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Performance of five plum rootstocks over 17 years to five commercial important plum cultivars in Norway

JONAS YSTAAS & ODDMUND FRØYNES
The Norwegian State Agricultural Research Stations, Ullensvang Research Station, Lofthus, Norway

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In a rootstock trial over 17 years the performance of the plum rootstocks St. Julien seedling, St. Julien A, Brompton, Myrobalan B and Marianna to the cultivars 'Rivers Early Prolific', 'Opal', 'Oullins Gage', 'Count Althan's Gage' and 'Victoria' was assessed. Tree vigour was affected by rootstocks in the following way: Myrobalan B > Brompton > St. Julien A, St. Julien seedling > Marianna. St. Julien A produced the highest yield to the semi-vigorous 'Opal' and the vigorous 'Count Althan's Gage', while Brompton and Myrobalan B were most productive to 'Rivers Early Prolific' and 'Victoria', both cultivars of moderate vigour. St. Julien A, however, had the highest yield efficiency for all cultivars with the exception of 'Rivers Early Prolific'. Depending on cultivar, fruit size was favourably affected by St. Julien A and Marianna, while trees on Myrobalan B produced smaller fruits. The content of soluble solids was higher in plums produced on Marianna than on Myrobalan B. In conclusion St. Julien A is recommended as a reliable semi-vigorous rootstock for plums.

Key words: Fruit quality, fruit size, plum, rootstock, yield, yield efficiency

Jonas Ystaas, Ullensvang Research Station, N-5774 Lofthus, Norway.

The main cultivars of plums grown commercially in Norway belong to the *Prunus domestica* L. species (Skard 1941). Rootstocks for plums cover several *Prunus* species without causing serious problems of incompatability (Glenn 1961). The classic work by Hatton (1936) on plum rootstocks resulted in selection of clonal rootstocks in preference to seedling rootstocks within four species (*Prunus domestica* L., *P. insititia* L., *P. ceracifera* Ehrh. and *P. munsoniana* Wight). From the comprehensive research activities on plum rootstocks carried out at East Malling Research Station over a 40-year period Glenn (1961) recommended the following rootstocks in addition to a few others:

Rootstock	Botanical species	Vigour
Myrobalan B	*Prunus cerasifera* Ehrh.	Vigorous
Brompton	*Prunus domestica* L.	Semi-vigorous
Marianna	*Prunus cerasifera* Ehrh. x *P.* munsoniana Wight	Intermediate
St. Julien A	*Prunus insititia* L.	Semi-dwarfing

These four rootstocks in addition to St. Julien seedling were included in a trial with five of the most widely grown plum cultivars in Norway ('Rivers Early Prolific', 'Opal', 'Oullins Gage', 'Victoria' and 'Count Althan's Gage') to assess their performance under the soil and climatic conditions prevailing in Norway.

While extensive rootstock trials in Great Britain (Glenn 1961) and Denmark (Dullum & Dalbro 1958) had given much valuable information about the best cultivar/rootstock combinations for standard, widely spaced trees, the present trial aimed at gaining information about the performance of these rootstocks in a more intensive planting system, where trees were formed as free spindles and tree height limited to three metres.

MATERIALS AND METHODS

A trial with four clonal and one seedling rootstock to five commercially important plum cultivars was planted in spring 1970 at Ullensvang Research Station, western Norway at latitude 60°N. The rootstocks included St. Julien seedling, St. Julien A, Marianna, Brompton and Myrobalan B. In order of ripening, the plum cultivars were 'Rivers Early Prolific', 'Opal', 'Oullins Gage', 'Count Althan's Gage' and 'Victoria'. The plant material was 2-year-old trees with 2-3 branches. The leader was cut back by planting. The trees were formed with a central leader as free spindles. The shoots were tied down to 60° during the initial three years and the height of the trees was kept at 3 m by pruning.

For each cultivar, the experimental design was a randomized block with four replications. Each plot had two trees of similar cultivar/rootstock combination. In order to facilitate the management of the trial, each cultivar was planted in two adjacent rows. This arrangement in fact combined five separate experiments representing five cultivars into one trial. Row distance was 5.5 m for the vigorous cultivars ('Count Althan's Gage', 'Oullins Gage') and the semi-vigorous 'Opal'. For cultivars of moderate vigour (Rivers Early Prolific', Victoria') 5 m was used.

Within the row, the distance was 3 m for all cultivars, providing a tree density of 606-667 trees/ha. The soil was a loamy sand high in organic matter (on an average 7%) and was of good fertility. Fertilizer application was monitored by soil analysis every third year. Soil management combined frequently mown grass in the alleyways with 1-m-wide herbicide strips along the tree rows.

Trunk girth was measured annually 25 cm above the graft union. Yield records of every tree on each plot were taken annually. Fruit weight was determined on random samples of 50 fruits from each tree. Samples of 10 fruits from each tree were taken to the laboratory for determination of soluble solids by an Atago Abbe refractometer at 20°C.

Heavy cropping cultivars like 'Opal' and 'Victoria' were thinned by lime sulphur or ethephon (Kvåle & Ystaas 1969; Kvåle 1978) combined with hand-thinning to obtain an optimal crop load.

RESULTS

Tree vigour

Tree vigour as measured by trunk circumference at the end of the experiment (17-year-old trees) was significantly affected by rootstocks (Table 1). Trees on Myrobalan B were more vigorous than on any other rootstock for all cultivars. Trees on Marianna were consistently smaller than those on any other rootstock for the five cultivars tested. While trees on Brompton were more vigorous than those on St. Julien A and St. Julien seedling.

Table 1. Trunk circumference of five plum cultivars as affected by rootstocks at the end of 17th growing season, mean values

	Trunk circumference, cm				
Rootstock	Rivers Early Prolific	Opal	Oullins Gage	Count Althan's Gage	Victoria
Myrobalan B	46.5	60.7	64.3	64.7	52.1
Brompton	43.2	59.7	60.2	56.4	46.5
St. Julien seedling	43.4	52.9	52.0	53.9	44.3
St. Julien A	40.6	54.8	51.0	55.4	39.1
Marianna	37.4	49.5	40.3	39.8	30.8
LSD (P=0.05)	4.8	6.5	8.0	4.3	5.7

Yield

The results are presented in order of ripening of the cultivars. 'Rivers Early Prolific' is a productive cultivar of moderate vigour. Trees of this cultivar on the semi-vigorous Brompton and vigorous Myrobalan B had significantly higher yields than those on the semi-dwarfing St. Julien A and Marianna, which had the smallest crop (Table 2, Figs. 1 and 2). The effect of rootstocks on yield, however, is quite different on the highly productive 'Opal', a semi-vigorous cultivar. Trees on St. Julien A had a significantly higher yield than those on any other rootstock. Trees on Brompton, which came next, had a 20% lower yield than those on St. Julien A. 'Oullins Gage' is a vigorous cultivar with a tendency to late cropping. Cumulative yields were almost similar on Brompton, Myrobalan B and St. Julien A. Trees on these rootstocks had significantly higher yields than those on Marianna. 'Count Althan's Gage' is a vigorous cultivar that comes slowly into bearing and is hardly a reliable cropper. Trees on St. Julien A had the highest yield, producing significantly more than those on Brompton, St. Julien seedling and Marianna. 'Victoria' is a very productive cultivar of moderate vigour. Trees on Myrobalan B had the largest accumulated yield, which was significantly higher than the yields obtained on St. Julien A and Marianna.

Table 2. Cumulative yield 1973-86, kg/tree of five plum cultivars as affected by rootstocks, mean values

Rootstock	Cumulative yield 1973-86, kg/tree				
	Rivers Early Prolific	Opal	Oullins Gage	Count Althan's Gage	Victoria
Myrobalan B	270	164	219	144	252
Brompton	273	215	230	116	242
St. Julien seedling	253	213	179	71	217
St. Julien A	188	268	215	169	204
Marianna	210	192	99	42	127
LSD (P=0.05)	52.4	52.4	79.8	44.6	47.6

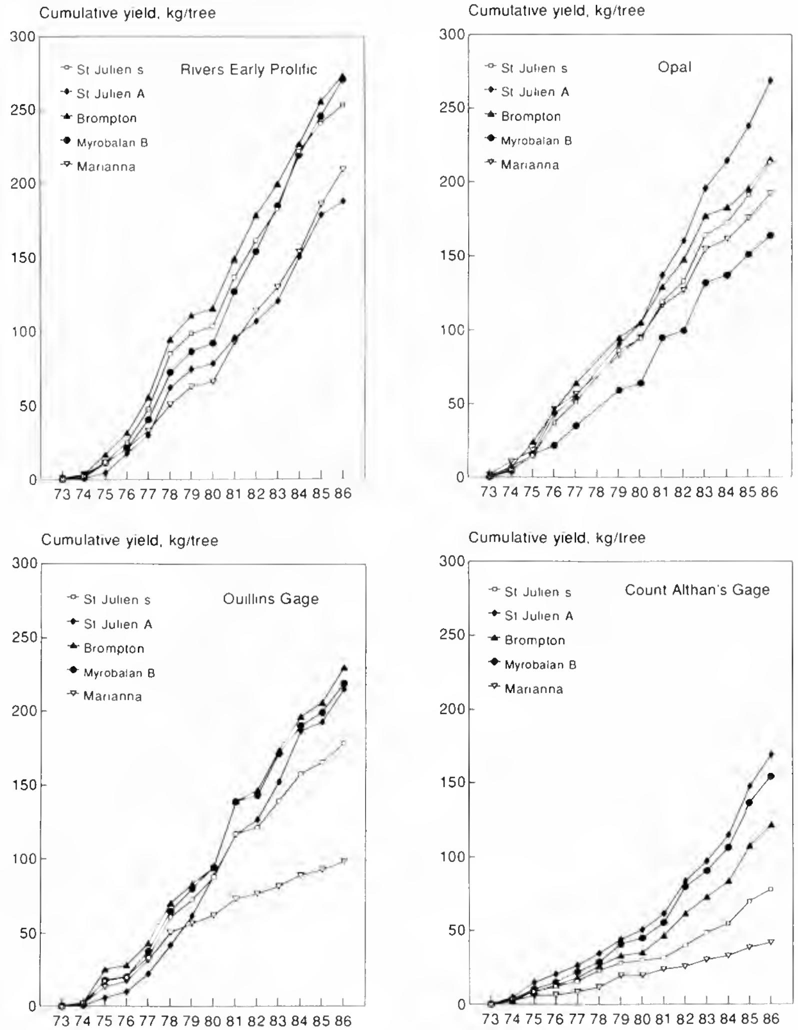

Fig. 1. Effects of five plum rootstocks on accumulated yield of four cultivars over the first 14 cropping years

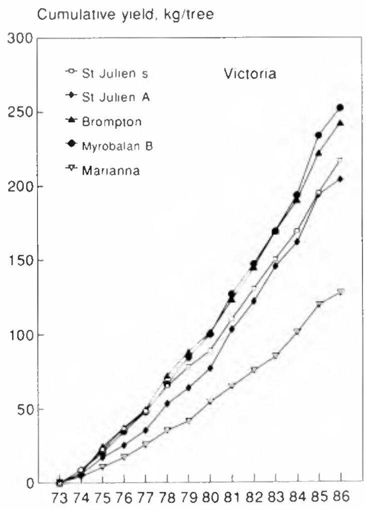

Fig. 2. Effects of five plum rootstocks on accumulated yield of 'Victoria' over the first 14 cropping years

Fruit size and fruit quality

Rootstocks exert an effect on fruit weight (Table 3). A trend towards larger fruits of 'Rivers Early Prolific', 'Opal' and 'Oullins Gage' were found on St. Julien A, while trees of 'Count Althan's Gage' and 'Victoria' produced their largest fruits on Marianna. The smallest fruits were produced on Myrobalan B.

Table 3. Effects of rootstocks on fruit weight of five plum cultivars over 14 years, mean values

	Fruit weight, g/fruit				
Rootstock	Rivers Early Prolific	Opal	Oullins Gage	Count Althan's Gage	Victoria
Myrobalan B	15	28	37	37	32
Brompton	15	30	37	40	34
St. Julien seedling	16	29	36	43	35
St. Julien A	17	30	40	43	34
Marianna	15	29	39	46	36
LSD (P=0.05)	0.8	1.1	NS	3.6	1.8

A similar pattern was found for fruit quality, as measured by the content of soluble solids (Table 4). Plums from trees on Marianna had the highest content of soluble solids for all cultivars, with the exception of 'Rivers Early Prolific'. Fruits of that cultivar had the highest soluble solids concentration on St. Julien A. With the exception of 'Oullins Gage', trees on Myrobalan B had fruits with the lowest content of soluble solids for all cultivars.

Yield efficiency

The accumulated yield over 14 cropping years in relation to trunk cross-sectional area of 17-year-old trees is presented in Table 5. The most yield-efficient trees were found on St. Julien A for all cultivars except 'Rivers Early Prolific'. In addition, trees of 'Victoria' on Marianna were as efficient as those on St. Julien A. In three out of five cultivars trees on Myrobalan B had the lowest yield efficiency.

Table 4. Effects of rootstocks on the content of soluble solids in fruits of five plum cultivars, means of 5 years (1982-86)

	Soluble solids, percent				
Rootstock	Rivers Early Prolific	Opal	Oullins Gage	Count Althan's Gage	Victoria
Myrobalan B	13.8	14.1	13.7	15.8	14.2
Brompton	14.3	14.6	14.0	15.9	14.8
St. Julien seedling	14.4	14.8	14.1	16.2	15.1
St. Julien A	16.0	14.5	13.4	16.1	14.3
Marianna	14.3	15.1	14.2	17.1	15.1
LSD (P=0.05)	1.1	0.6	NS	0.8	0.4

Table 5. Yield efficiency of five plum cultivars as affected by rootstocks, mean values

	Cumulative yield 1973-86, kg per tree/trunk cross-sectional area, cm^2				
Rootstock	Rivers Early Prolific	Opal	Oullins Gage	Count Althan's Gage	Victoria
Myrobalan B	1.56	0.56	0.67	0.44	1.17
Brompton	1.83	0.76	0.80	0.46	1.42
St. Julien seedling	1.70	0.95	0.86	0.31	1.39
St. Julien A	1.44	1.12	1.04	0.70	1.67
Marianna	1.86	0.99	0.77	0.34	1.69
LSD (P=0.05)	NS	0.16	NS	0.19	0.30

DISCUSSION

Tree vigour as affected by different plum rootstocks presented in Table 1 confirms the results reported by Glenn (1961), except that trees on Marianna are less vigorous than those on St. Julien A. Marianna should, according to the results obtained in this trial, be classified as semi-dwarfing in contrast to rootstock in-between the semi-vigorous Brompton and the semi-dwarfing St. Julien A as reported by Glenn (1961). Results obtained in a Norwegian rootstock trial (Husabø 1971) confirm that trees on Marianna are less vigorous than those on St. Julien A. In Danish rootstock trials (Dullum & Dalbro 1958; Christensen

1965) the results reported on the influence of rootstocks on tree vigour are in accordance with the sequence of vigour found in this experiment; Myrobalan B > St. Julien A, St. Julien seedling > Marianna.

When plum trees are widely spaced and yield is accumulated over a number of years, the rootstock effect on cropping appears to be an indirect one, the rootstock governing tree size, which in turn determines the amount of crop (Dullum & Dalbro 1958; Glenn 1961). This relationship is clearly demonstrated for cultivars of moderate vigour like 'Rivers Early Prolific' and 'Victoria' where Brompton and Myrobalan B have the highest cumulative yield per tree when spaced at 5 x 3 m. For more vigorous cultivars like 'Opal' and 'Count Althan's Gage' which utilized the allotted space completely, the semi-dwarfing St. Julien A have induced highest yields. The favourable effects of the semi-dwarfing rootstocks like St. Julien A and Marianna are even more evident when the cumulative yield efficiency is considered.

Fruit size and the content of soluble solids are important components of plum quality (Kvåle & Ystaas 1969; Vangdal 1985). Depending on cultivars, trees on Marianna and St. Julien A produce larger fruits than those on Myrobalan B. This finding is in accordance with results reported by Christensen (1965) and Husabø (1971). Glenn (1961), however, found that the effect of rootstock on fruit size was inconclusive.

The threshold value of soluble solids above which the fruit is found to have an acceptable taste quality was found to be 12.5% for plums (Vangdal 1980). All cultivar/rootstock combinations included in this trial meet this requirement. A clear effect of rootstocks on soluble solids concentration of plum fruits, however, was demonstrated when trees on Marianna and St. Julien produced plums significantly higher in soluble solids content than those on Myrobalan B in four out of five cultivars.

So, depending on cultivars, the less vigorous rootstocks may induce higher yield efficiencies as well as larger fruits of a higher content of soluble solids. This may be caused by a favourable shift in dry matter consumption within the tree from vegetative growth into fruit production.

CONCLUSION

If plum production is to remain economically viable, more intensive planting systems are required. Until a dwarfing rootstock that meets the requirement of moderate vigour, high productivity, satisfactory fruit size and excellent quality is identified, St. Julien A is to be preferred as the best rootstock available.

From the results obtained in this trial St. Julien A can be recommended as a reliable semi-dwarf rootstock of high yield efficiency and with a favourable influence on fruit size and fruit quality.

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N requirements of cabbage crops grown on contrasting soils. I: Field trials

HUGH RILEY[1] & GUNNAR GUTTORMSEN[2]
The Norwegian State Agricultural Research Stations
[1] Apelsvoll Research Station, Division Kise, Nes på Hedmark, Norway
[2] Landvik Research Station, Grimstad, Norway

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N fertilizer trials were performed with irrigated cabbage on soils with high and low water-holding capacity (loam and sand, respectively). Fertilizer rates from zero to 350 kg N/ha were employed. Total dry matter (DM) production, plant N concentrations and soil mineral N reserves (0-40 cm) were measured fortnightly during the growing season. Soil N reserves and plant N concentrations fell more rapidly on sand than on loam. Overall production was highest and optimum fertilizer requirements were lowest on the latter soil type. Suboptimal growth occurred when plant N concentrations were lower than a critical %N which is related to total DM. Apparent N recoveries were higher on loam than on sand, and generally declined with increasing fertilizer application. Implications for the modelling of crop response are discussed.

Key words: Apparent N recovery, critical %N, dry matter, freshweight, N-MIN in soil, plant nitrate, saleable yield, total %N.

Hugh Riley, Apelsvoll Research Station, Division Kise, N-2350 Nes på Hedmark, Norway.

Crop responses to nitrogen fertilizer differ between years at the same site, and within years on soils with contrasting moisture holding capacity, due to variations in nitrogen mineralization and leaching. Fertilization for optimal economic returns and nutrient use efficiency should take account of such variations. One approach is to measure actual levels of nitrogen in plant or soil during the growing season, and to adjust fertilization accordingly. However, such monitoring is usually expensive and/or impracticable, because of high labour and analysis costs and due to time constraints.

Another approach is based on the the modelling of plant growth and nitrogen uptake. Greenwood et al.(1986,1990,1991) have demonstrated how the optimum nitrogen concentration of plants ("critical %N") may be related to dry matter yield levels in a similar manner for a wide variety of plants. Only plants with a nitrogen content below the critical %N level exhibit growth responses to further nitrogen uptake. This concept has been incorporated into simple models which predict N uptake and plant growth from considerations of net mineralization in the soil and of water balance and nitrogen leaching

(Neeteson et al. 1987; Greenwood & Draycott 1989a, b).

This paper presents the results of multiharvest fertilizer trials with summer and winter cabbage grown on contrasting soils in two districts with somewhat differing rainfall. The aim of the paper is to assess the applicability of the critical N concept, whilst the suitability of a simple model for simulating nitrogen uptake and leaching will be discussed in a subsequent paper (Riley & Guttormsen 1994).

MATERIALS AND METHODS

Experimental design

Trials were performed in 1990 and 1991 at two locations (Kise 60°47'N, 10°49'E and Landvik 58°20'N, 8°31'E). Calcium nitrate was applied on main plots at planting at levels of 100, 200 and 300 kg N/ha in addition to a uniform basal dressing of PK fertilizer. A treatment with zero N application was included in order to allow calculations of apparent N recoveries. Main plot size was 30 and 60 m^2 for summer and winter cabbage respectively.

Each main plot was divided into three subplots. Top-dressings of 50 kg N/ha were applied on two of these plots, three and six weeks after planting respectively. This gave a range which varied between 0 and 350 kg N/ha, with increments of 50 kg N/ha (top- dressings were omitted on the zero treatment at Landvik). There were four randomized replicates in each trial.

White cabbage plants were raised under glass for four weeks in peat modules before transplanting. Both a summer variety (cv. Grenadier) and a winter variety (cv. Polinius) were included in all trials. The number of days from planting to harvesting for these varieties is normally around 75 and 145 days, respectively. The date of planting was 10 May at Landvik and 16 May at Kise. Plants were grown in three rows on 1.5 m beds, with 30 cm and 40 cm in-row spacing for summer and winter cabbage, respectively.

Soil physical properties

The trials at Landvik were carried out on adjacent sites on a sedimentary sandy soil, whilst at Kise two morainic loam soils with slightly different textures were used. Core samples, taken at 10-15 cm depth intervals in 3-4 representative profiles at each site, were analysed using standard laboratory procedures for pore and grain size distributions and air permeability. Mean results for each site are presented in Table 1.

The soil at Landvik is an almost pure sand, predominately medium sand (0.6-2 mm). The soils used at Kise may be classified as sandy loam and loam for the years 1990 and 1991 respectively. Total porosity was similar at all sites, and declined somewhat with depth. Moisture retention properties were, on the other hand, markedly higher in the two Kise soils than in the Landvik soil. Despite the difference in texture between the two Kise soils, their moisture retention properties were very similar.

Available water capacity (AWC) was in all cases considerably higher in the topsoil than in the subsoil. No roots were visible below 40 cm at Landvik, probably because of the coarseness of the soil, and only a few at Kise, probably because of high bulk density. Previous studies of water uptake and ^{32}P-recovery have indicated a maximum rooting depth for most crops of around 60 cm in the soils at Kise (Riley 1989). The capacity for plant-available water in the root zone is estimated to be around 55 mm at Landvik and 90 mm at Kise.

Table 1. Soil physical properties at the trial sites

Depth	Gravel[1] %	Sand[2] %	Silt[2] %	Clay[2] %	Bulk density Mg/m^3	Ignition loss %
LANDVIK						
0-30 cm	5	93	5	2	1.38	3.8
30-60 cm	13	97	2	1	1.51	0.8
60-90 cm	8	96	3	1	1.57	0.4
KISE 1990						
0-30 cm	11	61	23	16	1.49	5.5
30-60 cm	14	63	22	15	1.67	2.0
60-75 cm	-	-	-	-	-	-
KISE 1991						
0-30 cm	17	35	40	25	1.28	8.7
30-60 cm	25	50	36	14	1.79	3.6
60-75 cm	27	49	39	12	1.84	3.2

[1] Weight % of bulk sample. [2] Weight % of fine earth (<2 mm).

Depth	Total porosity %	Air capacity %	Air permeability μm^2	Moisture retention capacity pF2-3 %	pF3-4.2 %	pF4.2-7 %	AWC mm
LANDVIK							
0-30 cm	44	24	33	7	8	0.4	47
30-60 cm	38	29	43	4	4	0.8	25
60-75 cm	35	27	22	4	4	0.3	-
KISE 1990							
0-30 cm	43	10	7	6	17	11	67
30-60 cm	36	9	2	4	12	11	47
60-75 cm	-	-	-	-	-	-	-
KISE 1991							
0-30 cm	50	17	24	5	17	13	65
30-60 cm	34	10	15	3	12	9	43
60-75 cm	32	8	4	3	13	7	-

Water infiltration, assessed on the basis of air capacity and air permeability, is expected to be extremely rapid at Landvik, whilst at Kise it is moderately rapid in the topsoil, but somewhat lower in the subsoil. Together with the shallower rooting depth and lower moisture-holding capacity at Landvik, this suggests that this soil is more prone to leaching than the two soils at Kise.

Weather conditions and irrigation

Monthly data for each site are given in Table 2 for weather variables which characterize the temperature and moisture regimes in the trial years. Temperature levels were consistently highest at the more southerly site, Landvik. Temperatures were close to normal in most months, except in June 1991 which was colder and wetter than normal at both sites.

Table 2. Weather conditions and irrigation in the trial years

		May	June	July	Aug.	Sept.	May-Sept.
AIR TEMPERATURE °C							
Landvik	1990	11.9	14.2	16.2	15.7	10.2	13.6
Kise	1990	8.3	13.7	14.8	14.8	9.5	12.2
Landvik	1991	10.3	11.2	16.9	15.4	12.3	13.2
Kise	1991	8.9	10.5	16.3	15.2	10.0	12.2
GLOBAL RADIATION MJ/m^2							
Landvik	1990	591	527	608	487	235	2448
Kise	1990	561	552	509	416	231	2038
Landvik	1991	591	432	493	386	311	2213
Kise	1991	596	469	589	449	273	2376
POTENTIAL EVAPORATION mm							
Landvik	1990	80	66	82	70	41	339
Kise	1990	76	76	73	65	39	329
Landvik	1991	88	57	66	62	55	328
Kise	1991	95	60	73	68	56	352
PRECIPITATION mm							
Landvik	1990	37	93	98	168	170	566
Kise	1990	19	64	94	57	43	277
Landvik	1991	0	149	57	43	207	456
Kise	1991	10	136	52	29	58	285
IRRIGATION mm							
Landvik	1990	50	30	40	40	0	160
Kise	1990	36	0	20	13	0	49
Landvik	1991	75	0	75	50	25	225
Kise	1991	15	20	15	15	20	85

Potential evaporation, measured from an evaporimeter with an open surface area of 0.25 m^2 at Kise and calculated from weather data at Landvik using a formula derived for such an evaporimeter (Riley 1989), was broadly similar at both sites. This reflects the fact that levels of incoming radiation were also similar.

Conditions were relatively dry in May 1990, and extremely dry in May 1991. Somewhat different irrigation strategies were followed at the two sites, since a greater deficit (around 40 mm) was deemed permissible on the less drought-prone soils at Kise than at Landvik, where irrigation was usually given when the deficit reached around 20 mm. This resulted in much greater total amounts of irrigation (and possibly of leaching) at Landvik than at Kise.

Sampling and analytical methods

Plants were harvested at fortnightly intervals, starting three weeks after planting, in order to assess dry matter (DM) production and nitrogen concentrations. Six whole plants were cut at ground level on each subplot. Soil samples at 0-20 and 20-40 cm depths were taken at each harvest in order to assess mineral nitrogen levels.

Summer cabbage was sampled four to six times, depending on development rates in the individual trials, whilst winter cabbage was sampled nine times at Landvik and ten times at Kise. The length of the growth period was about two weeks shorter at Landvik than at Kise, in accordance with the temperature differences observed.

Levels of nitrate in the plant material were measured using an ion-selective electrode (Orion model 93-07) following extraction of fresh-frozen material by boiling in 0.2 M $CuSO_4$. Kjeldahl-N levels were measured following standard acid digestion.

The amount of nitrate included in the latter analysis is the subject of some uncertainty. A comparison of Kjeldahl-N with total-N analysed using a combustion elemental analysis technique (Perkin-Elmer) was therefore performed on a subset of 20 samples with nitrate content varying between 0 and 1.5% of DM. This suggested that about two thirds of the nitrate present in the plant is included in the Kjeldahl-N figures, irrespective of nitrate level.

Nitrate and ammonium levels in soil samples were analysed by the hydrazine reduction and salicyulate/cyanurate methods respectively, using autoanalyser spectrophotometry (SKALAR) following extraction of fresh or frozen samples by shaking in 1 M KCl for one hour (1:5 ratio). The sum of these fractions is designated "N-MIN", expressed on a quantitive basis after correction for moisture content and the dry bulk density of the soil. Standard values of 1.25 and 1.50 Mg/m^3 were used in the latter calculations, for the upper and lower soil horizons respectively.

Calculations

Critical N concentrations in the plant material were calculated from the individual plot DM data, using the formula given by Greenwood & Draycott (1989a):

$$\text{Critical }\%N = 1.35(1 + Be^{-0.26W}) \quad (1)$$

where W = DM Mg/ha and B = 3.07 for cabbage. Using the latter constant, this formula gives almost identical values to those obtained with a formula derived for arable crops (Greenwood et al. 1986). The calculated critical %N values were also used to estimate plant nitrate-N concentrations according to a relationship derived empirically for cabbage in England (Greenwood, pers. comm.). This makes use of the ratio between actual %N (x) and critical %N (y):

$$\%NO_3\text{-}N = (0.3580 * a - 0.5832) * b \quad (2)$$

where a = x and b = 1 when $x>y$, else a=y and $b = 0.37(x/y)^3$.

RESULTS

Soil mineral nitrogen levels

Total amounts of N-MIN found on different dates within the upper 40 cm are shown in Fig. 1 for the plots which did not receive top-dressing. Some extremely high values (600-1100 kg/ha), from the first sampling at Kise, are omitted. These were probably due to sampling error caused by incomplete dissolving of the fertilizer.

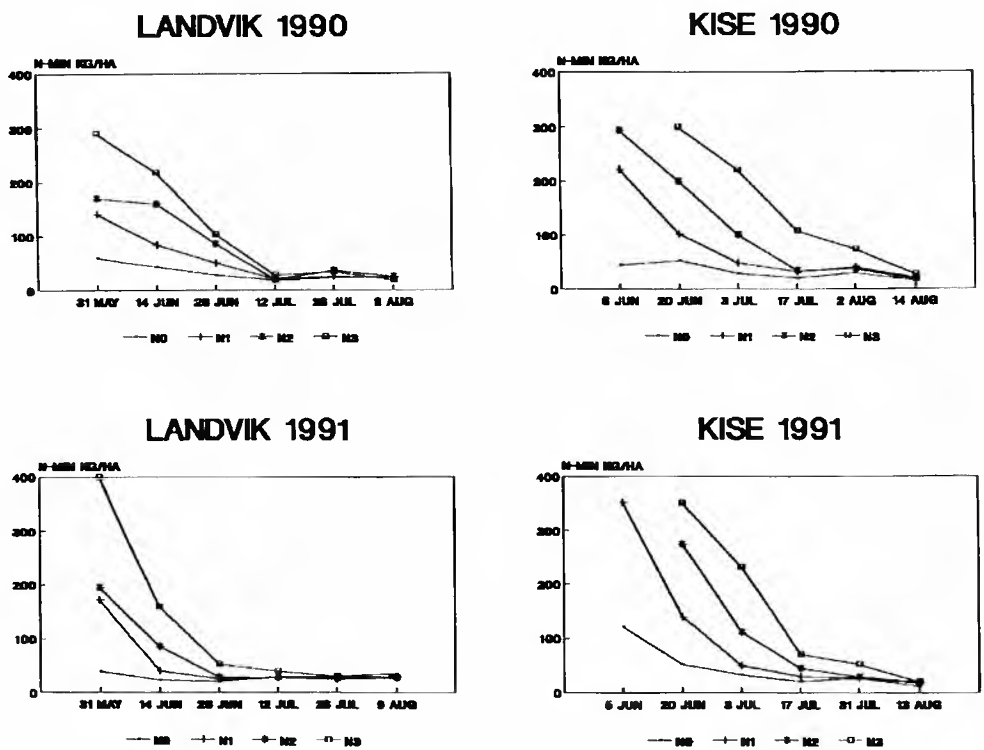

Fig. 1. Quantities of mineral nitrogen (N-MIN) found in soil at 0-40 cm depth following different levels of fertilization at planting: N0=0 N1=100 N2=200 N3=300 kg N/ha. Landvik = sandy soil, Kise = loamy soil

There was somewhat more available nitrogen at Kise than at Landvik throughout the first part of the season. Levels declined to about 25-35 kg N/ha on all plots by early July at Landvik. This level was not reached until about one month later at Kise. Top dressing with 50 kg N/ha resulted in levels which were on average about 10-20 kg N/ha higher than the above figures in late July/early August (data not shown).

The proportion of N-MIN present as nitrate declined from close to 100% shortly after planting to around 30-40% at Landvik and 50-60% at Kise by early August (Fig. 2). The proportion naturally increased with N application level, since N fertilizer was given in nitrate form. The greater decline at Landvik than at Kise suggests that more leaching may have occurred at the former site.

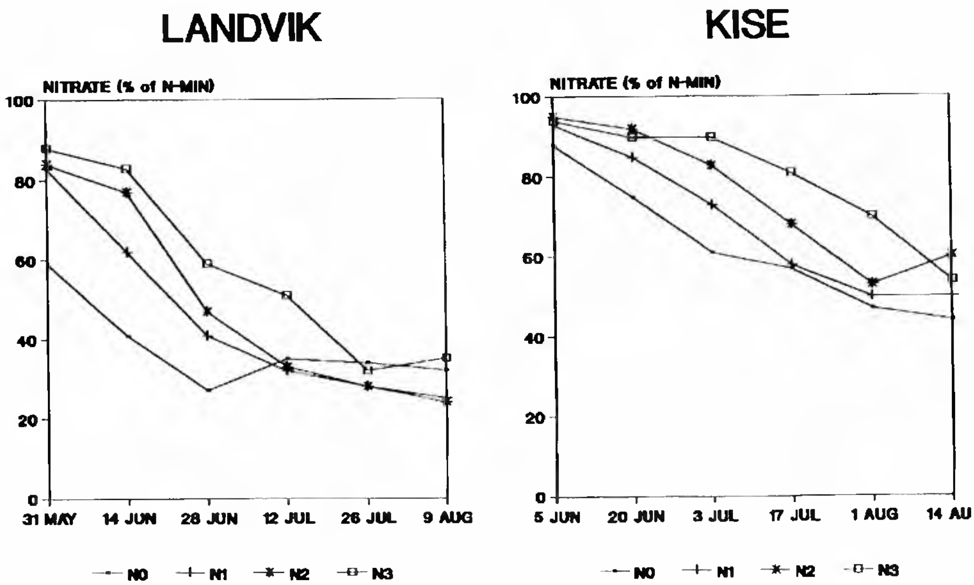

Fig. 2. Percentages of total N-MIN (0-40 cm depth) present as nitrate-N. Means of 1990 and 1991. Fertilizer levels as in Fig. 1. Landvik = sandy soil, Kise = loamy soil.

Nitrogen concentrations in plants

Trends in nitrate-N and Kjeldahl-N concentrations between years, sites and treatments were very similar for both summer and winter cabbage, though actual levels were somewhat lower in the former, because of its more rapid rate of development. Data are presented here for winter cabbage only.

The changes in nitrogen concentrations over time are shown in Fig. 3 for individual sites and years, averaged over all rates of fertilizer application. Levels of both Kjeldahl-N and NO_3-N declined from around mid-June onwards. Plants were clearly more N-deficient at Landvik than at Kise. At the latter site there were similar concentrations in both years, whilst at Landvik the decline was more rapid in 1991 than in 1990.

Concentrations of nitrate-N and Kjeldahl-N increased proportionally at both sites with increasing levels of nitrogen applied at planting (Figs. 4 and 5). The effect of top-dressing, however, differed between sites. At Kise, top-dressing with 50 kg N/ha gave intermediate concentrations compared with the relevant application rates at planting. This indicates that no benefit was gained by splitting the fertilizer application. At Landvik, on the other hand, top-dressing often resulted in higher concentrations than on plots which had received 100 kg N/ha more initially. Furthermore, the differences between treatments persisted throughout the season at Kise, whereas they almost disappeared by late August at Landvik.

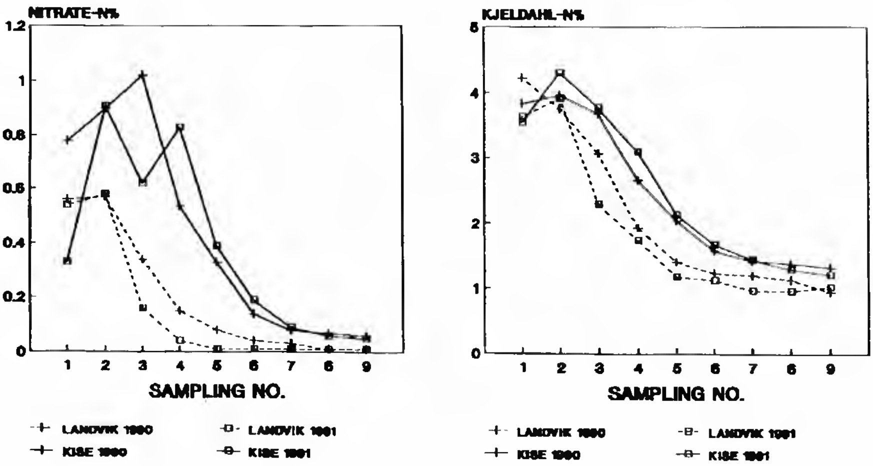

Fig. 3. Concentrations of nitrate-N and Kjeldahl-N in DM of winter cabbage at different times in the growing season. Means of all N fertilizer treatments. Sampling was at fortnightly intervals from 31 May at Landvik and from 5 June at Kise. Landvik = sandy soil, Kise = loamy soil

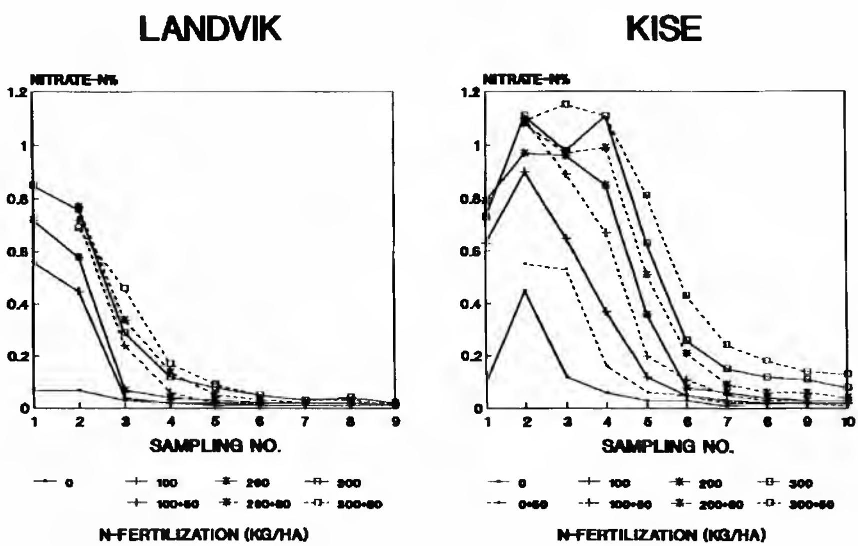

Fig. 4. Concentrations of nitrate-N in DM of winter cabbage at different times in the growing season at different levels of N fertilization. Dotted lines represent average values for plots which were top-dressed. Landvik = sandy soil, Kise = loamy soil

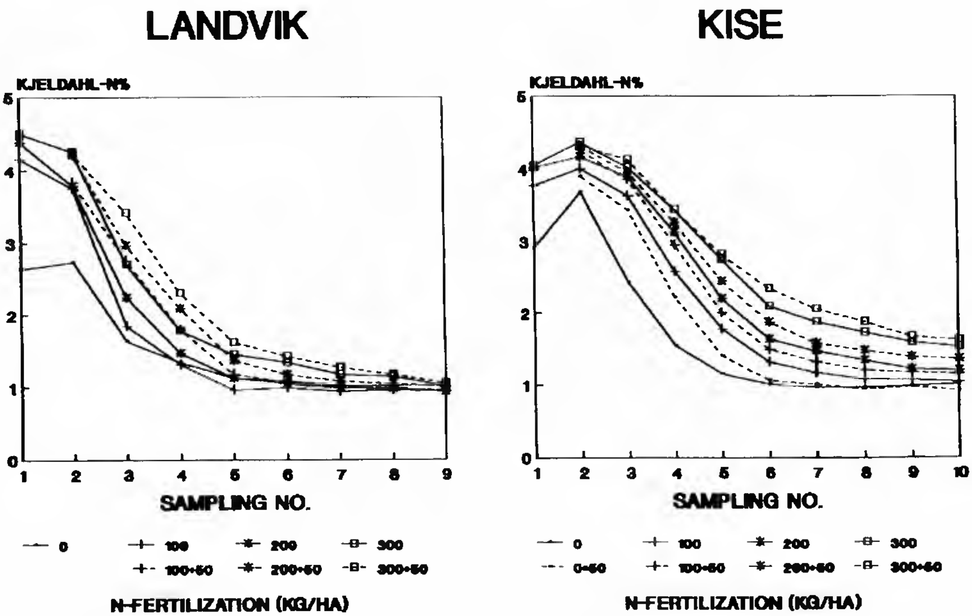

Fig. 5. Concentrations of Kjeldahl-N in DM of winter cabbage at different times in the growing season at different levels of N fertilization. Dotted lines represent average values for plots which were top-dressed. Landvik = sandy soil, Kise = loamy soil

Final yield levels

Yield data were averaged over the last two sampling dates in order to minimize the effect of sampling errors. Actual yield levels were similar in both years at Kise, whereas at Landvik they were much lower in 1991 than in 1990. There was, however, no interaction between year and fertilizer treatment at either site, and mean data only are therefore shown (Tables 3 & 4). Both freshweight (FW) and DM data refer to total above-ground plant material, but the proportion of FW comprised of cabbage heads at the final harvest is given as a percentage.

The percentage DM decreased in all cases with increasing N fertilizer, most markedly between application rates of 0 and about 150 kg N/ha. The effect of fertilizer rate on the proportion of heads was also greatest at this level.

For *summer cabbage* (Table 3) there was a marked difference between sites in the responses to N fertilizer. At Kise there was hardly any yield increase above 100 kg N/ha, and top-dressing had no effect except where no fertilizer was given at planting. At Landvik, on the other hand, yields increased up to the highest N fertilizer level. There was a beneficial effect of top-dressing, in most cases irrespective of timing, approximately in accordance with the relevant increase in total N supply.

Table 3. Final yields of summer cabbage (Mg/ha) on freshweight (FW) and dry matter (DM) basis. Figures refer to above-ground plant weights, averaged over the last two sampling dates in each year

N-fertilizer kg/ha			LANDVIK[1]				KISE[2]			
Plant-ing	Top-dressing 3 wks.	6 wks.	FW	%DM	DM	% heads[3]	FW	%DM	DM	% heads
0			10	13.9	1.4	0	46	11.8	5.1	40
0	50		-	-	-	-	79	9.7	7.4	55
0		50	-	-	-	-	70	9.7	6.6	53
100			39	12.3	4.4	21	122	7.6	9.1	64
100	50		48	11.0	4.9	20	116	7.7	8.8	63
100		50	48	10.4	4.8	32	117	7.5	8.7	64
200			46	12.0	5.2	35	125	7.4	9.1	64
200	50		57	10.0	5.5	41	123	7.1	8.6	65
200		50	59	9.7	5.5	46	124	7.3	8.9	65
300			67	9.7	6.1	54	135	7.0	9.3	65
300	50		66	9.4	5.9	39	122	7.1	8.6	63
300		50	82	8.6	6.8	52	128	7.1	8.9	64
s.e. of mean			5	0.4	0.3	7	5	0.2	0.3	1
1990			63	9.7	5.7	-	109	7.7	7.9	60
1991			42	11.7	4.4	34	108	8.5	8.7	60

[1] Means of 28.6/12.7 in 1990, and 12.7/26.7 in 1991, [2] Means of 17.7/30.7 in 1990, and 31.7/14.8 in 1991, [3] Data for 1991 only

Table 4. Final yields of winter cabbage (Mg/ha) on freshweight (FW) and dry matter (DM) basis. Figures refer to above-ground plant weights, averaged over the last two sampling dates in each year

N-fertilizer kg/ha			LANDVIK[1]				KISE[2]			
Plant-ing	Top-dressing 3 wks.	6 wks.	FW	%DM	DM	% heads	FW	%DM	DM	% heads
0			19	16.8	3.3	11	43	16.1	6.9	43
0	50		-	-	-	-	60	16.4	9.8	42
0		50	-	-	-	-	65	15.9	10.3	41
100			37	15.7	6.1	23	88	14.7	12.8	41
100	50		50	16.1	8.1	37	111	14.0	15.5	43
100		50	51	16.1	8.3	38	104	14.2	14.6	44
200			54	15.7	8.3	26	118	13.5	15.9	44
200	50		64	15.1	9.4	45	145	12.7	18.4	45
200		50	68	15.5	10.4	45	138	13.1	18.0	47
300			73	14.9	10.6	34	143	12.5	17.9	47
300	50		79	14.9	11.5	48	148	12.3	18.3	48
300		50	73	14.9	10.6	44	159	12.1	19.3	48
s.e. of mean			7	0.5	1.0	5	6	0.2	0.7	1
1990			81	15.9	12.3	34	106	13.6	13.8	44
1991			33	15.2	5.0	36	115	14.3	15.8	45

[1] Means of 6.9/20.9, [2] Means of 24.9/9.10

For *winter cabbage* (Table 4) yields increased up to the highest N fertilizer level at both sites. There was little evidence that top-dressing gave better nutrient utilization than would an equivalent total application given at planting. However, top-dressing at Landvik gave a much higher proportion of heads.

Apparent fertilizer-N recoveries

The apparent recovery of fertilizer-N in above-ground parts was calculated as the difference in N uptake between fertilized and non-fertilized plots, expressed as a percentage of the amount of nitrogen applied. Despite the relatively high variability which was found, there were clear differences between sites and years, and to some extent between summer and winter cabbage crops (Table 5).

Table 5. Apparent recoveries (%) of fertilizer nitrogen in above-ground plant material at final harvest (mean of the last two sampling dates)

		Level of N-fertilizer kg N/ha							
		50	100	150	200	250	300	350	Mean
SUMMER CABBAGE									
Landvik	1990	-	69	68	54	52	43	48	56
Landvik	1991	-	29	34	20	28	31	29	29
Kise	1990	73	101	80	74	65	60	50	72
Kise	1991	70	101	67	73	58	62	50	69
WINTER CABBAGE									
Landvik	1990	-	44	48	41	42	47	33	43
Landvik	1991	-	4	23	7	15	11	20	13
Kise	1990	66	80	72	61	75	79	75	72
Kise	1991	37	54	68	61	69	59	61	58
	Mean	62	60	58	49	50	49	46	

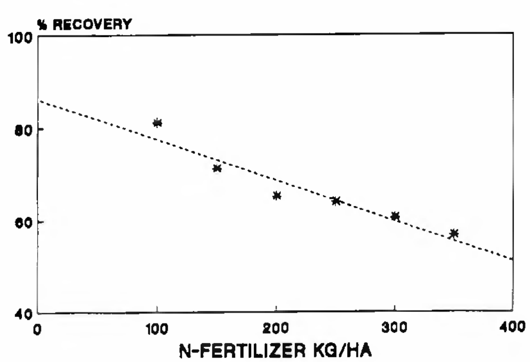

Fig. 6. Apparent recoveries of fertilizer nitrogen in relation to total amount of nitrogen applied. Means at four trials at Kise and one at Landvik

Recoveries were in all cases higher at Kise than at Landvik, reflecting the higher N concentrations at Kise. At both sites recoveries were somewhat higher in summer than in winter cabbage, possibly as a result of more rapid initial growth and N uptake in the former crop. At Landvik, recoveries were appreciably higher in 1990 than in 1991. There was a general decline in recovery rates with increasing level of fertilizer in both trial years at Kise and in summer cabbage in 1990 at Landvik. Average recoveries of these trials, which were probably little affected by leaching, are plotted against fertilizer level in Fig. 6.

Critical %N and DM responses

The differences ("deficiency/excess") between calculated values of critical %N and measured Kjeldahl-N values were plotted against measured levels of DM production on different dates (Figs. 7 & 8), starting with data from the third sampling (seven weeks from planting). Data for the first two samplings were not used as critical %N values were considerably higher than the measured Kjeldahl-N values, even on heavily fertilized plots. It may be that very young plants contained significantly more nitrate than was recovered in the Kjeldahl analysis.

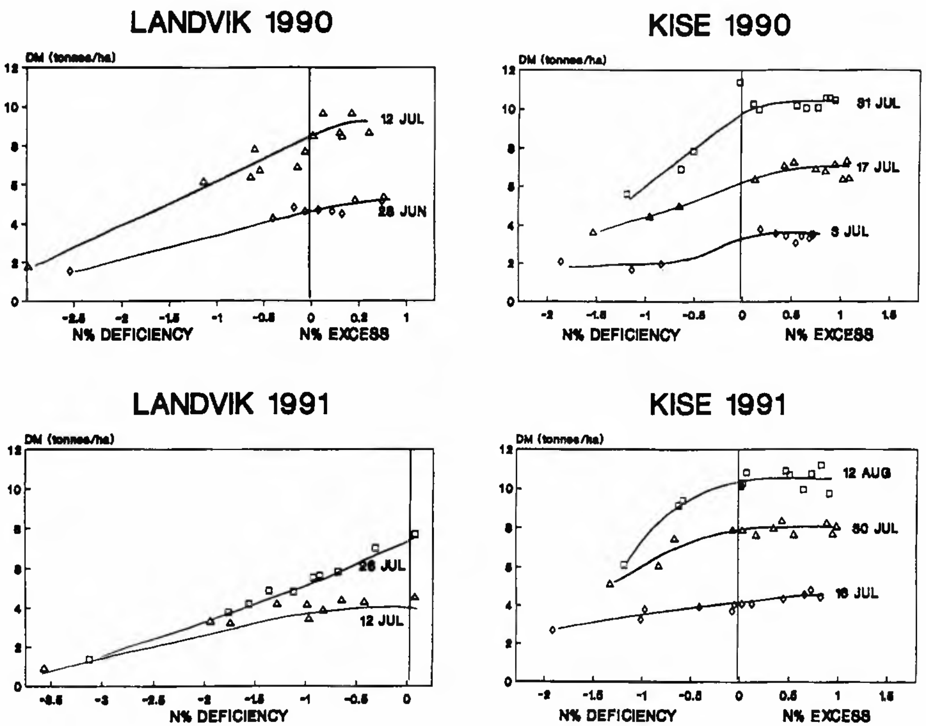

Fig. 7. DM production of summer cabbage at different times in the growing season, relative to the excess or deficiency of nitrogen in the plant, assessed by comparison of measured values with calculated critical levels. Landvik = sandy soil, Kise = loamy soil

DM production increased in all cases with diminishing degree of N deficiency, and levelled off when the measured concentration was in excess of the critical %N. For *summer cabbage* (Fig. 7), many of the treatments appeared to have an excess of nitrogen in both years at Kise, and to some extent at Landvik in 1990. Nearly all treatments were deficient at Landvik in 1991.

For *winter cabbage* (Fig. 8), there was often ample nitrogen in plants in mid-season, but more and more treatments became deficient as time went by. At Kise, the most heavily fertilized plots had sufficient nitrogen to maintain growth until the end of the season. At Landvik, however, all treatments had become deficient by the end of August in 1990, and in 1991 they were already deficient by the end of June.

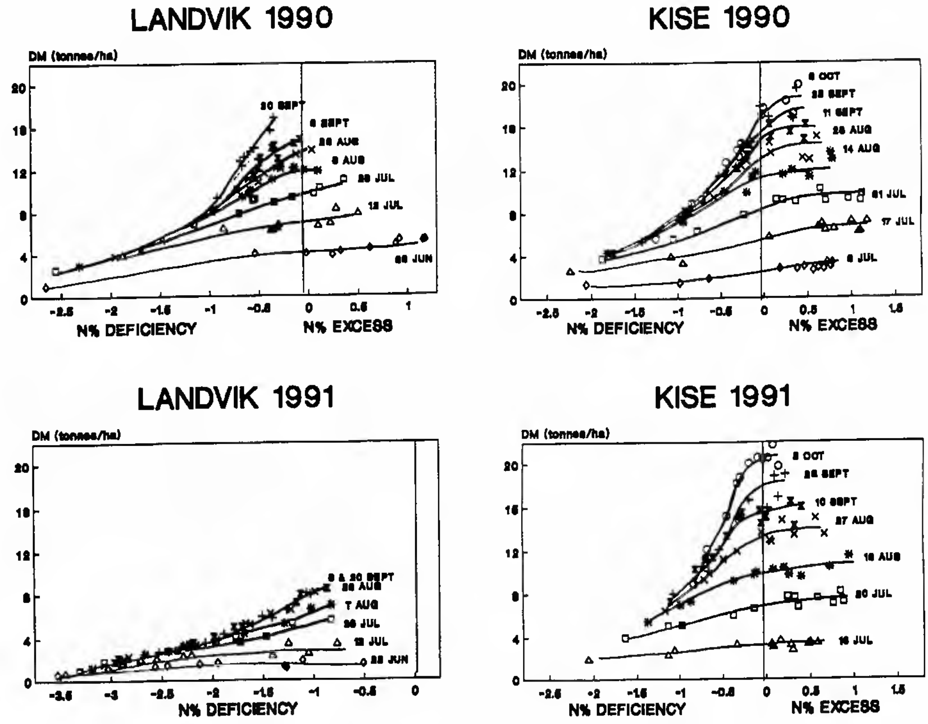

Fig. 8. DM production of winter cabbage at different times in the growing season, relative to the excess or deficiency of nitrogen in the plant, assessed by comparison of measured values with calculated critical levels. Landvik = sandy soil, Kise = loamy soil

The trials with winter cabbage showed remarkably similar yields at similar levels of deficiency. Final DM production was in all cases around 13 Mg/ha at a deficiency of 0.5%N, 8 Mg/ha at a deficiency of 1%N and 5 Mg/ha at a deficiency of 1.5%N. This suggests that the yield differences observed between sites were mostly due to differences in nitrogen supply.

Calculated versus measured plant nitrate

Regression of estimated plant nitrate-N against measured values suggested that the empirical equation tended to underestimate the true level of nitrate in plants by about 45%:

Estimated NO_3-%N = 0.03 + 0.55 Measured NO_3 -%N (n=1597, r=0.79)

Data plots revealed considerable variation, but no consistent differences in the data-fit between sites, level of fertilizer or timing of fertilizer application. New coefficients for the empirical relationship were calculated from the present data, giving the following equation:

$$\%NO_3\text{-}N = (0.860 * a - 1.617) * b \qquad (3)$$

where a and b are defined as for equation 2. This gave better agreement between estimated and measured values up to around 1% nitrate-N, but consistently overestimated values at higher concentrations. On average the overall overestimation was 20%.

Relationship between plant nitrate and final yield

An assessment of plant nitrate deficiency during early growth was attempted by regression of nitrate-N concentration against the number of days since planting (X_1) and relative final yield (X_2). The latter was calculated as the percentage of target yields, assuming values of 9 and 18 Mg/ha dry matter for summer and winter cabbage respectively. The following regression equation accounted for 50% of the variation in 328 observations:

$$NO_3\text{-}\%N = 0.33 - 0.0087\, X_1 + 0.0079\, X_2 \qquad (4)$$

The optimum range for nitrate-N concentrations (within 10% of target yield) is illustrated in Fig. 9.

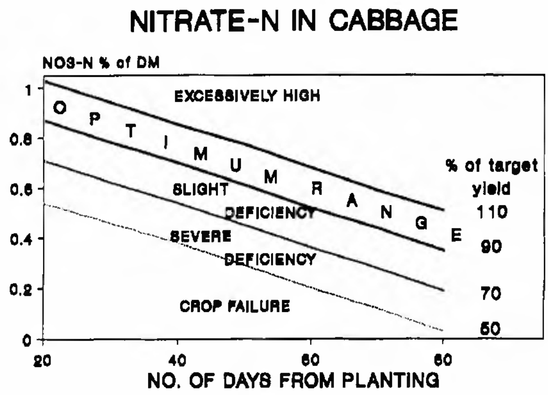

Fig. 9. The decline over time in levels of nitrate-N in cabbage plant DM corresponding to different levels of final yield

DISCUSSION

These trials illustrate the problem which is often encountered in practice when attempting to predict fertilizer needs, namely that optimum levels vary between soils and between years, due, at least partly, to differences in leaching losses.

The results on the loam soils at Kise are in agreement with those of Dragland (1982, 1984), who found no benefit from split N application rates to cabbage on soils similar to those used in this study. Critical %N values calculated for the data of Dragland (1982) showed that measured N concentrations were higher than the critical values, irrespective of fertilizer timing, except when no fertilizer was given at planting.

On the sandy soil at Landvik, however, it appears that better nitrogen economy can be expected from an even greater partitioning of fertilizer application. This topic will be explored in a subsequent paper dealing with model predictions.

The results of the present trials support the validity of the critical %N concept which is a prerequisite for the proposed method of modelling N responses. Some doubt arises, however, about the applicability of the method in young plant material (when plant DM is below about 1.5 Mg/ha). Measured Kjeldahl-N concentrations at this stage were usually well below the critical values even on heavily fertilized plots. Plants on these plots often had very high nitrate concentrations, but this is only partially reflected in the Kjeldahl-N figures. Better agreement might have been found by using an analytical method which included all the nitrate. Such a method was, however, not used in the original work from which the critical %N equation originated (Greenwood pers. comm.).

A further prerequisite for the modelling of N response is knowledge of the maximum rate of fertilizer recovery which may be expected in the plant component of interest (normally the above-ground leaves and stems in the case of vegetables). Recovery rates vary between crops, and generally increase with total DM yield up to around 4 Mg/ha (Greenwood & Draycott 1989b). On the other hand, recoveries in trials with vegetable crops normally decline with increasing levels of fertilizer application (Greenwood et al. 1989).

Maximum recovery rates may be estimated from the origins of linear regressions of recovery against fertilizer level. In the case of the trials included in Fig. 6, this indicates a maximum recovery rate of just over 85%. Recoveries of 79% were obtained in winter cabbage by Dragland (1982) with the use of 250 kg N/ha. Maximum recoveries of 79-85% for summer cabbage and of 55-70% for winter cabbage are typical in England (Greenwood & Draycott 1989a, Greenwood et al. 1989). The somewhat lower recoveries for winter cabbage there may presumably reflect greater exposure to leaching than under conditions at Kise.

Another important consideration in modelling is the lowest concentration level at which plant roots can extract nitrogen from the soil. Greenwood & Draycott (1989a) consider this to be about 0.46 kg N/ha/cm, which is equivalent to 18 kg N /ha for the depth sampled in these trials. Residual N-MIN levels of 20-40 kg/ha remained in the soil from August onwards, which is roughly in accordance with the above assumption. These figures also agree with the residual levels of nitrogen found in soil after cabbage grown in the Netherlands at similar fertilizer rates (Prins et al. 1988).

The empirical equation for nitrate concentration discussed in this paper is not of direct importance in the modelling of N response. Its main purpose is to provide information which may be used in assessing the effects of fertilizer practice on quality. The poor agreement between the equation derived in England and the results obtained here is possibly due to differences in uptake rates. Uptake is normally very rapid over a fairly short period in the early part of the growing season in Norway. This may lead to higher concentrations of nitrate accumulating at given levels of total N than would occur under conditions in England.

The decline in the optimum level of plant nitrate was broadly similar to that reported by Gardner & Roth (1989). The slightly higher values reported by them are probably due to the fact that leaf midribs only were sampled, whereas our data originate from whole plants (leaf plus stem). The relatively low correlation between early season plant nitrate and final yields found in our work suggests that this approach is likely to be of only moderate accuracy.

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Effects of ozone on young plants of *Betula pubescens* Ehrh. at different temperature and light levels

LEIV M. MORTENSEN,
Særheim Research Station, Klepp st., Norway/Agricultural University of Norway, Department of Horticulture, Ås, Norway

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Seedlings of *Betula pubescens* were grown at two ozone (O_3) concentrations (10 and 45 nmol mol^{-1} during 8 h day^{-1}) and four temperatures (12, 16, 20 and 24°C) over a period of 45 days in growth chambers. Increased concentrations of O_3 caused leaf injury (yellow stipples) which increased progressively with decreasing temperature. At the lowest temperature brown spots developed as a result of O_3 exposure. The increase in O_3 injury as a result of decreasing temperatures was correlated with decreases in leaf diffusion resistance and plant growth rate. Exposure of birch plants to 100 nmol mol^{-1} O_3 during the dark period caused the same amount of yellow stipples on young leaves as exposure during the light period. The older leaves developed brown spots through exposure during the light period only. Measurements of leaf diffusion resistance revealed that the stomata of the young leaves remained open during the dark period while the stomata of the older leaves partially closed.

Key words: *Betula pubescens*, diffusion resistance, growth, ozone, temperature

Leiv M. Mortensen, Særheim Research Station, N-4062 Klepp st., Norway.

Ozone (O_3) is known to cause growth reductions and yield losses in several species in the USA as well as in Europe (Guderian et al. 1985; Krupa & Kickert 1989). In Scandinavia, O_3 is the regional air pollutant that attracts most interest (Hoem et al. 1988), while sulphur dioxide and nitrogen oxides are generally considered as low level air pollutants (Joranger et al. 1986). The O_3 concentration is estimated to increase at the rate of 1-2% per year at ground level in Europe (Feister & Warmbt 1987), which means that the damaging effect of O_3 probably will increase in the future. *Betula pubescens*, which is the most widespread deciduous forest tree species in Scandinavia, has been shown to be sensitive to this pollutant (Mortensen & Skre 1990). This species grows at a wide range of temperatures from the lowlands up to about 1500 m a.s.l. in the south of Norway. Approximately the same O_3 levels seem to occur over this region irrespective of the elevation (Pedersen & Semb 1990).

Ozone episodes in Scandinavia may occur at all times of the day and night as a result of the long-range transportation of this pollutant in air masses (Joranger et al. 1986). In addition to the effect of O_3 at different temperatures, it was therefore of interest to study the effect of O_3 exposure during the dark period.

MATERIALS AND METHODS

O_3 and temperature

Seedlings of *Betula pubescens* Ehrh. (B2, location Løten, 60°45'N/11°30'E) were planted in a mixture of 25% perlite and 75% fertilized spaghnum peat in 0.3 l pots. Fifteen pots with one seedling per pot were placed in each one of the 16 chambers used in the experiment (Mortensen 1982; Mortensen et al. 1987). The initial dry weight per seedling was 0.4 g.

Two O_3 treatments (10 ± 3 and 45 ± 8 nmol mol^{-1} from 10.00 until 18.00 h) and four temperature treatments (12, 16, 20 and 24 ± 1°C) were applied, and the eight treatments were duplicated. Between 18.00 and 10.00 h the concentration was <10 nmol mol^{-1}. The daily maximum O_3 concentration was 55 ± 13 nmol mol^{-1} at the highest O_3 level. Ozone was generated from dry air, using a high-voltage ozone generator (Nomizon, Nordmiljø ab, Sweden). The O_3 concentration was measured by means of an O_3 analyser (Model 1008 AH, Dasibi Environmental Corp.). A scanner switched the air flows from the chambers to the O_3-analyser, and the concentrations were measured three times per hour in each one of the eight chambers. The mean and maximum concentrations during the eight-hour O_3 application period and the rest of the diurnal period were recorded separately by datalogger. The concentration of nitrogen oxides (NO_x) as measured by means of a Monitor Labs. Inc. (Model 8840) analyser was <10 nmol mol^{-1}.

Additional light was given by means of high pressure sodium lamps at a photon flux density of 120 ± 20 $\mu mol m^{-2}s^{-1}$ in 24 h day^{-1}. The light was measured by a Lambda LI-185B instrument (Licor Inc., Nebraska) with quantum sensor (400-700 nm) at the top of the plants. The total photosynthetic active photon flux including the daylight inside the chambers, was 15 mol m^{-2} day^{-1} as a mean for the experimental period (1 October until 15 November 1990). The natural outside radiation was measured at the meteorological station at Særheim, and these values were decreased by 50% as a result of the shading caused by the greenhouse and growth chamber constructions. The relative air humidity at 12, 16, 20 and 24°C was 80 ± 5, 80 ± 5, 70 ± 5 and 65 ± 5%, respectively. This corresponded to water vapour deficits of 2.8, 3.6, 7.0 and 10.4 mbar. The CO_2 concentration was 350 ± 20 μmol mol^{-1}.

The plants were watered with a complete nutrient solution which consisted of (mg l^{-1}): N, 188; P, 37; K, 242; Ca, 130; Mg, 41; S, 53; Fe, 2.0; Mn, 0.6; Zn, 0.14; Cu, 0.29; B, 0.34; Mo, 0.027; Co, 0.009, giving an electrical conductivity of 1.7 mS cm^{-1}. The soil salinity was kept between 1.5 and 2.0 mS cm^{-1}.

On termination of the experiment fresh and dry weights of leaves and stem, root dry weight, plant height, number of main leaves and branches >3 cm, and visible O_3 injury on the leaves were recorded. The O_3 injury (yellow stipples/brown spots) was scaled as follows: 0 = no injury; 1 = slightly visible stipples; 2 = distinct stipples, and 3 = leaf chlorosis and brown spots on the upper leaf surface.The mean relative growth rate was calculated by means of the equation:

$$W_2 = W_1 e^{RGR(T2-T1)}$$

where W_1 is the dry weight at time T1 (start of the experiment) and W_2 the dry weight at time T2 (termination of the experiment), and e the natural logarithm base.

The leaf diffusion resistance of the fourth leaf from the top (the last developed leaf) of the plants was measured on plants growing at the four temperatures and two O_3 concentrations. Six plants from each treatment were measured two times, 9.00-10.00 h and 13.00-14.00 h. The measurements were carried out at the end of the growth experiment. A porometer (Delta-T Devices, MK3, England) was used in order to measure the leaf diffusion resistance between 60 and 65% relative humidity. Before the measurements were taken, the porometer was placed in the chamber until the temperature had stabilized and then the measurements were carried out the lower leaf side. The resistance was very high on the upper leaf side due to lack of stomata. All six plants in a chamber were measured before the porometer was moved to the next chamber. The measurements followed the sequence 20, 16, 12, 24 and 20°C. A calibration curve was made for the different temperatures by using a calibration plate, and the diffusion resistances were then calculated.

All data were subjected to an analysis of variance (SAS Institute Inc., USA) with chambers as replicates in the growth experiment, and with plants as replicates in the measurements of leaf diffusion resistances.

O_3 and light

Six birch plants of the same plant material as before, were placed in each one of eight growth chambers. Each plant had 11 leaves. Four chambers were supplied with high pressure sodium light (Thorn SON XL-T) and four with fluorescent tubes (Philips TLD 33) at a level of 100 ± 10 $\mu mol m^{-2} s^{-1}$ photon flux density from 08.00 until 20.00 h. The two lamp types were used because their spectral distribution is different, particularly in the blue part of the spectrum. This difference in light quality might have had an effect on the stomatal function, and if so the lamp type might have influenced the results of the O_3 studies. Four of the chambers were supplied with O_3 during 8 h in the light period (10.00-18.00 h) and the other four chambers during 8 h in the dark period (22.00-06.00 h). The O_3 concentration in all chambers was 100 ± 10 nmol mol^{-1}, the CO_2 concentration 350 ± 30 μmol mol^{-1}, the temperature 16.0 ± 0.5°C, and the relative humidity 65 ± 10%. The experiment started on 26 November 1990, and lasted 21 days. The total photosynthetic photon flux including the daylight was 5.2 mol m^{-2} day^{-1} as a mean.

On termination of the experiment the number the of main leaves >3 cm, plant height, and yellow stipples and brown spots on the leaf surface were recorded. The stipples were visually recorded on the tenth leaf from the stem base (most injured) and the brown spots on the fourth leaf from the base. A scale from 0 to 3 was used in order to score the grade of leaf stipling: 0 = no visible stipples, 1 = weak stipples, 2 = distinct stipples, and 3 = strong stipling/leaf chlorosis. A similar scale was used to describe the amount of brown spots on the leaf surface: 0 = no visible spots, 1 = slightly visible spots, 2 = distinct spots, and 3 = spots on more than 50% of the leaf surface. The grading between 1 and 3 was given in 0.5 intervals. All data were subjected to an analysis of variance with chambers as replicates.

Six plants were used in measurements of the leaf diffusion resistance of leaf numbers 8, 12 and 18 from the stem base. This corresponded to leaves of three ages. The plant height was 40 cm. The plants were placed in a growth room at a temperature of 20.0±0.5°C, a relative humidity of 75±5% and a CO_2 concentration of 350±20 μmol mol^{-1}. The photon flux density was 120 μmolm^{-2}s^{-1} provided by means of fluorescent tubes (Philips TLD 33), and the photoperiod was 18 h day^{-1}. After one week the measurements of the leaf resistance were carried out at the end of the dark period, and after three and six hours in light. All data were subjected to an analysis of variance with plants as replicates.

RESULTS

O_3 and temperature

The only effects of increasing the O_3 concentration from 10 to 45 nmol mol^{-1} were found on the level of leaf injury and some variable effects on the shoot:root dry weight ratio (Table 1). The injurious effect of O_3 increased as the temperature decreased from 24 to 12°C. Increasing the temperature significantly enhanced the total dry weight, RGR, shoot:root ratio, plant height, number of branches and leaves. On most parameters the largest effect was found at temperatures up to 20°C.

Table 2. The effect of O_3 concentration and temperature on the leaf diffusion resistance in *Betula pubescens*. Significance levels: O_3 , $p<0.10$; temperature, $p<0.001$; O_3 x temperature, ns

	O_3 conc. (nmol mol^{-1})	Temperature (°C) 12	16	20	24
Diffusion resistance (s cm^{-1})	10	0.82±0.05	0.84±0.06	1.86±0.09	2.36±0.10
	45	0.95±0.05	0.94±0.10	1.84±0.14	2.82±0.31

The leaf diffusion resistance decreased as the temperature decreased (Table 2). The resistance was about three times higher at 24 compared to at 12°C. The resistance of leaves grown at high O_3 levels was slightly higher than that of leaves grown at low levels of O_3.

O_3 and light

Exposure of the plants to O_3 during the dark period gave the same amount of yellow stipples on young leaves (recorded on the tenth leaf from the base) as exposure during the light period (Table 3). Older leaves suffered more injury through O_3 exposure during the light (brown spots recorded on the fourth leaf from the basis) than during the dark period. The lamp type had no influence on the results. The number of leaves was 16 and the plant height 48 cm in all treatments (data not presented).

Table 1. The effect of O_3 concentration and temperature on growth (±SE) of *Betula pubescens*. Significance levels: ns, $p>0.05$; *, $p<0.5$; **, $p<0.01$; ***, $p<0.001$. L= 10 nmol mol^{-1} O_3 and M= 45 nmol mol^{-1} O_3

Temperature(°C)	Total dry wt (g)		RGR mg g^{-1} day^{-1}		Shoot: root ratio		Plant height (cm)		Leaf area (cm^2)		No. of branches		No. of main leaves		Leaf injury	
	L	M	L	M	L	M	L	M	L	M	L	M	L	M	L	M
12	1.75±0.43	1.56±0.36	32.2±5.7	29.5±5.4	3.1±0.4	3.4±0.3	19.2±3.0	20.0±4.7	200±52	176±42	6.9±0.9	7.1±1.3	7.6±1.1	7.5±0.3	0.0±0.0	3.0±0.1
16	3.20±0.20	2.52±0.04	46.3±1.4	41.0±0.4	4.5±0.4	3.7±0.1	28.8±1.2	27.0±0.2	336±90	261±53	10.1±0.3	9.2±0.6	10.1±03	9.4±0.6	0.0±0.0	2.4±0.0
20	4.12±0.04	4.04±0.21	52.0±0.3	51.5±1.1	5.3±0.4	5.2±0.1	35.4±0.4	35.4±0.4	435±56	406±46	12.0±0.3	11.4±0.1	12.4±0.6	12.8±0.5	0.0±0.0	1.1±0.8
24	4.47±0.25	4.61±0.08	53.8±1.3	54.5±0.4	6.0±0.1	4.7±0.4	40.0±0.4	39.2±1.7	494±15	404±11	12.1±0.4	13.0±1.0	14.3±0.8	14.5±0.2	0.0±0.0	0.4±0.4
Significance levels:																
O_3	ns		ns		*		ns		ns		ns		ns		***	
Temperature	***		***		***		***		**		***		***		*	
O_3 x Temp.	ns		ns		ns		ns		ns		ns		ns		*	

Table 3. The effect of O_3 exposure (100 nmol mol^{-1}) for 8 h day^{-1} during the light or dark period on the development of yellow stipples on younger leaves and brown spots on older leaves in *Betula pubescens*. Injury was scaled from 0 (no symptoms) to 3 (severe symptoms). Supplementary light was given 16 h day^{-1} by two lamp types (fluorescent tubes and high pressure sodium lamps)

Exposure time	Yellow stipples	Brown spots
Light	1.8±0.1	2.3±0.1
Dark	1.4±0.2	0.6±0.4
Exposure time (ET)	ns	*
Lamp type (LT)	ns	ns
ET x LT	ns	ns

The leaf diffusion resistance was significantly higher (77%) in old leaves (bottom position) than in the younger leaves when measured at end of the dark period (Table 4). The resistance decreased in leaves at all three positions when the light was turned on, but this effect was much more pronounced in older leaves compared with younger leaves.

Table 4. Leaf diffusion resistances (s cm^{-1}) in the dark and light period of *Betula pubescens* leaves at three different positions on the stem. Significance levels: Time, $p<0.001$; position, $p < 0.001$; time x position, $p<0.01$

Time	Leaf position		
	Bottom	Intermediate	Top
End of dark period	8.5±0.7	6.0±0.6	4.8±0.4
3-h after light on	3.2±0.3	2.2±0.1	2.2±0.1
6-h after light on	3.8±0.3	3.3±0.1	3.1±0.1

DISCUSSION

Betula pubescens was found to be relatively sensitive to O_3 in agreement with previous results (Mortensen & Skre 1990). The growth rate was enhanced by increasing the temperature up to 20°C in the present experiment, while no effect was found above 15°C in a previous experiment with birch seedlings of the same origin (Skre 1991). The present finding that the effect of O_3 increases with decreasing temperatures indicates that birch plants growing in the mountain areas at lower temperatures might be more injured by O_3 than plants growing in the lowlands at higher temperatures. Previous studies have shown a higher O_3 sensitivity of *Fraxinus americana* (Wilhour 1970) and *Pinus virginiana* (Davis & Wood 1973) when the plants were exposed to O_3 at low temperatures (10-16°C) than at high temperatures (27-32°C). Dunning & Heck (1977) found that the O_3 sensitivity of tobacco plants was independent on temperatures between 16 and 27°C, but decreased at higher temperatures. The observation by Winner et al. (1989) that the O_3 injury in different plant species increased with increasing altitudes might be explained by a decreasing temperature. The present measurements on birch showed that increasing O_3 injury at decreasing temperatures could be explained by a decrease in the leaf diffusion resistance and increased absorption of O_3. The water vapour deficit of the air generally decreases when the temperature decreases. It is well known that plants at low vapour deficits have more open stomata than plants at high deficits (Otto & Daines 1969; McLaughlin & Taylor 1981), and consequently more O_3 might be absorbed by the leaves.

The present results show that the birch leaves, particularly the younger ones, absorb O_3 also during the dark period due to lack of stomata closure. This means that O_3 exposure of the plants also during darkness might be injurious. This finding is in accordance with previous results for turnip, which was shown to be sensitive to night-time O_3 exposure due to partially open stomata (Winner et al. 1989).

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Reproductive effort in the arctic fox *Alopex lagopus*: A review

KARL FRAFJORD
Museum of Zoology, University of Bergen, Bergen, Norway

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This paper reviews the available information and hypotheses about litter size and reproductive effort in the arctic fox *Alopex lagopus*, considering both free-living populations and Norwegian farm foxes. The most important factor for reproductive success in free-living foxes is probably food, and there appear to be two different strategies of litter size. In regions with voles and lemmings, the arctic fox has large litters but breeds only in years when the numbers of small rodents are high. In regions without small rodents, the arctic fox has small litters but may breed more regularly or annually. The litter size of farm foxes seems to be in-between that of the two groups of native foxes, perhaps resulting from the diverse origin of farm foxes. A reduction in the litter size of farm foxes during the period 1977-92 was found, but most of this may indirectly have resulted from cross-breeding with red foxes *Vulpes vulpes* which started about 1982. An increase in the proportion of breeding females and a reduced mortality of pups may be more profitable than an increase in the number of pups per female.

Key words: Arctic fox, free-living populations, litter size, Norwegian farm foxes, reproductive effort.

Karl Frafjord, Tromsø Museum, Lars Thøringsv. 10, N-9006 Tromsø, Norway.

Recently, it has been claimed that the reproduction of farmed arctic foxes in Norway has declined and it was stated that the reproductive potential of the species has not been fulfilled (e.g. Loftsgaard 1985; Einarsson 1986; Fougner 1991). An increased reproductive effort may have great economic consequences, but few studies have been made. A reduced mortality may also be wanted for ethical reasons. In this paper I review the available data on reproduction in farmed Norwegian arctic foxes and discuss general theories and hypotheses about reproductive effort in this species. But first I review the available information on reproduction in natural free-living populations of arctic foxes.

REPRODUCTION IN FREE-LIVING ARCTIC FOXES

The arctic fox is a medium-sized canid with a circumpolar distribution (Garrott & Eberhardt 1987). Its main habitat is the arctic tundra region north of the tree-line, but arctic foxes are also found in the alpine tundra above the tree-line in Fennoscandia. In the vast regions of Siberia and North America most arctic foxes, generally more than 95%, are of the white colour morph. Blue foxes appear to be most common along the coast of islands such as Iceland and Greenland, where they are presumably afforded a better camouflage against the snow-free ground (e.g. Hersteinsson 1989). In Iceland, both regional and temporal variation in the proportion of white and blue foxes have been found, and the two colour morphs have slightly different litter size (Hersteinsson 1989).

Counting the number of pups at dens (older than three weeks) is notoriously difficult, because pups can rarely be individually identified and because all pups in a den are rarely observed at the same time (Frafjord 1984). Furthermore, pups may leave their natal den at an early age (Frafjord 1992a), and the exact age of the pups is rarely known. These difficulties can often result in underestimation of the litter size observed at dens. The accuracy of recording placental scars is also disputed and can result in overestimation of litter size (Lindström 1981; Prestrud 1992). Owing to the uncertainty and unreliability of these recording methods, it is difficult to compare litter sizes from various geographical regions. For example, litter size appears to be highly variable in different regions of Fennoscandia (Table 1). This may partly be due to observer error, but in the study with the largest litter size the pups in several of the dens may have come from two litters (Frafjord 1991a, 1992a).

Table 1. Litter size in arctic foxes reported by various sources (n = sample size)

Region	Litter size	Method[1])	n	Source
Alaska	8.3	P. scars	22	Anthony (1991)
Alaska	11.5	No. fetuses	21	Anthony (1991)
Alaska	4.8	No. pups	11	Fine (1980)
Alaska	2.8	No. pups	16	Berns (1969)
Canada	10.6	P. scars	118	Macpherson (1969)
Canada	6.7	No. pups	27	Macpherson (1969)
Canada	9.5	P. scars	16	Hammill (1983)
Canada	7.5	P. scars	?	Hall (1989, in Prestrud 1992)
Siberia	10.2	P. scars	?	Chirkova et al. (1959[2])
Siberia	7.1	No. pups	?	Chirkova et al. (1959[2])
Siberia	5.7	No. pups	?	Smirnov (1968)
Sweden	6.2	No. pups	57[3])	Calculated from Ericson (1984)
Sweden	5.2	No. pups	17	Angerbjörn et al. (1991)
Finland[4])	6.6/2.4	No. pups	10/28	Kaikusalo (1991)
Scandinavia	11.2	No. pups	5	Frafjord (1992a)
Iceland	5.4	P. scars	289	Hersteinsson (1992)
Iceland	3.9	H. reports	?	Hersteinsson (1992)
Svalbard	6.4	P. scars	102	Prestrud (1992)
Svalbard	5.3	No. pups	35	Prestrud (1992)
Svalbard	5.8	No. pups	5	Frafjord (1992a)

[1])Methods: P. scars = number of placental scars, No. fetuses = number of fetuses in pregnant females, No. pups = number of pups observed at dens, H. reports = hunting reports (number of pups killed at dens)

[2]) In Bannikov (1970)

[3]) Inhabited dens

[4]) Two periods: 1964-74 and 1985-91

In a review of the Greenland arctic fox, Bræstrup (1941) started a discussion about coastal and inland (lemming) foxes and about the supposed adaptability of the two colour morphs. Most of this discussion has suffered from a lack of data, but some questions are still interesting. One of these is the question of whether lemming foxes have larger litters than coastal foxes. The evidence is not conclusive (Table 1), but litter sizes in regions with voles and lemmings (North America and Siberia, $\bar{X}=9.2\pm1.3$ pups from studies of placental scars) appear to be larger than litter sizes in regions where small mammals are not a significant part of the diet (Iceland and Svalbard, $\bar{X}=5.9\pm0.7$ pups)(Mann-Whitney U-test, $z=1.94$, $p=0.05$, $n=7$).

Why should foxes in regions with voles and lemmings have larger litters than foxes in regions without small rodents? The argument is that voles and lemmings show great fluctuations in numbers, while coastal foods (e.g. sea birds) do not fluctuate much in numbers between years. Hence, in regions with small rodents most arctic foxes only breed in the peak population years of their main prey, i.e., at three- to four-year intervals (Macpherson 1969; Angerbjörn et al. 1991). Because few foxes survive more than five years (Hiruki & Stirling 1989; Hersteinsson 1992; Prestrud 1992) they may not have more than one to three breeding opportunities in their lifetime. On the other hand, foxes adapted to a stable and predictable food supply may be able to breed annually. Their reduced litter size may be due to less available food than in regions with peak numbers of small rodents, at least in wintertime. Thus the lifetime reproductive success of annual breeders may not be different from that of intermittent breeders. Putting it another way, arctic foxes are not able to invest in large litters every year. They have to choose between producing annual but small litters or intermittent but large litters. This difference is probably at least partly inherited. If it is not inherited but purely based on the individual fox's acess to food, we would expect a greater variability in the litter size in each region. Furthermore, arctic foxes mate in late winter when their food may not reliable reflect food availability in spring and summer. A more genetically determined litter size (or rather the number of fertilized eggs that implant in the uterus) may result in higher reproductive success than an environmentally determined litter size.

LITTER SIZE REDUCTION IN FREE-LIVING FOXES

Several theories have been put forward to explain the apparent reduction in the litter size of free-living arctic foxes prior to pup independence. This reduction or mortality is recorded by the difference in litter size between the number of placental scars and the number of pups found at dens (Macpherson 1969; Hersteinsson 1992). These theories are diminished by the fact that, mainly because of the difficulties in recording pup mortality and survival, it is not known whether such litter size reduction is abnormal and infrequent or whether it occurs regularly. However, as some foxes breed in less than optimal years or regions, their reproductive success is likely to be reduced. The problem facing a fox is how to adjust litter size to the available food in order to enhance the survival of the remaining pups, and to minimize the risk of losing the entire litter. This adjustment may theoretically be accomplished at any stage of the reproductive cycle (Table 2).

Few data exist on intra-uterine mortality or postnatal mortality of small pups. Yearly variation in the number of placental scars has been found (Macpherson 1969, recalculated by Angerbjörn et al. 1991). Although some young die of diseases (e.g. rabies, Smirnov 1968) and a few are killed by predators (Garrott & Eberhardt 1982; Frafjord 1991b), most mortality has been attributed to a lack of food (Macpherson 1969). Artificial feeding of foxes in Sweden increased the number of breeding attempts and pup survival, but not litter size (Angerbjörn et al. 1991; Tannerfeldt 1991). Mortality among pups has also been attributed to intralitter aggression (Macpherson 1969; see also Fine 1980), but this conclusion was not supported by Frafjord (1984) or Garrott et al. (1984). Cannibalism among pups is more likely to result when some pups have died, e.g. from starvation (Arvidson & Angerbjörn 1987; Sklepkovych 1989).

Table 2. Reduced reproductive effort in Norwegian farm-bred arctic foxes, percentages from Fougner (1991)

Factor	%
Females mated	82-95
Eggs fertilized	40-80
Loss before implantation	10-30
Loss of embryos	15-20
Loss at birth	?
Loss of young pups (<3 weeks)	20
Loss of older pups	5

Angerbjörn et al. (1991; see also Lindström (1988) for a discussion of red foxes *Vulpes vulpes*) suggested that female arctic foxes may regulate litter size according to her condition at any stage of the pregnancy, assuming that most females mate every year. Although the female is possibly able to regulate the number of ovulated eggs according to her condition at the time of mating, it is more difficult to explain resorption or abortion of healthy embryos (Frafjord 1992b). Thus prenatal losses in order to adjust litter size to the female's condition seem unlikely, even more so because such litter size reduction should take place prior to a severe reduction of the female's condition. Postnatal reduction of litter size by parents is not very likely either, other than as a consequence of differences in the competitive ability of pups. Small and weak pups may suffer from starvation when food is scarce.

REPRODUCTION IN FARMED ARCTIC FOXES IN NORWAY

Farm breeding of arctic foxes in Norway started in the first two decades of this century. The foxes originated from various parts of the species distribution range, but probably mainly from North America and Greenland. Thus, genetically, the farm-bred arctic fox is a mixture of many natural populations both from regions with large litter sizes and from those with small litter sizes. It has been suggested that foxes from North America (the "Alaska blue fox") were larger and more fertile than foxes from the arctic islands (the "Greenland blue fox"), which were more valued for their fur (Nes et al. 1987). Farm foxes are selected for their fur quality, but also for factors such as large body size and large litter size. The fur of blue foxes has been more highly valued than that of white foxes, and consequently most farm foxes today are blue foxes.

Several methods have been used to calculate litter size in farm foxes. I here use the number of pups per female, as given by the Insurance Association (Pelsdyrtrygdelaget). These have been summarized and discussed by several authors (Loftsgaard 1985; Einarsson 1986, 1988; Kulbotten 1991). The number of pups/female is given by the number of females in the farms by 1 February and the number of live pups by 15 July (Kulbotten 1991). From 1982, these figures also include cross-breedings between arctic and red foxes. To eliminate some of the error resulting from a variable proportion of cross-breeds, I recalculated litter size for 1982-91 from Kulbotten (1991, Table 1). I estimated the proportion of cross-breeds per pup (X% of one pup, assuming an average reduction in litter size by one pup in cross-breeds, Kulbotten 1991) and added this to the average litter size of arctic foxes. As no data on the proportion of cross-breeds were available for 1992, I calculated the average increase in litter size for 1982-91 given by the estimated litter sizes (0.14 pup/litter) and added this to the litter size for 1992 found in Eldøy (1992).

I also included the number of pups per litter, given in the annual reports from the Field Recording System (Peldsyrkontrollen), normally in the November issue of Pelsdyrbladet (1986-92). This figure gives the number of live pups per litter at the age of approximately three weeks, but is based on fewer farms (27% of all breeding females in 1991, Einarsson & Johannessen 1992). The number of pups/litter is also given for the various colour types of farm-bred arctic foxes. Naturally, pups/litter is higher than pups/female, because the latter also includes many barren females.

In Norway an average of 7.9 pups/litter has been estimated (Fougner 1991), which is intermediate between the two groups of natural populations reported above. The estimated values for prenatal mortality and mortality of pre-weaned pups are high (Table 2). Thus, the potential for improving the reproductive success of farm-bred arctic foxes appears to be high. A decline has been observed in recent years (Fig. 1), from 4.73 pups/female in the period 1977-84 to 4.41 pups/female in 1985-91 ($t=2.79$, d.f.$=13$, $p<0.05$). However, the number of pups per female was not correlated with the number of pups per litter during 1986-92 (Pearson's $r=0.06$, $p>0.05$, $n=7$). The reduction in pups/female during 1977-92 mostly resulted from more pups produced in the period 1977-82. That is, prior to the start of cross-breeding with red foxes and the introduction of artificial insemination.

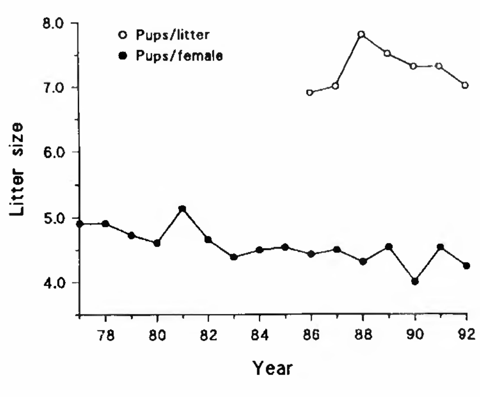

Fig. 1. Litter size in Norwegian farm-bred arctic foxes as recorded by the Insurance Association (pups/female) during 1977-92 and the Field Recording System (pups/litter) during 1986-92

When splitting pups/litter from the field recording system on blue foxes, white foxes, and shadow foxes (99.5% of all farm arctic foxes), a correlation was found only between blue and shadow foxes ($r=0.84$, $p<0.01$, $n=7$). The lack of correlation ($p>0.05$) between litter size in blue and white foxes and between shadow and white foxes indicates that multiple factors affect reproduction. I also calculated t-tests on pups/litter (as well as for pups/female) for the two periods 1986-89 and 1990-92, but found no differences in litter size between the two periods either for the total average, or for blue, shadow, or white foxes separately ($p>0.05$). This indicates that there has been no reduction in the number of surviving pups in Norwegian farms since 1986. For the period 1986-92 I found no difference in pups/litter between blue, shadow, and white foxes ($p>0.05$, means 7.26, 7.27, and 7.59 pups/litter, respectively). Thus in farms, white foxes (inland foxes) do not have larger litters than blue foxes (coastal foxes).

CONCLUDING REMARKS

Breeding of both free-living and farm-bred arctic foxes probably depends on the interaction of multiple and largely unknown factors. In free-living foxes food is probably the most important factor influencing the condition of both the female and her pups. However, other factors such as age and experience may also have an influence on the number of surviving pups. In farm-bred foxes with an artificial supply of food, factors other than food are probably more important. These factors include domestication, social dynamics (including kin-relations), interspecific relations, nutrition, health, captivity stress, housing conditions, climatic factors, and artificial selection. For example, in farm-bred red foxes social status may have an influence on the number of surviving pups (Bakken 1992; Braastad & Bakken 1992).

Calculations on the production of pups in farms are further complicated by, e.g., the fact that the death of females during the breeding period is not recorded, and by the fact that the litter size of cross-breds is included in the litter size for arctic foxes. Although I have attempted to correct for the latter error, my estimates may still be imprecise. Most of the claimed reduction in the number of surviving arctic fox pups, about 0.3 pup/female from the first to the second half of the period 1977-92, may have resulted from various effects of interbreeding with red foxes or from the effect of artificial insemination (see Fougner (1991) for a different conclusion). Thus, there may not actually have been a dramatic reduction in the number of pups/female.

Natural populations of arctic foxes seem to have adapted to one of two major strategies: large, intermittent litters in regions with voles and lemmings, or small, annual litters where voles and lemmings are not the staple foods. The litter size of farm-bred foxes seems to be in-between these two extremes, perhaps indicating a diverse origin of farm foxes. Even if these two strategies of litter size turn out not to be entirely genetically determined, it is probably worthwhile to pursue this line of reasoning further by experimental tests. If it is possible to separate the two strategies in farm foxes and identify the genetic factors, the potential to select for increased litter size would be higher. Despite the above arguments, it does not follow that selection for increased number of pups/litter is profitable. The potential for an increase in the proportion of breeding females and for a reduction in pup or embryo mortality may be greater (cf. Einarsson 1986).

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The effects of reduced doses of insecticide on aphids and their natural enemies in oats

PETER DENNIS, GARY L.A. FRY & MATTHEW B. THOMAS
Norwegian Institute for Nature Research, Urbygningen, Ås, Agricultural University of Norway

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Different application rates of the insecticide, dimethoate were added to 1 ha plots within a field of oats. The rates applied were 0, 10, 25, 50 and 100 % of the manufacturers recommended dose of 2.5 lha^{-1}, diluted in 400 l water. We analysed the impact of each dose rate on aphid populations, crop yield and beneficial arthropods. The density of diurnal predators, the activity-density of epigeal Carabidae and an index of predation rates were estimated in the plots prior to and on four dates after spray application. Aphid populations were reduced by all dimethoate doses. A limited recovery of aphids in 10 and 25% treated plots reached densities of 25% and 12% of those in control plots, respectively. Day-active beneficial arthropods, including populations of *Adalia septempunctata* (Coccinellidae), *Tachyporus* spp. (Staphylinidae) and Linyphiidae (Araneae) were significantly reduced in 25-100% dimethoate plots for 28 days after spraying despite limited recovery of their populations which reached about half the densities of populations in the control and 10 % plots. The extent of the recovery was related to the dilution of the dimethoate originally applied. The density of dead beneficial arthropods two days after spraying, indicated that mortality not emigration was responsible for the reduction in populations. The numbers of beneficial arthropods in traps also reflected spray concentration. No reduction was observed however, in the catches of carabids. The rates of removal of baits also indicated a reduction in beneficial arthropods between plots with increasing dose rate of pesticide. At harvest, lower yields of oats were obtained from control and 10 % plots, reflecting higher aphid populations in those plots. The most economic application rate was 25% of the manufacturers recommended dose, which achieved acceptable control of aphids under the conditions of the study.

Key words: Beneficial arthropods, insecticide, dimethoate, aphids, reduced rates, oats

Peter Dennis, Macaulay Land Use Research Institute, Craigiebuckler, Aberdeen AB9 2QJ Scotland, UK.

Insecticides are applied to cereal crops in a prophylactic manner over much of Europe (Wratten & Mann 1988). Many types of insecticide upset the balance between pests and their natural enemies (van Emden 1987). In particular, the broad spectrum insecticide, dimethoate, can cause long term (two month) reductions in the diversity and densities of natural enemies in cereals (Vickerman & Sunderland 1977). Furthermore, widespread use of full dose insecticides such as dimethoate can intensify pest problems in following years (Vickerman & Sunderland 1977). In sugarbeet, lack of food following full dose insecticide treatment reduced the next season's population of Coccinellidae more than direct toxicity (Heathcote 1963). Within season effects of pesticides on natural enemies also created a greater risk of pest resurgence. Carabid (Duffield & Baker 1990) and linyphiid spider (Thomas *et al.* 1990) densities recover after insecticide application mainly by invasion. Populations of these natural enemies diffuse in to sprayed fields from neighbouring unsprayed areas and non-crop habitats. This process is slower in larger fields.

For farmers to utilize the benefits of natural enemies, their populations must be protected within the crop. Labels on pesticide packaging commonly express dose rates higher than necessary to obtain full efficacy (Metcalf 1980). Applications of pesticides at lower doses could reduce the adverse effects of insecticides, in particular those with a broad spectrum of activity (Unal & Jepson 1991). Lowering inputs could maintain control over pest numbers but reduce environmental impact and encourage better survival of natural enemies within the sprayed area without compromising food production (Poehling 1989).

The application of optimal dose rates of pesticides could reduce the impacts of spray drift that infiltrates adjacent natural biotopes (Boatman *et al.* 1989). Within the crop, reduced dose rates of pesticides can achieve economic control of pests while minimizing impact on natural enemy populations (Kiritari 1976, Storck-Weyhermuller 1984, Taye & Jepson 1988). For example, reduced doses of pirimicarb used against pea aphid (*Acyrthosiphon pisum* Harr.) populations maintained the activity of aphid predators (Poehling 1988, 1989). Population growth of the pest was stopped or significantly reduced within five days by the combination of the pirimicarb and predator activity (Hellpap & Schmutterer 1982). Despite previous experimental work which tested the efficacy of reduced doses, few studies have investigated the impact of reduced doses of insecticides on the activity and predation pressure exerted by natural enemies in cereal crops. In the current work, four dose rates of the insecticide, dimethoate were applied to 1 ha plots marked out in an oat crop to investigate the effect on both the aphid pest and a selection of its natural enemy populations.

MATERIALS AND METHODS

On 5 July 1989, six one hectare plots within a single field of oats were either sprayed with 400 l water only (two plots as controls) or including 10% (0.25 l), 25% (0.625 l), 50% (1.25 l) or 100% (2.5 l) of the manufacturers recommended dose rate (MRDR; 200gai/l) of dimethoate (an insecticide commonly used by Norwegian farmers). A conventional tractor mounted sprayer was used, calibrated to apply 400 l ha^{-1}. The route for spraying was the same in each plot so that the area and pattern of wheel damage was kept constant. We analysed the effectiveness of each dose rate in controlling aphid populations, effects on beneficial arthropods and resultant crop damage. To aid interpretation, the percentage change in numbers of aphids and beneficial arthropods relative to control plots was calculated (Schaalje *et al.* 1989). A similar value, percentage "consumed" relative to control, was calculated from the number of baits removed in each treatment. All these parameters were tested using two-way analysis of variance (date by treatment, log transformed to normalise data).

Aphid counts

Aphids of the species *Sitobion avenae* (F.), *Rhopalosiphum padi* (L.) and *Metopolopium dirhodum* (W.) were sampled before (5 July) and after spraying (7, 11, 18 July and 2 August) by counting the numbers of each species and instar on 100 stems from each plot on each sampling date. The stems were picked randomly while walking a Z in each plot.

Natural enemy populations

Surface search

The density of diurnal predators was measured using surface search in 20 randomly placed quadrats (0.25 m^2) in the core area of each plot. A buffer of 10 m around each plot was not sampled to avoid direct edge effects between plots due to overspray of dimethoate or overspill of activity of invertebrates from adjacent plots. Natural enemies were counted after identification on the soil surface in each quadrat. The procedure was repeated during daytime on each of the sampling dates stated for the aphid counts. In addition, the numbers of dead predators were counted on two days after dimethoate application in five 0.25 m^2 quadrats per plot to investigate the level of mortality (direct or indirect) between plots.

Barrier pitfall traps

The activity-density during 24 h of ground active, in particular nocturnal Carabidae, was measured using barrier-pitfall traps. Each trap comprised a 1.5 m sheet of polyethylene stretched between two pitfall cups as described by Wallin (1985). Ten traps were constructed in each plot and traps opened the day before each sampling date stated for the aphid counts for 24 h before collecting the arthropod contents for laboratory identification and sorting.

Predation pressure

Feeding activity by predatory arthropods was measured as the predation pressure on baits placed out in the field. Aphids were killed by freezing and groups of ten were placed on 9 cm diameter paper discs, ten discs of baits were placed in each plot under a 20 cm diameter paper cover supported on two 8 cm long steel nails. The number of aphids that remained after 24h was recorded for each plot on each sampling date. Numbers removed during the 24h were assumed to be taken by natural enemies of aphids.

Yield

A small harvester was used to take five 1.5 m wide samples of oats from two 10 m wide strips left across each plot by a conventional harvester in late August 1989. Weights were measured for five samples taken from the two strips in each plot. The mean weight of the oats per plot was adjusted for the precise area of each cut and the moisture content of the grain samples. Thousand grain weight and weight per litre of grain were also recorded.

RESULTS

Effects on aphids

Aphid numbers declined in all plots two days after receiving dimethoate, contrasting with the control plot where increases in aphid populations occurred during the same period (Figs 1a & 6). Thirteen days after spraying, differences in the treatments reflected aphid population recovery in the 10% and 25% of MRDR plots (Fig. 6). However, these did not reach the levels of the control populations and by 18 July the maximum population of each treatment related inversely to the dose-rate (Fig. 1a). Full and 50% of MRDR showed no significant recovery in the aphid populations (Figs 1a & 6). In Scandanavia we would expect *R. padi* to be predominant and to cause damage to oat crops in early June (Rygg 1989). In this experiment, however, the aphid population comprised mainly *S. avenae* (Fig. 1b) and densities were highest in mid-June (Fig. 1a). *S. avenae* causes greater damage at lower populations because it feeds directly on the developing grain whereas *R. padi* feeds on the lower stems. The natural crash in aphid populations in all plots, after 18 July (Fig. 1a) was due to emigration induced as the crop ripened and became unsuitable as food.

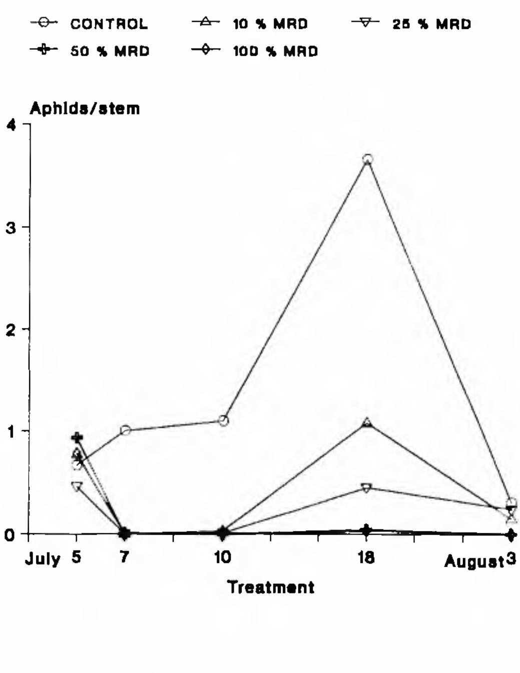

Fig. 1a. Aphid populations before and after spraying reduced doses of the insecticide dimethoate. Differences were tested between date and plot with two-factor analysis of variance, $\underline{F}_{20,2970} = 12.25$; $\underline{P} < 0.001$. Samples carried out before (5 July) and after (7, 11, 18 July and 2 August) the application of dimethoate at different doses (10, 25, 50 and 100 % recommended dose and control of water only)

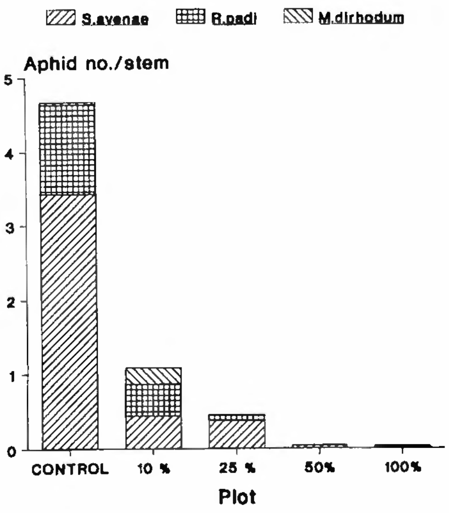

Fig.1b. The species composition of aphid populations when peak numbers were recorded on 18 July; there was a significant difference in the total number of aphids between plots at that time ($\underline{F}_{5,594}$ = 22.97; $\underline{P}<0.001$)

Effect on natural enemy populations

Surface search

There were significant between treatment and time effects on the density of beneficial arthropods from the surface search data ($\underline{F}_{20,511}$ = 5.54; $\underline{P}<0.001$; Figs 2a & 6). Populations of the aphid specific predator, *Adalia septempunctata* L. (Coccinellidae) were reduced in relation to the strength of dose rates applied ($\underline{F}_{20,511}$ = 4.33; $\underline{P}<0.001$; Fig. 2b). The captures of several species were lower in the 100 and 50% of MRDR compared with 25 and 10% of MRDR treatments and control plots. Bembidiinae ($\underline{F}_{20,511}$ = 5.56; $\underline{P}<0.001$), Staphylinidae ($\underline{F}_{20,511}$ = 4.82; $\underline{P}<0.001$), *Aloconota gregaria* Erichson (Coleoptera: Aleocharinae; $\underline{F}_{20,511}$ = 3.52; $\underline{P}<0.001$), *Tachyporus* spp. ($\underline{F}_{20,511}$ = 4.73; $\underline{P}<0.001$; Fig. 2c) and Linyphiidae ($\underline{F}_{20,511}$ = 2.85; $\underline{P}<0.001$; Fig. 2d) densities were significantly lower in the 100 and 50% of MRDR compared with 25 and 10% of MRDR plots on each date after the pesticide treatment. There were too few large Carabidae captured to conduct a statistical analysis although their numbers were included in the "beneficial arthropods" group. For all groups, greater reductions in the density of individuals were observed in plots receiving the highest doses of dimethoate (Fig. 2). The recovery of beneficial arthropod populations observed 28 days after spraying reflected the concentration of the insecticide application. The overall pattern in the results was that the lowest dose rates had less effect and allowed quicker recovery of populations of beneficials than the higher doses.

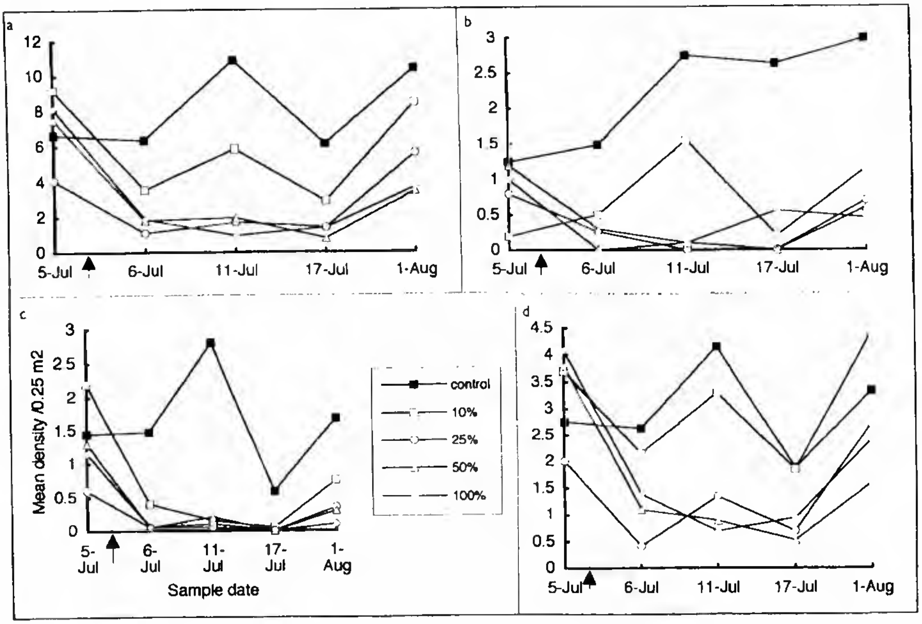

Fig. 2. Population densities (0.25 m^{-2}) estimated from surface search of: a, beneficial arthropod predators, b. *A. septempunctata* (Coccinellidae), c. *Tachyporus* spp. (Staphylinidae) and d. Linyphiidae (Araneae). Details of experimental treatments and sample dates given in Fig. 1a. legend

Knockdown is the immediate reduction in predator numbers after spraying, and was observed in each 1 ha plot that received dimethoate (Fig. 3). There was a significant reduction in numbers of beneficial arthropods detected by surface search from 5 to 7 July ($F_{20,511}$ = 5.54; $P<0.001$). and surface search (see Fig. 3a) showed that the reduction was due to mortality not emigration (surface search for dead beneficial arthropods on 7 July; $F_{5,24}$ = 5.50; $P<0.01$ for stenophagous and $F_{5,24}$ = 6.93; $P<0.001$ for polyphagous beneficial arthropods). A direct comparison between living and dead beneficial arthropods could not be made using analysis of variance because the density of dead arthropods was based on an accumulative total per plot whereas the sample of the live population was of the pattern of mobile individuals at a moment in time. However, the rate of change of living populations between 5 and 7 July was strongly related to the numbers of dead arthropods for each plot (Fig. 3b).

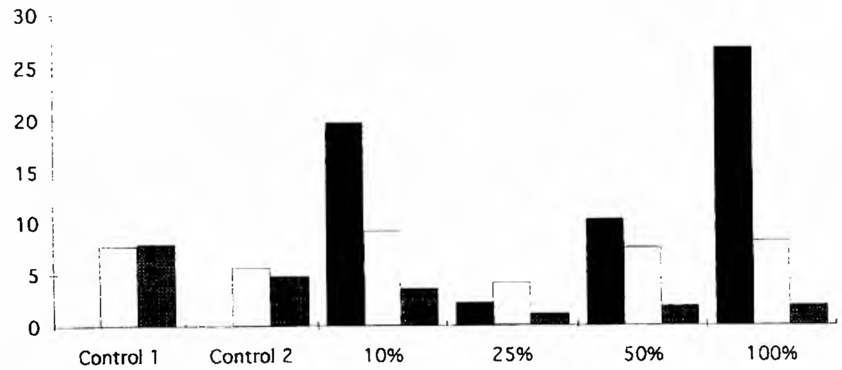

Fig. 3. Knockdown effect of different doses of dimethoate on beneficial arthropods sampled two days after spraying 1 ha plots. a. The density of beneficial arthropods alive in each plot before (5 July, □) and after (7 July, □) spraying, compared with the density of dead predators collected from quadrats on 7 July (■)

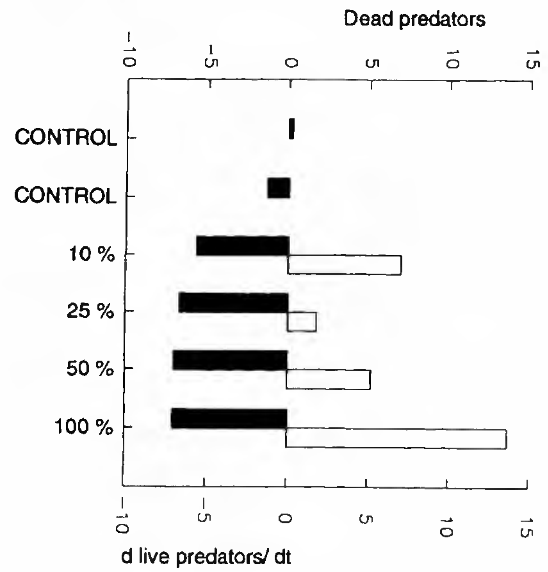

Fig. 3b. Dead predators were compared with the change in density of living predators (d live predators;) between 5 and 7 July (dt) and tested with linear regression ($\underline{r}$ = 0.86; y = -0.045 $\pm$ 0.0338x -0.13; $\underline{F}_{1,4}$ = 11.52; $\underline{P}<0.05$; $\underline{R}^2$ = 0.68).

Barrier pitfall traps

Plots receiving 25-100 % of MRDR dimethoate had a significantly reduced activity-density of *A. septempunctata* (Fig. 4a; $F_{20,254}$ = 4.78; $P<0.001$), Bembidiinae (Fig. 4b; $F_{20,254}$ = 2.38; $P<0.01$) and Linyphiidae (Fig. 4c; $F_{20,254}$ = 3.55; $P<0.001$) up to 13 days after insecticide application compared with control and 10 % of MRDR plots. This trend was still significant for *A. septempunctata* and Linyphiidae 28 days after the application of dimethoate (Figs 4a & b). However, large, nocturnal Carabidae, although significantly different in numbers between treatments on each date after spraying, did not show a consistent relationship with the concentration of dimethoate (Fig. 4d; $F_{20,254}$ = 7.05; $P<0.001$).

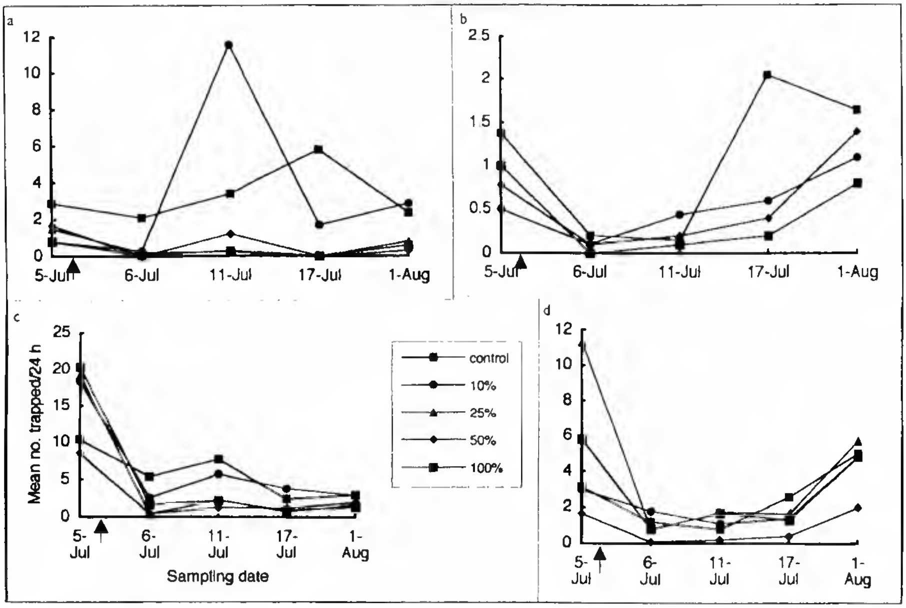

Fig. 4. Changes in activity-density of beneficial arthropods detected using barrier-pitfall traps in treatments that comprised reduced doses of the insecticide dimethoate (a. *A. septempunctata* (Coccinellidae), b. Bembidiinae (Carabidae), c. Linyphiidae and d. nocturnal Carabidae). Details of experimental treatments and sample dates given in Fig. 1a. legend. See Fig. 2 for key to symbols for the treatments.

Predation pressure

Predation as a measure of activity by natural enemies declined from 7 July (Figs 5 & 6). Levels of predation as a proportion of that in control plots declined to between 40% and <10% at six days after spraying, reflecting the mortality rates observed for beneficial arthropods (Fig. 6b). The variation in consumption rates of baits between treatments two days after application of dimethoate may reflect sub-lethal effects on the predators such as cessation of feeding. However, by 13 days, predation in the lower dose (10% and 25% of

MRDR) plots was c. 75% of the level in control plots but in the higher dose plots (50% and 100% of MRDR) it remained below 10% (Fig. 6c). By 2 August, the data indicated recovery from the insecticide effects but with high within plot variance (Fig. 5).

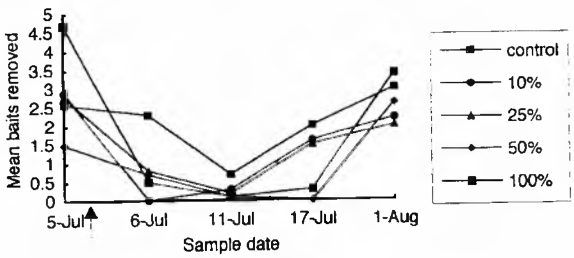

Fig. 5. The effect of different spray doses of dimethoate on the numbers of aphid-baits removed from ten paper discs placed in each plot for 24h. Two way analysis of variance for date by plot showed significant differences ($\underline{F}_{20,269}$ = 1.62; $\underline{P}$<0.05) between control plots and those receiving dimethoate. Quicker recovery of predation rate was observed in 10 and 25 % plots by 18 July and no significant between plot differences by 2 August. Details of experimental treatments and sample dates given in Fig. 1a. legend. See Fig. 2 for key to symbols for the treatments

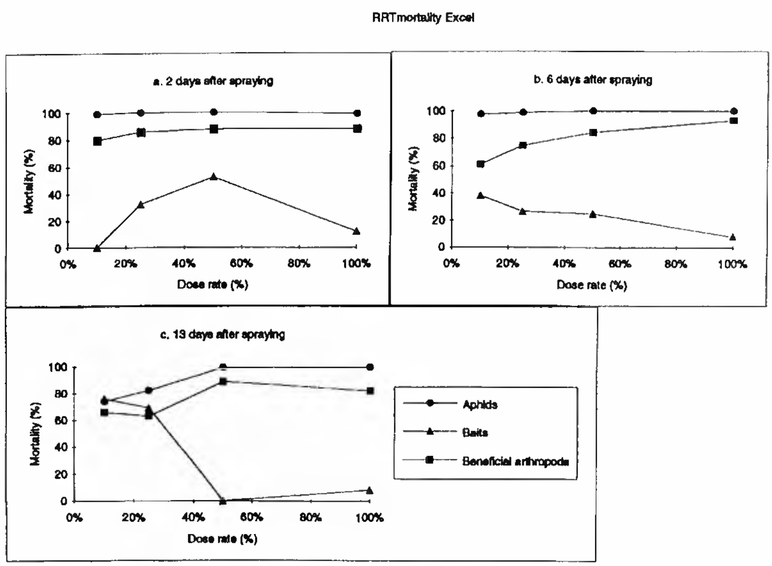

Fig. 6. The changes in densities of aphids and beneficial arthropods (surface search) and predation of artificial baits (as a proportion of that in control) in response to the application of different percentages of the recommended application rate of dimethoate (see Fig. 1a legend) a. two, b. six and c. 13 days after application

Yield

A pattern was observed between application rate, resultant aphid population levels and yield. The mean yield per plot, calculated from ten harvested samples per plot showed significant ($P<0.001$) reductions in yield for control and 10% of MRDR plots (Table 1). Moisture was not significantly different between plots (combined 95 % confidence range of 11.08 to 11.48 %; $F_{5,54}$ = 2.345; NS). Mass per litre of grain was significantly greater in plots receiving 25 % or more of MRDR dimethoate (control and 10 % of MRDR plot means 500.6-506.1 g; 25-100 % of MRDR plot means 528.4-536.0 g; $F_{5,54}$ = 10.19; $P<0.001$). Thousand grain weight was higher for 25-100 % of MRDR plots (37.0-38.3 g) than for control and 10 % of MRDR plots (34.8-35.6 g; $F_{5,54}$ = 8.41; $P<0.001$).

Table 1. Mean yield (± 95 % confidence limits) of oats expressed as tonnes ha^{-1} in experimental treatments in which the dose rate of dimethoate was varied. Different letters signify differences between yield in plots with different dose rates, tested using analysis of variance followed by Tukey's test ($F_{5,54}$ = 10.68; $P<0.001$).

Spray dose	Mean yield (tonnes ha^{-1})	95 % confidence limits
Control 1	3.51	3.202 - 3.812 a
Control 2	3.62	3.312 - 3.922 a
10 %	3.63	3.329 - 3.939 a
25 %	4.71	4.410 - 5.020 b
50 %	4.20	3.900 - 4.506 b
100 %	4.2	3.945 - 4.555 b

DISCUSSION

In this pilot study, the densities of aphid populations were significantly reduced by the different dose rates of dimethoate applied in each plot (Fig. 1a). The peak population of 1 $stem^{-1}$ *S. avenae* at flowering in the 10% of MRDR plot was an equivalent density to the economic threshold for this aphid species on flowering wheat in Germany (Basedow *et al.* 1983). Low densities of aphids at a late growth stage of the crop were appropriate for the use of low doses of insecticide in Germany because the reduction of aphids prevented yield loss in field experiments but did not allow time for the populations of the aphid to recover (Poehling 1988). In early aphid outbreaks, however, low dose rates were not effective because aphids that survived were able to reproduce before the natural decline phase of the population and reach densities that cause economic damage to the crop. Careful monitoring would be needed after spraying to detect an increase in the growth rate of aphids, despite the predation pressure exerted by the natural enemy population.

In the current study, lower application rates of insecticides gave economic benefits over full doses where they effectively controlled aphid populations. The 25% of MRDR maintained control of aphids, with no yield loss and produced the maximum economic benefit (NKr. advantage over control) for the farmer, NKr. 48.8 compared with full recommended dose, NKr. 195.0 ha^{-1} at 1989 prices. Similar economic benefits were shown for half MRDRs of pirimicarb, deltamethrin and dimethoate applied to small plots of oats and barley against aphids compared with full MRDRs in randomised plots in Norway (Rygg 1989; Fry 1991). Further experiments which reduced the MRDRs of pirimicarb and fenvalerate in Germany, showed that the high efficiencies of commonly used insecticides at full MRDR are unnecessary to gain cost efficient aphid control (Mann *et al.* 1991). The economic profitability of reduced rates depended on the extent of post-treatment recovery of the aphid populations, the cost of control and the crop value. The relative efficiency of MRDRs were dependent on the growth stage at which spraying took place and the size of the aphid population (Mann *et al.* 1991). Overall, reduced-rate applications would be most reliable when aphid populations were low and/or late. Although doses down to 25% of MRDR prevented aphid populations from causing yield loss in the current investigation, such work must be repeated to confirm that low doses could reliably control different size aphid populations at different growth stages of the crop, in all years and for different soil types, soil moistures and temperatures, factors which are considered in the manufacturers stated recommended dose.

The question remains, to what extent did the arthropod predators limit the recovery of the aphid population after spraying? The action of reduced insecticide application rates on beneficial arthropods would correspond to economic advantages if there was a delay or prevention of pest resurgence. The extent of the recovery of the arthropod populations related to the dilution of the dimethoate originally applied. The density of dead beneficial arthropods two days after spraying, indicated that mortality in sprayed plots as opposed to emigration, was responsible for the reduction in populations (Fig. 3). Despite the initial reduction (two days after application) in the activity and densities of beneficial arthropods in all plots that received dimethoate (Figs 2, 3 & 4), a quicker recovery of aphid feeding groups, six days after spraying, was observed in the lower MRDR plots (Figs 2, 4 & 6). The activity-density of beneficial arthropods in traps reflected the pattern of their numbers found from surface searching. Predation on baits of freeze-killed aphids reflected the relative abundance of the beneficial arthropods between the different proportions of MRDR plots on day six (Figs 5 & 6). At six and 13 days after spraying, predation in the 10 % and 25% of MRDR plots had recovered significantly compared with higher dose plots (Fig. 6). Experiments in Finland where the densities of predators were lowered, by using barriers or trenches in oats plots, led to an increase in *R. padi* populations of 0.1-1.3 times over plots with normal densities of predators and caused a subsequent 19-22% yield loss (Helenius 1990). Further experiments would be needed to seperate residual toxicity of different dose rate insecticides from predation pressure exerted by the surviving predator population. We also need to understand the role of immigration by predatory arthropods into crops after spray application and the viability of the sources of such populations given local or regional variation in the intensity of arable farming.

Particular groups of beneficial arthropods have different risks of exposure to pesticides, dependent on their ability to disperse, their overwintering location and timing of reproduction (Burn 1988, Jepson 1989). The limited effect observed here for nocturnal Carabidae was symptomatic of their low risk status although the experiment took place during the decline phase of adults of the previous generation and this was responsible for the overall decline in numbers captured (Fig. 4d). Their nocturnal activity on the ground avoids direct exposure to pesticide droplets at the time of spraying and later contact with the main sites of droplet deposition (the foliage). Furthermore, the dimethoate was applied before the period when adults of the next carabid generation were abundant and active on the soil surface of the crop (see Dennis & Fry 1992).

The observed effects on high risk groups suggest that long term effects could result. The densities of *A. septempunctata* and *Tachyporus* spp. in full dose plots remained at only c.15% the density in the control plots 28 days after spraying (Fig. 2b & c). Long-term exposure to annual spray schedules by high risk groups such as Tachyporinae, Linyphiidae and Coccinellidae have resulted in reduced activity in cereal fields which received high compared with low amounts of pesticide (Burn 1988). Conversely, the benefits of maintaining a high predation pressure in one season may be a reduction in the pest population of the following season (Heathcote 1963). High predation pressure on aphids combined with reduced rates of insecticide application may lower selection pressure for individuals expressing genes for insecticide resistance by fragmenting the development of pesticide resistant genes in the population.

Some environmental benefits of the more dilute active ingredient (a.i.) of reduced doses, particularly of broad spectrum insecticides, are lower residues in the plant tissues and soil of field and surrounding biotopes after application and less affect on non-target, beneficial organisms. Dimethoate caused 386 accidental wildlife poisonings, 47 against honeybees (1982-87), reported in the UK (Greig-Smith 1988) and run-off into waterways of pyrethroids such as Fenvalerate can kill fish (Ivens 1989). Current MRDRs of pesticide adversely affect populations of butterflies (Dover 1991) and insects essential as food for grey partridge chicks (Boatman *et al.* 1989). Our work suggests it is feasible to reduce the a.i. of insecticide applied to cereals by 25-50% but in practice insecticide represents a mere 7-8% of the 12 tonnes a.i. of pesticide applied annually to cereals in Norway (Norwegian Department of Agriculture, statistics for 1988). Of insecticides, 60% are applied to vegetable crops, therefore, to realise significant economic and environmental benefits, we must reduce inputs of pesticides to all crops. This cannot be undertaken without widespread monitoring and forecasting programmes to supervise the crop protection (Mann *et al.* 1991) although the 28 % lower costs (with no yield loss) of chemicals in supervised compared with conventional crop protection (Wahmhoff & Heitefuss 1989) could be improved with reduced MRDRs. More work is required to determine circumstances in plant protection programmes when reduced MRDRs of a wider range of pesticides would be appropriate and effective.

The combination of lower doses of physiologically selective pesticides (toxic to pest but not to predators, such as Sumicidin and Pirimor) is considered by Poehling (1989) the best approach for using the natural enemies present in crops. Many arable farmers today spray the cheaper, broad spectrum and most harmful products, for example dimethoate, which wastes the predation pressure exerted by aphid predators (Thomas *et al.* 1991). Reduced MRDRs are advocated to limit the side effects of broad spectrum pesticides, especially severe effects of full doses that occur immediately after spraying (Unal & Jepson 1991). In Norway, widespread use of broad spectrum compounds counteracts the beneficial influence of smaller field sizes (relative to European Community countries) which provide greater edge habitat where predators are active in higher densities (Dennis & Fry 1992).

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Vegetative, generative and quality characteristics of four blackcurrant (*Ribes nigrum* L.) cultivars

FINN MÅGE
Agricultural University of Norway, Department of Horticulture, Ås, Norway

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Four blackcurrant cultivars were evaluated for vegetative, generative and quality components over a period of four years. The new cultivars Ben Alder and Ben Tirran had the highest yield, and flowered and ripened more than one week later than Ben Nevis and Hedda. It was found that only Ben Nevis was susceptible to mildew, while Ben Tirran showed somewhat uneven ripening. Ben Alder is recommended for commercial growing because of its high yield, freedom from mildew and good fruit juice colour, although the fruits are small. Hedda can be recommended as an early cultivar, especially for home gardens, despite a somewhat lower yield, moderate fruit juice colour intensity, and low vitamin C content.

Key words: Blackcurrant, cultivars, fruit quality, yield.

Finn Måge, Agricultural University of Norway, Department of Horticulture, P.O. Box 5022, N-1432 Ås, Norway.

In blackcurrants, the cultivar choice both for commercial purposes and for home gardens has changed during recent decades. Breeding programmes are being carried out in different countries, and these include high yield, disease resistance, growth habit, frost resistance and high fruit quality among the important aims.

Cultivar testing is a continuous task, and recently a great many cultivars have been tested in Norway, both for agricultural properties (Heiberg & Måge 1991; Nes & Meland 1992) and for quality characteristics (Heiberg et al. 1992).

In Norway, Ben Nevis and Hedda are at present the predominant blackcurrant cultivars. The first is susceptible to mildew, and recommended for commercial production only. Hedda, on the other hand, is free from mildew, and is planted both commercially and in home gardens, despite a lower yield, spreading growth habit, low content of vitamin C and inferior fruit colour.

MATERIALS AND METHODS

At the Agricultural University of Norway, a field experiment with four blackcurrant cultivars was established in the spring of 1987. The cultivars included were Ben Nevis, Hedda, and two selections from the Scottish Crop Research Institute, recently named Ben

Alder and Ben Tirran. The plan used was a randomized block design, with four replicates and four plants in each plot.

The distance between the rows was 4.0 m, 1.5 m between the plants in the rows, and 2.0 m between the plots, making a total of about 1600 plants/ha.

The present planting was close to the site used for a similar experiment described earlier (Heiberg & Måge 1991), and the cultural practices were about the same as in the preceding experiment, except that the plants were sprayed only two to three times each year in the present experiment. The plants were pruned by hand each spring.

Fertilizers were applied by hand under the bushes. On the basis of results from leaf analyses in August 1989 (Table 4), more fertilizer was added in 1990 and 1991.

Chemical composition of the fruits was analysed in the same laboratory and in the same way as that described by Heiberg et al. (1992).

All data were subjected to analysis of variance, and LSDs were calculated to determine significant differences between cultivars at the $p < 0.05$ level.

RESULTS

Generative properties

Yield data in kg/ha are presented in Table 1. The differences between cultivars were statistically significant in three out of four years, and on an average of all years. The interaction between cultivar and year was also significant. Ben Tirran had the highest yield in all years except one, and Hedda the lowest yield in three out of four years.

Table 1. Yield in kg/ha of four blackcurrant cultivars in four years

	1988	1989	1990	1991	Average
Ben Alder	2060	5950	8910	7640	6140
Ben Nevis	740	3930	7960	6710	4835
Ben Tirran	2420	6060	7470	10050	6500
Hedda	180	2310	8780	5350	4155
Average	1350	4563	8280	7438	5408
p %	0.003	0.004	5.494	3.361	0.001
LSD					1582

The weight of 100 fruits was low in the two new cultivars Ben Alder and Ben Tirran (Table 2). It varied among years and the average weight was lowest in 1989 with 83 g, and highest in 1990 with 141 g. The differences between cultivars were significant every single year, and most pronounced in 1988, when the 100-berry-weight for Ben Alder was 57 g, and 110 g for Ben Nevis.

The number of flowers and fruits per raceme was somewhat higher in the two new cultivars (Table 2), and no statistical differences in weight of 100 racemes were found.

Table 2. Generative characteristics of four blackcurrant cultivars. Average of four years

	Number of flowers per raceme	Number of fruitlets per raceme	Weight of 100 berries (g)	Weight of 100 racemes (g)
Ben Alder	8.5	7.0	108	756
Ben Nevis	6.9	5.1	146	745
Ben Tirran	8.4	7.0	118	826
Hedda	7.0	5.6	141	790
Average	7.7	6.2	129	805
p %	0.000	0.000	0.000	6.972
LSD	0.85	0.78	15.0	-

Phenological data

Time of flowering was more than one week later in the two new cultivars, compared with that in Ben Nevis and Hedda (Table 3). Ben Tirran ripened latest, more than 10 days later than Hedda. The number of days for development was 80, with only small variations among cultivars.

Table 3. Phenological data of four blackcurrant cultivars, 1988-91

	Date of 50% open flowers	Date of ripening	Number of days for development
Ben Alder	May 16	August 2	78
Ben Nevis	May 8	July 27	80
Ben Tirran	May 17	August 7	82
Hedda	May 8	July 25	78
Average	May 12	July 31	80

Evaluation of fruit ripening was based on skin colour, but no detailed investigation was carried out. Ben Tirran, however, showed most uneven ripening on the racemes.

Vegetative growth and nutritional status

Ben Nevis had the most vigorous growth (Table 4), and Ben Alder had the smallest bushes. Form index, expressed as height divided by diameter, showed that Ben Alder had the most upright growth habit. The plants were pruned every spring and, on average for the four years, about twice as much branch material was removed from Ben Nevis compared to Ben Alder and Ben Tirran (Table 4).

Table 4. Vegetative growth of four blackcurrants cultivars as an average of four years

	Bush height cm	Bush diam. cm	Form index h/d	Number of shoots 50 cm or longer	Weight of prunings Kg/bush
Ben Alder	116	155	0.75	11	0.6
Ben Nevis	136	201	0.68	16	1.6
Ben Tirran	116	167	0.70	14	0.8
Hedda	120	171	0.70	14	1.0
Average	122	174	0.71	14	1.0
p %	0.000	0.000	0.082	0.011	0.000
LSD	7.5	16.5	0.06	4.5	1.03

The content of nitrogen in the leaves in samples from August 1989 was relatively low compared to the optimum interval (Table 5), and phosphorus and calcium was high. Cultivar differences were indicated, but as only two replicates were included, no statistical calculation was carried out. Little is known about the fertilizer demand of the new cultivars. Ben Alder had, for instance, about half a percent more nitrogen in the leaves than Hedda, and Hedda had twice as much boron as Ben Nevis (Table 5).

Table 5. Concentrations of N, P, K, Ca, Mg and B in leaves of blackcurrants sampled in August 1989. B is given as ppm of the dry matter, the others in percent

	Nitrogen	Phosphorus	Potassium	Calcium	Magnesium	Boron
Ben Alder	2.37	0.22	1.21	2.85	0.29	22.8
Ben Nevis	2.17	0.26	1.25	2.53	0.24	18.8
Ben Tirran	2.14	0.25	1.29	2.81	0.27	23.6
Hedda	1.87	0.35	1.23	2.50	0.24	35.7
Average	2.14	0.27	1.25	2.67	0.26	25.2
Optimum	2.6- 2.9	0.15-0.20	1.2-1.6	1.4-1.7	0.25-0.35	20-30

Leaf diseases

Only Ben Nevis was subject to mildew (*Sphaerotheca mors-uvae*) attack (Table 6). All cultivars displayed leafspot (*Pseudopeziza ribis*) symptoms, the most susceptible being Ben Alder and Ben Nevis. Blister rust (*Cronartium ribicola* Fisch.) appeared only in one year, and Ben Nevis was almost free, while Ben Alder was heavily infested.

Fruit quality factors

Ben Alder and Hedda had the lowest content of soluble solids in the fruit juice, and Ben Nevis the highest (Table 7). Hedda had the lowest content of titratable acid. Ben Alder had the most intense red colour, measured at 520 nm, and Hedda the lowest intensity. Ben Alder also had the highest colour quality (520/410 nm, and Hedda the lowest.

Table 6. Leaf diseases in four blackcurrant cultivars, average of four years. Scores from 0 to 5, (0=free)

	Mildew	Leafspot	Blisterrust
Ben Alder	0.0	1.8	1.1
Ben Nevis	2.8	0.7	0.3
Ben Tirran	0.0	1.3	0.8
Hedda	0.0	1.0	0.7
Average	0.7	1.2	0.7
p %	0.000	0.000	0.000
LSD	0.29	0.49	0.44

Table 7. Quality factors analysed in the fruit juice of four blackcurrant cultivars. Average of four years

	Solub. solids %	Titr. acids %	Colour at 520 nm	Colour at 410 nm	Colour Quality 520/410
Ben Alder	15.4	4.11	0.438	0.175	2.51
Ben Nevis	17.0	4.77	0.397	0.156	2.47
Ben Tirran	16.1	4.54	0.364	0.159	2.25
Hedda	15.4	3.32	0.202	0.096	2.15
Average	16.0	4.19	0.350	0.147	2.35
p %	0.000	0.000	0.000	0.000	0.004
LSD	0.94	0.21	0.578	0.270	0.289

The content of ascorbic acid varied from year to year, and from cultivar to cultivar, (Table 8). Hedda had a considerably lower content than the other cultivars, and the highest content was found in Ben Tirran.

Table 8. Ascorbic acid content in four blackcurrant cultivars in four years. Mg/100 g fresh fruit

	1988	1989	1990	1991	Average
Ben Alder	122	195	149	134	150
Ben Nevis	126	180	176	157	160
Ben Tirran	169	248	156	157	183
Hedda	64	74	79	70	72
Average	120	174	140	130	141
p %	0.362	0.000	0.000	0.000	0.000
LSD					23.6

DISCUSSION

A new blackcurrant cultivar should give a good crop, but important is also freedom from plant deseases. If the plants can be grown with less spraying, the growers will accept somewhat lower yields. In the present experiment only Ben Nevis was susceptible to mildew, and the two new cultivars Ben Alder and Ben Tirran both had higher yields than Ben Nevis, confirming the results from Nes & Meland (1992).

Ben Alder and Ben Tirran had small fruits, but for the processing industry this is preferable. For home gardens, on the other hand, larger fruits are preferred, and for this reason the two new cultivars are not ideal for this purpose.

The time of flowering was one week later in Ben Alder and Ben Tirran than in Ben Nevis and Hedda, which is important in areas where spring frost is a problem.

In this experiment Ben Alder had the smallest bushes, and Ben Nevis the largest. Ben Alder also had the most upright growth habit.

As to quality factors, the content of soluble solids was relatively high in all cultivars. Hedda had a low content of titratable acids, which may be desirable for home gardens, but not for the industry. Low colour intensity in Hedda also makes this cultivar unattractive for the processing industry.

The ascorbic acid content was especially low in Hedda which was also indicated in earlier studies (Heiberg et al. 1992). For this reason, and because of low colour intensity and low yield potential, Hedda should be replaced both for commercial production and for growing in home gardens if a new, good early cultivar becomes available.

Ben Tirran had the highest yield, but because of the uneven ripening, the cultivar is not recommended. In the present experiment the ripening was not evaluated in detail, so this property should not be considered fully documented in the present trial. If the berries do not drop until they are overripe, a cultivar with uneven ripening may be used. This was not studied in the present experiment, but further work is in progress.

Ben Alder has many good agricultural and quality properties and may be grown for the processing industry as an alternative to Hedda and Ben Nevis. Hedda is still recommended for home gardens but Ben Nevis cannot be recommended because of its susceptibility to mildew. Finally the ripening of Ben Tirran should be examined in greater detail.

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The effect of clear-cutting *Betula pubescens* Ehrh. (birch) on the plant species composition in a subalpine *Vaccinium myrtillus*-dominated pasture area

MARY HOLMEDAL LOSVIK
University of Bergen, Botanical Institute, Bergen, Norway

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Decline in grazing intensity is an important factor in the regeneration of *Betula pubescens*, which causes the reduction in pasture quality in the sense that the proportion of grasses, sedges and herbs is reduced. Clear-cutting of *B. pubescens* was thought to improve the pasture. In the Frudalen area in Sogndal two sites were clear-cut in spring 1990. The presence of species of Tracheophyta was recorded in 1989, 1990 and 1991 in 100 transect plots of 625 cm^2 in the experimental sites and in two adjacent control sites. The sites were dominated by *B. pubescens* and *Vaccinium myrtillus*. The vegetation was characteristic of the northern boreal vegetation region, and belongs to *Chamaemoro-Piceetum* K.-Lund 1962. The data were analysed using DCA and CCA ordination techniques (CANOCO) and regression analysis. Important gradients were light intensity and moisture (level). The vegetation changed with time. Vegetation in experimental sites was shown to be influenced by clear-cutting when compared with vegetation in the control sites. There was a greater increase in the number of species in the experimental plots than in the control plots. As the sites bordered on one another, the increase in species number in the control plots was probably due to the clear-cutting of the experimental sites. Grass, sedge and herb species colonized the plots and in the time-span allowed for in this study, it is concluded that clear-cutting has improved the quality of the pasture.

Key words: *Betula pubescens*, clear-cutting, herbs and grasses, subalpine pasture.

Mary Holmedal Losvik, Sogn and Fjordane College, N-5800 Sogndal, Norway.

Grazing intensity has been reduced in the Frudalen mountain pasture area during the last 40 years. Frequency and cover of species such as *Betula pubescens*, *Salix* spp., *Vaccinium myrtillus* and various ferns such as *Gymnocarpium dryopteris*, *Thelypteris limbosperma* and *Athyrium distentifolium*, have increased. The quality of the pasture has gradually deteriorated for the sheep and horses remaining in the area (see also e.g. Garmo & Nedkvitne 1985). An increase in the frequency of grasses, sedges and herbs, which are considered the best pasture plants, is required to improve pasture quality.

The aim of the present study was to test the following hypothesis: clear-cutting of *B.*

pubescens will cause an increase in the frequency of grasses, sedges and herbs and in this way will improve the pasture as more light will reach the field layer. Changes in the occurrence and frequency of species on two experimental sites cleared of *B. pubescens* were compared with two uncleared sites.

MATERIALS AND METHODS

Study area

Frudalen is situated in the municipality of Sogndal in the inner Sogn area, western Norway (Fig. 1). The valley is narrow with steep hillsides reaching 1200-1500 m a.s.l., and with

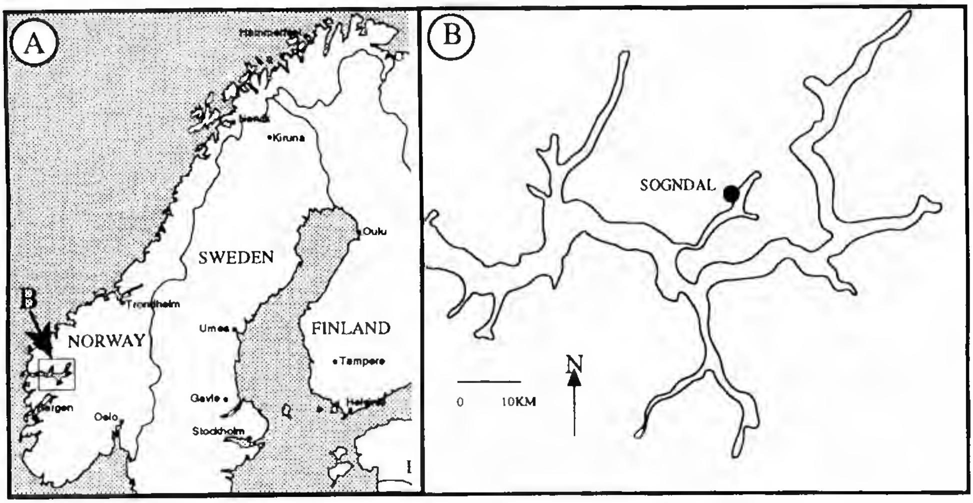

Fig. 1. The situation of Sogndal

the Frudalen river flowing through the valley bottom. The vegetation is characteristic of the northern boreal region (Dahl et al. 1986), and is dominated by birch forest with scattered patches of open grassland pasture and extensive areas of minerotrophic mires. In the valley bottom and on the lower hillsides it overlays morainic material or gneiss. The mean annual temperature is 5.0°C at the nearest weather station Fjærland (approximately 10 km, at sea level)(Det norske meteorologiske institutt 1982). In Frudalen the mean annual temperature is probably 2.5°C, having been adjusted to allow for the height above sea level. The annual precipitation is 1430 mm at Selseng (approximately 3 km). Mean snow cover is 460 mm (October-May) (Det norske meteorologiske institutt 1981). Melt water from the glaciers flows into the valley and together with the precipitation results in a permanently high groundwater level in the area.

Management

In the Sogndal valley 8-10 farms used Frudalen for summer farming for 200 years up until about 1955. The grazing animals in the valley in the summer season comprised 270 sheep, 290 lambs, 35 goats, 50 kids, 130 cattle and 25 horses. During the subsequent 30 years the number of animals was reduced, e.g. to 300 sheep, 400 lambs and 15 horses in 1986 (Rudsengen et al. 1989), thus representing a different type of grazing regime, as sheep are selective feeders amongst herbs and grasses (e.g. Sævre & Baadshaug 1984; Harris & O'Connor 1980; Torsteinsson 1980). Summer farming generally entailed clear-cutting of the tree layer, as large quantities of wood were needed for cheese-making and for cooking. The trees, mostly *B. pubescens*, have also been pollarded, but this practice ceased during World War II (Norvald Uglum pers. comm.). Aerial cables were constructed at several places to transport the wood and bundles of twigs down the hillside. The plant community structure in 1963 (aerial photographs) indicates that the field layer throughout Frudalen was dominated by grasses, sedges and herbs and that *Vaccinium myrtillus* was sparse as long as the old grazing regime continued. This is also confirmed by the land-owners (Sigbjørg Kvåle pers. comm.). At present the most widespread species in the area is *V. myrtillus* and only minor areas is dominated by grasses.

Sampling design, treatment and recording of data

The experimental area was 14 x 10 m^2, gently sloping towards NNE, with variable topography and situated approximately 500 m a.s.l. in a grove of *B. pubescens* with a trunk diameter of 50-70 mm. These trees were clustered in small groups, and some of them were less than half a metre apart, while other trees were 2-3 m apart. The stems were usually bent at the base as a result of snow pressure, and were 4-5 m in height. Close to the area was a sheep track, and in the experimental area sheep dung was recorded.

The experimental area was divided into four sites of equal size, i.e. two experimental sites and two control sites. One hundred plots, each 625 cm^2 in area, were systematically laid out in the sites along two systematically laid transects. Plots from different sites were at least 1 m apart. The plots were laid in groups of four or two and and each site comprised 25 plots. The transects and plots were permanently marked with wooden sticks. Plots without *Vaccinium myrtillus* or *V. uliginosum* on patches of minerotrophic mire were omitted.

On 26 June 1990, trees of *B. pubescens* in the experimental sites were cut and placed in heaps outside the lower end of the area under investigation. The stubble height was $<$ 10 cm.

The presence of species of Tracheophyta was recorded in each plot 1989, 1990 and 1991. Only individuals rooted in the plots were recorded. Nomenclature: Lid, J. 1985. Norsk, svensk, finsk flora. Universitetsforlaget, Oslo.

Data analysis

The variation in species composition was assessed by detrended correspondence analysis (DCA) and canonical correspondence analysis (CCA) in CANOCO (Hill 1979; Hill & Gauch 1980; Jongman et al. 1987; ter Braak 1986, 1987a, 1987b), using frequency in four grouped plots (= a quadrat) as a measure of cover. This resulted in 24 experimental quadrats and 24 control quadrats, each recorded for three years. Detrending was by segments with non-linear rescaling of the axes. Equal weight was given to all species and samples. Sample scores were weighted mean species scores. Time factor from 1989 to 1991 and clear-cut/not clear-cut were used as nominal variables.

Tests of significance by means of the trace statistic were carried out using unrestricted Monte Carlo permutation tests (ter Braak 1987b). Regression analyses were performed on number species, number of grasses, sedges and herbs and number of woody species in each plot, and time. Woody species comprised *Vaccinium myrtillus*, *V. uliginosum*, *Empetrum* sp. and *Betula pubescens*. Species of Pteridophyta are included in the group of grasses, sedges and herbs.

RESULTS

The field layer of the plot area was dominated by *Vaccinium myrtillus*, and, in addition, *Vaccinium uliginosum* and *Empetrum* sp. were frequent (Fig. 2). The occurrence of moisture indicator species such as *Carex nigra*, *Carex echinata*, *Juncus filiformis* and *Rubus chamaemorus* was characteristic of the vegetation type. Other common species were *Deschampsia flexuosa*, *Potentilla erecta* and *Cornus suecica*. In the ground layer *Sphagnum* spp. and *Polytrichum* spp. were frequent (Table 1).

Fig. 2. Part of the experimental area with one of the clear-cut sites

Vaccinium myrtillus, *V. uliginosum*, *Nardus stricta*, *Carex echinata* and *Juncus filiformis* showed little change from 1989 to 1991 both in experimental and in control plots. During the second season after clear-cutting *Empetrum* sp. decreased in frequency in the experimental plots, but had approximately the same frequency and was maintained in control plots. *Potentilla erecta*, *Cornus suecica*, *Rubus chamaemorus* and *Carex nigra* increased in frequency in the control sites more so than in the experimental sites, whilst *Deschampsia flexuosa* and *Trientalis europaea* increased in the experimental sites. *Agrostis capillaris* increased in the experimental sites, whereas in the control sites this species increased in the first season after clear-cutting, but later decreased to the same level prior to this investigation.

Table 1. Frequency of all species in 50 plots in experimental sites and control sites in 1989, 1990 and 1991

	Experimental sites			Control sites			
	1989	1990	1991	1989	1990	1991	
Vaccinium myrtillus	96	96	100	98	96	100	Vacc myr
V. uliginosum	42	46	44	30	30	34	Vacc uli
Nardus stricta	22	18	24	14	18	16	Nard str
Carex echinata	50	50	52	40	48	38	Care ech
Juncus filiformis	22	20	22	34	38	34	Junc fil
Betula pubescens	20	16	12	12	8	10	Betu pub
Empetrum sp.	42	36	28	30	24	26	Empe sp.
Carex nigra	74	78	82	44	46	56	Care nig
Potentilla erecta	68	78	72	46	54	60	Pote ere
Cornus suecica	40	50	52	44	44	62	Corn sue
Rubus chamaemorus	10	16	14	4	18	16	Rubu cha
Trientalis europaea	16	66	82	10	36	52	Trie eur
Deschampsia flexuosa	74	90	86	92	94	100	Desc fle
Agrostis capillaris	6	4	10	4	20	4	Agro cap
Gymnocarpium dryopteris	6	12	12	-	-	4	Gymn dry
Lycopodium clavatum	2	4	4	-	-	-	Lyco cla
Luzula pilosa	-	-	2	6	4	4	Luzu pil
Listera cordata	-	-	6	6	6	8	List cor
Salix sp.	2	2	-	-	-	-	Sali sp.
Deschampsia cespitosa	-	2	-	-	10	-	Desc ces
Eriophorum angustifolium	-	4	28	-	-	4	Erio ang
Carex cannescens	-	-	6	-	-	6	Care can
Carex magellanica	-	6	4	-	-	-	Care mag
Viola palustris	-	2	2	-	-	-	Viol pal
Carex panicea	-	4	-	-	-	-	Care pan
Athyrium filix-femina	-	2	-	-	-	-	Athy fil
Anthoxanthum odoratum	-	-	6	-	-	-	Anth odo
Sorbus aucuparia	-	-	2	-	-	-	Sorb auc
Eriophorum vaginatum	-	-	4	-	-	-	Erio vag
Polygonum viviparum	-	-	-	-	2	-	Poly viv
No. of species	17	23	25	16	18	19	

Additional species in the experimental area, but outside plots: *Molinia caerulea*, *Blechnum spicant*, *Juniperus communis*, *Thelypteris limbosperma*, *Dryopteris expansa*, *Calamagrostis purpurea*, *Luzula multiflora*

DCA ordination with frequency in 24 quadrats, each with four plots over three years, indicated a gradient of shade along the first axis (eigenvalue 0.21), with species such as *Vaccinium uliginosum*, *Empetrum* sp. and *Luzula pilosa* at the shaded end, and *Juncus filiformis*, *Rubus chamaemorus* and *Listera cordata* at the lighter end of the gradient (Fig. 3). The second axis (eigenvalue 0.17) may be interpreted as a moisture or level gradient, with *Carex echinata* and *Eriophorum angustifolium* at the moist or lower level end, and *Rubus chamaemorus* and *Cornus suecica* at higher levels or at the drier end of the gradient. DCA ordination of quadrats showed a larger variation in the data set along the first axis rather than along the second axis (Fig. 4). Experimental plot quadrats changed more than the controls from 1989 to 1991. The lengths of the gradients were 1.8 and 2.0 respectively.

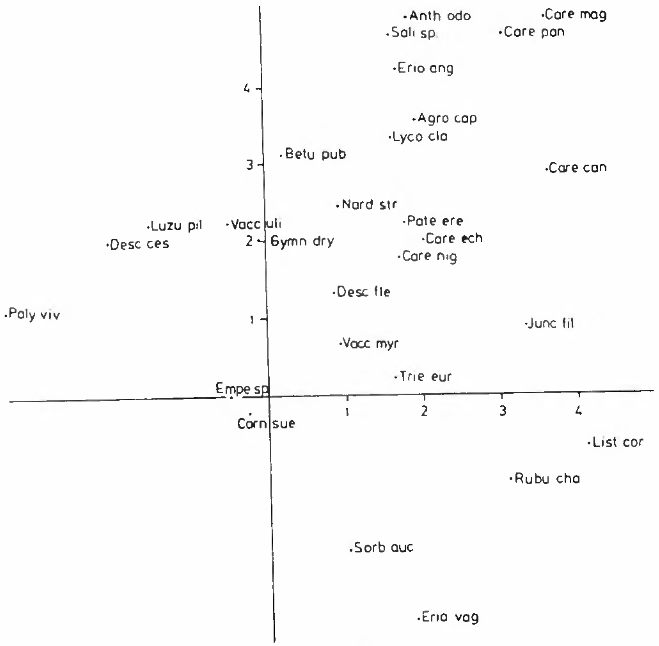

Fig. 3. DCA ordination with frequency of species in 24 quadrats in three years. Species abbreviations, se Table 1

CCA ordination with frequency of all species in 24 quadrats in three years, and the variables time and clear-cut not clear-cut, indicated that clear-cut/not clear-cut was correlated with the first axis (eigenvalue 0.065, $p = 0.01$). The time variable was weakly correlated both to axis 1 and to axis 2.

Regression analysis of number of species (S) in each plot against time, showed a significant increase in mean number of species both in the experimental and in the control plots, but the increase was larger in the experimental plots ($r = 0.37$ and 0.33, $p < 0.001$). There was no significant increase in number of woody species, but a significant increase in grasses, sedges and herbs ($r = 0.43$ and 0.3, $p < 0.001$).

DISCUSSION

The plant community represented in the plots belongs to *Vaccinio-Piceion* Br.-Bl. et al. 1939, association *Chamaemoro-Piceetum* K.-Lund 1962, with the characteristic species

Rubus chamaemorus, *Listera cordata*, *Trientalis europaea* and *Cornus suecica*, in addition to the species of *Spagnum* and *Polytrichum* (see also Nordhagen 1928; Kielland-Lund 1962, 1981; Kummen 1977; Fredriksen 1978; Rodvelt 1983). It is probably a subalpine birch forest type of this association, a grazing dependent *Caricion*-stage (Nordhagen 1928; Kielland-Lund 1981, p. 154) with species like *Carex nigra*, *Carex echinata* and *Juncus filiformis*.

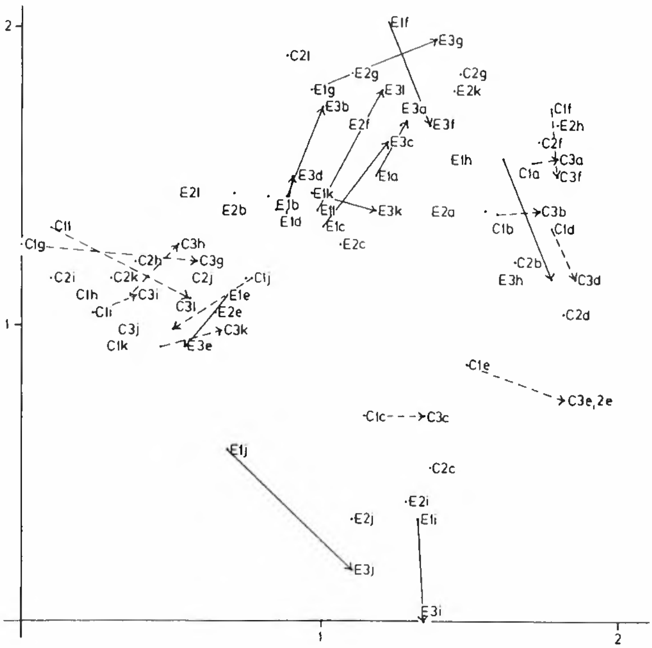

Fig. 4. DCA ordination of 24 quadrats in three years. E: experimental quadrats, C: controls, 1-3: 1989, 1990, 1991, a-1: quadrat symbols. Arrows indicate direction of changes 1989-91

Frudalen is considered a high quality summer pasture with a larger mean autumn weight of lambs than that of the rest of the Sogndal area (Hustveit 1987, p. 11). Sheep are selective grazers of grasses and herbs, but species of *Carex*, *Juncus* and leaves of trees and scrubs are also consumed, e.g. *Salix* spp. (Vigerust 1936; Selsjord 1966). In Norwegian subalpine forests, sheep graze grasses and herbs for four-fifths of the grazing time (Bjor & Graffer 1963). *Deschampsia cespitosa*, *Deschampsia flexuosa*, *Agrostis capillaris*, *Anthoxanthum odoratum* and *Carex* spp. are highly valued grazing plants in subalpine areas (Vigerust 1949; Selsjord 1960, 1966). *Deschampsia flexuosa* is selected more often in open pasture than in birch forest, probably because the palatability alters with sugar content (Selsjord 1968). Clearing of the tree layer may therefore increase grazing intensity. An increase in ferns is not desirable in the pasture and these should be controlled by more intensive grazing.

Selsjord (1965) found that birch forests with scattered birch trees and a field layer dominated by grasses, sedges and herbs are of higher grazing value compared with birch forests dominated by *Vaccinium myrtillus*. In Frudalen, the area dominated by *Vaccinium myrtillus* is steadily increasing.

The increase in *Deschampsia flexuosa* and *Trientalis europaea* in the experimental plots as opposed to the controls and the decrease in *Empetrum* in the experimental plots, is probably a result of less shaded conditions there than in the controls. The increase in e.g., *Cornus suecica* in the controls may be connected with the ongoing succession, especially in the uncleared sites. The increase in light-demanding grasses, sedges and herbs also in the control plots may be attrobutable to the close proximity of the buffer zones between sites which were too narrow. After clear-cutting of the experimental sites, additional light may have reached the control sites.

A gradient of light and moisture is interpreted along axis 1 of the DCA ordination. At the left end of the axis in Figs. 3 and 4 *Vaccinium uliginosum* and *V. myrtillus*, mixed with *Empetrum* sp., create a dense canopy, under which herbs, grasses and species of *Carex* are suppressed. On the right-hand side of the diagrams the species and plots of the areas which have a *Vaccinium* layer of low height can be seen. This constitutes an early stage of succession within the pasture, which is caused by the reduction in grazing intensity; while the high *Vaccinium* type shows a later stage of this process. The mosaic structure of the field layer is quite evident, with areas of low *Vaccinium* being frequently found close to trackways and open pasture. A moisture gradient is indicated along the second axis. This may indicate some overlapping, as open areas with a low *Vaccinium* carpet tend to be wetter and are at lower levels than those areas with a high *Vaccinium* layer. Birch colonizes more easily at high levels and the shade it affords may accelerate the local overgrowing of the vegetation. The gradients of overgrowth and level/moistness seemed to be the most important ones presented in the data.

CCA ordination confirmed this conclusion, as the environmental factors of time and clear-cutting, according to the eigenvalues, accounted for only a small part of the variation in the species composition. The ordination is still informative. Most of the species that changed marginally in frequency during the experiment, such as *Carex echinata* and *Nardus stricta*, are close to the centre of the diagram, whilst species that increased most in the control sites are connected to the centroid of no clear-cutting (Fig. 5). New species and species that increased most in the experimental sites are close to the 1991 centroid and are connected to the centroid of clear-cutting.

The variation according to moisture and shade is apparent in the CCA ordination of samples (Fig. 6), and as in the DCA ordination, the 1989 control quadrats showed larger variations than the experimental quadrats. The changes in species frequency and composition were greater in the experimental quadrats than in the controls. Four out of 12 control quadrats changed as much as most experimental quadrats, mainly because *Trientalis europaea* appeared in these quadrats. Three out of 12 experimental quadrats changed less than the others as no new species were recorded, or the frequencies of species which were newly recorded were low.

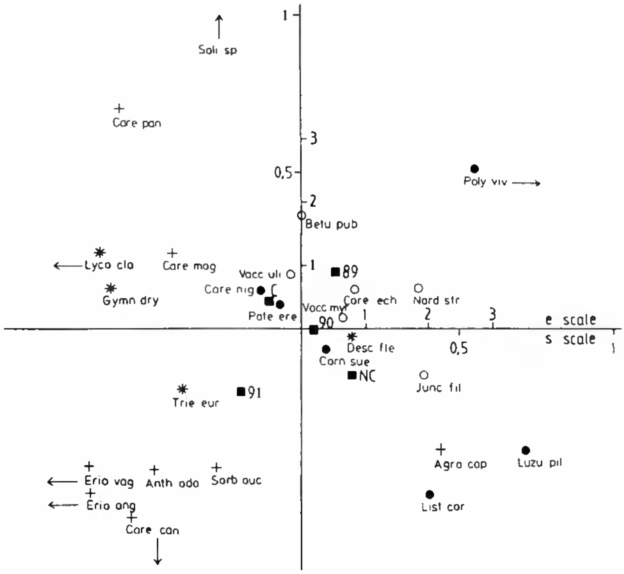

Fig. 5. CCA ordination with frequency of species in 24 quadrats 1989-91, and the environmental variables time and management. Stable species (solid circle), new species (+), species that increased most in experiment quadrats (*) and in control quadrats (circles). Solid quadrats are centroids of cleared (C) and un-cleared (CN). For species abbreviations, see Table 1

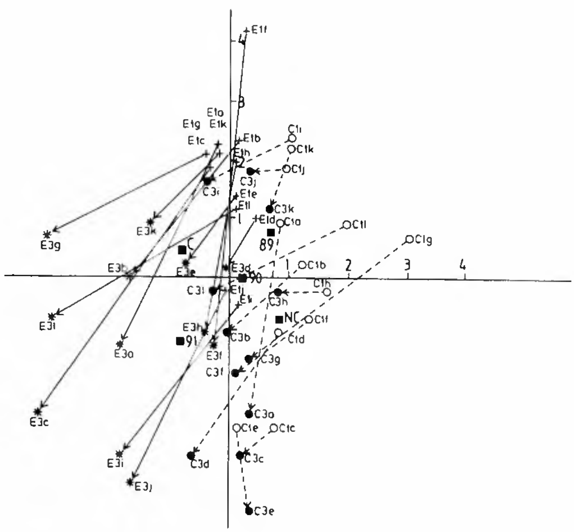

Fig. 6. CCA ordination with frequency of species in 24 quadrats 1989-91, and environmental variables time and management. In the figure, the 1990 quadrats are excluded. Experimental quadrats in 1989 (+) and in 1991 (*) and control quadrats in 1989 (circles) and in 1991 (solid circles). E: experimental quadrats, C: controls, 1-3: 1989, 1991, a-l: quadrat symbols. Arrows indicate direction of changes 1989-91

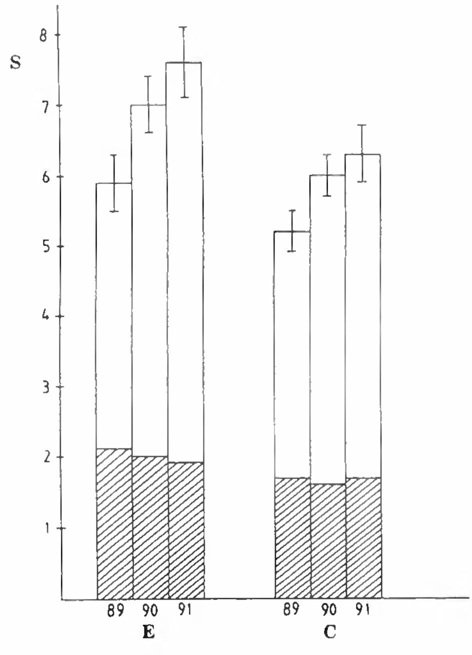

Fig. 7. Mean number of species (S) with standard deviation, mean number of woody species (hatches) and grasses, sedges and herbs (white) in experimental (E) and control (C) plots in 1989, 1990 and 1991

Both in the experimental plots and in the controls the regression analysis also showed an increase in species number with the time factor, as the clear-cutting of the experimental sites presumably resulted in better light conditions in the bordering control sites. The greater increase in grasses, sedges and herbs in the experimental plots, as opposed to those in the controls (Fig. 7), showed clearly the effect of clear-cutting on the number of species in the plots. In the experimental plots the mean number of grasses, sedges and herbs increased by 47.4% from 1989 to 1991. Earlier investigations revealed some effects of clearing of birch on the botanical composition of the field layer, and the increase in local grazing intensity (Graffer 1960).

CONCLUSION

The results of this study indicate that clear-cutting of birch forest will increase the proportion of grasses, sedges and herbs in a subalpine type of pasture. The aim of pasture management in the area is to maintain a birch forest with scattered birch trees together with a dense field layer dominated by grasses, sedges and herbs. Clear-cutting of the birch forest is not sufficient alone to restore overgrown neglected pasture areas. Increasing the grazing intensity by increasing the number of sheep and introducing cattle is necessary to achieve this aim. Goats would assist the birch control because of their browsing ability with woody species. A grazing regime would have to be determined. If clear-cutting were combined with light or medium fertilizing each year, the frequency of the species *Vaccinium*, *Calluna* and *Empetrum* would be reduced (Vigerust 1949; Graffer 1972). Clear-cutting once, followed by grazing management should be encouraged for the near future. Further experiments are necessary to reveal the effects of clear-cutting of *B. pubescens* over a longer time span and to investigate the effects of increased grazing intensities.

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Grass yield response to potassium fertilization on mineral soils in the inland of southern Norway

TOR LUNNAN
The Norwegian State Agricultural Research Stations, Løken Research Station, Heggenes, Norway

Lunnan, T. 1993. Grass yield response to potassium fertilization on mineral soils in the inland of southern Norway. Norwegian Journal of Agricultural Sciences 7: 345-357. ISSN 0801-5341.

Potassium (K) is an essential macro-nutrient in grass production. The response to K fertilization was determined on 56 mineral soils and in totally 189 experimental years. The material was grouped by the age of the meadows and by the soil content of exchangeable (K-AL) and non-exchangeable ($K-HNO_3$) potassium. Relative dry matter yields were subjected to linear regressions and to a Mitscherlich model. In the first production year, the response to K application was low. In older meadows the response was higher, but levelled out at rates of 100-150 kg ha^{-1} K. Both K-AL and $K-HNO_3$ should be taken into account when planning K fertilization for grass production in the area of Norway concerned.

Key words: Fertilizer application, grassland, potassium, soil fertility, yields.

Tor Lunnan, Løken Research Station, N-2940 Heggenes, Norway.

High-yielding forage crops remove considerable amounts of potassium (K) from the field. This need for K must be covered by release from the soil and application of animal manure or mineral fertilizer. Grasses have a high ability to utilize K reserves in the soil because of an efficient root system and a long period for nutrient uptake (Mengel & Kirkby 1987). In soils with high contents of exchangeable K, for instance after application of large amounts of animal manure, grasses can take up more K than needed for growth. Such a luxuriant consumption gives a high content of K in the forage. Animal mineral disorders such as grass tetany in cattle may be a result of excess fertilizer K application, causing Mg deficiency (Kemp & t'Hart 1957, Ødelien 1960).

The mountain and valley district in the interior of southern Norway has a continental climate, the mountains giving shelter from the oceanic climate along the western coast. The yearly precipitation in the region is normally 500-700 mm, but declines to below 300 mm in the driest parts of the Gudbrandsdalen valley. The precipitation is highest in July-September, whereas in May-June drought is common. Low precipitation gives a low potential for nutrient leaching. During the winter, the soil is usually frozen and covered with snow. The critical periods for leaching are rainy autumns and snow-melting periods in spring.

The land lies above the marine border of the last glacial period. Therefore the soils frequently have low clay contents. Many cultivated soils are derived from moraine and are influenced by the local bed rock. Some soils are derived from depositions in glacial lakes or rivers. The K content of the soil is highly dependent on the parent material. Parts of the area, especially in the northern Gudbrandsdalen valley, have high contents of acid-soluble or non-exchangeable K in the soil as a result of a high content of micas. Values of 200-300 mg K/100 g dry soil by an extract of 1M HNO_3 are not unusual here. However, most soils of this inland area have low non-exchangeable K contents. Values from 15 to 100 mg K/100 g soil (K-HNO_3) are common. Exchangeable contents of K (K-AL) are more dependent on the cultivation practices than on the soil (Semb & Øien 1961).

Many animal farms in these areas grow only forage crops. Meadows usually have a duration of three to six years. The use of animal manure influences the need for mineral fertilizer application. It is common practice to plow high amounts of manure under for use in annual forage crops or before the establishment of meadows, which results in a considerable residual effect of nutrients in the subsequent years. The need for K application on meadows therefore increases the first years after seeding (Hernes 1969, 1978; Bærug 1977a; Lunnan & Haugen 1993a).

Recently, however, there has been a shift toward using more manure on grassland on many farms. A more even distribution over time makes better use of the nutrients in the manure, especially of potassium and phosphorus. More of the nutrients are taken up directly by the plants than where large amounts of manure are plowed under, and less nutrients become unavailable by fixation in the soil or by leaching.

The use of K fertilizer has a great impact on the costs of grass production. In computer-based fertilizer programs like GJPLAN (SFFL 1990), the need for K is calculated on the basis of crop removal. Corrections are made for K in manure and the contents of K-AL and K-HNO_3 in the soil.

In earlier experiments low rates of nitrogen (N) were applied, and hence the need for K was lower than with higher N rates. This article summarizes experiments with K fertilization of mineral soils, in which higher N rates were used, performed by Løken Research Station.

MATERIALS AND METHODS

The investigation comprises 56 grassland field experiments in the mountain and valley region in southern Norway, from Oppdal in the north to Setesdalen in the south (Fig. 1). The distribution of the experiments was: 1 in Oppdal, 9 in Nord-Østerdalen, 9 in Trysil-Engerdal, 12 in Gudbrandsdalen, 15 in the Valdres-Land region, 2 in Hallingdalen, 1 in Numedalen, 4 in Telemark and 3 in Setesdalen.

The material includes five different series of experiments where rates from 0 up to 200 kg ha^{-1} K were applied (Table 1).

In all series factorial designs were used. In series 3/71, split application of K was compared with spring application only. Here 0 kg or 50 kg ha^{-1} K was applied after the first cut in addition to four K rates in spring, and there were three replicates. A 3x3x4-design without replicates was used in the series 510, with three N rates, three P rates and four K rates. In PK-Løken, two K rates was applied to four grasses; *Bromus inermis* Leyss., *Dactylis glomerata* L., *Phleum pratense* L. and *Festuca pratensis* Huds.. The series 506 had a 3x3x3-design without replicates (Lunnan & Haugen 1993a). Here three K rates and three N rates were applied to *B. inermis*, *D. glomerata* and *P. pratense*. In the series 508, three K rates and three N rates were applied, with two replicates.

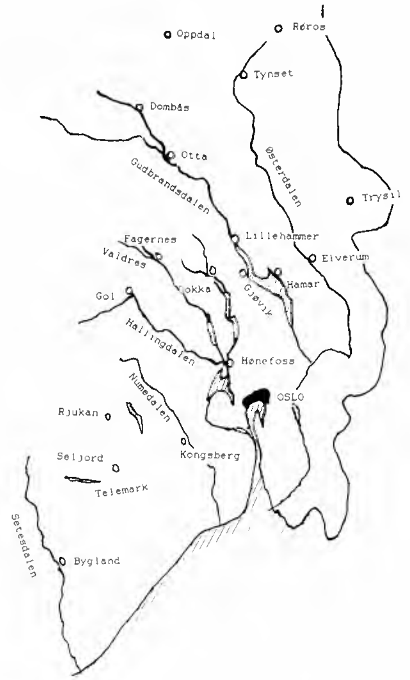

Fig. 1. Map over southeastern Norway

Table 1. Number of trials and potassium application rates (kg ha^{-1} K) used in five series of experiments

Series	No. of trials	Potassium rates				
3/71	21	0	50	100	150	200
510	14	50	100	150	200	
PK - Løken	2	0	100			
506	15	0	80	160		
508	4	50	100	150		

The field experiments were carried out in the period 1971-87, the trials lasting from one to seven years. Usually two cuts were taken in each year. Nitrogen rates differed between series, with average values from 150 to 180 kg ha^{-1} N per season. All fields were placed on mineral soils, 52 fields on sandy soil and 4 fields on silty soils. The content of organic matter varied from 3 to 10%, and the clay content was low. 40 of the fields were placed on moraine soils, the rest derived from depositions of glacial lakes or rivers.

Soil analyses og K were made when the experiments were established (Table 2). In soil samples from the 0-20 cm topsoil layer, exchangeable K (K-AL) was determined following the method by Egnér et al. (1960), and acid-soluble K (K-HNO_3) was determined following Reitemeier (1951). The variation in K values between sites was high. The distribution was skewed, with a few very high values. Only seven of the trials had acid-soluble K values above 100 mg/100 g soil. The values of K-AL and K-HNO_3 were positively correlated ($r=0.41$, $p= 0.002$).

Table 2. Mean values and variation of exchangeable K (K-AL) and of acid-soluble K (K-HNO_3) measured as mg per 100 g of dry soil in 56 experimental trials

	K-AL	K-HNO_3
Mean value	12.2	58
Standard deviation	8.4	54
Minimum	3.6	14
Maximum	48.0	300

Because of the heterogeneous application rates in the experiments (Table 1), relative dry matter (DM) yield was used in the calculations. Relative yield refers to absolute yield divided by maximum yield at high rates of K application. To reduce the variation in the individual experiments, and because of the low K response in young meadows, maximum yield was set to the average of rates $\geq$ 50 kg ha^{-1} K in the first production year, of rates $\geq$ 100 kg in the second year, and of rates $\geq$ 150 kg in the third or further years. Relative yield from individual observations thus can exceed 1.0.

The material was grouped by the age of the meadows in order to sort out residual effects. There were 50 experimental sites in the first production year, 47 sites in the second year and 43 sites with a total of 92 harvest years in older meadows.

For each age group, linear regressions of relative yield on K application rate were calculated for three classes of K-AL and K-HNO_3 in the soil.

Further, a Mitscherlich model was applied (Mitscherlich 1954), to investigate whether such a curvilinear approach could give a closer relationship between yield and K application. The function took the form

$$Y = A*(1-e^{-cx}), \qquad (1)$$

where Y represents the yield by the application of growth factor x, A is the maximum yield when x is in surplus, and c is a proportionality constant. For relative yield (RY), we get the form:

$$RY = Y/A = 1 - e^{-cx}, \qquad (2)$$

where x represents the total available K for the plants, calculated as:

$$x = K + a{*}K\text{-}AL + b{*}K\text{-}HNO_3 + d, \qquad (3)$$

where K represents the potassium application rate (kg ha^{-1}). The rest of Eq. 3 represents the release of K from the soil. Eq. 3 inserted in Eq. 2 finally gives

$$RY = 1 - e^{-c(K + a{*}K\text{-}AL + b{*}K\text{-}HNO3 + d)} \qquad (4)$$

The constant c, and the coefficients a, b and d, were adjusted to the material by using the NLIN procedure in SAS with Newton-Gauss non-linear regression (SAS Institute Inc. 1987). The same approach was used by Lunnan & Haugen (1993b) to calculate yield response to phosphorus fertilization on meadows.

RESULTS

The average yield level in these experiments was around 8 t ha^{-1} DM (Table 3). Even with no K application the yield was above 6 t DM in older meadows.

The yield response to K fertilization was weak in the first production year (Tables 3 and 4). On average, a relative yield of 0.99 was obtained without K application. Yield response was better correlated with K-AL than with K-HNO_3. In soils with a low content of K-AL, there was a significant positive response to K application. On the other hand, in soils with a high content of K-AL the response was significantly negative.

Table 3. Grass DM yield (t ha^{-1}) in the different series of experiments grouped by meadow age and K rates

			K application rate								
Series	Age	n	0	50	80	100	150	160	200	SE	p-value
3/71	1	19	8.62	8.88		8.89	8.96		8.91	0.09	0.05
3/71	2	18	7.93	8.61		8.76	8.82		8.88	0.17	0.002
3/71	>2	34	6.41	7.39		7.86	7.96		7.99	0.10	<0.001
510	1	12		7.93		8.00	8.06		7.94	0.10	>0.5
510	2	12		7.55		7.69	7.88		7.81	0.08	0.02
510	>2	29		7.88		8.06	8.26		8.32	0.05	<0.001
PK-L	1	2	11.47			11.41				0.01	0.18
PK-L	2	2	9.82			10.23				0.20	0.39
PK-L	>2	5	8.95			10.09				0.14	0.006
506	1	14	7.59		7.59			7.57		0.06	>0.5
506	2	12	7.73		8.16			8.29		0.08	<0.001
506	>2	22	6.95		7.87			8.24		0.09	<0.001
508	1	3		8.20		8.17	8.29			0.06	0.36
508	2	3		6.88		7.00	7.26			0.06	0.03
508	3	2		6.55		6.52	6.78			0.10	>0.5

In the second year, the response to K fertilization was higher. Both K-AL and K-HNO_3 were well correlated with yield response. The coefficient of determination, R^2, decreased with increasing content of K in the soil.

The yield response to applied K was very high in older meadows but decreased when the content of K in the soil increased. Both K-AL and K-HNO_3 gave good correlations with relative yield.

Table 4. Regression of relative yield on K application rate (kg ha^{-1} K) in 1st, 2nd and ≥3rd years and for different classes of K-AL and K-HNO_3 in the soil

	Number of observations	Regression equation	R^2 value	p value
1st year				
Average	50	0.9905 + 0.000068 K	0.015	0.09
K-AL ≤ 7	18	0.9565 + 0.000343 K	0.296	0.002
7 < K-AL < 15	18	1.0002 − 0.000011 K	0.001	>0.5
K-AL ≥ 15	14	1.0203 − 0.000176 K	0.089	0.025
K-HNO_3 ≤ 30	18	0.9489 + 0.000114 K	0.030	0.15
30 < K-HNO_3 < 60	19	0.9826 + 0.000137 K	0.063	0.04
K-HNO_3 ≥ 60	13	1.0080 − 0.000073 K	0.032	0.19
2nd year				
Average	47	0.9335 + 0.000462 K	0.196	<0.001
K-AL ≤ 7	17	0.8794 + 0.000814 K	0.366	0.001
7 < K-AL < 15	18	0.9392 + 0.000434 K	0.254	0.008
K-AL ≥ 15	12	0.9954 + 0.000059 K	0.008	>0.5
K-HNO_3 ≤ 30	14	0.8666 + 0.000951 K	0.412	0.001
30 < K-HNO_3 < 60	20	0.9324 + 0.000464 K	0.325	0.001
K-HNO_3 ≥ 60	13	1.0014 + 0.000008 K	0.000	>0.5
≥3rd year				
Average	92	0.8630 + 0.000867 K	0.372	<0.001
K-AL ≤ 7	31	0.8199 + 0.001145 K	0.540	<0.001
7 < K-AL < 15	34	0.8595 + 0.000884 K	0.379	<0.001
K-AL ≥ 15	27	0.9203 + 0.000508 K	0.195	0.004
K-HNO_3 ≤ 30	21	0.7953 + 0.001350 K	0.471	<0.001
30 < K-HNO_3 < 60	42	0.8645 + 0.000864 K	0.437	<0.001
K-HNO_3 ≥ 60	29	0.9149 + 0.000510 K	0.260	<0.001

The relationship between yield and K application was, however, more curvilinear than linear (Table 3). The yield increase was very high for low application rates, and the response for rates above 100 kg ha^{-1} K was usually low. The curvilinear relationship was well described by the Mitscherlich model (Table 5). The R^2-values showed a good fit to the model with the exception of the first-year meadows. All parameters were significantly different from zero at 5% level, with the exception of the d-value in the second year.

Table 5. Regression parameters in the Mitscherlich model RY = 1 - e^{-cx}, where RY is relative yield and x is total amount of available potassium for the grass. x = K + a*K-AL + b*K-HNO_3 + d, where K is potassum application, and the rest release of K from the soil

Meadow age	Number of observations	c	a	b	d	R^2
1	50	0.0363	9.07	-	33.2	0.133
2	47	0.0261	5.32	0.895	7.07	0.534
>2	92	0.0225	2.05	0.418	31.4	0.628
With c=0.0225:						
1	50	0.0225	14.4	-	58.2	0.128
2	47	0.0225	6.08	1.02	10.3	0.531

In the first year, K-HNO_3 as measured by the b-value, gave no significant improvement in the model and was therefore deleted. It was found that the values of c, a and b decreased with increasing age of the meadows. This indicates that the contribution of K from the soil was lowered.

Mitscherlich looked upon the c-value as a constant, and in this case it seems logical that the c-value is not influenced by the age of the meadows. If we keep the c-value constant at 0.0225, which was found in older meadows where the function gave the best fit to the data, the coefficients a, b and d are increased. A c-value of 0.0225 lies within the 95% confidence interval in the first and second years. Without soil and plant K analyses, it is difficult to predict which of the two models is the better one.

Response curves are shown in Fig. 2 with different values of K content in the soil. Here, a constant c-value of 0.0225 is used.

The Mitscherlich model used gave a good relationship between K and relative yield. There was no obvious pattern of the residuals, although the deviations were greatest at low relative yields.

The functions also give some information on the release of K from the soil. We see that the coefficients of the soil parameters decrease as the meadows get older. The contribution of K from the soil thus decreases, and the need for fertilizer increases. If, for example, the soil K values at the establishment of the grass are K-AL = 10 and K-HNO_3 = 40, the release of K from the soil is calculated to 124 kg ha^{-1} in the first year, 96 kg in the second year and to 69 kg for older meadows with different c-values. If we keep the c-value constant at 0.0225, the release is calculated to 202, 112 and 69 kg ha^{-1} K, for the first year, the second year and for older meadows, respectively. It can be seen that the choice of c-value has a large influence on the estimates of the contribution of K from the soil.

Split application of K gave yields similar to those with one dressing in spring (Table 6). K given in spring supplied the grass sufficiently for the rest of the season. There was no interaction between splitting and K rates.

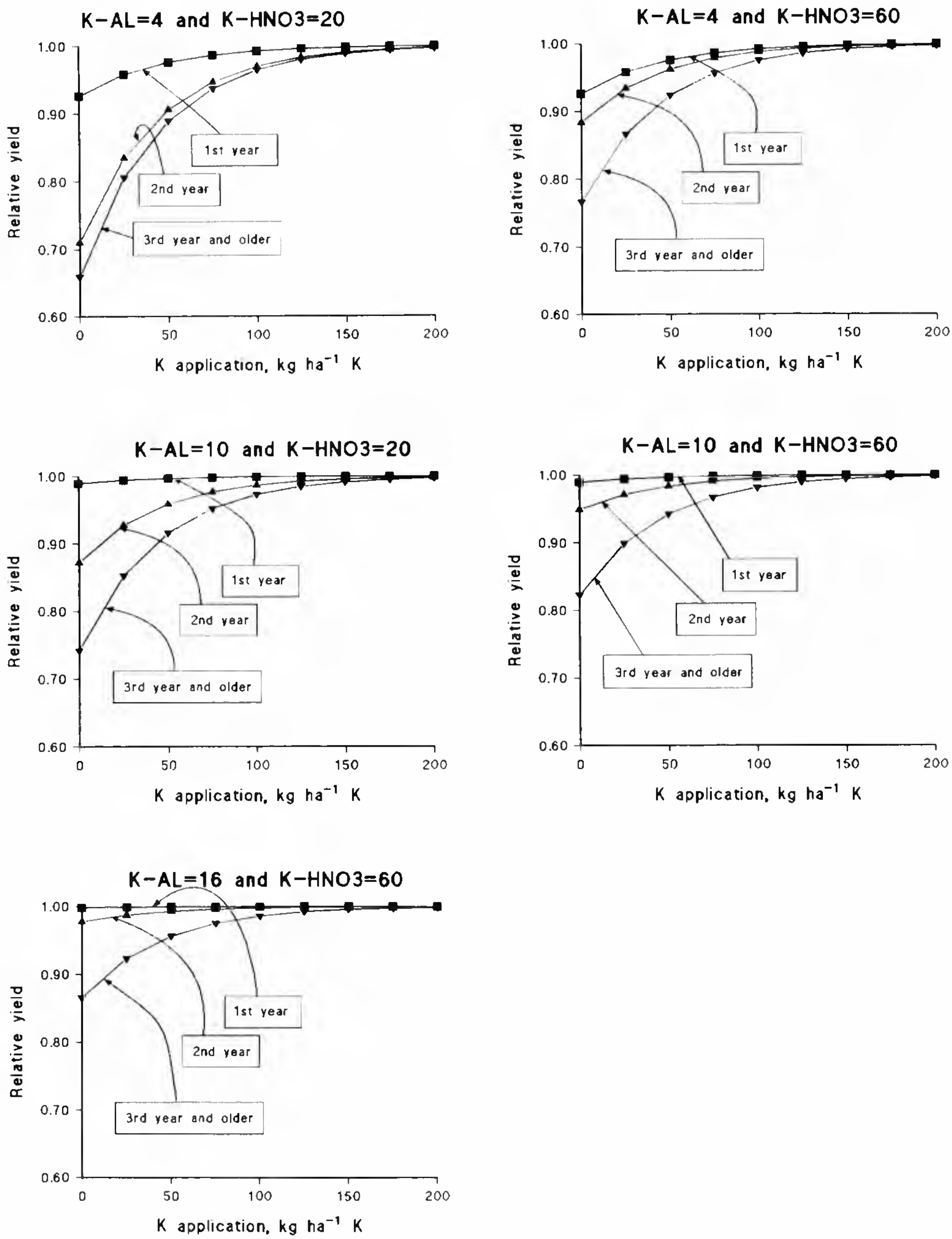

Fig. 2. Mitscherlich curves over relative yield and K fertilization for some combinations of K-AL and K-HNO_3 soil values in the seeding year

Table 6. Effect of split application of K on DM yield (t ha^{-1}). Split dressings of 0+50, 50+50 and 100+50 kg ha^{-1} K in spring and after first cut are compared with 50, 100 and 150 kg ha^{-1} K given in spring

	Production year 1	2	3	4	5	Mean value
Number of experiments	15	13	14	9	4	
K only in spring	8.96	8.70	7.51	8.08	7.98	8.25
Split application	+0.12	-0.11	-0.01	-0.04	-0.10	-0.03

DISCUSSION

A considerable proportion of the K in the grass originated from soil release. This is reflected in the high yield without K application, especially in young meadows (Table 3). However, even in old meadows considerable amounts were taken from the soil, according to the Mitscherlich model. Hernes (1969, 1978) found higher yield responses for K application on organic soils than on mineral soils. Organic soils have very small K reserves, and should therefore be well fertilized with K.

There was less need for application of K fertilizer in younger than in older meadows (Table 3), which was also found in other experiments from southeastern Norway (Hernes 1969, 1978; Bærug 1977a). This reflects a residual effect of previous manure applications, which lasts for at least two years. A more even distribution of manure over time by applying small amounts on meadows, improves the utilization of the potassium as well as of other nutrients in the manure. Along with applications of manure, supplements of cheaper N fertilizer or NK-fertilizer instead of NPK-fertilizer can also be used, thus making manure application on meadows more economical.

Grassland also improves the soil structure and increases the formation of aggregates. This gives a reduction in surface area of soil particles, and some K can be fixed and become unavailable for the plants (Mengel & Kirkby 1987). Grasses, however, have a considerable ability to take up K from the soil, and the amount of exchangeable K in the soil will be depleted by time. Practice has shown that the crop succeeding meadows is prone to K deficiency.

The effect of K fertilizer was poor in the first year meadows (Table 3). On soils with a large content of exchangeable K (K-AL > 15), there was even a statistically significant DM yield decrease after K application (Table 4). This might be attributable to high K concentrations in the soil which cause a reduction in the uptake of Mg.

The Mitscherlich model gave high correlations between relative yield and K supply for older meadows (Table 5). In Norway, with the current price of K fertilizer, the marginal DM yield should at least be 3 kg for one kg of K. Economic optimum rates, based on 3 kg DM, were calculated by derivation of the Mitscherlich function (Table 7). Soils with a very high content of K-HNO_3 had less need for K application. There were only seven experiments on soils with K-HNO_3-values above 100, so these results should be handled with care. Also in western Norway, however, it has been found that there is only a small need for K application on grassland with similar soils rich in micas (Håland et al.

1983).

Table 7. Economic optimum K fertilizer rates (kg ha^{-1}) according to the Mitscherlich model for meadows older than two years. The calculations are made for two yield levels and with combinations of different soil values of K-HNO_3 and K-AL in the seeding year

Yield level, t ha^{-1} DM	K-HNO_3/K-AL 20/4	20/10	60/4	60/10	60/16	100/4	100/10	100/16
5.0	113	101	97	84	72	80	68	55
10.0	144	132	127	115	103	111	98	86

Optimum rates of K fertilizer in this investigation are considerably less than the rates recommended in the computer program GJPLAN for fertilizer application (SFFL 1990), especially at the higher yield level. Also Dæhlin (1993) found small crop yield response at high K application to high-yielding cocksfoot (*Dactylis glomerata* L.). The exploitation of released K from the soil seems to be underestimated by the computer program. In addition, the program underestimates the residual effect of K from previous years on soils in southeastern Norway, with small nutrient losses through leaching.

A grass DM yield of 5.0 t ha^{-1} removes 100 kg K if the concentration of K is 2.0% of DM. However, the additional fertilizer rate in Table 7 is calculated to only 30 kg at the higher yield rate. A thorough examination of the individual experiments indicates that the relative yield response to K fertilizer was similar in experiments with high and low grass yields, when compared at the same level of K in the soil. This indicates that the growth factors which contribute to a high yield also give a higher release of K from the soil. Factors such as favourable water and temperature regimes, good environment for root growth, and good supply of other nutrients stimulate the uptake of K.

Hernes (1978) found a positive interaction between N and K application on grass yield. High N rates stimulate growth and the larger yield removes more K from the field. Therefore, higher yield responses of N were obtained with large K applications. The N x K interaction was less pronounced and not statistically significant in other Norwegian experiments (Foss & Furunes 1991; Lunnan & Haugen 1993a). Bærug (1977b) found a larger K removal when the N rate was increased. On an average of four K dressings, an application of 240 kg ha^{-1} N removed 43 kg more K from the field per year than an application of 120 kg N. The effect was most pronounced in the first production year. In the third year the effect was small at low K rates. The same stimulating effect on K release from the soil by N application was also found in experiments in Finland (Joy et al. 1973). This effect might be due to a larger root system, to replacement of K^+ by NH_4^+ on soil particles, and/or to increased cation uptake by application of NO_3^-.

Small K application rates led to a depletion of the soil reserves. Experiments have demonstrated that fertilizer rates have to be very high on meadows to maintain the soil content of exchangeable K (Hernes 1969, 1978; Bærug 1977a). The grass has a large potential for K uptake and high levels of exchangeable K lead to luxuriant consumption. Application rates in order to maintain high soil K levels lead to large K concentrations in the grass and reduce the uptake of other nutrients, such as Mg and Ca, and are therefore not economical.

On soils with small K reserves, application rates should not be too small. K deficiency results in high yield reductions. However, the grass yield response decreased sharply when the application rates reached 100-150 kg ha^{-1} K (Table 3). An even distribution of the fertilizer is important. Patches without fertilizer give low yield.

The relative yield was better correlated with exchangeable K (K-AL) than with acid-soluble K (K-HNO_3) in the first year (Table 4). In older meadows, the correlation between yield and the two soil K components was similar. On soils poor in clay in southeastern Norway, Uhlen & Semb (1962) also found similar correlation between yield increase by K application and the values of K-AL and K-HNO_3. Other experiments in southeastern Norway indicate a higher correlation between yield and K-HNO_3 than between yield and K-AL (Hernes 1978; Lunnan & Haugen 1993a). In western Norway, Håland et al. (1983) found the best correlation between grass yield and K reserves, i.e. the difference between K-HNO_3 and K-AL. Both K-AL and K-HNO_3 should be taken into account when calculating the need for K fertilizer.

Split application of K had no effect on yield (Table 6). This was also true on clay-rich soil in southeastern Norway (Bærug 1977a) and in experiments with cocksfoot (Dæhlin 1993). Small positive yield effects by split application have been found in western Norway and in Trøndelag (Lyngstad & Einevoll 1967; Foss & Furunes 1991). Positive yield effects by split application can only be expected on soils with very small reserves, such as on organic soils, or in districts with high precipitation. The results from mineral soils in southeastern Norway indicate no advantage from split application.

The K fertilizer regime may affect the mineral composition of the forage. When all the K is applied in spring, forage from the first cut contains more K and less Mg and Ca than with split application, and the relationship between these minerals is inverse in the second cut (Bærug 1977b; Foss & Furunes 1991). This effect is usually not important, but when the level of K in the forage is high, it could lead to animal disorders.

K application can also influence the botanical composition of the sward. Without K there is a decrease in cultivated grasses and an increase in weeds, according to Norwegian experiments (Lyngstad & Einevoll 1967; Foss & Furunes 1991; Lunnan & Haugen 1993a). In grass/clover mixtures, grasses are more competitive in K uptake than clover, which can suffer from deficiency and might disappear from the sward (Mengel & Kirkby 1987). The clover content, however, has been relatively little influenced by K application in Norwegian experiments (Sorteberg 1956; Foss 1971). It has been found that without K application there is a decline in clover content, but high K rates do not result in a higher clover content than medium K rates. This issue is now being investigated in an experiment performed by Løken Research Station.

In conclusion, these experiments demonstrate that grass yield losses caused by K deficiency can be large. However, the yield response to K application decreases rapidly with increasing K rates. On mineral soils in southeastern Norway, the application of K fertilizer to grassland should seldom exceed 150 kg ha^{-1} K even on soils with low reserves of K. The content of both K-AL and K-HNO_3 in the soil should be taken into account when the need for K fertilizer is calculated. Split application of K give no yield advantage on mineral soils, but might give a better mineral composition of the forage.

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Protein levels and antibiotics in feed for growing turkeys

OLAV HERSTAD
Agricultural University of Norway, Department of Animal Science, Ås, Norway

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An experiment on different protein allowances and feeds supplemented with the antibiotic avoparcin was carried out on a fastgrowing turkey strain. The three protein regimes included combinations of using Start feed (28% protein), Grower 1 (25% protein) and Grower 2 (21% protein). The amino acid profile (lysine and TSAA) in the feeds was adjusted to the recommendation given by the NRC (1984). Compared with the standard protein regime, Start feed (28%) from 0 to 4 weeks of age, Grower 1 (25%) from 4 to 8 weeks and Grower 2 (21%) from 8 to 11/13 weeks, it was found that male turkeys gained significantly more weight when fed the Grower 1 (25%) diet from 4 weeks to slaughtering. The feed conversion ratio measured for both sexes was also significantly improved for this particular protein regime. On a regime including Start feed (28%) from 0 to 6 weeks and Grower 2 (21%) from 6 weeks to slaughtering, the final body weight was reduced. It is concluded that for to day's fastgrowing turkeys the requirements for protein/amino acids can be higher than the recommendations given by the NRC (1984). Supplementing the feeds with the antibiotic avoparcin had no effect on growth rate, feed conversion or slaughter quality.

Key words: Amino acids, antibiotic, avoparcin, protein, turkey.

Olav Herstad, Agricultural University of Norway, Department of Animal Science, P.O. Box 5025, N-1432 Ås, Norway.

Compared with other meatproducing animals, growing turkeys have a high requirement for dietary protein. The NRC (1984) recommendations for total protein in feed for turkeys are: 28% from 0 to 4 weeks of age, 26% from 4 to 8 weeks, 22% from 8 to 11 weeks (8 to 12 weeks for males) and 19% from 11 to 14 weeks (12 to 16 weeks for males). These recommendations are given for diets increasing in metabolizable energy (ME) content from 11.7 MJ/kg in the starter feed to 12.1, 12.6 and 13.0 MJ/kg in the succeeding grower feeds. Different feeding intervals at each protein level for the two sexes reveal a higher protein requirement for males than for females after 11 weeks of age. Apart from the difference in growth rate and protein requirement between males and females, some strains have been developed with considerable differences in growth rate. The protein requirement is likely to be higher for fastgrowing strains than for slowergrowing strains.

In Norway, there has been a demand for ovenready dressed turkeys, weighing about 4.5 kg. The turkeys used have been of a relatively slowgrowing strain, reaching slaughter weight at 13-14 weeks of age. These turkeys were usually fed a Starter diet with about 26% protein from 0 to 8 weeks followed by one single grower feed diet containing about 21% total protein from 8 weeks to slaughtering. In 1990 a heavier turkey strain (Betina) was imported from France, which required a more updated feeding regime. As a result an experiment on protein levels in feeds for fastgrowing turkeys was carried out at the Department of Animal Science in February-April 1991. As a debate about the necessity of using antibioticsupplemented feed in poultry meat production is still going on, the feed was given with and without antibiotics.

MATERIAL AND METHODS

The experimental feeds

Three feeds with different protein levels were produced; Start feed with 28% protein, and two Grower feeds with 25% and 21% protein respectively. The protein regime used is illustrated i Figure 1.

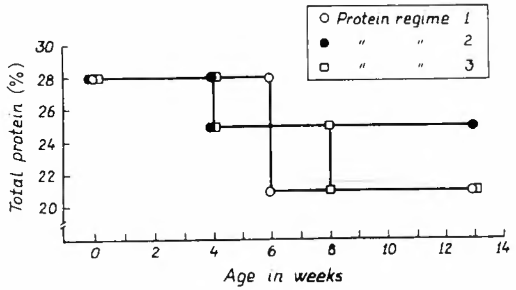

Fig. 1. The protein regimes used in the experiment

The experimental feeds, given as crumbles were divided into two and one part was supplemented with 15 mg avoparcin (antibiotic)/kg.

The feeds with different protein levels were adjusted to the amino acid profile, mainly according to the NRC (1984) recommendations for large turkeys. The diets were made up following a leastcost procedure and produced at a commercial feed mill (FK-Larvik). The composition of the diets and calculated content are presented in Table 1. The content of amino acids in the diets was analysed at "Uppsala universitets biomedicinska centrum, Institiutionen for naturvetenskaplig biokemi", Sweden. The calculated and analysed amino acid profile can be seen in Table 2.

As indicated in the table, there was general agreement between the calculated and analysed values of protein and amino acids. The lysine content in Grower diets 1 and 2 is slightly below the NRC (1984) recommendations for turkeys of 4-8 weeks (1.5%) and 8-12 weeks of age (1.3%).

An analysis of avoparcin was carried out at the Cyanamid Nordiska A/B, Copenhagen, and recoveries of 14.4, 21.2 and 15.7 mg/kg for the Start feed and Grower diets 1 and 2, respectively, were found. According to the analysis, avoparcin in Grower diet 1 was some higher than anticipated.

Table 1. Composition (in %) and content of experimental diets

	Starter	Grower 1	Grower 2
Herring meal	8.50	4.00	2.60
Meat and bone meal	6.00	6.00	6.00
Soybean meal	25.90	21.30	15.00
Rapeseed meal (Canola)	-	3.50	-
Maize gluten meal (65%)	3.80	4.50	3.00
Barley	5.00	10.00	10.00
Oats	25.00	24.70	27.00
Wheat	5.00	-	-
Maize/Maize grits	11.40	19.88	22.40
Wheat brand	3.60	-	8.10
Animal fat	4.00	4.00	4.00
Limestone meal	0.82	0.47	0.58
Monocalcium phosphate	0.05	0.68	0.31
Microminerals/salt	0.16	0.11	0.11
Vitamins	0.50	0.50	0.50
Methionine/lysine/treonine	0.27	0.30	0.29
Calculated content			
ME per kg, MJ	12.0	12.0	12.0
Total protein (%)	28.4	24.9	20.6
Digestible protein (%)	24.4	21.7	17.2
Protein per MJ (g)	23.7	20.8	17.2
Calcium (%)	1.2	1.1	1.0
Phosphorus (%)	0.85	0.85	0.75

Table 2. Calculated (c) and analysed (a) content of protein and amino acids in experimental feeds

	Starter		Grower 1		Grower 2	
	(c)	(a)	(c)	(a)	(c)	(a)
Total protein (%)	28.4	28.1	24.9	24.2	20.6	20.4
Lysine (%)	1.70	1.71	1.45	1.41	1.17	1.15
Methionine (%)	0.64	0.61	0.50	0.49	0.40	0.38
Cystine (%)	0.46	0.48	0.45	0.46	0.36	0.39
Threonine (%)	1.03	1.10	0.91	0.97	0.72	0.84
Tryptophane (%)	0.42	-	0.35	-	0.29	-

Birds and housing

The experiment was carried out in the experimental chicken house at the Department of Animal Science. Eight rooms, each with six litter pens varying in size from 3.05 m^2 to 3.91 m^2 with pens as replicates. At the start, 12 unsexed turkeys were allocated to each pen making a total of 576 turkeys (12x6x8). The turkeys were wingbanded for individual weight measurement at one day old.

The following temperature scheme was used: 1st week, 34°C; 2nd week, 31°C; 3rd week; 28°C, 4th week; 25°C, 5th week; 22°C and from the 6th week 20°C. Two lighting schemes were compared: longday lighting (18 h light and 6 h darkness) and intermittent lighting (2 h light and 2 h darkness). However, the effect of the lighting regime will not be discussed in this paper.

Registration of experimental data

Individual *live weight* was registered for all birds at the start of the experiment and at 2, 4, 6, 8, 11 and 13 weeks of age. One half of the birds were slaughtered at 11 weeks and the other half at 13 weeks. At the last weight control, the birds had been fasted for 10 h before they were weighed and put into boxes for transportation to slaughtering at a commercial poultry slaughterhouse. The sex of the birds was determined at the last weight control. The *feed intake* was measured for each pen on the same days that live weight was measured. *Feather quality* on the breast was judged subjectively at 6 weeks and before slaughtering, using a score from 1 to 5, with 1 indicating naked breast and 5 indicating full feather coverage of the breast.

Litter Quality in the pens was also judged subjectively at 6 weeks and before slaughtering with litter scores ranging from 1 (wet and cakey litter) to 5 (dry and porous litter). After slaughtering the carcasses were classified according to firstclass quality and down graded carcasses. The causes of downgrading, breast blisters, skinhaemorrhages and other injuries, were noted.

Statistics

The experimental data were analysed by the GLM procedure of the Statistical Analysing System (SAS 1990). For body weight, individual records were used as replicates and the analysis were accomplished separately for each sex. For feed conversion records, group (pens) were the replicates. The stastistical model was a factorial arrangement with 3 protein regimes * 2 antibiotic treatments (lighting shemes not included). For the slaughter quality data, a chi-square test was used.

RESULTS

Effect of protein/amino acid levels

The effects of the different protein regimes on growth, feed intake and feed conversion ratio (FCR) can be seen in Table 3. As shown in the table, the protein allowance had a significant influence on the growth rate and FCR. Up until 4 weeks of age, when all the birds were offered the high protein Start feed, there was no difference in feed intake and growth rate. Changing to Grower 1 (25% protein) at 4 weeks (regimes 2 and 3) reduced live weight and worsened FCR at 6 and 8 weeks. After 8 weeks, in males there was a significant response in growth rate to Grower 1 (25% protein) compared with Grower 2 (21% protein), but no significant difference between diets was found for the females. The feed intake was reflecting the growth rate. In the period 4-6 week, the feed intake was higher, although not signifikantly, and lower in period 6-8 week on Protein regime 1, providing the Start feed (28% protein) in the 4-6 week period and the Grower 2 (21% protein) in the 6-8 week period.

Table 3. Effect of feeding different protein regimes on performance of growing turkeys

			Protein regimes	
		1. 28-21%	2. 28-25%	3. 28-25-21%
No. of birds at start		192	192	192
Male/Female at slaughter		83/99	82/93	89/96
Live weight, 4 w.,	males (g)	1006	1036	1013ns
" " "	females (g)	861	887	881ns
" " 6 w.,	males (g)	2414a	2292b	2263b
" " "	females (g)	1968	1900	1897ns
" " 8 w.,	males (g)	3989b	4247a	4212a
" " "	females (g)	3185b	3430a	3482a
" " 11 w.,	males (g)	7173b	7725a	7277b
" " "	females (g)	5688b	6035a	5963a
" " 13 w.,	males (g)	9182b	9598a	9195b
" " "	females (g)	7062b	7415a	7502a
Feed intake/day,	0-4 w. (g)	41.7	42.4	41.5ns
	4-6 w. (g)	129.7	125.3	124.3ns
	6-8 w. (g)	197.2a	207.2ab	210.8b
	8-11 w. (g)	294.7	302.8	301.1ns
	8-13 w. (g)	315.1	337.1	326.7ns
Feed/gain ratio,	0-4 w.	1.35b	1.35b	1.31a
	4-6 w.	1.50a	1.58b	1.56b
	6-8 w.	2.00b	1.72a	1.75a
	8-11 w.	2.30ab	2.24a	2.38b
	8-13 w.	2.44a	2.57b	2.52ab
	0-11 w.	1.94b	1.87a	1.97b
	0-13 w.	2.10	2.11	2.08ns
Slaughter percentage				
11 weeks, males/females		73.7/73.6	74.4/74.2	73.6/74.8na
13 weeks, " "		72.8/74.8	74.2/74.5	74.7/74.3na
Feed/slaughter weight ratio				
Slaughter age 11 weeks,		2.63	2.52	2.60na
" " 13 weeks,		2.85	2.84	2.79na

Differences: Values with dissimilar letters are significantly different ($P < 0.05$), ns = nonsignificant differences, na = not analysed

From scores for feather- and litter condition taken during the growing period, no relation to the protein regimes could be observed (mean feather scores were 3.35, 3.33 and 3.40 for the three feeding regimes), but the females scored higher in feather condition (3.53) than the males (3.18). The litter condition was good for all protein regimes.

The values recorded for slaughter quality are presented in Table 5, where it can be seen that there was a very high percentage of downgraded carcasses (36%). The main causes of downgrading were breast blisters and skin haemorrhages on the wing region. The highest percentage of haemorrhages was registered in protein regime 2, on the Grower diet 1 with 25% protein to slaughtering. Also, the percentage of downgrading caused by breast blisters was high, but not significantly different between protein regimes. The frequency of breast blisters increased dramatically from slaughtering at 11 weeks to slaughtering at 13 weeks. Also, the breast blisters were much more prevalent in males than in females.

Effect of antibiotic supplement

As no significant interaction between protein levels and antibiotics was registered ($p > 0.05$), the performances of turkeys fed diets with and without antibiotics (avoparcin) are presented in Table 4.

There was no significant effect of antibiotic supplementation on the performance of the turkeys but there was a tendency to increased growth rate for the males, whereas the opposite tendency was observed for the females. Nor was there any effect of the antibiotic supplemented feed on feather scores, litter scores or slaughter quality.

Table 4. Effect of antibiotics on performance of turkeys

	With avoparcin	Without avoparcin
No. of birds at start	288	288
No. of deaths and exposed	18	17ns
Live weight at		
6 weeks, males (g)	2349	2295ns
females (g)	1906	1939ns
11 weeks, males (g)	7483	7307ns
females (g)	5849	5944ns
Feed/gain ratio, 0-11 weeks	1.92	1.91ns
Slaughter percentage	73.9	73.8na

Table 5 Registered slaughter quality

	No. slau-ghtered	No. disc-arded	Down-graded %	Causes of downgrading (%) Breast blisters	Haemorrh. in wing	Other injures
Protein regime:						
1 (28-21%)	179	5	31.0	16.6	11.5	3.5
2 (28-25%)	172	3	40.8	21.9	33.1	4.2
3 (28-25-21%)	181	7	36.2	23.6	9.8	2.9
Differences		ns	ns	ns	**	ns
With antibiotics	267	6	36.8	21.8	12.3	2.7
Without "	265	9	35.1	19.1	11.7	4.3
Differences		ns	ns	ns	ns	ns
Slaughter ages						
11 weeks	271	4	26.7	16.1	10.1	1.5
13 weeks	261	11	44.8	25.2	14.0	5.6
Differences		*	**	**	ns	**
Males	245	9	56.4	34.8	17.4	4.2
Females	287	6	18.9	8.5	7.5	2.8
Differences		ns	***	***	***	ns

Differences: ns = not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.005$

DISCUSSION

The response to protein allowances in mono gastric animals is dependent upon the amino acid profile in the protein. In many experiments on protein allowances for turkeys, the NRC (1984) recommendations are used as a standard for the amino acid profile (Leeson & Caston 1991; Sell et al. 1989 and Waibel 1991). However, the growth potential of turkeys has increased significantly over the recent years and large differences in growth rate as a result of protein and amino acid allowances have been reported. Below, some recommendations for lysine and TSAA from different authors are given as amino acids (g) per MJ of ME. The experimental diets used in this study, Start feed from 0 to 4 weeks, Grower 1 from 4 to 8 weeks and Grower 2 from 8 to 12 weeks, are also shown for comparison.

	0-4 weeks		4-8 weeks		8-12 weeks	
	Lysine	TSAA	Lysine	TSAA	Lysine	TSAA
Nixey (1989), males	1.57	1.02	1.34	0.94	1.10	0.82
Leeson & Summers (1991)	1.40*	0.91*	1.02	0.70	0.83	0.62
NRC (1984)	1.36	0.90	1.23	0.75	1.04	0.60
Present study	1.42	0.92	1.21	0.79	0.98	0.63

*Recommendations for 0-2 weeks

As indicated above, Nixey (1989) suggests a higher allowance of lysine and TSAA for large male turkeys than the general recommendation given by the NRC. For the experimental diets, a small deficit of lysine occurs in the Grower 2 diet (8-12 weeks) compared with the NRC standard. However, the specifications given by Leeson & Summers (1991) for lysine in the periods 4-8 and 8-12 weeks are lower than the NRC values.

The performance data obtained in the present experiment indicate that Grower diet 1 (25% protein) was limited in protein for males when introduced at 4 weeks of age. Furthermore, Grower 2 diet (21% protein) introduced at 8 weeks seemed to be deficient in protein for the males but not for the females. Using the NRC recommendation as a standard, lysine may be the limiting amino acid. Lesson & Caston (1991) compared a feeding regime with a reduced lysine content from 1.85% in the start diet of 12.3 MJ ME (1.50 g/MJ) to 1.12% in a diet of 13.3 MJ (0.84 g/MJ) used at 12 weeks with a higher protein allowance. There was no response in one of the experiments, but a response on increased protein allowance late in the experimental period was observed in another. Of two strains used, the BUT turkeys seemed to respond more favourably to high protein diets than Nicholas turkeys. However, on examing the amino acids/energy ratio, the lysine content in the control diets used at around 10 weeks of age was found to be lower than the NRC recommendation. Blair et al. (1989) found that the protein requirement of both male and female turkeys of different strains was higher (24% protein) in the 8-12 week period than the NRC standard of 21% protein. Summers et al. (1985) obtained the same performance at 12 weeks with heavy turkeys on diets with 12.2 MJ ME, decreasing in protein content from 28% protein to 25% and 22% with age, as on a higher protein regime.

Sell et al. (1989) found no effect on growth rate in Nicolas turkeys on diets varying in protein content from 83% to 118% of the NRC recommendations. However, breast weight and weight of breast meat were reduced significantly by feeding 82% of the NRC protein recommendation compared with 90% and more. That the protein allowance can have an influence on the proportion of organs and tissues is also demonstrated by Oju et al. (1988), who found that with underfeeding of protein up to 6 weeks of age, breast and thigh proportions were reduced.

It is generally accepted that protein and amino acid content in feed should be expressed in relation to energy content rather than as a percentage, as the birds on ad lib feeding largely regulate their feed intake to meet their energy requirements. However, Blair & Potter (1988) provided evidence to refute the concept that protein and lysine requirements increase proportionately in response to added ME from fat in turkey diets. Nor did Sell et al. (1989) find any interaction between protein level and ME level on performance in growing turkeys. Thus, to express protein or amino acid requirements in relation to energy content may also be questioned. Furthermore, the inconsistent response to increasing protein and amino acid allowance in reported experiments makes a more definite recommendation difficult. However, for turkeys with growth potential as used in the present experiment, the recommendations given by NRC the (1984) can be inadequate, particularly for the 8-12 week period.

In the present study a great many of the carcasses were downgraded because of breast blisters and haemorrhages in the wing region. The haemorrhages were probably caused by the individual handling of the birds before slaughtering and should not reflect a similar problem in commercial production. However, significantly more haemorrhages appeared with feeding regime 2, with the highest protein allowance. The breast blisters seemed to be related more to body weight at slaughtering than to the feeding regimes.

In the present experiment the protein feeds were given in a factorial design with and without supplementation of avoparcin. No response to the antibiotic supplementation was observed either on performance data or on slaughter quality. Salmon & Stevens (1990b) report a positive effect of virginiamycin supplementation to turkeys, while more inconsistent results have been found with flavomycin (Firman & Kirn 1989; Salmon & Stevens 1990a, Proudfoot et al. 1990). However, the effect of antibiotics on turkeys, as for broilers, is dependent upon many factors and is believed to be reduced under optimum feeding conditions and health managements. Buresh et al. (1986) report that the level of growth response for different antibiotics was greater in diets deficient in protein, choline and sulphur amino acids. Virginiamycin was more effective than the other three antibiotics. In the present study, the growth rate for the turkeys was very good, supporting the impression that the growth potential of the birds was achieved without the growth promoter.

CONCLUSION

The experimental results revealed that a protein regime including Start feed (28% protein) from 0 to 4 weeks of age, Grower 1 (25%) from 4 to 8 weeks and Grower 2 (21%) from 8 to 11/13 weeks and with an amino acid profile according to the NRC (1984) standard can, certainly for the 8 to 11/13 week period, be deficient in protein and amino acids for to day's fast growing turkeys. The male birds achieved a significantly higher weight at slaughtering when fed on the Grower 1 diet (25%) from 4 to 11/13 weeks than that on the

Grower 1 diet (25%) from 4 to 8 weeks and the Grower 2 diet (21%) from 8 weeks to slaughtering. The feed conversion ratio was significantly improved for both sexes on Grower 1 (25%) from 4 weeks of age to slaughtering. On a protein regime with Start feed (28%) from 0 to 6 weeks and Grower 2 (21%) from 6 weeks to slaughtering, the final body weight was reduced compared with that under the former regimes. Supplementing the feeds with the antibiotic avoparcin had no effect on growth rate, feed conversion or slaughter quality.

At slaughtering, many carcasses were downgraded because of breast blisters and skin haemorrhages. The downgrading was related more to the weight of the birds and the individual handling of the birds before slaughtering than to the protein regimes. Most haemorrhages were found on carcasses from turkeys on the highest protein allowance during the growing period.

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The effect on soil physical properties of undersown cover crops in cereal production in southeastern Norway

TROND BØRRESEN
Agricultural University of Norway, Department of Soil and Water Sciences, Ås, Norway

Børresen, T. 1993. The effect on soil physical properties of undersown cover crops in cereal production in southeastern Norway. Norwegian Journal of Agricultural Sciences 7: 369-379. ISSN 0801- 5341.

Cover crops, nitrogen application rates (0, 60 and 120 kg ha^{-1}) and four tillage systems were investigated in three factorial field experiments on loam and clay soil in southeastern Norway. Italian ryegrass, white clover and a mixture of the two were compared with treatment without cover crops. Autumn ploughing, autumn rotavating, spring rotavating and direct drilling were the tillage treatments. The soil structure was evaluated by volumetric relations, aggregate stability and air permeability in the soil. The cover crops did not affect the volumetric relationships in the soil. However, the aggregate stability was increased by the cover crop treatment as compared to treatments without cover crops. The tillage system had a greater effect on the soil physical properties than the cover crop treatments. Direct drilling increased the aggregate stability, but the bulk density was increased and the air capacity decreased compared with the effect of autumn ploughing. Nitrogen application rate did not affect the soil physical properties.

Key words: Cover crops, nitrogen application, soil physical properties, tillage system.

Trond Børresen, Agricultural University of Norway, Department of Soil and Water Sciences, P.O.Box 5028 N-1432 Ås, Norway

An undersown cover crop will continue to grow after the main crop is harvested. Reduced leaching of nutrients, fixation of nitrogen, higher total plant production, the safeguarding of the soil against erosion and improved soil physical conditions for plant growth are the possible effects of a cover crop. The purpose of this project was to investigate the effect of cover crops as a tool toward achieving a more sustainable plant production.

In Norway, cereals are normally cropped in monoculture systems. The straw residue is very often the only contribution to soil organic matter besides the plant roots. Cropping systems, which increase the soil organic matter, will very often improve the soil physical condition for plant growth (Macrae & Mehuys 1985). The aggregate stability is improved under ley and is reduced under arable crops (Tisdall & Oades 1982). Similar results have been reported for ryegrass by Tisdall & Oades (1979) and Reid & Goss (1981), who explain the improved stability by the increased content of organic matter in the soil.

This paper deals with the effect of cover crops in combination with nitrogen application rate and soil tillage system on soil physical properties in three field experiments.

MATERIALS AND METHODS

Soil and site characteristics

The experiments were located at Øsaker, Tune, (NGO-map no. 1913 IV Vannsjø, UTM-coordinates 32VPL 164774), at Sørås, Ås (NGO-map no. 1914 III Ski, UTM-coordinates 32VNM 006152) and at NLH, Ås (NGO-map no. 1914 III Ski, UTM-coordinates 32VNM 995154). The elevations above sea level are approximately 50 m at Øsaker, 90 m at Sørås and 70 m at NLH. The parent material is post-glacial clay in all trials. The soils were poorly drained in the natural condition and have therefore been tile drained. The soil at Øsaker and Sørås was a silty clay loam overlaying a clay and was classified as a humic haplaquept according to US Dept. Acric. (USDA) Soil Survey Staff (1975) (Table 1). The soil at NLH was a loam (0-60 cm) and was classified as a typic haplaquept (Table 1).

Table 1. Particle size distribution (%) for the soils at Øsaker, Sørås and NLH

Field	Depth	Clay[1]	Silt[1]	Sand[1]	Soil type[2]
Øsaker	0-20 cm	35	55	10	Silty clay loam
	20-40 cm	45	45	10	Silty clay
Sørås	0-25 cm	34	53	13	Silty clay loam
	25-40 cm	47	44	9	Silty clay
NLH	0-30 cm	21	40	39	Loam
	30-60 cm	22	54	25	Silty loam

[1]): Clay; <2 μm, silt; 2-60 μm, sand; 60-2000 μm
[2]): According to Njøs & Sveistrup (1977)

Experimental design and treatments

Øsaker and Sørås

The experiments were of a split-split plot factorial design with tillage treatments on superior main plots, nitrogen application rate treatments on main plots and cover crops treatments on subplots. The base plot was 4 m * 8 m at Øsaker and 4 m * 7.6 m at Sørås. There were three replicates. The experiments commenced in the spring of 1988 at Øsaker and the spring of 1989 at Sørås.

Tillage treatments were;

AP: Ploughing with a mouldboard plough to 22 cm depth in autumn and seedbed preparation by a tine cultivator in spring.

DD: No cultivation in autumn, direct drilling in spring. The cover crops were sprayed with glyphosate late in autumn.

AR: Cultivating with a rotavator to 10 cm depth in autumn and seedbed preparation by a rotavator in spring.

SR: No cultivation in autumn and seedbed preparation by a rotavator in spring.[1]

Nitrogen was added as calcium nitrate at 0 (N0), 60 (N1) and 120 (N2) kg ha^{-1}. Cover crops were sown with a conventional seed drill 1 to 7 days after the sowing date for the cereals. The treatments were: (a) no cover crop, (b) italian ryegrass (*Lolium multiflorum* Lam. var Italicum), (c) white clover (*Trifolium repens* L.), and (d) a mixture of (b) and (c). The cover crops were sown on the same plots every year during the research period. The seeding rates were: Italian ryegrass 25 kg ha^{-1}, white clover 10 kg ha^{-1} and for the mixture 5 kg ha^{-1} white clover and 10 kg ha^{-1} Italian ryegrass. The seed rates were reduced by one-half from 1990.

Basal dressing with fertilizer was 400 kg ha^{-1} PK fertilizer (7% P and 13% K). Crops grown were spring barley (*Hordeum vulgare* L.), spring oats (*Avena sativa* L.) and spring wheat (*Triticum aestivum* L.). The straw was removed from the plots. Annual weeds were controlled using Basagran.

NLH

The experiment was divided in two subfields, each with a split-plot factorial design with cover crop treatments on main plots and nitrogen application rate treatments on subplots. The base plot was 4 m * 6 m. There were four replicates in each subfield and the experiments were established in the spring of 1988. The cover crop treatments and nitrogen application rate treatments were the same as those for the other experiments. At NLH the soil was ploughed in autumn, and the cover crops were sown every other year (the first year on subfield I and the second year on subfield II).

Soil measurements

Soil physical measurements included particle size distribution, aggregate size distribution, aggregate stability, phase relationships, water release characteristics, bulk density and air permeability. The sampling was done two weeks after the date of sowing. Particle size distribution was determined by the pipette method according to Elonen (1971). The relative volume fractions of air, water and solids were determined from 100 cm^3 undisturbed soil samples (von Nitzsch 1936). Water release characteristics was measured using ceramic pressure plates (Richards 1947, 1948). The air porosity at -10 kPa matric potential (pF2) was determined with an air pycnometer (Torstensson & Eriksson 1936), and the total porosity was determined as the sum of air porosity and volumetric water content at -10 kPa matric potential (pF2). Air permeability was measured in laboratory at -10 kPa matric potential as described by Green & Fordham (1975). Aggregate size distribution was determined by dry sieving after the method by Njøs (1967) and aggregate stability was measured with a rain simulator in laboratory as described by Marti (1984).

RESULTS

There were no significant differences between the different cover crops with regard to the bulk density in soil depths of 5-10 cm (Tables 2 and 3). At Øsaker and Sørås the measurements were carried out after one and three years of continuous cover crops. During this period the bulk density had not changed as a result of the cover crops. At NLH the cover crops were sown only every other year and they had no effect on the bulk density.

Table 2. Bulk density (Mg m^{-3}) for 5-10 cm depth on N1 plots after one and three years of cover crops and different tillage systems at Øsaker and Sørås

	Øsaker		Sørås	
	1989	1991	1990	1992
No cover crop	1.39	1.22	1.12	1.31
Italian ryegrass	1.35	1.21	1.14	1.29
White clover	1.37	1.18	1.15	1.30
Mixture	1.39	1.21	1.11	1.34
SIG[1]/LSD-5%[2]	ns[3]	ns	ns	ns
Autumn ploughing	1.32	1.20	1.10	1.29
Direct drilling	1.47	1.26	1.18	1.31
Autumn rotavating	1.35	1.17	1.09	1.32
Spring rotavating	1.35	1.19	1.14	1.33
SIG/LSD-5%	*/0.02	*/0.05	*/0.06	ns

The interaction between cover crops and tillage was significant only at Sørås in 1990 ($p = 0.05$)
(1): SIG: significance level (ns, *, **, ***)
(2): LSD-5%: least significant difference at 5% level
(3): ns: not significant

Table 3. Bulk density (Mg m^{-3}) for 5-10 cm depth during four years of cover crops at three nitrogen application rates (main effects) at NLH

	1989	1990	1991	1992
No cover crop	1.17	1.09	1.08	1.19
Italian ryegrass	1.16	1.09	1.08	1.19
White clover	1.16	1.07	1.06	1.13
Mixture	1.16	1.06	1.08	1.22
SIG[1]/LSD-5%[2]	ns[3]	ns	ns	ns
0 kg N ha^{-1}	1.16	1.07	1.07	1.18
6 kg N ha^{-1}	1.18	1.09	1.09	1.19
12 kg N ha^{-1}	1.16	1.08	1.06	1.18
SIG/LSD-5%	ns	ns	ns	ns

The interaction between cover crops and nitrogen application rate was not significant ($p = 0.05$)
(1): SIG: significance level (ns, *, **, ***)
(2): LSD-5%: least significant difference at 5% level
(3): ns: not significant

The tillage treatments had a significant effect on the soil bulk density at Øsaker and Sørås (Table 2). Direct drilling resulted in significantly higher soil bulk density than the other tillage treatments, with the exception of the measurements taken after three years at Søràs. The nitrogen application treatments at NLH did not result in any significant differences in soil bulk density (Table 3).

The effects of cover crops, tillage system and nitrogen treatments on total porosity, airfilled porosity at -10 kPa matric potential, available water capacity and air permeability are presented in Figs. 1-4. Because of the small effect of the treatments on these properties, Figs. 1 and 3 show the average (aritmetric) for the measurements at Øsaker and Søràs and Figs. 2 and 4 the same for NLH.

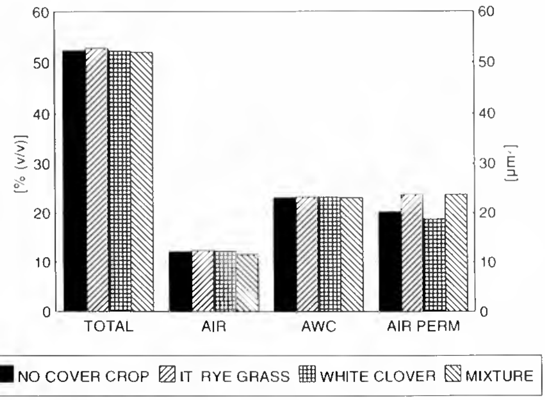

Fig. 1. Total porosity, airfilled porosity at 10 kPa matric suction, available water capacity (AWC, water between 10 and 1500 kPa matric suction) (% v/v), and air permeability (Air perm) (μm^2) for 5-10 cm depth on N1 plots on average of measurements after one and three years of cover crops at Øsaker and Søràs. Error bars indicate least significant difference at 5% level

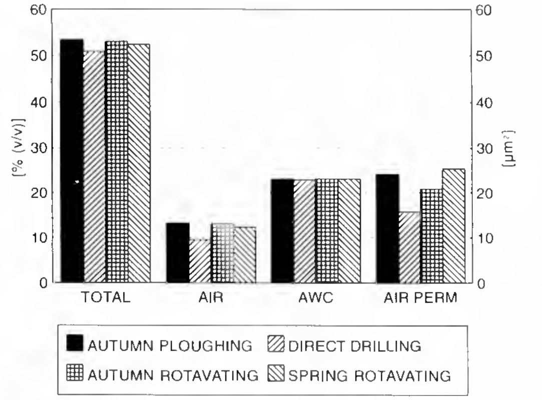

Fig. 2. Total porosity, airfilled porosity at 10 kPa matric suction, available water capacity (AWC, water between 10 and 1500 kPa matric suction) (% v/v), and air permeability (Air perm) (μm^2) for 5-10 cm depth on N1 plots on average of measurements after one and three years of different tillage systems at Øsaker and Søràs. Error bars indicate least significant difference at 5% level

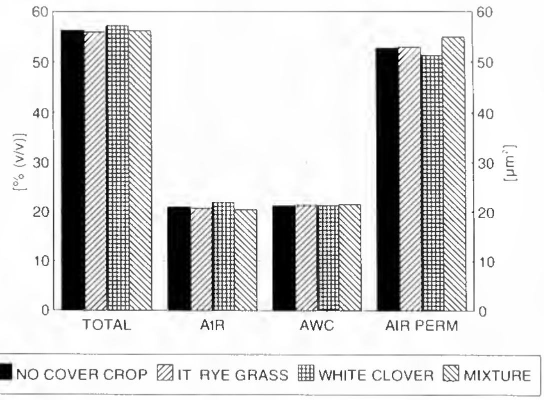

Fig. 3. Total porosity, airfilled porosity at 10 kPa matric suction, available water capacity (AWC, water between 10 and 1500 kPa matric suction) (% v/v), and air permeability (Air perm) (μm^2) for 5-10 cm depth on average of measurements during four years of cover crops at NLH. Error bars indicate least significant difference at 5% level

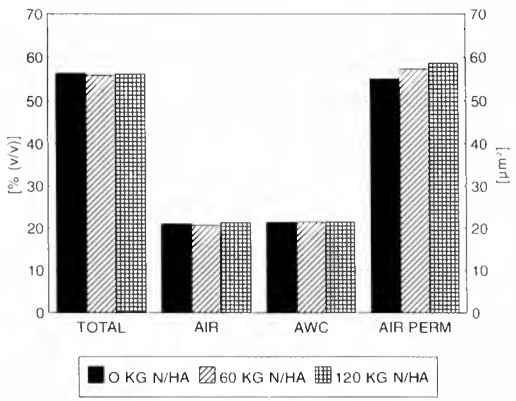

Fig. 4. Total porosity, airfilled porosity at 10 kPa matric suction, available water capacity (AWC, water between 10 and 1500 kPa matric suction) (% v/v), and air permeability (Air perm) (μm^2) for 5-10 cm depth on N1 plots on average of measurements during four years of different nitrogen application rates at NLH. Error bars indicate least significant difference at 5% level

The cover crops and nitrogen application rates did not affect total porosity, airfilled porosity at -10 kPa matric potential and available water capacity in these three experiments (Figs. 1, 3 and 4). The effects of cover crops and nitrogen application on water content at different matric suction were also small and not significant (not shown).

Direct drilling reduced the soil porosity significantly (Fig. 2). This reduction was found in the pores > 30 μm (air porosity at 10 kPa matric suction), but the available water capacity (pores between 0,2 μm and 30 μm) was not affected by tillage treatment.

Air permeability was measured at 10 kPa matric suction. In the 5-10 cm soil layer air permeability was slightly greater after treatment with Italian ryegrass and the mixture of Italian ryegrass and white clover on the clay soil (Fig. 1), but this result was significant only for the averaged results not for the single trials and years. On the loam soil there was no effect of Italian ryegrass on the air permeability compared with the treatment without cover crops (Fig. 3).

Direct drilling reduced the air permeability significantly on an average for the Øsaker and Søràs trials (Fig. 2). Autumn rotavated soil had also a lower air permeability than autumn ploughed soil. Nitrogen application rate did not affect the air permeability of the soil in the experiment at NLH (Fig. 4).

Aggregate stability after simulated rainfall was determined on the fraction 0.6-2 mm (Tables 4 and 5). Cover crops increased the aggregate stability for both years at Øsaker, but not at Søràs and NLH.

At Øsaker, direct drilling and spring rotavating gave higher aggregate stability compared with that under autumn ploughing. After three years (1991) with different tillage treatments autumn rotavating gave significantly higher aggregate stability than autumn ploughing, but not as high as that with direct drilling and spring rotavating. At Søràs direct drilling gave significantly higher aggregate stability compared with that under the other tillage treatments. Nitrogen application rate did not affect the aggregate stability at NLH (Table 5).

Table 4. Aggregate stability (g $100g^{-1}$) for the fraction 0.6-2 mm for 0-5 cm depth on N1 plots after one and three years of cover crops in different tillage systems at Øsaker and Søràs

	Øsaker		Søràs	
	1989	1991	1990	1992
No cover crop	69.7	46.9	76.7	64.6
Italian ryegrass	75.5	58.1	75.1	65.9
White clover	73.8	54.6	72.8	64.4
Mixture	75.0	56.8	74.2	65.8
SIG[1]/LSD-5%[2]	*/3.8	**	ns[3]	ns
Autumn ploughing	69.0	41.1	73.5	59.2
Direct drilling	75.4	63.1	79.2	74.1
Autumn rotavating	71.4	50.2	73.3	62.1
Spring rotavating	78.2	61.9	72.8	65.3
SIG/LSD-5%	ns	*	ns	*

The interaction between cover crops and tillage was significant only at Søràs in 1990 ($p = 0.05$)

(1): SIG: significance level (ns, *, **, ***)

(2): LSD-5%: least significant difference at 5% level

(3): ns: not significant

Table 5. Aggregate stability (g $100g^{-1}$) for the fraction 0.6-2 mm for 0-5 cm depth during four years of cover crops at three nitrogen application rates (main effects) at NLH

	1989	1990	1991	1992
No cover crop	79.3	75.2	65.5	67.0
Italian ryegrass	81.2	77.7	65.7	69.6
White clover	80.6	77.0	67.2	67.7
Mixture	81.4	76.5	68.3	67.0
SIG[1]/LSD-5%[2]	ns[3]	ns	ns	ns
0 kg N ha^{-1}	79.9	77.3	67.4	69.7
6 kg N ha^{-1}	81.4	75.4	65.9	67.6
12 kg N ha^{-1}	80.6	77.0	66.8	66.2
SIG/LSD-5%	ns	ns	ns	ns

The interaction between cover crops and nitrogen application rate was not significant ($p = 0.05$)
(1): SIG: significance level (ns, *, **, ***)
(2): LSD-5%: least significant difference at 5% level
(3): ns: not significant

Aggregate size distribution in the 0-5 cm layer was measured after seedbed preparation and sowing in the spring (not shown). The results revealed only small differences between cover crop treatments and nitrogen treatments in these experiments. The main effect of tillage system was that direct drilling gave the coarsest (big aggregates) and autumn ploughing the finest (small aggregates) seedbed judged from the size of the aggregates. Similar results are reported by Riley (1983). An interesting interaction was that cover crop treatments generally resulted in coarser aggregates and fewer fine aggregates in combination with direct drilling compared with the treatments without cover crop. This effect was not observed in combination with ploughing.

DISCUSSION

Cover crop treatments did not significantly affect the volumetric relationship in the soil in these trials. Rasmussen (1991) reported decreased bulk density in the plough layer as a result of ploughing down Italian ryegrass. Breland (1989) found small effects of ryegrass on the bulk density. The effect of cover crops on the soil volumetric relationship will depend on the type and amount of cover crops and the number of years with cover crop (Allison 1973; Macrae & Mehuys 1985). Benoit et al. (1962) concluded that the soil bulk density was first decreased after three years addition of ryegrass. The soil type is also an important factor for the effect of the cover crops on the soil volumetric relationship.

Aggregate stability of the surface soil seemed to be the soil physical parameter that was most influenced by cover crop treatments. The greater aggregate stability may be a result of a higher content of organic matter. In addition to being a stabilizer, organic matter provides good feeding conditions for the microorganisms and earthworms that have a positive effect on aggregate stability (Harris et al. 1965). Ram & Zwerman (1960) reported that aggregate stability was positively correlated with quality and quantity of the organic matter added to the soil. A gradual development towards more stable aggregates for soil cropped with cover crops is reported by Tisdall & Oades (1979) and Breland (1989).

As expected the tillage system affects the soil physical condition. Somewhat higher bulk density, lower total porosity, lower air porosity at 10 kPa matric suction and higher available water capacity as a result of reduced tillage and direct drilling as compared to ploughing is reported by several authors (Rydberg 1987; Mackie-Dawson & Morrice 1988; Rasmussen 1988). Decreased air permeability after reduced tillage has been reported by Riley (1983), Schønning (1988) and Riley & Ekeberg (1989).

CONCLUSIONS

In these experiments the effects of cover crops on soil physical properties have been small. Aggregate stability seemed to be higher after treatments with cover crops as compared with treatments without cover crops. The volumetric relationships in the soil were not affected after three years with cover crops. The soils at the trial locations have certainly had a good structure also without any cover crops. The effect of cover crops might have been more pronounced on soils with weaker structure.

The soil tillage system had a greater effect on the soil physical condition than had cover crops. Direct drilling increased soil bulk density and decreased total porosity, air porosity at 10 kPa matric suction and air permeability compared with autumn ploughing.

The nitrogen application rate had no influence on the soil physical properties of the soil.

ACKNOWLEDGMENTS

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NOTES

[1]): From 1991 this treatment was changed at Sørås to mouldboard ploughing to 22 cm depth in spring with following seedbed preparation by a tine cultivator.

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A comparison between meadow fescue and timothy silage
I. Feeding experiments with slaughter bulls

ASTRID JOHANSEN & LEIDULF NORDANG
The Norwegian State Agricultural Research Stations, Vågønes Research Station, Bodø, Norway

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The nutritional value and dry matter (DM) yield of meadow fescue (MF) and timothy (T) silage were evaluated in three experiments with 72 yearling bulls. The silages were fed *ad libitum* with two levels of concentrate supplement (1.5 and 3.0 kg). Both silages were well preserved but MF had a somewhat higher concentration of organic acids and a lower true protein:crude protein ratio than T. This was attributed to a higher buffering capacity in fresh meadow fescue grass. *In vivo* digestibility (sheep) of organic matter (DOM) was higher for MF than for T. In one experiment DM intake was significantly higher for T than for MF and at slaughter the carcasses had higher quality grades. Liveweight gain was not significantly different, however. In the other experiments no clear differences between the two groups were found. Despite the variations in fermentation quality it was concluded that MF was of no less value for bulls than T, even although MF was slightly ahead of T in morphological stage at harvest.

Key words: Bulls, carcass, chemical composition, digestibility, *Festuca pratensis*, liveweight gain, *Phleum pratense*, silage, voluntary intake.

Astrid Johansen, Vågønes Research Station, N-8010 Bodø, Norway.

Meadow fescue (*Festuca pratensis* Huds.) is known as a high-yielding grass that is better able to survive intensive management and grazing than timothy (*Phleum pratense* L.) whereas timothy has a better tolerence to low temperatures and ice-cover (Ravantti 1960; Sjøseth 1963; Andersen 1974). Meadow fescue and timothy are included in most of the seed mixtures used in Norway and are also grown as pure crops. In northern Norway, Schjelderup (1980) found a higher *in vitro* digestibility for grass and hay from meadow fescue than from timothy. Similar results have been found in France (Demarquilly & Weiss 1970; Demarquilly & Jarrige 1974). Although widely used only limited data about the ensilability of meadow fescue grass and the feeding value of the silage were found. Moreover, in practical farming it has been stated that meadow fescue has a lower palatability than timothy, but no experimental results have been found to confirm this theory.

Silage made from smooth meadow grass (*Poa pratensis* L.), another widely grown grass species, has been compared with timothy silage by Hole (1985a, b, c, d, e). The nutritive value estimated from *in vivo* digestibility trials with sheep was higher for smooth meadow grass silage than for timothy silage. However, dairy cows and bulls fed timothy silage had a higher feed intake and daily weight gain. These results were mainly explained by a poorer fermentation quality due to a higher buffering capacity of smooth meadow grass than of timothy. On this basis it was of great interest to examine meadow fescue silage, and a project including ensiling and digestibility studies, feeding experiments with sheep, dairy cows and bulls was started. The ensiling studies were published by Nordang (1992) and feeding experiments with sheep by Barvik *et al.* (1991). The present paper details the feeding experiments with bulls. In two subsequent papers digestibility trials and feeding experiments with dairy cows are discussed (Johansen 1993; Johansen & Nordang 1993).

MATERIALS AND METHODS

Feeds

In the years 1987-89 first cuts of the winter hardy meadow fescue cultivar Salten and the timothy cultivar Bodin were taken at Vågønes Research Station, Bodø (67°18'N) (Experiments 1-3). The grass species were harvested one to two weeks after the start of heading of timothy. In Bodø, meadow fescue usually reached the stage of heading about five days ahead of timothy (A. Larsen, personal communication). In Experiment 1 the harvesting of meadow fescue was completed before the harvesting of timothy in order to have both species at approximately the same stage of development. In Experiments 2 and 3 the grass species were harvested at the same time to eliminate the possible effect of the varying weather conditions during harvest on ensilability.

Inorganic fertilizer was applied in the spring (approximately 130 kg N ha^{-1}) and after the first cut. The swards were contaminated to some extent with other grass species, mainly smooth meadow grass, rough meadow grass (*Poa trivialis* L.), couch grass (*Elytrigia repens* L. Nevsky) and marsh foxtail (*Alopecurus geniculatus* L.). The amount of these species never exceeded 30% on a dry matter (DM) basis, but it was generally higher in the meadow fescue swards than in those with timothy. Only minor amounts of dicotyledonous weeds were found. Dates of harvest, DM yield and botanical composition of DM can be found in Table 1.

Table 1. Harvesting dates, dry matter (DM) yields and botanical composition of the swards

	Expt. 1		Expt. 2		Expt. 3	
	Meadow fescue	Timothy	Meadow fescue	Timothy	Meadow fescue	Timothy
Year of harvest	1987		1988		1989	
Date of harvest	8.-11.7	12.-15.7	12.-18.7		1.-8.7	
DM yield, t ha^{-1}	5.6	6.2	5.8	6.4	5.6	6.0
Botanical composition (% of DM):						
Sown grass species	70	95	67	90	87	90
Other grass species	20	2	30	4	13	6
Dicotyledonous weeds	10	3	3	6	0	4

The grass was direct cut using a flail harvester with the addition of 3 l per ton grass of formic acid (85%) in Experiment 1 and 4 l per ton grass of Foraform (64% formic acid plus 6% ammonia) in Experiments 2 and 3. The grass was ensiled in six wooden tower silos (diameter = 3.0 m, height = 6.0 m) and sealed with a thick plastic cover under water pressure (500 Pa). After about five months of storage the silos were opened at start of the feeding experiments.

A commercial concentrate mixture, Kunøtt A (Mix A), with the declared content of 12.5% digestible crude protein (DCP) produced by Felleskjøpet Trondheim was used in all the experiments. The composition of the mixture is detailed in Table 2.

Table 2. Composition of the concentrate mixture

	Expt. 1	Expt. 2	Expt. 3
Ingredient composition (%):			
Ground barley	50.0	31.0	48.0
Ground oats	12.0	16.0	14.0
Ground wheat		14.0	
Wheat bran	9.0	9.0	9.0
Extr. rape meal	8.0	9.0	11.0
Soybean meal	3.5	6.0	2.0
Guar meal	6.0	2.5	5.0
Molasses	6.0	6.0	6.0
Fat, bonemeal, etc.	2.6	3.1	1.8
Minerals and vitamins	2.9	3.4	3.2
Calculated chemical composition and nutritive values[1]:			
Dry matter (%)	88.1	87.5	86.8
In % of dry matter:			
Crude protein	17.8	17.7	17.7
Ether extract	4.8	4.8	4.5
Ash	6.7	6.2	6.3
DCP	14.5	14.3	14.3
AAT	9.5	9.2	9.5
PBV	2.9	3.1	2.6
ME, MJ kg DM^{-1}	11.6	11.3	11.6
FFE kg DM^{-1}	1.07	1.07	1.08
FEm kg DM^{-1}	1.02	1.00	1.02

[1] DCP=digestible crude protein; AAT=amino acids absorbed in the intestine; PBV=protein balance in the rumen; ME=metabolisable energy; FFE=fattening feed units; FEm=milk feed units

Experimental design and management of the animals

Three feeding experiments with yearling bulls of the NRF breed were conducted. The experiments started in late November. Prior to the experiments all animals had been on pasture during the summer. They were kept stalled for approximately two months before start of the experiments. In this period all animals were fed grass silage (mainly from timothy) *ad libitum* and 2.5 kg concentrates. During a preliminary period of two weeks, silage DM intake was recorded. The animals were then randomly allocated to one of four groups on the basis of liveweight, age and DM intake. A 2 x 2 factorial design was used with the following four groups:

1A: Meadow fescue silage (MF) + 1.5 kg concentrate (LC)
1B: Meadow fescue silage (MF) + 3.0 kg concentrate (HC)
2A: Timothy silage (T) + 1.5 kg concentrate (LC)
2B: Timothy silage (T) + 3.0 kg concentrate (HC)

The first two weeks of the experimental period were considered as a transition period and the data from this period were discarded from the computations. The bulls were housed in a tied-stall byre and given silage and concentrates on an individual basis. The feeds were offered at 0800 and 1330 hours in two equal portions, the concentrate given prior to the silage. Feed refusals were collected and weighed every morning before feeding and silage quantities were adjusted to about 110% of the consumption the previous day. Water was freely available. Number of animals, age and liveweight at grouping, DM intake during the preliminary period and the duration of the experiments are presented in Table 3. All the animals were slaughtered on the same day, with the duration of each experiment dependent on the amount of silage available. Liveweight was recorded on two consecutive days at grouping, two weeks after grouping and at the end of the experiment. In addition, the animals were individually weighed every fourth week. At slaughter, weights of carcass, of liver and of kidney fat were recorded and conformation and fat scores were determined.

Table 3. Number of bulls, mean DM intake (DMI) in the preliminary period, liveweight and age at grouping and duration of the experiments

	Expt. 1	Expt. 2	Expt. 3
No. of animals	24	24	24
Silage DMI (kg)	7.6	6.1	5.8
Liveweight (kg)	371	375	375
Age, days	440	420	442
Duration, days	111	97	96

Digestibility studies with sheep fed on silage sampled throughout the experimental period were carried out at the end of each experiment. Each of the two silages were fed separately to three or four adult wethers at maintenance level (approximately 900 g DM). The experimental period lasted 21 days with 11 days of adaptation followed by 10 days for collection of faeces. The animals were kept in digestibility cages and had free access to water.

Sampling procedures and chemical analyses
Grass samples were taken from each trailer load during filling of the silo and thoroughly mixed to give one sample per day per field harvested for chemical analysis. The DM content of the silages was determined weekly during the experiments. Every second week

samples of silage and silage refusals were taken for chemical analysis. Samples of the concentrate mixture were collected weekly, mixed at the end of each experiment and subsampled prior to analysis. Silage samples for the digestibility studies were collected four times. At the end of each experiment the samples were chopped, mixed and kept frozen in daily portions until two days before use. The daily faecal output from the sheep was bulked and frozen until the end of each trial. Ground and minced samples were retained for chemical analyses. Rumen fluid samples were collected from all bulls via the oesophagus on three occasions in each experiment. The samples were taken in the morning, about three hours after feeding the silage. The pH of the rumen fluid was measured immediately after sampling. The samples were preserved in 100% formic acid and the concentration of ammonia-N and volatile fatty acids (VFA) determined at the Department of Animal Science, Agricultural University of Norway.

The chemical analyses of the feeds and faeces were carried out at Holt Research Station, Tromsø. The methods used for analysing DM, ash, Kjeldahl-N, true protein, ammonia, crude fibre (CF) and ether extract are described by AOAC (1980). Water soluble carbohydrates (WSC) were analysed in fresh grass and silage as described by Pedersen & Lysnes (1991). Neutral detergent fibre (NDF), acid detergent fibre (ADF) and lignin (ADL) in silage and faeces were analysed according to Van Soest (1963 a, b) and Van Soest & Wine (1967) with modifications. The buffering capacity of the grass was determined using the Playne & McDonald method (1966) and organic acids and ethanol in the silages determined using gas chromatography (Pedersen & Lysnes 1991).

Calculations and statistical analyses

Silage DM was corrected for losses of volatile components, assuming that 80% of the formic, acetic, butyric, propionic and valeric acids and 100% of the ethanol are lost during oven drying at 103-105 °C. Crude protein (CP) was calculated as Kjeldahl-N · 6.25. Digestible crude protein was estimated from the CP content and the digestion coefficient for CP. In addition, amino acids absorbed in the intestine (AAT) and protein balance in the rumen (PBV) were calculated according to the AAT system (Harstad 1992). Rumen degradability of CP in silage was estimated using the equation formulated by Webster *et al.* (1982):

$$\%\ dg = 100 \cdot (g\ CP\ kg^{-1} - 22.5)/g\ CP\ kg^{-1}$$

Protein degradability of the concentrate mixture was calculated from the table values of the different ingredients (Skovbo Nielsen 1990). Energy values were estimated from the chemical composition of the feeds and the digestion coefficients obtained from *in vivo* experiments (silages) or the table values of Sundstøl *et al.* (1986) (concentrates). Gross energy (GE) and metabolizable energy (ME) were calculated according to Van der Honing & Alderman (1988). Net energy was calculated as feed units for fattening (FFE) and as feed units for milk production (FEm). FFE was calculated as described by Breirem & Homb (1970) using a value number of 80, and FEm was calculated according to Sundstøl & Ekern (1992).

The computation of daily liveweight gain based on the liveweight recorded after the transition period and the final liveweight (daily gain), or from 98% of warm carcass weight, provided a dressing percentage of 50 (corrected daily gain). The content of net energy in silage was computed by subtracting the amount supplied by the concentrate from the total requirement for maintenance and growth (Saue *et al.* 1978). The following equations were used to compute the FFE requirements for maintenance and growth:

Maintenance:	$0.0378 \cdot LW^{0.75}$ FFE	(Breirem 1987)
Growth :	2.5 FFE$\cdot \Delta LW$	(Saue *et al.* 1978)

where LW = weighed mean liveweight (kg) and ΔLW = corrected liveweight gain (kg). Assuming that 1 VEVI (feed units for intensively fed beef cattle) = 1 FEm =1650 kcal, the FEm requirements were calculated from the equations of Van Es (1978):

Maintenance:	$0.0478 \cdot LW^{0.75}$ FEm
Growth :	$(500 + 6 \cdot LW) \cdot \Delta LW / (1 - 0.3 \cdot \Delta LW) / 1650$

Statistical analyses were carried out using the General Linear Models procedure described by SAS (1987). The following model for analysis of covariance was used:

$$Y_{ijk} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + BX_{ijk} + e_{ijk}$$

where

μ = general mean
α_i = effect of i-th silage (i=MF,T)
β_j = effect of j-th concentrate level (j=LC,HC)
$(\alpha\beta)_{ij}$ = effect of silage and concentrate level interaction
B = slope of the covariate X_{ijk}
e_{ijk} = random error

DM intake obtained during the preliminary period was used as the covariate for feed intake. Liveweight at grouping was used as covariate for liveweight after the transition period, final liveweight and for carcass characteristics. Where $p > 0.05$, the covariate was considered as insignificant and discarded from the model. Variance analyses were used for rumen fermentation characteristics, growth rates and feed utilization. A model including only the effect of silage (α_i) was used when analysing the data from digestibility trials. Significant differences ($p < 0.05$) between means or LS means are indicated by different superscripts. When no superscripts are given this indicates that the values were not found to be significantly different.

RESULTS

Chemical composition of the forage

The chemical analysis of the concentrate mixture was analogous to that calculated from the ingredient composition (Table 2). DM content of the grass at cutting was variable (Table 4) and generally low, particularly in Experiment 3. The mean CP content was 13.3% for meadow fescue and 12.0% for timothy, whereas the true protein percentage was higher for timothy than for meadow fescue. In all experiments the buffering capacity of meadow fescue was higher than that of timothy.

Table 4. Chemical composition of meadow fescue and timothy grass at cutting

	Expt. 1		Expt. 2		Expt. 3	
	Meadow fescue	Timothy	Meadow fescue	Timothy	Meadow fescue	Timothy
Dry matter, %	15.9	19.6	22.5	18.4	15.6	15.4
In % of dry matter:						
Crude protein	13.4	14.9	12.6	10.3	13.9	11.7
Ether extract	4.1	4.4	3.0	4.0	3.3	3.1
Crude fibre	32.4	28.7	33.4	34.9	31.2	31.2
WSC[1)]	14.2	18.5	12.1	11.6	13.3	13.4
Buffering capacity[2)]	36.9	30.0	40.1	30.1	35.3	32.0
True protein, % of crude protein	79.0	79.2	65.6	83.8	70.1	79.5

[1)] WSC=water soluble carbohydrates [2)] mEq (100 g DM)$^{-1}$

In Experiment 1 DM content of meadow fescue silage was lower than that of timothy, but in the other two experiments no such difference was observed (Table 5). Silage DM content was lower in Experiment 3 than in the first two experiments. Generally, only minor differences in DM composition were observed between the two silages, but in Experiment 3 the CP content for meadow fescue was higher than that for timothy silage. Differences in NDF and ADF content were also small but ADL was somewhat lower in meadow fescue than in timothy silage.

Table 5. Chemical composition of meadow fescue and timothy silage

	Expt. 1		Expt. 2		Expt. 3	
	Meadow fescue	Timothy	Meadow fescue	Timothy	Meadow fescue	Timothy
No. of samples	7	7	6	6	6	6
Dry matter, %	22.5	24.2	22.7	22.9	21.5	20.8
In % of dry matter:						
Crude protein	12.8	13.1	11.6	11.6	13.4	11.9
Ether extract	4.9	4.9	3.5	3.6	4.0	4.9
Crude fibre	35.9	32.0	37.0	37.0	35.9	36.3
N-free extract	41.5	45.1	41.4	42.0	40.5	41.8
Ash	4.9	4.9	6.5	5.8	6.2	5.1
NDF[1)]	-	-	65.5	64.7	72.3	76.2
ADF	-	-	38.3	38.6	43.5	43.5
ADL	-	-	3.1	4.1	3.5	4.2
WSC[2)]	4.4	5.5	3.1	4.1	2.3	2.0

[1)] NDF=neutral detergent fibre, ADF=acid detergent fibre, ADL=lignin [2)] WSC=water soluble carbohydrates

Fermentation characteristics of the silages (Table 6) show that although the pH was below 4.2 for both silages it was slightly higher also in meadow fescue than in timothy. Acetic acid concentration was higher also in meadow fescue than in timothy silage, but only traces of propionic, butyric and valeric acids were detected. No differences in ammonia-N concentration between the two silages were found. The true protein content was variable, and somewhat lower for meadow fescue than for timothy silage. Generally, for both silages the fermentation quality was somewhat poorer in Experiment 3 than in Experiments 1 and 2.

Table 6. Fermentation characteristics of meadow fescue and timothy silage (Same samples as Table 5)

	Expt.1		Expt.2		Expt.3	
	Meadow fescue	Timothy	Meadow fescue	Timothy	Meadow fescue	Timothy
pH	3.9	3.8	3.9	3.8	4.1	4.0
Ammonia-N, % of total N	4.2	3.5	10.6	10.3	10.1	9.4
True protein, % of CP[1)]	51.0	57.9	54.2	62.2	39.6	41.3
In % of fresh silage:						
Formic acid	0.20	0.18	0.23	0.34	0.15	0.15
Acetic acid	0.43	0.34	0.46	0.45	0.62	0.59
Propionic acid	0.01	0	0.01	0	0.02	0.03
Butyric acid	0	0	0.01	0	0.01	0
Valeric acid	0	0	0	0	0	0
Lactic acid	1.12	1.20	1.72	1.12	1.44	1.88
Ethanol	-	-	0.09	0.17	0.40	0.33

[1)]CP = crude protein

Digestibility and nutritive values

The mean organic matter (OM) digestibility was 73.3% and 70.3% for meadow fescue and timothy silage, respectively (Table 7). In Experiments 1 and 2 significant differences between silages were seen for all measured coefficients, with those for meadow fescue higher than those for timothy. In Experiment 3 OM digestibility tended to be higher for timothy than for meadow fescue. The coefficients for NDF and ADF were significantly higher for meadow fescue than for timothy silage. A similar, but not significant effect was observed for CF. Generally, OM digestibility was lower in Experiment 2 than in the other experiments, but CP digestibility was lowest in Experiment 3. The rumen degradability of CP (dg) was calculated to be 82.1% and 81.5% for meadow fescue and timothy silage, respectively.

The estimated energy and protein values for the silages are presented in Table 8. All methods ranked the silages in the same order. In Experiments 1 and 3 the energy values were relatively high, partcularly in Experiment 1 and compared with those in Experiment 2. In two of the experiments meadow fescue silage had a higher energy content than timothy silage. Using either DCP or AAT, meadow fescue silage had higher values than timothy. The PBV value for meadow fescue silage was found to be negative in the first two experiments and positive in the third, wheras the opposite was noted for timothy.

Table 7. Digestion coefficients (%) and protein degradability (dg, %) of meadow fescue and timothy silage[1) 2)]

	Expt. 1			Expt. 2			Expt. 3		
	MF	T	SEM	MF	T	SEM	MF	T	SEM
Dry matter	78.1[b]	74.5[a]	0.7	69.7[b]	64.6[a]	1.4	72.0	73.1	0.7
Organic matter	79.9[b]	75.7[a]	0.8	70.8[b]	65.7[a]	1.6	73.9	74.1	0.6
Crude protein	76.5[b]	72.4[a]	2.3	72.5[b]	69.1[a]	1.1	60.3	64.3	2.0
Ether extracts	77.9[b]	74.1[a]	1.3	79.3[b]	72.0[a]	2.2	72.3[a]	79.6[b]	1.0
Crude fibre	85.4[b]	79.7[a]	1.4	73.0[b]	66.6[a]	2.5	80.3	78.9	0.7
N-free extracts	75.7[b]	73.8[a]	0.4	67.4[b]	63.2[a]	1.5	72.1	71.8	0.7
NDF	-	-	-	69.5[b]	62.3[a]	2.3	77.2[b]	75.8[a]	0.7
ADF	-	-	-	72.4[b]	66.2[a]	2.1	80.7[b]	78.2[a]	0.6
Protein dg	82.4	82.8	-	80.6	80.6	-	83.2	81.1	-

1) MF = meadow fescue silage; T = timothy silage; SEM = standard error of means; NDF = neutral detergent fibre; ADF = acid detergent fibre

2) Protein degradability calculated as: $dg = 100 \cdot (CP\ kg\ DM^{-1} - 22.5)/CP\ kg\ DM^{-1}$ (Webster *et al.* 1982)

Table 8. Estimated energy and protein values per kg DM of meadow fescue and timothy silage[1)]

	Expt. 1		Expt. 2		Expt. 3	
	MF	T	MF	T	MF	T
ME, MJ	11.3	10.8	9.9	9.3	10.3	10.4
FFE	0.86	0.82	0.75	0.70	0.79	0.80
FEm	0.97	0.91	0.82	0.76	0.86	0.87
DCP (g)	98	95	84	80	81	77
AAT (g)	78	74	70	66	74	74
PBV (g)	-6	4	-5	2	8	-8

1)MF = meadow fescue silage, T = timothy silage, other Abbreviations; see Table 2

Feed intake

The animal health was good and all animals were included in the statistical calculations. No interactions between silage and concentrate level were found and in the following observations only the main effects are presented and commented on. Daily intake of silage was 6.1 kg DM for group MF and 6.4 kg DM for group T, but only in Experiment 1 was the difference statistically significant (Table 9). Dry matter intake per 100 kg liveweight was not significantly different between the silage groups. All of the concentrate offered was consumed. Total net energy intake was variable and the means over all experiments were 4.9 FFE and 5.4 FEm for both groups. Only minor differences between silage groups were seen in total intake of DCP and AAT. In Experiments 1 and 2 total PBV was lower in group MF than in group T, but the values were positive for both groups. In the last experiment total PBV was positive in group MF while negative, but close to zero in group T.

Voluntary intake of silage was significantly depressed by 0.8, 0.6 and 0.5 kg DM in Experiments 1, 2 and 3 respectively, when the level of concentrate was increased from 1.5

kg to 3.0 kg. The total feed intake was greater at a high concentrate level (HC) than at a low level (LC). The DM intake was lower in Experiment 3 than in the other two experiments.

Table 9. Daily voluntary intake of silage and total feed consumption[1)]

	Expt. 1				Expt. 2				Expt. 3			
	MF	T	LC	HC	MF	T	LC	HC	MF	T	LC	HC
Silage intake:												
Kg DM	6.1[a]	6.7[b]	6.8[b]	6.0[a]	6.3	6.3	6.6[b]	6.0[a]	5.9	6.2	6.3[b]	5.8[a]
Kg DM (100 kg LW)$^{-1}$	1.43	1.48	1.55[b]	1.35[a]	1.49	1.48	1.58[b]	1.39[a]	1.35	1.38	1.46[b]	1.27[a]
Total feed consumption:												
DM, kg	8.1	8.7	8.2	8.6	8.3	8.3	7.9	8.7	7.8	8.1	7.6	8.4
FFE	7.4	7.6	7.1	7.8	6.9	6.5	6.2	7.2	6.7	7.0	6.4	7.4
FEm	7.9	8.1	7.7	8.2	7.3	6.9	6.6	7.6	7.1	7.4	6.8	7.7
DCP, g	884	923	850	958	809	789	730	869	754	748	676	827
AAT, g	667	684	646	705	626	601	573	654	620	644	587	677
PBV, g	17	83	31	69	26	77	31	72	96	-3	28	64

[1)] Abbreviations: MF=meadow fescue silage; T=timothy silage; LC=low concentrate level; HC=high concentrate level; DM=dry matter; LW=liveweight; Others, see Table 2

Animal performance

Differences in liveweight were generally small but in Experiment 3, animals in group T had significantly higher liveweights than those in group MF two weeks after grouping. No significant difference in carcass weight was found between the two silage diets and neither were any differences in growth rates observed. By increasing the concentrate level from 1.5 to 3.0 kg corrected liveweight gain increased 261, 275 and 381 g day^{-1} in Experiments 1, 2 and 3, respectively. In addition, carcass weight increased significantly in all experiments and this was also the tendency for the dressing percentage. In all experiments the liveweight increased almost linearly for all groups from two weeks after grouping to the final day. However, the increase was lower in Experiment 2 than in the other experiments.

Carcass characteristics

The carcasses were generally lean, with an average fat score of 3.2 and only a few carcasses were given the highest quality grade (Table 11). In Experiments 1 and 3 carcasses from group T had higher fat scores and greater weights of kidney fat than those from group MF. In Experiment 1 group T received significantly higher conformation scores than group MF.

Weight of kidney fat and, fat and conformation scores increased with the concentrate level in all experiments and a greater number of carcasses from the HC than from LC group received an "E" quality grade. Weight of liver, kidney fat and quality scores were generally lower in Experiment 2 than in the other experiments.

Table 10. Liveweight changes during the experiments, carcass weight and dressing percentage[1]

	Expt. 1				Expt. 2				Expt. 3			
	MF	T	LC	HC	MF	T	LC	HC	MF	T	LC	HC
Liveweight (kg)												
After two weeks	375	380	377	378	381	380	380	381	394[a]	400[b]	396	398
At slaughter	496	502	495	503	478	477	467[a]	493[b]	483	493	479[a]	497[b]
At slaughter:												
Carcass (kg)	251	257	248[a]	260[b]	237	234	229[a]	242[b]	243	246	237[a]	253[b]
Dressing %	50.6	51.2	50.1[a]	51.6[b]	49.6	49.0	49.0	49.6	50.2	50.0	49.3	50.9
LW gain, g day^{-1}:												
Uncorrected	1276	1289	1238	1328	1082	1080	969[a]	1193[b]	1083	1139	1012	1210
Corrected [2]	1343	1418	1250[a]	1511[b]	1038	975	869[a]	1144[b]	1119	1140	939[a]	1320[b]

[1] Meadow fescue silage; T=timothy silage; LC=low concentrate level; HC=high concentrate level; LW = liveweight

[2] Provided a dressing percentage of 50

Table 11. Weights of liver and kidney fat and carcass characteristics received at slaughter[1]

	Expt. 1				Expt. 2				Expt. 3			
	MF	T	LC	HC	MF	T	LC	HC	MF	T	LC	HC
Liver (kg)	6.4	6.8	6.3[a]	6.9[b]	5.5	5.3	5.3	5.5	5.9	6.0	5.8	6.2
Kidney fat (kg)	5.4[a]	6.4[b]	5.7	6.1	5.0	4.0	4.2[a]	5.6[b]	5.6[a]	6.1[b]	5.3[a]	6.4[b]
Fat score [2]	3.5[a]	4.3[b]	3.3[a]	4.5[b]	2.9	2.9	2.6	3.3	2.3	3.1	2.6	2.8
Conformation score	13.3[a]	14.1[b]	13.4	13.9	12.6	12.7	12.4	12.8	13.7	13.7	13.2[a]	14.2[b]
No of carcasses:												
Quality grade *E [3]	1	1	1	1	0	0	0	0	1	1	1	1
Quality grade E	3	7	3	7	2	2	1	3	6	3	2	7
Quality grade 1	8	4	8	4	10	10	11	9	4	8	8	4
Quality grade 2	0	0	0	0	0	0	0	0	1	0	1	0

[1] MF=meadow fescue silage, T=timothy silage, LC=low and HC=High concentrate level

[2] Fat score, scale 1 to 10 (10=fattest), Conformation score, scale 1 to 15 (15 best)

[3] Quality grades; *E=highest

Feed utilization

Feed consumption and net energy content of silage calculated from the energy requirements for the bulls can be seen in Table 12. No significant differences between the two silages were found from the computations. At the HC level the feed expenditure was lower than at LC level. The two net energy systems ranked the two silages similarly for feed expenditure but differences between the two systems were obtained for the calculated energy values of the silages. In two of the experiments FFE values were higher at LC than at HC, whereas the opposite relationship was found when calculated as FEm. In Experiments 1 and 3 the difference between concentrate levels was significant for FEm values. In Experiment 2 the feed expenditure was higher and the calculated energy values for the silages lower than in the other experiments.

Table 12. Feed utilisation and net energy values of silage calculated from liveweight gain[1)]

	Expt. 1				Expt. 2				Expt. 3			
	MF	T	LC	HC	MF	T	LC	HC	MF	T	LC	HC
FFE (kg LW-gain)$^{-1}$	5.7	5.4	5.8	5.3	6.7	6.9	7.3^{b}	6.3^{a}	6.4	6.3	7.1^{b}	5.7^{a}
FEm (kg LW-gain)$^{-1}$	6.1	5.7	6.2^{b}	5.6^{a}	7.2	7.3	7.8^{b}	6.6^{a}	6.7	6.7	7.5^{b}	5.9^{a}
FFE (kg DM)$^{-1}$	0.78	0.77	0.79	0.76	0.63	0.62	0.64	0.61	0.73	0.72	0.72	0.73
FEm (kg DM)$^{-1}$	1.13	1.15	1.05^{a}	1.23^{b}	0.82	0.80	0.79	0.84	1.01	1.00	0.91^{a}	1.10^{b}

1) MF=meadow fescue silage; T=timothy silage; LC=low concentrate level; HC=high concentrate level; LW=liveweight; DM=dry matter; FFE and FEm=fattening and milk feed units

Rumen fermentation

Mean values of rumen fluid analyses are presented in Table 13. In Experiment 1 no significant differences between main groups were obtained, but in Experiment 2 rumen pH was significantly higher and the total amount of acids was significantly lower for group MF than for group T. The proportion of acetic acid (C2), butyric acid (C4) over propionic acids (C3) was significantly lower for MF than T. In Experiment 3 differences were generally small but the concentration of ammonia-N was significantly higher for group MF than for group T.

Table 13. Rumen pH, total amount and molar proportion of volatile fatty acids, and concentrat of ammonia-N in rumen fluid[1)]

	Expt. 1				Expt. 2				Expt. 3			
	MF	T	LC	HC	MF	T	LC	HC	MF	T	LC	HC
pH	6.86	6.90	6.90	6.86	6.99^{b}	6.83^{a}	6.96	6.83	6.82	6.75	6.72^{a}	6.85^{b}
Total acids, mmol L-1	88.9	86.4	88.5	86.7	83.1^{a}	89.0^{b}	86.9	85.2	85.3	81.9	84.0	83.3
<u>In % of total acids</u>:												
Acetic acid (C2)	64.5	64.2	64.4	64.4	63.4^{a}	64.4^{b}	64.7	64.1	68.1	68.8	68.1	68.7
Propionic acid (C3)	19.9	18.8	19.0	19.6	21.3^{b}	18.7^{a}	20.3^{b}	19.7^{a}	17.5^{a}	18.1^{b}	17.8	17.8
Butyric acid (C4)	12.6	12.9	12.3^{a}	13.3^{b}	11.4^{a}	12.8^{b}	11.9	12.3	10.3^{b}	9.55^{a}	10.2	9.63
Iso-butyric acid	1.03	0.96	1.01	0.97	1.07	1.05	1.08	1.04	0.80	0.77	0.81	0.76
Valeric acid	1.43	1.52	1.53^{b}	1.41^{a}	1.58	1.58	1.59	1.57	1.59^{b}	1.38^{a}	1.47	1.50
Iso-valeric acid	1.34	1.27	1.42^{b}	1.19^{a}	1.31	1.35	1.35	1.30	1.77^{b}	1.45^{a}	1.61	1.61
(C2+C4):C3	4.00	4.13	4.04	4.09	3.54^{a}	4.14^{b}	3.76^{a}	3.91^{b}	4.52	4.35	4.43	4.45
Ammonia-N, mmol L-1	9.82	9.47	10.2	9.06	4.65	4.71	5.22	4.14	6.35^{b}	3.08^{a}	4.72	4.74

[1)] MF=meadow fescue silage; T=timothy silage; LC and HC = Low and High concentrate level

DISCUSSION

Forage characteristics

In previous investigations a higher content of CP, ash and sugar and a lower content of CF have been found in meadow fescue than in timothy when harvested at the same morphological stage (Oehring 1967; Demarquilly & Weiss 1970; Andersen & Østgård 1980; Schjelderup 1980). In Experiment 1 the opposite relationship was observed between the two grass species. In the later experiments chemical composition agreed relatively well with the literature, considering that meadow fescue was harvested at a slightly later stage of morphological development than timothy.

The main difference between the two grass species was the higher buffering capacity for meadow fescue than for timothy. The buffering properties of herbage are attributed to the anions, which are mainly organic acids salts (McDonald *et al.* 1991). Jones & Barnes (1967) have reported a higher total amount of weak organic acids in meadow fescue grass than in timothy, which partly explains the differences in buffering capacity. A high buffering capacity will elongate the initial fermentation period in which the pH is favourable for proteolysis and deamination (McDonald *et al.* 1991). The main products from these processes are acetic acid and non-protein nitrogen compounds (NPN), especially ammonia. In meadow fescue silage, acetic acid and ammonia-N were present in somewhat higher concentrations than in timothy silage and the true protein content was lower. Even greater effects on fermentation quality of the silage attributable to a high buffering capacity have been found for smooth meadow grass (Hole 1985a, c). The differences between meadow fescue and timothy silage were relatively small and in Experiments 1 and 2 both materials were considered as well preserved. In Experiment 3 the low DM content in fresh grass may have caused high losses of effluent and thereby of the additive. This probably explains the low content of formic acid and the poorer fermentation quality of both silages than in the other experiments. The higher concentration of ammonia-N in Experiments 2 and 3 compared with that in Experiment 1 may be partly due to the ammonia supplied with the additive.

Only small differences in chemical composition between the two silages were detected. In none of the other experiments in this project have any clear differences in chemical composition between silages been found (Barvik *et al.* 1991; Nordang 1992; Johansen & Nordang 1993). The main contrasts were the higher OM digestibility and energy values estimated for meadow fescue than for timothy silage. Similar differences between the two silages were found in feeding experiments with dairy cows (Johansen 1993; Johansen & Nordang 1993) and in feeding experiments with steers (Pestalozzi 1992, unpublished). On the other hand, no significant difference in OM digestibility was found in the ensiling studies or in the production experiments with sheep (Barvik *et al.* 1991; Nordang 1992). In Experiments 1 and 3 the OM digestibility of timothy silage was close to that found by Bergheim (1979a, b, c) for timothy harvested at the heading stage. The lower digestibility found in Experiment 2 is indicative of material harvested at a later morphological stage. The difference in OM digestibility between experiments may be associated partly with difficulties in identifying the stage of heading of a grass species and partly with natural variations between years.

The relatively high OM digestibility mainly explains the high energy values estimated for meadow fescue in Experiment 1. The generally higher DCP values for meadow fescue silage than those for timothy silage were due more to the differences in digestibility of CP than the differences in CP content. Different amounts of digestible carbohydrates largely explain the variation seen for AAT and PBV values, both within and between experiments.

Feed intake

Forbes (1988) reviewed the various approaches to forage intake prediction in which OM digestibility, DM concentration and fermentation characteristics were considered to be the most important feed factors. Furthermore, concentrate supplementation as well as a low content of CP in the total ration may limit the feed intake (Thomas & Thomas 1988).

In Experiment 1 the somewhat higher DM content may partly explain the significantly higher intake of timothy silage.

Moreover palatability effects which could be associated with the fermentation quality might have depressed the voluntary intake of meadow fescue silage compared with that of timothy. Among others, Ettala & Lampila (1978) and Miettinen *et al.* (1991) have shown that the amount of total acids, acetic acid, ammonia and the content of true protein (in % of CP) may affect silage intake significantly. However, in the present experiments the differences in fermentation quality between the two materials were relatively small, while the generally poorer fermentation quality in Experiment 3 might explain the generally depressed intake compared with the first experiments.

It has been shown that a low level of rumen degradable protein may reduce the digestibility of the ration and thereby limit the voluntary feed intake (Munksgaard *et al.* 1985). In experiments with growing bulls Andersen *et al.* (1986) found no reductions in feed intake or liveweight gain at lower PBV values than those observed in the present experiments. This makes it seem unlikely that protein shortage influenced the feed intake or liveweight gain of the bulls in these experiments.

The substitution rate (SR: the decrease in silage DM intake per kg increase in concentrate DM) was 0.61, 0.46 and 0.38 in Experiments 1, 2 and 3, respectively. The results from Experiments 2 and 3 were in good agreement with those found by Bergheim (1979c) and Hole (1985c). Phipps *et al.* (1987) found that there was an increase in SR with increasing OM digestibility for the silages, which may partly explain the higher SR in Experiment 1. Mean DM intake expressed per 100 kg liveweight was 1.45 kg, which is in good agreement with results from similar experiments (Bergheim 1979b; Hole 1985c).

Animal performance and feed utilization

The tendency of higher net energy values calculated for meadow fescue than for timothy were in good agreement with the values estimated from *in vivo* digestibility, although the calculated values differed less between the silages. This may partly be caused by altered energy utilization owing to the higher feeding level compared with the digestibility experiments. Carcasses from the timothy group received higher fat scores and had higher weights of kidney fat than those from the meadow fescue group. It is well known that the requirement of net energy increases with increasing fat content in the liveweight gain, but in the computations of FFE values the requirement for growth was considered equal in all groups (2.5 FFE kg gain^{-1}). Thus, the FFE value for timothy silage may actually be underestimated compared with that of meadow fescue silage. In contrast, the requirements for FEm increased with increasing liveweight gain (Van Es 1978). This may explain the higher FEm values calculated for timothy than for meadow fescue in Experiment 1 and the diminished difference between the two silages compared with the FFE values in the last two experiments. It may also explain the discrepancy between the two systems at low and high concentrate levels.

Moreover, according to Mould (1988) the assumption made in the computations that energy values of silages and concentrates are cumulative is probably not correct because associative effects between the feeds may have occurred. This is partly confirmed in digestibility experiments with sheep where no difference in OM digestibility between the two silage rations was found when 60% concentrate (on DM basis) was supplied (Johansen 1993).

Generally, the utilization of FFE was in good agreement with the Norwegian recommendations for growing bulls of an equivalent size and growth rate (Homb 1981), whereas the utilization of FEm was more efficient than expected according to standards given by Sundstøl & Ekern (1992). Furthermore, in previous comparisons higher FFE values were found when estimated from *in vivo* digestibility trials than when calculated from liveweight gain (Bergheim 1979b; Hole 1985c; Nordang 1990). The opposite relationship for FEm values corresponded well with similar computations from milk production in feeding experiments with dairy cows (Johansen & Nordang 1993). This might be associated with the equations used when computing the requirements which are based on data from other breeds than NRF. The lowered feed expenditure when increasing the concentrate level corresponded well with the results of Haugland & Matre (1974).

Despite the variations found in ensiling properties between the grass species it can be concluded that meadow fescue silage was of no less value for fattening of bulls than timothy silage, even when harvested at a slightly later stage of development. When discussing the use of grass species for forage production, factors other than the feeding value of the silages must also be considered. Among others, DM yield of the species is an important factor. In the present experiments DM yield of timothy was higher than that of meadow fescue, but in a series of experiments in northern Norway DM yields of both first and second cuts were found to be higher for meadow fescue than for timothy (A. Larsen, personal communication). The best result was found when the species were grown as mixed swards which is the most common farming practice in Norway. Thus, from both a nutritional point of view and the aspect of having a high DM yield, meadow fescue should remain an important species in seed mixtures.

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The effect of tungsten on nitrate reductase activity and nitrogen status of timothy (*Phleum pratense* L.) under various daylengths

ANNE KJERSTI BAKKEN
The Norwegian State Agricultural Research Stations, Kvithamar Research Station, Stjørdal, Norway

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Tungsten, a molybdenum analog inactivating nitrate reductase, was supplied to timothy plants before and during daylength treatment, to study the nitrogen and protein content in short- and long-day treated plants when the nitrate reducing step in protein synthesis was omitted. Ten-day-old plants grown with tungsten or molybdenum, were given short or long days for 10 days. All plants were fertilized with ammonium (5.5 mM) and nitrate (8.5 mM). For molybdenum plants, long-day treatments gave a lower nitrogen content than short days. A corresponding decrease from short to long days was not seen in the tungsten plants. Although this finding gives some support to the idea that the nitrate reduction step in protein synthesis in timothy is sensitive to the photoperiod, it can still not be concluded that NR is the control point for the ratio of assimilated nitrogen to assimilated carbon.

Key words: Night temperature, nitrate reductase,photoperiod, timothy, tungsten.

Anne Kjersti Bakken, Kvithamar Research Station, N-7500 Stjørdal, Norway

Long days stimulate dry matter production and induce generative development in timothy (*Phleum pratense* L.) (Evans & Allard 1934; Heide et al. 1985). In long days the ratio of assimilated nitrogen to assimilated carbon is lower than in short days, and there are indications that nitrate reductase (NR) (1.6.6.1), catalyzing the reduction of nitrate to nitrite, is sensitive to the photoperiod and thereby of importance for this ratio (Bakken 1993). Both NR activity and nitrogen and protein content were lower in timothy grown in long days compared with plants grown in short days. The activity of the enzyme is also regulated or modified by phytochrome (Jones & Sheard 1972; Schuster et al. 1987). Phytochrome is associated with the time measuring process and the induction of daylength responses in photoperiodically sensitive plants (Vince-Prue 1983), and might thus be the connection between daylength perception and photoperiodically regulated NR activity.

At one of its catalytic sites, NR has a prosthetic group containing molybdenum (Campbell & Smarelli 1986). Tungsten can compete with molybdenum for incorporation into the enzyme complex, resulting in an inactive enzyme (Notton & Hewitt 1971). Plants grown with tungsten will not be able to assimilate nitrate, and thus nitrogen assimilation and protein synthesis in such plants depend on ammonium as a source of nitrogen. Furthermore, daylength effects on nitrogen assimilation through NR activity should not be expected. The present investigation was designed to test these hypotheses.

MATERIALS AND METHODS

Experimental conditions and treatments

Timothy (*Phleum pratense* L., cultivar Bodin) was germinated at 20°C and grown in perlite (nr. 65, Ticon Perlite, Drammen, Norway) in a glasshouse at Kvithamar Research Station (63°29'N) in two successive experiments; the first sown on 21 December, the second on 28 January. From germination until start of daylength treatment the photoperiod was 12 h (natural daylight supplemented with light from SON-T high-pressure sodium lamps, minimum 190 μmol $m^{-2}s^{-1}$ at plant level). The temperature was 20°C/15°C day/night. An estimate for the incident global radiation (300-3000 nm) from germination until end of daylength treatment was made from data recorded at Værnes airport (located 5 km from Kvithamar Research Station) from 1970 - 1988. The daily mean global radiation during the periods corresponding to the growth periods was 7.0 MJ $m^{-2}d^{-1}$ for the first experiment and 45.2 MJ $m^{-2}d^{-1}$ for the second.

Daylength treatments with photoperiods of 12 and 24 h started 17 days after sowing. All plants were given 12 h PAR (photosynthetically active radiation) as described above. The daylengthening light in the long-day treatment was from incandescent lamps (0.8 - 1.1 μmol $m^{-2}s^{-1}$). During treatment the temperature was set to 20°C during the PAR period but reached maxima of 24°C on sunny days. During the rest of the diurnal period the temperature was either 10° or 15°C.

Seeds were imbibed and plants later watered with a nutrient solution consisting of 3.0 mM $Ca(NO_3)_2 \times 4H_2O$, 2.0 mM KNO_3, 0.5 mM NH_4NO_3, 1.0 mM $(NH_4)_3PO_4 \times 3H_2O$, 1.0 mM $(NH_4)_2SO_4$, 0.8 mM $MgSO_4 \times 7H_2O$, 1.0 mM $K_2HPO_4 \times 3H_2O$ and 0.2 mM NaCl in distilled water. The pH in this solution was adjusted to 4.8 with HCl. Micro nutrients were given according to Hewitt (1952): 100.4 μM $FeSO_4 \times 7H_2O$, 10.0 μM $MnSO_4 \times H_2O$, 1.0 μM $CuSO_4 \times 5H_2O$, 0.99 μM $ZnSO_4 \times 7H_2O$, 3.43 μM $Na_2B_4O_7 \times 10H_2O$ and 0.21 μM $Na_2MoO_4 \times 2H_2O$ or 500 μM $Na_2WO_4 \times 2H_2O$ in distilled water.

The experiments were of a factorial design with 3 replicates; 2 daylengths, 2 sampling times on each harvest day, 2 nutrient solutions (containing Mo or W) and 2 night temperatures. Each treatment consisted of 3 g (2 g in the second experiment) seeds sown in 5 l perlite in a 30 cm x 60 cm x 5 cm plastic tray. All treatments were watered with equal volumes of the nutrient solutions.

In the first experiment four additional treatments were added to test whether tungsten was toxic to the plants when molybdenum was available simultaneously. In these treatments all plants were grown in fertilized peat (containing Mo). Two trays were watered with the molybdenum solution and two with the solution containing tungsten.

Sampling and chemical analyses

Samples were taken at the start of daylength treatments and after 10 and 11 days of treatment in the first and the second experiment, respectively. Two samples from each treatment were taken, one after 2 h and another after 5½ h with PAR. In the first experiment NR activity was determined only in shoots from plants given 15°C at night, and in the second experiment only in shoots from plants supplied with molybdenum. Soluble protein, dry matter, nitrogen and nitrate content in plant shoots were analysed in all treatments. NR activity and soluble protein content in extracts made from fresh plant shoots (0.5 g) were determined as described by Bakken (1993). Total N and nitrate in samples (2 g) dried for 24 h at 70°C were determined by standard Kjeldahl methods and a nitrate selective electrode (Orion, model 93-07).

Statistical analysis

The data from the two experiments were analysed together and subjected to analysis of variance with main effects of daylength, micro nutrition, night temperature and sampling time of the day. All possible interactions between main effects were analysed, and all effects apart from the error element, were considered as fixed. The SYSTAT program (Wilkinson 1990) was used.

RESULTS

Plant status at start of daylength treatment

Plants given molybdenum were larger and had a lower dry matter content (% of fresh weight) and a higher nitrogen and protein content than those grown with tungsten (Tables 1 and 3). The NR activity in molybdenum plants was significantly higher than in plants grown with tungsten (Tables 1 and 3). A significant effect of sampling time on plant weight, on dry matter content and on the amount of protein per plant was also seen (Table 3). The weight of plants, the dry matter content and the amount of protein per plant increased from the first to the second sampling time on the day of harvest (data not shown).

Plant status after daylength treatment

The control plants grown in fertilized peat were on the average larger and had a higher protein, nitrogen and nitrate content than those grown in perlite (Tables 1 and 2). The same plants had a higher nitrogen and protein content and a lower nitrate content when watered with molybdenum than with tungsten and were smaller when they were given tungsten than molybdenum (Table 2).

Plants grown in perlite and watered with the molybdenum solution were significantly larger and had a higher protein, nitrogen and nitrate content than those watered with the tungsten solution (Tables 1 and 3). The NR activity in plants grown on tungsten was nearly zero (Table 1).

Plants from the 10°C treatment had a significantly lower protein, nitrogen and nitrate content and a higher dry matter content than those from the 15°C treatment (Tables 1 and 3). The differences in dry matter and nitrogen content between the 15°C and 10°C treatments were significantly larger for plants grown with tungsten than for molybdenum plants (Tables 1 and 3).

Table 1. Dry matter content, plant weight, nitrogen content, nitrate content, NR activity, protein content, and protein per plant in timothy shoots at start and after 10 (11) days of daylength treatment. Plants were given either molybdenum or tungsten, and the temperature at night (12 h darkness or 12 h day-lengthening light) was either 10° or 15°C. The values shown are the means of 12 samples, 6 from the first experiment and 6 from the second. -: Parameter not measured

	Start of treatment		After daylength treatment, 12 h photoperiod				After daylength treatment 24 h photoperiod			
	Molybdenum	Tungsten	Molybdenum		Tungsten		Molybdenum		Tungsten	
	10°C	15°C	10°C	15°C	10°C	15°C	10°C	15°C	10°C	15°C
Dry matter content (% of FW)	12.4	16.2	12.1	11.8	16.8	16.0	11.7	11.6	16.8	15.3
Plant fresh weight (mg)	9.2	5.4	51.1	50.6	16.3	19.6	57.8	54.5	13.2	18.8
Plant dry weight (mg)	1.1	0.9	6.3	6.0	2.8	3.2	6.7	6.4	2.2	2.9
Nitrogen content (% of DW)	6.56	4.78	5.79	5.81	3.84	4.09	5.37	5.40	3.69	3.94
Nitrate content (mg N x 100 g $(DW)^{-1}$)	964	780	932	933	615	768	880	999	598	735
NR activity (μmol NO_2^- x $g(FW)^{-1}$ x h^{-1})	8.83	0.78	3.40	2.10	-	0.00	1.98	2.50	-	0.13
Protein content (mg x $g(DW)^{-1}$)	137	100	99	97	60	68	90	97	63	70
Protein per plant (mg x $plant^{-1}$)	0.15	0.09	0.62	0.58	0.17	0.22	0.61	0.60	0.14	0.20

Table 2. Shoot weight and nitrogen, nitrate and soluble protein content in timothy plants grown in fertilized peat and watered either with a solution containing molybdenum or a solution containing tungsten. The values shown are the means of two samples, one from plants grown in 12 h photoperiod and one from plants grown in 24 h photoperiod

	Molybdenum plants	Tungsten plants
Plant dry weight (mg)	7.7	6.9
Nitrogen content (% of DW)	5.92	5.74
Nitrate content (mg N x 100 $g(DW)^{-1}$)	1242	1822
Protein content (mg x g $(DW)^{-1}$)	100	74

Table 3. Significant effects ($p < 0.05$) of daylength (D), micro nutrition (M), night temperature (T), sampling time of the day (S) and interactions on variables measured in the shoots from timothy plants at start and after daylength treatment. -: too few observations for the ANOVA.

	Start of treatment	After treatment
Dry matter content	M, S	M, T, MxT
Plant fresh weight	M, S	M, DxM
Plant dry weight	M, S	M
Protein content	M	M, T
Protein per plant	M, S, MxS	M
NR activity	M	M, DxT
Nitrogen content	M	D, M, T, DxM, MxT
Nitrate content	-	M, T

The nitrogen content in the shoots was higher at 12 h daylength than at 24 h daylength (Tables 1 and 3). The protein content and NR-activity decreased from short to long days only at the lower night temperature (Table 1). These two-factor interactions were significant at the 0.08 and 0.05 level, respectively.

An interaction between daylength and trace element was seen for plant fresh weight and nitrogen content (Table 3). The molybdenum plants were smaller when grown in short days than in continuous light, whereas the tungsten plants were smaller when grown in continuous light than in short days (Table 1). The effect of daylength on the nitrogen content was stronger for plants given molybdenum than those given tungsten (Table 1).

DISCUSSION

The status of the plants grown in fertilized peat give no indications of other toxic effects of tungsten on plants besides inhibition of nitrate assimilation. The tungsten plants grown in fertilized peat (containing small amounts of molybdenum) had no N-deficiency symptoms, and the protein and nitrogen content was nearly as high as in plants given molybdenum (Table 2). Other metabolic effects of tungsten can, however, not be fully eliminated as the availability of molybdenum in the substrate might have prevented tungsten uptake in the plants grown in peat.

For the plants grown in perlite, there were large differences in growth and in nitrogen and protein contents between those given tungsten and those given molybdenum, both before and after daylength treatment. This indicates that tungsten is easily absorbed and inhibits nitrate reduction in timothy. The small tungsten plants, low in nitrogen and protein and with a high dry matter content, seemed to suffer from N-starvation, even if considerable amounts of ammonium (5.5 mM) were available in the nutrient solution. A pH of 6-7 is thought to be optimal for the uptake of ammonium (Hageman 1984). In the present experiment the pH of the macro nutrient solution was quite low (4.8), and the uptake of ammonium might therefore have been inhibited. The lower nitrate content of timothy grown with tungsten compared to those grown with molybdenum, indicates that the roots absorb less nitrate when nitrate reduction is inhibited. Heimer et al. (1969) also found that the nitrate content of barley plants given tungsten in concentrations as in the present experiment was lower than of molybdenum plants.

An explanation for the lower nitrogen and protein content especially in the tungsten plants grown at the lower night temperature (Table 1), might be that the absorbtion and/or assimilation rate of ammonium was higher at the higher temperature. The ammonium absorbtion rate is found to increase with increasing root temperature in *Festuca ovina* (Rorison et al. 1983) and in *Hordeum vulgare* (Macduff & Hopper 1986). In the present experiment all plants experienced the same day temperature. An effect of the temperature in the non PAR period on the nitrogen and protein status of tungsten plants thus indicates that considerable amounts of the ammonium were absorbed and assimilated during this period.

The effect of daylength on the nitrogen content seen in the present study is in agreement with earlier findings of Bakken (1993). Plant growth was stimulated by long days, and the NR activity, the dry matter, nitrogen and protein content of timothy plants decreased with increasing daylength.

In the present experiment a decrease in protein content and NR activity from short to long days was seen only in the treatments with 10°C night temperature (Table 1). The temperature dependence of other long-day responses in timothy was investigated by Hay & Heide (1984) and Heide (1982) who found a greater long-day stimulation of dry matter production and flowering at lower temperatures. The temperature in these investigations was however constant during day and night. Junttila (1985) studied the effects of diurnal temperature fluctuations on shoot elongation in timothy (one year old and cold treated plants), and found elongation to be significantly stimulated by alternating temperature compared to a constant temperature. The apparently stronger long-day response at the lower night temperature in the present study, might be caused by a lower mean diurnal temperature as well as larger temperature fluctuations from day to night.

There was a greater decrease in the nitrogen content from short to long days in plants grown on tungsten than in plants grown on molybdenum, and at the lower night temperature the NR activity decreased from short to long days. These facts give some support to the idea that photoperiodic sensitivity in the nitrate reducing step in protein synthesis is the cause for the lower ratio of assimilated nitrogen to assimilated carbon in long days compared to short days. There was, however, no difference between tungsten and molybdenum plants in the way daylength affected the soluble protein content. Therefore it can still not be concluded that NR is the photoperiodically sensitive control point for the ratio of assimilated nitrogen to assimilated carbon.

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Competition between an established grass sward and seedlings of *Rumex longifolius* DC. and *Taraxacum officinale* (Web.) Marss.

ESPEN HAUGLAND
Norwegian Plant Protection Institute, Department of Herbology, Ås, Norway

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Effects of root and shoot competition from grasses on establishment of *Rumex longifolius* DC. and *Taraxacum officinale* (Web.) Marss. were investigated by planting seedlings of the two herbs into an established grass sward. The competition effects were evaluated at different nitrogen levels. In separate experiments shading cages and growth chambers were used to evaluate the effect of reduced light intensity on growth of *R. longifolius*, *T. officinale* and *Phleum pratense* L. Different rates of nitrogen affected the competition patterns between the grass sward and these dicots to only a limited extent. Root competition affected shoot dry weight much more than did shoot competition. Shading resulted in longer length of leaves and increased specific leaf area (SLA), which make the dicot seedlings less susceptible to competition for light. Shoot competition reduced root dry weight and increased shoot/root ratio, which in turn probably can reduce plant survival.

Key words: Establishment, grassland, nitrogen rates, root competition, *Rumex longifolius*, shoot competition, *Taraxacum officinale*

Espen Haugland, Norwegian Plant Protection Institute, Department of Herbology, Fellesbygget, N-1432 Ås, Norway

Rumex longifolius DC. and *Taraxacum officinale* (Web.) Marss. are two of the most troublesome dicotyledonous species in Norwegian grasslands. After renovation, meadows and pastures are often rapidly invaded by these and other species. If seeds of dicot species germinate in an established sward, they usually fail to establish, or the plants remain very small (Cavers & Harper 1967). The establishment depends on the capacity of seedlings to survive in competition with other plants.

In the establishment phase, the plants are competing for both above and below-ground resources. Soil moisture and nutrient supplies are main below-ground factors. Nitrogen may change the competitive capacity of different species in grassland (Dietl 1982), while Jeangros & Nösberger (1990) found no effect of potassium. The key aerial growth factor is light, where both quantity and quality are important. An understanding of the effect of these factors may be of importance in grassland management in order to reduce dicot infestation.

The aim of the present trials was therefore to investigate the relative importance of above-ground and below-ground competition between an established grass sward and seedlings of *R. longifolius* and *T. officinale* at different nitrogen levels, as well as to study the adaptability of a grass species and the two herbs to reduced light intensities.

MATERIALS AND METHODS

In three experiments, the two herbs were raised by seeding in potted trays in a greenhouse. The different treatments started three weeks after sowing, when the herbs had 3-4 permanent leaves and were 3-5 cm high.

Experiment 1:
The experiment was conducted at Ås, Akershus. The soil was characterized as sandy loam with 6 % organic matter, rich in plant available phosphorus and medium rich in potassium (P-AL and K-AL of 12 and 10 mg/100 g soil, respectively).

The technique used to separate effects of root and shoot competition between the grass sward and *R. longifolius* or *T. officinale* is essentially the same as that described by Jeangros & Nösberger (1990). The technique provides conditions of no competition, shoot competition only, root competition only, and both shoot and root competition between grasses and herbs. Seedlings of the two dicots were planted in the space between the sowing rows of a two-year-old meadow, sown with a mixture of *Phleum pratense* L., *Festuca pratensis* Huds. and *Poa pratensis* L. During the experimental periods the sward was dominated by *P. pratense* and *F. pratensis* in a ratio of approximately 75 and 25 per cent visually estimated. No root competition from the grass sward was achieved by driving PVC cylinders of 115 mm diameter and 225 mm length into the soil before the planting of one plant of *R. longifolius* or *T. officinale* inside each cylinder (Fig. 1). No shoot competition from the grass sward was produced by weekly cutting the grass to a height of approximately 15 cm.

In summary, the treatments for each dicot species were as follows: i) two levels of nitrogen (50 and 100 kg N/ha) given as calcium-nitrate (15.5% N) after planting, ii) root competition between the grass sward and the dicot, present (+) or absent (-) and iii) shoot competition between the grass sward and the dicot, present (+) or absent (-). All plots were given 39 kg P/ha and 116 kg K/ha as PK 7-21-fertilizer.

A split-plot design was used, with nitrogen level on main plots and competition treatments on randomized subplots. Four plants grew in each subplot. The experiments included three replications of each species, and the two dicot species were on adjacent fields.

Growing conditions
The trial was run for three growth periods (Table 1) to obtain different climatic conditions. Period 1 was unusually dry, cold and windy. Period 2 was dry and warmer than normal, while the soil moisture was kept close to field capacity (recorded by four tensiometers) by irrigation in period 3.

Table 1. Mean daily temperature and photosynthetic active radiation (PAR), and total precipitation in the growth periods of experiments 1 and 2

Growth period		Temperature °C	PAR E/m²	Rainfall mm
1	3 May - 12 June 1991	10.3	43.0	11.4
2	13 May - 10 June 1992	17.3	51.8	14.0
3	10 July - 12 August 1992	15.7	37.0	109.0

Measurements

At the end of each growing period the plants of the two herbs were cut at ground level and pooled within each subplot. At the end of period 1 shoot dry weight and leaf area were measured (LI-3100 Area Meter, Li-cor). At the end of periods 2 and 3 the plants were carefully dug up and divided into shoots and roots, and dry weights were recorded separately. Leaf length was measured on the four longest leaves. Specific leaf area (SLA) was calculated as leaf area:leaf weight (cm^2/mg) and shoot/root ratio as shoot dry weight:root dry weight (mg/mg).

Experiment 2:

This experiment was run during periods 2 and 3 (Table 1). *P. pratense* (cv. Grindstad) was sown in plastic pots (3.5 l). After emergence, the number of seedlings were reduced to five per pot. *R. longifolius* and *T. officinale*, raised in potted trays, were planted in the same type of pots, one plant per pot. A peat soil (84 % sphagnum + 10 % sand + 6 % clay, pH=5.8 and amended with a balanced mixture of plant nutrition) was used.

The three species were grown at different light intensities under outdoor conditions by placing five pots of each species into white wooden shade cages, 1.2 x 1.0 m wide and 1.0 m high, according to a method described by Erickson et al. (1972). Different spaces between the wood laths gave relative light intensities of 100, 40, 21 and 8 per cent, measured by a Sunfleck Ceptometer with 80 light sensors placed at 1 cm intervals along the probe (Decagon Devices, Inc.). The photosynthetic active radiation (PAR) in the experimental periods, recorded at a local meterological station, is given in Table 1. Assuming daylengths of 18 hours in period 2 and 17 hours in period 3, the mean photon flux densities on unshaded plants in the two growth periods were 800 and 600 $\mu mol \cdot m^{-2} \cdot s^{-1}$, respectively. Skuterud (1984) reported no significant differences in air temperature and relative humidity inside and outside the shade cages. All pots were irrigated to keep the soil moisture close to field capacity. The same measurements were taken as in experiment 1, periods 2 and 3.

Experiment 3:

This experiment was carried out in growth chambers with different photon flux densities. The plants were raised in the same way as in experiment 2, and the type and number of pots were the same. Photon flux densities of 375, 150, 100 and 40 $\mu mol \cdot m^{-2} \cdot s^{-1}$ were established (measured by the same Sunfleck Ceptometer as in experiment 2). Two growth chambers were used, giving 375 and 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$. The photon flux densities of 150 and 40 $\mu mol \cdot m^{-2} \cdot s^{-1}$ were obtained by placing a shade screen in one half of each growth chamber. No effect of the screen on air temperature or relative humidity could be detected. The day/night regime was 19/5 hours, with a temperature of 20/14 °C, and a relative humidity of 60/90%. The measurements were taken in the same way as in experiment 2.

Statistical analyses

In experiment 1, analysis of variance was carried out with the fertilizer treatment as the main plot factor and the competition treatments as subplot factors. Competition treatments were considered as factorial combinations of root competition (present or absent) and shoot competition (present or absent). The variables, except for SLA and shoot/root ratio, were transformed to logarithms to homogenize variances. Values of these variables are presented as geometric means. Analysis was carried out on the mean of leaf length within each subplot. The analysis of variance was performed separately for the two species. Comparisons of main effects were done by the Bonferroni t-test, and mean values with different letters are considered significantly different at the 5 %-level. In experiments 2 and 3, means are presented in a logarithmic scale to make proportional comparisons of the three species under different light conditions.

RESULTS

There was no significant effect of nitrogen level on the growth of seedlings of *R. longifolius* (Table 2). Root competition from the grass sward, however, significantly reduced shoot dry weight, shoot/root ratio, leaf area and leaf length of *R. longifolius*, while shoot competition increased leaf length. Both root and shoot competition resulted in reduced root dry weight. The shoot/root ratio indicated that root competition reduced shoot growth more than root growth. Shoot competition tended to give the opposite effect by reducing root growth more than shoot growth. Both root and shoot competition resulted in increased SLA.

There was no significant interaction between the root and shoot competition factors in the growth of *R. longifolius*. However, significant interactions in SLA were found between the shoot competition factor and growth period and the shoot competition factor and nitrogen fertilization (Table 3). In growth period 3 there was an increased response to shoot competition, and the higher N level enhanced the response to shoot competition.

Table 2. The main effects of nitrogen fertilization and root and shoot competition from a grass sward on the growth of seedlings of *Rumex longifolius* DC

	Shoot dry weight[1)4)] mg/plant	Root dry weight[2)4)] mg/plant	Shoot/root ratio[2)]	Leaf area[1)4)] cm^2/plant	Specific leaf area (SLA)[3)] cm^2/mg	Leaf length[2)4)] mm
Nitrogen fertilization:						
50 kg N/ha	88*a*	178*a*	0.90*a*	21*a*	0.38*a*	185*a*
100 kg N/ha	99*a*	135*a*	1.29*a*	26*a*	0.39*a*	200*a*
Root competition:						
-	178*a*	188*a*	1.46*a*	45*a*	0.38*a*	245*a*
+	49*b*	128*b*	0.73*b*	12*b*	0.40*b*	151*b*
Shoot competition:						
-	102*a*	198*a*	1.00*a*	23*a*	0.33*a*	179*a*
+	86*a*	121*b*	1.19*a*	24*a*	0.45*b*	206*b*

1) Total number of observations = 72.
2) Total number of observations = 48.
3) Total number of observations = 47.
4) Geometric means.
Means followed by the same letter do not differ significantly ($p > 0.05$).

Table 3. The interactions between shoot competition and growth period, and shoot competition and nitrogen fertilization, in specific leaf area (SLA) of *Rumex longifolius* DC. (N=47)

	Growth period		Nitrogen fertilization	
	2	3	50 kg/ha	100 kg/ha
Shoot competition:				
-	0.27	0.40	0.34	0.33
+	0.34	0.57	0.43	0.47
p-values	0.0001		0.009	

No significant effect was recorded of N level on the growth of seedlings of *T. officinale* (Table 4). Root and shoot competition from the grass sward affected *T. officinale* in almost the same manner as *R. longifolius*, by reducing both shoot and root dry weights. Shoot/root ratio, leaf area and leaf length were reduced by root competition, while shoot/root ratio, SLA and leaf length were increased by shoot competition.

Table 4. The main effects of nitrogen fertilization and root and shoot competition from a grass sward on growth of seedlings of *Taraxacum officinale* (Web.) Marss

	Shoot dry weight[1)3)] mg/plant	Root dry weight[2)3)] mg/plant	Shoot/root ratio[2)]	Leaf area[1)3)] cm²/plant	Specific leaf area (SLA)[2)] cm²/mg	Leaf length[2)3)] mm
Nitrogen fertilization:						
50 kg/ha	99*a*	78*a*	1.53*a*	31*a*	0.36*a*	143*a*
100 kg/ha	85*a*	53*a*	1.74*a*	30*a*	0.42*a*	157*a*
Root competition:						
-	151*a*	81*a*	1.97*a*	52*a*	0.40*a*	189*a*
+	56*b*	52*b*	1.30*b*	18*b*	0.38*a*	119*b*
Shoot competition:						
-	99*a*	87*a*	1.34*a*	29*a*	0.33*a*	140*a*
+	85*b*	48*b*	1.91*b*	31*a*	0.44*b*	159*b*

1) Total number of observations = 71.
2) Total number of observations = 47.
3) Geometric means.
Means followed by the same letter do not differ significantly ($p>0.05$).

Significant interactions between the nitrogen factor and the shoot competition factor were found in shoot dry weight, root dry weight and SLA of *T. officinale* (Table 5). There was almost no difference in shoot dry weight between the two levels of shoot competition at 50 kg N/ha, while shoot competition reduced shoot dry weight at 100 kg N/ha. The higher N level caused a greater difference in root dry weight between the shoot competition levels compared to the lower N level. The response of *T. officinale* in SLA to shoot competition was also larger at the higher N level.

There were significant interactions between the growth periods and shoot competition in shoot and root dry weights and leaf area of *T. officinale* (Table 6). The dry springs in periods 1 and 2 resulted in almost no difference in these three parameters between the two levels of shoot competition, while no shoot competition gave the higher values in period 3.

Table 5. The interactions between shoot competition from a grass sward and nitrogen fertilization in growth of seedlings of *Taraxacum officinale* (Web.) Marss

	Shoot dry weight[1)3)] mg/plant		Root dry weight[2)3)] mg/plant		Specific leaf area (SLA)[2)] cm^2/mg	
N kg/ha	50	100	50	100	50	100
Shoot competition:						
-	98	99	91	83	0.33	0.34
+	100	73	68	35	0.38	0.51
p-values	0.02		0.002		0.02	

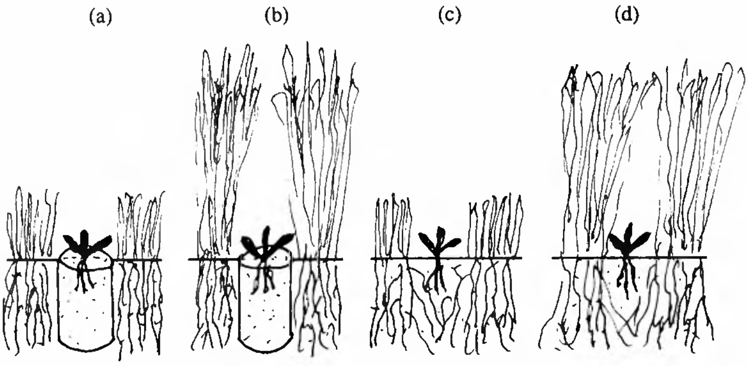
1) Total number of observations = 71.
2) Total number of observations = 47.
3) Geometric means.

Table 6. The interactions between shoot competition level from a grass sward and growth period in growth of seedlings of *Taraxacum officinale* (Web.) Marss

	Shoot dry weight[1)3)] mg/plant			Root dry weight[2)3)] mg/plant		Leaf area[1)3)] cm^2/plant		
Growth period	1	2	3	2	3	1	2	3
Shoot competition:								
-	76	56	242	45	178	18	17	89
+	85	47	156	32	74	23	17	76
p-values	0.03			0.006		0.03		

1) Total number of observations = 71.
2) Total number of observations = 47.
3) Geometric means.

Experiment 2:
R. longifolius, *T. officinale* and *P. pratense* all responded to reduced light intensities by a decrease in shoot dry weight, root dry weight and leaf area (Fig. 2 a, b, e). Relative light intensities of 40 % and 21 % increased leaf length compared to 100 % and *P. pratense* showed a greater response than did the weed species (Fig. 2d). SLA increased at reduced light intensity, though more strongly in *T. officinale* and *R. longifolius* than in *P. pratense* (Fig. 2f). A similar effect was found in shoot/root ratio, in which *T. officinale* responded more than the other two species to decreased light intensity (Fig. 2c).



	(a)	(b)	(c)	(d)
Root competition	-	-	+	+
Shoot competition	-	+	-	+

Figure 1. The arrangement of PVC cylinders and grass cutting used to produce a) no competition, b) shoot competition only, c) root competition only and d) both shoot and root competition between grasses and herbs

Experiment 3:
Reduced photon flux density reduced shoot dry weight and leaf area in *P. pratense* more than in the two dicots (Fig. 3 a, e), while the response in root dry weight was similar in the three species (Fig. 3b). A reduction of photon flux density from 375 to 150 and 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ resulted in increased leaf length, except in *T. officinale* which showed reduced leaf length at the latter photon flux (Fig 3d). At reduced photon flux, there was a tendency toward a greater increase in the shoot/root ratio in the two dicots than in the grass species (Fig. 3c). The curve shifts in Fig. 3c and f from 100 to 150 $\mu mol \cdot m^{-2} \cdot s^{-1}$ indicate that there may be an unidentified growth factor that varied between the two growth chambers used.

DISCUSSION

Shoot dry weight of both *R. longifolius* and *T. officinale* was more strongly affected by root than by shoot competition. The importance of root competition has been reported in several papers (Donald 1958; Rhodes 1968; King 1971; Snaydon 1971; Eagles 1972; Snaydon & Howe 1986; Jeangros & Nösberger 1990). It is frequently argued that root and shoot competition interact positively, which was also the conclusion of Donald (1958). However, in the present investigations these effects were simply additive. King (1971) also reported no such interaction, and Wilson (1988) concluded that this type of interaction is rather rare.

The reduced root dry weight and increased shoot/root ratio due to shoot competition can affect the survival potential of a plant through reduced carbohydrate reserves in the root. Exley & Snaydon (1992) showed that shoot competition between *Triticum aestivum* L. and *Alopecurus myosuroides* Huds. reduced the survival rate of *A. myosuroides* more than did root competition.

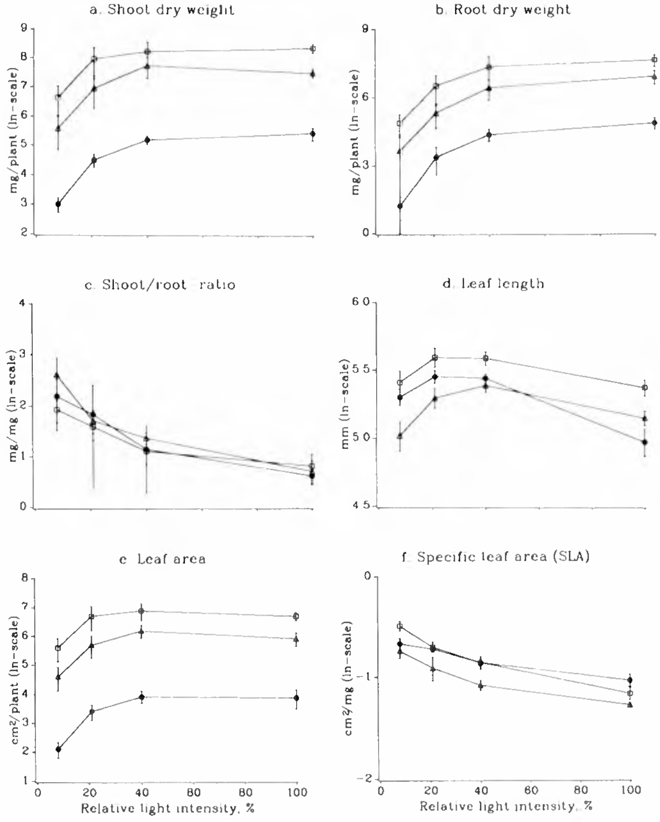


Figure 2. Effects of different relative light intensities on growth of *Phleum pratense* L. (-●-), *Rumex longifolius* DC. (-□-) and *Taraxacum officinale* (Web.) Marss. (-▵-). Bars indicate ± standard of the mean.

Leaf area, SLA and leaf length characterize the morphology of the shoot. Root competition reduced leaf area considerably in both dicot species, but affected SLA only slightly. Shoot competition produced increased leaf length, which positioned the leaves at a higher level of the canopy, and reduced the thickness of the leaves. This is typical of shaded leaves of dicots and is a compensation for reduced photon flux. Experiment 2 indicated that SLA was the only character in which the two dicots were better adapted to reduced light intensities than the grass cultivar investigated, while experiment 3 indicated better adaptation of the dicots in both shoot dry weight and leaf area. Jeangros & Nösberger (1992) reported that the lesser sensitivity of *Rumex obtusifolius* L. to reduced light intensities was mainly caused by a greater increase in SLA and a lesser decrease in net assimilation rate compared to *Lolium perenne* L.

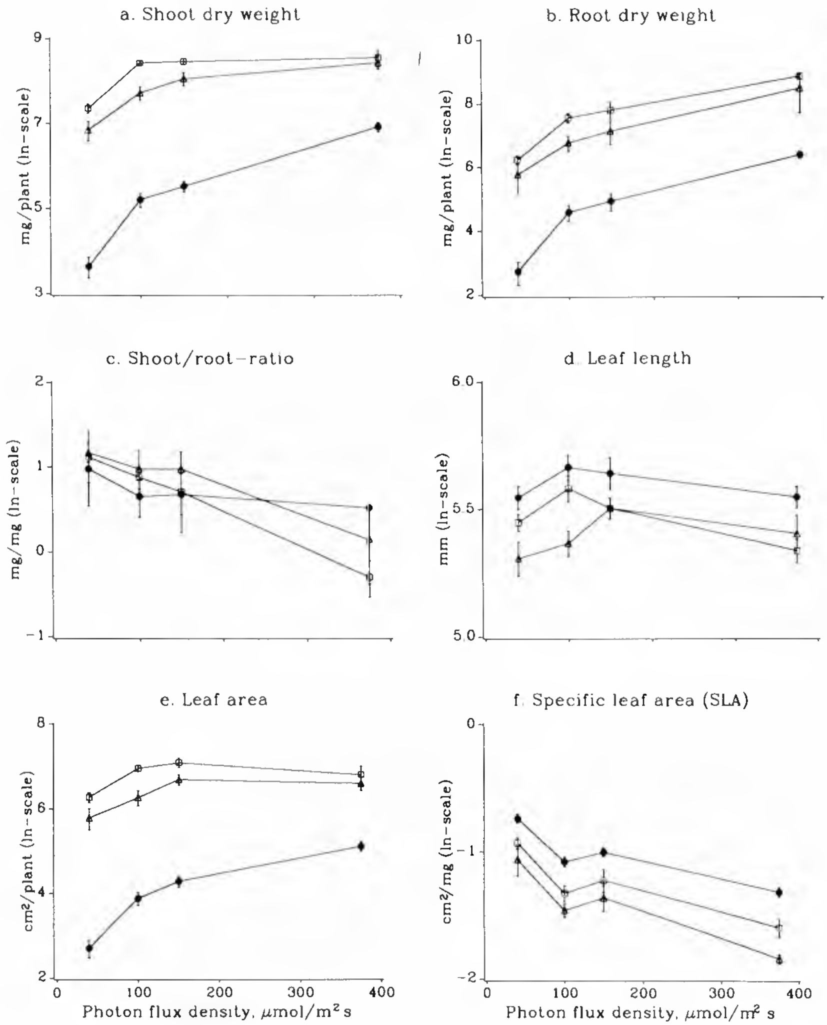


Figure 3. Effects of different photon flux densities on growth of *Phleum pratense* L. (-●-), *Rumex longifolius* DC. (-□- and T*araxacum officinale* (Web.) Marss. (-▵-). Bars indicate ± standard error of the mean

Another interesting question is whether it is possible to change the competition patterns by fertilization. Jeangros & Nösberger (1990) found that competition for N played a major role in the growth of *R. obtusifolius*, and that nitrogen fertilization favoured the establishment of the species. Dietl (1982) indicated that N fertilization would favour both *R. obtusifolius* and *T. officinale*. The present investigations showed limited effects of fertilization. This may be due to the dry conditions during two of the three growth periods. The higher level of N fertilization combined with shoot competition produced a reduced shoot and root dry weight in *T. officinale*. Simultaneously there was a considerable increase in SLA in both *T. officinale* and *R. longifolius*, indicating that these species compensated for inferior light conditions when the nitrogen supply was improved. These reactions were probably stimulated by the more vigorous growth of the grass sward.

Growing conditions may influence the effects of competition. In experiment 1 both of the spring periods were very dry, while the soil was kept close to field capacity during the third period. Although the soil moisture may be the main cause of different results between these periods, differences may also be attributed to other factors, for example changes in grass species composition after the first harvest. In *T. officinale*, the difference between shoot competition and no shoot competition reflected in shoot and root dry weights increased in period 3 compared with periods 1 and 2. This can be ascribed to a denser grass stand resulting from better water supply.

In conclusion, root competition seems to be the more important factor affecting establishment of *R. longifolius* and *T. officinale* in grassland. The morphological plasticity of the herbs makes them less vulnerable to shoot competition. From these investigations it seems difficult to control the two species by grassland management practices, because they are not sensitive to shoot competition. Shading may, however, reduce plant survival through reduced root dry weight and increased shoot/root ratio. Thus, to prevent establishment of these dicots in grass swards, gaps that reduce root competition should be avoided.

ACKNOWLEDGEMENTS

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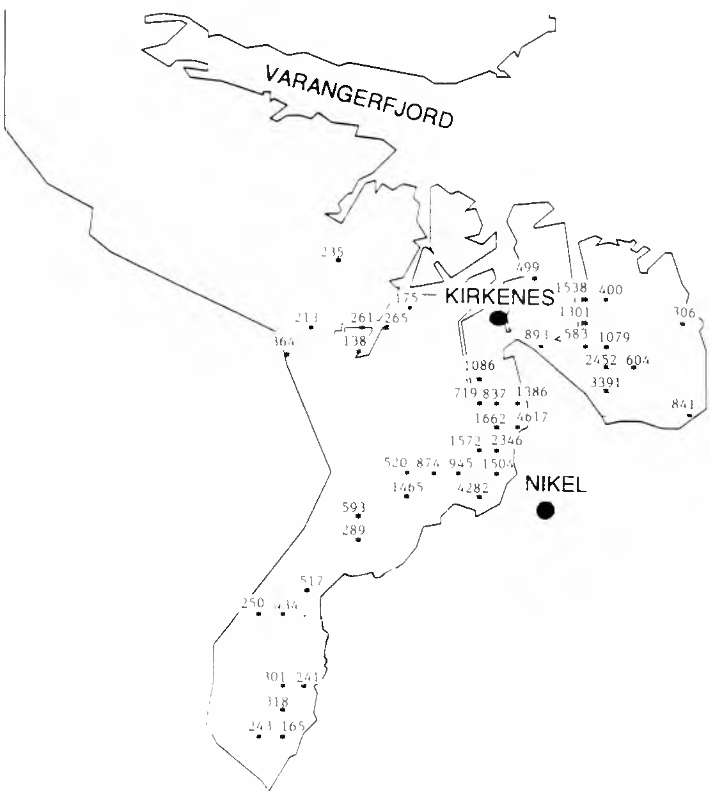
Correction

In the article "Methods of monitoring the effects of air pollution on forest and vegetation of eastern Finnmark, Norway", page 71-81, Vol. 1 1993 No. 1, the author is responsible for an error. The correct text to figure 10 is Copper (CU) instead of Nickel (Ni)

Fig. 10. Copper (Cu) in humus (μmol/kg) 1989



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