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Above- and below-ground biomass of boreal outlying hay-lands at the Sølendet nature reserve, Central Norway

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Studies of the above- and below-ground biomass of the field-layer species were carried out in permanent plots in two communities of rich fen and two communities of wooded grassland at the Sølendet nature reserve in the years 1992-94. The method used is based on the numbers of individuals of the species and their mean individual weights. The results show an overall tendency for biomass to decrease, both above and below ground, and for both the number of shoots and the ratio of above-ground/below-ground biomass to increase with increasing scything frequency. The highest biomass values were recorded in the tall-herb birch woodland, with total biomasses of about 4000, 9000 and 12,000 kg·ha^{-1} for plots scythed annually, biennially, or not scythed for more than 40 years, respectively. The lowest biomass values were found in the rich fen margin community, with total biomasses of about 1700, 2000 and 5300 kg·ha^{-1}, respectively. The number of individuals was highest in the open rich fen community (more than 6000 per m^2), and lowest in the overgrown, tall-herb community (1000 per m^2). There were also considerable differences in biomass values and in the numbers of shoots between years. It is postulated that this may partly be due to fluctuations in the climatic conditions, but the effect of some methodological bias is also stressed.

Key words: biomass, haymaking, mowing, aerial parts, underground parts, peatland, woodlands, boreal forests, Norway, marshes

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The effects of scything on the vegetation of fens, swamps and wet grasslands of upper boreal areas in Sweden have been studied by Elveland in a number of publications (e.g. Elveland 1984). However, he only included a few calculations of the hay yields. For a tall-growing sedge community (*Carex lasiocarpa, C. rostrata*) the field-layer yield was ca. 2000 - 2800 kg·ha^{-1}. In the boreal uplands of Norway, Moen (e.g. 1976, 1990) calculated the hay yield for a large number of hay fen communities. For areas of rich fen lawns (communities of the *Caricion atrofuscae* alliance) that had not been scythed for about three decades, the above-ground biomass values were about 1500-3000 kg·ha^{-1}. Experimental mowing using scythes led to the following conclusions (Moen 1990, 1995): After the first few

years, the field-layer biomass in the annually scythed plots had decreased to about one-third of the first harvest, whereas it was about two-thirds in plots scythed every other year, i.e. the practice of traditional haymaking on the outlying lands of upper boreal Norway.

The tall-herb birch communities of the upper boreal region (belonging to the *Lactucion alpinae* alliance) have been described by Nordhagen (1943). Holmen (1965) and Moen (1990) calculated the above-ground biomass values for these communities, recording values for the first year's yield (after abandonment for 3-4 decades) of 2500-5000 $kg \cdot ha^{-1}$.

Few papers in Fennoscandian publications have dealt with below-ground biomass of outlying upland communities (cf. Sjörs 1991 who surveyed the literature about fens). The most important studies were made during the course of the various International Biological Programme projects (e.g. Wielgolaski 1975; Sonesson 1980; Bliss et al. 1981). On the Hardangervidda in both a rich fen and a willow grassland community in the low alpine region, the IBP project found a ratio between above- and below-ground biomass for the vascular field-layer plants of 0.11 (when woody plants were excluded, the above-ground biomasses were 1150 and 720 $kg \cdot ha^{-1}$, respectively). In general for the wet to damp communities studied under the IBP programme for arctic/alpine areas, the same ratio was found to be as low as about 0.05 (Wielgolaski 1986). For communities with similar local environmental conditions, e.g. rich fens, the ratio was generally found to increase with lower latitude and altitude, and also usually to increase from community to community along the habitat gradient from wet to dry (cf. also Pearsall & Newbould 1957; Bernard 1973). Sjörs (1991) studied a wet, rich fen in central Sweden (*Carex limosa* and C. *lasiocarpa* as the most common species) where the below-ground biomass made up 93% of the total biomass. Sjörs (op. cit.) and Metsävainio (1931) also dealt with the depth distribution of the biomass of fen species. Sjörs (1988) reported living roots of *Menyanthes trifoliata* as deep as 93 cm below the surface.

The research programme to study the vegetation ecology of the hay fens and wooded grasslands of boreal Norway was started in the early 1970s (Moen 1990); in 1992 a new project was initiated, to obtain a better understanding of the processes underlying the observed influences of scything. The impact of scything on the number of individuals and on the biomass (above- and below-ground) of the field-layer species of four localities at Sølendet nature reserve was the subject selected for this study. Emphasis was laid on the differences in the biomass estimates for the different communities and species and on the annual differences. Previous papers (Aune et al. 1993, 1994, 1995a, 1996, in press) include preliminary results and the results of two years of studies for one locality in each paper. Aune et al. (1995b,) is a symposium proceedings, summing up the results from one fen and one wooded grassland locality.

The biomass studies of mosses were subjected to severe methodological limitations (Aune et al. 1994) and these results have not been included in this paper. The biomass values were found to be very high in the rich fen communities, and they were rather similar in all plots. The wooded grassland communities had a rather dense layer of mosses in the annually scythed plots, and a markedly decreasing trend with almost no moss layer present in the unscythed plots.

Aims

This present paper summarizes the results of three years of biomass studies of the field-layer species in two fen and two wooded grassland communities at Sølendet, and the main aims are:

- to compare the biomass figures (including number of individuals) for the different vegetation types;
- to compare the biomass figures with relevant climatic data;
- to compare the biomass figures with those cited in the literature;
- to evaluate the methods used.

The investigated area

The four localities studied

The investigations were conducted in the Sølendet nature reserve in the municipality of Røros in Central Norway. Four localities, representing four different plant communities, were selected for investigation. The studied localities are situated at 720-760 m a.s.l., at the transition between the middle boreal and northern boreal zones (Moen 1987). The localities consist of at least four permanent plots arranged as in Fig. 1, where all scythed plots have undergone a certain level of scything frequency since 1979 or earlier. The locality numbers, phytosociological classification, etc., follow Moen (1990). Localities 2 and 3 are in a rich fen vegetation of sloping fen (the *Caricion atrofuscae* alliance), with an inclination of 5°, a peat depth of 10-20 cm, and a pH of about 6.5. Locality 2 is a *Scirpus cespitosus-Carex hostiana-Campylium stellatum* type of rich lawn community on the fen expanse, and locality 3 a *Molinia caerulea-Kobresia simpliciuscula-Campylium stellatum* type of rich lawn community on the fen margin. A synopsis of the phytosociological analyses made in the two rich fen communities is presented in Table 3. Locality 5 is representative of the wooded grasslands of *Betula pubescens-Crepis paludosa-Campylium stellatum* type. It is characterized as open birch woodland, with a dense, rather

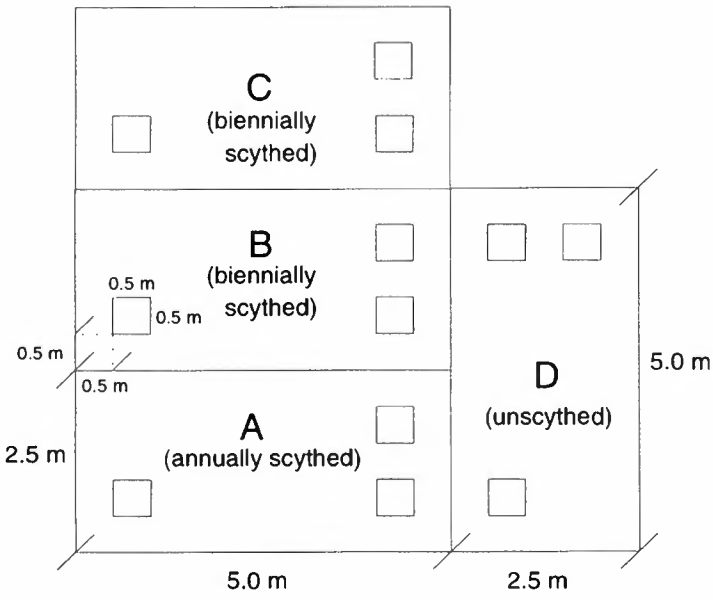

Fig. 1. Example of a sample area, showing four 12.5 m² permanent plots (A, B, C, D) used for scything and phytosociological analyses, and the 0.25 m² subplots used for counting individuals

Table 1. Monthly mean air temperatures (°C) in the years 1992-94 and temperature during the normal period 1961-90 at Røros (ca. 30 km south of Sølendet) adjusted for altitude according to Laaksonen (1976); the monthly precipitation (mm) in the years 1992-94 and the precipitation during the normal period 1961-90 at Brekken (ca. 5 km east of Sølendet)

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Year	May-July
Temperature														
1992	-4.6	-5.8	-2.1	-2.6	7.1	11.8	9.8	9.1	6.3	-4.4	-5.7	-7.6	0.9	9.6
1993	-6.1	-5.6	-5.5	0.8	6.4	6.0	10.7	8.4	3.7	-1.2	-8.4	-12.9	-0.3	7.7
1994	-11.7	-16.8	-5.6	0.6	3.7	7.5	15.3	10.2	4.8	-0.3	-3.1	-5.9	-0.1	8.8
Normal	-11.8	-10.2	-6.0	-1.2	5.0	9.6	10.9	9.9	5.6	1.2	-5.8	-9.7	-0.2	8.5
Precipitation														
1992	81	40	43	33	45	28	80	111	35	25	49	38	608	153
1993	30	63	27	9	78	60	124	92	34	76	16	34	643	262
1994	46	5	25	30	17	100	37	85	45	38	51	32	511	154
Normal	41	33	36	32	36	55	78	70	71	52	47	49	600	169

Source: Det Norske Meteorologiske institutt.

tall, field-layer dominated by herbs and graminoids, classified as belonging to the association *Deschampsio cespitosae-Salicetum lapponae* of the alliance *Lactucion alpinae*. The pH of the soil humus horizon is about 5.6. Locality 40 is representative of the tall-herb birch woodland of the grassland series, with either a sparse or no shrub layer and a dense field-layer dominated by herbs and graminoids. It is characterized as a *Betula pubescens-Aconitum septentrionale-Angelica archangelica* type of the subassociation *Geranietum sylvatici aconitetosum* of the alliance *Lactucion alpinae*. The pH of the soil humus horizon is about 5.9. A synopsis of the phytososiological analyses made in the two wooded grassland communities is presented in Table 4.

Climatic conditions

Table 1 shows the monthly mean air temperatures and monthly precipitation values for the years 1992-94, together with the values for the normal period 1961-90. Table 2 shows the effective temperature sums (ETS) for the years 1992-94. The effective temperature sum is expressed as degree-day units, with a threshold value of 5°C, using the following formula after Laaksonen (1979):

$$ETS = \sum_{i=1}^{n} (c_i - 5°)$$

where c_i denotes the mean temperature for day *i* in the vegetative period of the year. The vegetative period starts with the third day in the first 5-day period in the spring with a mean temperature of 5°C or more and no snow cover, and ends with the third day in the last 5-day period in the autumn with a mean temperature of 5°C or more and no snow cover. Thus, the ETS value expresses the sum obtained by subtracting 5°C from the mean temperature of each day in the vegetative period with a mean temperature above 5°C.

The climatic conditions during the three study years differed greatly, both in regard to temperature and precipitation (Table 1). The summer of 1992 was very warm, with an average temperature for May-July of 9.6°C, which is 1.1° above the normal average. The weather was particularly hot during May and June, with a mean temperature of ca. 2°C above

Table 2. Effective temperature sums, in degree-day units with a threshold value of 5°C (see further explanation in text), for Sølendet 1992-94. I: number of degree-day units before hay-cutting in the current year, II: number of degree-day units after hay-cutting in the previous autumn + number of degree-day units before hay-cutting in the current year

Year	I	II
1992	486	655
1993	308	465
1994	490	578

the normal value for both months. The weather was also rather dry, especially in June, when the precipitation was only 28 mm, or ca. 50% of normal precipitation. The summer of 1993, in contrast, was the coldest and wettest of the three years, with an average temperature for May-July of 7.7°C, which is 0.8° below the normal average, and a precipitation of 262 mm, or 155% of the normal precipitation for the months May-July. The month of July, with 124 mm, a value of almost 160% of the normal precipitation, was extremely wet. The summer of 1994 (May-July) was warmer and drier than 1993, with an average temperature of 8.8°C, which is 0.3° above the normal average, and a precipitation of 154 mm, or ca.90% of the normal precipitation for the three months together. In July, in particular, the weather was exceptionally hot and dry, with a mean temperature of 15.3°C, which is 4.4° above normal, and a precipitation of only 37 mm, or less than 50% of the normal value.

Material and methods

Sampling procedure

The fieldwork took place in the first week of August in all three years, at the peak of the species growth. In the sample plots, each measuring 12.5 m², three levels of scything frequency were studied: scythed every year, scythed every second year and unscythed. The numbers of individuals of all species and the biomass value of the field-layer were estimated and a phytosociological analysis was carried out in each plot. The numbers of individuals were calculated using the data obtained by counting in three smaller, representative subplots, each measuring 0.25 m² (0.5 x 0.5 m) (see Fig. 1). An "individual" is defined as the above-ground part of the plant that is readily counted in the field. For many species an "individual" is the whole above-ground part of the plant; for graminoids and other clonal species every separate shoot is an "individual". The method of indirect sampling, modified for non-recurrent sampling, was used to estimate the biomass of the species in the field-layer. This method is based on counting of individuals of all species in the plots and determining the mean individual weights of the dominant and subdominant species. The determination of the dominant and subdominant species was based on the phytosociological relevés of the plots. A number of individuals of each of the selected species (usually 10-30 individuals of each species) were dug up, an attempt being made to include as much of the root system as possible to a depth of about 10-30 cm. The samples were washed, divided into above-ground and below-ground parts, desiccated at 70°C to constant weight, and the mean weight of the individuals calculated. A more detailed description of the method can be found in Aune et al. (1994).

Vascular plant nomenclature follows Lid (1985) and bryophyte nomenclature is as given in Moen (1990: 96).

Correlation analysis

A correlation analysis was carried out for the two localities that were studied in all three years (i.e. localities 3 and 5) using Pearson's *r*, the product-moment correlation coefficient. The analyses were for the relationship between the number of individuals/the biomass values, and:

- the effective temperature sum of the vegetative period before hay-cutting in the present year (ETS-I);
- the effective temperature sum of the vegetative period after hay-cutting in the previous autumn, plus that for the vegetative period prior to hay-cutting in the present year (ETS-II);
- the precipitation in July (i.e. the main vegetative period before the hay harvest);
- the precipitation during the period June-July.

Significance levels were calculated by applying the usual t statistics in a two-tailed test according to Zar (1984).

Results

The values obtained from the biomass studies are presented in Tables 5-15. Tables 5-8 present the mean values for species, Tables 9-13 the mean values for the localities. Values for all three years are presented for localities 3 and 5, values for only 1993 and 1994 for localities 2 and 40. Separate species records for 1992 and 1993 for localities 3 and 5 have been published by Aune et al. (1994, 1995) respectively; with separate records for 1993 and 1994 for locality 40 in Aune et al. (1996, in press). Some preliminary records for localities 3 and 5 have also been published by Aune et al. (1993).

Number of individuals

The mean numbers of individuals for each species are listed in Tables 5-8, total and mean values for the field-layer in Table 9. The total mean number of individuals was highest for the rich fen community at locality 2, with about 6100-6700 individuals per m^2, and lowest for the grassland communities of localities 5 and 40, with about 1000-2200 individuals per m^2. The total mean number of individuals was higher in the scythed plots than in the unscythed one in localities 2, 5 and 40. In the grassland localities (5 and 40) there was a clear tendency for the number of individuals to increase with increasing scything frequency. In locality 2 the highest values were recorded in the biennially scythed plots. The values for locality 3 showed the opposite tendency to the other localities, with a decreasing number of individuals with increasing scything frequency.

The variation between years, expressed as the standard deviation (SD), was high in localities 3, 5 and 40, and particularly so in locality 3 with an SD of more than 20% of the total mean value for all scything frequencies (Table 9). In the annually scythed plot this variation was mainly accounted for by *Carex dioica* (Table 6), with extremely low values in 1993 (cf. Aune et al. 1994; variation from 432 to 1543 individuals). In the biennially scythed plots and in the unscythed plot, the variation was accounted for by all the dominant species (Table 6), which showed the same pattern as that for *C. dioica* in the annually scythed plot.

There was also a high variation in the unscythed plot in localities 5 and 40, with an SD of more than 22% and 35%, respectively, of the total mean value. This was mainly due to a variation in the dominant species, *Agrostis capillaris, Anthoxanthum odoratum* and *Deschampsia cespitosa* in locality 5 (Table 7), and in *Aconitum septentrionale* and *Deschampsia cespitosa* in locality 40 (Table 8).

Table 3. Synoptic table of the phytosociological analyses made in 1992-94 of plots in the rich fen communities at localities 2 and 3 at Sølendet, showing frequency of occurrence and mean degree of cover. Size of plots: 12.5 m². Cover scale in %: s: 0-1; u: 1-3.1; 1: 3.1-6.2; 2: 6.2-12.5; 3: 12.5-25; 4: 25-50; 5: 50-75; 6: 75-100

Locality no.	2	2	2	3	3	3
Scything frequency	Annually	Biennially	Unscythed	Annually	Biennially	Unscythed
No. of repeats	2	2	2	3	3	3
Betula nana	-	50-s	50-s	100-s	100-u	100-1
Betula pubescens	-	50-s	-	33-s	33-s	-
Salix cf. hastata	-	-	-	33-s	-	33-s
Salix sp.	50-s	-	-	-	-	-
Vaccinium vitis-idaea	-	-	-	-	-	67-s
Angelica sylvestris	-	-	-	-	33-s	-
Bartsia alpina	-	-	-	-	33-s	33-s
Crepis paludosa	-	50-s	-	-	-	67-s
Dactylorhiza cruenta	-	50-s	50-s	-	33-s	100-s
Dactylorhiza pseudocordigera	-	100-s	50-s	-	33-s	33-s
Equisetum palustre	100-3	100-u	100-u	100-s	67-s	33-s
Equisetum variegatum	100-u	100-s	100-u	100-s	100-s	100-s
Euphrasia frigida	100-s	100-u	100-u	100-s	67-s	100-s
Gymnadenia conopsea	-	50-s	-	-	33-s	100-s
Leontodon autumnalis	-	-	-	67-s	33-s	100-s
Listera ovata	-	-	50-s	-	33-s	-
Pedicularis oederi	-	100-s	100-s	67-s	67-s	100-u
Pedicularis palustris	-	-	50-s	-	-	-
Pinguicula vulgaris	100-s	100-s	100-s	100-s	100-s	100-s
Polygonum viviparum	100-u	100-s	100-s	100-u	100-s	100-s
Potentilla erecta	100-u	100-u	100-u	100-s	100-s	67-s
Pyrola rotundifolia	-	-	-	-	33-s	-
Rumex acetosa	-	-	-	-	33-s	-
Saussurea alpina	50-s	100-s	100-1	67-s	67-s	100-u
Saxifraga aizoides	100-s	100-s	100-u	100-u	67-u	100-s
Selaginella selaginoides	100-s	100-s	100-u	100-s	100-u	100-s
Succisa pratensis	-	50-s	50-s	67-s	67-u	100-2
Thalictrum alpinum	100-3	100-3	100-2	100-2	100-3	100-2
Tofieldia pusilla	100-u	100-s	100-s	100-s	100-s	100-s
Triglochin palustre	100-u	100-s	100-s	100-u	100-s	100-s
Carex buxbaumii	-	-	-	-	33-s	67-s
Carex capillaris	50-s	50-s	50-s	100-u	100-u	100-s
Carex dioica	100-3	100-3	100-2	100-2	100-3	100-1
Carex flava	50-s	50-2	100-u	100-s	67-s	33-s
Carex flava x hostiana	50-s	100-1	100-1	67-s	33-s	-
Carex hostiana	100-s	50-1	50-u	33-s	-	67-s
Carex panicea	100-u	100-u	100-2	100-u	100-2	100-2
Carex vaginata	50-s	-	-	-	33-s	-
Deschampsia cespitosa	-	-	-	33-s	67-s	100-s
Eriophorum angustifolium	100-2	100-1	100-1	100-u	100-u	100-u
Eriophorum latifolium	100-1	100-1	100-1	33-s	33-s	67-s
Eriophorum vaginatum	50-s	100-s	100-s	67-s	67-s	33-s
Festuca ovina	100-s	-	100-s	100-s	100-s	100-s
Juncus castaneus	-	-	-	33-s	-	-
Juncus triglumis	100-s	50-s	-	67-s	33-s	67-s
Kobresia simpliciuscula	100-s	50-s	50-u	100-u	100-1	100-1
Molinia caerulea	100-u	100-u	100-2	100-u	100-u	100-2
Nardus stricta	-	-	-	-	33-s	-
Scirpus cespitosus	100-2	100-4	100-4	100-3	100-3	100-3
Scirpus hudsonianus	-	-	-	-	-	33-s
Bryum pseudotriquetrum	100-s	50-s	100-s	67-s	67-s	67-s
Calliergon trifarium	100-u	100-s	100-s	67-u	-	100-u
Campylium stellatum	100-6	100-5	100-4	100-4	100-5	100-4
Ditrichum flexicaule	-	50-s	-	-	33-s	33-s
Drepanocladus revolvens	100-3	100-3	100-4	100-4	100-3	100-3
Fissidens adianthoides	-	50-s	50-s	-	67-s	67-s
Homalothecium nitens	-	-	-	-	-	33-s
Pleurozium schreberi	-	-	-	-	-	33-s
Tortella tortuosa	-	-	-	-	33-s	-
Aneura pinguis	100-u	100-s	-	-	-	-
Barbilophozia lycopodioides	-	-	-	-	-	33-s
Barbilophozia quadriloba	100-s	-	-	-	-	33-s
Lophozia borealis	100-u	100-s	50-s	100-s	100-u	100-u

Table 4. Synoptic table of the phytosociological analyses made in 1992-94 of plots in the wooded grassland communities at localities 5 and 40 at Sølendet, showing frequency of occurrence and mean degree of cover. Size of plots: 12.5 m². Cover scale in %: s: 0-1; u: 1-3.1; 1: 3.1-6.2; 2: 6.2-12.5; 3: 12.5-25; 4: 25-50; 5: 50-75; 6: 75-100. B: shrub layer

Locality no.	5	5	5	40	40	40
Scything frequency	Annually	Biennially	Unscythed	Annually	Biennially	Unscythed
No. of repeats	3	3	3	2	2	2
Betula pubescens B	-	-	33-s	-	-	-
Juniperus communis B	-	-	-	100-u	-	-
Salix nigricans coll. B	-	-	67-s	-	-	-
Juniperus communis	-	-	-	-	-	50-s
Vaccinium myrtillus	-	67-s	67-u	100-s	50-s	-
Achillea millefolium	-	-	-	100-2	50-1	-
Aconitum septentrionale	33-s	33-s	-	100-1	100-u	100-5
Alchemilla sp.	100-3	100-4	100-3	100-1	100-4	100-1
Angelica archangelica	-	-	-	100-1	100-2	100-2
Angelica sylvestris	100-s	67-s	100-s	100-s	100-s	50-s
Anthriscus sylvestris	-	-	-	100-s	50-u	100-u
Bartsia alpina	-	100-s	33-s	-	-	-
Botrychium lunaria	-	-	-	-	50-s	50-s
Caltha palustris	-	33-s	-	-	-	-
Campanula rotundifolia	-	-	-	-	50-s	-
Cerastium fontanum	67-s	33-s	100-s	-	50-s	50-s
Cicerbita alpina	-	-	-	-	-	100-s
Cirsium helenioides	-	33-u	100-u	-	-	-
Coeloglossum viride	33-s	33-s	-	-	-	-
Corallorhiza trifida	33-s	-	-	-	-	-
Crepis paludosa	100-2	100-3	100-2	100-3	100-4	100-1
Dactylorhiza fuchsii	100-s	100-u	100-s	-	50-s	-
Dactylorhiza maculata	-	33-s	-	-	-	-
Equisetum sylvaticum	100-u	100-u	100-s	-	-	-
Euphrasia frigida	-	-	-	-	50-s	-
Filipendula ulmaria	-	100-u	100-u	100-u	100-1	100-1
Galium boreale	100-u	100-s	100-u	100-s	50-s	100-s
Galium sp.	33-s	-	-	-	-	-
Geranium sylvaticum	100-s	100-u	100-3	100-u	100-4	100-3
Geum rivale	100-s	100-u	100-1	100-s	100-u	100-u
Gnaphalium norvegicum	-	33-s	-	50-s	100-u	100-s
Hieracium sect. Vulgata	-	-	100-s	50-s	100-u	100-s
Leontodon autumnalis	33-s	67-s	-	-	-	-
Melampyrum sylvaticum	-	-	-	-	-	100-s
Myosotis decumbens	-	-	67-s	100-s	100-u	100-s
Oxalis acetosella	-	-	-	-	-	100-s
Paris quadrifolia	100-s	100-s	100-s	100-s	100-u	100-s
Parnassia palustris	33-s	100-s	33-s	100-s	100-u	100-s
Pinguicula vulgaris	33-s	-	-	-	-	-
Polygonum viviparum	100-1	100-u	100-s	100-1	100-1	100-s
Potentilla erecta	100-s	67-s	100-u	-	-	-
Pyrola minor	100-u	67-s	100-s	-	-	-
Pyrola rotundifolia	-	-	-	100-u	100-u	100-s
Ranunculus acris	100-2	100-3	100-u	100-u	100-1	100-s
Ranunculus auricomus	33-s	33-s	-	100-u	100-s	100-s
Ranunculus platanifollus	33-s	-	-	50-s	-	-
Rhinanthus minor	33-s	-	33-s	-	50-u	-
Rubus saxatilis	-	-	-	100-s	-	-
Rumex acetosa	100-s	100-u	-	100-s	100-u	100-s
Sagina saginoides	-	-	-	100-s	-	-
Saussurea alpina	67-s	67-s	100-1	100-u	100-1	100-u
Selaginella selaginoides	100-s	67-s	-	50-s	100-u	50-s
Solidago virgaurea	100-s	100-s	100-u	100-u	100-1	100-u
Succisa pratensis	33-s	33-s	100-s	-	50-u	-
Taraxacum sp.	100-u	33-s	-	100-2	100-u	100-s

Locality no.	5	5	5	40	40	40
Scything frequency	Annually	Biennially	Unscythed	Annually	Biennially	Unscythed
No. of repeats	3	3	3	2	2	2
Thalictrum alpinum	100-u	67-s	-	-	-	-
Trientalis europaea	33-s	33-s	100-u	50-s	50-s	100-s
Valeriana sambucifolia	-	-	-	-	50-s	100-s
Viola biflora	-	33-s	-	100-1	100-1	100-2
Agrostis capillaris	100-3	100-3	100-u	100-3	100-2	100-s
Anthoxanthum odoratum	100-u	100-u	100-1	100-s	100-1	100-s
Calamagrostis purpurea	33-s	33-s	-	-	-	-
Carex capillaris	33-s	-	33-s	-	-	-
Carex nigra	100-s	100-s	100-s	100-s	-	-
Carex norvegica	-	-	-	100-s	-	-
Carex vaginata	100-u	100-s	100-u	100-s	-	-
Deschampsia cespitosa	100-3	100-3	100-3	100-u	100-u	100-1
Deschampsia flexuosa	100-u	33-u	100-u	100-u	100-u	50-s
Festuca ovina	33-s	-	-	-	-	-
Festuca rubra	100-s	100-u	100-u	100-s	100-s	50-s
Hierocloe odorata	33-s	-	100-s	-	-	-
Luzula multiflora	33-s	-	67-s	100-s	100-s	50-s
Luzula sudetica	100-u	100-s	100-s	-	-	-
Molinia caerulea	-	-	67-s	-	-	-
Nardus stricta	100-s	33-u	-	-	-	-
Phleum alpinum	100-u	100-u	67-s	100-s	100-s	100-s
Poa alpina	67-s	-	33-s	100-s	100-s	-
Poa nemoralis	100-u	100-u	100-u	100-u	100-1	100-s
Poa pratensis	33-s	33-s	100-s	100-s	50-s	100-s
Aulacomnium palustre	-	33-s	-	-	-	-
Brachythecium reflexum	-	-	-	-	50-u	100-s
Brachythecium salebrosum	-	-	33-s	100-2	100-1	100-s
Brachythecium sp.	-	-	-	50-s	-	50-s
Brachythecium starkei	-	33-s	67-s	-	-	-
Brachythecium velutinum	-	-	-	-	50-u	50-s
Bryum sp.	100-s	100-s	-	100-s	50-s	-
Campylium stellatum	67-s	33-s	33-s	-	-	-
Cirriphyllum piliferum	-	-	67-u	-	-	-
Climacium dendroides	100-u	67-u	67-s	100-u	50-s	-
Dicranum bonjeanii	-	33-s	-	-	-	-
Drepanocladus uncinatus	100-u	33-s	-	100-u	50-s	-
Fissidens adiantoides	33-s	67-s	-	-	-	-
Hylocomium pyrenaicum	33-s	-	33-s	-	-	-
Hylocomium splendens	100-3	100-1	100-s	100-s	100-u	-
Mnium spinosum	-	-	33-s	100-1	100-2	100-2
Mnium stellare	-	-	-	50-s	50-s	-
Plagiomnium ellipticum	-	33-s	-	-	-	-
Polytrichum juniperinum	33-s	-	-	100-s	100-s	-
Rhizomnium magnifolium	100-u	100-s	67-s	-	-	-
Rhodobryum roseum	100-u	100-u	100-u	50-s	100-s	100-u
Rhytidiadelphus sq./subp.	100-4	100-4	100-u	100-s	100-s	100-s
Barbilophozia lycopodioides	-	-	-	-	100-s	-
Barbilophozia quadriloba	-	67-s	-	-	-	-
Chiloscyphus pallescens	67-s	67-s	67-s	-	-	-
Lophocolea bidentata	-	33-s	-	-	-	-
Lophozia obtusa	-	-	-	-	50-s	-
Marchantia cf. alpestris	-	67-s	-	-	-	-
Pellia neeslana	100-s	67-s	33-s	-	-	-
Plagiochila porelloides	67-s	67-s	67-u	-	50-s	50-s
Scapania sp.	100-u	67-s	-	-	-	-

Table 5. Means and standard deviations for number of individuals and biomass values of dominant and subdominant species in the field layer of locality 2, a rich fen community of *Scirpus cespitosus-Carex hostiana-Campylium stellatum* type. A: above-ground; B: below-ground; T: total (A+B) biomass; - : values impossible to calculate, because the biomass was either estimated to be zero (both A and B) or only estimated in one year

Species	Annually scythed plot										Biennially scythed plots										Unscythed plot									
	No. of indiv. per m²		Biomass (kg·ha⁻¹) A				Biomass (kg·ha⁻¹) B				Biomass (kg·ha⁻¹) T				A/B ratio				No. of indiv. per m²		Biomass (kg·ha⁻¹) A				Biomass (kg·ha⁻¹) B				Biomass (kg·ha⁻¹) T				A/B ratio	
	mean	SD	mean	SD			mean	SD			mean	SD			mean	SD			mean	SD					mean	SD			mean	SD			mean	SD		
Equisetum palustre	1158	218	71	27			52	55			123	81			2.50	2.12			214	132					21	5			15	5			35	11			1.44	0.16		
Equisetum variegatum	94	54	16	16			21	14			38	31			0.66	0.30			61	40					8	4			23	20			31	24			0.47	0.26		
Euphrasia frigida	3	0	0	0			0	0			0	0			-	-			85	84					6	8			1	2			7	10			4.00	-		
Polygonum viviparum	121	8	33	9			99	16			132	25			0.33	0.04			35	37					9	13			52	73			61	86			0.17	-		
Potentilla erecta	9	6	0	0			0	0			0	0			-	-			72	92					4	6			13	18			17	24			0.32	-		
Saussurea alpina	0	0	0	0			0	0			0	0			-	-			9	8					0	0			0	0			0	0			-	-		
Saxifraga aizoides	5	1	0	0			0	0			0	0			-	-			31	3					0	0			0	0			0	0			-	-		
Selaginella selaginoides	32	11	0	0			0	0			0	0			-	-			40	27					2	3			1	2			4	5			1.60	-		
Thalictrum alpinum	1054	65	105	8			94	9			199	17			1.11	0.02			976	36					44	9			136	9			180	0			0.33	0.08		
Tofieldia pusilla	30	33	16	23			7	10			23	33			2.26	-			22	9					10	14			4	5			14	19			2.92	-		
Triglochin palustre	210	60	28	7			28	8			56	1			1.07	0.53			38	42					0	0			0	0			0	0			-	-		
Carex dioica	2313	760	141	124			150	111			290	235			0.88	0.18			2425	436					299	3			287	136			585	139			1.17	0.54		
Carex flava	0	0	0	0			0	0			0	0			-	-			21	29					36	51			32	45			68	96			1.14	-		
Carex flava x hostiana	4	5	0	0			0	0			0	0			-	-			33	46					85	120			199	281			284	402			0.43	-		
Carex panicea	6	3	0	0			0	0			0	0			-	-			80	90					102	145			81	114			183	259			1.27	-		
Eriophorum angustifolium	359	83	224	2			341	5			565	3			0.66	0.02			175	104					289	9			234	150			523	141			1.57	1.04		
Eriophorum latifolium	70	21	77	35			148	103			225	137			0.58	0.17			92	17					213	87			291	82			504	5			0.81	0.53		
Molinia caerulea	60	7	19	7			36	19			56	12			0.67	0.54			99	0					31	6			76	29			107	35			0.43	0.08		
Scirpus cespitosus	863	6	146	48			289	89			435	137			0.51	0.01			2209	1108					764	274			1151	700			1914	974			0.73	0.20		
Other species	44	47	0	0			0	0			0	0			-	-			35	16					0	0			0	0			0	0			-	-		
Total	6430	468	877	81			1266	13			2143	68			0.69	0.07			6747	746					1923	385			2594	404			4517	788			0.74	0.03		

Species	Unscythed plot									
	No. of indiv. per m²		Biomass (kg·ha⁻¹) A				Biomass (kg·ha⁻¹) B				Biomass (kg·ha⁻¹) T				A/B ratio	
	mean	SD	mean	SD			mean	SD			mean	SD			mean	SD
Equisetum palustre	44	7	3	2			3	0			6	1			1.03	0.67
Equisetum variegatum	98	7	31	13			78	46			109	34			0.54	0.48
Euphrasia frigida	135	82	7	6			2	0			9	6			3.67	3.30
Polygonum viviparum	5	0	0	0			0	0			0	0			-	-
Potentilla erecta	24	11	7	10			37	52			44	62			0.19	-
Saussurea alpina	52	12	23	16			37	31			60	47			0.67	0.11
Saxifraga aizoides	8	11	4	5			4	5			7	10			1.04	-
Selaginella selaginoides	73	20	7	9			2	3			9	12			3.00	-
Thalictrum alpinum	813	6	45	29			81	24			126	53			0.52	0.21
Tofieldia pusilla	14	2	0	0			0	0			0	0			-	-
Triglochin palustre	72	51	0	0			0	0			0	0			-	-
Carex dioica	1559	660	257	209			281	119			538	328			0.83	0.39
Carex flava	32	5	0	0			0	0			0	0			-	-
Carex flava x hostiana	20	18	53	75			40	56			93	131			1.35	-
Carex panicea	103	45	200	93			137	39			337	132			1.42	0.27
Eriophorum angustifolium	36	17	72	14			97	15			169	29			0.74	0.04
Eriophorum latifolium	35	14	147	107			244	125			390	233			0.56	0.15
Molinia caerulea	244	17	217	142			496	186			712	328			0.41	0.13
Scirpus cespitosus	2692	436	981	309			2900	2348			3881	2658			0.44	0.25
Other species	48	35	0	0			0	0			0	0			-	-
Total	6103	177	2054	142			4438	2372			6492	2514			0.53	0.25

Table 6. Means and standard deviations for number of individuals and biomass values of dominant and subdominant species in the field layer of locality 3 a rich fen community of *Molinia caerulea-Kobresia simpliciuscula-Campylium stellatum* type. A: above-ground; B: below-ground; T: total (A+B) biomass; - : values impossible to calculate, because the biomass was either estimated to be zero (both A and B) or only estimated in one year

Species	Annually scythed plot										Biennially scythed plots										Unscythed plot									
	No. of indiv. per m²		Biomass (kg·ha·¹)						A/B ratio		No. of indiv. per m²		Biomass (kg·ha·¹)						A/B ratio		No. of indiv. per m²		Biomass (kg·ha·¹)						A/B ratio	
			A		B		T						A		B		T						A		B		T			
	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD
Equisetum variegatum	93	17	4	7	4	8	9	15	0.93	-	54	26	5	5	6	7	11	13	0.91	0.22	36	1	3	3	7	7	10	9	0.36	0.07
Pedicularis oederi	1	2	0	0	0	0	0	0	-	-	9	16	0	0	0	0	0	0	-	-	27	17	8	14	20	35	28	49	0.41	-
Polygonum viviparum	46	12	3	4	5	9	8	14	0.49	-	61	11	7	9	30	34	37	42	0.21	0.05	48	12	1	1	6	11	7	12	0.10	-
Potentilla erecta	1	0	0	0	0	0	0	0	-	-	21	36	8	14	28	49	36	63	0.29	-	5	4	0	0	0	0	0	0	-	-
Saussurea alpina	0	1	0	0	0	0	0	0	-	-	10	17	0	0	0	0	0	0	-	-	43	7	4	4	16	17	20	19	0.32	0.28
Saxifraga aizoides	41	13	0	0	0	0	0	0	-	-	9	13	3	5	4	6	6	11	0.76	-	1	2	0	0	0	0	0	0	-	-
Selaginella selaginoides	6	3	0	0	0	0	0	0	-	-	76	78	4	4	1	2	5	6	4.75	3.18	84	30	4	5	1	1	5	5	5.75	5.30
Succisa pratensis	0	1	0	0	0	0	0	0	-	-	16	25	14	25	17	29	31	54	0.84	-	51	12	222	183	312	270	534	452	0.73	0.16
Thalictrum alpinum	405	240	51	62	69	57	120	119	0.58	0.30	638	221	86	43	93	38	179	74	0.93	0.27	595	59	46	17	54	26	101	38	0.94	0.49
Triglochin palustre	67	16	9	12	4	4	13	16	1.89	1.26	53	28	5	8	3	5	8	13	1.59	-	17	2	0	0	0	0	0	0	-	-
Carex capillaris	13	13	0	0	0	0	0	0	-	-	58	40	9	9	10	10	19	19	0.95	0.17	24	7	0	0	0	0	0	0	-	-
Carex dioica	1081	579	146	97	106	69	252	166	1.35	0.05	1589	1078	198	196	219	285	416	477	1.19	0.57	762	412	103	76	110	69	212	145	0.86	0.19
Carex panicea	58	12	53	19	55	1	108	20	0.97	0.35	168	63	135	46	150	91	285	136	1.02	0.30	158	8	157	39	277	155	434	149	0.68	0.33
Eriophorum angustifolium	44	23	30	31	53	55	84	86	0.58	0.03	33	7	32	29	49	43	81	70	0.66	0.27	19	10	17	14	25	22	42	36	0.66	0.06
Kobresia simpliciuscula	149	147	19	19	63	103	82	121	1.54	1.86	242	335	31	39	80	92	111	131	0.36	0.08	349	127	101	45	174	111	275	151	0.63	0.21
Molinia caerulea	113	40	30	26	74	56	105	82	0.40	0.10	194	52	47	6	193	107	240	113	0.30	0.16	282	34	232	89	1021	388	1253	468	0.23	0.05
Scirpus cespitosus	1975	204	332	117	544	101	876	22	0.65	0.34	1454	1009	176	135	339	205	515	337	0.48	0.12	2311	1185	601	480	1794	1430	2395	1443	0.49	0.35
Other species	72	31	0	0	0	0	0	0	-	-	156	64	0	0	0	0	0	0	-	-	142	105	0	0	0	0	0	0	-	-
Total	4164	975	677	191	979	339	1655	461	0.72	0.23	4839	1127	759	230	1222	454	1981	661	0.64	0.15	4952	1407	1497	547	3818	2205	5315	2524	0.44	0.19

Table 7. Means and standard deviations for number of individuals and biomass values of dominant and subdominant species in the field layer of locality 5, a wooded grassland community of *Betula pubescens-Crepis paludosa-Campylium stellatum* type. A: above-ground; B: below-ground; T: total (A+B) biomass; - : values impossible to calculate, because the biomass was either estimated to be zero (both A and B) or only estimated in one year

Species	Annually scythed plot										Biennially scythed plots										Unscythed plot									
	No. of indiv. per m²		Biomass (kg·ha⁻¹)						A/B ratio		No. of indiv. per m²		Biomass (kg·ha⁻¹)						A/B ratio		No. of indiv. per m²		Biomass (kg·ha⁻¹)						A/B ratio	
			A		B		T						A		B		T						A		B		T			
	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD
Alchemilla sp.	107	35	232	56	673	317	905	314	0.39	0.18	77	12	721	101	1180	401	1901	468	0.64	0.15	37	6	321	62	810	291	1132	335	0.43	0.15
Cirsium helenioides	0	0	0	0	0	0	0	0	-	-	0	0	0	0	0	0	0	0	-	-	4	1	10	17	4	7	14	24	2.63	-
Crepis paludosa	95	19	57	34	157	68	214	99	0.35	0.08	116	42	183	115	498	447	681	552	0.43	0.23	108	8	170	17	585	174	755	190	0.30	0.06
Equisetum sylvaticum	11	3	10	8	6	6	16	14	1.56	0.26	20	17	32	28	21	18	52	45	1.55	0.06	0	0	0	0	0	0	0	0	-	-
Galium boreale	32	6	10	6	5	5	15	11	4.17	4.20	5	6	3	4	1	2	4	6	2.21	-	70	8	37	20	33	15	69	33	1.08	0.35
Geranium sylvaticum	9	7	0	0	0	0	0	0	-	-	20	6	110	91	262	138	372	223	0.38	0.15	60	1	413	169	1300	340	1714	499	0.31	0.06
Geum rivale	14	8	4	7	7	12	11	19	0.56	-	19	7	33	49	66	81	100	129	0.42	0.22	23	8	254	108	544	378	798	315	0.86	1.01
Polygonum viviparum	107	41	37	18	134	10	171	24	0.27	0.12	25	27	14	24	27	47	41	72	0.52	-	6	4	0	0	0	0	0	0	-	-
Ranunculus acris	96	29	98	84	163	124	260	208	0.58	0.12	74	31	253	255	221	217	474	472	1.08	0.13	16	3	27	26	34	32	61	53	0.92	0.60
Saussurea alpina	0	1	0	0	0	0	0	0	-	-	3	4	0	0	0	0	0	0	-	-	22	3	43	4	35	9	78	6	1.28	0.47
Thalictrum alpinum	27	35	2	4	2	4	5	9	1.00	-	23	37	0	1	2	3	2	4	0.25	-	0	0	0	0	0	0	0	0	-	-
Trientalis europaea	0	1	0	0	0	0	0	0	-	-	0	0	0	0	0	0	0	0	-	-	53	24	12	11	9	8	21	19	1.40	0.07
Agrostis capillaris	506	39	169	38	214	89	383	126	0.83	0.16	367	189	236	116	680	872	916	941	0.85	0.59	129	69	61	38	80	37	141	75	0.70	0.23
Anthoxanthum odoratum	23	8	0	0	0	0	0	0	-	-	28	36	0	0	0	0	0	0	-	-	98	75	31	54	22	39	53	93	1.40	-
Carex nigra	0	0	0	0	0	0	0	0	-	-	14	25	0	0	0	0	0	0	-	-	36	31	31	54	31	54	62	108	1.01	-
Carex vaginata	31	25	0	0	0	0	0	0	-	-	24	18	14	24	12	21	26	45	1.16	-	62	22	74	29	102	40	176	66	0.75	0.19
Deschampsia cespitosa	309	51	260	46	292	120	552	92	1.04	0.62	432	166	524	197	615	213	1139	407	0.85	0.10	300	145	537	293	602	489	1139	744	1.08	0.68
Deschampsia flexuosa	149	37	11	11	25	22	36	32	0.42	0.25	20	20	0	0	0	0	0	0	-	-	53	6	0	0	0	0	0	0	-	-
Festuca rubra	41	46	0	0	0	0	0	0	-	-	24	42	25	43	8	14	33	57	2.97	-	41	28	13	22	5	9	18	32	2.41	-
Poa nemoralis	54	32	5	9	7	12	12	20	0.75	-	63	13	26	27	18	28	44	54	3.73	3.78	13	19	9	15	49	84	58	100	0.18	-
Other species	198	37	0	0	0	0	0	0	-	-	90	40	0	0	0	0	0	0	-	-	62	18	0	0	0	0	0	0	-	-
Total	1808	206	894	113	1687	574	2581	643	0.56	0.14	1444	107	2174	416	3611	1888	5785	2258	0.67	0.21	1191	263	2043	280	4246	374	6289	484	0.48	0.08

Table 8. Means and standard deviations for number of individuals and biomass values of dominant and subdominant species in the field layer of locality 40, a tall-herb birch woodland community of *Betula pubescens-Aconitum septentrionale-Angelica archangelica* type. A: above-ground; B: below-ground; T: total (A+B) biomass; - : values impossible to calculate, because the biomass was either estimated to be zero (both A and B) or only estimated in one year

Species	Annually scythed plot										Biennially scythed plots										Unscythed plot									
	No. of indiv. per m²		Biomass (kg·ha⁻¹)						A/B ratio		No. of indiv. per m²		Biomass (kg·ha⁻¹)						A/B ratio		No. of indiv. per m²		Biomass (kg·ha⁻¹)						A/B ratio	
			A		B		T						A		B		T						A		B		T			
	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD	mean	SD
Achillea millefolium	63	26	24	14	20	15	44	29	1.37	0.38	40	56	0	0	0	0	0	0	-	-	0	0	0	0	0	0	0	0	-	-
Aconitum septentrionale	8	5	0	0	0	0	0	0	-	-	21	23	132	187	160	226	292	413	0.82	-	265	93	2064	429	757	347	2821	776	2.90	0.76
Alchemilla sp.	34	2	124	57	347	184	471	241	0.36	0.03	54	20	455	128	903	381	1358	509	0.52	0.08	18	4	158	59	405	413	564	472	0.66	0.53
Angelica archangelica	29	1	78	8	305	141	382	132	0.29	0.16	14	4	127	40	263	87	390	127	0.48	0.01	26	13	1633	242	2552	518	4185	276	0.66	0.23
Anthriscus sylvestris	0	0	0	0	0	0	0	0	-	-	3	4	7	10	23	33	30	43	0.29	-	8	1	0	0	0	0	0	0	-	-
Crepis paludosa	84	1	254	71	536	106	790	177	0.47	0.04	76	6	279	8	305	30	584	21	0.92	0.12	37	11	103	29	205	52	308	24	0.54	0.28
Filipendula ulmaria	16	1	9	12	35	50	44	62	0.24	-	18	8	148	120	289	53	437	174	0.48	0.33	35	19	470	575	768	582	1238	1157	0.46	0.40
Geranium sylvaticum	75	59	118	142	549	666	666	808	0.22	0.01	139	127	647	539	3812	3305	4459	3844	0.17	0.01	86	18	552	325	1641	337	2193	12	0.36	0.27
Geum rivale	16	7	7	9	11	16	18	25	0.59	-	10	1	71	46	83	7	154	39	0.88	0.62	9	0	51	72	166	235	217	307	0.30	-
Polygonum viviparum	151	40	38	12	214	130	252	142	0.20	0.06	65	14	36	29	93	65	129	94	0.36	0.06	1	1	0	0	0	0	0	0	-	-
Pyrola rotundifolia	28	1	10	7	4	4	15	11	2.44	0.39	7	2	0	0	0	0	0	0	-	-	5	6	0	0	0	0	0	0	-	-
Ranunculus acris	68	16	62	55	94	11	156	66	0.63	0.51	44	10	56	27	59	10	114	37	0.92	0.30	8	1	0	0	0	0	0	0	-	-
Saussurea alpina	30	1	21	9	23	2	44	7	0.94	0.47	36	11	52	41	30	29	82	70	1.95	0.52	6	2	0	0	0	0	0	0	-	-
Solidago virgaurea	23	2	0	0	0	0	0	0	-	-	26	13	29	6	42	20	71	26	0.74	0.20	11	3	0	0	0	0	0	0	-	-
Taraxacum sp.	38	13	118	88	218	180	336	268	0.57	0.07	10	4	0	0	0	0	0	0	-	-	0	0	0	0	0	0	0	0	-	-
Viola biflora	108	44	11	1	53	38	64	39	0.26	0.17	159	134	30	36	57	44	88	80	0.41	0.31	163	45	24	29	48	24	73	5	0.75	0.97
Agrostis capillaris	839	394	243	114	229	7	472	122	1.05	0.46	415	122	168	54	138	38	307	16	1.32	0.75	4	5	0	0	0	0	0	0	-	-
Anthoxanthum odoratum	0	0	0	0	0	0	0	0	-	-	36	29	6	9	3	4	9	13	2.00	-	22	31	0	0	0	0	0	0	-	-
Deschampsia cespitosa	122	42	86	34	65	30	151	4	1.60	1.25	72	62	110	107	53	53	163	160	2.08	0.06	118	167	0	0	0	0	0	0	-	-
Deschampsia flexuosa	160	142	0	0	0	0	0	0	-	-	318	21	5	7	42	59	46	66	0.12	-	3	4	0	0	0	0	0	0	-	-
Festuca rubra	94	53	42	11	25	18	67	29	2.06	1.07	50	2	23	2	27	12	50	14	0.93	0.35	0	0	0	0	0	0	0	0	-	-
Poa nemoralis	63	15	0	0	0	0	0	0	-	-	48	10	28	32	28	32	57	64	1.01	0.01	2	3	0	0	0	0	0	0	-	-
Other species	120	35	0	0	0	0	0	0	-	-	92	3	0	0	0	0	0	0	-	-	87	56	0	0	0	0	0	0	-	-
Total	2163	209	1243	128	2729	1083	3972	1211	0.48	0.15	1746	313	2409	245	6411	2654	8821	2899	0.40	0.13	910	325	5055	1050	6544	1369	11599	2419	0.77	0.00

Biomass values

Above-ground biomass

The mean above-ground biomass values for each species are shown in Tables 5-8, total and mean values for the field-layer in Table 10. The highest values for the total mean above-ground biomass were estimated at locality 40 for all scything frequencies: about 1200, 2400 and 5000 $kg \cdot ha^{-1}$ respectively for the plots scythed annually, biennially and unscythed. The lowest values were estimated for locality 3 for all scything frequencies: about 700, 800 and 1500 $kg \cdot ha^{-1}$ respectively. The total mean value for the field-layer decreased with increasing scything frequency in localities 2, 3 and 40. For locality 5, the values estimated for the biennially scythed plots were a little higher than those for the unscythed plot.

There was a considerable variation between years, particularly in locality 3, with an SD of ca. 28-36% for all scything frequencies (Table 10). For the unscythed plot, much of the variation was due to fluctuations in the values of *Succisa pratensis, Molinia caerulea* and *Scirpus cespitosus*. For the scythed plots, a large part of the variation was due to fluctuations in the values for *Carex dioica* (Table 6).

Table 9. Number of individuals per m^2 in the field layer of the four plant communities at localities 2, 3, 5 and 40 at Sølendet, together with mean values and standard deviations

Scything frequency/year		Individuals per m^2			
		Loc. 2	Loc. 3	Loc. 5	Loc. 40
Annually scythed	1992	-	4855	2044	-
	1993	6099	3048	1665	2015
	1994	6761	4588	1716	2311
Biennially scythed	1992	-	5973	1348	-
	1993	6219	3720	1560	1967
	1994	7274	4823	1425	1524
Unscythed	1992	-	5467	1047	-
	1993	5977	3360	1032	1140
	1994	6228	6030	1495	680
Mean	Annually scythed	6430	4164	1808	2163
	Biennially scythed	6747	4839	1444	1746
	Unscythed	6103	4952	1191	910
SD	Annually scythed	468	975	206	209
	Biennially scythed	746	1127	107	313
	Unscythed	177	1407	263	325
SD in % of mean	Annually scythed	7.3	23.4	11.4	9.7
	Biennially scythed	11.1	23.3	7.4	17.9
	Unscythed	2.9	28.4	22.1	35.7

Below-ground biomass

The mean below-ground biomass values for each species are presented in Tables 5-8, total and mean values for the field-layer in Table 11. The highest values for the total mean below-ground biomass were estimated at locality 40 for all scything frequencies: about 2700, 6400 and 6500 kg·ha^{-1} respectively for plots scythed annually, biennially and un-scythed. The lowest values were also here estimated for locality 3 for all scything frequencies: about 1000, 1200 and 3800 kg·ha^{-1} respectively. The total mean value for the below-ground biomass of the field-layer decreases with increas-ing scything frequency in all localities.

With the exception of the scythed plots in locality 2 and the unscythed plot in locality 5, there was a considerable variation between years for all localities and plots. The SD varied between 20.9 and 57.7% of the mean value (Table 11). In locality 2, the variation in the unscythed plot was largely due to very wide variations in the values for *Scirpus cespitosus*

Table 10. Above-ground biomass of the field layer of the four plant communities at localities 2, 3, 5 and 40 at Sølendet, together with mean values and standard deviations

Scything frequency/year		Above-ground biomass (kg·ha^{-1})			
		Loc. 2	Loc. 3	Loc. 5	Loc. 40
Annually scythed	1992	-	750	964	-
	1993	819	461	955	1334
	1994	935	820	764	1153
Biennially scythed	1992	-	1000	1754	-
	1993	1651	543	2586	2582
	1994	2195	733	2183	2236
Unscythed	1992	-	1711	1755	-
	1993	2154	876	2061	4312
	1994	1953	1905	2313	5798
Mean	Annually scythed	877	677	894	1243
	Biennially scythed	1923	759	2174	2409
	Unscythed	2054	1497	2043	5055
SD	Annually scythed	81	191	113	128
	Biennially scythed	385	230	416	245
	Unscythed	142	547	280	1050
SD in % of mean	Annually scythed	9.3	28.2	12.7	10.3
	Biennially scythed	20.0	30.3	19.1	10.2
	Unscythed	6.9	36.5	13.7	20.8

Table 11. Below-ground biomass of the field layer of the four plant communities at localities 2, 3, 5 and 40 at Sølendet, together with mean values and standard deviations

Scything frequency/year		Below-ground biomass ($kg \cdot ha^{-1}$)			
		Loc. 2	Loc. 3	Loc. 5	Loc. 40
Annually scythed	1992	-	1366	1413	-
	1993	1275	732	2347	3494
	1994	1256	838	1301	1963
Biennially scythed	1992	-	1742	2486	-
	1993	2309	1020	5791	8288
	1994	2880	904	2555	4535
Unscythed	1992	-	6323	4409	-
	1993	6115	2172	3818	5576
	1994	2760	2960	4510	7512
Mean	Annually scythed	1266	979	1687	2729
	Biennially scythed	2594	1222	3611	6411
	Unscythed	4438	3818	4246	6544
SD	Annually scythed	13	339	574	1083
	Biennially scythed	404	454	1888	2654
	Unscythed	2372	2205	374	1369
SD in % of mean	Annually scythed	1.0	34.7	34.1	39.7
	Biennially scythed	15.6	37.2	52.3	41.4
	Unscythed	53.5	57.7	8.8	20.9

(Table 5). For locality 3, the variation was largely due to very high values for some of the dominant species in 1992: *Succisa pratensis, Molinia caerulea* and *Scirpus cespitosus* in the unscythed plot, *Carex dioica* in the biennially scythed plots, and *Kobresia simpliciuscula* and *Thalictrum alpinum* in the annually scythed one (Table 6; cf. also Aune et al. 1994). For locality 5, the variation was mainly due to very high values for some of the dominant species in 1993: *Alchemilla* spp. *Geranium sylvaticum, Geum rivale* and *Deschampsia cespitosa* for the unscythed plot, and *Crepis paludosa, Agrostis capillaris* and partly *Alchemilla* spp. for the biennially scythed plots (Table 7; cf. also Aune et al. 1995a). For locality 40, the variation was largely caused by variation in the values for *Geranium sylvaticum* in the scythed plots. In the unscythed plot the values for most of the dominant species showed wide variations (Table 8).

Total biomass

The mean total biomass values for each species are shown in Tables 5-8, total and

Table 12. Total biomass (above- + below-ground) of the field layer of the four plant communities at localities 2, 3, 5 and 40 at Sølendet, together with mean values and standard deviations

Scything frequency/year		Total biomass ($kg \cdot ha^{-1}$)			
		Loc. 2	Loc. 3	Loc. 5	Loc. 40
Annually scythed	1992	-	2115	2377	-
	1993	2094	1192	3302	4828
	1994	2191	1658	2065	3116
Biennially scythed	1992	-	2743	4240	-
	1993	3959	1562	8376	10871
	1994	5074	1637	4738	6771
Unscythed	1992	-	8034	6164	-
	1993	8269	3047	5879	9888
	1994	4714	4865	6823	13310
Mean	Annually scythed	2143	1655	2581	3972
	Biennially scythed	4517	1981	5785	8821
	Unscythed	6492	5315	6289	11599
SD	Annually scythed	68	461	643	1211
	Biennially scythed	788	661	2258	2899
	Unscythed	2514	2524	484	2419
SD in % of mean	Annually scythed	3.2	27.9	24.9	30.5
	Biennially scythed	17.5	33.4	39.0	32.9
	Unscythed	38.7	47.5	7.7	20.9

mean values for the field-layer in Table 12. The highest etimated mean values for total biomass were recorded at locality 40 for all scything frequencies: about 4000, 9000 and 12,000 $kg \cdot ha^{-1}$ respectively for plots scythed annually, biennially and unscythed. The lowest values were found in locality 3 for all scything frequencies: about 1700, 2000 and 5300 $kg \cdot ha^{-1}$ respectively. The mean value for the total field-layer biomass decreases with increasing scything frequency in all localities.

The results revealed the same pattern of variation for this parameter as that for the below-ground biomass, with a considerable variation between the years for all localities and plots, with the exception of the scythed plots in locality 2 and the unscythed plot in locality 5. The variation was highest in locality 3, where the SD varies between 27.9 and 47.5% of the mean value for all three plots (Table 12).

The above-ground/below-ground biomass (A/B) ratio

The mean A/B ratio values for each species are shown in Tables 5-8, and mean

Table 13. The above-ground/below-ground biomass ratio of the field layer of the four plant communities at localities 2, 3, 5 and 40 at Sølendet, together with mean values and standard deviations

Scything frequency/year		A/B ratio			
		Loc. 2	Loc. 3	Loc. 5	Loc. 40
Annually scythed	1992	-	0.55	0.68	-
	1993	0.64	0.63	0.41	0.38
	1994	0.74	0.98	0.59	0.59
Biennially scythed	1992	-	0.57	0.71	-
	1993	0.72	0.53	0.45	0.31
	1994	0.76	0.81	0.85	0.49
Unscythed	1992	-	0.27	0.40	-
	1993	0.35	0.40	0.54	0.77
	1994	0.71	0.64	0.51	0.77
Mean	Annually scythed	0.69	0.72	0.56	0.48
	Biennially scythed	0.74	0.64	0.67	0.40
	Unscythed	0.53	0.44	0.48	0.77
SD	Annually scythed	0.07	0.23	0.14	0.15
	Biennially scythed	0.03	0.15	0.21	0.13
	Unscythed	0.25	0.19	0.08	0.00
SD in % of mean	Annually scythed	10.3	31.7	25.1	30.0
	Biennially scythed	4.5	23.5	30.9	31.9
	Unscythed	47.4	43.0	15.6	0.1

values for the field-layer in Table 13. The values for mean A/B ratio showed a tendency to vary with locality. For localities 2, 3 and 5, the ratio was higher in the scythed plots than in the unscythed plot. For locality 40, the situation was the opposite. Here, the ratios for the scythed plots were among the lowest values (0.40 and 0.48), while the unscythed plot showed the very highest value (0.77).

With the exception of the scythed plots in locality 2 and the unscythed plot in localities 5 and 40, there is a considerable variation between years for all localities and plots; the SD values vary between 30.0 and 47.4% of the mean value for as many as 50% of all the plots (Table 13). For all localities, the variation could be explained by a wide variation in the A/B values for one or more of the most abundant species.

Table 14. Pearsons product-moment correlation coefficients between effective temperature sums (ETS) and production-ecological parameters of localities 3 and 5. I: ETS before hay-cutting in the current year, II: ETS after hay-cutting in the previous autumn + ETS before hay-cutting in the current year. Significant values in bold

Locality 3

ETS	Production-ecological parameter	Annually scythed	Biennially scythed	Un-scythed
I	No. of individuals	**0.988** *	0.850	0.983
	Above-ground biomass	0.986	0.813	0.987
	Below-ground biomass	0.615	0.358	0.632
	Total biomass	0.859	0.535	0.766
	A/B ratio	0.358	0.631	0.184
IINo. of individuals		0.962	**0.993** *	0.814
	Above-ground biomass	0.825	0.982	0.830
	Below-ground biomass	0.889	0.717	0.899
	Total biomass	**0.995** *	0.841	0.965
	A/B ratio	-0.068	0.246	-0.247

Locality 5

ETS	Production-ecological parameter	Annually scythed	Biennially scythed	Un-scythed
I	No. of individuals	0.588	-0.926	0.541
	Above-ground biomass	-0.479	-0.847	-0.037
	Below-ground biomass	**-0.997** **	**-0.999** **	**0.993**
	Total biomass	-0.974	**-0.992** *	0.746
	A/B ratio	0.933	0.939	-0.632
IINo. of individuals		0.874	**-0.999** **	0.137
	Above-ground biomass	-0.066	**-0.992** *	-0.453
	Below-ground biomass	-0.872	-0.923	0.853
	Total biomass	-0.790	-0.954	0.397
	A/B ratio	**0.998** **	0.708	-0.899

* ($0.05<p<0.1$), ** ($0.001<p<0.05$) and *** ($p<0.001$)

Correlation analyses

The results of the correlation analyses between the numbers of individuals/ biomass values and the climatic parameters in localities 3 and 5 are presented in Tables 14-15. The results revealed very few significant values, partly due to the few degrees of freedom in the analysis (values for three years only).

Effective temperature sum (ETS)
For locality 3, the results indicate a positive correlation with ETS, for both the number of individuals and the biomass values, though few values were significant. For the annually scythed plot, two values were significant at the $p<0.1$ level, the value between ETS-I (prior to hay-cutting in the present year) and number of individuals, and the value between ETS-II (previous autumn included) and total biomass, both showing positive correlations. For the biennially scythed plots, the value between ETS-II and number of individuals was the only significant one ($p<0.1$) (Table 14).
For locality 5, the results yielded both negative and positive correlations with ETS. For ETS-I the values for below-ground biomass were significant for all scything frequencies, yet showed negative correlations at the $p<0.05$ level for the scythed plots, and positive correlations at the $p<0.1$ level for the unscythed plot. For ETS-II, the values for the number of individuals and the above-ground biomass in the biennially scythed plots were significant at the $p<0.05$ and $p<0.1$ levels respectively (Table 14).

Precipitation
For locality 3, the results indicate a negative correlation with precipitation, both for the July value and for the June-July mean. The analysis revealed only two significant values, for below-ground biomass in the annually scythed plot and for total biomass in the biennially scythed plots, both in relation to the June+July mean precipitation ($p<0.1$) (Table 15).

For locality 5, the results indicate both positive and negative correlations with precipitation, positive for the biomass values for the scythed plots and negative for the biomass values for the unscythed plot. For the A/B ratio the results were the opposite. For July precipitation there was only one significant value, relating to the A/B ratio for the biennially scythed plots at the $p<0.1$ level. For the June+July precipitation there were two significant values for the biennially scythed plots, in regard to number of individuals and total biomass ($p<0.1$ and $p<0.001$ respectively). For the annually scythed plot, the value relating to the A/B ratio was significant at the $p<0.05$ level (Table 15).

Discussion

Changes in number of individuals and biomass caused by scything

Scything has a pronounced effect on several species. The following common species are among those found to increase in abundance (in both number of individuals and biomass) with increasing scything frequency: *Achillea millefolium, Polygonum viviparum, Ranunculus acris, Thalictrum alpinum, Triglochin palustre, Agrostis capillaris, Carex capillaris, C. dioica, Deschampsia flexuosa, Eriophorum angustifolium* and *Festuca rubra*. A number of other species decreased in abundance with increasing scything frequency: *Aconitum septentrionale, Angelica archangelica, Filipendula ulmaria, Saussurea alpina, Succisa pratensis, Carex panicea, Kobresia simpliciuscula, Molinia caerulea* and *Scirpus cespitosus*.

A few species show no clear trend in relation to scything frequency or are equally abundant in all plots: *Alchemilla* spp., *Potentilla erecta* and *Viola biflora*. For *Crepis paludosa*, the effect varied with the plant community, it decreased with increasing scything frequency in the open birch woodland (loc. 5) but increase in the tall-herb woodland (loc. 40).

The results agree well with those

Table 15. Pearsons product-moment correlation coefficients between precipitation and production-ecological parameters of localities 3 and 5. Significant values in bold

Locality 3

Precipitation of	Production-ecological parameters	Annually scythed	Biennially scythed	Un-scythed
July	No. of individuals	-0.793	-0.495	-0.952
	Above-ground biomass	-0.946	-0.437	-0.943
	Below-ground biomass	-0.163	0.131	-0.185
	Total biomass	-0.511	-0.067	-0.366
	A/B ratio	-0.760	-0.925	-0.631
June-July	No. of individuals	-0.840	-0.977	-0.844
	Above-ground biomass	-0.877	-0.698	-0.887
	Below-ground biomass	**-0.992** *	-0.826	-0.958
	Total biomass	-0.969	**-0.989** *	-0.829
	A/B ratio	0.041	-0.272	0.220

Locality 5

Precipitation of	Production-ecological parameters	Annually scythed	Biennially scythed	Un-scythed
July	No. of individuals	-0.131	0.634	-0.877
	Above-ground biomass	0.840	0.490	-0.445
	Below-ground biomass	0.913	0.860	-0.928
	Total biomass	0.963	0.809	0.973
	A/B ratio	-0.649	**-0.989** *	0.185
June-July	No. of individuals	0.093	**0.988** *	0.429
	Above-ground biomass	0.884	0.933	-0.867
	Below-ground biomass	0.806	0.962	-0.421
	Total biomass	-0.860	**1.000** ***	-0.164
	A/B ratio	**-0.999** **	-0.727	0.887

*(0.05<p<0.1), **(0.001<p<0.05) and ***(p<0.001)

obtained by Moen (1990) who includes a fuller discussion of the changes in floristic composition caused by scything. In general, concerning the life forms of plants, regular scything of fens and wooded grasslands leads to an overall reduction in shrubs (e.g. *Betula* spp., *Salix* spp.) and dwarf shrubs, and in the proportion of herbs, whereas the proportions of graminoids and bryophytes increase.

The total mean number of individuals per m² is higher in the scythed plots than in the unscythed plot for the most highly productive communities (locs. 40, 5 and 2). This agrees with the model of Grime (1979) (cf. also van der Maarel 1988; Tilman & Pacala 1993) which predicts low richness and diversity in productive habi-

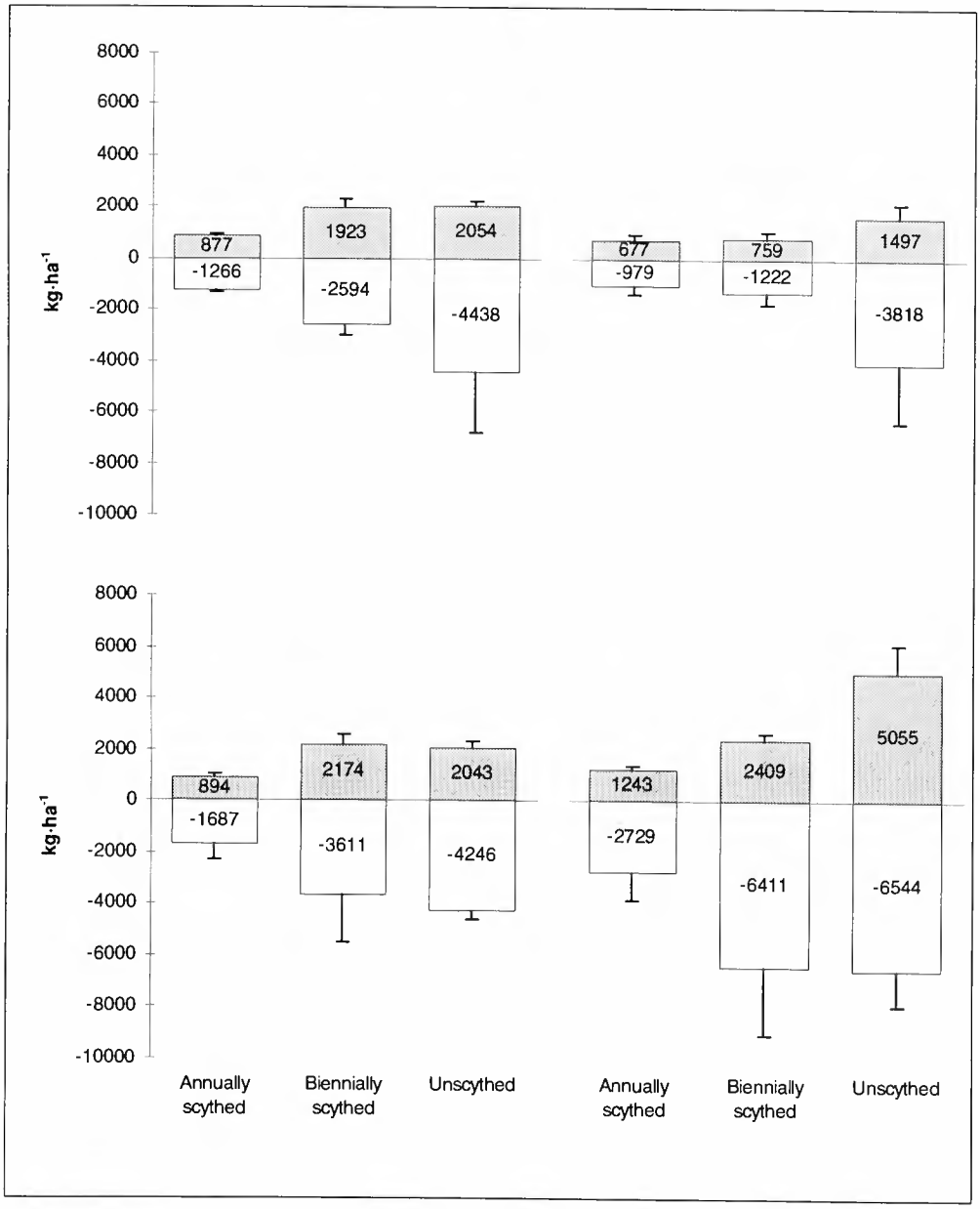

Fig. 2. Mean biomass values of the field-layer with standard deviations of the four plant communities at Sølendet. a: rich fen community of Scirpus cespitosus-Carex hostiana-Campylium stellatum *type (loc. 2), b: rich fen community of* Molinia caerulea-Kobresia simpliciuscula-Campylium stellatum *type (loc. 3), c: wooded grassland of* Betula pubescens-Crepis paludosa-Campylium stellatum *type (loc. 5), d: tall-herb birch woodland of* Betula pubescens-Aconitum septentrionale-Angelica archangelica *type (loc. 40)*

tats, caused by a few dominant species capturing the bulk of the available resources and thereby excluding other plants. Scything in highly productive communities makes more space and light available, and therefore the species diversity increases.

In locality 3, the opposite situation occurs, the number of individuals decreases with increasing scything frequency. In this less productive community, competition for light and space is not important. Scything (stress) thus leads to a reduction in the number of individuals.

Causes of variation between years

The results revealed a considerable variation between years. This variation is particularly pronounced for the below-ground biomass, for which the values in several plots have an SD of more than 30% of the mean value. This variation may have several causes, the main ones being variation in the climatic conditions and that arising from methodological errors (see further).

Climate

Three years is a short period in which to collect data for a correlation analysis. The results therefore revealed very few significant values, making it difficult to conclude whether or not the variation in climatic conditions can explain the considerable variation found between years. However, for the rich fen community on the fen margin (loc. 3) the overall picture is of an increase in the number of individuals/biomass values with increasing mean temperature and a decrease with increasing precipitation. This can partly be explained by the wet habitat occupied by this community. An increase in precipitation does not lead to higher growth, because water is not a limiting factor in this community, even though the groundwater level can vary considerably. Temperature, on the other hand, may be limiting.

For the open birch woodland (loc. 5), there is no overall trend correlated with either temperature or precipitation, and the trend also varies with both scything frequency and the climatic parameters. The negative correlation found between the ETS value and the below-ground biomass for the scythed plots may be explained by the strategy adopted by plants growing in a stressed situation (here due to scything). It is well known (e.g. as summarized by Fitter 1986) that scything forces the plants to mobilize large resources from their below-ground organs. This effect is reinforced in warm weather. The plants have to mobilize more resources from their below-ground organs to produce photosynthetic tissue the warmer the season is (i.e. higher irradiation). However, the biomass (and number of individuals) of the scythed plots still decreases with an increase in mean temperature despite this mobilization. The explanation may be that the below-ground system is too limited in extent and thus prevents any increase in production during dry periods, whereas the opposite situation exists in regard to precipitation; an increase in biomass and in number of individuals occurs with higher precipitation. The soil of the scythed plots is also much more exposed to solar irradiation, rapidly leading to drier conditions, than those found in the unscythed plots. For the unscythed plots the situation is the opposite of that for the scythed ones. Here, the warmer season leads to an increased production, with a corresponding increase in food reserve accumulation in the below-ground organs.

Methodological errors

Some methodological problems are discussed in previous papers concerned with these studies (Aune et al. 1994, 1996, in press). The two main causes of error are sampling errors and those caused by a weakness in the method used.

Sampling errors can occur for a number of reasons:

- Different persons carrying out the counting of individuals, which may lead to deviations in the number of individuals of different species counted in different years. For localities 3 and 5, other persons made the counts in 1992/1993 than those involved in 1994.
- Ignoring small individuals when sampling for biomass estimates. There is a certain possibility, when digging up the shoots, to choose the larger individuals and ignore the small ones.
- Weighing the samples (recording incorrect values, exchanging bags by mistake, etc.).
- Difficulties in identifying small sterile shoots. This is the case for some important species of both the rich fen communities (e.g. *Carex dioica, Kobresia simpliciuscula* and *Scirpus cespitosus*) and the grassland communities (e.g. *Aconitum septentrionale, Geranium sylvaticum* and *Ranunculus acris*).

The method used includes several "weaknesses", which may have led to either an underestimation or an overestimation of the biomass:

- Only the uppermost part of the below-ground material (usually down to 10-30 cm) was gathered, leading to an underestimation of the below-ground biomass. The roots of a number of mire species (cf. Metsävainio 1931; Sjörs 1991) can go much deeper. However, apart from *Eriophorum angustifolium*, species whose roots extend below 30 cm have mostly fine roots with a very limited biomass.
- Only the dominant and subdominant species were included in the biomass studies, i.e. the majority of species are omitted. However, the species omitted account for only 2-17 % of the total number of individuals in the studied plots, except for the unscythed plot at locality 40 (tall-herb woodland) where the omitted species account for 30%. Nevertheless, these species, on average, have a lower biomass than those studied. Hence, the underestimation amounts to only a few percent, even for the unscythed plot in locality 40.
- The method is based on determining the mean individual weight of selected species, from sampling a certain number of individuals. For species with a wide range in size, the mean individual weight can be overestimated or underestimated, because too few individuals are sampled (Aune et al. 1996, in press). This is particularly the case for some of the larger species in the tall-herb grassland (locality 40), e.g. *Aconitum septentrionale* and *Angelica archangelica*. For such species, including small individuals (seedlings) and large, flowering individuals, a stratified sampling (in size classes) should have been worked out.
- Difficulties in determining the border zone between the above- and the below-ground parts of plants may lead to either an overestimation or an underestimation of one of the biomass parts. The criterion used to separate the parts is that the above-ground part consists of green leaves and stems. However, for many plants, this criterion is difficult to apply, and the greater proportion of some species (e.g. *Molinia caerulea*) falls into the border zone itself.

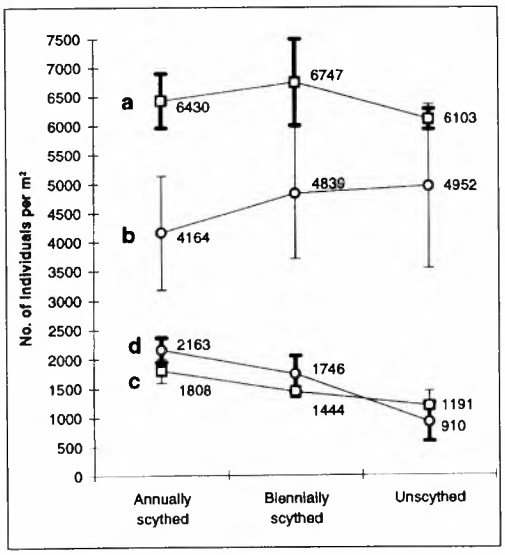

Fig. 3. Mean number of individuals of the field-layer with standard deviations of the four plant communities at Sølendet. a: rich fen community of Scirpus cespitosus-Carex hostiana-Campylium stellatum *type (loc. 2), b: rich fen community of* Molinia caerulea-Kobresia simpliciuscula-Campylium stellatum *type (loc. 3), c: wooded grassland of* Betula pubescens-Crepis paludosa-Campylium stellatum type *(loc. 5), d: tall-herb birch woodland of* Betula pubescens-Aconitum septentrionale-Angelica archangelica *type (loc. 40)*

Conclusions

Scything reduced the biomass in all four plant communities, both the above- and the below-ground biomass (Fig. 2). For the rich fen communities and the tall-herb community the biomass decreased distinctly for each increase in scything frequency. For the other grassland community (loc. 5) there is no distinct decrease until the plots have been scythed annually.

The field species biomass (above- and below-ground) was highest in the tall-herb birch woodland (a total of 12,000 $kg \cdot ha^{-1}$ in the unscythed plots) and lowest in the annually scythed plot of the rich marginal fen (1700 $kg \cdot ha^{-1}$).

The ratio between the above- and below-ground biomass was highest in the unscythed tall-herb community (0.8), and lowest in the scythed tall-herb and the unscythed fen communities (0.4).

The number of individuals was essentially higher in the rich fen communities than in the wooded grassland communities (Fig. 3). In these particular grassland communities, the number of individuals regularly increased from unscythed plots to the annually scythed plots. In the rich fen communities the tendency is less clearcut, and a decrease was even found in the lawn community on the fen margin (loc. 3).

Variation in the climatic conditions seems to be important in explaining some of the annual biomass variation.

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The effect of *Phytophthora palmivora* on *Hedera helix* L. at different temperatures

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Phytophthora palmivora caused a root rot of ivy (*Hedera helix* L.) 'Ester' at average diurnal temperatures between 20 and 30°C, but not at 15°C in a flow/ebb irrigation system. Root damage by *P. palmivora* was fastest developed at 25°C, and the greatest injury occurred also at this temperature. Wilting of shoots was correlated with root rot. Root rot was more severe during the summer than the winter. Control of *P. palmivora* root rot on ivy by maintaining plants at low temperatures is not acceptable in commercial production, because plant growth is reduced too much.

Key words: *Phytophthora palmivora*, *Hedera helix*, temperature.

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Decreased plant growth and death of plants due to root diseases have been a problem in the production of ivy (*Hedera helix* L.) as an ornamental pot plant. The problem has been aggravated by the introduction of the flow/ebb watering system for pot plants and the recirculation of nutrient solution. *Phytophthora palmivora* is a major cause of ivy root rot and death in Norway (Berge, 1989; Romstad et al., 1990) and in other countries (Chase, 1987; Rapp and Richter, 1984). It is also a pathogen on several other plant species, especially in the tropics where it attacks palm and cocoa, and in greenhouses where it has been isolated from *Dieffenbachia picta* and *Peperomia sp.* (Ark and Dewolfe, 1951; Tompkins and Tucker, 1947).Light, temperature, and air humidity interact to affect sporangium formation in *P. palmivora* (Rocha and Machado, 1973). Air humidity is the least important of these factors on formation of sporangia. On cocoa fruits, the optimum conditions for sporangium formation were good light conditions, temperatures around 25°C and relative air humidity of 80 %, and no sporangia were formed at 35°C or at 15 °C in the dark. The purpose of this research was to study the effect of *P. palmivora* on ivy at different temperatures, and to determine the effect of adjusting the temperature on a level unfavorable for the growth of the fungus in greenhouse ivy production. A preliminary report has been published (Myster et al., 1992).

Materials and methods

Cuttings of *Hedera helix 'Ester'* were rooted in 10 cm black plastic pots filled with limed and fertilized peat (Floralux); five single - leaf cuttings to each pot 14 days before the start of experiments. They were covered with clear plastic film for the first days of propagation to keep the humidity high. The air temperature was 20 ± 2°C.Plants were inoculated with a nutrient solution mixed with macerated mycelium of *P. palmivora* in daylight growth rooms. *P. palmivora* was isolated from *Hedera helix* and grown on potato dextrose agar. Mycelia from 43 culture dishes with a diameter of 9 cm were added to a tank of 200 liters. The temperature of the nutrient solution was 24 ± 3 °C. Before each watering, the temperature of both the uninfected and the infested nutrient solution was lowered to 16 ± 3°C. This was done in order to increase the amount of zoospores in the inoculated nutrient solution. The tanks with nutrient solutions were refilled each week. The plants were watered by means of a sub-irrigation system (flow/ebb) for 20 min. three times a week, as long as the experiments lasted. The solution was not recirculated.

The plants were placed in a phytotron at 15, 20, 25 and 30°C constant or with diurnal fluctuation between 15, 20, 25, and 30°C for ten hours and 15°C for 14 hours. The vapor pressure deficit was 5 mm Hg at all temperatures. Plants were fertilized with a fully compound nutrient solution with a conductivity of 2.2 mS/cm in experiment one and 1.4 in experiment two. Each treatment comprised 12 pots with five cuttings each.

Experiment 1: The experiment was carried out from January 24 to March 19, 1991, and included all treatments. Irradiance was natural daylight and 58 µmol m-2s-1 (4.000 lux) by means of SON/T lamps for 24 hours a day.

Experiment 2: This was carried out from May 23 to July 16,1991, under natural light conditions. Only two temperatures, 20 and 25°C, were used. The air temperature on hot days could increase 3-5°C in the 20°C room for a few hours.

Dependent variables recorded during experimental periods: Root rot was graded at each treatment on four plants each week. A scale from 0 to 6 was used, where 0 is healty roots and 6 is completely dead roots. Number of wilted plants were also counted. To reisolate *P. palmivora* from roots, petri dishes with selective PVP and PVPH agar (PVP agar contains Pimaricin-,Vancomycin, Pentachloronitrobenzene (Quintozene) and PVPH with Hymexazol added (Tachigaren)) (Tsao and Guy, 1977) were used. The roots were surface sterilized by dipping for 10 sec.in 70% ethanol and then for 90 sec.in 0.5 % sodium hypochlorite. After 21 and 47 days four roots from each treatment were isolated for growth of P. palmivora. The dishes were placed at 22°C. Growth of *P. palmivora* was recorded four days later.

Dependent variables at the end of the experiments: Root rot, number of wilting plants, fresh and dry weights of vines, length of vines, number of lateral breaks per vine were recorded. Dry weight of vines were tested by General Linear Model procedure in SAS/STAT (SAS Institute Inc.) at each level of temperature.

Results

Experiment 1 (winter): Severe root rot was recorded on plants inoculated with *P. palmivora* (qualified as 5 after a scale from 0-6, where 6 are completely dead roots) at 25/25°C after 26 days and at 30/

30°C after 40 days. All roots on inoculated plants at 25/25°C and 30/30°C were completely dead after 47 days. Root rot started to develop on inoculated plants (character 3) at 30/15°C after 33 days, at 25/15°C after 40 days and at 20/20°C after 47 days. There were just a few dead roots at the termination of the experiment at 20/15°C. At the end of the experiment the root quality of the inoculated plants declined up to an average growth temperature of 25°C, independent of whether constant or fluctuating temperatures were used (Fig. 1). A growth temperature of 30°C reduced the ability of *P. palmivora* to attack the roots to some extent. Root rot on inoculated plants at 15/15°C and plants not inoculated with *P. palmivora* was hardly observed. After 21 days, *P. palmivora* was reisolated from all roots on inoculated plants at 25/25°C. For plants at 15/15°C or 30/30°C, *P. palmivora* was found on one and two roots out of eight, respectively. The fungus was not reisolated from roots of plants at fluctuating temperature after 21 days. After 47 days, the fungus was reisolated from seven and eight out of eight roots for plants grown at 25/15°C or 30/15°C, respectively. Inoculated plants at 15/15 °C, 20/20°C or 30/30°C had zero, three and one infected roots out of eight, respectively, while roots from plants at 25/25°C were decayed. *P. palmivora* was not observed on roots from not inoculated plants.

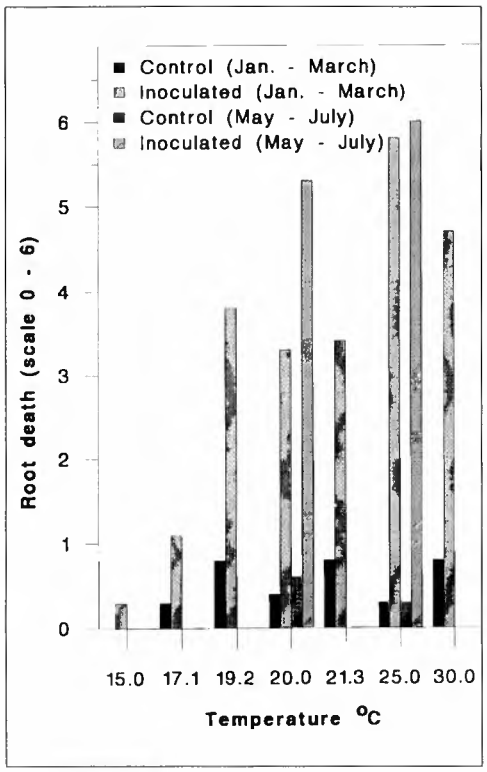

Fig. 1 Effect of temperature [(constant 15, 20, 25 or 30 °C or diurnal fluctuating 20/15 (=17.1 °C), 25/15 (=19.2 °C) or 30/15 (=21.3 °C)] on root death of Hedera helix 'Ester' without (control) or with inoculum of Phytophthora palmivora in the nutrient solution, scale 0-6 (0 = healthy, 6 = dead roots).

Dry weight of inoculated plants was reduced markedly at 25/25°C and 30/30 °C compared to the control plants, especially at 25°C at which uninoculated plants reached the highest dry weight (Fig. 2). At 25/15°C or 30/15°C the dry weight decreased with 26 and 33%, respectively. The reduction in dry weight at 20/20°C or 20/15°C was 15%. The fungus did not affect dry weight on plants grown at 15°C. On average, for all temperature treatments dry weight decreased 28% and fresh weight 36% on plants inoculated with P. palmivora compared to the control plants.

Number of wilted plants were correlated with root rot. Fresh weight of the plants showed the same pattern as dry weight. Plant vines were 25% shorter as an average for all temperature treatments on inoculated plants compared to the control (Fig. 3). Number of lateral side shoots on vines, longer than one cm, decreased 44% on inoculated plants. At average temperatures from 19.2 to 30 °C

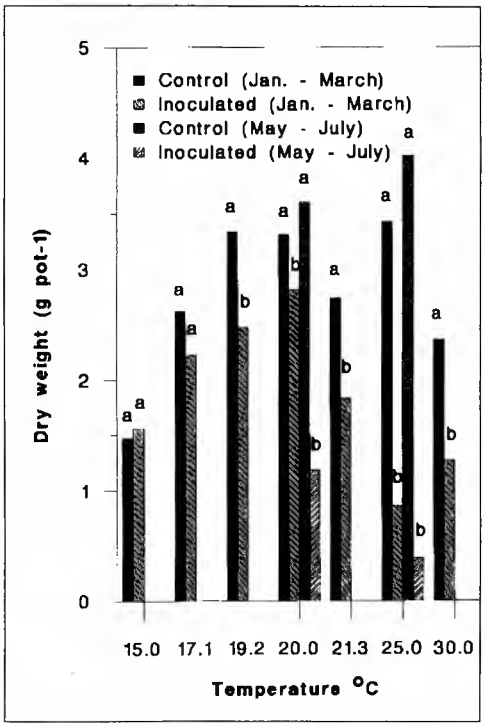

Fig. 2 Effect of temperature [(constant 15, 20, 25 or 30 °C or diurnal fluctuating 20/15 (=17.1 °C), 25/15 (=19.2 °C) or 30/15 (=21.3 °C)] on dry weight of vines of Hedera helix 'Ester' without (control) or with inoculum of Phytophthora palmivora in the nutrient solution. Dry weight was statistical tested at each level of temperature.

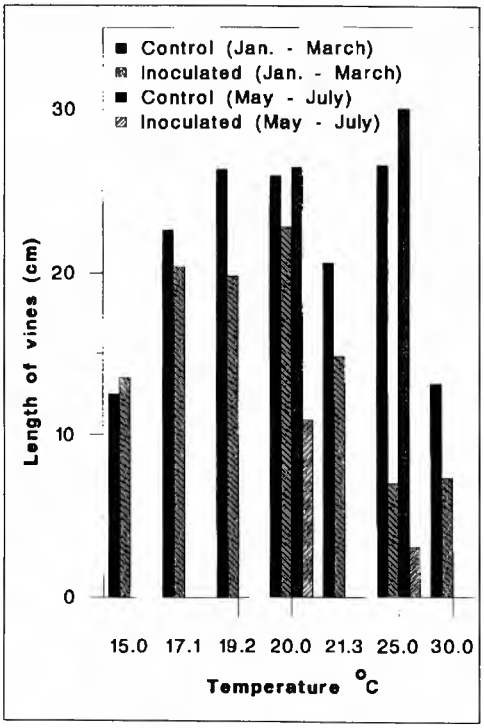

Fig. 3 Effect of temperature [(constant 15, 20, 25 or 30 °C or diurnal fluctuating 20/15 (=17.1 °C), 25/15 (=19.2 °C) or 30/15 (=21.3 °C)] on length of vines of Hedera helix 'Ester' without (control) or with inoculum of Phytophthora palmivora in the nutrient solution.

number of side shoots decreased from 87 to 99% on plants inoculated with P. *palmivora* compared to un - inoculated. Pictures of the plants inoculated with *P. palmivora* compared to the control are shown at constant temperature treatments (Fig. 4).

Experiment 2 (summer): Inoculated plants had much more root rot, and dry weight and length of vines decreased at the two temperature treatments (20/20 and 25/25°C) compared to control plants (Fig. 1, Fig. 2 and Fig. 3). Plants not inoculated with *P. palmivora*, had good root quality and made good growth.

Discussion

The optimum temperature for growth of *P.palmivora* was also the optimum temperature (25°C) for injury of the plants. When the plants had been grown at 20 or 30°C, sub optimal temperatures for the fungus, injury to the plants was a lot less than for plants grown at 25°C.

Fig. 4 Effect of 4 constant temperatures on Hedera helix 'Ester' without (usmitta) and with (Algesopp) inoculum of Phytophthora palmivora in the nutrient solution. Photo 54 days after start of experiment 1.

At 20°C, the dry weight of inoculated plants was reduced by 15% in the winter experiment and 67% in the summer experiment compared to the controls. This difference can be due higher irradiation (Rocha and Machado, 1973) and some higher leaf temperature in the middle of the day during part of the summer experiment.

Ivy grows well at 19-20°C and using lower temperature to reduce the injury of *P. palmivora* is not a good strategy in commercial ivy production, because lower temperatures reduce plant growth too much.

It is a general view that wet growing media often give conditions for attack of phycomycetes. In this experiment sub irrigation was used and all treatments were kept rather wet. Dead roots were first observed in the lower part of the pot at high temperature, while there were still healthy roots in the upper part. This can be because the lower part is wetter than the upper part because of the physical characteristics of the medium and/or that there was a heavier inoculum pressure of *P. palmivora* in the lower part of the medium because of the watering system.

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Juvenility and flowering in *Festuca pratensis* Huds.
1. Effects of plant age, cultivar and duration of primary induction treatments

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The effects of plant age (2, 4 and 6 weeks from seedling emergence) on the receptiveness to primary induction (6°C and natural short days for 12, 15 and 18 weeks) were studied in three Scandinavian cultivars of *Festuca pratensis* Huds. Tillering, leaf area expansion and the increase in plant dry weight and the content of water soluble carbohydrates during primary induction were studied and related to reproductive development after exposure to 15°C and continuous light (secondary induction). The experiment gave no indication of a distinct juvenile stage in seedlings of *Festuca pratensis*. The percentage of heading plants tended to decrease with increasing plant age at the shortest induction treatment and was generally more affected by the duration of primary induction than by plant age prior to induction. While a high proportion of tillers in the oldest plants remained vegetative after secondary induction, tillers that were laid down during primary induction usually flowered in the youngest plants. This suggests that flowering hormone(s) may be diluted in older plants and that tillers of *Festuca pratensis* have no, or a very short, juvenile stage. The north Norwegian cultivar 'Salten', which gives relatively low seed yields in commercial seed production, had less vigorous vegetative growth and developed fewer panicles per plant and shorter inflorescences than the south Norwegian cultivar 'Fure' and the Danish cultivar 'Senu Pajbjerg'.

Key words: Carbohydrates, dry weight, *Festuca pratensis*, flowering, growth rate, induction, juvenility, leaf area, meadow fescue, seed production.

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Juvenility in annual and perennial plants is often defined as the period after germination during which plants are unable to respond to flower induction stimuli (Salisbury & Ross 1985). However, Calder (1966) and Kleinendorst (1974) raised the question of whether juvenility in grass plants is a property of each individual tiller or of the plant as a whole. If each tiller, and not the entire plant, has to pass the juvenile stage, Salisbury and Ross' definition of juvenility may well be imprecise for grasses.

Most investigators have described juvenility in grasses as a property of the entire plant (e.g. Bean 1970; Calder 1963;

Cooper & Calder 1964; Heichel et al. 1980; Heide 1987; Heide 1994; Hare 1993; Hare 1994; Kozumplik & Christie 1972; Niemeläinen 1990). These studies show that the length of the juvenile stage in grass seedlings varies considerably and may also be absent in some species, such as *Lolium perenne*, which is able to respond to inductive stimuli already as germinating seeds (Cooper 1960).

Meijer (1984), on the other hand, used the juvenility concept on a tiller basis. He argued for the presence of a juvenile stage in tillers of *Poa pratensis* and *Festuca rubra* because tillers that emerged in less than 2 and 5 weeks, respectively, before the primary induction treatment did not become reproductive. Also Borg (1982) used juvenility on a tiller basis and stated that every newly developed tiller of *Poa pratensis* had to go through a juvenile stage.

The question of whether or not floral induction stimuli can be translocated from mother to daughter tillers, is fundamental for our understanding of juvenility in grasses. Most authors seem to agree that each individual tiller must be induced separately. This corresponds with the results by Garner & Loomis (1953), who found no translocation of induction stimuli within sods of *Dactylis glomerata*. On the contrary, Ikegaya (1984), working with the same species, reported that the induction stimuli of the main stem could be transferred to apices of lateral tiller buds at least in some cultivars. The possibility of translocation was also mentioned by Jewiss (1966), who argued that the flowering response could be transmitted from one single induced tiller to other tillers held under non-inductive conditions.

Theoretically, translocation may be possible because of the close vascular connection between parent and daughter tillers. Newly developed tillers are, according to Jewiss (1966) and Langer (1972), dependent on an external supply of minerals and carbohydrates from the main shoot until they have developed their own adventitious roots and produced 4-5 leaves. However, if translocation of inductive stimuli from mother to daughter tillers is possible, it makes little sense to define juvenility on a tiller basis.

Many attempts have been made to describe juvenility by means of morphological characteristics. Calder (1963) and Heide (1987) related juvenility in seedlings of *Dactylis glomerata* to leaf area. Leaf number and leaf area were also used by Bean (1970), who suggested that seedlings of *Festuca pratensis* need at least 4-5 leaves (25 cm^2 leaf area) in order to respond to floral induction. Since increasing light intensity is known to shorten the juvenile stage in the dicotyledonous species *Lunaria biennes*, carbohydrate content has also been suggested as a factor controlling the length of the juvenile stage (Wellensiek & Higazy 1961). Other possible characteristics include tiller age, apex size and the number of plastochrone cycles (Calder 1966; Cooper & Calder 1964).

Unless information on the dates of tiller emergence is provided, results concerning the length of the juvenile stage must always be interpreted in light of the subsequent induction treatment. For example, Kozumplik & Christie (1972) found that seedlings of *Dactylis glomerata* were not receptive to induction until eight leaves had appeared on the main shoot. This surprisingly high leaf number required for induction was probably due to the fact that plants were exposed to primary induction (10 h photoperiod and 10°C) for six weeks only. Any extension of the primary induction period would probably have shown smaller

tillers to enter a generative development, as demonstrated by Heide (1987).

In order to obtain further information about juvenility in *Festuca pratensis*, an experiment concerning the effect of plant age on the receptiveness to primary induction was carried out. Various genotypes were included because of the wide divergence in primary induction requirements found by Heide (1988a). An additional objective of the experiment was to find physiological explanations for the variation in seed yield among three Scandinavian cultivars of this species.

Material and methods

The experiment was carried out at the Norwegian Crop Research Institute, division Landvik and the Ås phytotron, during September 1993 through May 1994. Two Norwegian and one Danish cultivar of *Festuca pratensis* were used. Seeds of the two Norwegian cultivars 'Salten' (origin 67°N) and 'Fure' (origin 61°N) were obtained from the Basic Seed Centre (Skjetten, Norway), while seeds of the Danish cultivar 'Senu Pajbjerg' (origin 56°N) were obtained from the commercial Danish seed company DLF Trifolium.

Three groups of plants were sown at fortnightly intervals, from 2 to 29 September. Each group comprised 60 pots of each cultivar. The pots, which had a diameter of 8 cm, were filled with a mixture of 85% peat and 15% sand. The seedlings were thinned to one plant per pot after emergence and then grown in continuous light (150 µmol $m^{-2}s^{-1}$ from TL-33 fluorescent tubes) at 20°C for 2, 4 and 6 weeks from seedling emergence before transfer to primary induction on 19 October. The primary induction treatment was conducted in a phytotron compartment with natural daylight supplemented by 115 µmol $m^{-2}s^{-1}$ from high pressure mercury lamps (Philips HPI-T 400 W) for 8h per day. The temperature during primary induction was 6°C.

At the start of primary induction and again after 9 and 18 weeks of induction, 30 plants per cultivar (10 from each plant age) were sampled destructively and the following characters were recorded :

1. Plant height as measured to the top of the youngest fully expanded leaf on the main tiller (cm).
2. The number of visible tillers with base diameter < 1 mm, 1-1.5 mm, 1.5-2 mm, 2-3 mm, 3-4 mm and > 4 mm. (Tiller diameter was measured with a slide calliper 0.5 - 1 cm above tiller basis.)
3. Number of leaves with laminae longer than 1 cm above sheath of preceding leaf.
4. Leaf area (laminae) (cm^2).
5. Dry weight of shoots and roots) (g).
6. Percentage of water soluble carbohydrates (WSC) in the dry matter of shoots and roots.

Remaining plants (270 in total) were transplanted into 12-cm pots and transferred to secondary induction, at 15°C and continuous light (200 µmol $m^{-2}s^{-1}$ from TL-33 fluorescent tubes) after 12, 15 or 18 weeks of primary induction.

Percentage of flowering plants and the number of panicles per plant were used as the main criteria for flowering, while the number of days to heading of the first panicle was used as a criterion for the rate of flower development. In addition, culm length and inflorescence length were measured for the main reproductive tiller on each plant.

For vegetative characters recorded before or during primary induction, separate analyses of variance were carried out for each length of induction treatment.

For flowering characters, an overall analyses was conducted to examine the main effects of length of induction treatment, plant age prior to induction and cultivar, as well as their interactions. All analyses of variance were performed according to the procedure PROC GLM (Statistical Analysis System 1987). Significant differences were separated by $LSD_{0.05}$.

A traditional growth analysis (Radford 1967) for the primary induction period was based on leaf area and dry weight recordings after 0, 9 and 18 weeks of induction. In this analysis the main effects of plant age and cultivar were tested against their interaction.

In order to find the best morphological indicator of juvenility, an analysis of multiple regression was performed with the procedure PROC REG (Statistical Analysis System 1987). The models were set up to explain percentage of heading plants and the number of panicles per plant after 12, 15 and 18 weeks of induction by morphological characters recorded at the start of induction. Since the independent and dependent variables could not be determined on the same plants, these regression models were based on average values for each combination of cultivar and plant age (means of ten plants).

Results

Plant status at the start of primary induction.

Plant height

On average for cultivars, the 4-week-old plants were twice as tall, and the 6-week-old plants three times taller than the youngest plants at the start of primary induction (Table 1). Plants of 'Fure' were significantly taller than plants of 'Senu Pajbjerg'.

Number of tillers and tiller size

The number of tillers per plant in all cultivars was found to increase with increasing plant age (Table 1), the average tiller number being significantly higher in 'Fure' than in the other cultivars (Table 1).

Tiller base measurement showed that 93% of the tillers of the 2-week-old plants were less than 1.5 mm wide at the start of primary induction. The corresponding figures for 4- and 6-week-old plants were

Table 1. Effects of plant age (2, 4 and 6 weeks) and cultivar ('Fure', 'Salten' and 'Senu Pajbjerg') on plant height, tiller number per plant, leaves per plant, leaves per tiller, leaf area per plant (cm^2), leaf area per tiller (cm^2) and area per leaf (cm^2) at the start of primary induction. Means of 30 plants per treatment

Plant age/ cultivar	Plant height	Tillers per plant	Leaves per plant	Leaves per tiller	Leaf area per plant	Leaf area per tiller	Area per leaf
2	16.7	2.1	5.0	2.5	6.1	2.9	1.2
4	32.1	5.7	14.0	2.5	47.0	7.9	3.3
6	49.9	14.6	38.5	2.6	205.2	14.0	5.3
Fure	34.5	8.4	21.6	2.6	105.1	9.2	3.6
Salten	32.8	7.1	18.5	2.5	67.5	7.1	2.7
Senu P.	31.4	6.9	17.4	2.5	85.7	8.6	3.6
$LSD_{0.05}$ [1)]	1.8	1.3	3.5	n.s	24.1	1.8	1.0

[1)] LSD for comparison of main effects of cultivars and plant ages.

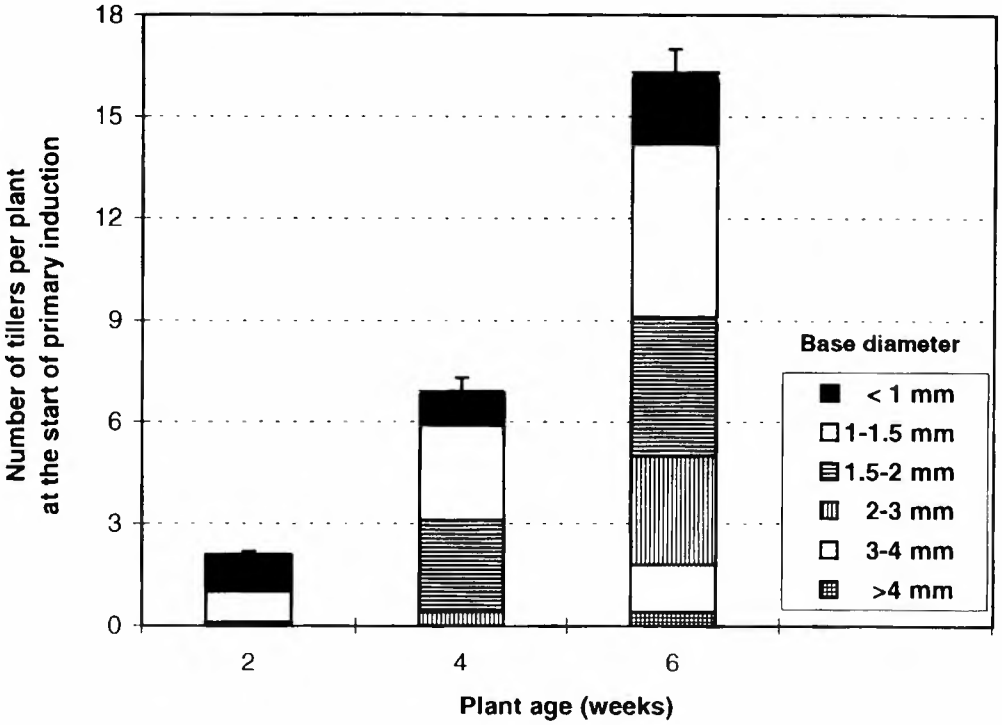

Fig. 1. The effect of plant age (2, 4 and 6 weeks) on the number and size distribution of tillers per plant at the start of primary induction. Average of three cultivars. Bars represent 1 SE for total tiller number

63 and 40%, respectively (Fig. 1). Classification of tillers according to diameter revealed no significant differences among cultivars.

Leaf number and leaf area

On average for all cultivars, an increasing plant age corresponded with a rise in the number of leaves per plant and with an increase in the area per plant, tiller and leaf. By contrast, the number of leaves per tiller was virtually unaffected by plant age and cultivar (Table 1).

On average for plant ages, 'Fure' had the highest number of leaves as well as the largest leaf area per plant and per tiller at the start of primary induction. The difference between 'Fure' and 'Salten' was significant for all of these parameters, 'Senu Pajbjerg' ranking mid-way between the two Norwegian cultivars. The number of leaves per tiller and area per leaf was not significantly influenced by cultivar, although the leaves tended to be smaller in 'Salten' than in 'Fure' and 'Senu Pajbjerg'.

Dry weight and carbohydrate content

Shoot dry weight closely reflected leaf area and the number of tillers and leaves per plant. On average for cultivars, the plants increased their total dry weight from 0.034 g per plant after 2 weeks to 0.35 and 2.1 g per plant after 4 and 6 weeks, respectively. Approximately 89% of total plant dry weight was found in the shoots after 2 weeks compared with 86

and 82% after 4 and 6 weeks, respectively. On average for plant ages, 'Fure' tended to have a higher total dry weight per plant than 'Salten' and 'Senu Pajbjerg' (Table 2).

The total amount of water soluble carbo-hydrates (WSC) increased, both on plant basis (data not shown) and tiller basis (Table 2), with increasing plant age. This was mainly a result of higher dry weight, but on average for all cultivars, 6-week-old plants also had a higher concentration of WSC in the dry matter of shoots and especially roots than younger plants (Table 2). 'Fure' and 'Salten' had significantly higher concentrations of WSC in root dry matter than 'Senu Pajbjerg'. 'Fure' also tended to have the highest carbohydrate content in mg per tiller (Table 2).

Plant growth during primary induction

Plant height

No distinct change in plant height was recorded in the 2-, 4- and 6-week-old plants during primary induction (Table. 3, cf. Table. 1). 'Fure' continued to be the tallest cultivar, but the difference from 'Senu Pajbjerg' was not significant after 18 weeks (Table 3).

Tiller number and size

The total number of tillers per plant increased, on average for plant ages and cultivars, from 7.5 at the start of primary induction to 17.6 and 36.8 after 9 and 18 weeks of induction, respectively. The 4- and 6-week-old plants had a higher tillering rate than the 2-week-old plants during the induction period (Fig. 2a). The highest tillering rate among cultivars was recorded in 'Senu Pajbjerg'. (Fig. 2b).
On average for cultivars and plant ages, the percentage of tillers with a base diameter greater than 2 mm increased from 23% at the start of primary induction to 50% after 18 weeks. The highest proportion of large tillers (> 2 mm) was found in the oldest plants (6 weeks) after both 9 and 18 weeks of induction (Fig. 3). No significant difference in tiller size was discovered among cultivars.

Leaf number and leaf area

The leaf number and leaf area per plant and per tiller increased with increasing length of primary induction in all plant ages and cultivars. The strongest response among cultivars was recorded in 'Senu Pajbjerg'. After 18 weeks of induction, on average for plant ages, the Danish cultivar had 31 and 48% more leaves per plant and a 42 and 118% larger leaf area per plant than 'Fure' and 'Salten', respectively (Table 3).

The number of leaves per tiller increased during the last 9 weeks of induction. However, as the number of leaves per tiller increased, the area per leaf became smaller, particularly in the oldest plants (Fig. 4). 'Salten' had the smallest leaves among cultivars after 18 weeks of induction (Table 3).

Dry weight and carbohydrate

The dry weight of roots and shoots increased during primary induction (Table 4, cf. Table 2). On average for plant ages and cultivars, 18% of total plant dry weight was found in the roots at the start of induction compared with 35 and 46% after 9 and 18 weeks, respectively. Among cultivars, the lowest total dry weight after 9 and 18 weeks was recorded in 'Salten' (Table 4), and this cultivar also had the lowest shoot/root ratio after 18 weeks.

Total plant dry matter, averaged for plant ages and cultivars, contained 12.5% carbohydrates at the start of primary induction compared with 26.8 and 28.2% after 9 and 18 weeks, respectively. However, a higher proportion of total plant

Table 2. Effects of plant age (2, 4 and 6 weeks) and cultivar ('Fure', 'Salten' and 'Senu Pajbjerg') on dry weight in shoots and roots (g), per cent water soluble carbohydrate (WSC) in shoot and root dry matter and the WSC content (in shoots and roots) calculated per tiller (mg) at the start of primary induction. Means of 30 plants per treatment

Plant age/ cultivar	Dry weight, shoot, g	Dry weight, root, g	% WSC, shoot	% WSC, root	WSC per tiller, mg
2	0.03	0.004	12.2	1.4	1.9
4	0.31	0.05	10.3	1.4	5.5
6	1.73	0.39	15.0	4.8	19.2
Fure	0.78	0.17	12.9	3.0	9.6
Salten	0.62	0.16	12.0	2.5	8.2
Senu P.	0.67	0.11	12.6	2.1	8.8
$LSD_{0.05}$ [1)]	0.18	0.04	2.0	0.3	2.0

[1)] LSD for comparison of main effects of cultivars and plant ages.

Table 3. Effects of plant age (2, 4 and 6 weeks at the start of primary induction) and cultivar ('Fure', 'Salten' and 'Senu Pajbjerg') on plant height (cm), number of leaves per plant, leaves per tiller, leaf area per plant (cm^2) , leaf area per tiller (cm^2) and area per leaf (cm^2) after 9 and 18 weeks of primary induction. Means of 30 plants per treatment

Prim. ind. (weeks)	Plant age/ cultivar	Plant height	Leaves per plant	Leaves per tiller	Leaf area per plant	Leaf area per tiller	Area per leaf
9	2	16.7	16.2	2.6	19.0	2.9	1.1
	4	36.3	49.1	2.6	153.4	8.3	3.1
	6	52.5	69.8	2.5	373.5	13.7	5.6
9	Fure	37.0	45.7	2.7	191.9	9.3	3.5
	Salten	33.1	38.5	2.4	156.9	7.0	3.1
	Senu P.	34.7	50.8	2.7	197.1	8.6	3.2
$LSD_{0.05}$ [1)]		2.3	7.0	0.2	30.2	1.4	0.6
18	2	17.2	54.4	3.7	77.7	4.8	1.3
	4	35.6	138.7	3.4	244.9	5.8	1.7
	6	51.8	164.0	3.0	448.3	8.4	2.8
18	Fure	35.9	111.9	3.4	251.3	6.8	2.0
	Salten	32.9	98.8	3.3	163.4	4.5	1.4
	Senu P.	35.3	146.4	3.3	356.0	7.8	2.3
$LSD_{0.05}$ [1)]		2.6	17.3	0.2	45.4	1.9	0.4

[1)] LSD for comparison of main effects of cultivars and plant ages.

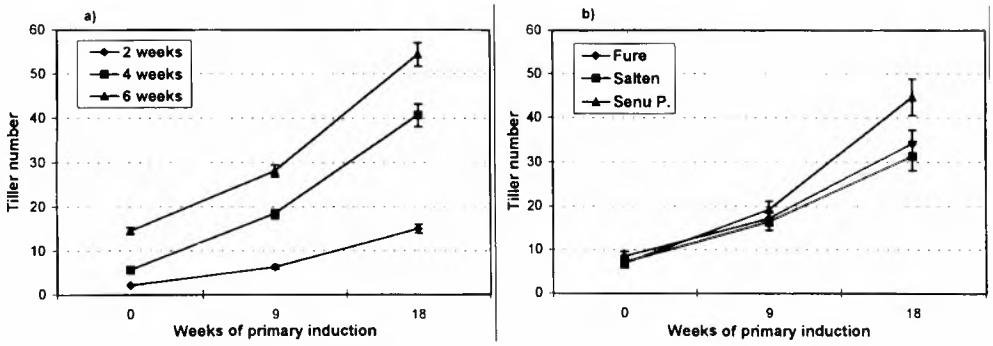

Fig. 2. Increase in total tiller number per plant as affected by (a) plant age prior to induction (2, 4 and 6 weeks), and (b) cultivar ('Fure', 'Salten' and 'Senu Pajbjerg'). Means of 30 plants per treatment. Bars represent ± 1 SE

carbohydrates was found in the roots after 18 weeks of induction compared with after 9 weeks. On average for plant ages, 'Salten' had the highest percentage of carbohydrates in roots and shoots both halfway through and at the end of the induction treatment. Calculations made after 9 and 18 weeks revealed that 'Fure' had the highest carbohydrate content per tiller (Table 4).

All the interactions between plant age and cultivar at the start of and during primary induction were either insignificant or gave little information in addition to that of main effects.

Growth analysis

Plants that were 6 weeks old at the start of primary induction had a lower relative growth rate (RGR) during the first 9 weeks of induction than 4-week-old plants. While the RGR of 2- and 4-week-old plants did not differ significantly during this first period, both the leaf area ratio (LAR) and net assimilation rate (NAR) tended to be higher in the youngest plants during the last nine weeks of induction, resulting in a significantly higher RGR. 'Senu Pajbjerg' tended to have a higher relative growth rate (RGR) than the Norwegian cultivars during the first nine weeks of induction (Table 5).

Flowering

Percentage of heading plants

The percentage of heading plants was lower after 12 weeks of induction than after 15 and 18 weeks (Table 6). Although the main effect of plant age was not significant, the 2-week-old plants had a higher percentage heading than the 4- and 6-week-old plants after 12 weeks of induction (Fig. 5a). However, after 15 and 18 weeks 90-100% of the plants headed, irrespective of plant age. Neither the main effect of cultivar nor the interactions cultivar* length of induction treatment and cultivar* plant age were significant.

The number of panicles per plant

The 18 weeks' induction period enabled the greatest number of tillers to become reproductive. After this period, on average for plant ages and cultivars, plants developed 88 and 5% more panicles per plant than after 12 and 15 weeks of induction, respectively (Table 6).

The number of reproductive tillers per

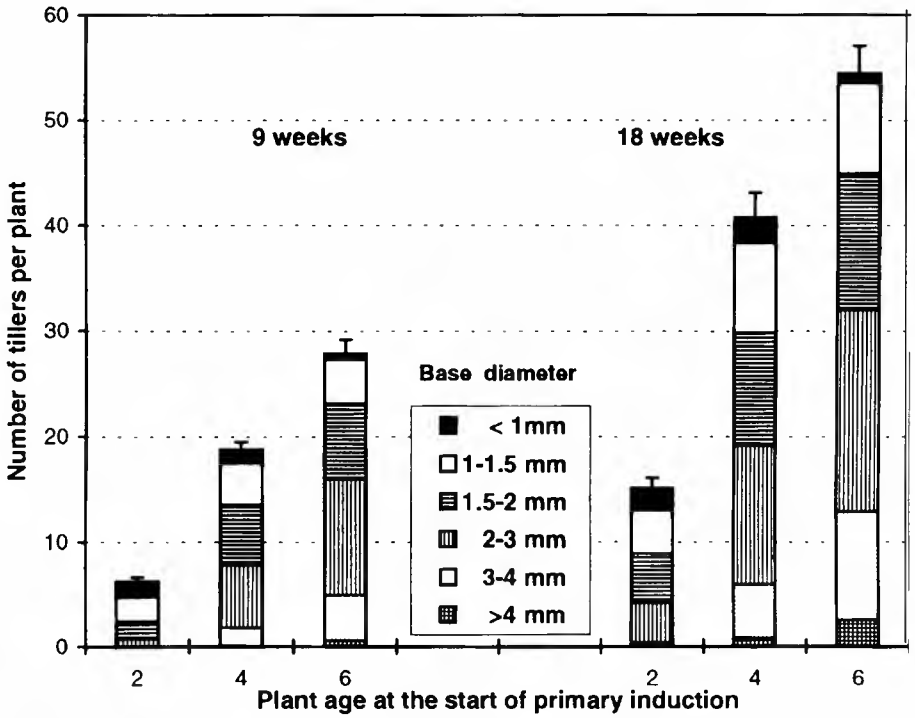

Fig. 3. The effect of plant ages at the start of primary induction (2, 4 and 6 weeks) on the number and size distribution of tillers per plant after 9 and 18 weeks of primary induction. Average of three cultivars. Bars represent 1 SE for total tiller number

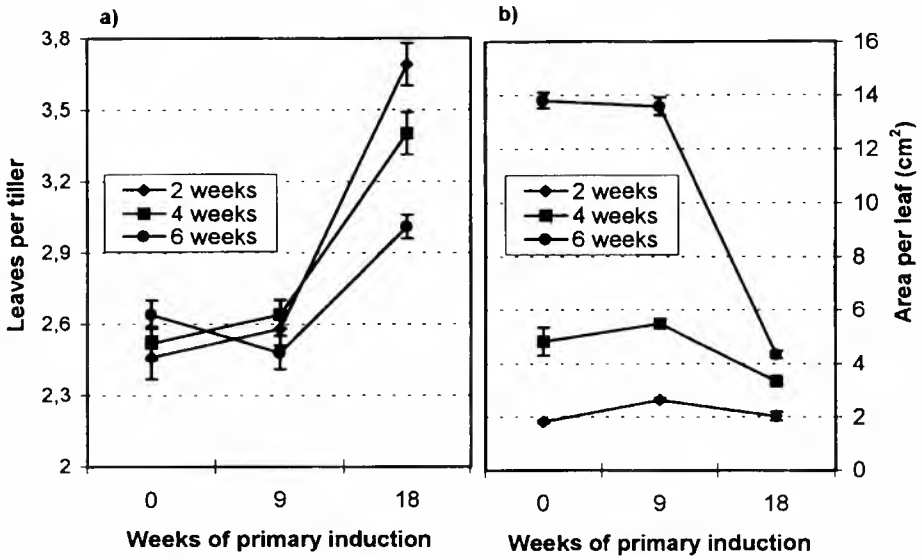

Fig. 4. The number of leaves per tiller (a) and area per leaf (b) as affected by plant age prior to induction (2, 4 and 6 weeks) and duration of primary induction (0, 9 and 18 weeks). Means of 30 plants per treatment. Bars represent ± 1 SE

Table 4. Effects of plant age (2, 4 and 6 weeks at the start of primary induction) and cultivar ('Fure', 'Salten' and 'Senu Pajbjerg') on dry weight in roots and shoots (g), percentage of water soluble carbohydrates (WSC) in shoots and roots (% of dry matter) and WSC content (in shoots and roots) calculated per tiller (mg) after 9 and 18 weeks of primary induction. Means of 30 plants per treatment

Prim. ind. (weeks)	Plant age/ cultivar	Dry weight, shoots, g	Dry weight, roots, g	% WSC, shoots	% WSC, roots	WSC per tiller, mg
9	2	0.2	0.05	22.9	7.0	6.5
	4	1.4	0.8	23.7	27.7	30.3
	6	4.2	2.3	25.9	30.8	67.9
9	Fure	2.1	1.2	24.7	22.2	41.2
	Salten	1.8	0.9	27.6	26.1	35.7
	Senu P.	2.0	1.0	20.0	17.3	32.4
$LSD_{0.05}$ [1]		0.3	0.2	0.8	2.5	6.0
18	2	0.6	0.3	13.0	30.1	11.9
	4	3.1	2.0	22.5	34.2	33.4
	6	6.7	4.5	28.3	31.6	63.7
18	Fure	3.6	2.31	21.9	32.5	41.0
	Salten	2.6	2.0	22.7	35.8	35.7
	Senu P.	4.3	2.5	19.3	27.7	32.4
$LSD_{0.05}$ [1]		0.6	0.3	1.3	1.6	5.9

[1] LSD for comparison of main effects of cultivars and plant ages.

plant was also strongly affected by plant age prior to induction. On average for cultivars and induction periods, plants that were 6 weeks old at the start of primary induction developed 95 and 28% more panicles per plant than the 2- and 4-week-old plants, respectively (Table 6). 'Salten' had significantly fewer panicles per plant than 'Fure' and 'Senu Pajbjerg'.

A significant interaction between plant age and length of primary induction revealed that the effect of plant age on panicle number was most marked after 15 weeks of induction (Fig. 5b).

Days to heading

On average for plant ages and cultivars, increasing the length of primary induction from 12 to 18 weeks decreased the time to heading by approximately 10 days. As a main effect, increasing the plant age prior to induction delayed reproductive development, while the effect of cultivar was not significant.

After 12 weeks of induction, the 2-week-old plants headed 6 and 13 days earlier than the 4- and 6-week-old plants, respectively. A similar tendency in differences between plant ages was noted after 15 weeks, but after 18 weeks the 2-, 4- and 6-week-old plants headed almost simultaneously (Fig. 6).

The two-factor interaction between cultivar and induction period was also significant in that 'Senu Pajbjerg' needed a longer time to heading than the Norwegian cultivars after 12 weeks of induction, whereas there was little difference between cultivars after 15 and 18 weeks (data not shown). No significant interaction between plant age and cultivar was discovered.

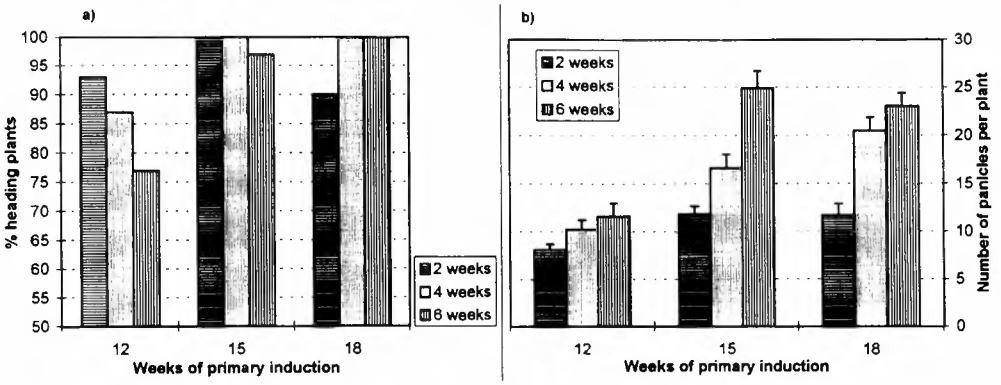

Fig. 5. Percentage of heading plants (a), and the number of panicles per plant (b), as affected by plant age prior to induction (2, 4 and 6 weeks) and primary induction duration (12, 15 and 18 weeks). Means of 30 plants per treatment. Bars in Fig. 5b represent 1 SE

Culm length

The culm length tended to increase with increasing length of induction (Table 6). 'Salten' developed shorter culms than 'Fure', on average for plant ages and induction periods (Table 6). Culm length was not affected by plant age prior to induction. The two-factor interactions were not significant for this character.

Length of the inflorescence

Contrary to culm length, inflorescence length decreased with increasing length of primary induction. On average for cultivars and plant ages, plants receiving 18 weeks of induction had 5.1 cm shorter inflorescences than plants receiving 12 weeks of induction. As a main effect inflorescence length also decreased with increasing plant age up to 4 weeks (Table 6). However, a significant interaction between plant age and induction period indicated that the 2-week-old plants had longer inflorescence than the 4- and 6-week-old plants only after 12 weeks (Fig. 7). When induction was prolonged inflorescences became shorter and after 18 weeks no difference in inflorescence length between plant ages was detectable.

On average for plant ages and induction periods, 'Salten' developed significantly shorter inflorescences than 'Fure' and 'Senu Pajbjerg' (Table 6).

The two-factor interactions between plant age and cultivar and between cultivar and induction period were either insignificant or not particularly meaningful.

Relationship between vegetative development before primary induction and flowering

Significant positive correlations (r = 0.9 or higher) were established among most of the vegetative characters at the start of primary induction (Table 7).

The analyses of regression revealed a strong relationship between the size of the individual tillers at the start of induction and the number of panicles per plant. The strongest influence was exerted by the average leaf area per tiller. Approximately 52, 92 and 78% of the variation in panicle number per plant after 12, 15 and 18 weeks of induction could be explained by this character alone (Fig. 8). Stepwise

Table 5. Effects of plant ages (2, 4 and 6 weeks at the start of primary induction) and cultivars ('Fure', 'Salten' and 'Senu Pajbjerg') on relative growth rate (RGR), net assimilation rate (NAR) and leaf area ratio (LAR) during the first (0-9 weeks) and second periods (9-18 weeks) of primary induction

	Period 1			Period 2		
Plant age/ cultivar	RGR (weeks)	NAR (mg cm^{-2} $week^{-1}$)	LAR (cm^2 mg^{-1})	RGR (weeks)	NAR (mg cm^{-2} $week^{-1}$)	LAR (cm^2 mg^{-1})
2 weeks	0.18	1.64	0.11	0.17	2.28	0.08
4 weeks	0.21	2.34	0.09	0.09	1.57	0.06
6 weeks	0.13	1.77	0.07	0.06	1.26	0.05
Fureq	0.17	1.95	0.09	0.09	1.51	0.06
Salten	0.15	1.88	0.09	0.11	1.94	0.05
Senu P.	0.20	1.93	0.10	0.12	1.67	0.07
$LSD_{0.05}$ [1)]	0.06	0.89	0.03	0.08	1.71	0.02

[1)] LSD for comparison of main effects of cultivars and plant ages.

Table 6. Main effects of duration of primary induction periods (12, 15 and 18 weeks), plant ages (2, 4 and 6 weeks at the start of primary induction) and cultivars ('Fure', 'Salten' and 'Senu Pajbjerg') on the percentage of heading plants, panicles per plant, days to heading, culm length (cm) and inflorescence length (cm). Means of 90 plants per treatment

	% heading plants	Panicles per plant	Days to heading	Culm length	Infloresc. length
12 weeks	86	9.9	42.1	121.0	22.8
15 weeks	99	17.7	33.4	123.3	19.3
18 weeks	97	18.6	32.5	127.0	17.9
2 weeks	94	10.5	33.4	122.7	21.0
4 weeks	96	16.0	36.3	126.1	19.4
6 weeks	91	20.5	37.6	122.8	19.3
Fure	96	16.7	35.2	128.8	20.8
Salten	91	13.4	35.2	119.0	18.4
Senu P.	94	16.7	36.9	123.6	20.5
$LSD_{0.05}$ [1)]	7	1.9	2.0	6.3	1.5

[1)] LSD for comparison of mean effects of induction periods, plant ages and cultivars.

regression did not reveal any additional character that might increase these coefficients of determination (r^2) significantly. The analyses showed that as the average leaf area per tiller prior to induction increased by 1 cm^2, the number of panicles per plant increased by 0.3, 1.2 and 1.0 after 12, 15 and 18 weeks of induction, respectively. Other characters that well described the number of panicles per plant, but with a lower coefficient of determination (r^2), were the average area per leaf and the average shoot dry weight per tiller. Surprisingly, the number of tillers per plant prior to induction, either as a total or in different categories according to base dia-

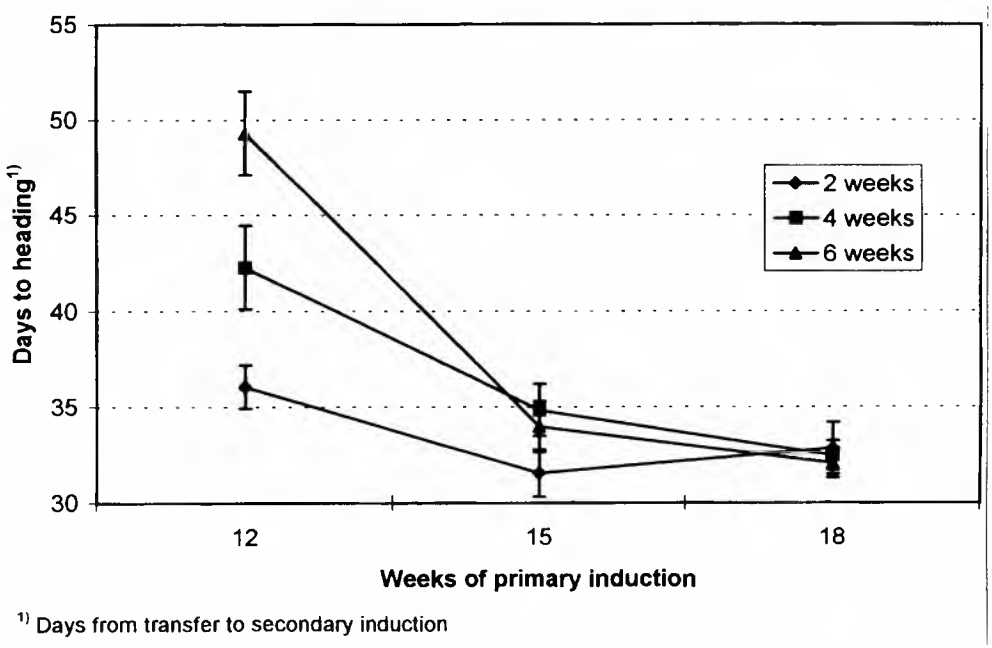

Fig. 6. The effect of plant age (2, 4 and 6 weeks) and induction periods (12, 15 and 18 weeks) on the number of days to heading. Means of 30 plants per treatment. Bars represent ± 1 SE

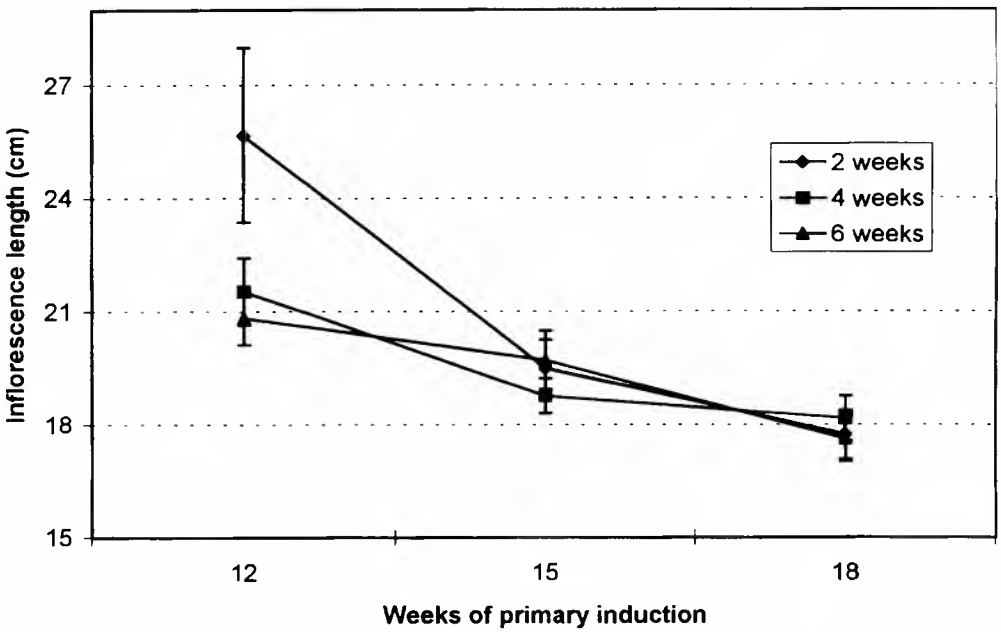

Fig. 7. The effect of plant age (2, 4 and 6 weeks) and induction periods (12, 15 and 18 weeks) on inflorescence length (cm). Means of 30 plants per treatment. Bars represent ± 1 SE

Table 7. Simple correlation coefficients (r) between morphological characters at the start of primary induction

	Tiller number/ plant	Leaf number/ plant	Leaf area/ plant	Dry weight/ plant	WSC/ plant (mg)	Leaf number/ tiller	Leaf area/ tiller	WSC/ tiller (mg)
Tiller number plant/	*	0.998	0.987	0.989	0.973	0.618	0.967	0.982
Leaf number/ plant		*	0.980	0.991	0.974	0.661	0.958	0.985
Leaf area/ plant			*	0.986	0.983	0.550	0.960	0.984
Dry weight/ plant				*	0.995	0.618	0.934	0.999
WSC/plant (mg)					*	0.568	0.908	0.995
Leaf number/ tiller						*	0.580	0.610
Leaf area/ tiller							*	0.929
WSC/ tiller (mg)								*

meter, did not explain the subsequent panicle production as adequately as characters expressing average tiller size. No significant relationship between morphological characters at the start of induction and per cent heading plants was discovered.

Discussion

This experiment revealed that the effect of the duration of primary induction was more important than plant age at the start of induction for the number of heading plants (Table. 6). Heide (1988a) found that 16-20 weeks at 6°C in 10 h photoperiod were needed for 'saturation' of primary induction in three Scandinavian cultivars of *Festuca pratensis*. Also, Cooper & Calder (1964) classified Welsh cultivars of the same species as having an extreme induction requirement. In the present experiment induction was clearly marginal after 12 weeks, at this length of induction the percentage of heading plants in fact decreased with increasing plant age (Fig. 5a). However, after the plants had received a sufficient period of induction (15 and 18 weeks), 90-100% reached heading, irrespective of plant age. The analyses of regression did not reveal any significant relationship between morphological characters prior to induction and per cent heading plants. Consequently, no significant indication of a juvenile stage in seedlings of *Festuca pratensis*, as suggested by Bean (1970), was discovered.

As expected, the number of vegetative tillers that were able to respond to inductive stimuli increased with increasing

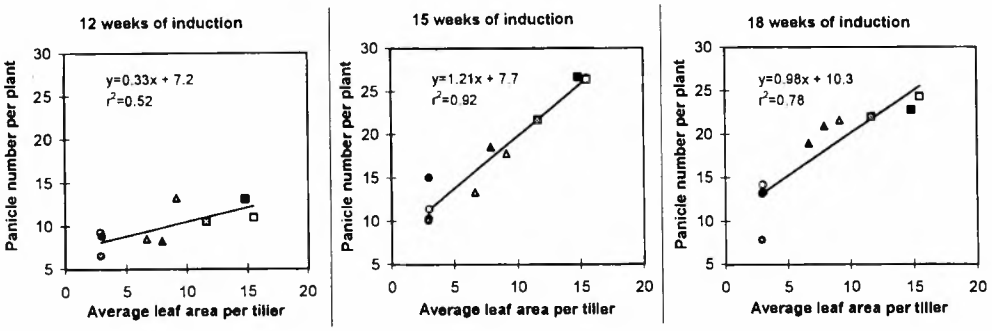

Fig. 8. Relationship between average leaf area per tiller at the start of induction and the number of panicles per plant after 12, 15 and 18 weeks' induction. (2-, 4- and 6- week-old plants at the start of primary induction are indicated by circles, triangles and squares, respectively. The cultivars 'Fure', Salten' and 'Senu Pajbjerg' are indicated by open, shaded and dark symbols, respec-tively)

plant age (Fig. 2a). This resulted in a higher panicle production in the oldest plants after 12, 15 and 18 weeks of induction (Table 6) and it appeared that the average leaf area per tiller was the vegetative character most closely associated with subsequent panicle production (Fig. 8).

However, the proportion of tillers present after 9 or 18 weeks of induction that ultimately flowered was higher in the younger plants. For example, after 18 weeks of primary induction 78, 50 and 42% of the tillers present at the onset of secondary induction became reproductive for the 2-, 4- and 6-week-old plants, respectively (Table 8). The high proportion of non-reproductive tillers in the oldest plants can not be explained either by insufficient leaf area (Table 3) or lack of carbohydrates (Table 4). The proportion of tillers with a wide base diameter also increased with increasing plant age (Figs. 1 and 3). This is clearly contradictory to the classical juvenility concept advocated by Calder (1966) and Bean (1970). The results in fact indicate that, at least in the smallest plants, tillers formed during primary induction had the same chance of becoming reproductive as tillers that were already present at the start of induction (Table 8). This can possibly be explained by the hypothetical flowering stimulus (florigen), which is produced in the leaves in response to photoperiodic induction and is transported via the phloem to the shoot apex, where it leads to evocation (Heide 1994). The florigenic signal(s) follows the carbohydrate stream from sources to sinks (Taiz & Zeiger 1991). Apices on small tillers that are not self-sufficient will be strong sinks for carbohydrates and will therefore also receive more florigen compared to apices situated on mature tillers. This might lead to a higher percentage of flower initiation in the non-mature small tillers. On the other hand, a general dilution of florigenic signals may explain the high percentage of non-reproductive tillers in the oldest plants. These results suggest that, at least when the conditions for primary induction are marginal, plants and tillers of *Festuca pratensis* may have an optimal age for transition from vegetative to reproductive development.

After 12 weeks of induction, the 2-week-old plants developed approximately 8 panicles per plant. However, only 6 vegetative tillers were registered in the youngest plants after 9 weeks of induction (Table 8). This indicates that tillers that were formed, or at least became visible, during the last 3 weeks of induction treatment became reproductive. Since the induction requirement, according to Heide (1988a) and Cooper & Calder (1964), far exceeds 3 weeks, these latest developed tillers must have been induced while still in the leaf sheath or as very young buds at the base of the parent shoot (Kleinendorst 1974). Alternatively, transmission of flowering stimuli from fully induced mother tillers to small undeveloped daughter tillers, as suggested by Ikegaya (1984) and Jewiss (1966), may have occurred. A different, but analogous situation was found in *Festuca vivipary* in which Heide (1988b, 1994) demonstrated that only viviparous plantlets, which were still attached and thus received flowering stimuli from the parent plant, became reproductive. By contrast, detached viviparous plantlets remained vegetative, even after extended primary induction treatments with low temperature and short days. Although these suggestions require further investigation, the possibility of transfer of flowering stimuli from mother to daughter tillers raises the question of whether it is at all relevant to talk about a juvenile stage in individual tillers of *Festuca pratensis*.

Increasing the length of primary induction increased the number of panicles per plant, on average for plant ages and cultivars (Table 6). However, while 4-week-old plants exhibited an almost linear increase in panicle production with increasing length of induction, 2- and 6-week-old plants appeared to be saturated after 15 weeks. For the oldest plants, this result may possibly be explained by lack of space and reduced light intensity because of mutual shading after the last plants had been transferred to the secondary induction chamber. Ryle (1966) found that a reduction in light intensity to 50% of full daylight reduced the number of panicles in plants of *Festuca pratensis* by approximately 40%.

The number of days to heading was influenced by both plant age prior to induction and the duration of the primary induction treatment. After 12 weeks of induction the main tillers of 2-week-old plants headed significantly earlier than those of older plants (Fig. 6). The early heading indicates that the shoot apices of the youngest plants reached the optimal hormonal concentration for flowering earlier than those of older plants. Faster accumulation because of less competition from shoot apices possibly explains this difference in hormonal concentration. Apparently, older plants, which had more

Table 8. The effect of plant age (2, 4 and 6 weeks at the start of primary induction) on the number of tillers per plant after 0, 9 and 18 weeks of induction and panicles per plant after 12 and 18 weeks of induction. Means of 30 plants per treatment

	Tillers per plant			Panicles per plant	
Plant age	0 weeks	9 weeks	18 weeks	12 weeks	18 weeks
2 weeks	2.1	6.2	15.1	8.1	11.7
4 weeks	5.7	18.6	40.8	10.2	20.5
6 weeks	14.6	28.1	54.4	11.6	23.0

shoot apices to be saturated, needed longer exposure to inductive conditions since no significant difference among plant ages on the number of days to heading was found after 15 and 18 weeks of induction. The number of days to heading, on average for plant ages and cultivars, decreased with increasing length of primary induction (Table 6), which is in good agreement with earlier induction studies (Heide 1988a, 1990).

At the start of primary induction 'Fure' had more tillers, higher dry weight and greater leaf area per tiller than the other cultivars (Tables 1 and 2). However, 'Senu Pajbjerg' grew faster during primary induction than the other cultivars and had after 18 weeks a significantly larger leaf area and more tillers and leaves per plant than 'Fure' (Table 3, Fig. 2b). This difference in the ability to grow at low temperatures and in short days can probably be explained by the fact that 'Senu Pajbjerg' originates from a latitude farther south than 'Fure' and 'Salten'. The genetical mechanism for growth cessation was not so prevalent in the Danish cultivar as in the two Norwegian cultivars, and this compensated for the early lead of 'Fure' in subsequent panicle production (Table 6). On the other hand, 'Senu Pajbjerg' had the lowest concentration of WSC in roots and shoots (Table 4), which undoubtedly indicates that this cultivar will be less persistent under harsh winter conditions than 'Fure' and in particular 'Salten'.

Preliminary results from field experiments at Landvik (58°N) showed 'Fure' and 'Senu Pajbjerg' to be approximately equal with regard to seed production, both yielding 1000-1100 kg ha^{-1}, whereas 'Salten' produced only 600 kg ha^{-1} (Havstad, unpublished results). In 1993 and 1994 the average Norwegian seed yields of 'Fure' and 'Salten' were 655 and 500 kg ha^{-1}, respectively. This is compatible with the present results, showing that 'Salten' not only had a less vigorous growth habit, but also produced fewer panicles per plant and shorter inflorescences than the other cultivars (Table 6).

Acknowledgements

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Exogenous chorionic gonadotropin and breeding efficiency

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The mink breeding season occurs annually and lasts for approximately three weeks. Therefore, on the commercial mink ranch this is a very work-intensive period. We sought to reduce this work intensity by increasing breeding efficiency through estrus synchronization with human chorionic gonadotropin (hCG) administration. Mink were injected with either saline or 250 IU of hCG between March 8th and 12th. Saline-treated animals were then immediately subjected to normal breeding practices, whereas in hCG-treated animals breeding was attempted 8 days following hCG injection. Breeding efficiency, defined as the number of successful matings divided by the total number of breeding attempts, was significantly improved by 14% with hCG administration. There was no significant difference between the two groups in the number of animals that bred, but it was observed that a significantly lower percentage of hCG-treated mink whelped. Thus, while exogenous hCG was effective in synchronizing estrus in female mink and in facilitating breeding efficiency, it also resulted in a significant decrease in the total number of offspring produced. We conclude that commercial application of estrus synchronization in mink may not be of economic value to the commercial mink industry.

Key Words: Mink, hCG, eCG, Synchronization, Estrus

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There are numerous periods throughout the year that are critical to the economic success of commercial mink ranches. The breeding season, however, is one of the most critical and it is during this period that the workload is very high. One procedure that has proven successful in reducing the workload associated with the breeding of agricultural animals has been the synchronization of breeding (1, 2). Although this procedure has been applied in the mink industry (3), it has not been investigated thoroughly. Herein we report a field study investigating the synchronization of estrus in the mink with exogenous chorionic gonadotropin.

The mink breeding season occurs during the month of March in the northern hemisphere (4). The animal is an induced ovulator (5). If breeding occurs early during the period of female receptivity, the mature follicles ovulate and a new wave of follicles develop 7-8 days later (6). Superfetation (the presence of several fetuses of different age in the uterus due to fertilization of ova liberated at successive periods of ovulation) can occur in the mink (7, 8, 9). This phenomenon manifests itself in the mink due to the existence of embryonic diapause and delayed implantation.

Mink husbandry has demonstrated that

maximal litter size can be obtained by breeding mink three times over two estrous periods. The general practice in the United States is to breed mink on day 1 and then rebreed the female two times, 7-8 days later (5, 10, 11). It is well established that most of the offspring result from the terminal breeding (12). Therefore, during the first 10 days of the breeding season (approximately 1-10 March) the rancher is attempting primarily to breed female mink to determine exactly when the second or terminal estrous period will occur. An alternative approach would be for the rancher to wait until the middle of March, and mate the mink only once. In those instances where the rancher breeds the animals during the first 10 days of the season, the initial breeding can be considered as an attempt to synchronize the breeding herd. Our aim in this investigation was to induce ovulation with hCG administration and thereby synchronize estrus in normal-breeding mink, thus obviating the need to breed mink during the first 10 days of the breeding season.

Materials and Methods

Animals

Female mink (*Mustela vison*) were maintained under standard ranch conditions (12). Animals were fed six times per week with wet mink feed consisting of 39% crude protein and 19% fat. During the breeding season the animals were fed every day. Water was available at all times. Normal breeding practices consisted of moving the females into the male's cage. Prior to use in the study, males were evaluated for sperm motility and count. Retrospectively, fertility was confirmed in all males based on the fact that these males had sired litters. Breeding attempts were controlled by the investigators and equalled the number of times the females were placed with the males. The females were closely watched to determine their receptivity to breeding. If the male was successful in mounting the female and intromission occurred (confirmed visually by the posture of the animals), the animals were left together for 15-20 min (13). This was defined as a «successful breed». If the female was non-receptive, the animals were separated within 5 min. This was defined as an «unsuccessful breeding attempt». Successful breeding attempts are assumed to represent animals in estrus, while unsuccessful events represent non-receptive and therefore anestrous animals.

The patterns of breeding success were defined as follows: Single -bred successfully during only one estrous period. Doublebred successfully during two different estrous periods (7-8 days apart). Triple-bred successfully three times during two different estrous periods. The third breeding was within 8-24 h following the second breeding.

Study

Human Chorionic Gonadotropin Synchronization of the Breeding Cycle.

The objective of this study was to synchronize estrus in normal-breeding mink. Two hundred female mink of the pink variety were used in this study. The animals were homozygous for the Moyle-Olsen buff, the ambergold, the gunmetal, and the platinum genes. The mink were assigned to either of two groups. All animals in Group 1 (n = 104) received 250 IU human chorionic gonadotropin (hCG) i.m. (lot #32H0001, Sigma Chemical, St. Louis, MO). One subgroup of approximately 20 mink was treated on 8th March, a second on 9th, a third on 10th, a fourth on 11th, and a fifth on 12th of

March. This treatment was designed to induce ovulation (14) and thereby obviate the need to breed the female during the first estrous period. Females were all subjected to normal breeding practices beginning eight days after hCG treatment (March 8th + 8 days, March 9th + 8 days, etc.). For all animals, breeding was terminated on 21 March. Animals in Group 2 (n = 96) were all treated with saline i.m. (0.25 mL) on March 8th and subjected to normal breeding practices from that date to the end of the breeding season. Animals were monitored for number of successful and unsuccessful breeding attempts, date of breeding, parturition, and litter size (live kits only, counts taken within 24 h of parturition).

Statistical Analysis

Data were analyzed with the aid of a computer-based data management system (RS1, BBN Corp., Cambridge, MA) and statistical software program (SPSSPC, SPSS Inc., Chicago IL). Data, expressed as per whelping females and per all females (whelping plus non-whelping), were analyzed for breeding attempts, successful breeding attempts, percentage bred, percentage whelped, litter size (live kits only), and gestation length from last mating. Breeding efficiency, as an estimation of workload, was defined as the number of successful breeds divided by the total number of breeding attempts (successful and unsuccessful breeds). Significant treatment effects were identified by Student's t-test or a completely randomized one-way analysis of variance followed by Duncan's Multiple Range test and chi-squared analysis where appropriate. An alpha of 0.05 was selected for statistical significance.

Results

Human Chorionic Gonadotropin Synchronization of the Breeding Cycle.

Breeding endpoints are presented in Table 1. To make meaningful comparisons of the breeding patterns it must be understood that hCG treatment was substituted for the first breeding. This is based on the knowledge that hCG induces ovulation in the mink (6, 10). Therefore, the breeding of hCG-treated mink, although technically only representing their first and second breeding, is equivalent to double and triple breeding of untreated mink. Cognizant of this working definition, we observed a significantly larger proportion of hCG-treated mink being successfully triple mated.

There was no difference in the percentage of animals that bred, 100% in saline-treated and 97% in hCG-treated mink. There was, however, a significant difference in the number of breeding attempts necessary to accomplish the successful matings. The mean number of breeding attempts for saline-treated mink bred was 4.4 ± 0.1, but only 2.6 ± 0.1 attempts were necessary for the hCG-treated mink. It should be noted that these means do not include the hCG injection as a breeding attempt. The manipulation is justified based on the fact that an i.m. injection of a mink requires 15 sec rather than the approximate 15 min required in handling a mink for a breeding attempt.

We observed that the breeding efficiency, defined as breeding success/breeding attempts, was significantly higher (14%, $p < 0.05$) in the hCG-treated group than in the saline-treated group (Fig. 1). Workload was further reduced because all of the hCG-treated females bred on their target dates.

Table 1. Breeding parameters in mink treated with hCG

Treatment	Total Number of Females	Number of Mated Females	Breeding Attempts[1] (mean ± SEM)	Breeding Pattern[2]
Saline (control)	96	96	4.4±0.1*	5 single 11 double 80 triple
hCG	104	101	2.6±0.1	«inj» single 6 double 95 triple

[1]Breeding Attempts equalled the number of times the females were placed with the males.
[2]Breeding pattern defined as:
Single – bred successfully during only one estrous period
Double – bred successfully during two different estrous periods
Triple – bred successfully three times during two different estrous periods, the third breeding occurring within 8-24 hrs following the second breeding
«inj» single – by definition, the hCG injection replaces the initial breeding

*Denotes a significant difference ($p<0.05$) between the treatment groups

The percentage of breeding females that whelped is illustrated in Fig. 1. Chi-squared analysis revealed that a greater number of saline-treated animals whelped per breeding female compared with hCG-treated animals ($p < 0.05$). Litter size per whelping female was not significantly different for the two treatment groups (Table 2). In contrast, when all females were considered, the hCG-treated group averaged significantly smaller litter sizes. This was due to the fact that 21% of the hCG-treated females that bred did not whelp, whereas only 11% of the saline-treated mink did not whelp. Gestation lengths were within the normal range (15) for both treatment groups (50 ± 1 for saline-treated and 47 ± 1 for hCG-treated mink) when measured from the last breeding date. The average last breeding day for both groups was March 8th.

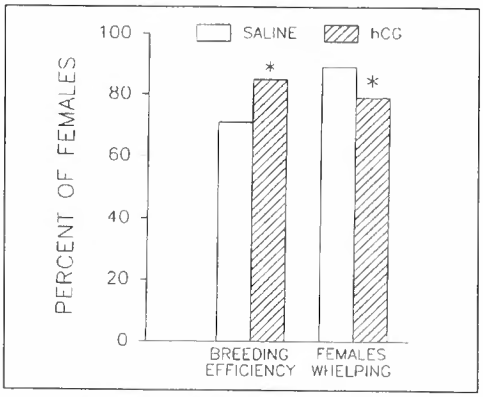

Fig. 1. The percentage of breeding efficiency and whelping in saline and hCG-treated female mink is illustrated. Breeding efficiency is defined as the number of successful breeds divided by the total number of breeding attempts (successful plus unsuccessful). The breeding efficiency was significantly greater for hCG-treated females ($p<0.05$). There was a significantly lower precentage of hCG-treated mink whelping ($p<0.05$).

Table 2. Reproductive performance in mink treated with hCG

Treatment	Number of Mink	Number of Mink Bred	Number of Whelping Mink	Number of Live Kits at 24 h Per (Mean ± SEM) Whelping Females	All Females
Saline	96	96	86	5.1±0.3	4.5±0.3
hCG	104	101	80*	4.5±0.3	3.3±0.3*

* Denotes a significant difference ($p<0.05$) between the treatment groups

Discussion

Synchronization of the reproductive cycle in agricultural animals is an established practice in animal husbandry. The artificial regulation of estrus with exogenous hormones is used in cattle, swine, and sheep (1). On an economic level, synchronization of estrus results in more efficient use of labor by allowing a large group of females to be brought into estrus at a predetermined time. The animals can then be bred or artificially inseminated by genetically superior sires on a single day (2). It is recognized, that artificial insemination is not practiced in mink ranches. A wide variety of synthetic and non-synthetic compounds, such as GnRH agonists, gonadotropins, and prostaglandins, have proved beneficial in synchronization of estrus in livestock (16). However, important factors, such as costs, availability, side effects of the drugs, and the need for careful monitoring of the animals must all be considered when assessing the economic value of estrus synchronization.

Our current knowledge of mink reproductive physiology (9) suggests that synchronization of estrus may be of economic value to the mink industry. Both eCG and hCG have been used in the past by commercial mink ranchers to stimulate ovulation and induce mating (7, 9, 13, 17, 18). The eCG in non-equine species functions mainly by stimulating follicle development and has some LH-like action, while hCG functions much like LH and is used for induction of ovulation (19). In cases of human infertility, exogenous gonadotropin administration is standard practice when functional ovarian tissue is present (20). The dose selected for use in the mink was based on human studies and adjusted for animal weights.

This study was designed to address workload and breeding efficiency related to mink ranchers who practice triple breeding methods with their herd. This requires breeding mink on day 1 and then double breeding the females 7-8 days later. Recognizing the amount of work each breeding attempt represents, we sought to replace the day 1 breeding with hCG. The findings of the present study demonstrate that exogenous hCG results in synchronization of estrus in animals treated in this way. As a result, it reduces the work effort of mink ranchers during the breeding season since the need to mate the mink the first time can be bypassed. Owing to the induction of ovulation with exogenous hCG, the mink rancher knows the exact day on which a female returns to estrus.

It has previously been shown that a single injection of hCG early in the breeding season induces ovulation in the same manner as copulation (6, 10). Injecting an animal, however, requires much less time and effort than does breeding. In addition, the rancher can also synchronize the breeing herd so that a specified number of females will be in estrus on a predetermined date while others will be receptive on different days. In contradistinction, standard breeding practices require females to be paired with males to identify the first estrous period. Frequently, females are not receptive when first paired with a male and the rancher must then attempt to breed the female on another day. Our study suggests that hCG treatment increases the breeding efficiency by 14%. This means a reduction, by a similar percentage, in the workload of each individual worker. It should be recognized that the present study may not be relevant to mink ranchers who practice only double breeding of their mink. That is, those who start breeding later in the season (later than March 12th) and breed mink on day 1 and then rebreed them 8-24 h later (day 1 + 1).

The results of this study further showed that 97% of the hCG-treated females bred, but only 79% of these animals actually whelped. The saline-treated group showed a higher percentage (89%) of whelping females. This suggests that the 250 IU of hCG, although synchronizing estrus, had a significant detrimental effect on reproductive function. When administered to humans as part of an *in-vitro* fertilization regimen, hCG has also been shown to exert adverse effects (21). These included a significant occurrence of ovarian cysts that was associated with ovarian hyperstimulation syndrome. The complications we encountered with hCG administration may be avoided with a lower dose.

Another approach to the present research design could have been to breed all animals for the first time (both hCG-treated and saline controls) 8 days following the injection. Because breeding at this later date is not common ranch practice, and this study was designed to enhance common ranch procedures, the two groups were not bred for the first time on similar dates. Moreover, the study was designed so that the hCG treatment would substitute for the «first breeding» in the control group, in those ranches that practice triple-breeding procedures. The present study demonstrates that hCG treatment is effective in synchronizing estrus of female mink and thus reduces the workload during the breeding season. This treatment also resulted in a reduction in the percentage of animals whelping suggesting that additional research is necessary if hCG is ever to become part of normal ranch practice.

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Ozone Sensitivity of *Betula pubescens* Ehrh. at different growth stages after budburst in spring

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Plants of *Betula pubescens* at different growth stages in spring (swollen buds, visible leaves, unfolded leaves and well-developed leaves) were subjected to three O_3 concentrations (23, 56 and 77 nmol mol^{-1} O_3 in 10 h day^{-1}) for three weeks. Visible leaf injuries (yellow stipples and brown spots) developed first in plants with the most developed leaves at the start of O_3 exposure. However, when the plants were harvested 16 days after the end of exposure, the percentage of the total leaf biomass with O_3 injury was not significantly different between plants at the different growth stages. No leaf injuries were recorded at the lowest O_3 concentration, while 11 and 22% of the leaf biomass suffered injury at 56 and 77 nmol mol^{-1}, respectively. No significant effects of O_3 were found on shoot and root dry weights. The results are discussed in relation to the accumulated O_3 dose over 40 nmol mol^{-1} (AOT40).

Key words: *Betula pubescens*, growth stage, leaf injury, ozone dose.

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Tropospheric ozone (O_3) is regarded as an air pollutant that could cause growth reduction of sensitive plant species in Europe (UNECE 1994), including Scandinavia (Skärby et al. 1994). In Norway, about 50 native species have been investigated, and *Betula pubescens* (birch) has been identified as being among the most sensitive tree species (Mortensen & Skre 1990; Mortensen 1994a,b,c; Mortensen 1995, 1996). *Betula pubescens* is the most widespread deciduous tree species in Scandinavia, and is also the predominant tree-line species. It has been suggested that an accumulated O_3 concentration over 40 nmol mol^{-1} (AOT40) should be used when defining a critical level for O_3 (UNECE 1994). The AOT40 during the growth season in southern Norway has been found to be close to the level that might cause growth reductions in birch (Tørseth et al. 1996).

April-May is often the time during the growth season when the O_3 levels are the highest in Norway (Mortensen 1996). This is also the time for budburst of birch. When evaluating the effect of O_3 pollution on growth of this species it is therefore very important to know the O_3 sensitivity at the early growth stages (from budburst to well-developed leaves). An O_3 exposure experiment was therefore conducted with *Betula pubescens* plants at different growth stages after budburst. In addition, it was also of interest to discover whether the light

conditions during the preceding autumn would affect the leaf physiology and O_3 sensitivity the following spring.

Material and methods

Plants of *Betula pubescens* Ehrh. (Kvinesdal, 58°20'N) were propagated from seed under a controlled environment in 1995. The first objective was to produce plants at a height of about 30 cm and at a physiological status comparable with that found in spring in Norway, i.e. dormancy fully released. In addition, these plants should include those which during the previous short-day treatment (induction of growth cessation) had received two different light regimes. The growth chambers used (2.5 m^2 growing area) have been described earlier in Mortensen & Nilsen (1992), and were placed in a greenhouse compartment. Supplementary lighting at different photosynthetic photon flux densities (PPFD) was supplied, in addition to the daylight by means of high pressure sodium lamps (Philips SON-T Plus). The light was measured by means of a Lambda LI-185B instrument with quantum sensor (400-700 nm). The daylight was measured at the Meteorological Station at Særheim Research Centre, and this value was decreased by 50% because of shading from the greenhouse and growth chamber constructions.

The propagation schedule was as described in Table 1. On 10 February the seedlings were planted in a mixture of 50% standard fertilized peat (Floralux, Nittedal industrier AS, Norway) and 50% perlite in 150 ml pots, one seedling per pot. The chilling (1-2°C) was performed in a refrigerated room.

At the beginning of August a test showed that budburst occurred after about one week at 15°C. The objective was now to produce plants at four different stages of leaf development before the experiment started. This was done by moving the plants from the 1-2°C treatment to the

Table 1. Climatic conditions during the propagation of *Betula pubescens* after one week in a greenhouse at 21°C. PPFD = photosynthetic photon flux density; PAP = total number of photosynthetic active photons (supplementary light + daylight until 21 April)

Period	Temperature (°C)	Daylength (h)	Suppl. PPFD μ(îmol m^{-2} s^{-1})	Total PAP (mol m^{-2} day^{-1})
30 Jan. - 10 Feb.	16.0±0.5	20	175	15
10 feb. - 10 Apr.	15.0±0.5	20	175	18
10 Apr. - 26 Apr.	10.0±0.5	12	325 and 550	14 and 24
26 Apr. - 1 June	8.0±0.5	12	325 and 550	14 and 24
1 June - 1 July	1.0-2.0	10	75 and 300	3 and 11
*1 July ->	1.0-2.0	10	75	3

*Foliage dropped off the plants

growth chambers (15.0±0.5°C) on four different dates: 14 August, 24 August, 30 August and 5 September. Before the plants were moved to 15°C they were planted in 1.0 l pots in the same substrate as that used before. The plant material at the start of the experiment (5 September) therefore included low- (LL) and high-light (HL) grown plants (given during the short-day treatment) at four leaf developmental stages:

- Stage 1 (G1): Swollen buds (directly from 1-2°C).
- Stage 2 (G2): Visible leaves (6 days at 15°C).
- Stage 3 (G3): Elongating/unfolded leaves (12 days at 15°C)
- Stage 4 (G4): Well-developed leaves (22 days at 15°C).

A number of 36 LL and 36 HL plants at each of the four growth stages (G1, G2, G3 and G4) were divided equally among six growth chambers. Each chamber therefore contained 48 plants including 8 pretreatments. The temperature during the experiment was 15.0±0.5 for 12 h (08.00-20.00 h) and 10.0±0.5°C for 12 h day^{-1} (20.00-08.00 h), and supplementary light was supplied at a level of 300 µmol m^{-2} s^{-1} for 17 h day^{-1} (05.00-22.00 h). The total number of photosynthetic active photons (supplementary + daylight) as the mean for the experimental period (5 September - 11 October) was 25 mol m^{-2} day^{-1}. The relative air humidity was 90±3% and the CO_2 concentration was 350±30µmol mol^{-1}, as measured by infrared gas analyser (PP-Systems, Model WMA-2, UK). The pots were watered regularly with a complete nutrient solution in order to maintain the electrical conductivity at about 2.0 mS cm^{-1}.

Three O_3 concentrations (23 nmol mol^{-1} O_3 as the control, and 56 and 77 nmol mol^{-1} O_3 during 10 h day^{-1} (10.00-20.00 h)) were applied for 21 days (5-25 September), two growth chambers per concentration (Table 2). The O_3 concentration for the rest of the day (20.00-10.00 h) was <20 nmol mol^{-1}. From 26 September until the end of the experiment (11 October) no O_3 was added. The accumulated O_3 dose over a concentration of 40 nmol mol^{-1} (AOT40) was calculated on a daily basis for all chambers (Fig. 1), and the total for the whole experimental period is presented in Table 2. Ozone was generated from oxygen using a high-voltage generator (Nomizon, Normiljø ab, Sweden). The O_3 concentration was measured twice an hour by a scanner switching the air flows from the chambers sequentially to an O_3 analyser (Monitor Labs. Inc., Model 8810).

Table 2. Mean O_3 concentrations during the 10 h exposure period and accumulated O_3 doses over 40 nmol mol^{-1} (40 ppb) (AOT40) during the 21 days exposure period (5-25 September) in the six growth chambers. 1 nmol mol^{-1} = 1 ppb

	Chamber no.					
	1	2	3	4	5	6
O_3 conc. (nmol mol^{-1})	55.0	22.9	75.6	56.2	77.9	22.1
AOT40 (ppb-h)	3469	13	8172	3992	8693	18

During the experiment the time of first visible O_3 injury was recorded for the individual plants. At the end of the experiment the dry weight of leaves which had dropped off the plants, the dry weight of leaves with visible O_3 injuries (yellow stipples/brown spots), the dry weight of the remaining leaves, the dry weight of shoot and root, and of plant height were all recorded. All data were subjected to an analysis of variance using the PROC GLM procedure (SAS Inc., Carey NC, USA).

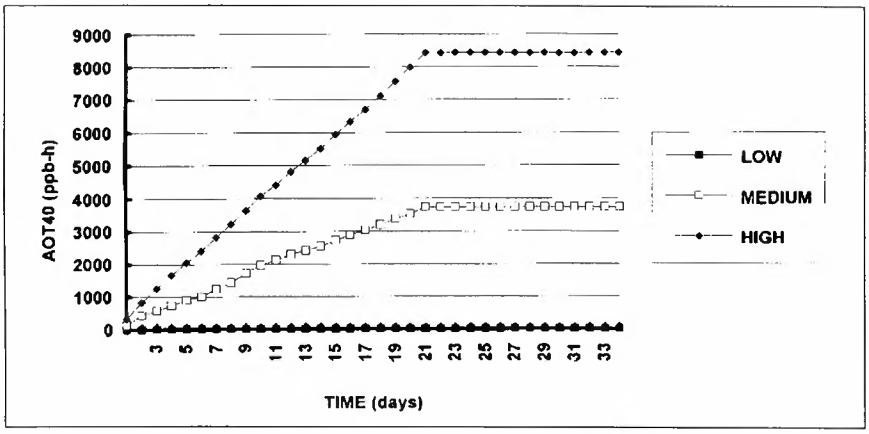

Fig. 1. The accumulated O_3 dose over 40 nmol mol^{-1} (ppb) O_3 (AOT40 in ppb-h) at low (23 ppb), medium (57 ppb) and high O_3 concentrations (77 ppb). Cumulative values are given during the experimental period as means of two parallel chambers.

Measurement of the diffusion resistance of leaves

The leaf diffusion resistance was measured on leaves at different stages of development, from newly unfolded to fully expanded. For pratical reasons, it was impossible to take measurements on the leaves before unfolding. A porometer (Delta-T Devices, MK3, England) was used to measure the resistance between 60 and 65% relative humidity.

Results

At the time the LL plants were removed out from the chilling treatment, the shoot and root dry weights were 1.6 and 1.2 g, respectively. The corresponding values for the HL plants were 2.1 and 1.9 g. The height of both plant groups was 30 cm. Before the experiment started on 5 September 1995, a significant leaf biomass (1.7 g leaf dry weight per plant in both LL and HL plants) had developed in the G4 plants.

Development of visible O_3 injuries

The first O_3 injuries (yellow stipples and brown spots) were observed on leaves of the G4 plants, followed by the G3, G2 and G1 plants with time (Fig. 2). The injuries were first observed at the highest O_3 concentration (77 nmol mol^{-1}) and then at the medium concentration (56 nmol mol^{-1}). No injuries were observed at the lowest O_3 level. On the basis of Figs. 1 and 2 it appears that 50% of the G3 and G4 plants developed visible injuries at an AOT40 value of about 2.5 ppm-h at medium O_3 and 4.0 ppm-h at high O_3. At end of the O_3 exposure period the 50% limit was passed by the G1 and G2 plants only at the highest O_3 level (Fig. 2) at an AOT40 value of about 8.0 ppm-h (Figs. 1 and 2). Generally, there were no differences between LL and HL plants, and the mean values for the two treatments are therefore presented. In the course of 16 days (26 September-11 October) after the O_3 exposure had stopped, O_3 injuries continued to develop in new leaves and in plants where no

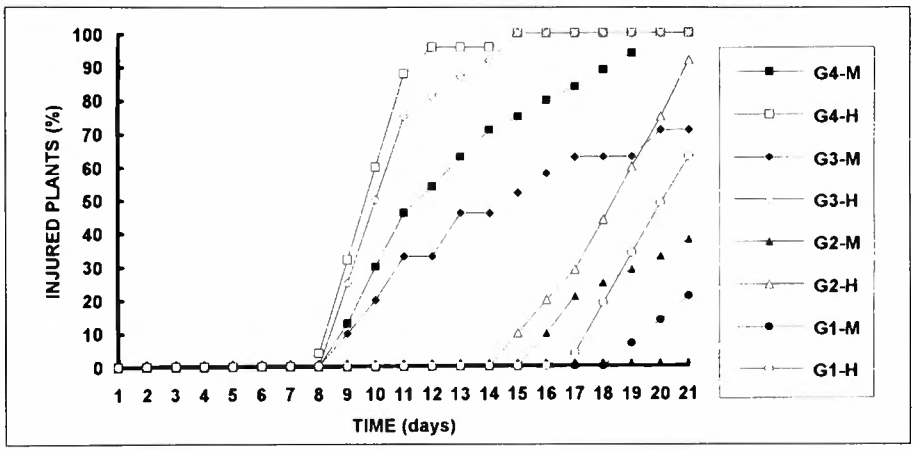

Fig. 2. The development of visible leaf injuries caused by medium (-M) and high (-H) O_3 concentrations during the three-week O_3 exposure period, in plants at different growth stages (G1, G2, G3 and G4) at start of the exposure.

injuries had been observed during the O_3 exposure period. At the end of the experiment (11 October) 80-100% of all plants, irrespective of pretreatment light level and growth stage, had developed visible O_3 injuries at medium and high O_3 levels.

Plant growth

An increase in the O_3 concentration did not significantly affect the shoot or root dry weight, or the shoot:root dry weight ratio, irrespective of the growth stage or pretreatment PPFD level (Table 2). The dry weights of leaves, total shoot and root increased with increasing growth stage (i.e. longer growth period). The pretreatment PPFD level increased the root dry weight and decreased the shoot:root ratio (Table 2). An increase in the O_3 concentration resulted in a greater decrease in plant height in G4 plants than in plants at other growth stages, and slightly more so in HL than in LL plants (Table 2).

Leaf drop occurred at the highest O_3 concentration, particularly in G4 plants and also slightly in G3 plants, while only G4 plants were affected at medium O_3 level (Table 2, Fig. 3). The dry weight of all leaves with visible O_3 injuries as a percentage of the total leaf dry weight increased with increasing O_3 concentrations, but this percentage was not significantly different between the plants at different growth stages or at different pretreatment PPFD level (Table 2).

Leaf diffusion resistance

The leaf diffusion resistance was not significanly different between newly unfolded leaves and well-developed leaves (Table 4).

Discussion

An interesting feature was that despite the development of severe leaf injuries caused by O_3, the dry weights of the different plant parts were not affected. This is in contrast to earlier findings with the

Table 3. Effects of different O_3 treatments on growth (±SE) of Betula pubescens pretreated at low (LL) and high (HL) PPFD levels during the previous short-day treatment. The O_3 exposure started at four different growth stages (different leaf development) of the plants

	Dry weights (g)				% leaf biomass		
	Leaves	Total shoot	Root	Shoot:root ratio	Height (cm)	Dropped	Injured
O_3-conc. (nmol mol^{-1})							
22	6.1	12.0	3.4	3.5	66	0.0	0.0
	±0.7	±1.4	±0.3	±0.1	±4	±0.0	±0.0
56	6.2 1	2.0	3.7	3.2	63	0.2	11.0
	±0.7	±1.3	±0.4	±0.1	±3	±0.1	±1.7
77	6.4	12.2	3.5	3.4	64	0.9	21.7
	±0.7	±1.4	±0.2	±0.1	±3	±0.3	±1.5
Growth stage							
1	3.8	7.1	2.2	3.2	51	0.0	11.0
	±0.1	±0.2	±0.1	±0.1	±1	±0.0	±3.1
2	4.3	8.5	2.8	3.0	55	0.0	8.8
	±0.2	±0.4	±0.2	±0.1	±1	±0.0	±2.5
3	6.6	12.7	3.5	3.6	68	0.2	12.1
	±0.2	±0.4	±0.1	±0.1	±1	±0.1	±3.3
4	10.3	20.0	5.6	3.6	83	1.2	11.7
	±0.2	±0.3	±0.2	±0.1	±1	±0.4	±3.2
PPFD level							
Low	6.1	11.6	3.2	3.5	63	0.3	11.8
	±0.6	±1.1	±0.3	±0.1	±3	±0.1	±2.3
High	6.4	12.6	3.9	3.2	65	0.4	10.0
	±0.5	±1.0	±0.3	±0.1	±3	±0.2	±2.0
Significance levels:							
Ozone (O_3)	ns	ns	ns	ns	**	***	***
Growth stage (S)	***	***	***	***	***	***	ns
Light (L)	ns	**	***	**	*	ns	ns
O_3 x S	ns	ns	ns	ns	ns	***	ns
O_3 x L	ns	ns	ns	ns	ns	ns	ns
O_3 x S x L	ns	ns	ns	ns	*	ns	ns

same species, where significant growth reductions accompanied the development of leaf injuries (Mortensen 1994c, 1995, 1996). The present experiment, however, differed from earlier experiments in that the plant growth was allowed to continue for a period after the O_3 exposure. This might to some extent have decreased the overall O_3-effect. Nevertheless, the question still remains why an O_3 injured leaf biomass of up to about 20% of the total did not cause a reduction in biomass

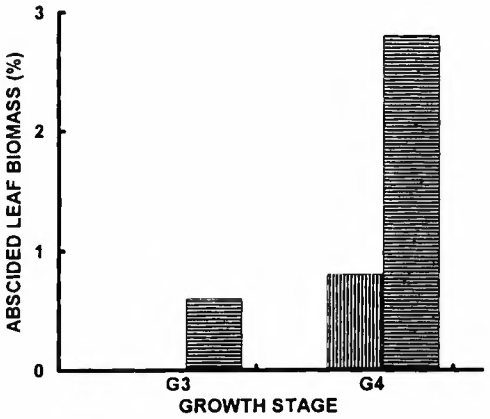

Fig. 3. The dry weight of abscided leaf dry weight at low (always zero) medium ( ) and high ( ) O_3 concentrations as percentage of the total leaf dry weight at end of the experiment. From plants at different growth stages (G1, G2, G3 and G4) at start of the experiment.

Table 4. The leaf diffusion resistance (s cm^{-1}) of leaves of different sizes/developmental stages (from newly unfolded to fully expanded). Standard errors are given (±SE, n=5). No significant effect was found (p>0.05)

	Leaf development		
	Unfolded	Intermediate	Expanded
Diffusion resistance (s cm^{-1})	1.65±0.05	1.59±0.04	1.55±0.01
Leaf width /length (cm)	2.5/3.5	4.5/5.5	7.0/8.0

production. In order to answer this question it is important to know how fast the leaf injury developed compared with the development of new leaves. The present results reveal that it takes about two weeks from emergence of a new leaf until visible injuries are observed. During this time about five new leaves were produced on the shoot, and the shading caused by these leaves resulted in very low light levels at the site of the injured leaf. In a plant stand with a dense and fast-growing foliage, it is probably the case that at the time the leaf injury reaches a sufficient level to decrease the photosynthetic rate, the shading from other leaves would already have made the leaf unproductive anyway. This might explain the lack of effects on plant dry weight by AOT40 doses of up to 8 ppm-h which previously have been found significantly to decrease the dry weights of this species (Mortensen 1996). In earlier experiments small seedlings have always been used, whereas in the present experiment plants were grown from a height of about 30 up to 50-80 cm.

The first O_3 injuries on leaves were observed 8-10 days after start of exposure in G3 and G4 plants, which means that the injured leaves were already unfolded at the start of O_3 exposure. The O_3 dose at which the injuries appeared in the present experiment (AOT40 = 2.5-4.0 ppm-h) was at about the same level as that in a previous study (Mortensen 1996). Starting the O_3 exposure when plants were at the G1 or G2 stage took a much longer time before the leaf injuries appeared. Visible injuries continued to develop in new leaves after the O_3 exposure had stopped. This indicates that after the critical level for injuries had been reached, it took some time before any injury became visible. No injuries were observed on leaves until some days after they were unfolded, despite a relatively high AOT40 dose (>4 ppm-h) on these leaves. This perhaps indicates that a particular physiological stage of the leaf must be reached before the visible injuries develop. In spite of a much later development of visible injuries in G1 and G2 plants as compared with G3 and G4 plants, the percentage injured leaf biomass of the total was the

same. The reason for this has already been discussed, and was probably due to a delay between the time the injurious O_3 dose had been reached and the time when the injuries became visible in young, developing leaves. On the basis of the present results it seems that the O_3 sensitivity of birch is relatively independent of the stage of leaf development in spring. This was supported by the measurements which showed that the leaf diffusion resistances were the same in recently unfolded leaves as those in large, well-developed leaves. This indicates that the O_3 absorption rate was independent of leaf development. These measurements were conducted on leaves at low O_3 concentrations, but earlier measurements have shown that the diffusion resistance is relatively little affected by the O_3 concentration (Mortensen 1993).

The present results indicate that high O_3 concentrations in late April (new leaves appearing) might be as harmful as high O_3 concentrations in May-June (well-developed leaves). In the lowlands of southern Norway the budburst often occurs in the middle of April. However, because of low temperatures the leaf development can often stop during the subsequent two to three weeks. In future studies, it would be of great interest to study the effect of O_3 under such conditions. In the present experiment the temperature (15/12°C) was comparable with the mean temperature in June in the coastal areas of South Norway, and therefore the plants were growing relatively quickly. No effects of light conditions during the preceeding growth cessation phase were found on the O_3 sensitivity of leaves after budburst. Previous experiments have shown that increasing the light level during plant growth decreases the O_3 effect in birch (Mortensen, unpublished results) as well as in other species, such as clover (Sanders et al. 1994) and wheat (Mortensen 1990). However, it seems that the light conditions during the bud formation phase in autumn have little effect on the O_3 sensitivity of the leaves after budburst the following spring.

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The Kvithamar field lysimeter
I. Objectives, methods and results of soil analyses

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The Kvithamar field lysimeter at Stjørdal in central Norway was constructed in order to measure nutrient leaching in surface runoff and in drainage discharge from agricultural soil in humid areas of Norway. Ploughing and application of pig slurry in autumn and spring were compared in barley crops. The soil at the lysimeter is a uniform, sandy clay loam of marine origin, representative of large areas suitable for cereal production below the marine limit in central Norway. After an experimental period of four years, pig slurry applied in the spring resulted in the highest content of nitrate- and ammonium-N in the upper subsoil layer (40-60 cm). Autumn ploughing and autumn application of pig slurry gave approximately the same level of readily available phosphorus and potassium in the topsoil as treatments without fertilizer, but the level of readily available phosphorus and total-N in erosion material was highest for the treatment with autumn ploughing and autumn application of pig slurry. Although the total erosion loss was negligible, autumn ploughing increased the soil erosion by 73% compared with spring ploughing.

Key words: Erosion, fertilizer, leaching, nitrogen, phosphorus, pig slurry, potassium, runoff, sulphur.

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Dairy cattle or pig production, combined with cereal growing, has been the main agricultural activity in central Norway for many years. Application of animal slurry before ploughing in the autumn has until recently been a prevailing practice. Limited storage, a short growing season, variable climate in the spring and relatively cheap commercial fertilizers are some of the reasons why many farmers apply slurry on the fields before ploughing in the autumn. From the farmers' side, it is also convenient to apply slurry in autumn when labour and machinery are not usually used for other farming activities.

During the last two decades recommendations and legislative regulations have been given in order to avoid water pollution, caused by soil erosion, surface runoff, and leaching of plant nutrients in pipe drainage from the arable fields. Soil and crop research institutions were encouraged to start investigations on different soils and under different climatic conditions (Anon 1988). The investigations were to be carried out in order to obtain documentation of pollution risks in relation to the various fertilizing and soil

tillage practices in different parts of the country. Results from such investigations have so far been published by Tveitnes (1988), Uhlen (1989), Eltun (1994), Oskarsen & Amdal (1994), Riley & Eltun (1994), and Uhlen (1994). Similar studies have been conducted in the other Scandinavian countries and in different European countries (Brogan 1981; Brink & Jernlås 1982; Dam Kofoed et al. 1986; Bertilsson 1988; Torstensson et al. 1992; Lindén et al. 1993; Thomsen et al. 1993). Modelling of surface runoff and pipe drainage, particularly with regard to loss of nitrogen from manure or slurry, has been carried out by Borg et al. (1990) and Hansen & Svendsen (1994).

In this study a comparison of equal amounts of plant nutrients in animal slurry and commercial NPK fertilizers was included in the experimental design. Pig slurry was supplied and ploughing accomplished in autumn or in spring. The aims of the investigation were to compare grain yields, and nutrient loss in drain water, surface runoff and erosion material.

In the present report experimental methods and results of the soil analyses will be communicated. In future articles in this journal nutrient leaching, crop yields and nutrient balances will be presented and discussed.

Materials and methods

The site and climate

The experimental site is located at Kvithamar Research Centre, Stjørdal, in Mid-Norway, 40 km east-northeast of Trondheim city, approximately 63°29'20"N, 10°52'40"E, and 27-29 m above sea level. The experimental area slopes gently towards the south (1-2% slope).

According to the Critchfield's classification (1966), Kvithamar has a humid continental climate with long, cold winters, and cool summers (Table 1). There is usually some snow from the middle of December to the beginning of April. The length of the period with frozen ground and the depth of frost vary between years, but the ground is usually frozen during the period with snow and the depth of frost is normally less than 50 cm. The annual precipitation was 892 mm (as the mean for the years 1961-90) at Værnes in Stjørdal, and 410 mm was recorded during the growing season May-September (Table 1).

Table 1. Mean precipitation, temperature and days with frost at 10 cm and 20 cm soil depths.

Month	Prec.[1] mm	Temp.[1] °C	Frost[2] 10 cm	20 cm	Month	Prec. mm	Temp. °C	Frost 10 cm	20 cm
Jan.	63	-3.2	2	0	Aug.	87	13.4	0	0
Feb.	52	-2.4	13	7	Sep.	113	9.8	0	0
Mar.	54	0.5	15	10	Oct.	104	6.1	0	0
Apr.	49	3.9	5	2	Nov.	71	0.9	0	0
May	53	9.4	0	0	Dec.	84	-1.5	8	0
Jun.	63	12.6	0	0	May-Sep	410	11.8	0	0
Jul.	94	13.9	0	0	Year	892	5.3	43	19

[1] Precipitation and air temperature at Værnes, 5 km distant, means for the years 1961-90.
[2] Days with frost at 10 and 20 cm soil depths at Kvithamar, means for the years 1991-94.

Reclamation and cropping history

Up until recent days the experimental area has been described as «The Kvithamar Bog». The reclamation took place in the late 1890s, and the original peat layer might have been 50-60 cm thick. Three old drain systems were identified, and put out of action, when the lysimeter was installed in 1989. Drainage, liming, fertilizing and tillage promoted subsidence and mineralization of the organic compounds in the topsoil, and after a number of decades subsoil clay was ploughed up, and mixed into the topsoil. Today, it is difficult to imagine the original trait of bog, although the relatively high humus content in the plough layer perhaps gives an indication of this.

The cropping history as far back as 1950 was a 6-year rotation including barley/oats, root crops/potato, barley as nurse crop, and 3-year ley. In this period only small, or moderate, quantities of manure and commercial fertilizers were supplied. In the years from 1950 to 1975 the field was used for vegetable growing, mainly cruciferous and leek crops, and the fertilization was heavy. After 1975 barley, oats and ley have prevailed, and optimal quantities of NPK fertilizer have been supplied.

Soil type

In the Kvithamar area, marine deposits tend to prevail. Silt and clay are dominating grain-size fractions, although a considerable content of sand is present at some locations (Reite 1983). The superficial deposits are underlain by metasedimentary and metavolcanic rocks of assumed late Precambrian to Ordovician or possibly Silurian age (Reite 1994). The upper marine limit in the Stjørdal watercourse is located at 180 m above present sea level.

The soils at Kvithamar Research Centre have been systematically mapped and described (Solbakken 1987). The major soil type on the experimental site is a poorly drained silty clay loam, with an average of 6% sand, 62% silt and 32% clay in the layer at 30-40 cm depth. The clay content is 39% between 80 and 180 cm depth. According to Soil Survey Staff (1975), the soil is a Typic Cryaquept (Sveistrup et al. 1994) and according to the Canada Soil Survey Committee (1978) the dominating soil is an Orthic Humic Gleysol. A smaller part of the area has silt loam in the layer at 30-40 cm depth, but in general there are only minor differences in textural components at the experimental site (Table 2). pH is found to increase from 5.8 in the plough layer to 7.0 and 8.3 at 80-100 cm and 160-180 cm depths, respectively. Free calcium carbonate can be found in the subsoil below 1 m depth. The degree of base saturation in the clayey subsoil at Kvithamar is normally higher than 70% below 30 cm depth (Solbakken 1987; Sveistrup et al. 1994). The content of readily available phosphorus and potassium (AL-extraction) was moderately high in the plough layer, and the content of cations generally increases with depth (Table 3). The content of organic matter in the topsoil is high (Table 3), but varies slightly patchwise on the site.

Experimental design

Six treatments for fertilizing and ploughing were defined for the first experimental period (1991-94):

1. Autumn ploughing, pig slurry supplied before ploughing.
2. Autumn ploughing, pig slurry supplied in the spring.
3. Autumn ploughing, NPK fertilizer

Table 2. Uniformity test of soil particle size (mm), for the 30-40 cm layer, mean values for the separate treatments. Data in weight percent

Treat-ment	Gravel	Sand			Silt			Clay
	>2.00 mm	2.0 0.6	0.6 0.2	0.2 0.06	0.06 0.02	0.02 0.006	0.006 0.002	<0.002 mm
1.	0.0	0.7	1.0	3.4	15.4	29.3	18.0	32.3
2.	0.0	0.7	0.8	3.9	14.8	27.9	18.5	33.4
3.	0.6	0.7	1.8	3.7	15.2	28.6	17.8	32.1
4.	0.0	0.8	1.1	5.4	16.7	28.6	16.8	30.6
5.	0.3	0.4	0.9	3.3	14.1	29.5	17.6	34.1
6.	0.4	0.6	1.2	3.2	15.1	30.0	16.9	32.9
$LSD_{5\%}$	0.6	0.7	0.7	2.0	1.7	1.9	1.3	1.9
Level of sign.	ns	ns	ns	ns	*	ns	ns	ns

Table 3. Mean values of soil properties, at three depths, sampled in autumn 1990 before start of the experimental treatments. Means of 18 plots.

Depth cm	pH	v.w. kg/l	lg.loss %	Kjeldahl N %	P-AL	K-AL	K-HNO_3	Mg AL	Ca-AL
					(mg/100 g air dry soil)				
0-20	5.8	1.02	11.7	0.62	9.2	7.8	138	14	268
st.err[1)]	0.0	0.01	0.3	0.03	0.1	0.1	2	0.1	7
40-60	6.5	1.18	2.4	–	10.4	10.7	329	19	164
st.err[1)]	0.0	0.01	0.1	–	0.1	0.2	3	1	1
80-100	7.0	1.20	2.2	–	13.8	13.3	366	32	152
st.err[1)]	0.0	0.00	0.1	–	0.2	0.1	2	1	1

[1)]Standard error

supplied in the spring.

4. Spring ploughing, pig slurry supplied in the spring.
5. Spring ploughing, NPK fertilizer supplied in the spring.
6. Spring ploughing, no plant nutrients supplied.

Three replications of each treatment were arranged in a randomized block design. Each of the 18 plots measured 36 m x 8 m. The experimental layout is illustrated in Fig. 1. After spring ploughing the field was tine cultivated. Mineral fertilizer and slurry were applied on the plots, and as soon as possible thereafter the field was harrowed and spring barley was sown. A uniformity trial was performed in 1990, and the experimental treatments started after crop harvest the same year.

Pig slurry and fertilizer

Forty metric tons of pig slurry per hectare was supplied each year. According to chemical analyses of the slurry, the following amounts of plant nutrients were supplied

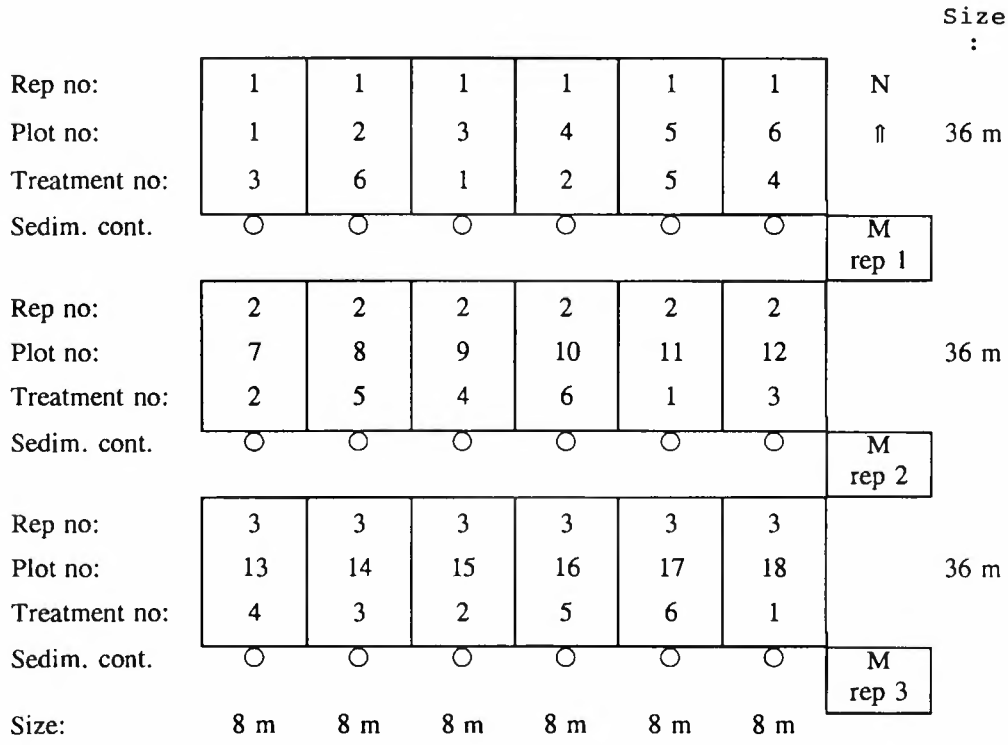

Fig. 1. Layout of The Kvithamar field lysimeter, showing the experimental grid, the sedimentation containers for erosion meterial and the measuring houses (M) for drainage discharge and surface runoff

per hectare, each year: 72 kg ammonium-N (112 kg Kjeldahl-N), 27 kg P, 50 kg K, 34 kg Ca, 13 kg Mg and 6 kg S. The corresponding amounts for NPK fertilizer were: 75 kg N, 27 kg P, 50 kg K and 29 kg Ca. Concentrations of Mg and S were low, and not declared, in the fertilizer applied.

Lysimeter installation

Along the middle of each plot at a depth of 1.0 m, a perforated 2" plastic drain pipe were placed to collect drain water. The pipes were covered with a 10 cm thick layer of sawdust as filter material. From the lowermost end of each plot the drain water were led through nonperforated pipes to the cellars of the measuring houses. The surface runoff water from the separate plots was caught by boards covered with plastic sheets from the separate plots, and directed into sedimentation containers, and then further through non-perforated pipes to the measuring houses. One measuring house was built for each replication (block) of the experiment. Each house was the catchment for the pipes with drain and runoff water from six plots, totalling 12 pipes. The pipes terminated at a tipping bucket, which was connected to dataloggers. The water flow was measured continuously, and at the same time water was sampled proportionally to the water flow for chemical analyses.

To avoid the inclusion of runoff water from neighbouring areas, interception ditches were filled with gravel, above the

blocks. During the time of the year with no crop on the plots, plastic covered boards were dug 5 cm down in the topsoil along the plot borders to ensure that surface water did not invade adjacent plots.

Soil density, porosity, water retention and soil analyses

Stainless steel cylinders of 100 cm^3 were used to obtain undisturbed soil samples from the topsoil (7-12 cm) and subsoil (25-30 cm) after grain harvest in the year before start of the experimental work. Systematically, the plots of three future treatments on all three replications were sampled. Four cylinders were taken at each depth at each plot. pF-analysis for determination of water retention in soil samples was conducted according to Richards(1948). A summary of the measurements is presented in Table 4. Particle-size analysis of soil samples was conducted according to Elonen (1971).

Chemical analyses

Chemical analyses of soil samples, pig slurry, plant material and of water were conducted according to standard methods.

Crop productivity

A uniformity trial was performed in 1990, in which barley was grown on all plots. This provided yield data which could be used to evaluate possible effects of soil variability on productivity. The results in Table 5 reveal that there is no significant overall difference in inherent soil productivity of the plots used to represent the six treatments in the experiment.

Measurements

The following variables were registered (a more detailed description of the variables and measuring methods will be given in the articles dealing with the results):

Weather (at a standard, automatic weather station 200 m to the southwest of the site):

- air temperature 10 and 200 cm above ground and soil temperature at 10, 20 and 50 cm depths;
- precipitation and snow depths.

Weather at Værnes airport, 5 km distant (official data from the Norwegian Institute of Meteorology):

- air temperature, mean per month (1961-90);
- precipitation, total per month (1961-90).

Table 4. Soil density, porosity and water retension (pF) in topsoil (7-12 cm) and subsoil (25-30 cm).

Soil depths	Density g/cm^3 Dry bulk	Sol-ids	Volume (%) of solids	Volume of water (%) at 0,1 bar	1,0 bar	3,0 bar	15 bar
Topsoil							
Mean	1.13	2.26	49.8	48.4	40.5	36.1	12.5
St.err[1)]	0.02	0.02	0.6	0.6	0.6	0.6	0.2
Subsoil							
Mean	1.76	2.50	70.5	31.0	27.3	24.2	16.2
St.err[1)]	0.01	0.01	0.3	0.4	0.7	0.8	0.8

[1)] Standard error

Table 5. Relative crop productivity of the separate treatments, calculated on the basis of a dummy trial in 1990.Barley grain with 15% moisture, kg per hectare

Barley yield	Treatment 1	2	3	4	5	6	LSD 5%	CV %
Kg grain/ha	3610	3700	3590	3550	3570	3620	170[1)]	5
Rel. yield %	100	103	100	98	99	100		

[1)] Not significant (F=0.69)

Water flow:
- drainage discharge and surface runoff from each plot was registered each hour, and proportional water samples for chemical analyses were collected automatically.

Yield:
- standard yield and quality measurements for the barley crop, chemical composition included.

Pig slurry:
- Chemical composition was determined in samples in the autumn and spring.

NPK fertilizer:
- Two types of Fullgjødsel from Norsk Hydro were compared, one low in cadmium (1 mg Cd/kg P), and the other high in cadmium (400 mg Cd/kg P). To ensure equal amounts of all macronutrients, particular analyses of the fertilizers were obtained from the manufacturing company. The investigation on cadmium will be published separately.

Soil characteristics:
- Soil physical properties were analysed for each plot in topsoil and subsoil before start of the experiment.
- Soil chemical properties were analysed for three depths on each plot before start and at termination of the experimental period, four years later.

Statistical methods

The experiment was treated as a randomized block experiment in the analysis of variance. The LSD method was used to determine significant differences between the treatments. For the tests of variablity, means and standard errors are given.

Level of significance is denoted by * for 95%, ** for 99%, *** for 99.9% probability, and ns for not significant.

Results

Plant nutrients in soil

The different fertilizer treatments influenced the amount of different plant nutrients in the topsoil (0-20 cm). The following results are based on the soil sampling in autumn 1994.

Phosphorus

During the experimental period there was a reduction in the level of readily available phosphorus (P-AL) (Tables 3 and 6). In the plough layer (0-20 cm) the P-AL value for the treatment without fertilizer was significantly lower compared with spring application of pig slurry on spring ploughed land (treatment 4). Application of pig slurry in the autumn showed approximately the same P-AL status as treatment without fertilizer (Table 6). In the plough layer there was a tendency

Table 6. P-AL phosphorus in soil samples from six treatments at three depths, at termination of the experiment, autumn 1994.

Treatment	0-20 cm	40-60 cm	80-100 cm
1. Pig slurry in autumn, AP[1)]	5.5	7.3	11.2
2. Pig slurry in spring, AP	6.0	7.1	11.1
3. NPK fertilizer, AP	5.7	7.4	11.4
4. Pig slurry in spring, SP[2)]	6.8	6.6	11.0
5. NPK fertilizer, SP	6.4	6.9	10.1
6. No fertilization, SP	5.4	7.5	10.9
$LSD_{5\%}$ ..	1.2	1.4	1.6
Level of significance*	ns	ns	ns

[1)]AP: autumn ploughing [2)] SP: spring ploughing

toward higher P-AL values on spring ploughed plots, com-pared with autumn-ploughed plots, although this trend was not significant. In the two subsoil layers no significant differences in P-AL values were recorded for the different experimental treatments.

Potassium

In the topsoil the highest values for readily available potassium (K-AL) were found on fertilized and springploughed treatments (Table 7). Pig slurry applied in the autumn and ploughed in immediately (treatment 1) had K-AL values at approximately the same level as plots with no fertilization (treatment 6). On plots where NPK fertilizer and pig slurry were applied in the spring, the K-AL values were discernibly higher on springploughed plots compared with autumnploughed plots. After use of the same amount of NPK fertilizer, significantly higher K-AL values were found for springploughing, compared with autumnploughing. In the subsoil layer at 40-60 cm the lowest K-AL values were found on unfertilized plots (treatment 6). In this layer the

Table 7. K-AL potassium in soil samples from six treatments at three depths, at termination of the experiment, autumn 1994.

Treatment	0-20 cm	40-60 cm	80-100 cm
1. Pig slurry in autumn, AP[1)]	7.4	9.2	13.0
2. Pig slurry in spring, AP	9.0	9.6	12.9
3. NKP fertilizer, AP	8.1	10.2	13.2
4. Pig slurry in spring, SP[2)]	9.1	9.4	13.0
5. NPK fertilizer, SP	9.3	10.3	12.5
6. No fertilization, SP	7.1	8.6	12.8
$LSD_{5\%}$	1.2	1.0	0.6
Level of significance	*	*	ns

[2)] AP: autumn ploughing [2)] SP: spring ploughing

treatments with NPK fertilizer had significantly higher K-AL values than unfertilized soil, whilst the plots with slurry came in an intermediate position. In the deepest subsoil layer (80-100 cm) no significant differences could be found.

Mineral nitrogen

In the topsoil (0-20) the nitrate-N content was significantly influenced by fertilizing practices (Table 8). As expected, the unfertilized plots had the lowest concentration, but pig slurry applied in the autumn also showed low values. NKP fertilizer applied on springploughed soil also showed a low nitrate content, while the highest nitrate-N concentrations were found after use of NKP fertilizer applied on autumnploughed land and pig slurry applied in spring. On plots where NPK fertilizer was applied, the nitrate-N content was significantly higher on autumnploughed plots, compared with springploughed plots.

For ammonium-N, too, the lowest content was recorded on unfertilized plots (Table 8). On the other hand, the highest content was found where pig slurry was applied in the spring on springploughed soil, and the level was significantly higher than that for NPK fertilizer.

In the upper subsoil layer analysed (40-60 cm) the nitrate-N content was significanly higher where pig slurry had been applied in the spring, compared with autumn applications and unfertilized plots (Table 8). The data show a tendency toward a higher content of nitrate-N after use of pig slurry. The concentration of ammonium-N followed the same pat-tern as that for nitrate-N, and therefore the sum of the two investigated fractions of mineral nitrogen adds up to a signific-antly enhanced level in the soil where pig slurry had been applied. NPK fertilizer also enhanced the total mineral nitrogen in the soil, but not significantly, compared with unfertilized soil.

In the deepest subsoil layer analysed (80-100 cm), no significant differences in content of mineral nitrogen contents were found. For nitrate-N there was a tendency toward a lower content on unfertilized soil (Table 8).

Table 8. Mean nitrate-N (Nit) and ammonium-N (Amm)(µg per 100 g dry soil) content in soil samples at three depths, at termination of the experiment, autumn 1994

Treatment	0-20 cm			40-60 cm			80-100 cm		
	Nit	Amm	Sum	Nit	Amm	Sum	Nit	Amm	Sum
	(µg/100g)			(µg/100g)			(µg/100g)		
1. Pig sl., aut. AP[1])	67	138	205	39	31	70	51	53	104
2. Pig sl., spr. AP	92	140	232	63	67	130	47	67	114
3. NKP fertil. AP	95	131	226	51	47	98	49	54	103
4. Pig sl. spr. SP[2])	85	167	252	62	67	129	51	45	96
5. NPK fertil. SP	71	132	203	50	45	95	49	61	110
6. No fertil. SP	60	96	156	41	31	72	39	59	98
$LSD_{5\%}$	22	32	44	18	39	40	28	32	34
Level of significance	*	*	**	*	ns	**	ns	ns	ns

[1]) AP: autumn ploughing [2]) SP: spring ploughing

Sulphur in soil

As will be communicated in future reports, the loss of sulphur in drain water was relatively high in this investigation (50 kg sulphate-S per hectare, per year). On that background it was interesting to examine the sulphur content in the soil. A summary of the analyses of the topsoil (0-20 cm) is presented in Table 9. No significant results for differences in treatment were recorded. In the topsoil the average content of total S was close to 50 mg per 100 g of dry soil. In the subsoil layers the content was <10 mg per 100 g.

Erosion material

Erosion material was collected continuously in traps at the lowermost end on all plots. During the experimental period the sediment was taken out, dried, weighed and analysed on five different occasions.

Quantities

Although the erosion was moderate on this gently sloping field, a significantly larger loss of soil in autumnploughed plots was registered, compared with spring-ploughed plots (Table 10).

Chemical properties of erosion material

For autumnploughed plots the loss on ignition was significantly higher where pig slurry was applied before ploughing (Table 11).

Readily available phosporus was highest in erosion material from plots where pig slurry was applied in the autumn, and lowest where the slurry was applied in the spring. Material from unfertilized plots, and from plots supplied with NPK fertilizer had medium P-AL values (Table 11).

Readily available potassium was significantly lower in erosion material from plots where no fertilizer was applied (Table 11). On autumnploughed land the

Table 9. Mean values of total sulphur in the topsoil (0-20 cm) for the separate treatments. mg per 100 g of dry soil.

	Treatments						LSD
	1	2	3	4	5	6	5%
Total-S	48	46	52	47	49	48	7[1]

[1] Not significant (F=0.65)

Table 10. Mean values for soil erosion on autumn and spring ploughed plots, for separate periods, and in sum for 4 years. Kg dry soil per hectare

Time for ploughing	May 1992	Oct. 1992	June 1993	June 1994	Oct. 1994	Sum for 4 years
Autumn	11.9	12.2	21.1	23.9	8.5	77.5
Spring	5.7	5.8	7.6	19.3	6.5	44.9
$LSD_{5\%}$	5.8	7.0	8.2	7.6	2.0	21.7
Level of sign.	*	ns	**	ns	*	**

Table 11. Mean values for chemical characteristics in erosion material collected from the separate plots. Average of foursampling times

Treatment	Ignition loss %	Kjeldahl N%	P-AL	K-AL	K-HNO_3	Total S (mg/100g)
			mg/100g air dry soil			
1. Pig sl., aut. AP[1)]	12.2	0.63	19.6	51	298	79
2. Pig sl., spr. AP	9.8	0.54	13.8	59	354	55
3. NPK fertil. AP	9.0	0.49	15.4	50	359	53
4. Pig sl., spr. SP[2)]	10.4	0.59	13.1	53	343	58
5. NKP fertil. SP	10.4	0.59	16.5	52	330	59
6. No fertil.SP	11.0	0.50	14.5	44	297	58
$LSD_{5\%}$	1.7	0.12	4.4	7	38	13
Level of significance	*	*	*	**	**	**

[1)] AP: autumn ploughing[2)] SP: spring ploughing

erosion material from plots where pig slurry was applied in the spring had significantly higher K-AL values. Potassium extracted with nitric acid showed lowest values in erosion material on plots where pig slurry was applied in the autumn and on unfertilized plots. Potassium extracted in 1N nitric acid also showed the lowest values for unfertilized plots and plots where pig manure was applied before ploughing in the autumn.

For Kjeldahl-N, the highest values in erosion material were found on plots fertilized with pig slurry in the autumn, and the lowest values on unfertilized plots and where NPK fertilizer was used on autumnploughed soil (Table 11).

The concentration of total-S was significantly highest in erosion material from plots where pig manure was applied in autumn. Pig slurry and NPK fertilizer applied in the spring did not raise the S concentration, compared with plots without fertilization (Table 11).

Texture of erosion material

Table 12 presents the mean values for particle size of erosion material for autumn- and springploughed plots separately.

No significant differences between the two ploughing times were registered. On the other hand, the content of clay was considerably higher in the erosion material compared with the topsoil from the same plots (see Table 2).

Discussion

A comparison of the P-AL values at the start (Table 3) and at termination of the trial (Table 6) reveals a considerable lower phosphorus content in the soil at termination. This may be due to relatively small applications of P in the period of experimentation, compared to previous practice. Loss of phosphorus through erosion and drainage is not thought to have contributed significantly to that decline, as will be communicated in future reports. The P-AL fraction usually

Table 12. Mean values of soil particle size in erosion material from autumn- and springploughed plots. Data in weight percent. Average of four sampling times

Time for ploughing	Sand 2.0 – 0.6 mm	Sand 0.6 – 0.2 mm	Sand 0.2 – 0.06 mm	Silt 0.06 – 0.02 mm	Silt 0.02 – 0.006 mm	Silt 0.006 – 0.002 mm	Clay < 0.002 mm
Autumn	2.3	4.3	4.0	7.3	12.0	12.1	57.9
Spring	2.6	5.1	4.5	9.0	12.1	11.7	54.8
$LSD_{5\%}$ [1)]	1.0	1.5	1.0	1.3	1.4	1.0	4.5

[1)] $LSD_{5\%}$ not significant for any particle-size group

amounts to 10-20% of the total P content in the soil (Krogstad & Løvstad 1988), and in this way it is possible that some of the readily available phosphorus may have been more strongly absorbed to the soil particles during the experimental period, thus being rendered unprovable by the AL-method.

As expected, the lowest content of plant nutrients in the topsoil was found for the unfertilized soil. The level of readily available potassium and phosphorus in the topsoil at the treatment with slurry application and ploughing in autumn was approximately at the same as that for unfertilized soil, while the highest level of organic matter, total-N and readily available phosphorus in erosion material was found in the treatment with slurry application and ploughing in autumn. This indicates that the combination of slurry application and ploughing in autumn causes more loss of plant nutrients than the same operation carried out in the spring.

Although autumnploughing caused an increase in erosion loss of 73% compared with spring ploughing, the total erosion loss was small. The small quantities of erosion material were a result of the gentle slope of 1-2%, to a plot length of only 36 m, and relatively few days with heavy rain and snow-melt. However, the suspended dry matter in the runoff also represents erosion, and will be discussed in future articles. As will be seen in future articles, most of the surplus precipitation passed through the soil and escaped through the drain pipes. A considerable internal soil erosion took place through cracks and other macropores, and in that way a larger portion of soil was lost in the drain water discharge, compared with surface runoff. Oskarsen & Amdal (1994) have reported correspondingly small quantities of runoff water and erosion material from a recently drained field with a steeper slope at Skjetlein in Trondheim.

Acknowledgements

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slurry, plant material, water, and pF-analyses were carried out at the laboratories at Holt Research Centre, Tromsø. Mineral nitrogen in soil samples was analysed at Apelsvoll Research Centre, division Kise. Thanks are also extended to the staff and the co-workers of the above mentioned laboratories.

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The Kvithamar field lysimeter II. Pipe drainage, surface runoff and nutrient leaching

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Nutrient losses after different treatments with slurry and commercial fertilizer, combined with autumn or spring ploughing, were investigated in a four-year period on a silty clay loam soil in central Norway. Approximately 75 % of the water came through the drainage pipes, and 25% as surface runoff. Surface runoff mainly occurred in periods with melting snow or heavy rain on frozen soil. Most of the eroded material was found as suspended in the water from the drainage pipes, and there was very little surface erosion in the experimental period. Greatest losses of nitrogen and phosphorus were found when pig slurry was applied before ploughing in autumn, and the highest losses were found in the winter months. Autumn ploughing caused significantly higher losses of nitrogen and phosphorus than spring ploughing. There were also significantly higher losses of nitrogen and phosphorus from treatments receiving NPK fertilizer compared to treatments receiving only pig slurry.

Key words: Clay soil, erosion, fertilizer, leaching, nitrogen, phosphorus, pig slurry, potassium, runoff.

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Animal manure is a very valuable source of plant nutrients, but also a source of water pollutants. In Norway most of the cattle and pig manure is stored as slurry. In districts in central Norway dairy or pig farming combined with cereal production is common. In Norway, as in many other countries, the focus has been on pollution from agriculture, mostly concentrated on runoff and leaching of plant nutrients. Application of slurry in autumn before ploughing has been a common practice, due to shortage of storage and a short growing season. Such application has been reported to increase loss of nitrogen by leaching or denitrification during autumn and winter (Brink & Jernlås 1982; Paul & Zebarth 1993), but a good cover crop could almost prevent such loss (Bertilsson 1988). Effects on leaching and runoff of different cropping systems using mineral fertilizer and slurry in the Nordic

countries have been investigated by Uhlen (1978), Torstensson et al. (1992), Lindén et al. (1993) and Thomsen et al. (1993).

The aim of this investigation was to register nutrient leaching in drainage discharge and surface runoff from agricultural soil in humid areas of Norway.

In this paper the effects of autumn and spring ploughing, autumn and spring application of pig slurry and use of NPK fertilizer on nutrient loss by runoff and leaching, and loss of soil material by erosion, in a field lysimeter in central Norway are presented. Another aspect was to include analyses of runoff water from an uncultivated soil of the same type, under natural forest. A detailed description of the objectives and methods used in this experiment is presented in Myhr et al. (1996).

Material and methods

Experimental design

The lysimeter included six treatments randomized within each of three replications, making 18 plots measuring 36 m x 8 m. The treatments concerned time of ploughing, time of fertilizing and kind of fertilizer:

1. Autumn ploughing, pig slurry supplied before ploughing,
2. Autumn ploughing, pig slurry supplied in the spring,
3. Autumn ploughing, NPK fertilizer supplied in the spring,
4. Spring ploughing, pig slurry supplied in the spring,
5. Spring ploughing, NPK fertilizer supplied in the spring,
6. Spring ploughing, no plant nutrients supplied.

After spring ploughing the plots were tine cultivated, and fertilizer and slurry were applied to the plots. As soon as possible thereafter the field was harrowed and spring barley sown. A more detailed description of the experiment treatments can be found in Myhr et al. (1996).

Soil type

A detailed description of the soil type is presented in Myhr et al. (1996). The soil type is a poorly drained silty clay loam, with 6% sand, 62% silt and 32% clay, a Typic Cryaquept according to Soil Survey Staff (1975). The content of organic matter is approximately 11% in the top layer.

The weather in the experimental period

The weather conditions were recorded at an automatic climate registration station 200 m distant from the field lysimeter. The number of parameters registered increased during the experimental period. Temperature and precipitation were measured every hour during the whole period. At the end of the period frost in soil was also registered. Temperature and precipitation levels during the experimental period are shown in Figs. 1 and 2. The means for 1961-90 are given for Værnes, situated 5 km south of Kvithamar.

The winter 1993/94 was cold with frozen soil and stable snow cover. The other winters, however, were mild with almost no frost in the soil. The mild winters had a considerable amount of precipitation, most of it as rain.

Measurement of water flow

A description of the installation of the lysimeter can be found in Myhr et al. (1996). The surface runoff water and the pipe drainage water from each of the 18 plots ran into separate tipping buckets, making a total of 36 buckets. All the

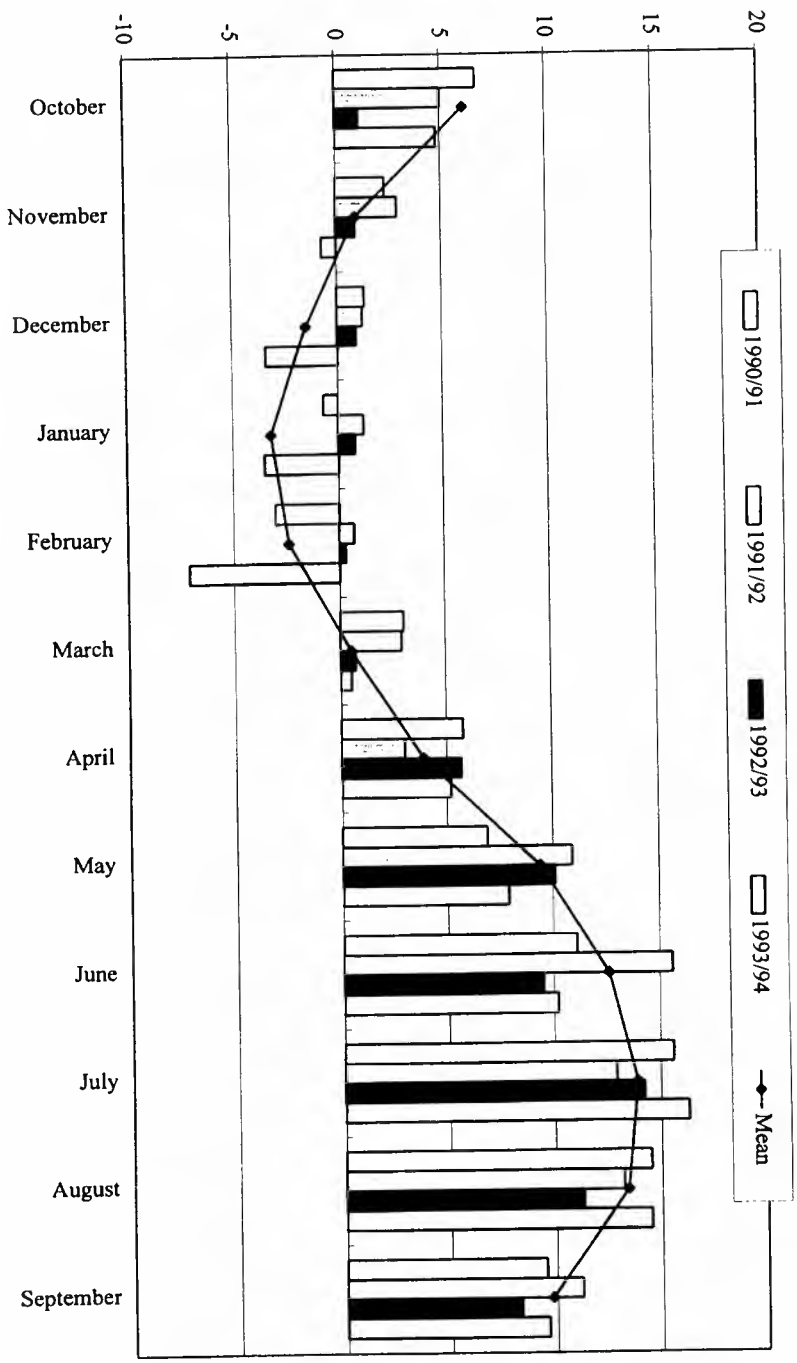

Fig. 1 Temperature at Kvithamar (°C) in the experimental period. Mean is from Værnes (5 km distant) for the period 1961-90.

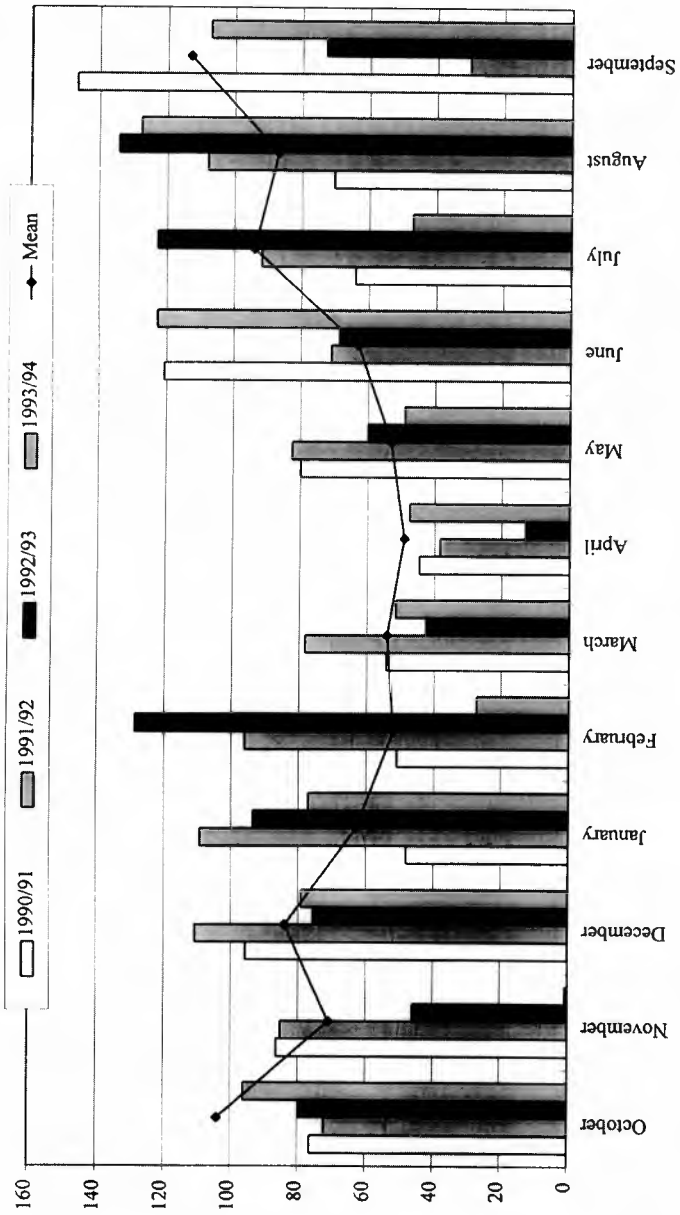

Fig.2. Precipitation at Kvithamar (mm) in the experimental period. Mean is from Værnes (5 km distant) for the period 1961-90.

buckets were connected to a datalogger, which recorded all tips, and gave information about the water flow each hour of the experimental period. As a supplement to the datalogger all the buckets had a mechanical counter. The buckets were calibrated for three litres. The exact volume of the different buckets was measured before the experiment started, and by recalibration once a year.

Chemical analyses of the water

For every second tip of the tipping buckets a sample of approximately 5 ml water was caught by a tube running into a sample container. Consequently the samples were taken proportionally to the water flow. There was one sample container for each tipping bucket, stored in the cellar of the measuring houses. Once a month a one litre representative sample was taken from each of the sample containers and sent for analysis to the Chemical Analysis Laboratory at Holt Research Centre, Tromsø. The analyses were done according to the Norwegian Standard for chemical analysis of water samples. In some cases nutrient concentrations were not detectable, and in such an event the value was set to 0 (zero).

Treatments 1, 2, 3 and 5 only were analysed during the first seven months. From 2 May 1991, however, all plots were analysed whenever there was sufficient water in the sample containers. In dry periods there was of course neither information about water flow nor water chemical analyses.

The number of parameters analysed at Holt increased during the experimental period. All the samples were analysed for total suspended dry matter, total suspended ash, total phosphorus, total dissolved phosphorus, phosphate-phosphorus, total nitrogen, nitrate-nitrogen, ammonium-nitrogen, calcium, magnesium and total potassium. From 1 February 1991 sulphur was analysed, from 1 January 1992 dissolved potassium was analysed, from 1 March 1992 total sodium was analysed, and from 1 January 1993 chlorine was analysed.

According to the Norwegian Standard for analysis of water, the samples should be analysed within 24 hours after they were collected or preserved in sulphuric acid. In our case the sample containers were filled more or less continuously for one month before the samples were collected and sent to the laboratory. The storage temperature was seldom higher than 5 °C, and never higher than 11 °C. Turtola (1989) found that samples stored for two weeks at 4 °C before analysis caused insignificant changes in nitrate-N, total-P and phosphate-P, but a significant decrease in ammonium-N. However, after 12 weeks' storage at the same temperature the concentrations of total-N and nitrate-N had increased by 13% and 12% respectively, and those of total-P and phosphate-P had decreased by 6% and 3%. Since we know that sampling proportional to water flow gives better estimates of the nutrient losses than the same amount of discrete samples, the errors related to sampling and analysing seem to be relatively low in our investigation, we assume an error rate of less than 10% for total-N, nitrate-N, total-P and phosphate-P.

From the middle of June 1993 water samples were collected for chemical analyses, on the same days as those from the field lysimeter, from a small creek running through a forest pasture located at a distance of 7 km from the lysimeter. The soil in the area is not given a detailed description, but can be characterized as a marine deposit of silt loam and silty clay

loam. The elevation is about 20-150 m a.s.l. The dominating vegetation in the lower part of the basin is old alder (*Alnus incana*). In the higher part of the basin there is a greater abundance of spruce (*Picea abies*), and in the whole basin there is some bird-cherry (*Prunus padus*), wych elm (*Ulmus glabra*) and rowan (*Sorbus aucuparia*). The herb vegetation in the lower part consists of nitrophile species such as ostrich-fern (*Matteuccia struthiopteris*), raspberry (*Rubus idaeus*), meadow-sweet (*Filipendula ulmaria*), willow-herb (*Epilobium angustifolium*) and nettle (*Urtica dioica*). Since the samples were not taken proportionally to the water flow, and the size of the basin was not measured, it is therefore not possible to calculate nutrient losses per hectare. Only concentrations of nutrients can be compared.

Statistical methods

In periods with no runoff the monthly values were set to zero (and not to missing data). The data were analysed on the basis of the analysis of variance with yearly totals as experimental units. The different LSD results were used for comparison. All the data analyses were carried out with the help of the software package Statistical Analysis System (SAS).

Results

Water flow

Most of the runoff came through the drainage pipes. As a mean of the six treatments in 4 years 75% of the water came through the drainage pipes, and the rest as surface runoff. The different treatments had a very similar pattern of water flow. Treatment 4 had relatively more surface runoff than the other treatments. This pattern is due more to soil sedimentation in the drainage pipes than the effect of the treatment. The treatments ploughed in the autumn had a slightly higher runoff (both surface and pipe runoff) than those ploughed in the spring, but the differences were small.

Precipitation and runoff varied from time to time over the year. The relationship between pipe drainage and surface runoff also varied, according to precipitation and temperature. Monthly data are shown in Table 1, and graphs based on 24-h-data are shown in Figs. 3 and 4.

Surface runoff mainly occurred in periods with melting snow or heavy rain on frozen soil. The most dramatic surface runoff episode took place toward the end of March and at the beginning of April 1994. The winter had been cold, and there was a 40-50 cm layer of snow. Suddenly, the temperature increased, and an intensive snowmelt occurred. The soil was still frozen, and consequently all the runoff was on the surface. The maximum runoff was 37 mm per day. After some days with high temperatures, the ice in the soil melted, and the rest of the excess water drained through the pipes. The maximum drainage runoff, however, was found several days after the maximum surface runoff.

Also in periods with protracted precipitation, causing the soil to be completedly filled up with water, there was some surface runoff. This was found in the winters 1991/92 and 1992/93, with a maximum runoff of 12-15 mm per day. The runoff that took place in the winter 1992/93 differed from the «normal» pattern. Normally there was very little difference in surface runoff between autumn and spring ploughing. In this particular winter, however, the spring-

Table 1. Precipitation (P), pipe drainage (Pd) and surface runoff (Sr) in mm. Means of six treatments in the months from October 1990 to September 1994

	1990/91			1991/92			1992/93			1993/94		
Month	P	Pd	Sr	P	Pd	Sr	P	Pd	Sr	P	Pd	Sr
October	76	53	2	72	41	3	80	46	6	96	64	10
November	86	52	2	85	62	3	46	19	12	1	6	0
December	96	77	8	111	79	7	76	56	22	79	3	25
January	48	31	8	109	197	32	94	40	12	77	0	20
February	51	0	0	96	82	10	129	110	39	27	0	0
March	54	10	49	78	62	4	42	102	14	52	0	115
April	45	31	12	38	3	0	13	11	0	48	47	159
May	80	16	0	82	12	1	60	15	0	49	8	0
June	121	39	2	63	0	0	69	1	0	123	47	1
July	64	8	1	92	0	0	123	22	0	47	5	0
August	70	9	0	108	54	1	134	62	4	128	37	1
September	147	99	5	30	7	0	73	49	2	107	55	8
SUM	938	425	89	964	599	61	939	533	111	834	272	339

ploughed treatments had a much higher runoff than the autumnploughed treatments. This is due to a better permeability through the soil on the autumnploughed plots. During the same period there were many episodes with drainage pipe runoff, and the autumnploughed plots had a higher maximum drainage than the springploughed plots. The maximum was approximately 30 mm per day in January 1992, and 27 mm per day in February 1993. In the winter 1990/91, too, there were some episodes with a maximum runoff of 28 mm per day.

Overall, the surface runoff and the pipe drainage followed the same patterns with distinct episodes. The surface runoff, however, had a more distinct episode pattern than the pipe drainage, and the surface runoff episode was almost finished when the pipe drainage episode began. The pipe drainage was more stable, and after the most distinct episode the drainage continued for a long time at a low level.

Generally, the runoff was at its highest outside the growing season. This was due to higher precipitation in the autumn and winter than at other times of the year. At the same time there was no crop use of water, and low temperature caused a minimum of evaporation.

During the summer months there was seldom any surface runoff. The showers were not heavy enough to saturate the pores in the soil and thereby cause surface runoff. Some of these showers, however, contained more water than the soil was able to maintain, and therefore at times pipe drainage occurred also during the summer months.

Erosion and losses of soil

There were two kinds of erosion causing soil loss: surface erosion caused by the surface runoff water, and inside erosion caused by the water sinking through the soil profile to the drainage pipes.

Most of the eroded material was found as suspended matter in the water from the

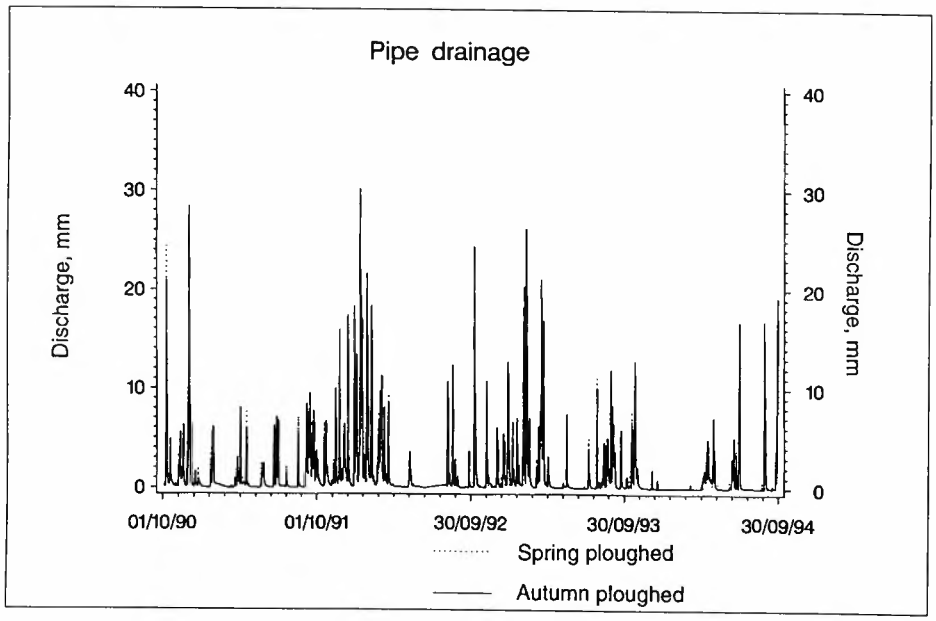

Fig.3. Pipe drainage (mm) in the experimental period. Mean of respectively spring ploughed and autumn ploughed treatments.

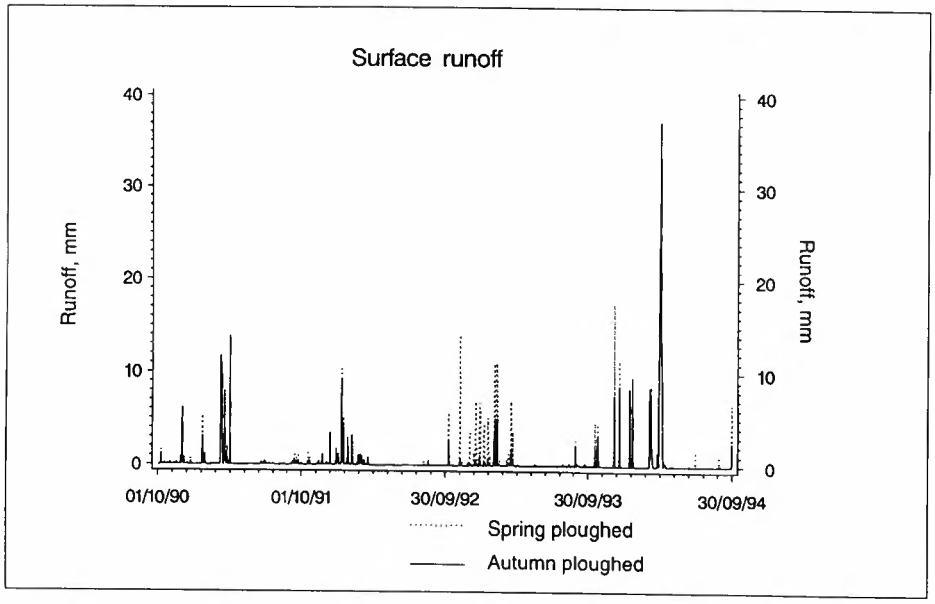

Fig.4. Surface runoff (mm) in the experimental period. Mean of respectively spring ploughed and autumn ploughed treatments.

drainage pipes. Some was also found suspended in the surface runoff water, and some as sedimented material in the sedimentation containers. The amounts of soil losses of the different kinds are shown in Table 2.

Monthly amounts of suspended dry matter, as means of the four-year experimental period, are shown in Table 3. The months with data 0 were either dry, or the content of dry matter was not detectable.

There was very little surface erosion in the experimental period. This is due both to the very flat land (1-2% slope), and to most of the water being drained through the pipes. The erosion was related to precipitation, the water content of the soil, and whether the soil was frozen or not. Relationships regarding the surface-eroded soil that sedimented in the traps are discussed more fully by Myhr et al. (1996). Surface erosion never took place in the months May to October, most of it occurring in the months December to March. There was no significant difference between the treatments in surface erosion.

There was also a moderate soil loss as suspended matter in the pipe drainage water. As for the surface erosion, the inside erosion was related to precipitation, the water content of the soil, and whether the soil was frozen or not. In April to July there was almost no inside erosion. Most inside erosion took place in August to March, with the months December to February reflecting maximum levels. There were significant differences between the treatments concerning inside erosion, with significantly ($p<0.001$) higher soil loss with autumn ploughing than with spring ploughing. As mentioned earlier, there was better permeability through the soil during the winter on the autumn-ploughed plots than on the spring-ploughed plots.

Nutrients in the runoff water

Concentrations of plant nutrients in the runoff water are listed in Table 4.

Nitrogen

The content of total-N in the surface runoff water was moderately different between the treatments. The total-N content of the drainage water was 3-4 times as high as that in the surface water, and with greater differences between the treatments. In the surface water the content of nitrate-N was about half that of total-N, while the amount of nitrate-N was somewhat higher in the drainage water. With the exceptoin of treatment 1, the drainage water had a much lower content of ammonium-N than the surface water. The water from forest pasture had a higher

Table 2. Loss of soil from the different treatments as means of the 4-year experimental period. Kg dry soil per hectare per year

	Treatment					
	1	2	3	4	5	6
Sedimented soil	20	13	25	13	12	10
Suspended in surface runoff	45	45	75	63	20	31
Suspended in pipe water	1029	502	709	246	328	274
Sum	1094	560	809	322	360	315
Ash (suspended)	959	500	708	280	316	277
Organic matter (suspended)	135	60	101	42	44	38

Table 3. Dry matter suspended in water from respectively pipe drainage (Pd) and surface runoff (Sr) each month, as means of the 4-year experimental period. Kg per hectare per year

	Treatment											
	1		2		3		4		5		6	
	Pd	Sr	Pd	Sr	Pd	Sr	Pd	Sr	Pd	Sr	Pd	Sr
January	239	18	190	25	190	30	78	15	65	8	72	11
February	196	4	70	2	115	2	41	9	67	1	24	6
March	45	15	30	10	44	17	20	2	26	4	22	2
April	7	4	7	5	13	7	8	4	7	4	5	4
May	7	0	3	0	4	0	5	0	8	0	4	0
June	8	0	6	0	8	0	5	0	5	0	8	0
July	6	0	4	0	4	0	4	0	4	0	8	0
August	42	0	22	0	25	0	12	0	25	0	38	0
September	43	0	25	0	33	0	18	0	22	0	35	0
October	156	0	40	0	51	0	19	0	18	0	25	0
November	82	0	32	0	52	4	29	2	29	0	21	0
December	200	8	110	9	191	23	33	35	50	5	34	10
Sum	1031	49	539	51	730	83	272	67	326	22	296	33

content of total-N and nitrate-N, and a lower content of ammonium-N than the surface water from any of the lysimeter treatments.

Phosphorus

The content of total-P was higher in the drainage water than in the surface water, while the content of dissolved total-P and phosphate-P was highest in the surface water. The amount of particular phosphorus (the difference between total-P and dissolved total-P) was about 85% in the drainage water and about 33% in the surface water, on average for all treatments. The water from forest pasture had a lower content of different P fractions than the water from any of the lysimeter treat-ments.

Potassium

The content of total-K was 3-5 times higher in the drainage water than in the surface water. The differences between the treatments were moderate. The proportion of particular K (the difference between total-K and dissolved K) was about 25% in the surface water and about 42% in the drainage water, on average for all treatments. The mean loss of total-K and dissolved K was lower from the forest pasture than from any of the lysimeter treatments.

Sulphur, calcium, magnesium, sodium and chlorine

The content of all these elements was much higher in the drainage water than in the surface water. The differences between the treatments were not considerable. The content of these elements in the water from forest pasture was higher than that of the surface water, but lower than that of the drainage water.

Table 4. Concentrations of plant nutrients in the analysed water (mg per litre). Means (arithmetial averages) for the period June 1993 - October 1994

	Pipe drainage water							Surface runoff water							Forest
	Treatment							Treatment							
	1	2	3	4	5	6	$LSD_{5\%}$	1	2	3	4	5	6	$LSD_{5\%}$	pasture
No. of observations	36	36	36	36	36	36		12	12	12	12	12	12		14
Total-N	4.62	3.68	4.25	3.49	5.76	2.69	1,55	1.27	1.06	1.11	0.97	1.32	1.13	0,39	1.52
Nitrate-N	2.89	2.36	3.07	2.34	4.51	1.43	1,54	0.58	0.42	0.49	0.34	0.53	0.63	0,29	1.18
Ammonium-N	0.34	0.03	0.03	0.02	0.02	0.03	0,25	0.31	0.27	0.21	0.25	0.34	0.16	0,11	0.01
Total-P	0.32	0.25	0.24	0.17	0.20	0.23	0,05	0.12	0.11	0.12	0.15	0.18	0.13	0,06	0.04
Dissolved total-P	0.05	0.04	0.03	0.03	0.03	0.03	0,01	0.08	0.06	0.08	0.11	0.13	0.09	0,04	0.01
Phosphate-P	0.04	0.02	0.02	0.02	0.02	0.02	0,01	0.07	0.05	0.07	0.09	0.12	0.08	0,04	0.01
Total-K	12.12	11.73	12.38	11.17	10.55	10.02	1,63	2.52	2.73	2.82	3.17	2.99	2.24	1,12	1.24
Dissolved K	5.77	6.93	6.97	8.16	6.51	4.83	0,71	1.90	1.87	2.06	1.65	2.68	1.89	0,91	0.98
Sulphate-S	11.78	11.96	16.13	15.24	9.96	10.84	4,08	0.67	0.76	0.85	0.55	0.88	0.65	0,63	2.97
Calcium (Ca)	32.33	37.74	37.93	45.70	36.73	29.71	5,32	2.37	3.81	3.17	3.31	4.75	2.95	2,07	30.85
Magnesium (Mg)	17.68	15.39	15.30	20.02	14.01	12.08	5,25	0.57	0.70	0.68	0.73	1.01	0.70	0,26	3.41
Sodium (Na)	33.74	48.16	44.25	58.96	40.64	35.13	8,42	3.76	3.93	3.74	3.70	4.14	3.97	1,16	8.46
Chlorine (Cl)	47.13	74.50	56.75	86.06	61.93	47.51	13,31	6.51	6.77	7.10	7.36	7.19	6.56	2,58	13.97

Correlations between water discharge and concentrations of plant nutrients

For all treatments there was a positive correlation between surface runoff and concentration level of ammonium-N (R^2 between 0.16 and 0.31). For nitrate-N there was a dilution effect of runoff, shown by the negative correlation between runoff and concentration of nitrate-N for treatments 3 and 4 (R^2 0.13 - 0.14). For treatment 1 there was a negative correlation between runoff and concentration of total potassium ($R^2 = 0.18$).

There was a significant positive relationship between drainage water discharge and concentration level of suspended dry matter for all treatments with the exception of treatment 1 (R^2 between 0.07 and 0.23). Also in drainage water there was a dilution effect for nitrogen. For all treatments, excluding treatment 1, a negative correlation between drainage water discharge and total-N (R^2 between 0.05 and 0.11) and drainage water discharge and nitrate-N was found (R^2 between 0.06 and 0.10). There was a pronounced dilution effect for dissolved potassium in drainage water. The negative correlation between dissolved potassium and drainage water discharge was significant for all treatments (R^2 between 0.13 and 0.39). For phosphorus there was a significant correlation between water discharge and total-P for the treatments 2 and 3 (R^2 0.08 - 0.11), and a positive correlation between dissolved total-P and water discharge for treatment 3 ($R^2 = 0.14$), but for treatments 4 and 5 the same relationship showed a negative correlation (R^2 0.05 - 0.07). There was a negative correlation between water discharge and dissolved phosphate-P for treatment 6 ($R^2 = 0.06$).

Losses of plant nutrients

An overview of plant nutrient losses is presented in Tables 5 and 6.

Although treatment 6 did not receive any kind of fertilizer during the experimental period, it did not have the lowest nutrient loss. For most of the nutrients, treatment 4 had a lower loss than treatment 6. This confirms that the content of nutrients in the soil was quite high, and that the natural leakage was not unimportant. The high nutrient content is due to the previous vegetable growth on the field lysimeter area, decribed by Myhr et al. (1996).

Nitrogen

There was a significant difference between treatments concerning loss of total-N, nitrate-N and ammonium-N with the pipe drainage water. The loss of nitrogen was significantly higher from treatment 1 than from any other treatment, especially during the winter months

It was only when slurry was supplied in the autumn that there was more than a «natural» loss of ammonium-N. Concerning total-N and nitrate-N with the pipe drainage water, there was a significantly higher loss from the autumn-ploughed treatments 2 and 3 than from the spring-ploughed treatments 4 and 5 ($p=0.004$ for total-N and 0.012 for nitrate-N). Also for nitrate-N in the surface runoff water there was a significantly ($p=0.019$) higher loss from the autumn-ploughed than from the spring ploughed treatments.

There was also a significantly higher loss of total-N ($p=0.019$) and nitrate-N ($p=0.011$) from the NPK-fertilized treatments (treatments 3 and 5) than from the treatments with slurry (treatments 2 and 4), but the differences were not large.

For all treatments approximately half of the total nitrogen loss was nitrate-N.

Table 5. Losses of plant nutrients, dissolved in the pipe drainage water, as means of the 4-year experimental period. Kg per hectare per year

	Treatment						P-value	LSD5%
	1	2	3	4	5	6		
Total-N	25.3	12.2	13.4	6.1	11.4	7.6	<0.001	3.8
Nitrate-N	15.8	6.8	7.8	2.8	6.8	3.3	<0.001	2.7
Ammonium-N	1.6	0.1	0.1	0.1	0.1	0.1	<0.001	0.4
Total-P	2.2	1.3	1.5	0.6	1.0	0.9	<0.001	0.4
Dissolved total-P	0.3	0.2	0.1	0.1	0.1	0.1	<0.001	0.1
Dissolved phosphate-P	0.2	0.1	0.1	0.0	0.1	0.1	<0.001	0.1
Total-K	80.1	58.8	70.5	37.4	53.2	42.4	<0.001	13.5
Dissolved K	17.7	15.0	16.6	13.3	14.8	11.9	0.004	3.0
Sulphate-S	39.6	35.8	46.0	33.6	35.8	35.4	<0.001	5.4

Table 6. Losses of plant nutrients, dissolved in the surface runoff water, as means of the 4-year experimental period. Kg per hectare per year

	Treatment						P-value	LSD5%
	1	2	3	4	5	6		
Total-N	1.5	1.3	1.5	1.6	0.9	0.9	0.018	0.7
Nitrate-N	0.6	0.5	0.5	0.2	0.2	0.2	0.06	0.3
Ammonium-N	0.3	0.2	0.2	0.3	0.2	0.2	0.12	0.1
Total-P	0.2	0.2	0.3	0.4	0.2	0.2	0.02	0.1
Dissolved total-P	0.1	0.1	0.1	0.1	0.1	0.1	0.02	0.04
Dissolved phosphate-P	0.1	0.0	0.1	0.1	0.1	0.0	0.03	0.05
Total-K	4.0	5.2	6.6	7.2	3.7	3.4	0.03	2.7
Dissolved K	1.6	1.8	2.3	4.1	2.1	1.8	<0.001	1.0
Sulphate-S	0.9	1.4	1.5	1.8	1.1	0.9	0.67	1.0

Phosphorus

There were significant differences between treatments concerning loss of total-P, dissolved total-P and dissolved phosphate-P with the pipe drainage water and with the surface runoff water.

The loss of P with the pipe drainage water was significantly higher from treatment 1 than from any other treatment, especially during the winter months. There was a significantly higher loss of total-P ($p<0.001$) from the autumn-ploughed treatments 2 and 3 than from the spring-ploughed treatments 4 and 5.

There was also a significantly higher loss of total-P ($p=0.017$) from the NPK-fertilized treatments (treatments 3 and 5) than from the treatments with slurry (treatments 2 and 4).

Most of the P-loss from all treatments was particular phosphorus.

Potassium

There was a significant difference between treatments concerning loss of total-K ($p<0.001$) and dissolved K ($p=0.004$) with the pipe drainage water. Only about a quarter of the total K loss in drainage water was dissolved K, while about half of the total K loss with surface runoff was dissolved K.

In drainage water there was a significantly ($p=0.003$) higher loss of total-K from autumn-spread than from spring-spread slurry. There was also a significantly ($p<0.001$) higher loss of total-K from autumn-ploughed than from spring-ploughed treatments (2 and 3 vs. 4 and 5); and a significantly ($p=0.006$) higher loss of total-K from NPK-fertilized treatments (3 and 5) than from slurry-supplied treatments (2 and 4). There were no significant contrasts for dissolved K.

In surface water there were no significant contrasts between treatments concerning loss of total-K. The highest loss of dissolved K came from treatment 4, but there was little difference between the other treatments.

Sulphur, calcium, magnesium, sodium and chlorine

The loss of sulphate-S was significantly higher from autumn-ploughed treatments than from spring-ploughed treatments ($p=0.002$), and significantly higher from NPK-fertilized treatments than from slurry-supplied treatments ($p=0.002$).

There were no significant differences between treatments for loss of calcium, magnesium, sodium or chlorine in drainage water.

In surface runoff the highest loss of sulphur, calcium, magnesium, sodium and chlorine came from treatment 4, but little difference was found between the other treatments.

Discussion

Since the different treatments had very similar water flow patterns and amounts of runoff water, the differences between nutrient loss were caused by differences in nutrient concentration in the runoff water. The differences in nutrient loss between treatments, presented in Tables 5 and 6, do not directly reflect the differences in nutrient content in the water, presented in Table 4. This is due to the fact that the nutrient concentrations from the different treatments did not have the same pattern of variation in relation to the water flow.

The content of nitrate-N was much higher in the drainage water than in the surface water, while ammonium-N showed an opposite trend. This was also found by Uhlen (1989), but the N-content was much lower at Kvithamar than at Ås (Uhlen 1989, 1994) and in Denmark (Hansen 1990). The loose soil in the first years after start of the experiment caused a relatively high loss of particular P with the drainage water. At Ås the highest content of total-P was found in the surface water (Uhlen 1989), and the concentration was higher at Kvithamar than at Ås and in Denmark (Hansen 1990). The K-content in the surface water was a little higher at Kvithamar than at Ås (Uhlen 1989), but in the drainage water the K-content was about 10 times higher at Kvithamar. The soil type contains large amounts of K, and a lot of the K loss is from the K-bank in the soil. Compared to the nutrient concentrations in the water from spring grain plots at Ås (Uhlen 1989), Kvithamar had a higher level of S in the drainage water, but a little lower S-content in the surface water. Kvithamar had a slightly higher content of Ca and Mg, and a 3-5 times higher content of Na and Cl (highest

in the drainage water). The high content of Na and Cl is due to the fact that the soil at Kvithamar is a marine deposit, located 27-29 m above present sea level, whilst the upper marine limit is found at 180 m a.s.l.

Two explanations can be given for the high content of N in the water from the creek in the uncultivated area. First the N-fixating bacteria that live symbiotically with the roots of the alder. Second, the leaf-fall from the alder every autumn. As mentioned before, it is not possible to calculate the nutrient loss per hectare in the uncultivated area. The annual loss of nitrate-N from old spruce forests in southern Sweden was measured to be as high as 7 kg per hectare (Nilsson 1990). The average loss for larger areas was calculated to be 5 kg N per hectare, which is 100 % higher than calculated some years earlier.

The highest runoff and leaching of plant nutrients were found in special episodes in the winter period. Heavy rain on soil without frost caused many episodes with high drainage discharge, and considerable amounts of nitrogen, phosphorus and soil particles were lost through the drainage system in such episodes. Similar patterns of losses of phosphorus and nitrogen have been reported from clay soils in Sweden (Ulén 1995), and from sandy clay soils in Denmark (Hansen et al. 1989). Loss of suspended material in pipe drainage in the winter period have also been recorded at Skjetlein, 50 km west of Kvithamar (Oskarsen & Amdal 1994). However, heavy rain and melting snow on frozen soil caused high losses of plant nutrients by surface runoff at Kvithamar, similar to results on a clay soil at Ås (Uhlen 1978). The surface runoff contributed to a greater part of the total runoff in Finland (Turtola & Jaakkola 1995) than at Kvithamar.

Highest losses of nitrogen and phosphorus were found when pig slurry was applied before ploughing in autumn. High losses of nitrogen after slurry application in autumn have been found previously (Brink & Jernlås 1982, Paul & Zebarth 1993). In previous investigations, applications of slurry have not been reported to cause significant leaching of phosphorus (Uhlen 1978; Gerritse 1980; Unwin 1980; Furrer & Stauffer 1986; Dam Kofoed & Søndergård Klausen 1986). In our investigation significantly more phosphorus was lost in pipe drainage water in the winter period when slurry had been applied in autumn than for other treatments. It is reasonable that this loss is related to macroporous flow and inside erosion after heavy rain on thawed soil in winter, as found by Ulén (1995). The average annual loss of total-P (average of treatments, sum of surface and drainage water) was 1.5 kg per ha. Turtola & Jaakkola (1995) found the average annual loss of total-P from barley to be 1.2 kg per ha in southwest Finland, with most of the loss occuring after the growth period. Uhlen (1989) found the average annual loss to be 0.6 kg per ha from spring grain in southeast Norway. The percentage of particular phosphorus at Kvithamar (72% on average) was mostly transported with the drainage water, and was slightly higher than that found by Turtola & Jaakkola (1995).

At Kvithamar there were significantly higher losses of nitrogen and phosphorus from treatments with NPK fertilizer applied in spring compared to pig slurry applied in spring. In a Danish investigation the opposite trend was found, with significantly higher losses from treatments with slurry (Thomsen et al. 1993).

The combination of humid climate and poorly drained clay soil at Kvithamar may cause considerable losses of nitrate by denitrification, which was not measured at Kvithamar. Since the total amounts of nitrogen applied to the soil are greater in the treatments with slurry compared to the treatment with NPK fertilizer, other losses of nitrogen by ammonia volatilization and denitrification may also be of importance. It is also interesting that there is a considerable loss of nutrients from the treatment with no additional fertilizer at Kvithamar. Compared with unfertilized crops, leaching of nitrate increased only slightly when recommended amounts of nitrogen fertilizer were used in the study by Thomsen et al. (1993).

The positive effects of spring ploughing in reducing nitrogen and phoshorus losses compared to autumn ploughing are also supported by other investigations in Norway (Ludvigsen 1995). Hansen et al. (1989) reports increased N-loss after lack of K, and points out a reduced N-loss after the balanced support of a fertilizer.
The results from this investigation provide a basis for practical conclusions and recommendations. Ploughing in the spring should be preferred rather than ploughing in the autumn, and if animal slurry is supplied, it should be spread in the spring rather than in the autumn.

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