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Vegetation dynamics during the establishment phase of an energy forest on a riverside in south-western Sweden

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Abstract

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The succession of ground vegetation was studied in a meadow in SW Sweden during four years after planting with *Salix viminalis*. Two older stands (11 and 18 years) were included as reference points for the next stage of succession. Random, permanent plots were used and the data were analysed with cluster analysis, principal components analysis and detrended correspondence analysis. Before energy forest was planted meadow species were dominant and constituted more than half of the mean field-layer cover. The first year after planting of willow, the vegetation decreased drastically in cover but then recolonized quickly. The change in vegetation was very rapid during the first years but a stabilization was evident already after four years. Ten species present in the original meadow were found in all years in the energy forest while three species disappeared. Species number varied from 33 to 45, depending on year. The dominant herbs four years after planting were *Cirsium arvense* (10% cover), *Filipendula ulmaria* (10%) and *Galeopsis tetrahit* (9%). Ruderal species became increasingly common during the succession, while meadow and fen species decreased. The spring flora was outstanding in the two older reference stands. Comparisons are made with other successions and an attempt is made to use the results to judge the impact of future large-scale energy forestry on flora and vegetation.

Key words: Succession, willow, *Salix*, coppice, short rotation forestry, biomass energy, principal components analysis, detrended correspondence analysis, cluster analysis.

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Introduction

This paper presents results from a conservation-orientated study on the flora and vegetation of energy forests. A background to energy forestry and the vegetation study is given by Gustafsson (1987).

As a part of the vegetation study, the succession during the early establishment of an energy forest on a meadow in the south-western part of Sweden was studied. The results from a parallel study on a peat bog in east-central Sweden are presented by Gustafsson (1988).

The aim of the present study was to describe the change in flora and vegetation starting with the original meadow, through four years of willow cultivation (1978–1982); to describe the rate of change from year to year; to assess the period needed for the vegetation to stabilize; to study the changes in vegetation throughout a growing season and to apply the results to large-scale energy forestry.

Methods

The sites

The main area of investigation (Ätran) is situated alongside the River Ätran, about 8 km east of the centre of Falkenberg in the province of Halland (Fig. 1). The river flows through a cultivated valley, the soils of which are based on quaternary deposits composed of fine material such as clay and sand. The bedrock consists of gneiss (Svedmark, 1893). The

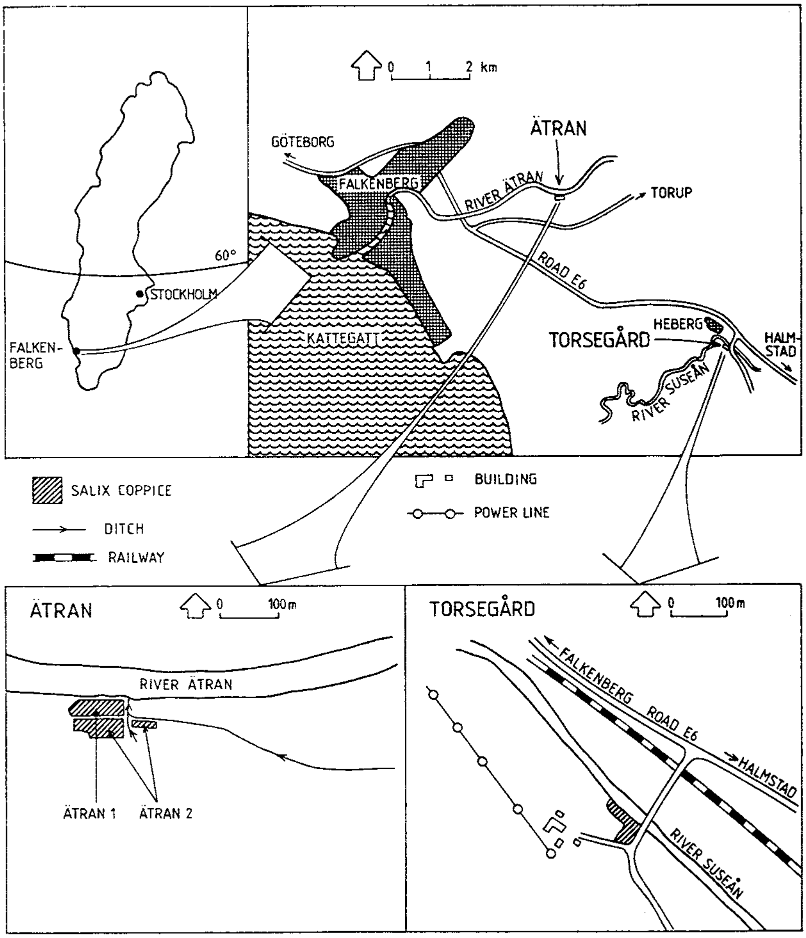

Fig. 1. Map of the sites.

Table 1. *Climatic data for the sites. All data taken from the climatic station at Varberg, about 30 km north of the sites*

Precipitation, monthly 1978–1982, mm[a]

Year	Total	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
1978	672	52	25	114	6	7	52	55	112	131	26	63	29
1979	697	48	16	58	66	55	24	68	98	44	33	107	80
1980	829	36	40	23	23	31	123	64	82	81	104	102	120
1981	811	35	59	91	5	50	89	88	35	48	142	118	51
1982	755	53	27	50	19	81	91	3	173	32	58	73	95

Mean annual precipitation 1931–1960: 695 mm[b]

Temperature, mean monthly 1978–1982 °C[a]

Year	Mean	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
1978	7.3	0.7	−0.3	1.2	5.0	11.8	15.5	15.5	15.9	11.2	9.4	7.3	−2.7
1979	6.3	−4.6	−4.8	0.5	4.8	10.5	16.1	14.8	15.1	12.5	6.7	4.5	0.1
1980	6.9	−2.4	−3.6	0.1	5.3	10.6	15.6	17.0	15.8	13.3	7.4	2.0	1.6
1981	7.0	−1.2	−0.3	1.5	5.1	13.2	14.3	16.2	15.8	13.4	8.0	4.3	−5.9
1982	7.8	−5.5	−2.2	2.6	5.8	10.2	14.4	18.3	17.4	13.7	9.3	6.4	2.7

Mean annual temperature 1951–1980: 7.5°C[c]

Heat sum = 1391 (Annual sum of average daily (1961–1974) temperatures above 6°C)[d]

Growing season = 19/4–8/11 213 days (Number of days with average daily (1961–1974) temperatures above 6°C)[d]

Frost frequency = 5.7 (Average number of days (1961–1974) during the growing season with minimum temperatures below 0°C)[d]

[a] From:SMHI, climatic section, Oct. 1983. [b] From: SMHI (1973). [c] From: Eriksson (1982). [d] From: Perttu & Huszar (1976).

willow beds are found on soil of brown earth type. The area is usually flooded during spring and the ground-water level is high throughout the year.

The climate of the study area is maritime with relatively mild winters and fairly cool summers. The yearly precipitation is 695 mm, the growing season is 213 days, which is long compared to the rest of Sweden, and the frost frequency is low. The years 1980 and 1981 had higher precipitation than normal and the years 1978–1981 all had a lower mean temperature than the average. The summer of 1982 was exeptionally warm and dry. The climate is described in detail in Table 1.

In the autumn of 1978 two small areas (0.3 ha and 0.1 ha, Fig. 1), which were formerly grazed, were ploughed and harrowed. Hereafter they are treated as one stand (Ätran 2). *Salix viminalis* was planted in April 1979. Fertilizers were applied at a rate of 50 kg N/ha in 1981 and 90 kg N/ha, in 1982. Weeds were removed by hand early in June during the first two years and a herbicide (Roundup) was used between rows in the eastern section in 1979. The willow was cut with a brush saw about 1 dm above the ground each year during the period 1979–1982. At the time of the last analysis (July 1982) the shoots measured 1.5–2 m in height and the stand was very dense.

Two older willow beds were included for comparison. One (Ätran 1, 0.2 ha) bordered on Ätran 2. It was planted with *S. viminalis* in 1971. The other stand (Torsegård, 0.2 ha) was situated in another riverside area 7 km south-east of Ätran and was planted with the same species in 1964. (Fig. 1). The treatment of Ätran 1 and Torsegård was similar to that of Ätran 2.

More information on the history, biology and management of the stands is given in Gustafsson (1985, 1987).

Sampling

The edge zones around the stands (2–10 m) were omitted from the analysis in order to avoid possible edge effects. Large plots were placed centrally within the Ätran stands (Ätran 1: 10×40 m, Ätran 2: 25×60 m, 10×35 m). At Torsegård three plots (10×10 m) were placed at random (not overlapping). Within the plots, quadrats 0.5×0.5 m were placed at random. At Ätran 1 there was a total of 75 quadrats, at Ätran 2 there were 120 and at Torsegård there were 75. Ätran 2 was analysed every summer during the period 1978–1982 and in spring and autumn of 1981. The quadrats became permanent after the soil cultivation in the autumn of 1978. Ätran 1 and Torsegård were analysed in spring, summer and autumn 1981. The dates of analysis were:

	Year				
Site	1978	1979	1980	1981	1982
Ätran 1				20–21 V, 1–2 VII, 15 IX	
Ätran 2	15–16 VI	5–7 VII	2–4, 7 VII	18–19 V, 30 VI, 1–3 VII, 13–14 IX	7–9 VII
Torsegård				21–22 V, 3 VII, 16 IX	

In the quadrats, the cover (cov) (Persson, 1975) for vascular species and bryophytes was estimated using a percentage scale. For Ätran 2 it was: $0<cov\leq 1$, $1<cov\leq 2$, $2<cov\leq 3$, $3<cov\leq 4$, $4<cov\leq 5$, $5<cov\leq 10$, $10<cov\leq 20$, $20<cov\leq 30$, ... $90<cov\leq 100$ and for Ätran 1 and Torsegård: $90<cov\leq 10$, $10<cov\leq 50$, $50<cov\leq 100$. The Ätran 2 data were converted to the coarser scale during part of the data treatment. The apparent cover (Persson, 1975) for all field-layer and bottom-layer species respectively was recorded in each quadrat using the detailed cover scale. These measurements are termed "apparent field-layer cover" and "apparent bottom-layer cover", in accordance with the apparent cover concept of Persson (1975).

All species not occurring in the quadrats but present in the stands were noted. If a species was found flowering or fruiting in a quadrat, it was recorded as such.

In many cases it was impossible to distinguish between different species of grasses, particularly in their sterile state, and consequently all grasses were estimated collectively ("*Poaceae*"). The names of all grass species occurring in a stand were noted.

Nomenclature

The nomenclature for vascular plants follows Lid (1974) and for mosses Nyholm (1954–69). "Meadow species" is used in the sense of Andersson (1981) and Gustafsson (1987).

Data analysis

Species cover

The BMDP program P1D (Dixon & Brown, 1979) was used to obtain mean cover and standard error. When the coarser cover scale was used, the centres of the intervals were used (5%, 30%, 75%) in order to avoid overestimation of cover.

Grouping of stands/years/seasons

A cluster analysis was performed on the summer data from Ätran 2, 1978–1982, Ätran 1 and Torsegård, 1981, with BMDP program P2M (hierarchic, agglomerative, average linkage method). Euclidian distance was used as a measure of dissimilarity. The data were in the form of the coarse cover scale. Runs with different number of species were tested. The result was similar when species with a mean cover of 1% or more and up to 5% or more were included. When all species were included, the rare species distorted the run.

A principal components analysis (PCA) based on a correlation matrix and with varimax rotation, was performed on the same data set with BMDP program P4M. The quadrats were united into groups of five, to fit the limited capacity of the program. The mean factor scores per stand each year were used in the presentation.

A detrended correspondence analysis (DCA) was performed on the May-July-September 1981 data for all stands using program DECORANA (Hill & Gauch, 1980). Species occurring five times or more in the dataset were included in the DCA. Rare species were downweighted.

Frequency and reproductive effort.

Quadrat frequencies for species and for species present in a reproductive stage were calculated using the program FENRUT (Svensson, 1982).

Results

The results presented below are mainly from the analysis of Ätran 2 (1978–1982) but also from the stands Ätran 1 and Torsegård. Additional data on the vegetation of the stands are presented in Gustafsson (1987).

Before being converted to energy forest, the Ätran 2 site was an open meadow, rich in herbaceous species, of which the most dominating were *Trifolium repens* (13% cover), *Carex acuta* (11%), *Ranuculus repens* (7%), *Ranuculus acris* (6%), *Achillea millefolium* (5%), *Carex disticha* (5%), *Cirsium vulgare* (5%), *Juncus effusus* (5%), *Filipendula ulmaria* (3%). The vegetation covered 97% of the ground and the cover of grasses was 46%.

Meadow species constituted 57% of the total mean field-layer cover ("Poaceae" exepted), fen species 29% and ruderals 13%.

Four years after the planting of willow, the species composition had changed considerably. The mean apparent field-layer cover had decreased to 85% and the grasses had increased to 57%. The most dominant herbs were *Cirsium arvense* (10%), *Filipendula ulmaria* (10%), *Galeopsis tetrahit* (9%) and *Taraxacum vulgare* coll. (6%). Ruderals constituted 51% of the total mean field-layer cover ("Poaceae" excepted), fen species 24%, meadow species 22% and woodland species 2%. The corresponding values for the 11-year-old stand Ätran 1 were ruderals 82%, fen species 1%, meadow species 13% and woodland species 4%, and for the 18-year-old stand Torsegård ruderals 90%, fen species 3%, meadow species 7% and woodland species 1% (Gustafsson, 1987).

The cluster analysis and the PCA (Figs. 2, 3) give graphical representations of the change between years. The dendrogram shows that the planting year (1979) had the lowest degree of similarity and that similarity increased in the order: 1979, 1978, 1980, 1981, 1982. Torsegård and Ätran 1 are included as old stands and as possible next stages of sucession. They are linked at quite a high level of similarity and in turn they link with the 1980-1981-1982 group. The PCA corresponds well to the cluster analysis and the years 1978 and 1979 also are extremes here. The Ätran 2 stand seems to be developing towards a vegetation similar to the one at the old stand of Ätran 1. The rate of change can be estimated from the distance between the stands in the diagram. Change was very rapid at the beginning of succession, but in 1980 it started to slow down considerably. Contrary to the dendrogram, Torsegård has an isolated position in the PCA, suggesting that it differed from the Ätran stands.

If the whole time series at Ätran 2 (0, 1, 2, 3, 4, years) and Ätran 1 (11 years) is considered, the species can be divided into different groups, based on the time of their appearance during the succession (Table 2). Three species present in the original meadow did not reappear in the stands: *Carex leporina*, *Luzula multiflora* and *Sium latifolium*. A number of species only were present in the oldest stand (Ätran 1), among them *Galium aparine*, *Geum urbanum*, *Prunus padus*, *Ribes rubrum* and *Rubus idaeus*. *Cirsium arvense*, *Galeopsis tetrahit* and *Urtica dioica* were found only in the coppices, not in the original meadow. Ten species were present in the meadow and in the stands in all years, among them being *Achillea ptarmica*, *Cirsium vulgare*, *Rumex acetosa* and *Vicia cracca*. During the first years of cultivation, several annuals germinated. They grew for one or two years and then disappeared (*Bidens tripartita*, *Juncus bufonius*, *Rhinanthus angustifolius*, *Spergula arvensis*, *Veronica agrestis* and *Viola arvensis*). There was a tendency for more perennials to be found in the older stands.

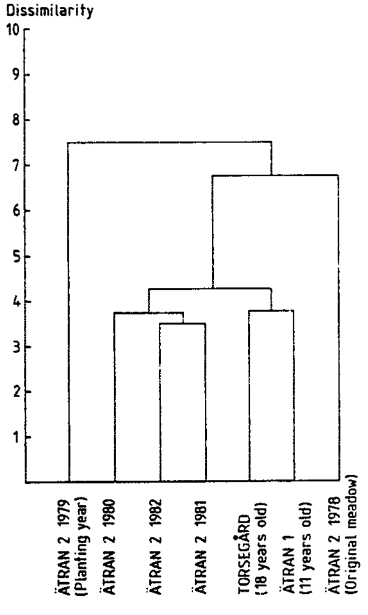

Fig. 2. Cluster analysis of the stands. Species with a mean cover of 5% or more in any stand and year were included in the analysis.

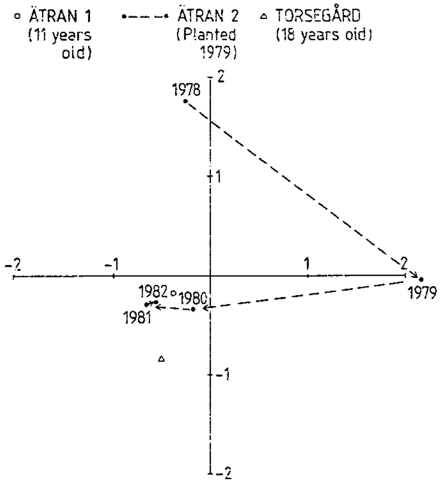

Fig. 3. Principal components analysis (PCA) of the stands, based on the same data set as the cluster analysis (Fig. 2). The axes indicate the mean factor scores per stand each year.

Table 2. *Categories of species in willow stands of different ages. Data are taken from Ätran 2 (0–4 years old) and Ätran 1 (11 years old). Based on records of species cover in random 0.5×0.5 m quadrats with the cover scale (%): 0<cov≤10, 10<cov≤50, 50<cov≤100. Note that this cover scale is different from the one used in Figure 4*

	AGE OF WILLOW COPPICE (YEARS)					
CATEGORY OF SPECIES	0	1	2	3	4	11
Present in original meadow but absent from coppice						
Carex leporina	------					
Luzula multiflora	— — —					
Sium latifolium	— — —					
Present in young coppice but absent from old coppice						
Anthriscus sylvestris			— — —	— — —	------	
Cardamine pratensis	— — —	— — —	· · ·	— — —		
Carex acuta	======			— — —	— — —	
C. disticha	------			— — —	— — —	
Filipendula ulmaria	------	— — —	------	▪▪▪▪▪▪	▪▪▪▪▪▪	
Galium palustre	— — —	— — —	— — —	— — —	— — —	
Lysimachia thyrsiflora	— — —	— — —	— — —	— — —	— — —	
Matricaria inodora		— — —	— — —	— — —		
Mentha arvensis	— — —	— — —	— — —	— — —	— — —	
Myosotis caespitosa	— — —	------	— — —			
Plantago major	— — —	======	------	— — —	— — —	
Polygonum aviculare	— — —	------		— — —		
P. lapathifolium	— — —	------	— — —	— — —	— — —	
Potentilla anserina	------	— — —	— — —	— — —	— — —	
Rumex crispus		— — —	— — —	— — —	— — —	
Trifolium repens	▪▪▪▪▪▪	======	======	— — —		
Permanent in coppice but absent from original meadow						
Cirsium arvense		------	------	======	======	— — —
Galeopsis tetrahit		------	— — —	------	======	▨▨▨▨▨▨
Urtica dioica		— — —	— — —	— — —	------	------
Present in old coppice only						
Brachythecium rutabulum						— — —
Galium aparine						· · ·
Geum urbanum						— — —
Prunus padus						· · ·
Ribes rubrum						— — —
Rubus idaeus						------
Senecio vulgaris						— — —
Tussilago farfara						· · ·
Valeriana sambucifolia						· · ·
Permanent species						
Achillea millefolium	------	— — —	— — —	------	— — —	— — —
A. ptarmica	------	— — —	— — —	------	— — —	— — —
Cerastium fontanum	------	------	------	— — —	— — —	— — —
Cirsium vulgare	▪▪▪▪▪▪	------	------	— — —	— — —	· · ·
Ranunculus acris	======	— — —	— — —	------	— — —	------
R. repens	▪▪▪▪▪▪	======	▨▨▨▨▨▨	▨▨▨▨▨▨	— — —	— — —
Rumex acetosa	— — —	------	------	------	------	— — —
Stellaria graminea	— — —	— — —	— — —	------	— — —	— — —
Taraxacum vulgare coll.	------	------	------	======	======	— — —
Vicia cracca	------	— — —	— — —	------	------	------
Temporary species						
Alnus glutinosa				· · ·	· · ·	· · ·
A. incana				· · ·		
Angelica sylvestris				· · ·		
Atrichum undulatum		— — —				
Bidens tripartita		— — —				
Brachythecium albicans		— — —				
Carex hirta	— — —					— — —
C. nigra	— — —			— — —		
C. sp.			— — —		— — —	
Ceratodon purpureus		======				
Chenopodium sp.	— — —	— — —				
Cirsium palustre	— — —	— — —				— — —
Epilobium adenocaulon				— — —	— — —	— — —
E. montanum				— — —	— — —	— — —

Table 2. *(continued)*

	AGE OF WILLOW COPPICE (YEARS)					
CATEGORY OF SPECIES	**0**	**1**	**2**	**3**	**4**	**11**
E. palustre			– – – – – –			
Equisetum arvense		– – – – – –		– – – – – –		– – – – – –
Galeopsis speciosa					– – – – – –	· · · · · ·
Glechoma hederacea	– – – – – –	– – – – – –		– – – – – –		– – – – – –
Gnaphalium uliginosum		----------				
Juncus bufonius		==========	– – – – – –			
J. effusus	----------		– – – – – –	– – – – – –	– – – – – –	– – – – – –
Lathyrus pratensis				· · · · · ·		
Lychnis flos-cuculi	– – – – – –		– – – – – –	· · · · · ·		
Lycopus europaeus		– – – – – –			– – – – – –	
Myosotis arvensis					– – – – – –	
Ranunculus flammula		– – – – – –	– – – – – –			
Rhinanthus angustifolius		– – – – – –				
Rorippa palustris		----------	– – – – – –	· · · · · ·		– – – – – –
Rumex acetosella		– – – – – –	– – – – – –			
Scuttelaria galericulata				– – – – – –		
Sonchus arvensis				– – – – – –	– – – – – –	– – – – – –
Spergula arvensis		– – – – – –	– – – – – –			
Stachys palustris				– – – – – –	– – – – – –	– – – – – –
Stellaria media		– – – – – –		– – – – – –		
Trifolium hybridum				· · · · · ·		
Veronica agrestis		– – – – – –				
V. scuttelata			– – – – – –			
Viola arvensis		– – – – – –				

Explanation of symbols:

· · · · · ·	present (outside quadrats)
– – – – – –	0<cov≤1 (%)
----------	1<cov≤5 (%)
==========	5<cov≤20 (%)
▨▨▨▨▨▨▨▨▨▨	20<cov≤100 (%)

In Figure 4, the change in cover for some species during the years 1978–1982 at Ätran 2 is shown. *Anthriscus sylvestris*, *Filipendula ulmaria*, *Galopsis tetrahit* and *Urtica dioica* increased in cover over the years. *Ranunculus acris* decreased from 6% in 1978 to less than 1% in 1982. *Cirsium arvense* and *Taraxacum vulgare* coll. increased between 1979 and 1981 but were levelling out during 1981–1982. *Ranunculus repens* increased 20% in cover between 1978 and 1980 but then drastically declined to less than 1% in 1982. The mean apparent field-layer cover was fairly constant: 85%–97%. Bryophytes (3 species) were recorded only in 1979, the first year of cultivation, and *Ceratodon purpureus* was the most dominating species (7%). The number of vascular plant species recorded within and outside of quadrats changed over the years: 33 in 1978, 42 in 1979, 36 in 1980, 45 in 1981 and 34 in 1982.

The grasses decreased slightly after soil cultivation but recolonized quickly. Their cover was 46% in 1978, 30% in 1979, 47% in 1980, 47% in 1981 and 57% in 1982. In 1978, 13 species of grasses were recorded. After soil cultivation in 1979, the number of grass species was much lower (4) but then increased from year to year (1980:5, 1981:10, 1982:11). *Agrostis tenuis*, *Poa trivialis* and *Holcus lanatus* were found in all years. *Alopecurus geniculatus*, *Lolium perenne* and *Poa supina* were recorded only in the meadow. *Dactylis glomerata* started colonizing in 1982.

The quadrat frequency of species provides information on the pattern of dispersion. Highly frequent species with low cover can be expected to be quite evenly dispersed. Such species were *Carex leporina*, *Cerastium fontanum*, *Gnaphalium uliginosum* and *Rorippa palustris*. Low frequency and high cover indicates a clumped dispersion. Such species were *Carex acuta*, *Juncus effusus*, *Epilobium adenocaulon* and *Urtica dioica*.

The reproductive effort differed considerably between species and years. Figure 5 shows the percentage of quadrats in which a species was recorded flowering or fruiting during the years 1978–1982. There was a tendency for most species to increase their reproductive effort one or two years after planting and then to decrease. Species with increased reproduction immediately in the first year after soil cultivation were, among others, *Achillea ptarmica*, *Filipendula ulmaria* and *Ranunculus repens*. In the original meadow *Ranuculus acris*, *Rumex acetosa* and the grasses were recorded with a high frequency of

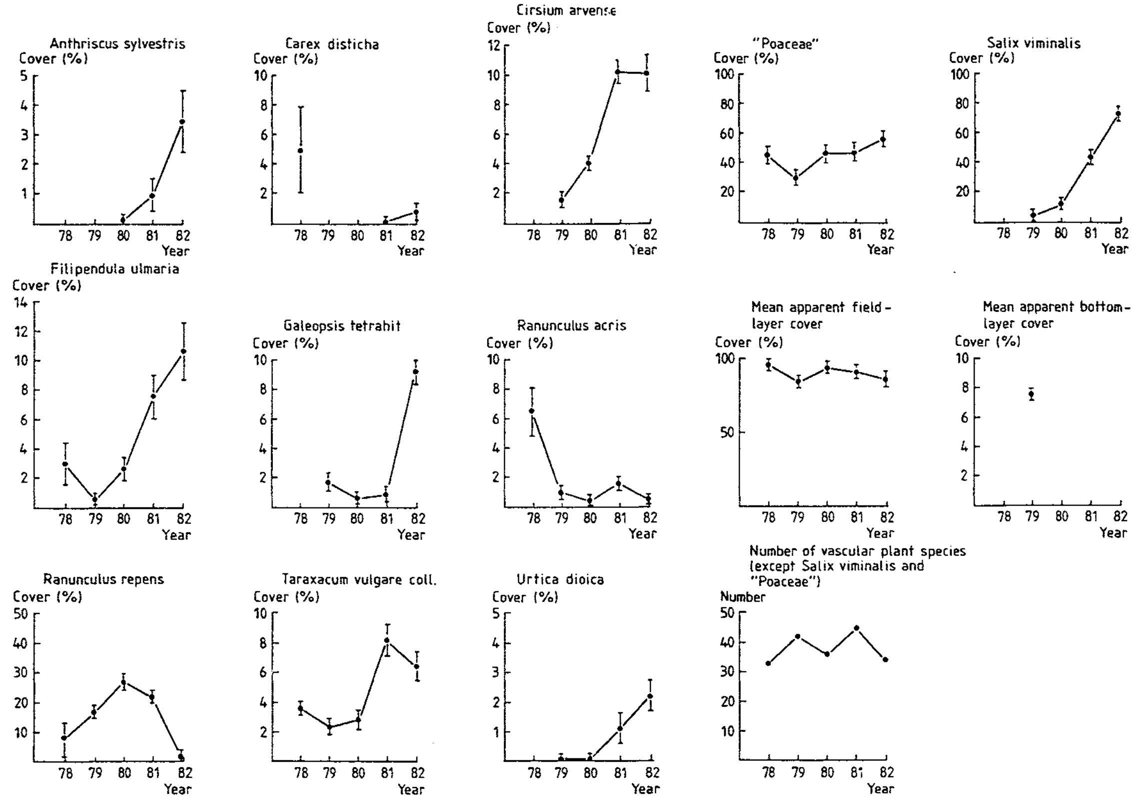

Fig. 4. Mean cover (%) for a selection of species, mean apparent field-layer cover and bottom-layer cover (%), number vascular plant species recorded within and outside quadrats at Ätran 2, during the years 1978–1982. Vertical bars indicate standard error of the mean. Note the different scale on y-axis. The mean covers are based on cover estimates in random quadrats, in the scale:
$0<\mathrm{cov}\leq 1$, $1<\mathrm{cov}\leq 2$, $2<\mathrm{cov}\leq 3$, $3<\mathrm{cov}\leq 4$, $4<\mathrm{cov}\leq 5$, $5<\mathrm{cov}\leq 10$, $10>\mathrm{cov}\leq 20$ ... $90<\mathrm{cov}\leq 100$.

flowers or seeds (84%, 90%, 83% respectively). During the first summer after soil cultivation and planting (1979) these plants reproduced to a minor extent only (6%, 19%, 1%). Subsequently they increased their reproduction but there was a tendency towards a decline in 1981–1982.

There was a great difference in vegetation between the seasons in all three stands. From most points of view there was a peak in vegetational development in July. The mean apparent field-layer cover was largest in July. The grasses also had their largest cover in July in all three stands. When cover of all herbaceous species is calculated, the same peak in July appears. The number of field-layer species was largest in July in Ätran 2 and Torsegård, while it decreased as the year progressed in Ätran 1.

Many single species followed the same trend, with a peak in July, e.g. *Cirsium arvense* and *Taraxacum vulgare* coll. A few increased in cover throughout the growing season, e.g. *Filipendula ulmaria*, *Rubus idaeus* and *Urtica dioica*, and a few decreased, among them *Ranunculus acris*. Most species followed the same pattern in all three stands. One exception was *Galeopsis tetrahit*, which had a peak in July at Ätran 1 and 2 but decreased throughout the growing season at Torsegård.

When species occurring in one season only are counted in a stand, it can be seen that the spring aspect is outstanding at Ätran 1 and Torsegård (Table 3). The percentage of unique species (unique to a particular stand at a particular time of the year) is high in May (Ätran 1 37%, Torsegård 32%). The July and September flora is much less spectacular (Ätran 1 9%, 12%, Torsegård 6%, 0%). Species recorded in spring but not later were, e.g. *Anemone nemorosa*, *Luzula multiflora* and *Ranunculus ficaria*. At Ätran 2 the percentage of unique species was much lower, for May and for July 18% and for September 3%.

The DCA (Fig. 6) yielded information on the similarity between stands in different seasons. Each stand forms a distinct group with the May-July-September records quite close together.

Table 3. *Species occurring in one season only. Percentage is based on the total number of species recorded per stand during the growing season 1981, on and outside quadrats, "Poaceae" and Salix viminalis excepted*

Stand	Date	Species recorded once, %	Species
Ätran 1	May	37	Anemone nemorosa Cardamine pratensis Carex sp Chamaenerion angustifolium Galium palustre Luzula multiflora Myosotis caespitosa Plantago major Stellaria media Trifolium repens Atrichum tenellum Brachythecium sp Mnium affine Pellia sp Pohlia nutans
	July	9	Rorippa palustris Senecio vulgaris Valeriana sambucifolia
	Sept.	12	Cirsium vulgare Galium aparine Myosotis arvensis
Ätran 2	May	18	Juncus articulatus Matricaria inodora Myosotis caespitosa Ranunculus flammula Rorippa palustris Trifolium pratense Brachythecium rutabulum
	July	18	Carex nigra Epilobium montanum Lathyrus pratensis Lychnis flos-cuculi Polygonum aviculare Polygonum lapathifolium Scutellaria galericulata Trifolium hybridum
	Sept.	3	Carex sp
Torsegård	May	32	Anemone nemorosa Equisetum arvense Ranunculus ficaria Brachythecium rutabulum Brachythecium sp Pohlia nutans
	July	6	Stellaria media
	Sept.	0	-

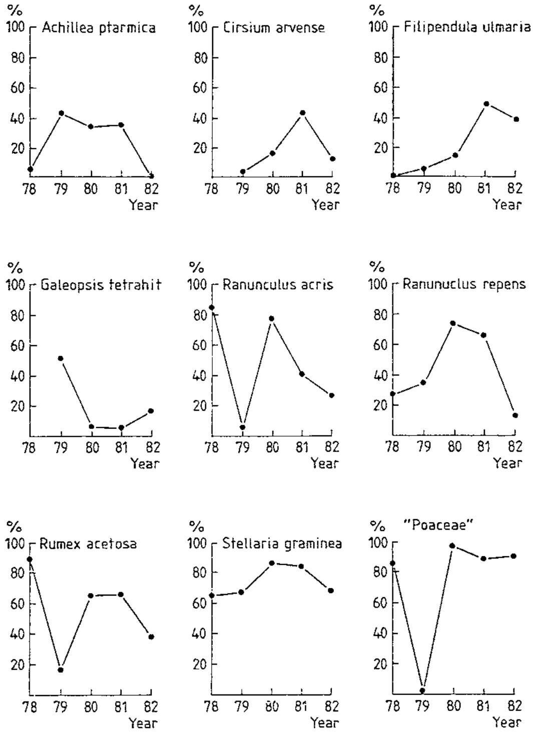

Fig. 5. Reproductive effort of species at Ätran 2, 1978–1982. Percentage of quadrats in which a species was recorded flowering or fruiting. Based on number of quadrats in which a species was present.

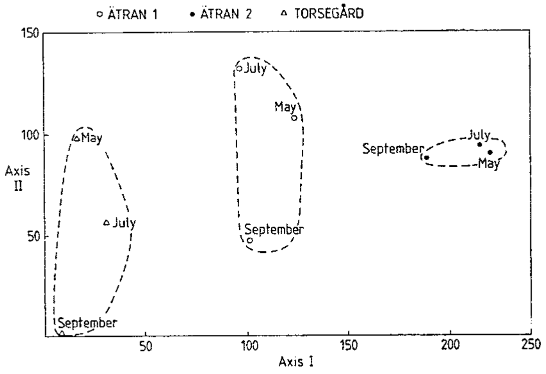

Fig. 6. Detrended correspondence analysis (DCA) on the willow coppices Ätran 1, Ätran 2 and Torsegård in May–July–September 1981.

The frequency of flowers/ fruits for different species was generally highest in July (*"Poaceae"*, *Achillea millefolium*, *Cerastium fontanum*, *Galium palustre*, *Ranunculus repens*, *Stellaria graminea*, *Vicia cracca* and others). A few species increased in reproductive effort over seasons, e.g. *Achillea ptarmica* and *Galeopsis tetrahit*. A minority of species had highest reproduction in spring, among these *Taraxacum vulgare* coll.

Discussion

Aspects of vegetation dynamics in energy forests

Three cyclical changes are important to the flora of coppices. First, there is a succession during the rotation. Here rotation is used in the sense "intervals between harvests". In long-rotation coppice woods there is a distinct sequence of phases throughout the cycle. In early studies on coppices in England a "light phase" and a "shade phase" were distinguished (Adamson, 1912; Salisbury, 1924). During the "light phase", which occurs after cutting, the flora from before the harvest flourishes and at the same time new species colonize from dormant seeds, and incoming propagules from the margins of the wood and the surrounding area. On the whole there is a strong response in vegetation, particularly in the second season after cutting (Peterken, 1981). Another effect of coppicing is a spectacular increase in the flowering of many shade-tolerant plants as well as that of typical spring species (Rackham, 1975). As the canopy closes, the field layer becomes scattered, poorly-grown and apparently impoverished (Peterken, 1981). In energy forests harvested annually, this development naturally does not occur. Instead, a mixture of species from different successional phases is established, as can be seen from the investigated stands. In the stands both shade-tolerant and light-tolerant species were present. Although it was not investigated in detail, a spatial pattern can be found in the annually cut stands, with shade-tolerant species close to the stools and light-tolerant species in clearings, openings and margins.

Secondly, there is a change throughout the year from the development of leaves in spring to leaf abscission in autumn. The vegetation is highly affected by the reduction in light caused by the foliage. The irradiance beneath a deciduous canopy is known to decrease to only a few per cent from spring to summer (Anderson, 1964). This seasonal change is influenced by the rotation time. The spring flora is likely to become relatively more developed in long-cycle stands since light intensity is very low in an old stand during autumn but the light during spring is less affected by the age of the shoots.

Thirdly, there is a succession of species throughout the whole existence of a coppice. A willow stand can reach an age of at least 50 years before it must be replanted owing to decreasing productivity (Stott, 1956). During the life cycle of a stand, propagules of new species will constantly reach the site and some species will establish themselves. Also, some existing species will disappear due, for example, to competitive exclusion. The data presented suggest that typical spring species need some years to colonize a stand. The two oldest stands had an outstanding spring flora but the young stand did not. For instance, *Anemone nemorosa* grew at Ätran 1 which borders on Ätran 2 and it is probably only a matter of time before *A. nemorosa* colonizes Ätran 2.

Species performances during the succession

The pattern of succession on a ploughed surface is very difficult to predict since it is influenced by random events such as availability of seeds, conditions suitable for germination of different species, etc. (Keever, 1983).

When the meadow was ploughed, this favoured a number of potential weed species which were already present in the vegetation or in the seed bank. In the first year after ploughing, species with fast-germinating seeds colonized, e.g. *Gnaphalium uliginosum*, which sets seeds only 3 weeks after germination (Hultén, 1960); also *Plantago major*, *Juncus bufonius* and *Rorippa palustris*. *Juncus* spp. are reported to be common in the seed bank in agricultural soils (Chippindale & Milton, 1934). These early colonizers are sensitive to competition and disappeared or became very rare during subsequent years. The mortality of *Plantago major* is highly density dependent (Palmblad, 1968).

Some of the original species on the contrary were disfavoured by cultivation. The soil became too dry for the sedges *Carex acuta* and *C. disticha*. Also *Juncus effusus* decreased drastically. This species is known to decrease when the soil dries out (Korsmo, 1954).

Ranunculus repens in environments with low competition can produce stolons with daughter rosettes, 20 cm or longer (Sarukhán & Harper, 1973). This mode of growth made it possible for the species to increase very rapidly in cover during the early years. *Trifolium repens* has the same mode of growth and also was common the first years after ploughing. These species were competed out when the field layer closed. *Trifolium repens* is sensitive to a canopy of grasses (Jones, 1933). The two species probably also suffered from diminished light during high and late summer, due to the closure of canopy. In contrast, *Ranunculus acris* produces daughter rosettes only a few millimetres from the parent (Harper, 1977) and this species increased very slowly after soil cultivation.

Cirsium arvense and *Filipendula ulmaria* increased in cover every year after the ploughing. But these species were very rare in the 11-year-old stand. The difference in the stands might be due either to more favourable conditions for establishment in the younger stand, or to the inability to survive in the long run under the low light intensities in high and late summer.

Galeopsis tetrahit had a very high cover (36%) in the oldest stand but was much less common in the younger stand (9%). The presence of this annual species is very fluctuating, due to differences in conditions for germination in different years (H. Fogelfors, pers. comm.). It spreads its seeds early in July, before the closure of canopy and thus it is well adapted to a *Salix* coppice harvested every year. It is therefore surprising that it was much less common in the younger stand. It spreads easily when an area is flooded, as the Ätran site is during spring, and could be supposed to have colonized the younger stand much more quickly (H. Fogelfors, pers. comm.)

Taraxacum vulgare coll. was more common in the younger than in the older stand. It had an opportunity to establish from seeds the first years after ploughing when there were many safe sites, and enough light for the rosettes to form during establishment. In an older and denser stand, the established individuals persist, but expansion is very unlikely. *Taraxacum vulgare* coll. is present in many willow coppices in Sweden but never with a high cover (Gustafsson, 1987).

Urtica dioica increased in cover over the period of study. It is favoured by a high nitrogen content in the soil and thus was promoted by the fertilization of the energy forest. *Urtica* grows well even at low light intensities and thus can tolerate the conditions in a rather dense stand.

An established energy forest attracts birds, and as a consequence, bird-dispersed seeds can reach a stand. *Rubus idaeus* is known to spread in this way (Oosting & Humpreys, 1940) and its presence in the 11-year-old stand was most probably due to bird dispersal.

Comparisons with other successions

The succession at Ätran deviated considerably from a succession in an energy forest on a former peat bog in Jädraås, east central Sweden, in that it stabilized much more quickly and it changed less between years. Four years after planting at Jädraås the vegetation was still changing rapidly (Gustafsson, 1988). Unfortunately, no older stands existed for comparison at Jädraås and it is difficult to judge when the rate of change will slow down and what the mature vegetation will look like. But it is evident that the ground flora of this energy forest will be very different from that at Ätran. Very few species are mutual, among them being *Rubus idaeus*, *Sonchus arvensis* and *Taraxacum vulgare* coll. The grasses, which covered more than 50 % at Ätran, were absent at Jädraås. One similarity was the mean apparent field-layer cover, which was high in both areas (70–91%, depending on plot, at Jädraås; 85% at Ätran).

The most important reason for the divergence in vegetation between the two sites was the large difference in starting points. The ground vegetation in the energy forest at Ätran was relatively similar to the one in the original meadow. Many species from the meadow were able to recolonize the willow bed. The propagules of almost all establishing species were already present at the site when the succession started, either in the seed bank or as surviving vegetative tissue after the soil cultivation. At Jädraås, the vegetation in the energy forest was of a very different type compared to the original peat-bog vegetation. *Sphagnum* spp. covered about 75% in the peat bog but less than 1% in the energy forest stands four years after planting. Many bog species did survive after soil cultivation but mostly in very low quantities. Instead, new species like *Chamaenerion angustifolium*, *Epilobium adenocaulon* and *Epilobium palustre* became dominant. Another difference between the Jädraås and Ätran sites was the difference in surrounding vegetation. The Jädraås site is surrounded by woodland and mires. The closest meadow or arable field is one kilometre away. In contrast, Ätran is situated in the middle of a farming area. At Jädraås, weeds and meadow species have little chance of becoming established. At Ätran, it might take many years before seeds from woodlands and bogs reach the willow stand.

Comparisons can also be made between the energy forest succession at Ätran and the change following a harvest in other coppice woods. Early in this century, some investigations were made of coppiced woodlands in England. Salisbury (1916, 1918, 1924) mainly studied oak-hornbeam woods. These woods, which were cut at intervals of up to 20 years, were very ancient and had a rich flora. He found that the development of the flora was well correlated with light. The spring flora was very rich, while a depletion occurred later in the season. In old coppices, the importance of margins, edges and paths became considerable, since a large part of the species stock was restricted to these light spots.

Adamson (1912) studied the effext of coppicing. He stated that the vegetation became very mixed and that grasses became very numerous after cutting. He pointed out the importance of increased light in the formation of the flora during the early years after coppicing, but he also stressed the significance of increased evaporation, which occurs after cutting. A number of more recent investigations have been made on coppices. Ford & Newbould (1977) studied a *Castanea sativa* coppice cycle, and found that the production of the ground vegetation was highest two years after cutting, and that it was negatively correlated to the tree biomass. The species number increased up to five years and then declined.

In a study of an oak-ash-maple-hazel woodland during the first 30 years after coppicing, Ash & Barkham (1976) found a rise in species number early in the coppice cycle but a decline after the closure of the canopy (4–9 years). The species number tended to decline with time even if conditions were constant. They also found a positive correlation between number of species and light transmission and between number of species and pH.

Pons (1976,1977) made an ecophysiological study of the field layer of an ash coppice. He studied *Geum urbanum* as an example of a closed canopy plant and *Cirsium palustre* as an example of a pioneer plant. *G. urbanum* developed well in the light phase during spring, and later adapted to the darkness beneath the canopy and developed well both vegetatively and generatively. *C. palustre,* in contrast, retrogressed when the light diminished, at least in the generative phase. This species is known to establish from seeds after the removal of canopy.

Aspen stands are frequently cut in Utah in the United States of America for livestock forage and wildlife habitat. Three years after cutting, the biomass of the ground vegetation had doubled. The annuals increased their biomass five-fold. The vegetation gradually became increasingly similar to the stage before cutting (Bartos & Mueggler, 1982)

Many analyses of abandoned fields have been made, especially in North America (e.g. Bard, 1952; Bazzaz, 1968, 1979; Keever, 1950, 1983; Pickett 1982) and some have been made in the Nordic countries (e.g. Bråkenhielm, 1977; Jukola-Sulonen, 1983). The development of abandoned farmland resembles in many respects the succession throughout the existence of a coppice wood. The different developmental stages recognized by, e. g., Pickett (op. cit.) with annuals followed by perennial herbs and later invasion by shrubs, also can be found in long-rotation coppices.

Although similar to abandoned fields and coppice woods, the energy forests have unique qualities. The main difference compared to abandoned fields is the immediate presence of a shrub layer. The very frequent harvests make the energy forests different from other coppice woods. Very frequent harvests are usually associated with agricultural systems, but in these the soil is cultivated much more frequently than in energy forests.

Seasonal dynamics

Some investigations have been made (mostly regarding biomass) on the seasonality of meadow vegetation and deciduous woodland vegetation. The biomass and the cover of ground vegetation are known to be well correlated (Persson, 1979), thus investigations on biomass as well as on cover can be used in comparisons with the results presented here.

The timing of the peak of the vegetational development varies considerably with the type of vegetation. In an abandoned field in Finland, the total green biomass was rather constant from mid-June until late August (Törmälä & Raatikainen, 1976). The species stock in this area was very similar to that in the investigated Falkenberg stands. Traczyk (1968) studied a meadow community in Poland *(Stellario-Deschampsietum)* and found that the peak standing crop occurred in August.

Kubicek & Simonovic (1975) analysed two deciduous woods in Czechoslovakia. They found early peaks of biomass of the herbaceous layer in both communities. In the *Primula veris – Carpinetum* it occurred in May and in the *Carici pilosae – Carpinetum* in June. One analysis of some Lake District (UK) woodlands suggested that the biomass remained fairly constant throughout the seasons, but this could partly be an artefact due to insufficient sampling (Frankland et al., 1963). Persson (1975) analysed a Swedish hazel coppice with standards. He found a long maximum in standing crop for the field-layer total from early June until late August.

It should be pointed out that the July peak found in the Falkenberg stands does not certainly coincide with the highest cover during the season. It might just as well occur earlier or even later. The analyses must be made more frequently in order to decide this.

When individual species are studied, the time of the peak is more complex. The peak of the grasses in July is in contrast to the results of Persson (op. cit.), who found that the standing crop of the graminaceous plants steadily increased from May to September. The tree and shrub layers at Persson's sites were not as dense as in willow stands, and this probably permitted the grass species to develop late in the season. Many meadow grasses are known to have a markedly bimodal growth curve, with a minimum during high summer. Maxima occur some weeks before midsummer and late August or the first half of September (Rappe, 1963). These late maxima are not reached in the willow stands. Kosonen (1969) studied the seasonal growth rhythm (late July–late September) for various herbaceous species in an *Arrhenaterum pubescens* meadow, and found two peaks in biomass during the growing season for some species, e.g. *Geum rivale* and *Rumex acetosa*.

The species which increased in cover late in the season may be divided into two categories. Some species, such as *Anthriscus sylvestris*, *Filipendula ulmaria* and *Urtica dioica*, are shade tolerant and strong competitors when the light diminishes. Others (e.g. *Stachys palustris*) probably increase late in the season due to their internal growth rhythm, with a late summer maximum.

Methods used

The sampling procedure was not completely identical in the three stands. In the Ätran stands the random quadrats were placed directly within the whole stands, except in the edge zones which were omitted from the analysis. At Torsegård the stand first was subdivided into three random 10x10 m plots, into each of which 25 small random quadrats were placed. The reason for the different procedure at Torsegård was purely practical. The angular shape of this stand made direct sampling of small quadrats very difficult. It was much easier and quicker to subdivide the stand first into large plots.

A coarse cover scale was used for Torsegård and Ätran 1 and a finer scale was used at Ätran 2. There is a great risk of miscalculation for mean cover when using very coarse cover scales, but on the other hand, the time for field analysis decreases considerably. The fine cover scale for Ätran 2 was converted to the coarser one when comparisons were made between the stands, and gave an opportunity for comparison of the two scales. When this was done for the year 1982, it was revealed that the mean cover of species with very low mean cover (less or much less than 1%) was very much overestimated by the coarser scale. But when the results are presented, integers are used and thus differences in cover below 1% are of no consequence. Mean covers up to about 15% were also overestimated, but not seriously. As an example, the coarse scale gave 11% for *Cirsium arvense*, 7% for *Taraxacum vulgare* and 4% for *Anthriscus sylvestris* and the fine scale gave 10%, 6% and 3%. On the other hand, species with high covers were underestimated in the coarse scale. For instance, the coarse cover scale gave 50% and 66% cover for "Poaceae" and mean apparent field-layer cover respectively, while the finer scale gave 57% and 85%. But on the whole, the two cover scales agreed well and thus the coarser scale in most cases probably gave quite accurate estimates of the means.

Application to large-scale energy forestry

The investigated stands can be viewed as typical energy forests, provided there is no drastic change in general energy forest management in the future. Important management factors which influenced the ground vegetation in the Falkenberg stands were moderate fertilization, annual harvests and very low use of herbicides. If energy forests are managed more intensively, this may radically alter the vegetation.

When applying the results to large-scale energy forestry, we may conclude that when a stand becomes established in an open field dominated by common meadow vegetation, it will give many original species the opportunity to survive in the coppice but that there will be a shift towards a dominance of very common ruderals. The ground vegetation will stabilize fairly rapidly. The cover of vegetation and probably the species number will decrease if the rotation time increases. When a stand has reached an age of about ten years, the spring aspect is likely to have a large proportion of unique species compared with the summer and autumn aspects.

As has been shown in a study on the ground vegetation of Swedish willow coppices (Gustafsson, 1987), a very great variation will probably be found between various energy forest stands. In order to be able to predict even in very broad terms the composition of a willow stand, a thorough knowledge is necessary of past and present management, soil properties, availability of propagules and life histories of invading species.

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