

IMPRIMATUR POUR LA THÈSE

Etude du boisement des tourbières hautes de
la chaîne jurassienne : typologie et dynamique
de la végétation - approche dendroécologique et
dendrodynamique des peuplements arborescents

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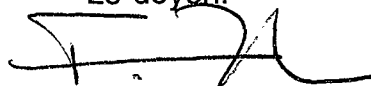
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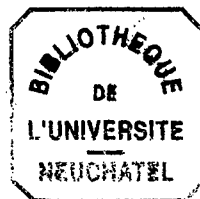
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Stand structure, invasion, and growth dynamics of bog pine (*Pinus uncinata* var. *rotundata*) in relation to peat cutting and drainage in the Jura Mountains, Switzerland

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Abstract: A description of bog pine stands (*Pinus uncinata* Ramond var. *rotundata* (Link) Antoine) on uncut oligotrophic mires affected by drainage and nearby peat cuttings at three sites of the Jura Mountains (Switzerland) is given. In all sites, three situations were chosen: (i) central parts of the bogs, (ii) surfaces near cutting walls and bog margins, and (iii) intermediate situations. Population structures were characteristic for each situation. In the open and wet central parts of the bogs, trees were scattered, small, and uneven aged. In the intermediate situations, tree density was higher, and the stand was multilayered with taller and uneven-aged individuals. Near the edges of the bogs or close to the peat cutting walls, the trees were tall, even-aged, and younger with a high growth rate. The nonsynchronous colonization of the bog pine trees on the three sites indicates that local factors such as drainage and peat cuttings in the vicinity of the uncut surfaces were more influential than climate factors. Radial growth patterns, very similar between the sites and the various pinewood stands, and the numerous common pointer years reflect local and regional climate fluctuations. The pinewood development on uncut bogs in the Jura Mountains thus represents a recent dynamics, which is strongly linked to human activities.

Résumé : Une description des peuplements de pins à crochets (*Pinus uncinata* Ramond var. *rotundata* (Link) Antoine) de marais oligotrophes de la chaîne jurassienne (Suisse), perturbés par des drainages et l'exploitation de la tourbière, est donnée. Dans tous les sites, trois situations ont été choisies : (i) parties centrales des tourbières, (ii) surfaces proches des murs d'exploitation et bords de tourbières et (iii) situations intermédiaires. Les structures de populations étaient caractéristiques de chaque situation. Dans les parties ouvertes et humides des zones centrales des tourbières, les arbres étaient disséminés, petits et d'âge inégal. En situations intermédiaires, la densité des arbres était plus élevée et les peuplements étagés, avec de grands individus d'âge très différent. En bordure des tourbières ou à proximité des murs d'exploitation, les arbres étaient grands, de même âge et plutôt jeunes, avec un taux de croissance élevé. La colonisation asynchrone des pins dans les trois sites suggère que des facteurs locaux comme les drainages et l'exploitation de la tourbe à proximité des surfaces intactes ont été plus importants que les facteurs climatiques. Les patrons de croissance radiale, très semblables entre les sites et les différentes situations, de même que les nombreuses années caractéristiques communes, reflètent les fluctuations climatiques locales et régionales. Le développement des pinèdes sur les surfaces non exploitées des tourbières de la chaîne jurassienne représente ainsi une dynamique récente qui est fortement liée aux activités humaines.

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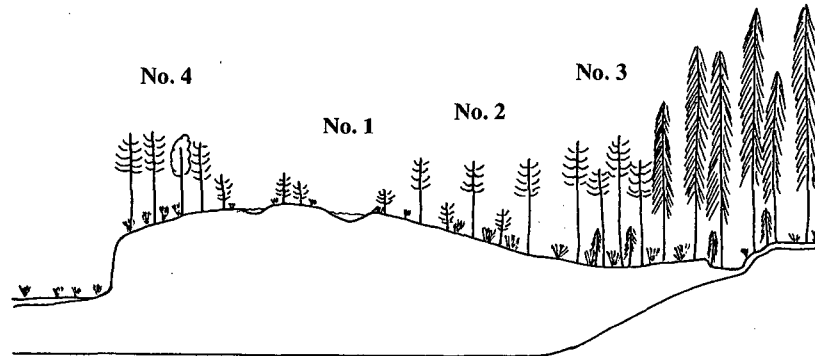
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Introduction

Raised bogs of the Jura Mountains are generally of limited size, mostly less than 20 ha, which is typical in this karstic environment where many geological and geomorphological features condition their development. Impermeable autochthonous and allochthonous substrates, synclines, and ancient glacial valleys with moraine ridges are features explaining the local geographical distribution of these bogs. Nevertheless, the growth dynamics of the Jura bogs was considerable during the post-glacial period and several metres of peat have built up. This sustained the peat-cutting industry, which flourished from the 18th century up to the middle of the 20th century. Nowadays, about 90% of the original bog areas in Switzerland have disappeared and only about 1500 ha are left (Grünig et al. 1984, 1986). In such areas, where whole uncut bogs are rarely found, vegetation changes have occurred even in uncut portions as an indirect

Fig. 1. The four major bog pine dominated vegetation types in the uncut oligotrophic mires of the Jura (after Freléchoux 1997): (No. 1) *phytocoenoses* type with *Pinus uncinata* var. *rotundata*, *Andromeda polifolia* L., and *Sphagnum rubellum* Wils. in open and wet situations of the central part of the bogs, where trees are scarce and of small size; (No. 2) *phytocoenoses* type with *Pinus uncinata* var. *rotundata*, *Vaccinium uliginosum* L., and *Sphagnum fuscum* (Schimp.) Klinggr. representing layered tree stands of medium size and with a higher density; (No. 3) *phytocoenoses* type with *Pinus uncinata* var. *rotundata*, *Vaccinium myrtillus* L., *Sphagnum capillifolium* (Ehrh.) Hedw., and *Dicranum polysetum* Sw. of dense and tall tree stands near the edge of the mire and its bordering spruce forest; (No. 4) *phytocoenoses* type with *Pinus uncinata* var. *rotundata*, *Betula pubescens* Ehrh., *Vaccinium myrtillus*, *Sphagnum capillifolium*, and *Dicranum polysetum* of rather dense and tall tree stands near the peat cutting area.



result of earlier peat cutting in the vicinity. This activity led to the drying-up of the peat and the development of tall bog pines. Reille (1991) stressed the drastic increase of pine pollen abundance in the recent past within the peat profiles.

The bog pine (*Pinus uncinata* Ramond var. *rotundata* (Link) Antoine) is known to be a hybrid between *P. uncinata*, which is a tall and monocormic species located in the western part of Europe (Pyrenees) and *Pinus mughus* Scopoli, which is a prostrate polycormic species with a more easterly distribution in Europe (Sandoz 1982, 1987). In the Jura Mountains, *Pinus uncinata* var. *rotundata* is found in contrasting extreme ecological situations such as rocky limestone environments and ombrotrophic bogs.

On histosols, the high groundwater table is an important limiting factor for the development of trees. Its influence on the survival and growth of seedlings has been demonstrated for many bog tree species (Müller-Dombois 1964; Lieffers and Rothwell 1986, 1987). Oxygenation of the upper soil layers has proved to be critical for many species, either at the seedling stage or later for the adult plants (Boggie 1974, 1977; Coutts and Philipson 1978a, 1978b), the oxygen transport ability within the woody roots representing a key property in adaptation to waterlogging (Philipson and Coutts 1978, 1980). Drainage is known to stimulate the growth of bog trees (Seppala 1969; Payandeh 1973; Stanek 1977; Stravinskene 1983; Dang and Lieffers 1989), and this applies also to bog pine (Grünig 1955; Schulthess 1990, in Schweingruber 1996).

Several authors have considered the bog pine stands of uncut and bulky oligotrophic peats to be a climax vegetation of these ecosystems (Richard 1961; Matthey 1964; Royer et al. 1978; Buttler et al. 1983). More recently, Freléchoux (1997) and Freléchoux et al. (2000) have reassessed the role of the bog pine in these ecosystems and came to the conclusion that there are four elementary coenotaxa representing (i) *phytocoenoses* developing in the open and wet central part of the bogs, where trees are scattered and small (Fig. 1, No. 1); (ii) *phytocoenoses* with layered tree stands of medium size and with a more dense coverage (Fig. 1, No. 2);

and (iii) *phytocoenoses* with dense and tall trees, developing generally near the edge of the bog (Fig. 1, No. 3) or close to the peat cuts (Fig. 1, No. 4). They all belong to the same (primary) successional series, driven by both autogenic and allogenic processes, and represent local polyclimaxes induced by differential waterlogged situations.

Since there is not necessarily a relationship between the size and the age of the trees (e.g., Harper 1977), a more precise dendroecological investigation of the bog pine populations was needed to get a better knowledge of their structure in relation to human impacts. In particular, knowledge of the relationship between age structure and tree morphology was necessary to get a better understanding of the population dynamics, and tree ring analyses can provide information on their stability and reactions to disturbances (Lorimer 1985; Cherubini et al. 1996). Most pine species are known to be heliophilous and pioneer in open sites and, therefore, develop rapidly after disturbances such as climate change, fire, deforestation, or insect invasion (Richardson and Bond 1991). Drainage of peat bogs may also act as a disturbing factor, which in turn can trigger bog pine invasion processes.

In this paper we aim at (i) describing the structural characteristics of some pine stands representative of three typical *phytocoenoses* that can be found along the ecological gradient from the centre to the margin of the bogs in the Jura Mountains, (ii) showing the colonization dynamics of these populations (cohorts), (iii) quantifying their radial and apical growth, (iv) relating dendroecological measurements to historical events, and (v) relating dendroecological measurements to groundwater measurements.

Materials and methods

Study sites

The dendroecological survey was carried out at three different sites: (i) the Bois des Lattes site (BL; 46°58'27"N, 6°43'02"E, 1000 m a.s.l.), (ii) the Cachot site (LC; 47°00'27"N, 6°39'57"E, 1050 m a.s.l.), and (iii) the Pontins site (LP; 47°07'43"N, 6°59'22"E, 1100 m a.s.l.). All three sites were partly mined from the 18th century up to the end of World War II. The vegetation of

Table 1. General characteristics of the pinewood stands, number of phytocoenoses types according to Fig. 1, cover estimates of

Plot	Pinewood type	Phytocoenoses type	No. of pines	Sampling plot area (m ²)	Density (trees/ha)	Basal area (m ² /ha)	Cover estimation			
							Tree layer (%)	Shrub layer (%)	Herb layer (%)	Moss layer (%)
Bois des Lattes										
BL1	Low pinewood stand	2	40	100	4000	19.0	0	30	75	100
BL2	Intermediate pinewood stand	2	73	96	7604	44.2	0	80	80	85
BL3	Tall pinewood stand	4	48	128	3750	73.2	80	10	70	85
Le Cachot										
LC1	Low pinewood stand	1	81	240	3375	16.1	0	40	35	100
LC2	Intermediate pinewood stand	2	113	240	4708	30.6	0	50	60	85
LC3	Tall pinewood stand	4	47	240	1958	54.3	50	15	90	80
Les Pontins										
LP1	Low pinewood stand	1	95	96	9896	19.6	0	40	70	95
LP2	Intermediate pinewood stand	2	65	80	8125	53.1	60	30	90	90
LP3	Tall pinewood stand	3	32	144	2222	52.5	40	10	95	90

^aStandard deviations are given in parentheses.

^bFor the plot LP3, values are given for the two tree height subgroups, <8 and >8 m, respectively (see explanation in the text).

the nine plots on the three sites belongs to the four major bog pine dominated vegetation types described for uncut oligotrophic bogs affected by drainage (Fig. 1, Table 1).

The Bois des Lattes and the Cachot sites lie on Quaternary clay deposits covering a Tertiary bedrock (marine molassic sandstone of the Helvétien) (Matthey 1971a), whereas the Pontins site has developed on an autochthonous marl layer of the upper Jurassic (Argovian). All soils are oligotrophic and acid (3.5 < pH < 4.5) fibric histosols of more than 2 m depth in the Pontins site (Buttler et al. 1983), more than 3 m depth in the Bois des Lattes site (Ischer 1935), and about 5 m depth in the Cachot site (Spinner 1926).

The Jura Mountains are under the double influence of humid winds from the Atlantic Ocean (westerlies) and continental anticyclones (originating in the east). The climate is predominantly oceanically influenced with a mean annual precipitation of about 1500 mm. Rainfall is rather low from February to April and in October (mean monthly precipitation of 100–110 mm) and high in June (mean monthly precipitation >140 mm). According to Matthey (1971b), the mean annual temperature in the bogs is about 4°C, and the monthly means in the period from June to September range from 9.7 to 13.3°C, with values under 0°C possible at any time. In the bogs, air humidity is saturated during the night and misty conditions are frequent.

Structure of pine stands (density, height, diameter, and age)

Nine plots were investigated, representing on each site the three types of bog pine stands with small, medium, and tall trees. Different measurements were made (Table 1). Each plot was chosen so that the surfaces had a homogeneous patterned vegetation (tree height and cover; shrub type, height, and cover; presence of wet-dry, light-shade characteristic species) and also enough trees for the dendroecological investigations. All tree individuals were counted, mapped, and their main morphological characteristics measured. Height was measured directly with a folding rule for the small trees or with a clinometer (Suunto) for taller individuals. Diameter and basal area of the stems were calculated from the circumference at the base. The tall trees were cored at 15–40 cm above the ground with an increment borer (two perpendicular cores were taken), whereas small trees were cut and sliced at their root collar. Age underestimation due to coring above root collar was assessed for each stand by dividing mean coring height by mean annual apical growth. Seedlings less than 4 years old were not taken

into account. This material was prepared in the laboratory to obtain information on the age of each tree and to allow the construction of skeleton plots. Mean annual growth of each tree was calculated as the ratio between corrected height (tree height minus coring height) and age. Pairwise comparisons between some of these measurements were tested by Spearman's rank correlation.

Skeleton plot

This visual method for ring-width analysis was first developed by Douglass (1939) to allow cross dating between different radii and recognition of anomalies such as missing or false rings. It was used later by Stokes and Smiley (1968) and Schweingruber et al. (1990). Additionally, this method aims at recognising individual-specific characteristic rings (i.e., event years based on ring width, latewood width, or abrupt growth changes) and characteristic years (pointer years), which represent the reaction of a whole stand (Schweingruber et al. 1990; Weber and Schweingruber 1995). These measurements are essential for the reconstruction of bog dynamics, which would be more difficult to demonstrate on measured, continuous ring-width sequences. For example, the best event years permit a good cross dating of tree ring sequences in a population. Secondly, the event years and pointer years show annual (short-term) reactions of individuals and tree populations respectively. Thirdly, abrupt growth change curves maximize medium-term fluctuations, high-frequency signals being suppressed. The main objective is to show the dendroecological differences both between the plots of one site, and between the different sites, to separate climate effects from those resulting from drainage. Visual readings were carried out with a stereomicroscope (Olympus SZ-ST) equipped with a micrometric eyepiece (0.05-mm graduations). Data handling, calculations, and graphical display followed Weber (1994). Skeleton plots were drawn for all plots except BL1 and LP1, where the trees were too small.

Abrupt growth change means (AGCm)

The construction of the radial growth curve of each tree is based on abrupt growth changes, which can be recognised and quantified by successively comparing all the ring widths using the largest ring as a reference in each radius (Schweingruber et al. 1990). Each ring is characterized by a growth-reduction class, based on estimations: class 0 (0–40% of reduction), class -1 (40–55%), class -2 (55–70%), and class -3 (>70%). Thus, two successive abrupt

different vegetation layers, and groundwater levels in the nine plots in the three sites.

Mean height (m) ^a	Mean diameter (cm) ^a	Mean age (years) ^a	Mean apical annual growth (cm/year) ^a	Mean groundwater level (cm)
2.07 (0.99)	6.8 (3.9)	73 (52)	3.29 (1.65)	-13.6
2.88 (1.49)	7.5 (4.2)	117 (45)	2.26 (0.96)	-14.8
9.22 (1.27)	15.4 (3.2)	125 (17)	7.24 (1.23)	-29.0
2.37 (1.45)	6.6 (4.1)	71 (34)	3.11 (1.25)	-14.5
8.38 (1.92)	7.8 (4.7)	106 (45)	3.00 (1.34)	-21.1
9.44 (1.18)	18.2 (4.7)	92 (10)	9.97 (1.34)	-31.9
1.72 (1.18)	4.2 (2.7)	85 (26)	1.83 (0.94)	-12.9
4.60 (2.33)	8.0 (4.3)	102 (17)	4.13 (1.75)	-14.5
3.63 (1.22), 13.08 (0.86) ^b	5.8 (1.6), 22.2 (3.9) ^b	88 (11), 116 (7) ^b	4.03 (1.42), 10.82 (0.82) ^b	-16.6

growth changes fix the limits of a period of relatively constant and homogeneous growth of the tree.

For each plot and each year, the mean abrupt growth change curve (AGCm) was calculated by using, for all the corresponding years, the abrupt growth change information obtained from the different trees growing within the plot. The weighted mean was calculated by using the median value of each class and not the semiquantitative variables as suggested by Weber (1994):

$$\text{AGCm} = \frac{\sum_{i=1}^k f_i x_i}{n}$$

where x_i is the median percentage value of the AGC reduction class i , expressed relative to the maximum growth (the largest ring: 100%) of the radius ($x_0 = 0.8$, which means 80% of the maximum growth; $x_{-1} = 0.525$; $x_{-2} = 0.375$; $x_{-3} = 0.15$); f_i is the frequency of reduction class i ; and n is the number of rings (radii) recorded for the current year. Thus, the mean of the relative growth for each year ranged between 15 and 80% of the maximum growth. To avoid misleading interpretations, the AGCm curves were drawn only for the period in which more than half of the radii were represented in the corresponding years.

Abrupt growth changes

In the abrupt growth change readings from each tree, the year in which growth increases or decreases in comparison with the previous year, can be considered as an event year. For each plot and each year, the abrupt growth change pointer years can be quantified by expressing the proportion of radii which have reacted positively (AGC_{inc}) or negatively (AGC_{dec}):

$$\text{AGC}_{\text{inc}} = 100 \left(\frac{f_{\text{inc}}}{n} \right)$$

$$\text{AGC}_{\text{dec}} = 100 \left(\frac{f_{\text{dec}}}{n} \right)$$

where f_{inc} is the frequency of AGC growth increase, f_{dec} is the frequency of AGC growth decrease, and n is the number of rings (radii) recorded for the current year.

Because of the low sensitivity of trees in bogs, a rather low threshold of 20% was chosen for interpreting AGC pointer years, as suggested by Schweingruber et al. (1990).

Ring width weighted (RWw) and latewood width weighted (LWw)

In a sequence of rings along a radii, rings that are particularly wide (positive reaction) or narrow (negative reaction) or that present a particularly high (positive reaction) or low (negative reaction) latewood width compared with their neighbouring rings can be identified as event years and quantified. Each ring was characterized by estimating a reaction factor, using a scale with five classes according to Schweingruber et al. (1990) and Weber (1994): class ± 5 (very pronounced positive or negative reaction) to ± 1 (very low positive or negative reaction). The five classes are considered as quantitative variables.

For each plot and each year, the weighted mean positive and negative reactions were calculated for both the ring width and the latewood width and expressed in percent of the maximum possible reaction, according to Schweingruber et al. (1990) and Weber (1994):

$$\text{RWw}_{\text{pos}} \quad \text{or} \quad \text{LWw}_{\text{pos}} = 100 \left(\frac{\sum_{i=1}^k f_i y_i}{5n} \right)$$

where RWw_{pos} or LWw_{pos} is the ring width weighted or latewood width weighted positive reactions, f_i is the frequency of positive reactions of class i , y_i is the reaction factor of the class i (1 to 5), and n is the number of rings (radii) read for the current year.

$$\text{RWw}_{\text{neg}} \quad \text{or} \quad \text{LWw}_{\text{neg}} = 100 \left(\frac{\sum_{i=1}^k f_i y_i}{-5n} \right)$$

where RWw_{neg} or LWw_{neg} is the ring width weighted or latewood width weighted negative reactions, f_i is the frequency of negative reactions of class i , y_i is the reaction factor of the class i (-1 to -5), and n is the number of rings (radii) read for the current year.

Here again, because of the low sensitivity of trees in bogs, a rather low threshold of 20% was chosen for interpretation of ring

Fig. 2. Relation between height and age of the trees in the different pinewood stands. Sites are as follows: BL, Bois des Lattes; LC, Le Cachot; LP, Les Pontins. Plots are as follows: (1) low pinewood stands; (2) intermediate pinewood stands; (3) tall pinewood stands.

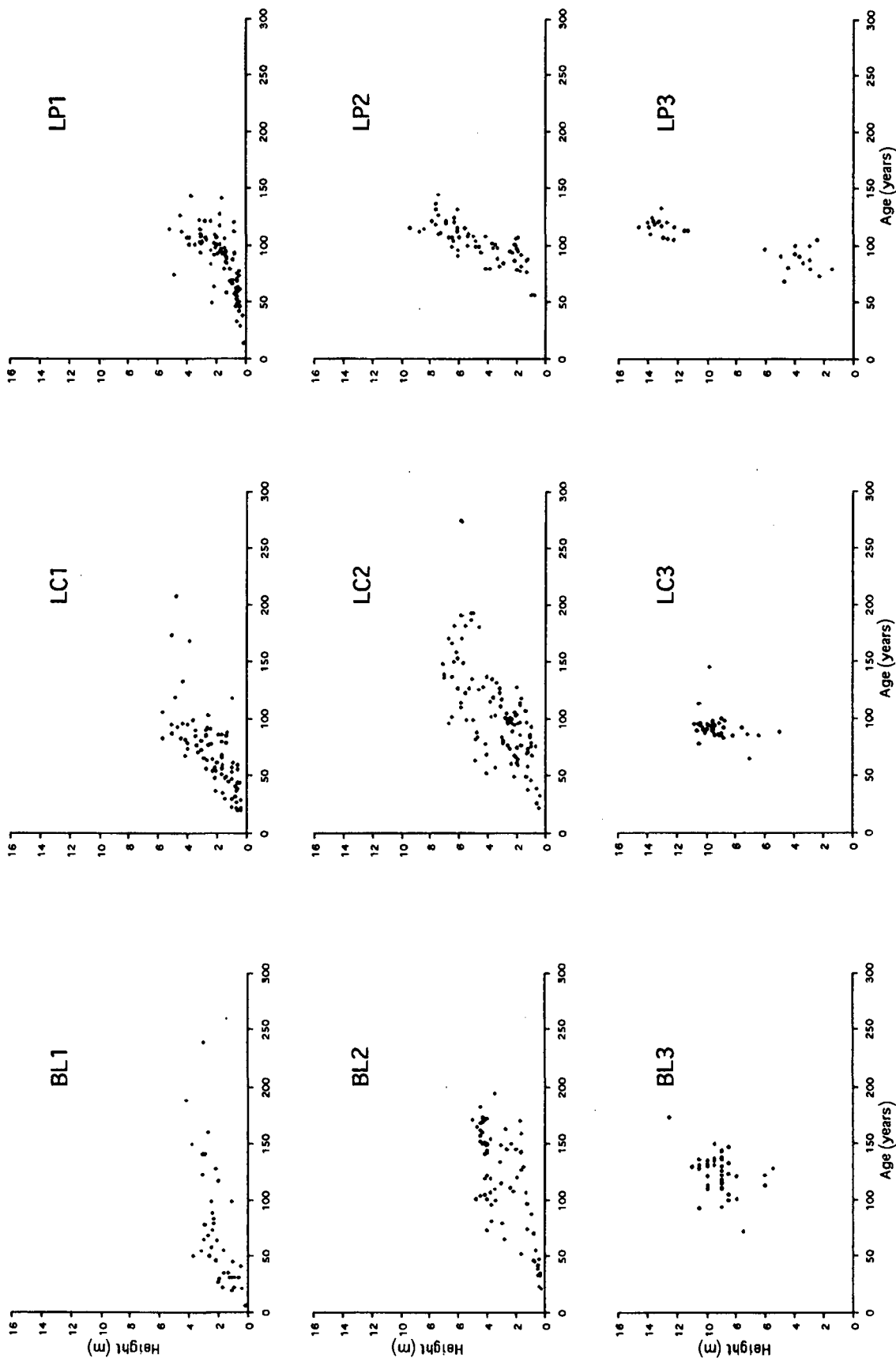


Table 2. Spearman's rank correlations between height, diameter, and age of the pine trees in the different plots.

Plot ^a	No. of pines	Height vs. age	Diameter vs. age	Height vs. diameter
BL1	40	0.736	0.793	0.947
BL2	73	0.664	0.643	0.903
BL3	48	0.283ns	0.398 ($P = 0.0064$)	0.601
LC1	81	0.763	0.798	0.937
LC2	113	0.707	0.714	0.939
LC3	47	0.329 ($P = 0.0258$)	0.487 ($P = 0.0009$)	0.570
LP1	95	0.780	0.790	0.932
LP2	65	0.808	0.784	0.940
LP3, <8 m ^b	14	0.163ns	0.421ns	0.560
LP3, >8 m ^b	18	0.382ns	0.279ns	0.262ns

Note: The P values not given are <0.0001 . ns, not significant.

^aSites are as follows: BL, Bois des Lates; LC, Le Cachot; LP, Les Pontins. Plots are as follows: (1) low pinewood stand; (2) intermediate pinewood stand; (3) tall pinewood stand.

^bFor LP3, correlations are given for the two tree height subgroups, <8 and >8 m.

width weighted and latewood width weighted pointer years, according to Schweingruber et al. (1990).

Groundwater measurements

Groundwater measurements have proved to be very informative in comparing the vegetation of wetlands and assessing their ecology (Klötzli 1969; Feldmeyer-Christe 1990). On each of the three plots of the sites BL, LC, and LP (Table 1), five piezometers were installed in the lowest situations. They were built with 5 cm diameter PVC tubes and up to 160 cm length, perforated along the wall and with an open lower end. On plot LC1, four piezometers were placed in an open area, and four others, within groups of trees. Measurements were made weekly during the May to October growing season (22 weeks, 21 in plot BL3). Results are presented by means of duration curves, which show the cumulative number of days on which the groundwater is above a certain level.

Results

Density and basal area of the pinewood stands

Pines densities ranged from 1900 to 10 000 individuals/ha, and the basal areas, from 16 to 74 m²/ha (Table 1). Highest densities were reached in the stands of intermediate size (except on LP2 plot), while densities were lower in the central, wetter parts of the bogs, where the trees are scattered and smaller. In all three tall pinewood stands, the densities were much lower because of a lack of regeneration, while the basal areas were generally high.

Height and diameter of the pinewood stands

In the central, wet parts of the bogs (BL1, LC1, LP1), trees were rarely higher than 5 m (Table 1, Fig. 2). In the intermediate pinewood stands (BL2, LC2, LP2), trees were layered with heights ranging from 1 to 8 m. In BL2 and LC2 there was a tendency towards a separation between a dominant and a dominated stratum. Trees of the tall pinewood stands BL3 and LC3 showed a rather limited range of heights (8–11 m), and on the LP3 plot there was a clearly bimodal distribution; the dominant stratum ranged from 12 to 15 m, and the undergrowth, from 2 to 5 m. Similar trends were observed for the diameters.

Age structure of the pinewood stands

Age underestimation due to coring above root collar was 4 years for small bog pine stands, 5–8 years for medium bog pine stands, and 3–5 years for tall bog pine stands. In the central wet and open parts of the bogs (BL1, LC1, LP1), trees of various ages coexisted (Table 1, Fig. 2). They were generally less than 120 years old, but some of them exceeded 200 years in age. In the intermediate pinewood stands (BL2, LC2, LP2), trees were also of varying ages, specially on BL2 and LC2 plots, but the mean age was higher compared with the low pinewood stands. Many trees exceeded 150 years in age, with one individual reaching 275 years on LC2 plot. Compared with the previous plots, the age structure was quite different in the tall pinewood stands: rather young trees of similar ages on BL3 and LC3 plots and two successive cohorts on LP3 plot. Spearman's rank correlations between height, diameter, and age are given in Table 2.

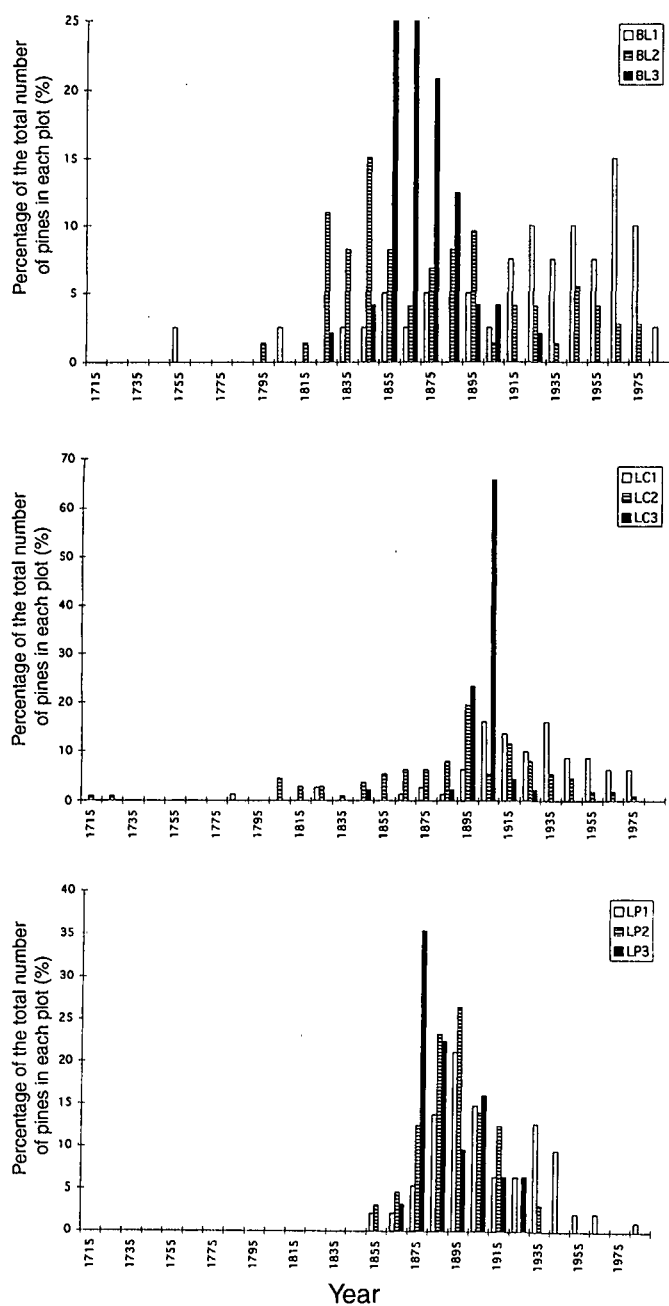
Mean annual apical growth of the pine trees

The mean annual apical growth of the trees was very low in the low pinewood stands (1.8–3.3 cm/year), a little higher in the intermediate pinewood stands (2.3–4.1 cm/year), and much higher in the tall pinewood stands (7.2–10.8 cm/year) (Table 1).

Colonization dynamics of the pine trees

In the central wet and open part of the Bois des Lattes site (plot BL1), the colonization dynamics of the pine trees has been very progressive in the past 200 years, but the process has accelerated since the turn of this century (Fig. 3). On plot BL2, colonization dynamics showed two rapid increases, the first in 1815 and the second in 1865. The closing up of this intermediate pinewood stand did not allow good undergrowth development. In the tall pinewood stand of this same site (BL3), colonization was very intense between 1815 and 1915, and no regeneration has occurred since. On the Cachot site (LC), colonization started around 1800 and increased progressively. From 1885 to 1915, there was massive colonization, especially in the tall pinewood stand of plot LC3. Colonization was less drastic on plots

Fig. 3. Colonization dynamics of the pine trees in the different pinewood stands. Data are grouped in decades. Sites are as follows: BL, Bois des Lattes; LC, Le Cachot; LP, Les Pontins. Plots are as follows: (1) low pinewood stands; (2) intermediate pinewood stands; (3) tall pinewood stands.



LC2 and LC1 and slightly delayed in the latter one. Colonization ceased shortly after that period on plot LC3, whereas in the intermediate and low pinewood stands (plots LC2 and LC1), it continued but decreased regularly. On the Pontins site (LP), colonization was very rapid in all three plots in the period after 1845, and no older trees were found. This colonization process occurred first in the tall pinewood stand of plot LP3, where a second invasion phase intervened around 1905 and gave rise to the present undergrowth. The invasion dynamics stopped almost simultaneously during the period

1935–1945 on plots LP3 and LP2, whereas there was a temporary increase around the World War II period on plot LP1.

Radial growth of the pine trees

On the Cachot and Pontins sites (LC and LP) and especially in their tall pinewood stands, it was seen that the initial growth of the trees was very high at first and decreased steadily afterwards (Fig. 4). On the whole, the AGCm curves show similar major fluctuations within and between sites, most probably in relation to general climate conditions. Maximal growth occurred in the periods 1925–1930, 1951–1955, and 1984–1986 and minimal growth in the periods 1919–1922, 1940, and 1970–1980.

Pointer years

Pointer years can be identified and quantified on the basis of abrupt growth changes, ring width, and latewood width. Comparing the seven plots for which the skeleton plot was available, it appears that the period between 1900 and 1990 shows many common positive or negative reactions (Table 3). Some of these reactions are common to the three sites: 1951, 1958, 1970, and 1985 for ring width and 1932, 1948, 1956, 1958, 1960, 1973, and 1985 for latewood width. Some reactions are common to only two sites: 1923 for abrupt growth changes (BL + LC) and 1973 (BL + LC) and 1980 (LC + LP) for ring width. Finally, some others are apparent on one site only: 1955 (BL) and 1968 (BL) for ring width and 1925 (LC), 1937 (BL), and 1955 (BL) for latewood width. Ring width readings and especially latewood width readings permitted a very good cross dating of all radii. The following reactions are particularly noticeable: 1932, 1948, 1973, and 1985. Among these, the best reaction is a very low latewood production in 1948, which appears in all plots.

Groundwater measurements

Duration curves of the ground water levels are distinct between the different sites and plots (Fig. 5). There is a clear gradient from the central parts of the bogs, hosting pinewood stands of small size, towards the edges or the peat cutting walls where the trees are tall. On plots BL3 and LC3, the drying up of the peat is most pronounced, with two preferential levels at –20 and –40 cm. On plot LC1, there is a noticeable difference in the data from the piezometers installed in wet lawns as compared with those installed within small bog pine bunches. Plots BL1, BL2, LC1 (within trees), and LC2, representing low and intermediate pinewood stands, show rather similar curves. On LP site, the groundwater behaviour in the three pinewood stands is similar. The relation between the mean groundwater level and the mean size of the trees on the different plots and sites is given in Fig. 6.

Discussion

Stand structures and tree characteristics in relation to the location in the bog

Similar patterns of bog pine stand structures and tree characteristics could be found in the three sites, but differences appeared between plots, depending on their location within the bogs. In the central wet parts of the bogs, bog pines were scattered (low basal area), small, uneven aged, and grew

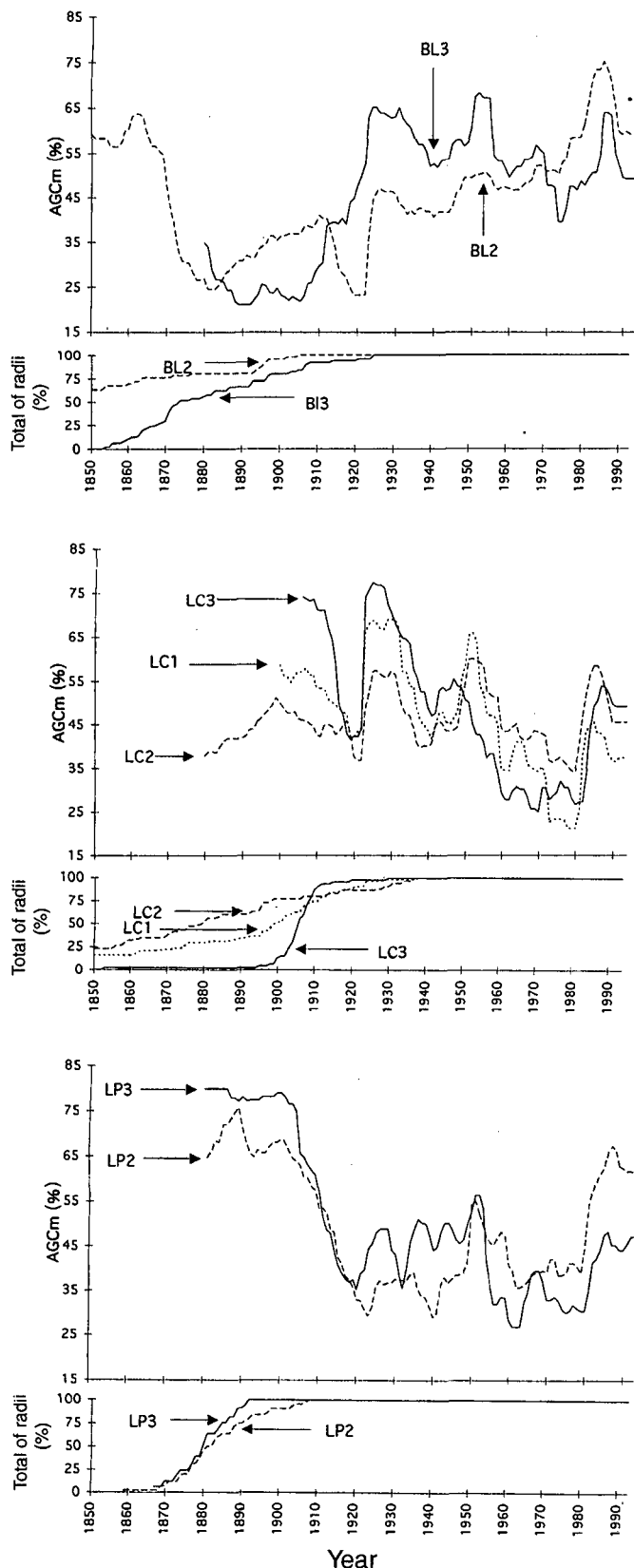


Fig. 4. Abrupt growth changes means (AGCm) of the pinewood stands of seven plots. Curves are drawn only for the period in which more than half of the radii were represented in the corresponding years (see total radii curves: Tot. rad.). Sites are as follows: BL, Bois des Lattes; LC, Le Cachot; LP, Les Pontins. Plots are as follows: (1) low pinewood stands; (2) intermediate pinewood stands; (3) tall pinewood stands. Number of pine trees and radii considered, respectively, are as follows: BL2 (30, 46); BL3 (41, 50); LC1 (42, 64); LC2 (49, 70); LC3 (47, 47); LP2 (26, 44); LP3 (18, 33).

in accordance with the main hydrological gradient, which most often runs from the centre of the bogs towards the margins. The rather wet soils of LP site, even under the tall pine trees, is probably due to a rewetting process, which is confirmed by the number of dead and declining trees observed since 1995, specially in plot LP3. According to Tüxen (1976), Schmatzler and Tüxen (1980), Schulthess (1990, in Schweingruber 1996), and Schneebeili (1991) this mortality could be due to intensive mineralization, subsidence, and compaction of the peat that has brought the groundwater level closer to the rooting zone of the trees. Similarities between sites and differences between plots are well confirmed by vegetation investigations (Freléchoux 1997; Freléchoux et al. 2000).

Climatic versus historical and human factors

All three sites were strongly subjected to human influence from the 18th century until the 1980s. Bogs were drained, cut over, and used for agriculture. While the original mire surface in the Ponts-de-Martel Valley (Bois des Lattes site) covered 1500 ha, the remaining surfaces today total 130 ha, and in drained uncut situations, only 18 ha of pinewood remains (Grünig et al. 1986). Two thirds of the 120 ha of pine forests in the Bois des Lattes disappeared between 1890 and 1935 (Ischer 1935). In the Brévine Valley (Cachot site), 90% of the original mire surfaces have disappeared and have been reclaimed for agriculture. More precisely, in the Cachot site, 70% (60 ha) of the raised bog disappeared between 1845 and 1996 (Matthey et Borcard 1996). On the Bois des Lattes (BL) and Cachot sites (LC), the progressive colonization of pine trees on the plots representing low and intermediate stands reflects the first interventions that took place in these bogs. It can be assumed that, on these two sites, the plots with tall stands invaded rapidly, because of their proximity to peat cuttings, with the result that old trees were overgrown and suppressed by the new cohort of younger trees. On the Pontins site (LP), all three plots underwent a sudden and simultaneous invasion in the middle of the 19th century. The ancient cutting walls near our plots were made between 1800 and 1900 (Buttler et al. 1983). The drained uncut surfaces covered by bog pine stands represented in 1983, and still represent today, 12% of their original surface. The latest high impacts in the studied bogs occurred during World War I (1914–1918) and World War II (1939–1945).

Although aerial photographs and more precise historical references are generally lacking or imprecise, we can reasonably believe that the nonsynchronous colonization of bog pines (Fig. 3) reflects the most influential site-specific human impacts.

slowly. Near the ancient cutting walls and the bog margin, bog pine cover was denser (high basal area), and the tree were tall, even aged, and grew faster (Table 1, Fig. 2). Intermediate features occurred in intermediate situations. This is

Table 3. Main pointer years, number of positive and negative reactions, and total of pointer years between 1850 and 1995 for abrupt growth changes, ring width, and latewood width for seven plots in three sites.

Pointer years	Abrupt growth changes (AGC)							Ring width weighted (Rww)							Latewood width weighted (Lww)							
	BL7	BL5	LC12	LC14	LC15	LP2	LP3	BL7	BL5	LC12	LC14	LC15	LP2	LP3	BL7	BL5	LC12	LC14	LC15	LP2	LP3	
1919								-57	-29	-28												
1922										-32	-82	-49	-36					-47	-23	-29		
1923	48	31	60	34	78				20													
1925						20				29	30	27					22	29				
1932																						
1937									22													
1940																						
1948									-24													
1951		26	22	20				41	32	52	26	63										
1955								30	34													
1956		-40																				
1958									30	23												
1960			-33	-29					-53	-48	-25	-30										
1967			-20						36													
1968									21	32												
1970									-24	-32												
1971																						
1973		-30	-33	-23					-67	-49	-43	-37										
1976		22						27	44													
1980																						
1985	34								42	49	27											
No. of positive reactions	2	5	5	3	2	4	3	7	15	9	6	8	8	2	12	12	13	6	8	6	5	9
No. of negative reactions	2	4	5	2	2	2	3	12	19	8	8	12	10	6	5	6	6	9	9	11	9	9
Total of pointer years	4	9	10	5	4	6	6	19	34	17	14	20	18	8	17	18	19	15	17	17	14	14

Note: For AGC, values are the proportion of positive or negative reactions, expressed as a percentage of the number of rings in the corresponding year. For Rww and Lww, values are weighted means of positive or negative reactions, expressed as a percentage of the maximum possible reaction according to the number of rings in the corresponding year. The threshold chosen for interpreting pointer years is 20%.

Fig. 5. Groundwater duration curves in the pinewood stands of nine plots. Sites are as follows: BL, Bois des Lattes; LC, Le Cachot; LP, Les Pontins. Plots are as follows: (1) low pinewood stands; (2) intermediate pinewood stands; (3) tall pinewood stands. In LC1, measurements have been done in open and wet lawns and within drier pine bunches.

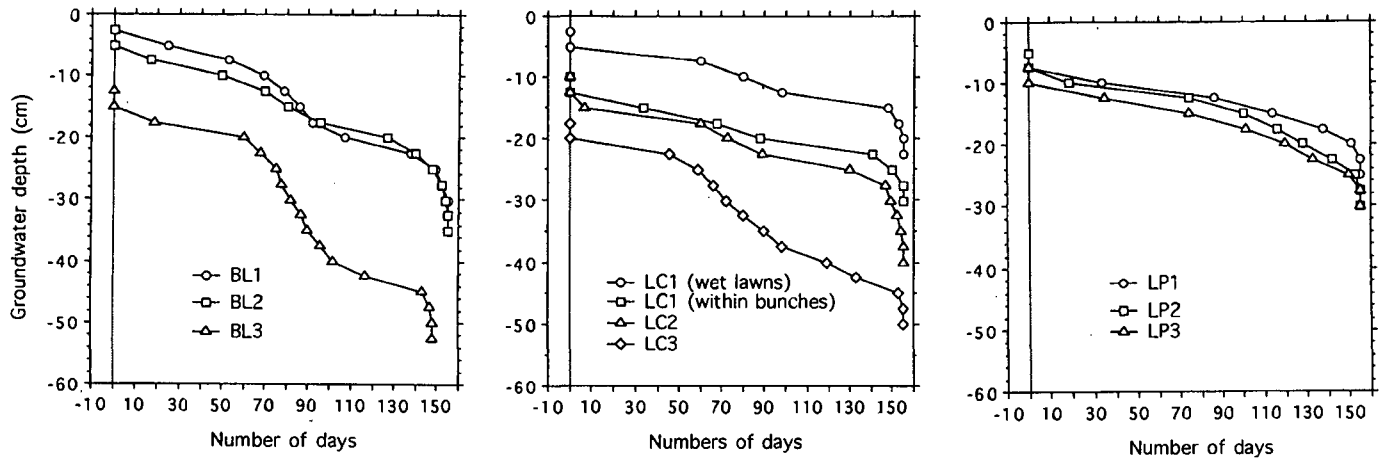
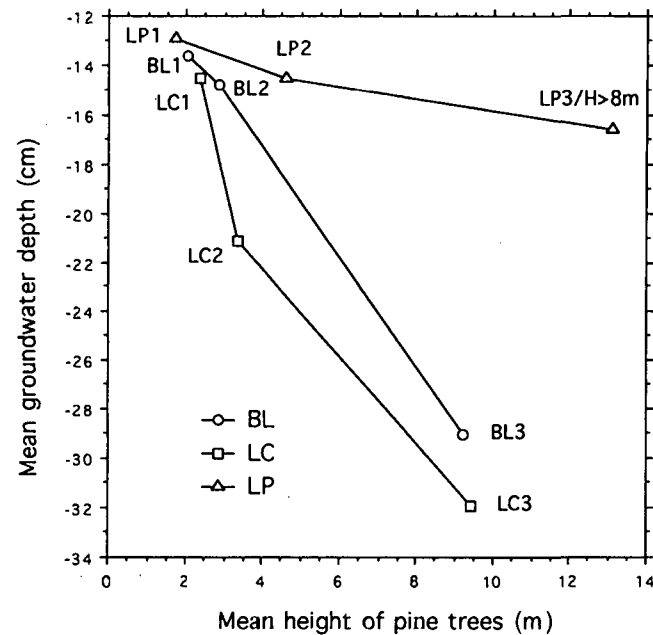


Fig. 6. Scatterplot of the relation between mean groundwater depth and mean height of the pine trees in the different pinewood stands. Sites are as follows: BL, Bois des Lattes; LC, Le Cachot; LP, Les Pontins. Plots are as follows: (1) low pinewood stands; (2) intermediate pinewood stands; (3) tall pinewood stands.



The period after World War II shows new tree invasion patterns on all these three sites, especially in the plots with low bog pine stands (Fig. 3). This could be due to increasing autogenic or allogenic processes. Among allogenic factors in relation to human activities, drainage and exploitation have a prominent role and occurred locally at the margin of the studied bogs and on adjacent agriculture land until 1960–1980 (i.e., 1942 at BL and LC sites). Nevertheless, we cannot exclude some influences of climate change in the pine colonization patterns.

Since 1920, many common fluctuations of AGCm curves (Fig. 4) and many common pointer years (Table 3) indicate

that radial growth depends on regional climate factors. On the contrary, before 1920, AGCm curves show site-specific fluctuations (Fig. 4). The high relative radial growth observed in several sites and plots (i.e., BL2, LC3, LP2, and LP3) in the early phase of tree settling, especially in the marginal parts of bogs, is characteristic of the post-colonization period. Common pointer years in one or two sites only (Table 3) could reflect local climate or human factors.

Disturbances versus regeneration of bog pine

Light and groundwater level seem to be the main key ecological factors determining bog pine establishment (Schmid et al. 1995). In the open and wet central part of bogs, where pine trees are scarce and small, enough light reaches the soil surface to promote bog pine seed germination and seedling growth. Furthermore, herb layer coverage, i.e., the *Vaccinium* layer, is low and the moss carpet plays a favourable nursery role: Ohlson and Zackrisson (1992) showed that humidity created by the *Sphagnum* layer promotes the seed germination best, as compared with the drier *Pleurozium schreberi* (Brid.) Mitt. layer, but their further development was then threatened because of the wetness, once the roots of pine reached the water level. The lowering of a few centimetres of the water table may improve these conditions and promote tree colonization, mainly on hummocks and dry lawns, where small groups of trees are located. We can imagine a positive feedback reaction in that dynamics, trees contributing to further drying up, as observed by Schulthess (1990) in Schweingruber (1996).

Near the margin of raised bogs, there is a general lowering of the water table, as a result of natural or artificial drainage. In a natural situation, this favours bog pine growth, but in extreme artificial situations such as the proximity of high cutting walls, this could also lead to a decline of bog pines, as suggested by Ischer (1935). In BL3 and LC3, near the cutting walls, bog pines have had the same quick colonization pattern and grew tall in optimal conditions (Fig. 3). As no old pines were found, we suppose that the remaining pines of the previous cohort have been overtopped by the later trees. Once the trees form a dense canopy, almost no

regeneration occurs because of the lack of light at the soil surface. The sparse *Sphagnum* cover and the accumulated *Vaccinium myrtillus* L. litter are other factors that then hamper the germination and survival of pine seeds (Ohlson and Zackrisson 1992; Jäderlund et al. 1996).

The age structure of tree stands may be described by means of mathematical models, where recruitment and mortality rates are the main parameters (Hett and Loucks 1976). Nevertheless, disturbances, climatic fluctuations, and competition among cohorts are other important parameters when considering age and size structure and may alter the classical patterns recognised in stable tree stands, as was demonstrated by Agren et al. (1983), Agren and Zackrisson (1990), and Lorimer (1985). The even-aged trees in the tall pine-wood stands are indicative of a previous strong disturbance event, in contrast to the low pinewood stands, where recruitment happened more regularly (Lorimer 1985; Bergeron and Gagnon 1987; Conkey et al. 1995). Although we did not take into account the seedlings less than 4 years old, none of the studied bog pine stand showed a reverse J-shaped age structure indicative of a good recruitment.

Successional pattern

On the contrary to observations made in other regions (Munaut and Casparie 1971; McNally and Doyle 1984a, 1984b; Hörnberg et al. 1995; Pilcher et al. 1995; Arseneault and Payette 1997; Segerström 1997), there is scant evidence in the literature concerning Jura bogs of sub-fossil tree layers (Favre et Thiébaud 1907; Spinner 1926, 1930; Ischer 1935; Joray 1942; Hubschmid and Lang 1985; Reille 1991). Thus, pine development on a large scale in the Jura bogs represents a recent dynamic pattern, as can be seen in most of the palynological records (Reille 1991). The low pollen abundance of *Pinus* in the former stratigraphical layers, as compared with surface layers, could be explained both by the scarcity of bog pine, which has probably always existed on bogs as small individuals, and by the stress exerted on the trees by the high water table levels, which allowed only limited pollen production (Giertych 1967; Ellenberg 1978, in Reille 1991).

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DYNAMICS OF BOG-PINE-DOMINATED MIRES IN THE JURA MOUNTAINS, SWITZERLAND: A TENTATIVE SCHEME BASED ON SYNUSIAL PHYTOSOCIOLOGY

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Abstract: A description of the bog-pine (*Pinus uncinata* var. *rotundata*) dominated vegetation of uncut oligotrophic mires affected by drainage is given. Surveys were carried out at 17 sites along the Jura Mountains (Switzerland and France) in 1993, 1994, and 1995. Raised bogs of the Jura are generally of small size, and most vegetation changes in them have occurred as a result of the indirect impact of peat cutting. This activity led to the peat drying out and to colonization by trees, in particular by bog-pines.

Integrated synusial phytosociology was used to describe the vegetation where bog-pine, spruce, and birch occur. Two spatio-temporal levels of organization were considered: the synusia and the phytocoenosis. At the phytocoenosis level, four vegetation types representing bog-pine stands of uncut and deep oligotrophic peats are described with their constitutive synusial composition. They represent: (1) phytocoenoses developing in the open, wet central parts of the bogs, where trees are scattered and of small size, (2) phytocoenoses with layered tree stands of medium size and with a higher density, and (3) phytocoenoses with tall trees, developing generally near the edge of the bogs or close to peat cuttings. A generalized qualitative dynamic model of the vegetation in relation to the development of bog-pine trees was developed. It shows the spatial and temporal organization of the constituent synusiac, as well as other underlying hypothetical functional relations.

The different bog-pine-dominated vegetation types described in this study appear to have coexisted since the origin of the Jura bogs as a result of local polyclimaxes induced by differential waterlogged situations. They probably all belong to the same (primary) successional series, but have been affected by both autogenic and allogenic processes. During the development of the bogs the balance between the different communities changed. In particular, the vegetation types with dense and tall pine trees have undergone a drastic expansion since the Jura bogs were first affected by drainage.

INTRODUCTION

The raised bogs of the Jura Mountains are generally of small size, most of them less than 20 ha, which is typical for this karst environment. Impermeable autochthonous and allochthonous substrates, synclines and ancient glacier valleys with moraine ridges are features that explain the local geographical distribution of these bogs. Despite these limiting features, the growth dynamics of the Jura bogs were considerable during the postglacial period, leading

to the formation of peat of several metres deep. This was an opportunity for the peat-cutting industry, which was important mainly from the 18th century to the middle of the 20th century. Today, about 90% of the original bog surfaces in Switzerland have disappeared with only about 1,500 ha remaining (GRÜNIG et al. 1984, 1986). Even where entire uncut bogs are found, vegetation changes have occurred as a result of the indirect impact of peat-cuttings which took place in the vicinity. This activity led to the drying out of peat and to the colonization by tall bog-pines (*Pinus uncinata* var. *rotundata*). REILLE (1991) stressed the significant increase in pine-pollen deposition in the recent past, in comparison with the rates established for earlier layers within the peat profiles.

The bog-pine – *Pinus uncinata* var. *rotundata* (LINK) ANTOINE – is considered by SANDOZ (1982, 1987) to be a hybrid between *P. uncinata* RAMOND, which is a tall and monocormic species located in the western part of Europe (Pyrenees) and *P. mughus* SCOP., which is a prostrated polycormic species with an eastern distribution in Europe. Bog-pine is distributed between the Jura Mountains and the High Tatras, including the Vosges, the Black Forest, the Bavarian Forest, Southern Bohemia, North-West Austria, mountain ranges in the northern part of the Czech Republic, and the Bohemian-Moravian Uplands (NEUHÄUSL 1972, SANDOZ 1987, FELDMEYER-CHRISTE 1990).

In histosols, the ground-water table is an important limiting factor for the development of trees. Its influence on the survival and growth of seedlings has been demonstrated for many bog-tree species (MÜLLER-DOMBOIS 1964, LIEFFERS & ROTHWELL 1986, 1987). Drainage is known to stimulate the growth of a number of bog trees (SEPPALA 1969, PAYANDEH 1973, STANEK 1977, STRAVINSKENE 1983, DANG & LIEFFERS 1989) and this applies also in the case of *Pinus uncinata* var. *rotundata* (GRÜNIG 1955, SCHULTHESS 1990, SCHWEINGRUBER 1996). The moss carpet is another factor that plays an important role in the rooting of seedlings. OHLSON & ZACKRISSON (1992) showed that a *Sphagnum* carpet, because it is moist, promotes the seed germination of some *Picea* and *Pinus* species more than drier *Pleurozium schreberi* carpets. The high moisture content of the *Sphagnum* carpet, however, is a threat to the survival of these seedlings.

While some authors consider the bog-pine-dominated mire vegetation in the Jura to be a local climax (RICHARD 1961, MATTHEY 1964, ROYER et al. 1978, BUTTLER et al. 1983), others disagree and suggest that in some mires the bog-pines might have been planted (FELDMEYER-CHRISTE 1990, REILLE 1991). Some authors classified this kind of vegetation as a *Pino rotundatae-Sphagnetum* KÄSTNER et FLÖSSNER 1933 (CHASTAIN 1952, RICHARD 1961, nomenclature according to OBERDORFER 1977), but only those communities on drier soils and with dense populations of tall trees were included in these studies. The bog-pine also develops in the wetter parts of the mires, where it grows to a smaller height, and is either isolated or in small groups. Our observations suggest that there is more than one type of bog-pine-dominated vegetation, varying within the broad range of ecological conditions where bog-pines are found. This is reflected in the uncertainties of the literature when classifying the bog-pine-dominated vegetation of Central European mires: some authors include the *Pino rotundatae-Sphagnetum* in the class *Vaccinio-Piceetea* BR.-BL. in BR.-BL. et al. 1939 (OBERDORFER 1957, RICHARD 1961, KRISAI 1960), and others in the class *Oxycocco-Sphagnetea* BR.-BL. et TX. 1943 (MOORE 1968, NEUHÄUSL 1969, 1972, DIERSSEN 1977, 1980, ROYER et al. 1978). More recently, OBERDORFER (1992) and NEUHÄUSL (1992) referred to the pine-dominated communities of tall trees with a paucity of mire species as *Vaccinio uliginosi-Pinetum rotundatae* OBERD. 1934 (class *Vaccinio-Piceetea*).

This paper describes the bog-pine-dominated vegetation of the uncut oligotrophic mires of the Jura Mountains. A typology is given based on the synusial organization of the phytocoenoses in order to formulate a theoretical dynamic qualitative model relative to the water level and the extent to which the bogs have dried out.

METHODS

Study area

The survey of tree-dominated bog vegetation was carried out at 17 sites along the Jura Mountains (15 sites in Switzerland and 2 sites in France) in 1993, 1994, and 1995, within the geographical limits: 46° 33' to 47° 17' N, 6° 5' to 7° 11' E and at altitudes ranging between 930 and 1,250 m a.s.l. The climate is predominantly oceanic, under the combined influence of humid winds from the Atlantic (Westerlies) and continental anticyclones, with a mean annual precipitation of about 1,500 mm. Rainfall is rather low from February to April and in October (monthly 100–110 mm), and high in June (monthly > 140 mm). With reference to MATTHEY (1971), the mean annual air temperature in bogs of the study area is about 4 °C; monthly means in the period from June to September range from 9.7 °C to 13.3 °C, with values under 0 °C being possible throughout the year. Air humidity is saturated during the night and misty conditions are frequent.

Integrated synusial approach

Integrated synusial phytosociology (GILLET et al. 1991, GILLET & GALLANDAT 1996) was used to describe the vegetation. Based on the BRAUN-BLANQUET (1964) approach, this method aims at describing complex vegetation structures and at emphasizing the dynamic links between the various constituent elements. Among several spatio-temporal organization levels, we only considered the first two levels (Fig. 1):

(i) The synusia (BARKMAN 1973) is an elementary one-layered concrete vegetation unit (patch) directly linked to uniform environmental conditions (microclimate, microtopography, soil, biotic factors). Thus, every synusia is a floristically, physiognomically and ecologically homogeneous vegetation unit. In the field, the vegetation structure is first assessed and the vegetation stand divided into synusiae. A synusial relevé is a quantitative description (abundance-dominance values according to BRAUN-BLANQUET 1964) of the species occurring in the sample plot of any selected concrete patch.

(ii) The phytocoenosis (GUINOCHET 1973, BARKMAN 1973, WESTHOFF & VAN DER MAAREL 1978) is a complex of synusiae that are functionally strongly linked both in space (mosaics, stratification) and time (seasonal aspects, regeneration cycles). The phytocoenotic relevé consists of a quantitative description (abundance-dominance values according to BRAUN-BLANQUET 1964) of the elementary synusial syntaxa observed in a concrete phytocoenosis.

Synusial phytosociology has several advantages over the Braun-Blanquet method. For instance: (1) It is a very detailed approach to studying vegetation aiming at discerning and interpreting both the horizontal and vertical micro-heterogeneity of the phytocoenosis. The synchronic approach can also lead to the interpretation of succession patterns. (2) Vegetation layers within the phytocoenosis may represent different environmental conditions. For example, abiotic conditions such as water-table depth, light or pH are very different for a bog-pine tree of the dominant layer and for a *Sphagnum* plant in the moss carpet. Further,

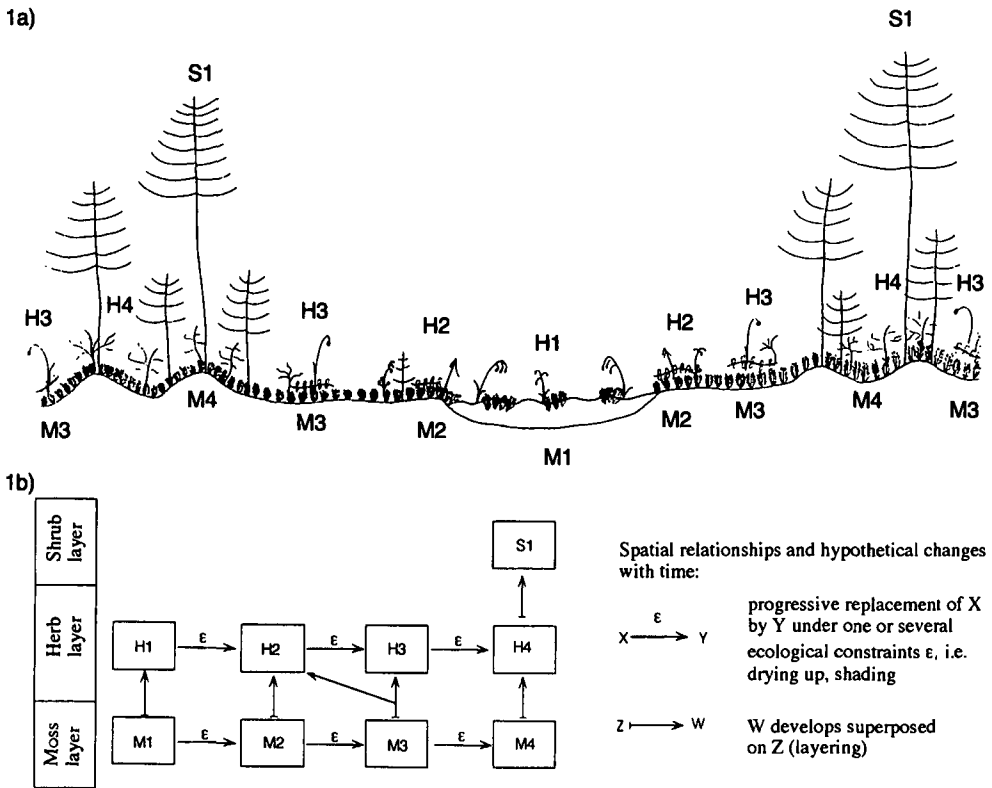


Fig. 1. Theoretical example of the synusial organization within a phytocoenosis representing a wet central part of a bog with hollows, wet lawns and hummocks sparsely covered by small bog-pine trees. 1a: Sketch of the location of the different synusiae in the phytocoenosis. 1b: Dynamic diagram representing the spatial and temporal hypothetical relationships between the synusiae in relation to tree colonization. M1 and H1: moss and herb synusiae of hollows; M2 and H2: moss and herb synusiae of wet lawns; M3 and H3: moss and herb synusiae of dry lawns; M4 and H4: moss and herb synusiae of hummocks; S1: shrub synusia of bog-pine.

changes in the vegetation, either as a result of natural evolution or anthropic impact, may occur variously in the different layers.

The vegetation was described by means of 94 phytocoenotic relevés of the main woodland communities dominated by bog-pine (*Pinus uncinata* var. *rotundata*), spruce (*Picea abies*) and pubescent birch (*Betula pubescens*) (FRELÉCHOUX 1997). Bog-pine woodlands were found on deep uncut bogs. Spruce forests were found along the edges of uncut raised bogs and colonized ditches after exploitation. Birch woodlands are scarcer and most often found on cleared, unexploited surfaces and in the wetter ditches. 767 synusial relevés were carried out simultaneously in all these phytocoenoses. A typology was carried out by comparing and classifying these relevés in synusial elementary syntaxa (elementary typological units of this organization level) with numerical tools combining various methods step-by-step using MULVA-5 software (WILDI & ORLÓCI 1996, WILDI 1989). More precisely, three macro-applications were performed separately on the data of each layer: moss, herb, shrub and tree. The first application yielded various classifications: (i) a classification of relevés and species based on presence-absence transformed data, van der Maarel similarity matrix and complete linkage clustering; (ii) a classification of relevés based on the Euclidean distance

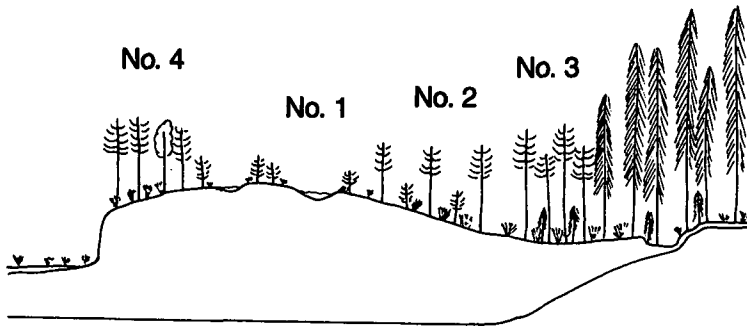


Fig. 2. The four major bog-pine-dominated vegetation types in the uncut oligotrophic mires of the Jura. No. 1: coenotaxon with *Pinus uncinata* var. *rotundata*, *Andromeda polifolia*, and *Sphagnum rubellum* in open and wet situations; No. 2: coenotaxon with *Pinus uncinata* var. *rotundata*, *Vaccinium uliginosum*, and *Sphagnum fuscum* with slightly denser tree canopies; No. 3: coenotaxon with *Pinus uncinata* var. *rotundata*, *Vaccinium myrtillus*, *Sphagnum capillifolium*, and *Dicranum polysetum* of dense and tall tree stands near the edge of the mire and its bordering spruce forest; No. 4: coenotaxon with *Pinus uncinata* var. *rotundata*, *Betula pubescens*, *Vaccinium myrtillus*, *Sphagnum capillifolium*, and *Dicranum polysetum* in rather dense and tall tree stands near the peat-cutting area.

matrix of the co-ordinates of principal coordinate analysis and minimum variance clustering; (iii) a classification of relevés based on the Euclidean distance matrix of the co-ordinates of correspondence analysis of presence-absence transformed data and minimum variance clustering and (iv) a classification of relevés and species based on square-root transformed data and the adjustment of vectors to unit length, on a cross-product similarity matrix and minimum variance clustering. The optimal number of groups of relevés and species was determined after comparing, for the various classifications, the successive fusion levels in the clusterings. The second application compared the combined classifications by mean of concentration analyses. Based on the best combination of relevés and species classification, the third application led to the re-allocation of relevés and species in order to optimize the final classification by means of a sum of squares K-means algorithm. In the same way as for the synusia, the phytocoenotic relevés were compared using the same numerical tools and classified into elementary coenotaxa (= the elementary typological units of this organization level).

The ecological indicator values of the species for important factors such as soil moisture, light, nutrient status and acidity were used according to LANDOLT (1977) for vascular plants and DÜLL (in ELLENBERG et al. 1991) for the bryophytes. The mean values for each synusia were calculated by weighting the ecological values of the species with their dominance percentage. The mean and the standard deviation were calculated for each synusial elementary syntaxon. Field drawings representing the location of each synusia within each phytocoenosis (see example in Fig. 1a) and the calculated mean ecological indicator values served to interpret spatial and temporal relationships and thus to formulate the functional hypotheses that are represented in the dynamic schemes (Fig. 1b). A comparison of all the individual dynamic schemes of each phytocoenosis allowed a qualitative generalized model to be developed that summarizes the hypothetical processes characterizing the succession from unwooded peatlands to bog-pine-dominated vegetation.

The nomenclature of vascular plants follows TUTIN et al. (1964–1980), and that of bryophytes CORLEY et al. (1981) and GROLLE (1983).

Table 1. Synthetic tabular representation of the elementary coenotaxa that constitute the bog-pine-dominated vegetation of the uncut oligotrophic mires of the Jura Mountains. Each coenotaxon is described by a list of syntaxa, numbered according to Tab. 2 to 5 and Appendix. Relative frequency (RF) classes are indicated for each syntaxon in each coenotaxon; r: syntaxon represented in less than 10% of the relevés or in a single relevé; I: 10% ≤ RF ≤ 20%; II: 20% < RF ≤ 40%; III: 40% < RF ≤ 60%; IV: 60% < RF ≤ 80%; V: RF > 80%. Mean abundance-dominance values are also indicated according to the Braun-Blanquet scale. Syntaxa that do not show relative frequencies of 10% or higher in any of the coenotaxa are not listed. Those syntaxa given in Tab. 2 to 5 and used in the generalized qualitative dynamic model (Fig. 3) are indicated with an asterisk (*).

Coenotaxon No.	1	2	3	4
Number of relevés	10	18	8	5
Total number of elementary syntaxa	24	24	25	17
Tree layer syntaxa				
T5*	.	II:3	IV:3	.
T6	.	.	II:4	.
T8*	.	.	.	V:4
Shrub layer syntaxa				
S101*	V:2	V:3	II:2	.
S102*	r:3	II:2	II:2	r:2
S103*	.	.	r:2	IV:2
S108	.	.	II:2	.
Herb layer syntaxa				
H208*	III:1	r:4	.	.
H201*	IV:4	.	r:1	.
H202*	IV:3	.	.	.
H203*	IV:2	V:4	IV:1	V:3
H205*	.	r:4	V:5	III:4
H206*	.	.	II:1	r:1
Moss layer syntaxa				
M314*	III:1	.	.	.
M310	I:1	I:+	.	.
M329	I:1	r:2	.	.
M330	r:1	II:2	.	.
M311	r:+	I:+	.	.
M312*	III:2	I:1	r:1	.
M343	II:+	I:1	III:1	.
M307	I:3	.	r:2	r:2
M306*	IV:4	IV:3	II:2	.
M305	r:2	II:4	.	r:2
M302*	I:3	II:3	r:1	r:3
M304*	r:3	III:3	V:3	III:3
M326	.	r:2	r:1	II:1
M336	.	II:1	III:+	II:1
M327*	r:2	.	IV:2	III:3
M333	.	r:2	.	II:1
M334	.	.	II:+	r:1

RESULTS

The numerical analysis of the 767 synusial relevés led to 83 synusial elementary syntaxa (FRELÉCHOUX 1997): 12 for the tree synusiae, 10 for the shrub synusiae, 14 for the herb synusiae, 47 for the moss and lichen synusiae. The numerical analyses of the 94 phytocoenotic relevés enabled us to identify 12 elementary coenotaxa: 5 for the bog-pine-dominated vegetation, 2 for the spruce-dominated vegetation and 5 for the pubescent birch-dominated vegetation. Among the 5 bog-pine-dominated coenotaxa, 4 are characteristic of uncut deep oligotrophic peats (Fig. 2) and these are the primary objects of interest in this paper. The main elementary syntaxa occurring in these coenotaxa are presented in Appendix. Tab. 1 presents the 4 elementary coenotaxa with their elementary syntaxa assemblages and Tab. 2 to 5 give the species assemblages of the main characteristic and differential elementary syntaxa that have been used in the qualitative generalized dynamic model of Fig. 3 and which explain most of the spatial structure of the vegetation.

Coenotaxon No. 1 is a community type with *Pinus uncinata* var. *rotundata*, *Andromeda polifolia*, and *Sphagnum rubellum*. In it, the trees are scattered and of small size. They are generally spread out or growing on hummocks alternating with hollows and very wet lawns. This coenotaxon includes some associations recognized in classical phytosociology such as: *Caricetum limosae* BR.-BL. 1921, *Sphagnetum magellanicum* (MALCUIT 1929) KÄSTNER et FLÖSSNER 1933 and *Pino rotundatae-Sphagnetum* KÄSTNER et FLÖSSNER 1933 (*pro parte*) (nomenclature after OBERDORFER 1977). Coenotaxon No. 2 is a community type with *Pinus uncinata* var. *rotundata*, *Vaccinium uliginosum*, and *Sphagnum fuscum*. It represents phytocoenoses in intermediate situations

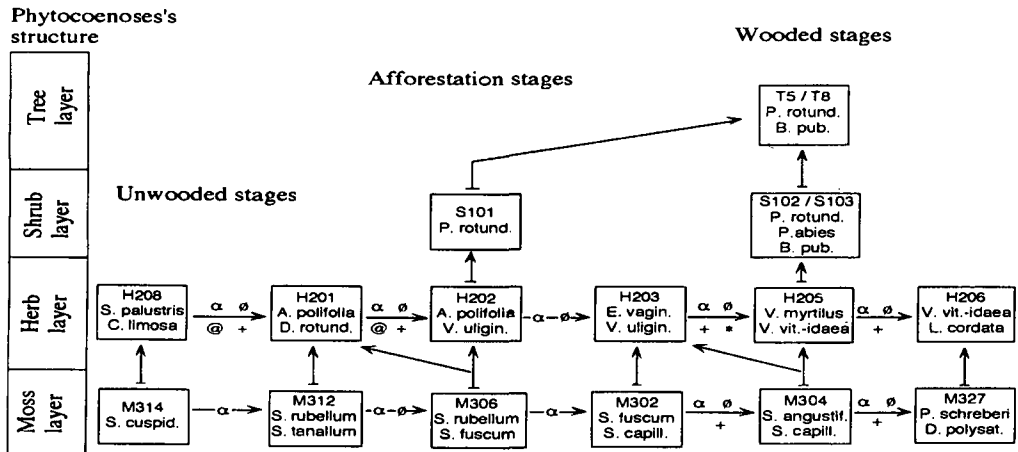


Fig. 3. Generalized qualitative dynamic model of the vegetation in relation to the development of bog-pine trees on oligotrophic mires affected by drainage. The diagram is drawn with the elementary syntaxa occurring in the four bog-pine-dominated coenotaxa described in Fig. 2 and in Tab. 2 to 5. The hypothetical relations are derived from the synchronical description of the vegetation and from comparisons of the calculated ecological significance of the different syntaxa (Fig. 4). Lichen or hepatic-dominated synusia are not included and only the main syntaxa explaining most of the vegetation spatial structure are considered. Spatial relationships and hypothetical changes with time: $X \xrightarrow{\epsilon} Y$ – progressive replacement of X by Y under an ecological constraint ϵ . Constraints are: α – soil becomes drier; @ – soil becomes more acid; + – soil becomes less acid; * – soil nutrients increase, peat mineralization; + – soil nutrients decrease; \emptyset – light decreases; $Z \mapsto W$ – W develops superposed on Z (layering).

with layered tree stands of medium size and high density. Vigorous *Vaccinium uliginosum* forms a dense layer. This coenotaxon includes a number of recognized associations such as: *Sphagnetum magellanici* (incl. *Sphagnetum fuscum* LUQUET 1926) and *Pino rotundatae-Sphagnetum (pro parte)*. Coenotaxon No. 3 is a community type with *Pinus uncinata* var. *rotundata*, *Vaccinium myrtillus*, *Sphagnum capillifolium*, and *Dicranum polysetum* comprising tall tree stands near the mire edge and its bordering spruce forest. Coenotaxon No. 4 is a community type with *Pinus uncinata* var. *rotundata*, *Betula pubescens*, *Vaccinium myrtillus*, *Sphagnum capillifolium*, and *Dicranum polysetum* consisting of rather dense tall tree stands adjacent to peat-cuttings. Its vegetation is closely related to coenotaxon No. 3, although with birch developing. In these two last coenotaxa, the *Vaccinium myrtillus* layer is very vigorous. Together they include a number of classical associations including *Pino rotundatae-Sphagnetum (pro parte)* and *Vaccinio uliginosi-Pinetum rotundatae*. Species of the *Oxyccoco-Sphagnetum* are rare, those of the *Vaccinio-Piceetea* being more frequent.

The mean ecological indicator values of the herb and moss synusia are shown in Fig. 4, and the generalized qualitative model of the vegetation dynamics on oligotrophic mires affected by drainage is given in Fig. 3. In the course of tree colonization, some of the elementary syntaxa of hollows (M314, H208) and of wet lawns (H201, H202, M312, M306) disappear, whereas the *Vaccinium* strata gain in importance, first dominated by *Vaccinium uliginosum* (H203) and then by *V. myrtillus* (H205). This dynamic process is marked by shifts in the combination of mosses. Species such as *Sphagnum cuspidatum*, *S. tenellum*, *S. rubellum*, *S. fuscum*, and *S. capillifolium* are transient (ANDRUS et al. 1983), while *S. angustifolium* and *S. magellanicum*, which have a greater ecological amplitude are, therefore, less affected by the tree colonization (Tab. 5). The spread of *Sphagnum tenellum*, in such bogs, may be due

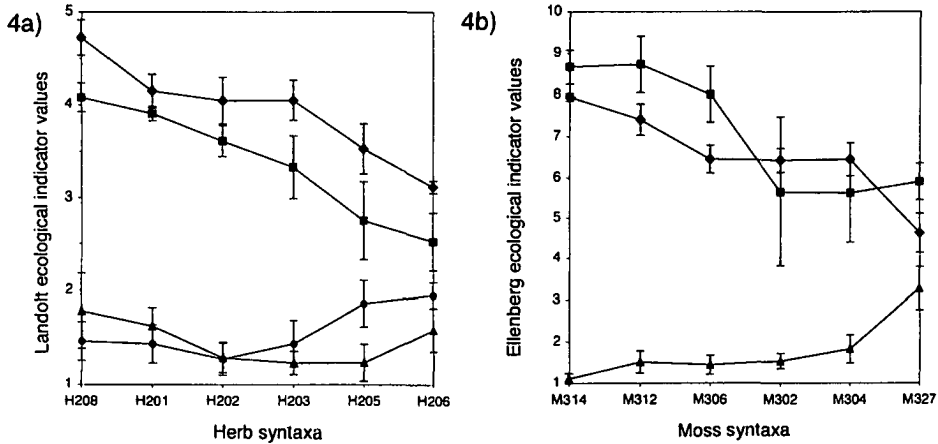


Fig. 4. Mean ecological indicator values ± 1 standard deviation for the herb and moss syntaxa, numbered and ordered according to Tab. 4 and 5 and Fig. 3. Scales for ecological indicator values are given according to LANDOLT (1977) for the herb syntaxa (Fig. 4a, scale from 1 to 5) and according to ELLENBERG et al. (1991) for the moss synusiae (Fig. 4b, scale from 1 to 9). Soil humidity value F (◆): 1 (dry) to 5 or 9 (wet); Light value L (■): 1 (shade) to 5 or 9 (light); Reaction value R (▲): 1 (acid) to 5 or 9 (neutral to alkaline); Nutrient value N (●): 1 (nitrogen poor) to 5 or 9 (nitrogen rich).

to the hygrophilous nature of the species, which can cope with summer droughts. Some other mosses are also favoured by dryness in the open and well-lit environments of the bogs; these include *Aulacomnium palustre*, *Dicranum affine*, and *Polytrichum strictum*. In more shaded locations beneath dense canopies of pine trees, species such as *Hylocomium splendens*, *Pleurozium schreberi*, *Dicranum polysetum*, and *Ptilium crista-castrensis* increase in abundance on the driest hummocks, competing with the *Sphagnum* species. Seedlings of *Pinus* were more frequently encountered in the open and wet situations (H201, H202) or in the presence of a low *Vaccinium uliginosum* layer (H203). By contrast, *Picea abies* and *Betula pubescens* seedlings were more frequent in dry situations with a *Vaccinium myrtillus* and *V. vitis-idaea* layer (H205, H206) (Tab. 4) and were missing in the wet and open parts of the bogs (H208, H201, H202). Thus, it appears that seedlings and saplings of *Pinus uncinata* var. *rotundata* survive at a better rate in more open and wet environments, which confirms the observations of SCHMID et al. (1995).

DISCUSSION

The four coenotaxa that describe the bog-pine-dominated vegetation on uncut oligotrophic mires affected by drainage in the Jura Mountains are often found in concentric arrangements on small bogs that are often bog remnants. They can be easily distinguished if their synusial organization is considered, including both vertical layers and horizontal patches.

A dendroecological study of the tree stands (FRELÉCHOUX 1997, FRELÉCHOUX et al. 2000) allowed interesting insights into the vegetation dynamics. In coenotaxon No. 1, representing open and wet situations, pine trees were small (0–5 m) and showed reduced width and top growth. Their populations consisted of individuals of uneven ages. In coenotaxon No. 2, showing a slightly denser tree canopy, trees were of medium size (0–8 m) and also of uneven ages, but some individuals were very old (maximum 375 years old). By contrast, in coenotaxa No. 3 and No. 4, where dense tree stands have developed, most trees grew fast, reaching

Table 2. Synthetic tabular representation of the principal tree synusial elementary syntaxa of bog-pine-dominated vegetation in the uncut oligotrophic mires of the Jura Mountains. Relative frequency (RF) classes are indicated for each species in each syntaxon; r: species represented in less than 10% of the relevés or in a single relevé; I: $10\% \leq RF \leq 20\%$; II: $20\% < RF \leq 40\%$; III: $40\% < RF \leq 60\%$; IV: $60\% < RF \leq 80\%$; V: $RF > 80\%$. Mean abundance-dominance values are indicated according to the Braun-Blanquet scale. Species that do not show relative frequencies of 10% or higher in any of the syntaxa are not listed. A short description of each syntaxon is given in Appendix.

Tree layer syntaxon	T5	T8
Number of relevés	11	7
Total number of species	1	3
<i>Pinus uncinata</i> var. <i>rotundata</i>	V:5	V:4
<i>Betula pubescens</i>	.	V:1
<i>Picea abies</i>	.	V:1

Table 3. Synthetic tabular representation of the principal shrub synusial elementary syntaxa of bog-pine-dominated vegetation in the uncut oligotrophic mires of the Jura Mountains (see complete explanation in Tab. 2). A short description of each syntaxon is given in Appendix. Rare species are not listed.

Shrub layer syntaxon	S101	S102	S103
Number of relevés	42	10	20
Total number of species	1	3	6
<i>Pinus uncinata</i> var. <i>rotundata</i>	V:5	V:5	V:2
<i>Betula pubescens</i>	.	III:+	V:4
<i>Picea abies</i>	.	III:+	III:1
<i>Sorbus aucuparia</i>	.	.	I:+

heights of 10–15 m and constituting even-aged and relatively young populations (maximum 150 years). These observations highlight the distinct population dynamics of *Pinus* in these four different communities.

The primary vegetation succession that leads towards *Pinus* forest is outlined in Fig. 5. When comparing the vegetation units described by NEUHÄUSL (1992) with the coenotaxa described here, it appears that the *Pino rotundatae-Sphagnetum*, which is considered to be a local climax, corresponds to coenotaxa No. 1 and No. 2, which have trees of small to medium size. On the other hand, the *Vaccinio uliginosi-Pinetum*, which is considered to be a post-climax community, corresponds well to coenotaxa No. 3 and No. 4, which both have tall trees. In fact, the coenotaxa belong to the same (primary) successional series, but have been affected by both autogenic and allogenic processes. According to ZOBEL (1988), increasing oligotrophy and acidity are the main forcing functions of autogenic processes. On the other hand, it seems clear that bog evolution has been conditioned by

allogenic factors such as climate shifts over thousands of years and more recently by such anthropic impacts as drainage and peat cutting. It is, therefore, permissible to consider the first part of the dynamics (coenotaxa No. 1 and No. 2) as being chiefly dependent on autogenic processes and the second part (coenotaxa No. 3 and No. 4) on allogenic processes. The later stages result from the combination of the indirect effects of active drainage in the vicinity (peat cutting) and of natural drainage that is more pronounced in small raised bogs. Although GUINOCHET (1955) suggested that there is a succession from pine forest towards spruce forest, this is not possible on uncut oligotrophic, poorly-drained, deep-peat soils since spruce trees growing on these are generally of limited size and show obvious signs of chlorosis.

The high mortality of pine trees at some sites suggests that succession could proceed towards wetter heathlands. The subsidence and compactness of the peat soils as a result of intensive mineralization could explain this phenomenon (SCHNEEBELI 1991, SCHULTESS 1990, SCHWEINGRUBER 1996). This would also indicate that a cyclic process could take place with an alternation of wooded, dry peat-bogs and open wet mires. Indeed, tree establishment would require favourable ecological conditions, in particular enough light and moisture, which are

Table 4. Synthetic tabular representation of the principal herb synusial elementary syntaxa of bog-pine-dominated vegetation in the uncut oligotrophic mires of the Jura Mountains (see complete explanation in Tab. 2). A short description of each syntaxon is given in Appendix. Rare species are not listed.

Herb layer syntaxon	H208	H201	H202	H203	H205	H206
Number of relevés	7	10	8	50	25	7
Total number of species	27	21	13	37	38	14
<i>Carex chordorrhiza</i>	II:1	r:+
<i>Carex limosa</i>	V:2	r:+
<i>Scheuchzeria palustris</i>	V:1	II:+
<i>Eriophorum angustifolium</i>	III:+	II:1	.	r:+	.	.
<i>Carex echinata</i>	III:1	II:+	.	l:1	.	.
<i>Menyanthes trifoliata</i>	III:2	r:1	.	r:1	.	.
<i>Carex lasiocarpa</i>	III:2	III:1	r:1	r:1	.	.
<i>Carex rostrata</i>	III:2	r:+	.	r:1	r:2	.
<i>Betula nana</i>	.	I:+	.	r:1	.	.
<i>Carex pauciflora</i>	III:1	IV:1	III:1	I:1	.	.
<i>Drosera rotundifolia</i>	r:+	V:1	IV:1	r:1	.	.
<i>Scirpus cespitosus</i>	III:2	IV:3	IV:2	r:+	.	.
<i>Vaccinium oxycoccus</i>	V:2	V:1	V:2	V:2	I:1	.
<i>Andromeda polifolia</i>	IV:1	V:2	V:2	V:1	r:+	.
<i>Eriophorum vaginatum</i>	IV:2	V:2	IV:2	V:2	IV:2	r:1
<i>Dactylorhiza maculata</i>	II:1	I:+	r:1	I:+	r:1	r:+
<i>Carex nigra</i>	r:1	II:1	.	I:1	I:+	r:+
<i>Potentilla erecta</i>	II:+	.	.	.	r:1	.
<i>Vaccinium uliginosum</i>	II:1	II:1	V:2	V:2	V:2	.
<i>Calluna vulgaris</i>	.	IV:2	V:3	V:2	IV:1	.
<i>Vaccinium vitis-idaea</i>	r:1	.	.	III:1	V:2	V:3
<i>Vaccinium myrtillus</i>	r:1	.	.	IV:2	V:3	IV:3
<i>Listera cordata</i>	.	.	.	r:+	I:+	V:1
<i>Melampyrum pratense</i>	r:+	.	r:+	II:1	I:1	.
<i>Dryopteris carthusiana</i>	.	.	.	r:2	II:1	r:+
<i>Anthoxanthum odoratum</i>	.	.	.	r:+	I:2	.
<i>Luzula multiflora</i>	I:1	.
Tree seedlings						
<i>Pinus uncinata</i> var. <i>rotundata</i>	r:+	V:+	IV:+	III:+	II:+	r:1
<i>Picea abies</i>	.	.	.	I:+	III:1	III:2
<i>Betula pubescens</i>	r:+	.	.	r:+	III:1	r:+
<i>Sorbus aucuparia</i>	.	.	.	r:1	II:1	.
<i>Abies alba</i>	.	.	.	r:+	I:+	r:+

not fulfilled when a dense layer of *Vaccinium* remains. It is unlikely that such a cyclic process has occurred on a large scale in the small Jura bogs. Nevertheless, it might well be the case that small transient patches of pine forest have developed in the past. Such ancient woodland phases have been demonstrated elsewhere by stratigraphical analyses of peat bogs and the discovery of fossil trees (MUNAUT & CASPARIE 1971, McNALLY & DOYLE 1984a, 1984b, PILCHER et al. 1995). In the Jura bogs there is little macrofossil evidence for such ancient pine forests. Nevertheless, layers with much higher pine-pollen content and associated macroremains, which indicate that there were several pine forest phases during the Atlantic and Subboreal periods, were identified by REILLE (1991) in one of the largest bogs of the Jura Mountains (Frasne, France).

Following REILLE (1991) and FELDMEYER-CHRISTE (1990), it is proposed that the phytocoenoses with tall and dense bog-pine trees (coenotaxa No. 3 and No. 4) have appeared

Table 5. Synthetic tabular representation of the principal moss synusial elementary syntaxa of bog-pine-dominated vegetation in the uncut oligotrophic mires of the Jura Mountains (see complete explanation in Tab. 2). A short description of each syntaxon is given in Appendix. Rare species are not listed.

Moos layer syntaxon	M314	M312	M306	M302	M304	M327
Number of relevés	8	12	40	23	39	13
Total number of species	7	17	29	20	28	24
<i>Sphagnum subsecundum</i>	II:1	.	r:1	r:1	.	.
<i>Drepanocladus fluitans</i>	II:1	.	r:1	.	.	.
<i>Sphagnum cuspidatum</i>	V:5	III:2	I:+	.	.	.
<i>Sphagnum angustifolium</i>	II:2	I:1	V:2	III:2	V:2	II:2
<i>Sphagnum tenellum</i>	r:2	V:4	I:+	.	.	.
<i>Sphagnum papillosum</i>	.	III:2	r:+	r:1	.	.
<i>Sphagnum magellanicum</i>	.	IV:1	V:2	V:2	V:2	I:1
<i>Mylia anomala</i>	.	II:+	I:+	.	.	.
<i>Cephalozia connivens</i>	.	.	I:+	.	r:+	.
<i>Sphagnum rubellum</i>	.	V:2	V:2	r:2	r:2	.
<i>Sphagnum fuscum</i>	.	r:1	IV:2	V:2	.	.
<i>Aulacomnium palustre</i>	.	r:1	V:1	III:1	III:1	r:1
<i>Dicranum affine</i>	.	r:+	III:1	III:1	II:1	I:1
<i>Sphagnum capillifolium</i>	.	r:2	II:1	V:3	V:2	r:2
<i>Polytrichum strictum</i>	.	r:1	V:1	V:2	V:1	r:2
<i>Hylocomium splendens</i>	.	.	.	r:+	II:+	V:2
<i>Pleurozium schreberi</i>	.	.	II:1	II:1	III:1	V:3
<i>Dicranum polysetum</i>	.	.	.	r:+	II:1	V:1
<i>Sphagnum centrale</i>	.	.	r:1	.	I:1	.
<i>Ptilium crista-castrensis</i>	I:1	IV:1
<i>Dicranum scoparium</i>	I:1	III:1
<i>Rhytidiadelphus loreus</i>	r:1	II:1
<i>Rhytidiadelphus triquetrus</i>	.	.	.	r:+	r:+	II:2
<i>Sphagnum girgensohnii</i>	.	.	r:2	.	II:1	.
<i>Sphagnum russowii</i>	.	.	r:1	.	I:2	.

recently on the Jura bogs as a result of continuous human impact since the 18th century (peat cutting, drainage). It is, however, probable that the bog-pine has always existed in this ecosystem since the onset of the post-glacial period. Its distribution earlier was probably different from that of today, most populations having developed on the fens or in association with the spruce forest at the bog margins, but possibly also in isolated stands or individually on the oligotrophic bog (FRELÉCHOUX 1997). Contrary to REILLE (1991) and FELDMEYER-CHRISTE (1990), we do not believe that bog-pines were ever planted in the Jura bogs, at least not on a large scale. Based on historical documents, BÉGEOT & RICHARD (1996) have proved that bog-pines were never planted in the large mire of Frasné (France), unlike some other tree species. Recently MITCHELL et al. (in press) stressed that forest clearance in the vicinity of the bogs in the Jura Mountains could have changed their local climate, increasing the influence of winds and the drying up of the peat surface, thus permitting bog-pine encroachment. The survival potential of *Pinus uncinata* var. *rotundata* is very high and has allowed this species to thrive in many ecological situations, such as wet and oligotrophic environments. The small contribution of *Pinus* in the former stratigraphical layers, as compared to surface layers, can be explained by the stress exerted on the plants by a high water table, which allowed only limited pollen production (GIERTYCH 1967, ELLENBERG 1978). In conclusion, the different bog-pine-dominated vegetation types described in this study have

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APPENDIX

List of the 30 synusial elementary syntaxa of bog-pine-dominated vegetation presented in Tab. 1, with a short description. Not listed are 13 elementary syntaxa that were accidental. Syntaxa numbers are those kept from the whole typology (FRELECHOUX 1997). The letters T (trees), S (shrubs), H (herbs) and M (mosses) come before the number according to their respective layer. Those syntaxa which explain most of the vegetation spatial structure and which were used for the generalized dynamic model (see Fig. 3 and Tab. 2 to 5) are marked with an asterisk (*).

- T5*. Monospecific tree layer syntaxon with *Pinus uncinata* var. *rotundata*. Both *Picea abies* and *Betula pubescens* are missing. Synusiae occur in closed, medium or tall pine forests.
- T6. Tree layer syntaxon with *Pinus uncinata* var. *rotundata*, *Betula pubescens*, and *Sorbus aucuparia*. Synusiae occur in closed, tall pine forests.
- T8*. Tree layer syntaxon with *Pinus uncinata* var. *rotundata*, *Betula pubescens*, and *Picea abies*. Synusiae occur in closed, tall pine forests.
- S101*. Monospecific shrub layer syntaxon with *Pinus uncinata* var. *rotundata*. Synusiae occur in open to closed pine forests.
- S102*. Shrub layer syntaxon with dominance of *Pinus uncinata* var. *rotundata*. Both *Picea abies* and/or *Betula pubescens* are present. Synusiae occur in open to closed pine forests.
- S103*. Shrub layer syntaxon with *Betula pubescens* and *Pinus uncinata* var. *rotundata*. The pubescent birch is more dominant. Synusiae occur in the understorey of half-closed to closed tall pine forests.
- S108. Shrub layer syntaxon with *Picea abies*, *Betula pubescens*, and *Sorbus aucuparia*. Synusiae occur mainly in spruce forests.
- H201*. Herb layer syntaxon with *Drosera rotundifolia*, *Carex pauciflora*, *Andromeda polifolia*, *Eriophorum vaginatum*, *Vaccinium oxycoccos*, *Pinus uncinata* var. *rotundata*, *Scirpus cespitosus*, and *Calluna vulgaris*. Synusiae occur on wet lawns at the edges of the hollows.
- H202*. Herb layer syntaxon close to H201. Most of the hygrophilous plants are missing. Here *Vaccinium uliginosum* is more frequent and has greater cover. Synusiae occur on less wet lawns.
- H203*. Herb layer syntaxon with *Vaccinium uliginosum*, *Calluna vulgaris*, *Eriophorum vaginatum*, *Vaccinium oxycoccos*, *Andromeda polifolia*, and *Vaccinium myrtillus*. Synusiae occur on drier lawns and hummocks.
- H205*. Herb layer syntaxon with *Vaccinium myrtillus*, *V. vitis-idaea*, and *V. uliginosum*. Synusiae occur on drier and more shaded hummocks in pine, birch, and spruce forests.
- H206*. Herb layer syntaxon with *Vaccinium vitis-idaea*, *Listera cordata*, and *Vaccinium myrtillus*. Synusiae occur in very shaded locations mainly in spruce forests. It also occurs in the tall pine forests, in the understorey of the tall and dense *V. myrtillus*-layer.
- H208*. Herb layer syntaxon with *Carex limosa*, *Scheuchzeria palustris*, *Vaccinium oxycoccos*, *Andromeda polifolia*, and *Eriophorum vaginatum*. Synusiae occur in well-lit and moist situations, in hollows and in the wettest borders in the middle of raised bogs.
- M302*. Moss layer syntaxon with *Sphagnum capillifolium*, *S. fuscum*, *S. magellanicum*, and *Polytrichum strictum*. Synusiae occur in half-light locations on dry lawns and hummocks in pine- and birch-wooded bogs.
- M304*. Moss layer syntaxon with *Sphagnum capillifolium*, *S. magellanicum*, *S. angustifolium*, and *Polytrichum strictum*. Synusiae occur in shady and dry locations in pine, birch and spruce forests, mainly under a *Vaccinium*-layer.
- M305. Moss layer syntaxon with *Sphagnum angustifolium*, *S. magellanicum*, *Polytrichum strictum*, and *Aulacomnium palustre*. The dominant moss is *Sphagnum angustifolium*. Synusiae occur mainly in ditches after peat cutting and form very wet lawns.
- M306*. Moss layer syntaxon with *Sphagnum rubellum*, *S. magellanicum*, *Polytrichum strictum*, *Aulacomnium palustre*, *Sphagnum angustifolium*, and *S. fuscum*. Synusiae occur in open and wet locations, on wet lawns at the borders of the oligotrophic hollows in the middle of the raised bogs.
- M307. Moss layer close to M306, with *Sphagnum rubellum*, *S. magellanicum*, *S. angustifolium*, and *S. fuscum*. A number of mosses, including *Polytrichum strictum*, *Aulacomnium palustre*, and *Dicranum affine* are missing. Synusiae occur on the wettest and most oligotrophic lawns at the borders of the oligotrophic hollows.

- M310. Moss layer syntaxon with *Sphagnum rubellum* and the hepatics *Kurzia pauciflora*, *Mylia anomala*, *Cephalozia connivens*, and *Calypogeia sphagnicola*. Synusiae occur on well-lit and moist lawns or on wet, bare or trampled peat. Hepatics might point to increasing peat mineralization.
- M311. Moss layer syntaxon poor in species with *Sphagnum cuspidatum* and *S. magellanicum*. Synusiae sometimes relictual on well-drained raised bogs, sometimes pioneer on wet peat after peat cutting.
- M312*. Moss layer syntaxon with *S. rubellum*, *Sphagnum tenellum*, *S. magellanicum*, *S. papillosum*, and *S. cuspidatum*. Synusiae occur on the wettest borders of the oligotrophic hollows.
- M314*. Moss layer syntaxon poor in species with *Sphagnum cuspidatum* and *Drepanocladus fluitans*. Synusiae occur only in the most oligotrophic hollows.
- M326. Moss layer syntaxon poor in species, with only *Pleurozium schreberi* and *Hylocomium splendens*. Synusiae occur in very dry and half-shaded locations, chiefly in birch forests, but also in pine forests.
- M327*. Moss layer syntaxon with *Pleurozium schreberi*, *Hylocomium splendens*, *Dicranum polysetum*, and *Ptilium crista-castrensis*. Synusiae occur under the dry and shadiest locations, only in tall pine forests.
- M329. Moss layer syntaxon with *Dicranum affine*, *Polytrichum strictum*, and *Pleurozium schreberi*, but with *Hylocomium splendens* missing. Synusiae occur in light and dry locations in open pine- and birch-wooded bogs.
- M330. Moss layer with *Aulacomnium palustre*, *Sphagnum angustifolium*, and *Pleurozium schreberi*. Synusiae occur in meso-oligotrophic locations in wooded fens but also in pine-dominated raised bogs. In these bogs, the presence of *Aulacomnium palustre* may point to increasing peat mineralization.
- M333. Moss layer syntaxon with *Dicranodontium denudatum* and *Tetraphis pellucida*. Synusiae occur in dry situations on rotted wood or on bare peat.
- M334. Moss layer syntaxon with *Dicranodontium denudatum*, *Sphagnum capillifolium*, *S. magellanicum*, and *Mylia anomala*. Synusiae occur in wet, shady locations on bare peat.
- M336. Hepatic-dominated moss layer syntaxon with *Cephalozia connivens*, *Mylia anomala*, *Kurzia pauciflora*, *Calypogeia sphagnicola*, *Calypogeia neesiana*, and *Dicranodontium denudatum*. Synusiae occur on bare or trampled peat.
- M343. Lichen syntaxon with *Cladonia rangiferina* (L.) WEBER ex WIGG and *Cladonia arbuscula* (WALLR.) FLOTOW. Synusiae occur in dry, light to shady locations in several pine-dominated coenotaxa.