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Alkali-treated straw as feed for ruminants: Digestibility of treated straw in sheep and voluntary intake and growth of heifers fed on treated straw

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The objective of this study was to investigate how the nutritive value of cereal straw as feed for ruminants could be improved. Barley straw was treated with anhydrous ammonia and NaOH solution (dip treatment). The digestibility of NH_3-treated and dip-treated straw assessed by sheep was significantly increased compared with that of untreated straw. The low level of N content in the tested diet affects the intake of dip-treated straw as determined in grwing heifers. Supplementation of urea to the diet increases roughage intake.

Key words: Dip treatment of straw, heifers, NH_3, sheep and urea.

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Treatment of straw with an alkali solution such as sodium hydroxide calcium hydroxide, anhydrous ammonia, aqueous ammonia, or urea makes roughage as a feed for ruminants possible. Extensive studies on this subject have been carried out in recent years (Jackson 1977, Sundstøl 1988).

Improvement of the feeding value of roughage using NaOH solutions was first carried out by means of the Beckmann method. Since then, many modifications to this method have been made in order to avoid using large amounts of water for washing the straw, dry matter loss and environmental pollution (Wilson & Pigden 1964, Rexen et al. 1975). Sundstøl's (1981) dip treatment eliminated any pollution problems. Straw treated in this way has a digestibility similar to that treated by the Beckmann method. Ammonia treatment is one of the alternatives to NaOH treatment. Treatments with anhydrous or aqueous ammonia or urea have the advantage over other alkali treatments in that they increase the nitrogen content of the straw (Waiss et al. 1972, Sundstøl et al. 1978).

In present experiments both NaOH treatment of straw and anhydrous ammonia treatment of straw were studied as the main feeds for heifers and the digestibility of treated straw by sheep was evaluated.

MATERIALS AND METHODS

Preparation of alkali-treated straw

NH_3-treated straw (stack method)

After combine harvesting of the grains, barley straw was baled, stacked, and treated with anhydrous ammonia according to the stack method described by Sundstøl et al. (1978). The anhydrous ammonia was injected through a perforated metal pipe from a pressure tank containing anhydrous ammonia (30-50 kg anhydrous ammonia was used per ton of straw). The hole left when the pipe was withdraw was then taped.

NaOH-treated straw (dip treatment method)

The method of alkali treatment used, termed the «Dip treatment», is described by Sundstøl (1981). Dip treatment is a modified version of the original Beckmann method and follows these principles:

> Soaking of the straw in a solution of 15 g NaOH$\cdot$l^{-1}
> Time of soaking should be 30 min-1 h
> Time of dripping should be about 2 h
> Time of ripening should be 3 - 6 days

The solution of the NaOH lye was replenished by adding 6-6.5 kg NaOH per 100 kg straw treated.

Digestibility experiment with sheep

The digestion trial was conducted on 18 mature, male sheep using 6 sheep on each of the three types of straw: untreated straw, HN_3-treated straw and dip-treated straw. The trial comprised an 11-day preliminary period, and a 10-day total collection period. The sheep were given about 900 g dry matter (DM) of straw and in addition either 60 g herring meal or 15 g urea, 10 g salt and 10 g mineral mixture daily. The animals had free access to water throughout the trial. The sheep were fed twice a day at 07.30 and 14.30 with equal portions given at each feeding.

During the collection period, faeces and urine were quantitatively collected daily from each sheep.

Samples of feeds and excreta were prepared for chemical analysis of DM, ash, crude fibre (CF), crude protein (CP) and nitrogen-free extracts (NFE) by difference (AOAC 1980). Neutral detergent fibre (NDF), acid detergent fibre (ADF) and lignin were determined according to Goering & van Soest (1970).

Feeding trial with heifers

Twenty 11-18 month-old heifers, weighing 250-300 kg at the start, were used for the growth studies. The trial followed a 2^2 completely random factorial design and lasted for 159 days.

During a fourteen-day preliminary period all the animals were fed the same diet. At the end of the preliminary period the heifers were allotted to their treatment groups and then individually fed on experimental diets for the remaining 145 days with the following combination of feeds: treatments A_1, A_2, B_1 and B_2 (see Table 1). After 10 weeks of poor performance by the heifers on dip-treated straw, urea was added to the lye at 2.25% of straw weight in order to increase the N-intake of the B diets. During the entire experimental period straw was offered at a rate resulting in 10-15% refusals. Water was available at any time, and the consumption was recorded. All heifers received 100 g mineral and 20 g vitamin mixture daily.

The animals were weighed on two consecutive days every second week at 12.00. Concentrates and treated straw samples were taken regularly once a week for DM determination and chemical composition analysis.

Table 1. Feeding plan for heifers

	Roughage diet	
Supplements:	NH_3-treated straw (Ad lib)	Dip-treated straw (Ad lib)
1 kg concentrate + 0.1 kg herring meal	A_1	B_1
1.1 kg concentrate without herring meal	A_2	B_2

Table 2. The chemical composition of feeds used in digestion and N-balance studies in sheep

	Dry matter	Organic matter	Nx6.25	Ether extract	Crude fibre	NFE	Ash	NDF	ADF	Lignin
	$g \cdot kg^{-1}$	----------	----------	----------	$g \cdot kg^{-1}$	DM	----------	----------	----------	----------
Untreated straw	869	962	51	14	442	456	38	723	437	52
NH_3-treated straw	870	972	103	10	453	406	28	718	495	49
NaOH-treated straw	250	880	52	8	404	416	120	452	344	40
Herring meal	936	889	787	103	9		111			
Urea	974	100								

Blood samples were taken before the morning feeding on three occasions during the experimental feeding period: at the start, in the middle and at the end of the trial. The samples were analysed for Na, Ca, K, Mg and PO_4-P using an atomic absorption spectrophotometer (AOAC 1980).

Rumen samples were taken four times during the course of the experiment for pH and ammonia concentration determinations (Logsdon 1960) and volatile fatty acids (VFA) were determined by gas chromatography (PYE-Unicam GCD) using a glass column packed with Chromosorb 101, 60-80 mesh (Johns-Manville). The column temperature was 175°C and the carrier gas (N_2) flow rate was 75 ml/min. Detection was by hydrogen flame ionization and quantities were expressed as an integrator (HP3380A).

Statistical analysis of data was the analysis of the variance, using the general linear models (GLM), procedure of the statistical analysis system (SAS 1985).

RESULTS AND DISCUSSION

Digestibility with untreated straw, NH_3-treated straw and dip-treated straw diets supplemented with either urea or herring meal

Chemical composition of feed

For the digestibility and balance studies, untreated, NH_3-treated and dip-treated barley straw from the same batch were fed along with supplements of either urea or herring meal. The chemical composition of feeds is given in Table 2. (discussed later). Because of the added ammonia and NaOH, the N and ash content was higher for NH_3-treated and dip-treated straw, respectively, as compared with untreated straw. The reduction in NDF and ADF content due to dip treatment was greater than can be explained by the increased ash content.

Apparent digestibility of the diets

The apparent digestibility values (in vivo) for the three types of diets which contain various types of straw are given in Table 3. These are the values given obtained for the complete diets. The differences in digestibility of DM and organic matter (OM) between untreated, NH_3-treated and dip-treated straw are statistically significant ($p<0.05$). There was, however, no difference between urea and herring meal supplementation regarding its effect on ration or straw digestibility. DM and OM digestibilities were equally high in diets with urea and herring meal supplements. The mean digestibility coefficients for DM and OM were increased by 10 and 21 percentage units for NH_3-treated straw and dip-treated straw respectively as compared with untreated straw (Table 3).

Digestibility coefficients of crude protein (N x 6.25) for both untreated and NH_3-treated straw were significantly higher ($p<0.05$) than those for dip-treated straw, although there was no significant difference between untreated and NH_3-treated straw. The latter was better than the former by 4 percentage units. Treatment of straw with ammonia, unlike treatment of straw with sodium hydroxide (Table 3), increases both the nitrogen content and its digestibility. The values obtained in this study were similar to those reported by Orr et al. (1985). However, the lower digestibility of CP (N x 6.25) in the diets containing alkali-treated straw has been reported earlier (Garrett et al. 1974, Oji & Mowat 1977).

Table 3. Apparent digestibility of various compositions of the diets fed to sheep

Treatments		Dry matter	Organic matter	Nx6.25	Ether extract	Crude fibre	N.F.E.	N-balance
Untreated straw	Urea	$48.1^{c}\pm4.2$	$50.4^{c}\pm4.$	$62.7^{a}\pm5.8$	$49.9^{a}\pm6.3$	$55.8^{c}\pm5.4$	$48.5^{c}\pm2.4$	$-3.0^{b}\pm4.0$
	Herring meal	$48.6^{c}\pm1.9$	$51.3^{c}\pm1.7$	$59.8^{a}\pm2.5$	* $69.1^{a}\pm2.3$	$54.2^{c}\pm2.9$	$45.7^{c}\pm1.9$	$-1.8^{b}-0.8$
NH_3-treated straw	Urea	$58.3^{b}\pm1.4$	$61.8^{b}\pm1.4$	$67.2^{a}\pm1.2$	$43.2^{b}\pm9.6$	$71.0^{b}\pm1.6$	$55.0^{b}\pm1.6$	$2.3^{a}\pm3.3$
	Herring meal	$58.3^{b}\pm2.0$	$59.8^{b}\pm2.6$	$63.6^{a}\pm4.8$	* $61.5^{b}\pm1.8$	$70.4^{b}\pm1.4$	$50.1^{b}\pm5.4$	$3.8^{a}\pm2.19$
NaOH-treated straw	Urea	$68.8^{a}\pm1.1$	$69.8^{a}\pm1.1$	$58.2^{b}\pm1.2$	$33.0^{b}\pm3.6$	$83.5^{a}\pm1.5$	$64.1^{a}\pm1.5$	$1.1^{a}\pm0.6$
	Herring meal	$70.1^{a}\pm1.1$	$71.3^{a}\pm1.7$	$55.5^{b}\pm4.0$	* $64.5^{b}\pm4.7$	* $88.5^{a}\pm1.7$	$58.9^{a}\pm1.6$	* $2.57^{a}\pm0.5$

Differences between means with the same superscripts (a, b, c or none) are not significantly different ($P > 0.05$). Significant differences within straw treatments are indicated by asterisks.

Digestibility of ether extract of untreated straw was significantly different from both NH_3-treated and dip-treated straws ($p<0.05$). This result differs from that reported by Wanapat et al. (1985), where digestibility of ether extract was found to be 41% and 36% for NH_3-treated and NaOH-treated straw, respectively, which was higher than that for untreated straw (25.4%). Within each treatment of straw, digestibility of ether extract in the herring meal group was superior to that in the urea group ($p<0.05$). This is perhaps because of the substantial amount of highly digestible ether extract in the her ring meal itself.

Obviously, digestibilities of CF and NFE were statistically significantly different ($p<0.05$) among the three treatments of straw. Supplements of urea ver sus herring meal apparently had no significant effect on straw digestibilities except in dip-treated straw, where CF was positively affected and NFE negatively affected by herring meal supplementation ($p<0.05$). It should be borne in mind, however, that NFE is estimated by difference.

N-balance was significantly lower ($p<0.05$) for untreated straw than for both NH_3- and dip-treated straw. No significant differences were shown between urea and herring meal groups for untreated and NH_3-treated straw, but for dip-treated straw a positive effect of herring meal was observed ($p<0.05$).

Growth study in heifers on diets based on straw treated with either ammonia (NH_3) or NaOH (dip-treated) with and without extra protein (nitrogen) supplement

Chemical composition of feed

The chemical compositions of NH_3-treated straw, dip-treated straw and concentrates are given in Table 4. It was decided that urea should be added to the lye in order to increase the N-content of the dip-treated straw; this was because of the poor intake and growth on dip-treated straw with concentrates without herring meal. The amount applied was estimated as being commensurate with the amount of N in NH_3-treated straw at a similar intake of straw DM. As indicated in Table 4, the protein content (N x 6.25) in DM of dip-treated straw was thus raised from 4.8% in feed offered during period 1 to 12.5% in feed offered during period 2, as

Table 4. Chemical composition of the different treatments of straw and concentrates

	Dry matter	Organic matter	Crude protein (Nx6.25)	Ether extract	Crude fibre	NFE	Ash	NDF	ADF	Lignin
	$g \cdot kg^{-1}$	----------	----------	----------	$g \cdot kg^{-1}$	DM	----------	----------	----------	----------
NH_3-treated straw	755	966	115	14	481	356	34	782	554	70
NaOH-treated straw (Period 1 without urea)	255	866	48	10	437	371	134	651	506	88
NaOH-treated straw (Period 2 with urea)	248	870	125	12	434	300	130	652	478	75
Concentrate with 10% herring meal	898	947	168	47	61	668	57	404	70	29
Concentrate without herring meal	900	946	108	50	61	727	54	656	23	37

compared with 11.5% in NH_3-treated straw DM.

As expected, the ash content was lower and the fibre content somewhat higher for NH_3-treated straw than for dip-treated straw. The chemical composition of untreated, NH_3-treated and dip-treated barley straw in this study (Tables 2 and 4) was similar to that obtained in other studies with the same treatment (Wanapat et al. 1985). The Maillard reaction phenomenon was observed in this study (Buettner 1978, Saenger et al. 1982).

DM content of straw depends largely on the water content at harvest, storage conditions and treatment. The barley straw used in this study was harvested in mid-September. Straw for NH_3 treatment was prepared directly from the field after harvesting, using the «stack method». Both untreated straw and straw for dip treatment were baled just after harvesting, then barn-dried and stored inside for more than 8 weeks prior to the start of the growth study.

CP content (here defined as N x 6.25) of NH_3-treated straw in these studies, as in the experiments conducted by Garrett et al. (1979), was increased to twice that of untreated straw. When urea was added to the NaOH lye during period 2, the crude protein content was increased to more than twice that of dip-treated straw without urea (Table 4). However, the availability of added urea is not known.

It has been suggested that about 50% of the nitrogen increase can be accounted for as ammonia-N, with the remaining 50% in some more tightly bound form (Waiss et al. 1972, Solaimen et al. 1979). NaOH treatment apparently affected CF content, while NH_3 treatment did not (Tables 2 and 4). Both types of treatment reduced the NDF content, and the ADF content tended to be lower after NaOH treatment than after NH_3 treatment, and similar to the results reported by Orr et al. (1985) and Wanapat et al. (1985).

Feed intake of heifers

Treated straws were offered ad libitum throughout the experiment and supplemented with restricted amounts of concentrate, minerals and vitamins. The experimental period of 145 days was divided into two phases, period 1 comprising the first 67 days and period 2 the subsequent 71 days and a transition period of 7 days. The only treatment difference was the addition of urea to the NaOH lye for the dip treatment in period 2. Values for the mean live weight of the animals together with feed intake are given in Table 5, respectively.

The animals consumed all concentrates offered throughout the experiment. During period 1, intake of straw DM was significantly higher for NH_3-treated straw than for dip-treated straw. Also, herring meal supplements significantly improved the intake by about 20% for the latter type of straw. During period 2, the roughage intake was generally higher, particularly for dip-treated straw. Thus, during this period no significant differences were observed in straw DM intake between treatments. The great improvement in straw intake for NaOH diets during period 2 may be attributable to increased N-intake. Improved ad libitum intake of straw after NH_3 and NaOH treatments as observed in the present study is in agreement with reports by Homb (1948) and Sundstøl (1981). Thus, both the treatments applied seem generally to improve ad libitum feed intake of low quality roughage in cattle. In the present study (period 1), the DM intake of NH_3-treated straw was significantly higher than that of dip-treated straw in spite of the higher digestibility of the latter. Inclusion of 100 g herring meal in the concentrates did not influence the intake of NH_3-treated straw, but improved the intake of dip-treated straw by 15-20%.

When urea was added to the NaOH lye, the difference in intake between NH_3-treated and dip-treated straw evened out. The highest intake was obtained for dip-treated straw supplemented with

Table 5. Live weight and ad lib intake of treated straws of heifers (±SD)

	NH_3-treated straw		Dip-treated straw	
	Conc.with 10% herring meal	Conc.without herring meal	Conc.with 10% herring meal	Conc.without herring meal
Period 1 (67 days)				
Mean live weight (kg)	347.2±38.5	336.9±25.2	325.4±25.6	319.5±30.4
Feed intake:				
straw DM kg/d,	4.8^{a}	4.9^{a}	3.8^{b}	3.1^{c}
straw DM g/kg.$W^{0.75}$	60.6^{a}	62.1^{a}	49.6^{b}	41.0^{c}
dietary CP (N*6.25), g/d	718	664	349	256
Period 2 (71 days)				
Mean live weight (kg)	390.2±40.9	367.1±26.4	364.5±27.3	348.5±33.0
Feed intake:				
straw DM kg/d,	5.8	5.6	6.0	5.4
straw DM g/kg.$W^{0.75}$	66.1	67.0	71.9	66.9
dietary CP (N*6.25), g/d	823	750	915	888

Superscript see Table 3.

Table 6. Mean live weight gain of heifers

	NH_3-treated straw	Dip-treated straw
Period 1 (67 days) $g \cdot d^{-1}$:		without urea
Conc. with 10% herring meal	628	31
Conc. without herring meal	372	-216
Period 2 (71 days) $g \cdot d^{-1}$:		with urea
Conc. with 10% herring meal	611^{b}	809^{a}
Conc. without herring meal	489^{c}	733^{a}

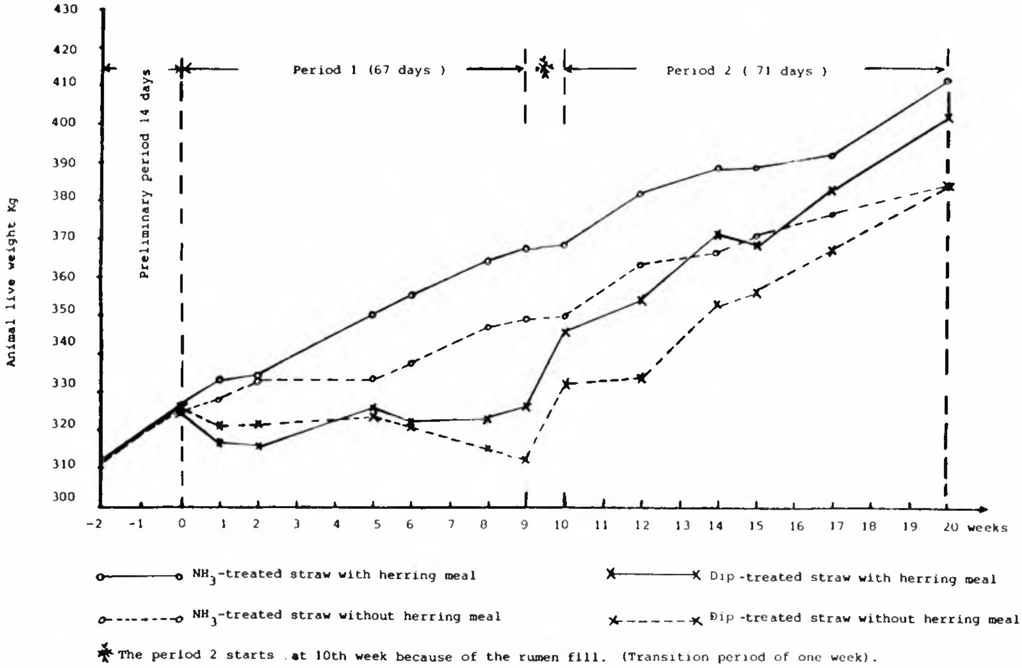
Superscript see Table 3.

either urea or herring meal. These results concur with those obtained by Borhami et al. (1983), who showed that supplementation of urea improved digestibility of NaOH-treated straw in lambs, and with Deschard et al. (1988), who showed that both the intake and live weight gain of steers were increased by NaOH-ensiled wheat plus urea. In the present study there is very good agreement between rumen ammonia concentration and ad libitum straw intake, which again underlines the importance of an adequate supply of soluble protein (nitrogen) for high intake and favourable utilization of treated straw. Also, the result indicates that NPN sources like urea may be an effective N-source in such diets.

Live weight gain of heifers

The mean daily live weight gain for the various treatment groups and periods of the growth study are given in Table 6 and the corresponding curves for live weights are given in Figure 1. During period 1, live weight gain was best for the animals on NH_3-treated straw supplemented with concentrates with 10% herring meal. The animals on this treatment gained significantly better than the heifers on the other treatments. During this period the animals on dip-treated straw performed

Fig. 1. Live weight of experimental heifers during the growth study



rather poorly, particularly those supplemented with low protein concentrates, which caused a considerable loss in body weight. Thus, for period 1, significant differences in live weight gain were observed between both straw treatments and concentrate supplements.

Judging from the low rumen ammonia content in the animals fed on dip-treated straw during period 1, the poor performance following low feed intake in these treatment groups may be attributable to shortage of soluble nitrogen available for the rumen microbes.

Such an indication is strengthened by the fact that when urea was added during period 2, both feed intake and daily weight gain improved for the NaOH-fed animals. In fact, during period 2 the animals on dip-treated straw had a rather high level of live weight gain that was significantly higher than that of the animals on NH_3-treated straw, irrespective of type of concentrate supplement given. Live weight gains obtained in animals fed on NH_3-treated straw were quite satisfactory and in line with results obtained by Matre (1978). The live weight gain on dip-treated straw with urea during period 2 was extremely high and much better than that reported by Koers et al. (1969) and Kategile & Frederiksen (1979). Arnason (1980), on the other hand, reported that even higher daily weight gain was obtained with bulls fed on 2.1-2.3 kg concentrates in addition to straw ad libitum. The results indicate that a satisfactory performance may be obtained in young cattle on diets based on either ammonia- or NaOH-treated straw supplemented with moderate amounts of concentrate. Although, not included in the heifer studies, both the sheep studies and studies reported elsewhere (Horton 1978, Sundstøl & Matre 1980) indicate that the improved performance of treated straw may be due to a combination of improved intake and increased energy values after treatment.

Table 7. Mean water consumption of heifers

	NH$_3$-treated straw			Dip-treated straw		
	Drinking water kg·d^{-1}	Water in feeds kg·d^{-1}	Water kg·kg^{-1} feed DM	Drinking water kg·d^{-1}	Water in feeds kg·d^{-1}	Water kg kg^{-1} feed DM
Period 1				(	without urea	)
Conc. with 10% herring meal	19.6	1.7	4.4	15.0	11.1	7.1
Conc. without herring meal	19.6	1.7	4.4	14.0	9.2	7.5
Period 2				(	with urea	)
Conc. with 10% herring meal	23.7	2.0	4.5	24.6	17.7	7.3
Conc. without herring meal	23.5	1.9	4.6	27.9	15.9	8.4

Water intake of heifers

The animals were given free access to water throughout the experimental period. The consumption was measured for each pen (5 animals) and the results are given in Table 7. During period 2, consumption increased, apparently as a result of increased feed consumption. Water consumption per kg of feed DM intake was similar for treatment groups within each of the two methods of straw treatments. However, the animals on dip-treated straw consumed on average 65-70% more total water per kg DM consumed for the two periods. Thus, NaOH treatment apparently led to increased water consumption because of the excess sodium which has to be excreted.

Effect of diets on rumen ammonia-N and pH

During periods 1 and 2 rumen samples were taken by stomach tubes approximately one hour after the morning and one hour before the afternoon feeding of concentrates. The samples were subject to ammonia and pH analyses. Results are given in Table 8. Rumen pH was normal for all diets and much the same for the morning and afternoon samples, with no significant difference between treatments. Ammonia concentration, on the other hand, was generally lowest for the afternoon sample during period 2. For dip-treated straw, the rumen NH$_3$-N concentration was extremely low for all samples during period 1 and significantly lower than for NH$_3$-treated straw irrespective of concentrate supplement. Satter & Slyter (1974) indicated that rumen microbial synthesis may be related to the available nitrogen, with synthesis at a concentration of rumen ammonia between 5 and 8 mg per 100 ml rumen liquor. Urea application to the NaOH lye raised not only the N content of the subsequent straw (Table 4) but also significantly increased the rumen NH$_3$-N content (Table 8). As already indicated, the improved N supply may explain the difference in straw intake and live weight gain between periods 1 and 2 for these treatment groups. In the present study, there was good agreement between rumen ammonia concentration and ad libitum straw intake, which underlines the importance of an adequate supply of soluble protein (nitrogen) for high intake and favourable utilization of treated straw. Also, the result indicates that the sources like urea may be an effective N source in such diets.

Blood plasma mineral status of heifers

In order to check the mineral status of the experimental animals, blood samples were taken three times during the course of the study: prior to start, at 8 weeks (period 1) and at 14 weeks (period 2). The results are given in Table 9. All blood

Table 8. Ammonia-N concentration and pH in rumen liquor of heifers (±SD)

	Morning sampling		Afternoon sampling	
	pH	NH_3-N mg.100ml^{-1}	pH	NH_3-N mg.100ml^{-1}
Period 1				
NH_3-treated straw				
Conc. with 10% herring meal	6.9±0.1	9.9±2.6	7.0±0.1	9.4±1.6
Conc. without herring meal	6.9±0.2	10.7±2.7	7.0±0.2	9.9±2.8
Dip-treated straw without urea				
Conc. with 10% herring meal	7.2±0.2	0.6±0.3	7.2±0.1	1.1±0.5
Conc. without herring meal	7.4±0.3	0.6±0.3	7.4±0.0	0.5±0.3
Period 2				
NH_3-treated straw				
Conc. with 10% herring meal	7.1±0.2	13.7±3.8	7.0±0.2	10.5±1.4
Conc. without herring meal	7.0±0.2	18.7±5.7	6.8±0.2	9.8±2.3
Dip-treated straw with urea				
Conc. with 10% herring meal	7.3±0.1	12.7±3.0	7.2±0.1	9.1±3.3
Conc. without herring meal	7.3±0.2	11.4±3.3	7.4±0.1	6.0±1.5

plasma mineral concentrations were within the normal range, with no significant differences between treatments. Blood plasma analysis of Ca, Ma, Na, K and P (Table 9) indicated normal values were similar for all treatment groups throughout the experimental period of 4½ months (Table 9).

It may be concluded that throughout the experimental period all animals used in this study remained in very good health. However, the intake of Na on NaOH-treated diets was high.

Excessive amounts of Na are excreted in the urine (Nelson et al. 1955). Arnason (1980) fed young bulls on NaOH-treated straw and observed health problems after about two weeks. The animals developed diarrhoea and did not thrive. Furthermore, the blood serum concentration of P and Mg became significantly reduced below normal level. On the other hand, Kristensen (1984) carried out a long-term experiment with heifers fed on NaOH-treated straw as the only roughage from the beginning of the first pregnancy until the third lactation. No clinical health problems were observed. Of the 20 heifers used in the present study 14 were inseminated during the course of the experiment. Conception rates were good, with only one animal on NH_3-treated straw without herring meal and one animal on dip-treated straw with herring meal not conceiving after the first insemination.

SUMMARY

The stack method of NH_3-treated barley straw (30 kg anhydrous ammonia per ton of straw) and the dip treatment method of NaOH-treated straw (1.5% NaOH solution) were carried out in digestibility experiments with sheep and feeding trials with heifers.

Table 9. Mineral concentration in blood plasma of heifers (±SD)

	NH$_3$-treated straw		Dip-treated straw	
	Conc.with 10% herring meal	Conc.without herring meal	Conc.with 10% herring meal	Conc.without herring meal
Calcium mmol·l^{-1}	(normal values 2.3 - 3.9)			
Pre-experiment	2.65±0.2	2.47±0.1	2.61±0.3	2.50±0.1
8 weeks	2.66±0.1	2.61±0.1	2.57±0.2	2.72±0.4
14 weeks	2.46±0.1	2.40±0.1	2.44±0.2	2.37±0.0
Magnesium mmol·l^{-1}	(normal values 0.6 - 1.2)			
Pre-experiment	0.88±0.1	0.78±0.1	0.86±0.1	0.90±0.1
8 weeks	0.94±0.1	0.88±0.1	0.92±0.1	0.95±0.1
14 weeks	0.94±0.1	0.84±0.0	0.86±0.1	0.89±0.1
Potassium mmol·l^{-1}	(normal values 4.1 - 5.6)			
Pre-experiment	4.15±0.1	3.99±0.3	4.10±0.1	3.83±0.2
8 weeks	4.40±0.2	4.50±0.2	4.50±0.4	4.10±0.5
14 weeks	4.20±0.4	4.09±0.3	3.98±0.3	3.60±0.5
Sodium mmol·l^{-1}	(normal values 131 -157)			
Pre-experiment	150±14.4	153±5.1	151±16.9	153±1.8
8 weeks	156±3.4	158±10.8	160±11.8	147±10.7
14 weeks	142±14.6	144±10.5	147±13.3	143±9.9
PO$_4$-P mmol·l^{-1}	(normal values 1.3 -2.3)			
Pre-experiment	1.96±0.1	2.01±0.1	2.01±0.2	1.9±0.3
8 weeks	1.65±0.3	1.69±0.1	1.84±0.1	1.7±0.1
14 weeks	1.68±0.3	1.77±0.0	1.83±0.2	1.8±0.3

Anhydrous ammonia increased the CP content (N x 6.25) of treated straw from 51 to 103-115 g/kg DM. Ash content of dip-treated straw was raised from 38 to 120-130 g/kg DM due to NaOH treatment. Both treatments decreased the cell wall content (NDF) of straw, especially the treatment with NaOH. The digestibility of untreated, NH$_3$-treated and dip-treated straw supplemented with either urea or herring meal was determined in 18 mature wethers at a maintenance level of feeding. The digestibility of DM and OM was significantly increased by 10 percentage units for NH$_3$-treated straw and by 20 percentage units for dip-treated straw when compared with untreated straw.

There was apparently no difference between urea and herring meal supplements as to the effect on straw digestibility.

Twenty 11 to 18-month-old heifers weighing 250-300 kg at the start were used. The heifers were allotted to four diet groups and were fed individually for 145 days after a 14-day preliminary period. The four diets were as follows:

A1: NH$_3$-treated straw ad libitum + 1 kg concentrate + 0.1 kg herring meal.
A2: NH$_3$-treated straw ad libitum + 1.1 kg concentrate.
B1: Dip-treated straw ad libitum + 1 kg concentrate + 0.1 kg herring meal.
B2: Dip-treated straw ad libitum + 1.1 kg concentrate.

After 10 weeks (period 1) with poor performance in the heifers fed on dip-treated straw, urea was added to the lye at 2.25% of straw weight in order to increase N-intake of the B diets during period 2.

Straw DM intake (g/kg $W^{0.75}$) of heifers fed on NH_3-treated straw in period 1 was significantly higher than that of heifers fed dip-treated straw ($p<0.05$), 60.6, 62.1, 49.6 and 41.0 for treatments A1, A2, B1 and B2, respectively. The DM intake in period 2 was not significantly different between either treated straw or supplementation, 66.1, 67.0, 71.9 and 66.9 for treatments A1, A2, B1 and B2 respectively. Live weight gain in period 1 was significantly different for all treatments ($P<0.05$), 628, 372, 31 and -216 g/d for A1, A2, B1 and B2, respectively. In period 2 the corresponding figures were 611, 489, 809, and 733 g/d, the difference between straw treatments being significant ($p<0.05$).

Rumen pH was normal for all diets and with non-significant difference. The rumen NH_3-N concentration for heifers fed on dip-treated straw in period 1 was extremely low (0.5-1.1 mg NH_3-N/100ml). Adding urea to the lye in period 2 not only raised the N content of the straw but also significantly increased the rumen NH_3-N content.

The concentrations of Ca, Mg, K, Na and PO_4-P in blood plasma were within the normal range in all diets throughout the experiment.

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Dip-treated straw supplemented with urea or soybean meal as feed for heifers

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Xu, S. & Å.T.Randby, 1991. Dip-treated straw supplemented with urea or soybean meal as feed for heifers. Norwegian Journal of Agricultural Sciences 5: 123-129. ISBN 0801-5341.

A comparative study was conducted with 15 heifers fed on grass silage and dip-treated straw supplemented with urea or soybean meal. The daily gains (g/d) of the heifers were 990, 800 and 930 for animals fed on grass silage, dip-treated straw with urea and dip-treated straw with soybean meal, respectively. The magnesium concentration (mmol/l) in blood plasma was lower when the heifers were fed dip-treated straw with either urea or soybean meal as compared with that when grass silage was used as feed.

Key words: Dip-treated straw, grass silage, heifers, urea

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Studies on dip treatment of straw with NaOH have been going on for more than 10 years (Sundstøl et al. 1979). Less water is required with this method, less organic matter is lost and less pollution is caused compared with the traditional Beckmann method. Since straw has a very low crude protein content (N*6.25), urea is used for increasing the N content of dip-treated straw. Satisfactory results have been obtained in experiments where dip-treated straw constituted the main part of the diet for heifers (Randby & Mo 1983), bulls (Xu et al. 1991) and milking cows (Randby & Xu 1988).

In the present experiment the effects of a combination of grass silage and dip-treated straw supplemented with either urea or soybean meal on rumen fermentation, blood composition and growth rate of heifers were compared with the effects when the heifers were fed only grass silage and 1 kg barley meal.

MATERIALS AND METHODS

Dip-treated barley straw in this experiment was prepared as described by Sundstøl (1981). The principles were:

Soaking straw in a solution of 15 g NaOH/l.
Time of soaking, 0.5-1 hour.
Time of ripening, 3-6 days.

The solution of the NaOH lye was replenished by adding 6-6.5 kg NaOH per 100 kg straw.

Four steel vessels (275 * 140 * 165 cm) were used, two for dip-treated straw with urea (A), the other two for dip-treated straw without urea (B). The solution in vessel A was replenished at the rate of 7.1 kg NaOH, 3.4 kg urea and 0.5 kg Na_2SO_4 (Silva and Ørskov 1988) per 100 kg dry straw treated. The mean concentration of the NaOH solution throughout the experiment was 14.8 g NaOH, 12.5 g urea and 2.1 g Na_2SO_4 per litre. The solution in vessel B was renewed at the rate of 6.5 kg NaOH per 100 kg dry straw and the mean concentration was 14.9 g NaOH per litre.

The silage used in this study was prepared in 1986 from perennial grasses and the botanical analysis showed 26% cocksfoot (*Dactylis glomerata*), 26% (*Agropyron repens*), 20% smooth meadow grass (*Poa pratensis*), 13% red top (*Agrotis tenuis*), 12% timothy (*Phleum pratense*) and 3% meadow fescue grass (*Festuca pratensis*).

Fifteen 14 to 17 month-old heifers, weighing about 340 kg at the start, were divided into three groups on the basis of live weight. The experiment lasted for 13 weeks, the first three weeks constituting a preliminary period when all the heifers were fed the same diet followed by a two-week transition period and an eight-week experimental period when the following three treatments were compared:

Group 1 : 6.3 kg DM grass silage + 1 kg barley meal.
Group 2 : 4.7 kg DM dip-treated straw with 208 g urea + 2.1 kg DM silage + 1 kg barley meal.
Group 3 : 4.7 kg DM dip-treated straw without urea + 2.1 kg DM silage + 1 kg soybean meal.

Both concentrates and roughages were fed in restricted amounts throughout the experiment. Diets were formulated so as to be nearly isonitrogenous for the three groups. Seventy-five grams vitamin-mineral mixture (Vita-Mineral) were given to all heifers daily. All animals were equipped with an electronic collar and placed in three pens with electronic doors to allow individual feeding. Water was available at any time. Feed offered and any feed residues were recorded daily.

Dry matter (DM) content of the roughages was determined every week in order to adjust the amount of feed according to the plan. The rest of the sample was frozen for later determination of DM, ash, crude fibre (CF), crude protein (CP), and nitrogen-free extracts (NFE) by difference (AOAC, 1980). The heifers were weighed five times on three consecutive days at 12.00 throughout the experiment. Blood samples for the analysis of Na, K, Ca and Mg concentrations (AOAC 1980) were taken through the jugular vein in heparinized tubes on three occasions, (three hours after morning feeding), once in the preliminary period and twice in the experimental period. The samples were analysed by atomic absorption spectrophotometer. The concentrations of urea in the blood plasma were determined as described by Kapalan (1987). Samples of rumen liquor were collected three times on two consecutive days by means of a vacuum pump via a stomach tube. The first part of the sample was discarded. pH was measured using a pH meter immediately after sampling. Ammonia-N of the rumen liquor preserved with formic acid was determined by automated colorimetric indophenol reaction (Logsdon 1960) and the level of volatile fatty acids (VFA) was determined by gas chromatography (PYE-Unicam GCD), using a glass column packed with Chromosorb 101, 60-80 mesh (Johns-Manville). The column temperature was 175°C and the carrier gas (N_2) flow rate was 75 ml/min. Detection was by hydrogen flame ionization and quantities were expressed at an integrator (HP3380A). Statistical treatment of data followed the procedure for analysis of variance (MSTAT 1984). The components of blood and rumen liquor in the experimental

Table 1. Chemical compositions of the feeds

	Grass silage	Dip-treated straw with urea	Dip-treated straw without urea	Barley meal	Soybean meal
Dry matter %	23.9	26.7	26.1	87.2	89.7
pH	3.93				
NH3-N,% of total N	3.9				
Formic acid,%	0.23				
Propionic acid,%	0.01				
Lactic acid,%	1.37				
Acetic acid,%	0.37				
Butyric acid,%	0.00				
In DM g/kg:					
Ash	59	154	152	24	62
N * 6.25	183	155	60	130	501
Ether extract	61	15	14	20	16
Crude fibre	291	342	361	54	64
NFE	407	413[1)]	413	772	357

1) NFE = Nitrogen free extract same as for straw without urea

Table 2. Feed intake and live weight gain of heifers fed grass silage and dip-treated straw with urea or soybean meal (56 days, ±SD)

	Grass silage	Dip-treated straw with urea	Dip-treated straw with soybean meal
DM intake (kg/d):			
Silage	6.1	2.1	2.1
Dip-treated straw		4.5	4.6
Barley meal	0.92	0.92	
Soybean meal			0.95
Total DM intake, kg/d	7.0	7.5	7.7
DM intake, g/kg.$W^{0.75}$	83.4	90.4	91.0
Live weight (kg):			
Initial weight	340±34	340±36	345±41
Final weight	395±42	384±36	397±48
Daily gain, g/d	990±230	800±200	930±130

period were corrected by means of the data in the preliminary period using covariance analysis.

RESULTS

The chemical composition values for silage, dip-treated straw with or without urea, barley meal and soybean meal are presented in Table 1.

The values for the DM content of silage in Table 1 are the means of first cut (mid-June) and second cut grass (mid-August). The fermentation quality of grass silage was good (Breirem & Homb 1970). As urea was mixed into the NaOH solution of vessel A, the protein equivalent (N*6.25) content of the treated straw was more than double that of treated straw without urea. The barley straw used in this experiment was harvested in September 1986 and stored in an air-dried barn. The quality of original straw was good. Feed consumption and live weight gain of the heifers are given in Table 2.

Table 3. The pH, ammonia-N and VFA concentrations in rumen liquor of heifers fed silage and dip-treated straw with urea or soybean meal

		Grass silage	Dip-treated straw with urea	Dip-treated straw with soybean meal
pH		6.9	6.7	6.7
Ammonia-N	mmol/l	15.8	15.7	17.9
Total VFA	mmol/l	91.0	100.4	100.1
Individual VFA, Mol%:				
Acetic acid		61.5	64.8	61.0
Propionic acid		20.5	18.6	20.3
Isobutyric acid		1.2a	0.7c	0.9b
Butyric acid		12.9	13.4	15.4
Isovaleric acid		2.2a	1.4b	1.5b
Valeric acid		1.6a	0.9b	1.2b

Means with the same superscript are not significantly different ($P<0.05$)

At the beginning of the experiment 3.8 kg urea per 100 kg straw was used, but intake of treated straw with urea soon decreased because of lower palatability. The amount of urea was then reduced to 3.0 kg per 100 kg straw. The mean urea consumption by the heifers in Group 2 was approximately 141 g/d. The DM intake (g/kg.$W^{0.75}$) was slightly higher for the animals fed on treated straw than for the silage fed animals. There was no statistically significant difference in daily gain between the groups. The heifers fed silage or dip-treated straw supplemented with soybean meal had higher growth rates than those fed dip-treated straw with urea. The pH, ammonia-N content and VFA of rumen liquor are given in Table 3.

The pH of rumen liquor was not affected by feed ration. The ammonia-N content in the rumen liquor of heifers fed dip- treated straw with urea was as high as that of heifers fed silage, while heifers fed dip-treated straw supplemented with soybean meal had a slightly higher content of ammonia-N. There was no significant difference in total amount of VFA between groups. The silage fed heifers had a higher content of isobutyric acid, isovaleric acid and valeric acid than those fed dip-treated straw ($p < 0.05$).

The concentrations of urea and certain minerals in the blood plasma of the heifers fed on the different diets are presented in Table 4. The urea content in blood plasma was higher for the silage fed group than that for the groups fed dip-treated straw ($p < 0.05$). The blood magnesium concentration was lower when the heifers were given dip-treated straw than when they were given silage ($p < 0.05$). There were no health problems during the experiment.

Table 4. The concentrations of urea and certain minerals in blood plasma (mmol/l)

	Grass silage	Dip-treated straw with urea	Dip-treated straw soybean meal
Urea	5.09a	3.92b	4.13b
Calcium	2.54	2.58	2.49
Magnesium	0.92a	0.78b	0.77b
Potassium	3.96	3.94	3.99
Sodium	139	144	142

Superscripts see Table 3

DISCUSSION

Urea mixed into the NaOH solution increased the CP content (N*6.25) of dip-treated straw (Xu 1986). Ash content of dip-treated straw was also increased as a result of the NaOH added (Sundstøl & Wanapat 1983). The heifers were fed the same amounts of estimated net energy (fattening feed units, FFU) and CP (N*6.25) in the present study. The average daily consumption levels of FFU and CP were 5.42 and 1.23 kg for the silage fed group, 5.44 and 1.20, and 5.46 and 1.14 kg for the heifers fed dip-treated straw supplemented with urea and soybean meal, respectively. The average daily gains of the animals fed silage or dip-treated straw plus soybean meal were superior to those of animals fed dip-treated straw supplemented with urea. However, if a daily gain of about 600 g for dairy heifers is recommended (Kristensen 1984), treated straw can be used as the essential roughage in the diet and urea can be substituted for an expensive protein source, like the soybean meal used in this experiment.

Straw treated with NaOH did not alter the pH of rumen liquor in this experiment. In other words, ruminal pH remained almost constant although animals were fed a large proportion of NaOH-treated straw. Sundstøl (1981) reported that straw per se neutralizes the NaOH, and after eight days of ripening, dip-treated straw was entirely neutralized, but the sodium content remained unchanged.

The ruminal pH was slightly higher for the silage fed heifers (Table 3) than for the heifers in the treated straw groups. This may be due to the lower concentration of VFA (Mullen 1973). As a result of feeding isonitrogenous diets the ammonia-N concentration in the rumen liquor did not differ significantly in spite of different sources of nitrogen. This does not necessarily mean that ammonia-N was utilized at the same level by the animals. Davis & Stallcup (1967) showed that ammonia-N in rumen liquor from steers fed a urea supplemented diet was higher than that of animals fed a soybean meal supplemented diet. The amount of protein N in the rumen liquor, however, was the opposite.

Compared with most other N-sources, feed urea is rapidly hydrolysed in the rumen into ammonia, which may be used for microbial protein synthesis or absorbed across the rumen wall and resynthesized into urea in the liver. Saxena et al. (1971) found a lower urea concentration in the blood when feeding NaOH-treated oat straw (1.5% w/v solution) with urea compared with untreated straw supplemented with urea. They suggested that the alkali treatment probably increased the rate of energy release from straw, which in turn improved the N utilization by the rumen microbes. The lower urea concentration in the blood from heifers fed dip-treated straw with urea as compared to that of the silage fed heifers in this experiment (Table 4) was probably due to the peak of urea concentration in the blood for heifers fed treated straw with urea being reached before sampling, whereas the peaks for soybean meal or silage fed animals occurred later.

Magnesium in blood plasma is the only mineral that shows any significant difference between heifers fed silage and those fed dip-treated straw (Table 4). This phenomenon has been noted in many other experiments (Moseley & Jones 1974, Arnason 1980, Randby & Xu 1988). O'Connor et al. (1988) reported that as Na increases in the diet, renal fractional excretion of Mg increases, and vice versa. Mg supplementation should therefore attract special attention when animals are fed NaOH-treated roughages.

SUMMARY

The experiment was conducted with fifteen, 14 to 17-month-old heifers, weighing about 340 kg at the start. The three feed rations compared were:

Group 1. Grass silage (6.1 kg DM) + 1 kg barley meal.

Group 2. Dip-treated straw with urea (4.5 kg DM) + grass silage (2.1 kg DM) + 1 kg barley meal.
Group 3. Dip-treated straw (4.6 kg DM) + grass silage (2.1 kg DM) + 1 kg soybean meal.

The average values for DM content of silage, dip-treated straw with urea and dip-treated straw were 23.9%, 26.7% and 26.1% respectively; respective values for CP (N*6.25) content were 18.3%, 15.5% and 6%.

The daily gains (g/d) of heifers fed silage, dip-treated straw with urea and dip-treated straw with soybean meal were 990, 800, and 930 respectively. The ruminal pH was not influenced by the diets. The ammonia-N concentration (mmol/l) in the rumen liquor of heifers fed dip-treated straw with urea was similar to that of heifers fed silage, whereas it was slightly higher for heifers fed dip-treated straw supplemented with soybean meal.

There were no significant differences in total VFA concentration (mmol/l) between the treatment groups. The silage fed animals had a higher concentration of isobutyric acid, isovaleric acid and valeric acid in the rumen liquor compared with those fed dip-treated straw ($p < 0.05$). The urea concentration (mmol/l) in blood plasma of heifers fed silage was higher (5.09 mmol/l) than those fed dip-treated straw with urea (3.92 mmol/l) or dip-treated straw with soybean meal (4.13 mmol/l).

The magnesium concentration (mmol/l) in blood plasma was lower when the heifers were fed dip-treated straw with either urea or soybean meal as compared with that when they were fed silage (0.78 and 0.77 vs 0.92. $p < 0.05$).

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The performance of bulls fed dip-treated straw vs. grass silage

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The experiment was carried out with 15 bulls to compare their performance when fed dip-treated straw with urea or soybean meal with their performance when fed grass silage. The daily gains of bulls fed grass silage, dip-treated straw with urea or soybean meal were 0.99, 0.80 and 0.81 and corrected daily gains (dressing percentage, 50%) 1.22, 0.95 and 0.99 (kg/d), respectively. The relative weights of kidneys (in percent of carcass) were 0.45 and 0.44% for bulls fed dip-treated straw and 0.37% for bulls fed grass silage ($p < 0.05$).

Key words: Dip-treated straw, bulls, grass silage, urea.

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In recent years more effective methods for improving low quality roughages, e.g. cereal straw, as feed for ruminants have been developed. Many feeding experiments have been carried out to study the effects of alkali-treated barley straw on the performance of cattle (Mo 1978, Sundstøl 1983/84, 1988, Homb 1984). Xu (1986) reported on an experiment with heifers fed dip-treated straw (Sundstøl 1981) supplemented with concentrates. Randby and Xu (1988) carried out an experiment with dairy cows in which dip-treated straw constituted 60% of dry matter (DM) in the ration.

DM intake is increased by dip treatment with NaOH and the digestibility of treated straw was found to increase by 15-20 percentage units compared to that of untreated straw (Sundstøl et al. 1979). However, it is still an interesting issue as to whether the animals can tolerate the amounts of Na fed through NaOH-treated and unwashed straw over a long period of time (Kristensen et al. 1977).

The present experiment was therefore planned as a study of the performance of bulls fed dip-treated straw at more than 50% of DM in the ration compared with bulls fed grass silage. Two sources of nitrogen as supplements to the dip-treated straw were compared.

MATERIALS AND METHODS

Silage-making

Grass silage for the experiment was prepared from the first (mid-June 1987) and second cuts (mid-August 1987) of a mixture of timothy and meadow fescue at Hellerud Experimental Station.

Treatment of straw

Barley straw was dip-treated according to the method described by Sundstøl (1981). The straw was soaked in a solution of 15 g NaOH/l for about 0.5-1 h and allowed to ripen for 3-6 days before being given to the animals.

Fifteen 12 to 14-month-old bulls, weighing 350-450 kg were divided into three groups on the basis of live weight. The experiment lasted for 187 days and included a 10-day preliminary period in which the same diet was given to all animals, followed by a 177-day experimental period. The treatments were:

Group 1:	6.1 kg DM silage + 2.5 kg barley meal.
Group 2:	4.7 kg DM dip-treated straw with urea + 2 kg DM silage + 2.5 kg barley meal.
Group 3 :	4.7 kg DM dip-treated straw without urea + 2 kg DM silage + 1.4 kg soybean meal + 1.2 kg barley meal.

The feed supply of both concentrates and roughages was restricted on the basis of the Norwegian Feed Unit system (FU). One FU is equivalent to the net energy value of 1 kg barley. Four-and-a-half FUs of silage is equivalent to about 6.1 kg DM for group 1. Three FUs of dip-treated straw is about 4.7 kg DM for groups 2 and 3. Two-and-a-half FUs of concentrate is 2.5 kg for all three groups.

Urea as 3% of air-dry straw was mixed into the NaOH solution for Group 2. The diets were formulated so as to be nearly isonitrogenous for the three groups. One hundred grams vitamin-mineral mixture (Vita mineral) was given to all bulls daily. Each of five bulls was equipped with an electronic collar for opening the electronic door to allow for individual feeding. The feed offered and the residues were recorded daily. Water was available at any time and the group consumption was measured. The animals were weighed every fifth week throughout the experiment. At slaughter the carcasses were commercially prepared and classified at the slaughterhouse. Liver, kidneys and kidney fat were weighed.

Feed samples were taken every week for DM determination and composite samples for chemical analysis. The samples of dip-treated straw were freeze-dried. The DM, ash, crude fibre (CF), ether extract (EE), crude protein (N*6.25, CP) were analysed according to AOAC (1980) and nitrogen free extracts (NFE) were calculated by difference. The statistical analysis of data was the analysis of the variance, using the General Linear Models (GLM) procedure of the statistical analysis system (SAS 1985).

RESULTS

The chemical composition values for dip-treated straw with or without urea, silage and concentrates are given in Table 1. The pH of grass silage was slightly higher than that of the silage used in the experiment with heifers (Xu et al. 1991) and the organic acids in grass silage were within the normal range according to Breirem & Homb (1970).

The N content of the dip-treated straw was increased by adding urea to the NaOH solution. It was about three times as high as dip-treated straw without urea. The ash content was higher for unwashed dip-treated straw as compared with silage and concentrates, because of the NaOH added.

The feed and water intake and live weight gains of bulls are given in Table 2.

The average daily gains throughout the experimental period of 177 days were 0.99, 0.80 and 0.81 kg/d for bulls fed silage, dip-treated straw with urea and dip-treated straw with soybean meal, respectively. The difference between the bulls fed silage and bulls fed dip-treated straw was significant ($p<0.05$). At the

Table 1. The chemical composition values of the feeds

	Grass silage	Dip-treated straw with urea	without urea	Barley meal	Soybean meal
Dry matter,%	20.9	25.1	24.9	86.7	88.4
pH	4.25				
NH_3-N in % total N	7.43				
Formic acid,%	0.37				
Propionic acid,%	0.01				
Lactic acid,%	0.91				
Acetic acid,%	0.61				
Butyric acid,%	0.00				
<u>In dry matter</u>, g/kg					
Ash	62	147	149	23	69
N * 6.25	185	123	38	113	484
Ether extract	64	27	28	24	15
Crude fibre	344	428	443	51	79
N-free extract	345	342	342	789	353

Table 2. Feed and water intake and performance of the bulls (average of 177 days, ±SD)

	Grass silage	Dip-treated straw with urea	Dip-treated straw with soybean meal
DM intake (kg/d):			
Silage	5.9	2.0	2.0
Dip-treated straw + urea	-	4.6	-
Dip-treated straw	-	-	4.8
Barley meal	2.0	2.0	0.9
Soybean meal	-	-	1.3
DM intake g/kg.$W^{0.75}$	76.6	85.7	89.6
Live weight:			
Initial, kg	395.4 ± 27.9	395.4 ± 39.2	395.5 ±32.6
Final , kg	573.3 ± 38.1	536.8 ± 41.6	538.0 ±37.6
Daily gain ,kg/d	$0.99^{a}\pm0.13$	$0.80^{b}\pm0.07$	$0.81^{b}\pm0.08$
Carcass ,kg	305.7 ± 17.6	281.4 ± 25.7	285.3 ±22.9
Dressing percentage, %	53.6	52.4	53.0
Corrected daily gain, kg/d (50% of carcass)	1.22a±0.13	0.95b±0.15	0.99b±0.13
Fat content of carcass,1)	1.6a±0.5	1.0b±0.0	1.0b±0.0
Drinking water intake, l/d	12.5	19.0	20.0
Total water intake,l/d,2)	35.0	40.0	42.0
Total water intake,l/kg DM	4.5	4.7	4.7

Means with the same superscripts are not significantly different ($p<0.05$)

1) Judged visually , score 1: little fat; score 2: normal

2) Including water in the feed

end of the experiment the carcasses of the silage-fed bulls were 24.3 and 20.4 kg heavier than those of bulls fed dip-treated straw with urea and soybean meal, respectively.

Because of the high dressing percen-

Table 3. Weights of liver, kidneys and kidney fat of the bulls at slaughter (± SD)

	Grass silage	Dip-treated straw with urea	Dip-treated straw with soybean meal
Liver weight, kg	6.12 ± 0.70	5.64 ± 0.59	5.26 ± 0.74
Kidneys, kg	1.12 ± 0.11	1.25 ± 0.09	1.26 ± 0.16
Kidney fat, kg	7.55 ± 1.65	6.12 ± 2.75	5.56 ± 1.61
Liver/Carcass, %	2.01	2.01	1.85
Kidneys/Carcass,%	0.37^a	0.45^b	0.44^b
Kidney fat/Carcass,%	2.48	2.14	1.94

Superscripts see Table 2

tage of the bulls (more than 50%), the corrected daily gain was 1.22 kg for bulls fed silage, 0.95 kg for bulls fed dip-treated straw with urea and 0.99 kg for bulls fed dip-treated straw with soybean meal. The bulls fed urea as a source of nitrogen grew at almost the same rate as those fed soybean meal as the source of protein. The carcasses of the silage fed bulls had a normal fat content of the carcasses while the dip-treated straw fed bulls had a lower fat content, regardless of being supplemented with urea or soybean meal.

When drinking water and water in the silage and dip-treated straw were taken into account the average water intake of the bulls was 35.0, 40.0 and 42.0 l/d for those fed silage, dip-treated straw with urea and dip-treated straw with soybean meal, respectively. NaOH treatment seems to increase water intake because of the excess sodium which has to be excreted. The weights of liver, kidneys and kidney fat of the bulls are given in Table 3.

There was no significant difference in weight of liver, kidneys and kidney fat between the groups. As a proportion of carcass weight, the kidneys of the bulls fed dip-treated straw were significantly heavier than those of the bulls fed silage ($p < 0.05$).

DISCUSSION

The weather conditions in the harvest season may affect the quality of straw (Kjos et al. 1987). Barley straw used in this study was harvested and baled in September 1987, when the precipitation was at 101 mm, about four times as much as in 1986. The straw had a high moisture content and some of the bales grew mouldy during storage. This probably affected the nutritive, the palatability and the digestibility of the straw.

It was mentioned that both roughages and concentrates were fed strictly according to the plan. More residuals were observed from the silage-fed group compared with the dip-treated straw fed groups. This did not affect the growth rate because of the higher energy content of the silage than that of dip-treated straw.

Studies of live weight and carcass gain of bulls or steers fed NaOH-treated straw processed in different ways are reported on by Kristensen et al. (1977), Pirie & Greehalgh (1978), Henriksen (1978), Garrett et al. (1979) and Deschard et al. (1988). Among these experiments, the effect of increasing the proportion of NaOH-treated roughages in the ration was tested. The more the treated roughage in the diet (from 30% up to 70%), the greater the growth response as compared with the same proportion of untreated roughages in the diet.

The interactive factors, such as breed of animal, concentrate levels of the diet, etc., make it difficult for a comparison to be made between the experiments. An experiment with heifers under similar conditions was conducted by Randby & Xu (1988), who obtained live weight gains of 800 g/d for heifers fed about 60% dip-treated straw with urea supplemented with 1 kg barley meal and 930 g/d for heifers fed the same amount of dip-treated straw plus 1 kg soybean meal. The live weight gain of the bulls fed dip-treated straw in the present study was probably affected by the poor quality of the straw.

The dressing percentages of bulls were almost the same (Table 2) for both the silage and the straw fed groups, which was in agreement with Pirie & Greehalgh (1978). The corrected daily gain depicts the growth response rate more precisely than the daily gain.

Levy et al. (1977) found increased body fat deposition in bulls when NaOH-treated wheat straw was compared with untreated straw. In the present study, the fat content in the carcass of bulls fed on dip-treated straw was lower than in carcasses of animals fed silage, but it was also lower than normal for Norwegian bull carcasses.

About 90 ml water intake per g Na from NaOH was calculated in the present study, which is close to the value reported by Singh & Jackson (1971) and Maeng et al. (1971). The higher water intake may partly be explained by a higher DM intake for bulls fed treated straw.

Feeding animals with dip-treated straw does not seem to affect the liver weight. The weight of the kidneys was significantly increased by about 0.07 units ($p < 0.05$) when expressed as a percentage of the carcass weight. Arnason (1980), who fed bulls with NaOH-treated straw, found that the kidneys were heavier than those from bulls fed untreated straw, but no pathological abnormality was found. On the other hand, kidney weight was unaffected when steers were fed whole-crop cereals ensiled with either NaOH or NaOH plus urea (Deschard et al. 1988).

SUMMARY

The experiment was carried out with fifteen bulls weighing 350-450 kg at the start. The bulls were fed dip-treated straw with urea or dip-treated straw with soybean meal as compared with grass silage.

The averages for DM content of grass silage or dip-treated straw with urea and without urea were 20.9%, 25.1% and 24.9%, respectively; for CP (N*6.25) content they were 18.5%, 12.3% and 3.8%, respectively.

The daily gains of bulls fed silage, dip-treated straw with urea or with soybean meal were 0.99, 0.8 and 0.81, respectively; the corrected daily gains (dressing percentage, 50%) were 1.22, 0.95 and 0.99 (kg/d), respectively. The fat content of the carcasses was normal for the silage fed group but lower than normal for the groups fed dip-treated straw ($p < 0.05$).

The weight of the kidneys, liver and the relative weight of the liver (expressed as percentage of carcass) were not significantly different between the groups. The relative weights of the kidneys for bulls fed dip-treated straw were 0.45% and 0.44% and 0.37% for bulls fed grass silage ($p<0.05$). There were no health problems observed in bulls fed 50% dip-treated straw in the diet over a period of six months.

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Polledness and associated traits in goats

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Data presented by Haugen (1960) on polledness and associated traits in Norwegian goats were examined and discussed in relation to reports by other workers. It was concluded that the data were consistent with the following hypotheses:

a. Polledness is determined by a single dominant autosomal gene.
b. The same gene is responsible for most cases of intersexuality in polled goats. This effect is recessive and is restricted to genetic females (sex chromosomes XX).
c. The skewed sex ratio (excess of males) in many goat populations occurs because a large proportion of intersexuals are erroneously classified as males.
d. About one-half of the genetic males which are homozygous for the gene for polledness are completely sterile.
e. Polled females are more prolific than horned females.

Haugen's data also indicated that polled bucks sired larger litters than horned bucks. Later research is not consistent on this point.

Key words: Bucks, goats, hermaphroditism, intersexuality, polledness, prolificacy, sex ratio, sterility.

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The wild ancestors of the domestic goat had horns. Although most of the present day goat breeds are horned, polled individuals occur sporadically in many of them. In some breeds polledness has been established as a breed characteristic, e.g. in the Saanen.

Some goatkeepers prefer polled goats because they are easier to handle and less likely to hurt one another when fighting. But of more practical importance is the association between polledness and other traits. One such trait is *intersexuality* (hermaphroditism), a defect which has a rather high frequency rate in many breeds of goats and whose association with polledness is well documented. The *skewed sex ratio* often observed in polled goats and the problem of *sterile bucks* are a part of the intersexuality complex. *Prolificacy* (litter size) is another trait which appears to be related to polledness.

One of the more comprehensive sets of data on polledness and associated traits in goats was collected by Haugen (1960) in Norwegian goats. The data were obtained by means of questionaires distributed to goat breeders and extension officers, and included information on more than 4000 goat kids. Each kid was classified as either a male, a female or an intersexual. Information on sire and dam with respect to presence/absence of horns was also collected, and the number of kids in each parturition was recorded. The data were summarized and presented in tabulated form, but no tests of significance were carried out. The interpretation was therefore sometimes inadequate and not fully justified by the data, while other findings deserved more attention than they were given. The purpose of this paper is to re-examine the data collected by Haugen and to discuss his results in view of both earlier and more recent reports by other workers.

Inheritance of polledness

Asdell & Crew (1925) and Lush (1926) found that polledness in goats is caused by a single dominant autosomal gene (symbolized by P). The data presented by Haugen support this hypothesis, as only one out of 499 kids from the mating of two horned animals was polled (Table 1). This single polled kid can probably be ascribed to a mistake either in recording of parentage or in classification polled/horned (see later).

Haugen noticed, however, that when one of the parents had horns and the other was polled, there was a larger proportion of horned kids among males than among females (54.9% of male kids had horns, but only 40.5% of female kids, see Table 1). He concluded that «the heredity of horns is partly sex-linked».

A χ^2-test confirms that the proportion of horned kids differed significantly between the two sexes ($\chi^2=11.01$, $P<0.005$). The proportion of horned males did not deviate significantly from the 50% expected when all polled parents were heterozygotes ($\chi^2=2.52$, $P>0.05$), but the proportion of horned females was significantly less than 50% ($\chi^2=9.67$, $P<0.005$).

Haugen mentioned that it was sometimes difficult to determine whether or not a kid was going to develop horns, as many of the kids were slaughtered shortly after birth. He suggested that the number of kids classified as horned might be too low. Ricordeau & Bouillon (1969) found that horns appeared at an earlier age in male than in female kids. The discrepancy between the two sexes might therefore be due to bias in classification. Haugen's conclusion that the inheritance of horns is dependent on sex is probably not justified.

Polledness and intersexuality

Asdell (1944) forwarded the hypothesis that intersexuality in goats is caused by a single recessive gene which acts only on females, and is linked with the gene causing polledness. This was supported by Eaton (1945), who added that the close association between intersexuality and polledness might be explained either by complete linkage or as a result of a gene with pleiotropic effects (».... a single gene may be responsible for both the polled and the hermaphroditic characters«). The data collected by Haugen were in good agreement with the Asdell/Eaton hypothesis, as almost all kids classified as intersexuals were polled and resulted from the mating between a polled male

Table 1. Number of polled and horned kids born from various types of parents. After Haugen, 1960

Parents		Number of male kids		Number of female kids	
Sire	Dam	Polled	Horned	Polled	Horned
Polled	Polled	910	229	636	180
Polled	Horned	109	130	131	92
Horned	Polled	12	17	29	17
Horned	Horned	0	270	1	228

Table 2. Sex ratio and frequency of intersex among kids born from various types of parents. After Haugen, 1960

Parents	No. of kids	Sex distribution, pct. Male	Female	Intersex
Both polled	2260	55.5 ± 1.1[a)]	37.4 ± 1.0	7.1 ± 0.5
One or both horned	1225	49.3 ± 1.4	50.3 ± 1.4	0.4 ± 0.1

a) Standard errors calculated by present author

and polled female (Table 2). A few years later Nes et al. (1963) confirmed by karyotyping that the intersexual kids were usually genetic females (cf. also review by Hulot & Basrur, 1969).

Matings between two polled animals also resulted in a considerable excess of male kids. A skewed sex ratio in some breeds of goats had been reported previously by several authors. Likewise sterility of bucks had been recognized as a problem. Brandsch (1959) proposed that both the skewed sex ratio and the sterility among bucks were a part of the intersexuality complex, and that the sterile males were actually females which had been masculinized to such a degree that they were erroneously classified as males. In a postscript to Haugen's paper it was pointed out that 37.4% of the kids from the mating of two polled animals were females. If the actual sex ratio is 0.50, this means that the rest of the females (12.6% of all kids) were classified either as intersexuals or as males (pseudo-males). The segregation ratio in females was thus 37.4:12.6, or very close to the 3:1 ratio expected if all polled parents were heterozygous for the recessive gene causing intersexuality.

According to the Asdell/Eaton hypothesis all polled female goats which can be used for breeding are heterozygotes, as homozygous polled females would develop intersexuality. Haugen estimated that 7.8% of the polled does in his data were homozygous, but this estimate was based on very limited evidence, and his data were in no way in contrast to the Asdell/Eaton hypothesis.

On the male side the situation is less clear. Haugen reported that 25 out of the 138 polled bucks represented in his material sired no horned offspring, and therefore might be considered homozygous for the gene for polledness. However, most of these bucks had rather few offspring, and might not have been detected even if they were heterozygous. The proportion of intersexuals among offspring of these 25 bucks was 6.3%, only slightly higher than for all polled bucks (5.6%). This suggests that most, if not all, of the bucks which left no horned offspring, were nevertheless heterozygotes.

Haugen suggested that homozygosity for the gene for polledness in bucks was often associated with a certain type of sterility. This was later confirmed by Soller et al. (1963). Weber (1967) found two types of sterility (or reduced fertility) in polled bucks, testicular hypoplasia and seminal congestion. The first type occurs in pseudo-males (genetic females), the second in genetic males which are homozygous for the gene causing polledness. Ricordeau et al. (1972) estimated that more than half of the genetic males homozygous for the gene for polledness were completely sterile.

Of the 166 intersexual kids in Haugen's data five had one horned and one polled parent. Four of the intersexual kids were themselves classified as horned. Both these findings are in contrast to the hypothesis that intersexuals are homozygous for the gene for polledness. Apart from any possible recording errors, it is likely that some of these cases of intersexuality can be of a different, non-genetic origin. Many cases of intersexual horned kids have been reported, and some of these might be of the same type as the freemartin condition in cattle twins.

Polledness and prolificacy

Haugen reported the average number of kids born per parturition from polled and horned parents (Table 3), but did not comment on the findings. However, his data indicate very clearly that polled goats gave birth to more kids than horned goats (+0.16 kids per parturition = +12%). This over-prolificacy of polled females was confirmed later in studies by Soller & Kempenich (1964), Ricordeau (1969), Hancock & Louca (1975), and Constantinou et al. (1981).

Table 3. Prolificacy of polled and horned parents. After Haugen (1960)

Parents Sire	 Dam	No. of births	Average number of kids per birth
Polled	Polled	1464	1.54
»	Horned	403	1.38
Horned	Polled	58	1.40
«	Horned	468	1.26

Haugen's data also indicated that on average polled bucks sired larger litters than horned bucks (+0.13 kids = 9%). Ricordeau (1969), who was able to distinguish between homozygous and heterozygous polled bucks, found a significantly larger litter size from homozygous than from heterozygous polled bucks, while the latter did not differ significantly from the horned bucks. Hancock & Louca (1975) found no difference of importance between polled and horned bucks in their data (all polled bucks were heterozygotes).

Haugen mentioned that births in which an intersexual occurred had a much higher number of kids than all births combined (1.70 vs. 1.47 kids on average) but did not give any interpretation for this occurrence. This difference is mostly spurious, as the probability of an intersexual individual occurring in a set of twins is nearly twice as high as for a single kid.

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A lysimeter study on the nitrogen balance in soil

II. Fate of ^{15}N-labelled nitrate fertilizer applied to grass

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Calcium nitrate labelled with 9.80% ^{15}N was applied to meadow fescue and Italian ryegrass in a 3-year lysimeter experiment. The treatments consisted of 120, 240 and 360 kg N ha^{-1} applied, partly in spring and partly after the first harvest, to mineral soils from three sites. The recovery percentages of applied N were sigificantly higher at the 240 and 360 kg N rates compared with those at the 120 kg rate, whereas fertilizer utilization differed only slightly for the three soils. The recovery of fertilizer N in the grass crop for the 3-year period, averaged over soils and N rates, was 66%. The percentage of total N from fertilizer retained in the 0-20 cm topsoil at the end of the experiment decreased with increasing N rates and varied from 20 to 25% for the three soils. Losses of fertilizer N through leaching were extremely low. Unaccounted-for losses of fertilizer N on the three soils were from 8 to 14%, and were probably caused by denitrification. Calculations for the 3-year period gave higher values for crop removal of fertilizer N by the isotope method than by difference measurements.

Key words: Grass, denitrification, ^{15}N, leaching of N, N balance, N uptake.

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The amount of fertilizer N recovered in grass is normally greater than that recovered in arable crops. Numerous experiments with non-labelled N have shown recovery values of 50-80% in grassland herbage in humid regions (Whitehead 1970). Leaching losses of N from grass are generally considered to be small on most soil types, except when the soil is heavily fertilized.

Studies on ^{15}N fertilizer applied to grass are partly based on experiments with single year ^{15}N treatments and partly on repeated ^{15}N applications over several years. In a 3-year lysimeter study with labelled N applied to soft chess, Jones et al. (1977) found that recovery percentages of N after 3 years of annual spring fertilization with 100 kg N ha^{-1} were: 59% of N applied in herbage, 24% remaining in soil and roots, 3% leached, while 14% was undetected. Nitrogen fluxes in intensive grassland were studied by Triboi (1987) in lysimeters on established grasses with labelled fertilizer (360 kg N ha^{-1}). Fertilizer N recovered in herbage was 45% during the first year and amounted to 56%, including residual effects, in the subsequent year. The amount of N retained in the soil after two years was 40% of that applied, whereas leaching and other losses were small. Dowdell & Webster (1980) found 43-54% recovery of N in the herbage of perennial ryegrass during the first growing season in a lysimeter experiment with labelled nitrate fertilizer (400 kg N ha^{-1}), and 54-60% was recovered after the residual fertilizer N in the following year was taken into account. Results from the same experiment published by Webster & Dowdell (1985) showed that about one-third (32-35%) of applied N was retained in the soil after 5-7 years, and the total ^{15}N measured in yield, soil and leaching amounted to 93-98%. The remaining 2-7% was assumed to be lost by denitrification.

Kissel & Smith (1978) determined the disposition of ^{15}N labelled fertilizer nitrate applied to coastal Bermuda grass on a swelling clay in a field experiment over two growing seasons, applying 560 kg N ha^{-1} during the first year. Fertilizer N recovered in the forage during the first season amounted to 49% of that applied, and the residual effect in the following year was 7%. About 40% of applied N remained in the soil at the end of the first year. In a field study by Whitehead & Dawson (1984), where plots of perennial ryegrass each received three applications of N (130 kg N ha^{-1}), the first of which was labelled with ^{15}N, 53% of fertilizer N was recovered in the subsequent four harvests. The amount of fertilizer N retained in stubble, roots and soil was approximately 21%. Westerman et al. (1972) found a recovery of 51-52% in a field experiment with ^{15}N labelled urea and oxamide applied to a Sorghum-Sudan grass hybrid, whereas 25-31% was retained in the soil.

The present lysimeter experiment was conducted to determine the fate of labelled fertilizer N applied annually to barley and grass on three soil types during a 3-year period. The results with barley have already been reported (Lyngstad 1990).

MATERIALS AND METHODS

Information on the construction of the lysimeters and physical and chemical characteristics of the sandy loam (samples 1 & 3) and silty loam (sample 2) soils used are presented elsewhere (Lyngstad 1990).

In May 1975 meadow fescue (*Festuca pratensis* Huds.) was sown at the rate of 50 kg ha^{-1} after fertilizer materials corresponding to 120 kg N, 60 kg P and 120 kg K were broadcast on each lysimeter and mixed with the surface soil. The following year four N treatments were applied: 1. Control; 2. 120 kg N ha^{-1}; 3. 240 kg N ha^{-1}; 4. 360 kg N ha^{-1}. The nitrogen was applied to the soil surface as a solution of calcium nitrate labelled with 9.80% ^{15}N. The lysimeters received two-thirds of the N in spring and one-third after the first harvest. Each treatment was in three replicates.

As the grass sward was greatly damaged during the following winter it was decided to proceed with annual ryegrass (*Lolium multiflorum* L.) for the subsequent two years. The ryegrass was sown at a rate of 100 kg ha. The N applications were repeated in the second and third years. Half of the fertilizer N was applied prior to sowing in the spring and mixed with the upper 10 cm of the soil, and half was surface-applied after the first harvest. All lysimeters were treated with 60 kg P and 300 kg K per ha annually as superphosphate and potassium sulphate, respectively. Half of the K was applied in spring and half after the first harvest.

The grass sward was cut twice during 1976 and three times during the subsequent two years. The final harvest during the three years was in the middle or toward the end of September. Natural precipitation levels during the growing season up to the final harvest in 1976, 1977 and 1978 were approximately 150, 270 and 330 mm, respectively. Because of moisture stress each lysimeter was given extra irrigation amounting to 200 mm in 1976 and to 80 mm in 1977.

The drainage water was sampled during the period from May to November, when the lysimeters were covered against frost. Hydrochloric acid was added to the water samples for preservation until analysed. NO_3-N in the drainage water was determined by reducing the nitrate to ammonia with Devarda's reagent, distilling and titrating. The concentration of ^{15}N in the samples was determined with an emission spectrometer (Jasco N 150).

Soil samples were taken from the lysimeters at the end of the experiment. Plant and soil samples were analysed for total N by a Kjeldahl procedure modified to include NO_3-N with salicylic acid, followed by analysis of isotope ratios.

RESULTS

Grass yields

In the first year, fertilizer N increased yield significantly in all three soils (Table 1). The total application of 240 kg N generally gave a significantly higher yield than 120 kg at the two successive harvests, whereas the 360 kg N rate only slightly affected yields compared with the 240 kg rate. Owing to a partly damaged grass sward no significant yield increase beyond 80 kg N was obtained at the first harvest in soil sample 3. Though extra water was applied, grass yields

Table 1. Yields of grass at different rates of fertilizer N application in three successive years

N applications kg ha^{-1} year^{-1}	Soil No.	Grass yields at different harvests, t dry matter ha^{-1} 1976 1st	1976 2nd	1977 1st	1977 2nd	1977 3rd	1978 1st	1978 2nd	1978 3rd
0	1	0.72	0.96	2.76	1.33	1.03	2.82	0.96	0.43
120		3.16	1.85	3.33	4.09	1.12	5.60	4.25	0.67
240		4.60	2.58	4.29	5.24	1.42	6.38	5.41	1.10
360		4.67	2.63	3.63	6.59	2.13	7.00	6.12	1.63
LSD 5%		0.63	0.14	0.59	0.62	0.22	0.46	0.48	0.15
0	2	0.64	0.73	1.57	0.80	0.81	2.32	0.96	0.34
120		2.89	2.06	3.55	3.55	0.88	4.64	4.11	0.64
240		4.03	3.02	4.40	4.93	1.60	5.50	5.36	1.05
360		3.91	3.25	4.35	6.28	2.29	6.17	5.68	1.43
LSD 5%		0.75	0.56	0.60	0.24	0.35	0.46	0.28	0.24
0	3	1.02	0.83	1.11	1.01	1.02	2.36	1.06	0.40
120		3.12	1.81	2.73	3.77	1.03	4.47	3.88	0.86
240		3.38	3.05	3.31	5.38	1.35	5.45	4.87	1.32
360		4.00	2.85	3.23	5.85	2.59	5.39	4.86	1.64
LSD 5%		1.45	0.66	0.48	0.53	0.27	0.37	0.27	0.19

were depressed by water shortage in the first year.

The second year results showed that 180 kg N applied in spring gave no increase in grass production above 120 kg N at the first harvest, whereas a repeat application of the same N rates resulted in higher yields as well as greater responses to N at the second harvest, especially at the higher N rate. The lower yields at the first harvest were probably a result of lack of water. Residual effects of N at the third harvest occurred only at the two higher N rates. Calculated as average values for the three soils, these effects amounted to 7 and 16% of the total yield increases by the 240 and 360 kg N rates, respectively.

In the third year, grass yields and responses to fertilizer N at the first harvest were higher compared with those in the second year. This was probably the effect of an earlier sowing of ryegrass in the third year combined with a sufficient water supply. Yields at the second harvest were lower than those at the first harvest. Residual effects of applied N on yield at the third harvest were noticeable at all N rates. Averaged over all soils the effects of 120, 240 and 360 kg N were 6, 9 and 13% of the total yield increases, respectively. The residual effects at the two higher N rates were thus of the same order as those in the second year.

N concentrations in the grass crop

The N concentrations of the crop as affected by N rates are shown in Fig. 1 for the separate harvests in the three years averaged over all soils. The N content of fescue grass was mainly unaffected by the lower N rate at both the first and second harvests in 1976, whereas the two higher N rates resulted in marked increases in the N concentrations. The N concentrations in the ryegrass crop at the first two harvests increased at all N rates in the second year, the increase being very high at the two higher N rates at the first harvest. The extremely high values for the N concentrations at the first harvest may partly have been due to residual effects of N applied in the previous year. In the third year the N concentrations followed the same pattern as those in the second year, except for a much lower increase by the higher N rate at the first harvest because of higher grass yields. The N concentrations in ryegrass at the third harvest were lower on fertilized lysimeters than on non-fertilized lysimeters in both the second and third years.

The variations in N concentrations of the grass crop among the three soils were generally small. The variations seemed to be related to differences in yield or yield responses to fertilizer N.

Fertilizer N uptake

Plant uptakes of ^{15}N, expressed as percentages of the amounts applied, are given in Table 2 for the three N rates at the separate harvests in the three soils. Crop recovery of fertilizer N applied to meadow fescue in 1976 was considerably lower compared with that for the ryegrass crop in the two succeeding years. Averaged over soils and N rates the total uptake percentages of applied N were 43, 83, and 72% in 1976, 1977 and 1978, respectively. The low recovery values in 1976 were partly related to insufficient water supply and partly the result of damaged plant cover of the meadow fescue. The uptake values in the second and third years reflected both the effects of yearly fertilizer application and the residual effects from previous years. The higher recoveries of applied N in 1977 and 1978, however, were mainly related to increased water supply compared to 1976.

With the exception of the first harvest in 1976, the higher N rates resulted in significantly higher recovery percentages of fertilizer N than the lower N rates. As discussed later, this seemed to be related to different immobilization rates of N in the soil.

Table 2 reveals how the recovery percentages of isotope N at the second

Table 2. Isotope recoveries at different rates of N fertilizer applied to grass

N applications kg ha^{-1} year^{-1}	Soil No.	^{15}N recoveries in grass yields, % 1976 1st	1976 2nd	1977 1st	1977 2nd	1977 3rd	1978 1st	1978 2nd	1978 3rd
120		44.0	41.3	57.0	76.3	6.2	55.5	68.9	4.1
240		47.1	48.0	71.2	83.9	5.2	62.3	73.2	4.2
360		43.3	48.2	64.9	95.9	5.9	68.5	74.2	4.7
LSD 5%		4.4	3.9	5.6	7.6	1.0	5.6	4.3	0.5
120		37.7	41.1	57.2	77.8	5.4	52.6	71.1	3.9
240		41.4	51.2	77.4	84.4	5.3	57.8	75.2	3.9
360		35.5	56.9	73.4	94.2	5.7	62.3	74.3	4.0
LSD 5%		4.0	7.9	5.6	5.9	1.5	4.4	2.7	1.1
120		36.2	38.4	51.4	77.4	5.5	54.5	67.7	5.5
240		36.7	47.7	64.0	86.7	4.8	61.4	71.8	4.8
360		39.1	52.0	59.4	96.9	7.9	64.9	68.8	5.1
LSD 5%		6.4	9.3	7.3	3.0	2.4	6.4	4.9	0.9

harvest were generaly higher than at the first harvest. This was probably a result of residual effects of the spring-applied N, though other factors could have been involved. The very high recovery percentages of fertilizer N at the two higher rates at the second harvest in 1977 indicate considerable residual effects of the spring-applied N.

The isotope N taken up by ryegrass at the third harvest generally amounted to 4-5% of the total fertilizer N applied in 1977 and to 5-6% of that applied in 1978. The uptake percentages of residual N at the third harvest were not significantly affected by N rates and differed only slightly from soil to soil. These results would therefore indicate minor differences in the percentages of plant-available N from residual sources at the different N rates in the subsequent years.

The total crop recovery of fertilizer N varied somewhat from soil to soil in separate years. Averaged over the 3-year period, however, the N recovery of applied N differed only slightly among the soils, amounting to 67, 66 and 65% in soil samples 1, 2 and 3, respectively.

The values for fertilizer nitrogen taken up by the crop, estimated as the difference between N removed in fertilized and unfertilized plots and measured by the isotope dilution method, are given in Table 3. The results include the 3-year period and indicate the average values for the three soils. The isotope method gave higher values for the yield removal of fertilizer N compared with the values by the difference method at all N rates. These results were consistent on all soils in the separate years. Like the experiment with barley (Lyngstad 1990), the difference method resulted in greater variability for fertilizer N removal by the crop, as indicated by the standard deviation values in Table 3.

Non-fertilizer N uptake

Values for soil N uptake on the three soils in different years are given in Table 4. In the first year fertilizer N decreased the utilization of soil N by fescue grass on all soils at both harvests, the effect increased with increasing N rates. In 1977, too, average values for the three ryegrass harvests showed significantly lower soil

Table 3. Crop removal of fertilizer N as measured by ^{15}N and difference methods. Average values for the 3-year period

N applications kg ha^{-1}	Fertilizer N removed by crop, kg ha^{-1}	
	^{15}N method	Difference method
120	71.1 ± 2.6	60.3 ± 4.6
240	158.8 ± 5.5	149.4 ± 7.4
360	244.0 ± 7.1	234.2 ± 12.1

Table 4. Amounts of non-fertilizer N in total grass yields at different fertilizer rates

N applications kg ha^{-1} year^{-1}	Soil No.	N uptake, kg ha^{-1}		
		1976	1977	1978
0		26.8	71.5	44.6
120		14.4	37.7	46.2
240	1	10.7	39.5	47.3
360		8.0	49.3	43.6
LSD 5%		3.0	8.9	6.3
0		16.8	40.5	38.6
120		11.3	25.3	29.1
240	2	5.6	36.4	30.5
360		3.9	36.1	31.7
LSD 5%		2.9	6.4	4.5
0		21.0	39.6	38.8
120		15.5	28.3	33.6
240	3	14.9	30.8	38.2
360		7.3	39.2	33.8
LSD 5%		4.7	4.2	3.3

N uptake in fertilized lysimeters compared with values by the zero N treatment. The effect of fertilizer N was most pronounced at the second and third harvests and at the lower N rates. In 1978, soil N uptake was, on the whole, not significantly affected by the N rates.

Leaching of N

The amounts of drainage water from the lysimeters with grass were generally higher compared with those from the corresponding barley experiment (Lyngstad 1990). This is explained by the lower total yield of grass compared with total yield of barley, resulting in lower water consumption and consequently of a higher water content in the soils at the end of the growing seasons. In the first and second years the higher levels of additional water applied to grass may also have contributed to the increased leaching losses compared to barley. Drainage water from the different lysimeters varied from almost zero to about 250 mm.

Fertilizer N lost by leaching was negligible in all soils and at any N rate during the experimental period. Losses of nonfertilizer N were also small, as indicated in Table 5. The highest values were obtained in 1976, as a result of an exceptionally rainy autumn. The drainage water decreased with increasing ferti-

Table 5. Yearly leaching of non-fertilizer N from the three soil types. Average values for all N rates

Soil No.	Leaching, kg N ha^{-1} 1976	1977	1978
1	2.2	0.6	1.6
2	2.1	0.4	0.6
3	2.8	0.4	0.7

lizer rates, especially in 1977 and 1978, reflecting a higher water use in the fertilized lysimeters, and resulting in lower soil N losses from the N treatments.

The small leaching losses of N under grass, despite greater water drainage compared to the lysimeters grown to barley, indicate the great efficiency of grass to absorb nitrogen in the soil. As the lysimeters were covered during the winter months, the lower N losses under grass were related to the prolonged uptake period in autumn compared with the lysimeters grown to barley.

Fertilizer N in soil

Soil samples from the top 20 cm of the lysimeters were analysed for total N from fertilizer at the end of the experiment. Subsoil samples were not analysed for residual fertilizer N because of too low a total N concentration. The contents of ammonium- and nitrate-N in the subsoil were low and unaffected by fertilizer treatments. Only small amounts of inorganic N were found in the 0-20 cm layer. Most of the residual fertilizer N was therefore assumed to be immobilized in organic form in the soil.

The fractions of fertilizer N remaining in the soil at the end of the experiment were higher compared with the results of the barley experiment (Lyngstad 1990). The residual N percentages were highest at the lower N rate and decreased markedly at the higher rates on all soils (Table 6). Higher levels of fertilizer N were retained by the silty loam soil than by the sandy loams. On average for N rates, about 28% of the isotope N remained in soil sample 2 and about 23% in soil samples 1 and 3.

Nitrogen balance

The relative lower plant uptake of labelled N at the 120 kg N rate compared to the two higher rates in this experiment was compensated by higher fractions of fertilizer N immobilized at the lower N rate in the three soils. As a result, the unaccounted-for losses, averaged over all soils, were approximately the same at all N rates, amounting to 10-12% of that applied. On two of the soils the unaccounted-for losses were somewhat higher at the 360 kg N rate compared with those at the lower rates.

The N balance for the 3-year period is given in Table 7 as separate values for the three soils and averaged over the N rates. Fertilizer N rates recovered in grass yields plus that retained in the soils after a 3-year period were, on the average of the three N rates, 88, 92 and 86% for soil samples 1, 2 and 3, respectively. As leaching losses were negligible in all soils the unaccounted-for losses, which were assumed to be a result of denitrification, made up the rest of the

Table 6. Fertilizer N remaining in the soil (0-20 cm) after three years of treatment

Soil No.	Fertilizer N found kg N ha^{-1} 120 kg N	240 kg N	360 kg N	LSD 5%	% of N applied 120 kg N	240 kg N	360 kg N
1	107.6	145.0	188.7	26.4	29.9	20.1	17.5
2	124.9	194.1	230.5	33.3	34.7	27.0	21.3
3	101.1	150.9	210.8	19.6	28.1	21.0	19.5

Table 7. Nitrogen balance after a 3-year period of annual nitrogen applications. Average values for three N rates (240 kg N ha^{-1} $year^{-1}$)

Soil No.	1	2	3
Removed by grass yield	483.2	477.4	464.5
Leaching	0.8	1.4	0.4
Present in total soil N (0-20 cm)	147.1	183.1	154.3
Unaccounted-for losses	88.9	58.1	100.8

applied N. The amounts of unaccounted-for losses were determined by difference and thus included accumulated errors of sampling and analyses. Since subsoil samples were not analysed for residual fertilizer N, the values for unaccounted-for losses also included any fertilizer N possibly remaining in the subsoil.

DISCUSSION

The average fertilizer N recovered for the three soils and the three N rates in the total grass crop for the 3-year period amounted to 66% compared with 69% in the barley crop (Lyngstad 1990). The lower utilization of fertilizer N by grass was due to poor growth of meadow fescue in the first year, caused by water shortage and a damaged grass sward. In the second year the utilization of fertilizer N by grass was higher compared with utilization by barley, whereas the uptake pecentages of applied N were about the same for the two crops in the third year.

The uptake percentage of applied N in 1977 and 1978 also included residual effects in previous years. The recoveries of isotope N at the third harvest in these two years indicated the same percentages of remineralized N at all fertilizer rates, amounting to a few percent of the applied N. However, the low plant utilization of fertilizer N in 1976 probably resulted in a considerable residual potential, which may have contributed to the high recovery of isotope N in 1977.

The residual levels of fertilizer N in the soil after the 3-year period of grass were relatively higher than N levels after barley, which was a result of greater amounts of N being caught up in stubble and roots in the grass lysimeters. The precentage of isotope N retained in soil under grass decreased markedly with increasing N rates, whereas in the barley experiment the residual N percentages were unaffected by N rates. The decrease in the residual N fractions with increasing N rates in the grass experiment may be related to the higher N application rates compared with N rates in barley and to the relative low grass yields. As to the soils, a greater part of the applied N was retained in soil sample 2 as compared with soil samples 1 and 3.

The increase in the crop recovery percentages of applied N as a result of higher N rates at the first and second harvests must be seen mainly in relation to the decrease in the fractions of isotope N immobilized in soil with increasing N rates. Increased uptake efficiency following the increasing N rates may also have contributed to the observed differences in uptake values among the N rates, whereas differences in residual effects of N did not seem to be involved, judging from the uptake values at the third harvest (Table 3).

On average for the N rates, the unaccounted-for losses were 12, 8 an 14% for soil samples 1, 2 and 3, respectively. These losses were smaller than those in the barley experiment (Lyngstad 1990), indicating a more efficient uptake of N by grass roots.

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Slurry application techniques for grassland: effects on herbage yield, nutrient utilization and ammonia volatilization

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Field experiments were carried out in southern Norway to study the effects of broadcast spreading, band spreading with band spacings of 200 and 400 mm, and slurry injection (600 mm tine spacing) on herbage dry matter yield and nutrient utilization. The wind tunnel method was used to study ammonia volatilization from broadcast spreading and band spreading with band spacings of 200 and 400 mm. Band spreading of slurry on grassland gave dry matter yields that were not significantly different from those resulting from broadcast spreading of slurry. But nitrogen utilization of applied slurry was clearly influenced by the application technique. Slurry injection resulted in a significant increase (100%) in the degree of utilization as compared with the other techniques; and band spreading resulted in less ammonia volatilization than broadcast spreading, particularly during the first hours after application, when the difference was clearly significant. However, as the ammonia evaporation continued with time, so this difference decreased.

Key words: Ammonia volatilization, application technique, field trials, nutrient utilization, slurry.

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The use of slurry on grassland has been much discussed. From the practical point of view the odour problem is well known, as is scorching. In addition, ammonia volatilization can cause serious pollution problems. The ammonia volatilization represents a loss of nitrogen which has to be replaced with fertilizer. Developments in slurry application techniques are not only necessary in order to overcome the pollution problems, but are also necessary toward making better use of the nutrients in the slurry.

Slurry injection is one technique that has been developed to overcome these problems. Poor yields caused by wide tine spacing and damage to the soil surface, and high draught forces and low capacities as a result of narrow working widths, seem to be common conclusions (Ronningen 1974, Godwin et al.1985). On the other hand, recent research has revealed that various constructions influence the performance of injectors and the yield response. Hann et al.(1987) concluded that if the tine leg angle was increased, the damage to the soil surface would be reduced. They also found that using press rollers behind the injectors significantly increased the dry matter yield ($p<0.05$).

Rodhe et al. (1988) found that band spreading with band spacings of 250, 375, and 500 mm all gave a herbage yield response of 40-60% as compared to herbage yield response with fertilizers. The differences between the yields obtained with various band spacings were small, but there was a tendency toward higher yields after band spreading than after broadcast spreading.

Research into factors affecting ammonia volatilization has also been carried out. After a four-year study of ammonia volatilization from liquid dairy manure applied in early May, Beauchamp et al.(1982) found that volatilization followed a diurnal pattern with maxima occurring shortly after midday and minima occurring during the early morning hours. The magnitude of the daily flux values tended to decrease with time. The flux values increased with temperature and were suppressed by rainfall. Over a period of 6 or 7 days following the time of manure application, between 24 and 33% of the ammoniacal N applied in the manure was lost through volatilization. Five days after manure application, the relatively large quantities of ammoniacal N remaining in the manure layer were still subject to potential volatilization. Hoff et al.(1981), Christensen (1986), Hall & Ryden (1986), Döhler & Wiechmann (1988) have shown that ammonia volatilization increases with temperature and with wind speed but decreases with rain and with relative air humidity. Ammonia volatilization can be avoided by

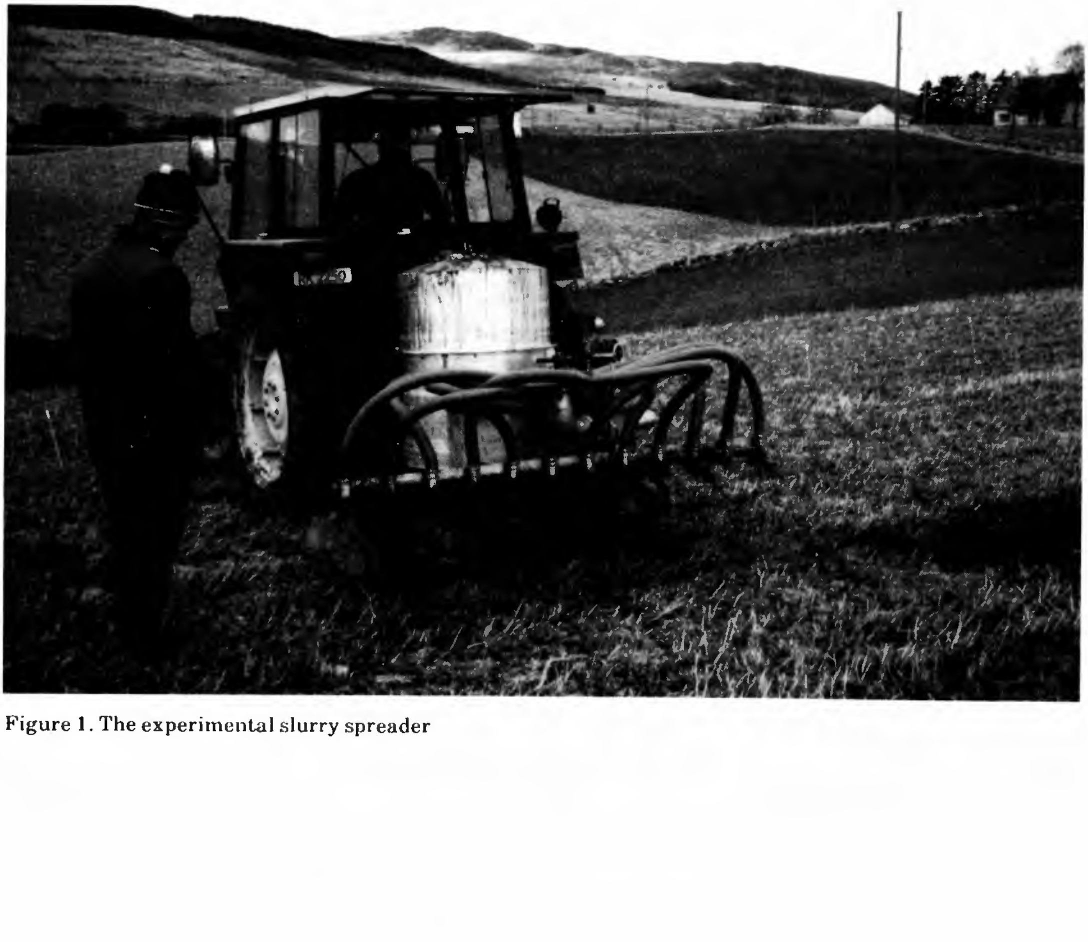

Figure 1. The experimental slurry spreader

Figure 2. The band-spreading equipment

means of slurry injectors. Hoff et al. (1981) found that the ammonia volatilization was only 2.5% after slurry injection.

The objective of this study was to test out the band-spreading technique. Field plot experiments were used. The band-spreading technique was compared with the soil injection and broadcast spreading techniques. First, a comparison had to be made of the herbage yield response to the different methods, and then any differences in response between the 200 and 400 mm band spaces were investigated. In order to explain the results obtained from the herbage yield response investigation, nutrient utilization was calculated, and ammonia volatilization was investigated.

MATERIALS AND METHODS

Experimental slurry spreader

The spreader (Fig. 1) has a 540 l tank and is attached to the tractor through the normal three-point linkage. A positive displacement pump (lobe rotor type) is driven by an auxiliary engine. The pump delivery is in close proportion to the speed of the pump. The application rate, then, is a function of the rotational speed of the pump, the tractor travelling speed, and the spreading width.

To provide an even, crosswise distribution and a constant spreading width (2.5 m), a system based on a distribution chamber with one central inlet and 12 evenly spaced, peripheral outlets was developed. In this chamber there is a driven rotor through which the slurry flows, leaving its periphery through one chamber outlet at a time. The rotor is driven by the pump engine. Each of the 12 outlets can either be connected to its own lip spreader (broadcast spreading) through 50 mm hoses, or be connected to band-spreading equipment through the same hoses (Fig. 2). This equipment was based on curved runner furrow openers from a seed drill. A simpler version based on dragging hoses was rejected. A hoe type furrow opener was also rejected. When the dragging hoses were used, much of the slurry contaminated the plant leaves, and when the hoe type was used the grass did not slide away from the coulter tip with the result that it slid on top of the vegetation.

Every other hose on the band-spreading equipment could be connected to the neighbouring coulter, and the band spacing could thereby be doubled from 200 to 400 mm.

Yield response and nutrient utilization

The experimental slurry spreader was used in the field experiments as well as a slurry injector. The injector had 4 tines (600 mm apart) and the working depth chosen was 100 mm.

A total of 12 field experiments were conducted at Ås, Jæren and Skien in 1987 and 1988. Slurry was applied to the plots in 7 field experiments in early May and 5 field experiments in late June. Each field experiment included 18 plots, each measuring 2.5 x 8.0 m; six treatments; and 3 replications of each treatment. The treatments were: lip spreading of slurry; band spreading, spacing 200 mm; band spreading, spacing 400 mm; slurry injection; control; and fertilizer. With slurry the applied dose was 50 t per ha, and with fertilizer the applied dose was 100 kg N per ha in the composite fertilizer of type A from Norsk Hydro. This was estimated to give a nitrogen dressing similar to that of the slurry treatments. Table 1 summarizes the results of the analyses of the chemical contents of the slurry used in the experiments. Slurry from the farm on which the experiments were located was used. Samples were taken at the time when slurry was applied, frozen down immediately and brought to the laboratory for analysis. We can see from Table 1 that the values of the dry matter content varied greatly in the experiments. But these values were not correlated with the contents of any of the chemical components that were analysed, although there were also large variations in these values. In the Jæren 3 experiment the dose was reduced from 50 to 40 t per ha because of the high nitrogen concentration in the slurry. This content was found by means of the Agros method for analysis of ammoniacal nitrogen, which was carried out before application of slurry on the plots.

In the Ås experiments the soil was of a sandy loam type. In the Jæren experiments the soil consisted of a loamy sand, a sand, and an organic type for the Jæren 1, 2 and 3 experiments respectively. At Skien the soil was of a silt type.

In all experiments except the one of June application at Skien, where cocksfoot was the predominant plant type, the predominant plant types were timothy and clover (10-20%).

Table 1. Dry matter (DM) content and chemical composition of the slurries used in the field experiments

Site	Spreading time	DM (%)	Total N (g/kg)	$NH4^{+}$-N (g/kg)	Total P (g/kg)	Total K (g/kg)
Jæren 1	May 1987	8.8	3.6	1.8	0.62	3.7
Jæren 2	»	4.6	2.5	1.4	0.67	3.4
Jæren 3	»	6.0	4.2	2.8	0.80	7.1
Ås	»	6.9	2.8	1.4	0.83	3.0
Jæren 1	June 1987	8.3	3.9	1.8	0.71	4.0
Jæren 2	«	8.6	3.8	2.0	0.69	3.9
Ås	«	6.6	2.8	1.6	0.54	2.6
Skien	May 1988	10.1	4.5	2.6	0.61	3.9
Skien	June 1988	14.0	4.8	2.5	0.76	3.9

The crop resulting from the May application was cut in early June, and that from the June application in early August. Samples were collected for the standard analysis of dry matter content and nutrient content.

The statistical computer program Systat was used for the statistical analyses.

Samples for plant analyses were collected from each treatment within each experiment. Nutrient utilization was determined for N, P and K given by the equation:

$$X_{ut} = \frac{(YD_m - Y_c D_{mc})100}{VD} \times 100\,\%$$

where

X_{ut} = N, P or K utilization (in percent)
Y = N, P or K content in plant analyses (kg per 100 kg dry matter)
Y_c = N, P or K content in plant analyses (kg per 100 kg dry matter) from the control treatment
D_m = dry matter yield (kg per ha)
D_{mc} = dry matter yield from the control treatment
V = N, P or K content in slurry samples (kg per tonne slurry)
D = application rate of slurry (tonnes per ha)

Ammonia volatilization

The ammonia volatilization study was carried out in 1988. The wind tunnel method was chosen. Four tunnels were constructed, each consisting of a piece of polycarbonate sheet (2.0 x 1.2 m) which was bent into a frame measuring 0.5 x 2.0 m to form a tunnel. A fan was connected to one end of the tunnel through an adaptor and a one metre tube. The fan was a Nowenco ACN 400. The fan air speed was adjusted with a frequency converter so that an average wind speed of 1.2 ms^{-1} was attained, this being the lowest practical wind speed that could be used if the air stream in the tunnel was to be uninfluenced by the wind speed outside the tunnel. The wind speed is probably lower so near the soil surface, but, on the other hand, it had to be taken into account that the diffusion in nature is free to a convectional flow in all directions, while the diffusion in a wind tunnel will be more directed into a horizontal flow.

Each tunnel was connected to a vacuum pump through hoses (10 mm diameter) and ammonia traps. To trap the ammonia, the sampled air was bubbled through bottles with 200 ml of 2% boric acid. The vacuum pumps were calibrated to pump 4.0 $lmin^{-1}$.

The test period of five days took place in early May. A quantity of slurry (5 lm^{-2}) was placed onto the ground in the area where three of the tunnels were placed. The application techniques of broadcast spreading and band spreading with band spacings of 200 mm and 400 mm were used. The fourth tunnel was used as a control. Samples were taken every 6 h during the first two days, then samples were taken every 12 h. The samples were brought to the laboratory for analysis.

Temperature and relative air humidity were sensed both inside and outside the tunnels, and the signals from the thermocouples and the Phillips capacity sensor for air humidity registration were digitalized and recorded on a data logger.

RESULTS AND DISCUSSION

Yield response and nutrient utilization

In the figures and tables used in this chapter the treatments of broadcast spreading; band spreading, band spacing of 200 mm; band spreading, band spacing of 400 mm; injection; control; and fertilizer, will be abridged to B, S20, S40, N, 0, and FERT respectively.

The results from the May field experiments are given in Fig. 3 and those from the June field experiments are given in Fig. 4. Higher yields were generally observed after the May applications than after the June applications ($p < 0.001$), which can easily be seen from

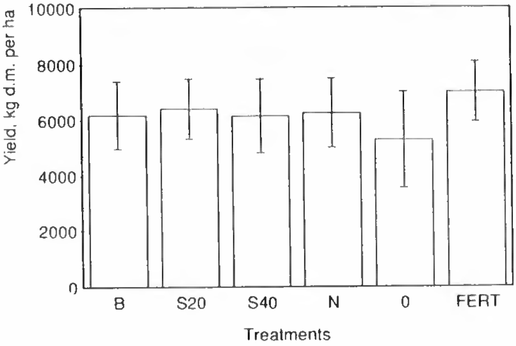

Figure 3. Effects of different treatments on the dry matter yields after the May application of slurry

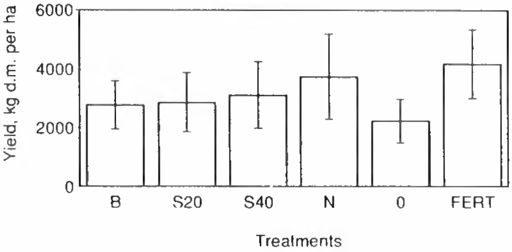

Figure 4. Effects of different treatments on the dry matter yields after the June application of slurry

Figs. 3 and 4. There were significant differences between the experimental sites ($p < 0.001$) as well as between the treatments ($p < 0.001$). There were interactions between sites and application times ($p < 0.001$), between sites and treatments ($p < 0.001$), and between application times and treatments ($p < 0.005$). There were very small differences between the treatments with broadcast spreading and those with band spreading (not significant). When slurry was applied in May, the injection technique resulted in a dry matter yield on the same level as that of the other slurry application techniques.

The unusual weather conditions (high precipitation) at Ås caused very abnormal yields (Fig. 3), and therefore the control plots gave yields that were not significantly different from those of the other treatments. Differences between sites and between treatments were found to be significant ($p < 0.001$). Interaction between sites and treatments was found ($p < 0.001$). This could be explained by the high yields on the control plots and by the relatively low yields on the injection plots at Ås. By using contrast tests it could be proved that there were no significant differences between the slurry-treated plots.

Statistical analysis of the June application experiment showed significant differences between sites and between treatments ($p < 0.001$). Interaction was observed ($F = 2.863$). From Fig. 4 it can be observed that the yields from the injection treatments varied widely between the sites, thus explaining the interaction found. The yields from the surface application techniques were not significantly different in a contrast test, but the various injection yields were found to be significantly different ($p < 0.01$). There were significant differences between the fertilizer plots and slurry plots, and between the control plots and slurry plots. In the literature (Rønningen 1974, Godwin et al. 1985) the general conclusion is that slurry injection results in a lower herbage yield than that with broadcast spreading. One explanation for the high yield found in the June experiments may be weather conditions and/or soil type, which are documented as having an influence on the yield response (Godwin et al.1985). Very few reports on slurry injection have focused on the injection times (before or after the first cut). One explanation that the author cannot prove may be the difference in plant root growth from May to June. When injection is carried out in spring, the plant roots are weak and the cut-off that may result from injection will damage the plant roots. The plant roots are normally stronger and therefore the cut-off caused by the injector will not have the negative effect on plant growth.

When slurry was spread on the soil surface, the effect of the slurry was about 40-60% that of the fertilizer, which is much the same as the effect found by Rodhe et al.(1988).

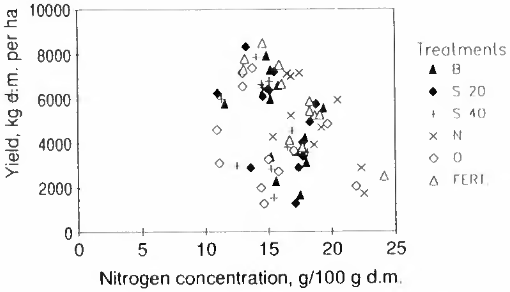

Figure 5. Nitrogen concentration versus dry matter yields for various treatments

Nutrient utilization

Fig. 5 shows a plot of nitrogen concentrations versus dry matter yields split into treatments. There is a slight tendency toward higher nitrogen concentrations as the dry matter yield decreases. The nitrogen concentration varies a lot even for yields on the same level. In most of the cases slurry as well as fertilizer application resulted in higher nitrogen concentrations.

The calculated nitrogen utilization values in Table 2 indicate large variations between the different sites as result of very large standard deviations (SD). From the variation analysis it can be concluded that there were no differences between experimental sites, but there were some differences between times of application ($p < 0.10$). No interactions were found. All treatments except the fertilizer treatment resulted in lower nitrogen utilization when application took place in June (4-11 percentage points lower). Significant statistical differences were found between treatments ($p < 0.01$) (both application times), and a multiple range test (Tukey's T-test) indicated that there were no differences between the various surface application techniques for slurry. Slurry injection resulted in a nitrogen utilization no different from the utilization in the fertilizer treatment. This may be explained by the minimal ammonia volatilization (according to Hoff et al.1981 and Hall & Ryden 1986) and the good contact between ammonia ions and the soil colloids brought about by this technique.

The calculated phosphorus and potassium utilization values are given in Tables 3 and 4. There are small differences between the various treatments, but a slight tendency towards better utilization after fertilizer application can be found for the potassium utilization values.

Table 2. Nitrogen utilization in percent of applied nitrogen

Treatments	May application Mean	SD[1]	June application Mean	SD	All data Mean	SD	Grouping[2]
B	22	13	13	8	19	12	A
S20	21	14	16	21	19	7	A
S40	20	14	9	18	15	16	A
N	49	28	42	12	42	22	B
FERT	41	28	42	12	42	22	B

[1]: SD = standard deviation
[2]: Tukey's T-test ($p=0.05$) gives a critcal value of 21 (%)

Table 3. Phosphorus utilization in percent of applied phosphorus

Treatments	May application		June application		All data	
	Mean	SD[1]	Mean	SD	Mean	SD
B	10	7	6	4	8	6
S20	10	8	9	7	10	8
S40	10	10	6	6	8	8
N	10	9	12	10	11	9
FERT	15	10	15	6	15	8

1): SD = standard deviation

Table 4. Potassium utilization in percent of applied potassium

Treatments	May application		June application		All data		
	Mean	SD[1]	Mean	SD	Mean	SD	Grouping[2]
B	26	14	12	8	19	14	B
S20	24	15	20	12	23	14	A B
S40	25	12	15	14	21	13	A B
N	25	15	24	22	25	17	A B
FERT	33	12	37	12	35	12	A

1): SD = standard deviation
2): Tukey's T-test (p = 0.05) gives a critcal value of 15 (%).

Ammonia volatilization

The experiment took place in early May 1988. Slurry with an ammonia content of 2.2 g per kg slurry (9% DM) and at rates of 5 kg m^{-2} (50 t ha^{-1}) was applied at 15.00 h on the 9 May. Fig. 6 indicates that the conditions inside the tunnels differed from the conditions outside the tunnels because of a higher temperature and a lower relative air humidity during daytime and lower temperature and higher air humidity during night-time. This probably promoted the volatilization process. There was no rainfall during the experimental period, and the air humidity during daytime was very low.

In terms of volatilization resulting from the application techniques, two variations were found. First, the volatilization as a result of the broadcast spreading was much higher than that resulting from the band-spreading techniques in the first 10 h after application. The very low first value from the 400 mm band spacing cannot be explained. Second, the volatilization as a result of broadcast spreading dropped to zero within 30 h, while the volatilization as a result of band spreading did not reach zero for the next 10 and 40 h for the 200 mm and 400 mm band spacings respectively. Very little ammonia seems to have been transported from the slurry layer into the soil, and therefore the ammonia remaining in the slurry layer is potential for volatilization. This conclusion was also reached by Beauchamp et al.(1982). The herbage yields found in the field experiments can also be explained by this conclusion.

With all application techniques there was an increase in volatilization the day after spreading.

During the first 17 h after spreading the volatilization was 37% lower with the 200 mm spacing and 74% lower with the 400 mm spacing as compared with broadcast spreading. In the subsequent hours there was more volatilization from the

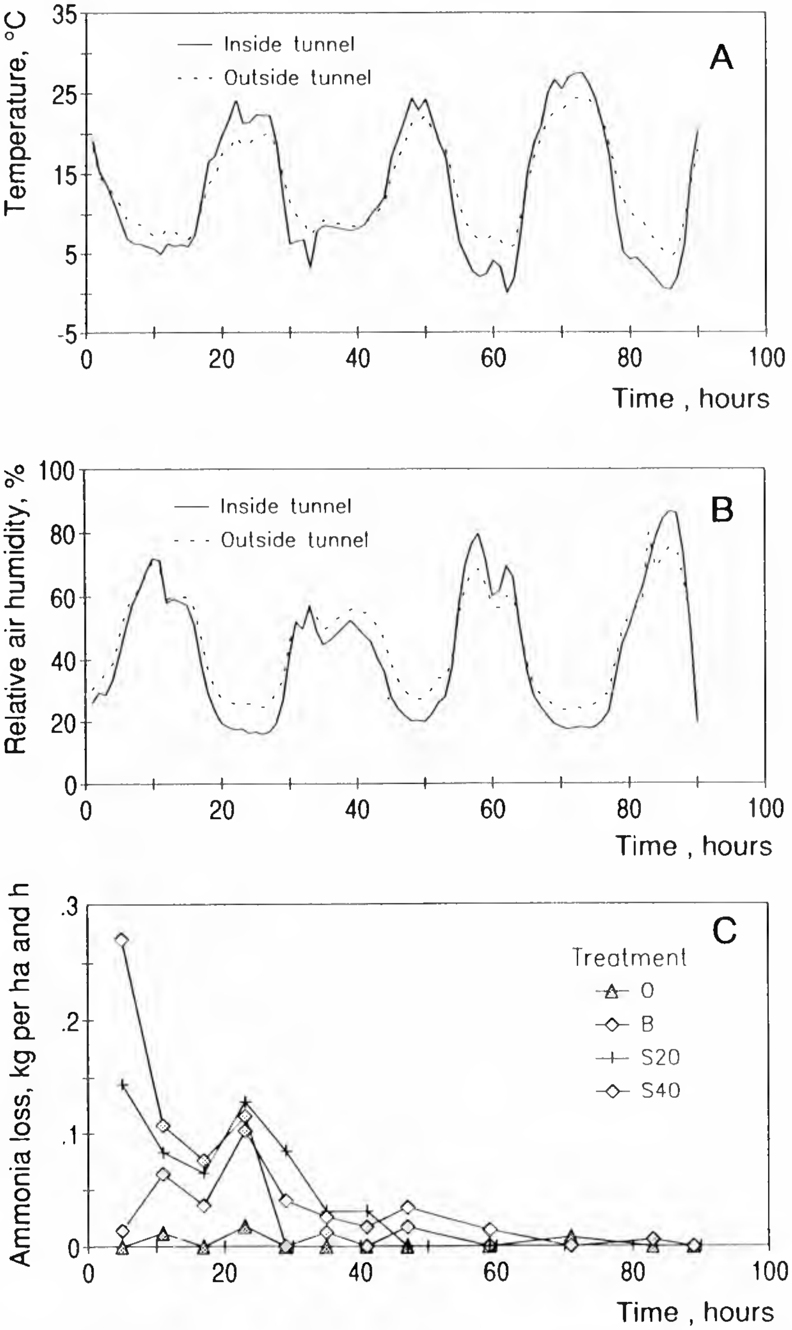

Figure 6. Temperature (A) and relative air humidity (B) inside and outside the wind tunnel, and ammonia volatilization (C). In Fig. C the spreading techniques are broadcast spreading (B) and band spreading with band spacing of 200 mm (S20) and 400 mm (S40). 0 is the control (no treatment). Hour 0 = 15.00 h

band-spread slurry than from the broadcast slurry. After five days the measurements were terminated. In total 8% less ammonia had then evaporated from the band spread-slurry, band spacing 200 mm, and 38% less from the band spread-slurry, band spacing 400 mm, than had evaporated from the broadcast slurry.

SUMMARY

Band spreading of slurry on grassland resulted in dry matter yields that were not significantly different from those resulting from broadcast spreading of slurry. In the experiments surface application of slurry resulted in a yield increase of about 25% compared with that of plots without slurry application. The effect of the slurry was about 40-60% that of the fertilizer.

Slurry injection in May gave dry matter yields on the same level as those resulting from other slurry application techniques. Slurry injection in June gave dry matter yields that sometimes differed greatly from those resulting from other slurry application techniques. In some of the experimental fields the dry matter yields did not differ significantly from those from the fertilizer plots.

Nitrogen utilization of applied slurry was influenced by the application technique. Slurry injection gave a significant increase in the degree of utilization compared with the other techniques. This can be explained by the minimal ammonia volatilization and the good contact between ammonia ions and the soil colloids brought about by this technique.

Some reduction in ammonia volatilization could be expected with the band spreading of slurry. During the first hours after application the reduction was very significant, but since the ammonia that did not evaporate in the first period after spreading tended to evaporate later, this difference decreased. This can explain the yield response results and the values for the nitrogen utilization.

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Vegetative and reproductive growth of *Poa pratensis* L. as influenced by soil compaction

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Aamlid, T.S. 1991. Vegetative and reproductive growth of *Poa pratensis* L. as influenced by soil compaction. Norwegian Journal of Agricultural Sciences 5: 163-181. ISSN 0801-5341.

Three ecotypes of *Poa pratensis* L. collected from loose ('Herøya') or densely compacted ('Foss', 'Sunnvollen') soils and typical genotypes of the commercial cultivars 'Leikra' and 'Lavang' were propagated vegetatively and planted in six field trials at two compaction levels. On a sandy loam or a loamy sand, compaction reduced both vegetative and reproductive growth, the lateral spread of rhizomes being more affected than growth within tufts. On a loam or a silt loam or a silty clay loam, growth was generally enhanced by compaction. Both dry matter production and seed yield were higher in 'Sunnvollen' than in the other ecotypes, the two commercial cultivars ranking last for thousand seed weight and seed yield. Though there were some tendencies, no significant compaction-ecotype interaction was detected. The results are discussed in relation to soil physical analyses, especially penetration resistance, air-filled porosity and air permeability.

Key words: Adaptation, ecotypes, rhizomes, seed production, soil air relations, soil density, soil strength, soil types, yield components.

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One of the most serious problems in modern agriculture is soil compaction. Based on normal Norwegian farm practice, Njøs (1971) calculated that each point in intensively managed grasslands was covered by tractor wheels four times per season. In cereal production, the corresponding number was 1.6-2.5, but according to Eriksson et al. (1974) four to five or even more coverings are not uncommon.

Most concern about compaction seems to be devoted to annually tilled soils (for recent reviews see Soane et al. 1981, Boone 1988, Håkansson et al. 1988), probably because perennial grasses are generally known to prevent the deterioration of soil structure caused by traffic, trampling, heavy rains and so on (Håkansson 1965, Wiklert 1964). However, in areas where direct ensiling is the prevailing method of grass conservation and slurry is distributed to the fields by heavy tankers, traffic often impairs soil structure in grasslands as well (Tveitnes & Njøs 1974, Myhr & Njøs 1983, Frost 1988). Even the treading of grazing animals has been reported to increase bulk density of the topsoil to harmful levels (Tanner & Mamaril 1959, Edmond 1966); this aspect may attract more attention and stimulate to renewed interest in grazing systems in the future.

Soil compaction is also a major concern in sportsfields and other recreational grasslands (Beard 1973, Håbjørg 1988). Though the direct wear and abrasion injury associated with various kinds of sports may be more conspicuous, the cumulative effect of foot and wheel traffic on soil physical properties will often be more deleterious in the long run. Beard (1973) calculated that a 90 kg football player would exert a static ground pressure equivalent to 1.04 MPa when wearing shoes with cleats and two to three times this value when running. Madison (1971) in fact considered compaction to be the 'foremost problem of turfgrass management'.

Mainly because of its high tolerance to wear injury, smooth meadow grass (*Poa pratensis* L.) is one of the main species of amenity grasslands. This species is also utilized for fodder production, mainly in long-lasting or permanent pastures. Because of its dependence on rhizomes, compacted soils might be expected to restrict the performance of this species in particular. As demonstrated by Fisher (1964), circumnutational growth movements may aid rhizomes in soil penetration; nevertheless, Shearman & Watkins (1985) found that compaction reduced the lateral spread of 17 out of 20 cultivars of smooth meadow grass.

In Norway, the basic seed of smooth meadow grass is partly produced on silty clay loams at Hellerud, approximately 30 km northeast of Oslo. In order to control *Poa annua* L. and *Alopecurus geniculatus* L., plants of *Poa pratensis* L. are commonly raised in a greenhouse and transplanted into the field at a row distance of 60 cm. Under these conditions, it is frequently observed that unfavourable soil structure delays or inhibits closure of the sward (R. Hillestad pers. comm.).

The objective of the research described in this report was to elucidate the influence of physical soil properties on growth, development and seed production of smooth meadow grass on different soil types. Besides two commercially available cultivars, three edaphic ecotypes were included in a first attempt to examine possible adaptation to adverse physical soil conditions.

MATERIALS AND METHODS

Six experimental fields were established on various soils at Landvik (ca. 280 km southwest of Oslo), and at Hellerud and Leirsund (ca. 30 km northeast of Oslo) in 1987 and 1988 (Table 1). Each field included six replicates, all divided into two

Table 1. Location, year of establishment, textural composition, organic matter content (OM) and soil type (Hillel 1982) at the six experimental fields

Field	Loc.	Year	Sand	Silt[1]	Clay	OM[2]	Soil type
			%	%	%	%	
1	Landvik	1987	83	12	5	3.5	Loamy sand
2	Landvik	1988	72	22	6	9.5	Sandy loam
3	Landvik	1988	26	61	13	7.9	Silt loam
4	Hellerud	1987	11	64	25	6.5	Silt loam
5	Hellerud	1988	7	61	32	4.5	Silty clay loam
6	Leirsund	1987	46	46	8	2.7	Loam

[1] 0.002 - 0.06 mm.

[2] % OM = % ignition loss - (1 + (0.05 · % clay)) (Riley 1979)

Table 2. Date, estimated water content (Wc.), and number of wheelings (No.) for the compaction treatments at the experimental fields

Field	First compaction treatment[1]			Second compaction treatment		
	Date	Wc.	No.	Date	Wc.	No.
1	June 12	Wet	2	August 5	Wet	2
2	June 23	Dry	4			
3	June 23	Moist	4			
4	June 22	Wet	1			
5	June 20	Dry	2	August 30	Wet	1
6	July 2	Moist	2	August 12	Moist	2

[1] Immediately before planting.

main plots. Before planting, one of the main plots was tilled with a cultivator harrow (fields 1,2,3) or a rotary hoe (fields 4,5,6); the other one was covered, wheel track by wheel track, with a tractor weighing a total of 24.8 kN (Landvik) or 23.2 kN (Leirsund/Hellerud). The number of passages was subjectively adjusted for the soil water content, and in some cases additional wheeling was carried out approximately two months after planting (Table 2).

Vegetatively propagated plants of five ecotypes of smooth meadow grass - each consisting of two to six tillers - were sorted according to their size and transplanted into the fields. The main plots comprised 15 plants (three of each ecotype) which were randomly distributed at a distance of 1 m. Two of the ecotypes were typical genotypes of the commercially available cultivars 'Leikra' and 'Lavang'. The remaining three were collected in the Grenland region, approximately 180 km southwest of Oslo; 'Foss' and 'Sunnvollen' from extremely compact soils of permanent wheeltracks (penetration resistance > 5 MPa; a great amount of gravel and stones in the soil complicated the measurement at the latter location), and 'Herøya' from a rather loose soil close to an old fence pillar (penetration resistance 0.75 MPa).

Basic fertilization prior to soil tillage was 40 kg N ha^{-1} in NPK fertilizer 16-7-12. When considered necessary, the fields were irrigated after planting; otherwise no irrigation was applied. Because of very wet conditions when preparing the soil at field 4, most of the plants died within a few weeks of planting; therefore, on 27 July 1987, non-compacted plots were retilled, and, with occasional exceptions, plants from both soil treatments were replaced with new ones. Nevertheless, growth was generally very poor in this field, and little importance will be attached to the results.

In both the year of establishment - after the final compaction treatment had been carried out - and the subsequent seed production year, soil strength (Taylor 1974) was measured at 0-10 and 10-20 cm depths with an Eijkelkamp hand-operated penetrometer. The surface areas of the probes, all of them with 60° cone angles, were 1.0, 2.0 or 3.5 cm^2. Ten measurements were carried out per main plot; the lowest and highest values were disregarded, and the mean value of the remaining eight was included in statistical analyses (Børresen 1987).

For determination of soil bulk density, porosity and pore size distribution, 100 cm^3 cylindrical soil samples were taken from undisturbed soil at 5-10 and 20-25 cm depths at the same time as the first assessment of penetration resistance. Four cylinders were taken from each depth of the compacted and uncompacted main plots in one replicate per field. Because of incomplete measurements of soil specific weights, total porosity was determined as the volumetric water content at complete saturation. This method may involve an underestimation of 2 to 4 percentage units (Riley 1979, 1983c). The pore size distribution was determined using traditional pF techniques (Riley 1979), assigning the pore equivalent diameter to extraction pressures as follows: 30 µm = pF 2, 3 µm = pF 3 and 0.2 µm = pF 4.2 (Børresen 1987). The air permeability at pF 2 was measured as described by Green & Fordham (1975).

In October 1987 and 1988, plants from three replicates of each field were excavated and brought into the laboratory for assessment of vegetative growth and development (Aamlid 1990b). Plants in the remaining three replicates were left in the fields for seed production studies in the following year. No mowing or fertilization was carried out in autumn, but in the subsequent spring, 30 and 40 kg N ha^{-1} were applied in NPK fertilizer 14-6-16 and 16-7-12 at Landvik and Leirsund/Hellerud, respectively.

Prior to seed harvest in 1988 and 1989, the lateral spread of each plant was assessed as the greatest distance between panicles and rhizomes. Seed yield and its components were determined according to the procedure described by Aamlid (1990b). Speed of germination (10 days) and germination capacity (28 days) were recorded for seeds from fields 1 and 6.

RESULTS

Soil physical conditions

Compaction greatly increased penetration resistance on all fields (Table 3). The effect was generally more marked at 0-10 cm than at 10-20 cm depths. An exceptionally high resistance was measured on field 4 in the year of establishment, but, unlike the other fields, this effect was largely weakened during the following

Table 3. Penetration resistance (MPa) at different soil depths on uncompacted (Uc.) and compacted (C.) plots at six experimental fields in the year of establishment (Year 1) and one year later (Year 2). W/w indicates the soil water content (weight %) on uncompacted plots on days when penetration resistance was measured

		0-10 cm				10-20 cm			
Field	Year	Uc.	C.	Sign.[1]	W/w	Uc.	C.	Sign.[1]	W/w
					Loamy sand / sandy loam				
1	1	0.39	1.30	**	18	0.82	1.31	**	19
	2	0.63	1.97	*	16	1.18	1.93	*	14
2	1	0.86	2.11	**	31	1.16	1.90	ns	43
	2	0.99	1.64	**	27	1.55	1.77	*	26
					Silt loam /silty clay loam				
3	1	1.04	1.82	*	32	1.36	1.63	*	35
	2	0.89	1.32	**	33	1.18	1.41	**	35
4	1	1.29	4.22	*	30	1.75	3.40	*	29
	2	0.97	1.40	ns	31	1.19	1.62	ns	33
5	1	0.54	1.01	*	30	0.68	0.98	*	29
	2	0.88	1.23	*	-	1.03	1.13	ns	-
					Loam				
6	1	0.61	1.65	*	27	0.87	1.60	*	26
	2	0.40	0.93	*	32	0.82	1.10	ns	29

[1] In this report $P \leq 0.001$, $0.001 < P \leq 0.01$ and $0.01 < P \leq 0.05$ are denoted by ***, **and *, respectively.

Table 4. Dry bulk density and air permeability at two depths of uncompacted (Uc.) and compacted (C.) plots on different soil types

	Bulk density (kg dm^{-3})				Air permeability (µm^2)			
	5-10 cm		20-25 cm		5-10 cm		20-25 cm	
	Uc.	C.	Uc.	C.	Uc.	C.	Uc.	C.
				Loamy sand / sandy loam				
Field 1	1.32	1.60	1.52	1.50	12.0	4.2	6.7	4.5
Field 2	0.90	1.25	1.18	1.36	41.8	2.1	14.4	13.9
				Silt loam / silty clay loam				
Field 3	0.99	1.17	1.10	1.29	20.8	0.2	2.4	1.6
Field 4	1.23	1.45	1.39	1.54	7.2	1.6	1.4	1.4
Field 5	1.38	1.43	1.46	1.50	8.0	6.2	2.9	0.3
				Loam				
Field 6	1.14	1.42	1.30	1.39	12.9	1.7	13.0	2.6

winter. With the exception of this field, the relative effect of compaction on soil strength was in fact greater and more persistent on coarse- than on fine-textured soils.

The bulk density of the topsoil layer was increased more by compaction on the sandy soils at Landvik and on the loam at Leirsund than on the heavier soil types (Table 4). At a 20-25 cm depth, however, the soil in field 1 was rather dense even in the uncompacted state, and no effect of compaction was detectable. The same conclusion was valid for both depths in field 5.

With the exception of the surface layer in field 3, the highest air permeabilities on uncompacted plots were recorded on sandy soils. The effect of compaction on the topsoil was most severe in field 2, and even more so in field 3, where the permeability was reduced to about 1% of that measured on uncompacted plots. The clayey soils at Hellerud seemed to maintain a reasonable air permeability in the topsoil even on compacted plots, but at a 20-25 cm depth, the absolute effect of compaction was in fact most pronounced in field 6.

With the exception of field 5, compaction generally decreased the total porosity of the topsoil layer (Fig. 1a). The effect could wholly be ascribed to a severe reduction in the volume of coarse, air-filled pores (>30 µm). On the sandy soils at Landvik, the volume of such pores exceeded 10% (v/v) even after compaction, but on heavy soils, volumes below 5% occurred. As an average for all fields, the available soil water capacity (pF 2-4.2) was 2.3 percentage units higher on compacted than on uncompacted plots.

In three out of six fields, compaction clearly reduced total porosity at a 20-25 cm soil depth (Fig. 1b), but the effect on pore size distribution was not as evident as it was for the surface soil. In many cases, the volume of pores below 3 µm actually seemed to be more affected than the volume of pores beyond this limit.

Vegetative plant growth

Effects of compaction

Because of the split plot design, offering only 2 degrees of freedom for the error term, the main effects of compaction on plant growth were often statistically nonsignificant; nevertheless, the tendencies were generally clear enough. The most remarkable result was a clear distinction between soil types as to plant response to compaction.

On the most coarse-textured soil (field 1), compaction greatly reduced plant diameter and the number and weight of rhizomes and tillers outside

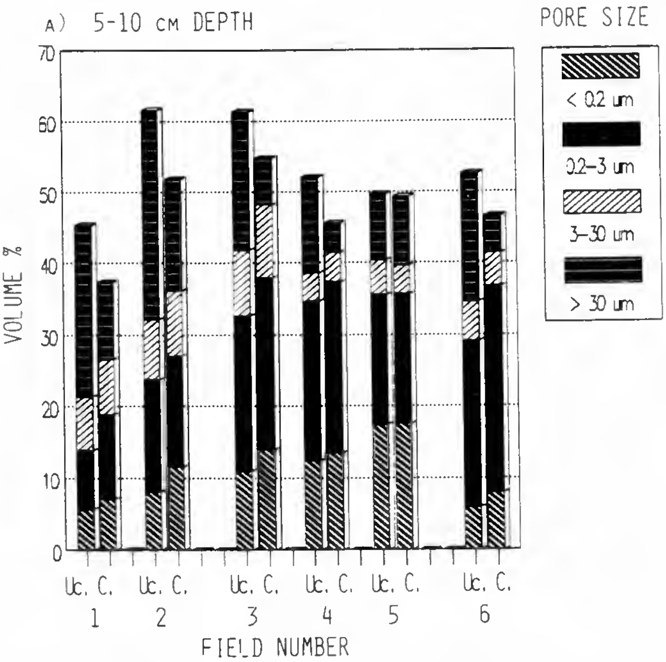

Figure 1. Pore size distribution at two soil depths in six experimental fields as influenced by compaction. Uc. = uncompacted, C. = compacted

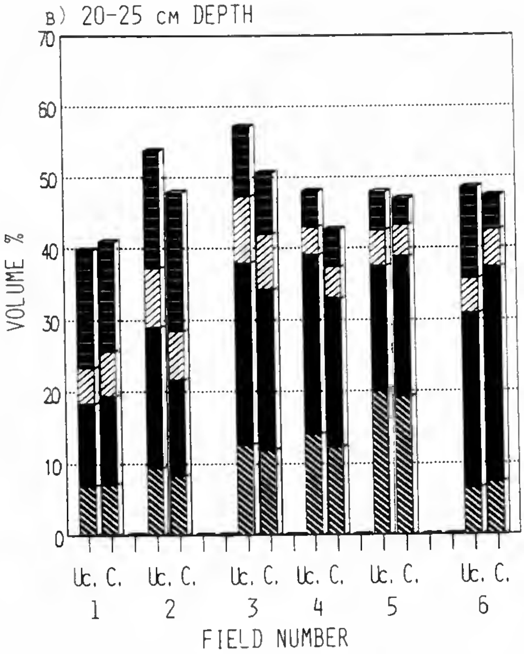

Table 5. Rhizome number per plant and plant diameter as related to uncompacted (Uc.) and compacted (C.) plots on different soil types. Means of five ecotypes. The rhizome number was counted on excavated plants in autumn in the year of establishment; plant diameter was monitored as the distance between the outermost panicles in the following year of seed production

	Rhizome number			Plant diameter (mm)		
	Uc.	C.	Sign.	Uc.	C.	Sign.
			Loamy sand / sandy loam			
Field 1	77.3	49.8	ns	531	275	**
Field 2	46.1	47.3	ns	379	280	**
			Silt loam / silty clay loam			
Field 3	40.4	68.7	ns	236	317	ns
Field 4	4.4	7.4	ns	151	179	ns
Field 5	46.2	43.6	ns	218	296	*
			Loam			
Field 6	25.5	31.4	ns	353	271	**

Table 6. Number of tillers within tufts and number of tillers from rhizomes as related to uncompacted (Uc.) and compacted (C.) plots on different soil types. Means of five ecotypes

	Tillers within tufts			Tillers from rhizomes		
	Uc.	C.	Sign.	Uc.	C.	Sign.
			Loamy sand / sandy loam			
Field 1	55.6	55.6	ns	112.0	65.5	ns
Field 2	33.7	38.8	ns	48.3	38.4	ns
			Silt loam / silty clay loam			
Field 3	49.4	80.7	**	40.9	89.8	*
Field 4	14.7	19.3	ns	5.1	11.9	ns
Field 5	43.3	60.6	ns	48.3	58.0	ns
			Loam			
Field 6	76.2	83.5	ns	23.2	31.9	ns

tufts (Tables 5 and 6, Fig. 2). Though a slight increase in the weight, but not in the number, of tillers within tufts was recorded, total dry matter accumulation was reduced by 30% on the compacted plots as compared with the uncompacted controls.

On average for ecotypes, compaction reduced plant diameter and dry matter production outside tufts also at field 2, but, since this was largely compensated by increased growth within tufts, the difference in total dry weight was marginal.

With very few exceptions, compaction enhanced rhizome formation, tillering and dry matter accumulation on the loam at Leirsund (field 6) and on the fine-textured soils at Landvik and Hellerud. As in the sandy soils mentioned above, compaction seemed to impair the lateral spread of the rhizomes at field 6, but this was clearly not the case in fields 3, 4 and 5.

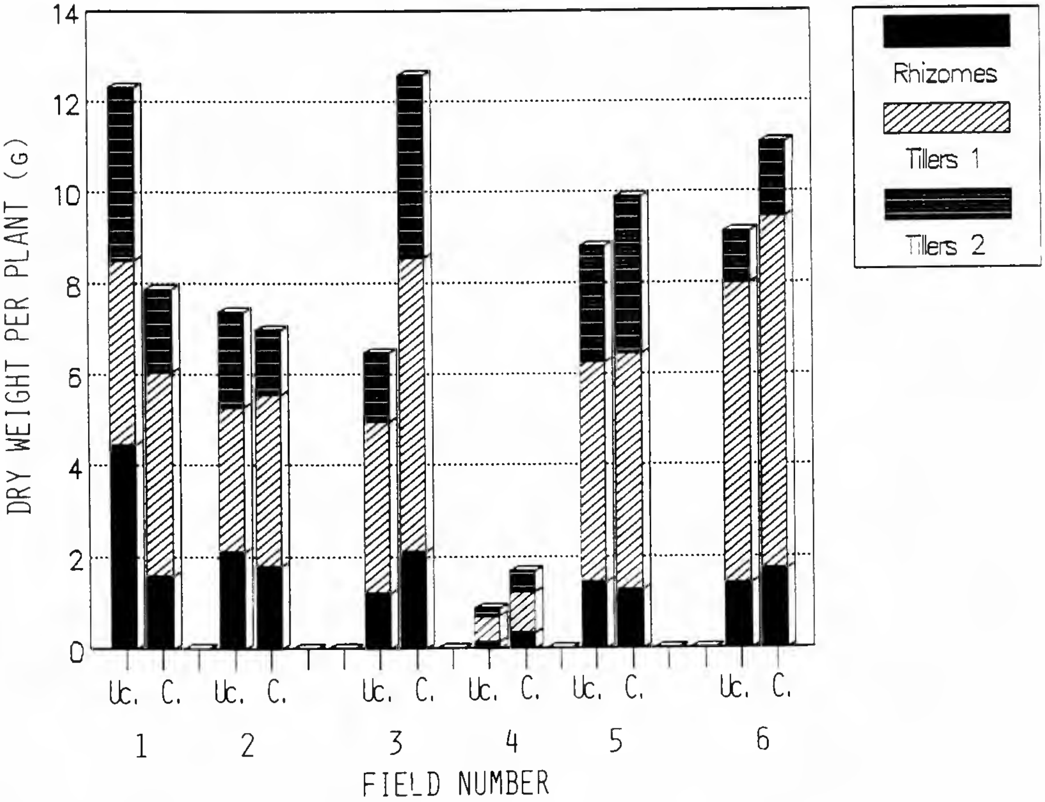

Figure 2. Dry weight of rhizomes, tillers within (tillers 1) and outside (tillers 2) tufts as influenced by soil compaction on six experimental fields. Means of five ecotypes. Uc. = uncompacted, C. = compacted

Table 7. Plant height, plant diameter, rhizome number, number of tillers within and outside tufts and total tiller number for five ecotypes of *Poa pratensis*. Means of uncompacted and compacted plots on six experimental fields

Ecotype	Plant height mm	Plant diameter mm	Rhizome number	Tiller number		
				Within tufts	Outside tufts	Total
'Leikra'	220	293	30.1	43.1	22.2	65.3
'Lavang'	156	279	83.6	38.9	91.0	129.9
'Foss'	130	324	37.3	52.1	44.9	97.0
'Sunnvollen'	164	347	35.2	93.4	62.4	155.8
'Herøya'	144	210	17.2	27.4	18.5	45.8
Significance	***	**	***	***	***	***
$LSD_{0.05}$	27	72	22.3	20.7	25.6	35.0

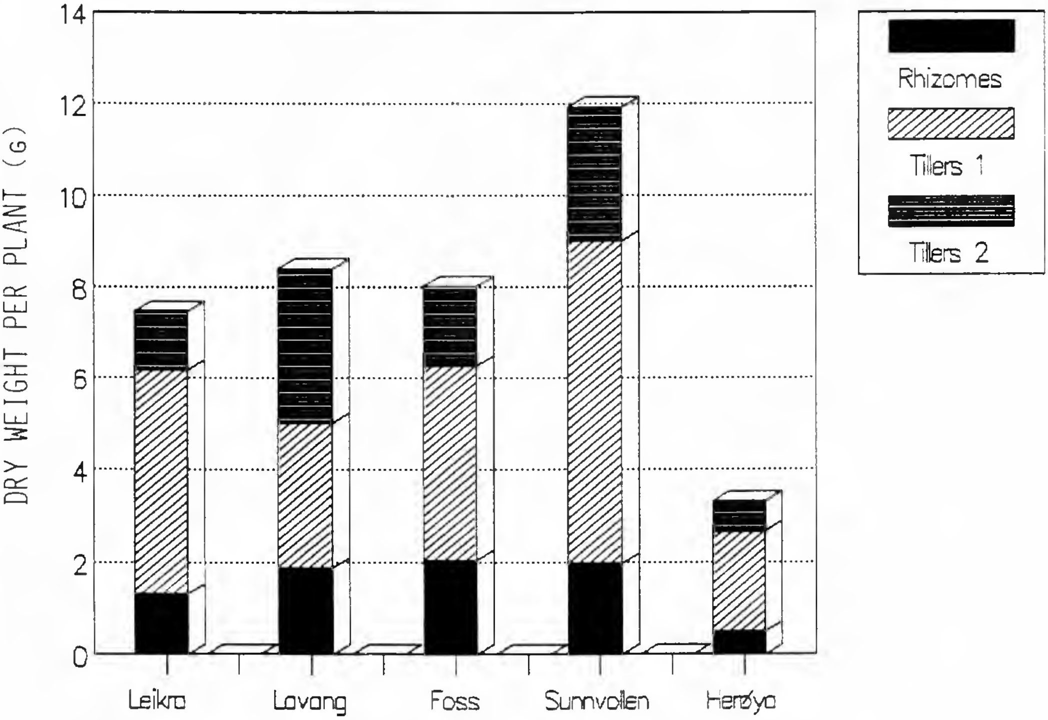

Figure 3. Dry weight of rhizomes, tillers within (tillers 1) and outside (tillers 2) tufts in five ecotypes of *Poa pratensis*. Means of two compaction treatments and six experimental fields

Ecotypes

The main effects of ecotype were analysed using the ecotype·field interaction as the error term. Whilst 'Leikra' developed significantly higher plants than the other ecotypes, 'Foss' generally exhibited a decumbent growth habit (Table 7). Along with 'Sunnvollen' this ecotype seemed to occupy a larger surface area than 'Leikra', 'Lavang' and 'Herøya', the last mentioned being especially inferior both in this respect and with regard to total dry matter production (Fig. 3). Because of an abundant formation of rhizomes, and a high proportion of the rhizomes emerging as tillers, 'Lavang' had the highest number and weight of tillers outside tufts. However, since 'Sunnvollen' had more than twice as many tillers within tufts, this ecotype also had the greatest dry matter production.

Compaction · ecotype interactions

Significant compaction · ecotype interactions were recorded at four out of six experimental fields, but the results were often contradictory, even within soil groups. In an overall analysis using the field · compaction · ecotype interaction as the error term, compaction retarded lateral growth more in 'Sunnvollen' than in the other ecotypes (Table 8a). 'Sunnvollen' was also the only ecotype which attained a higher dry weight on uncompacted than on compacted plots (Table 8b). None of these effects were significant, however.

Seed production

On an average for fields and compaction treatments, blowing of the threshed seed (Statens frøkontroll 1987a) gave significantly lower pure seed percentages for

Table 8. Effect of compaction on (a) plant diameter and (b) dry weight per plant (except roots) of five ecotypes of *Poa pratensis*. Means of six experimental fields

	'Leikra'	'Lavang'	'Foss'	'Sunnvollen'	'Herøya'
(a)			Plant diameter (mm)		
Uncomp.	308	294	339	390	224
Comp.	278	264	307	303	197
C./Uc.	0.90	0.90	0.91	0.78	0.88
Significance of interaction: ns (P=0.40)					
(b)			Dry weight per plant (g)		
Uncomp.	5.70	7.43	7.80	12.45	3.14
Comp.	9.29	9.37	8.24	11.43	3.51
C./Uc.	1.62	1.26	1.06	0.92	1.12
Significance of interaction: ns (P=0.11)					

Table 9. Intercept and regression coefficients with significance levels in the full model of contributions to seed yield per plant (mg) in four ecotypes by the components: Number of panicles per plant (PN), number of seeds per panicle (SN) and thousand seed weight (TSW) (mg) when included in this order in the models

	'Leikra'	'Lavang'	'Foss'	'Sunnvollen'	'Herøya'
Intercept	-9644	-6169	-13049	-25494	-10810
PN	67.3***	28.6***	89.3***	84.3***	81.7***
SN	12.4***	25.8***	36.7***	66.3***	19.6***
TSW	26.6**	13.6*	13.6*	29.5**	19.5***

Table 10. Simple correlation matrices among seed yield (SY) per plant and its components: Number of panicles per plant (PN), number of seeds per panicle (SN) and thousand seed weight (TSW) in five ecotypes

	PN	SN	TSW	PN	SN	TSW
		'Leikra'			'Lavang'	
SY	0.94***	0.36ns	0.27ns	0.89***	0.57**	0.24ns
PN		0.10ns	0.15ns		0.20ns	-0.31ns
SN			0.07ns			-0.21ns
		'Foss'			'Sunnvollen'	
SY	0.95***	0.37*	0.58***	0.97***	0.39*	-0.03ns
PN		0.09ns	0.40*		0.20ns	-0.17ns
SN			0.58**			0.20ns
		'Herøya'				
SY	0.95***	0.51**	0.43*			
PN		0.30ns	0.25ns			
SN			0.43*			

'Leikra' and 'Lavang' than for the other ecotypes:

'Leikra'	'Lavang'	'Foss'	'Sunnvollen'	'Herøya'
79.0	78.0	86.1	86.7	86.7

The three principal yield components contributed significantly to total seed yield in all ecotypes (Table 9); this result must be interpreted in view of the low intercorrelations found between the yield components (Table 10). Panicle number explained 79-94% of the total variation in seed yield.

Seed yield per plant was reduced significantly by compaction on both sandy soils at Landvik (Fig. 4). The number of panicles from rhizomes was more reduced than the corresponding number within tufts. In field 2 seed number per panicle and thousand seed weight were slightly higher on compacted than on uncompacted plots (Table 11), but this could far from compensate for the scarcity of panicles after compaction.

On average for the heavier soils at Landvik and Hellerud, compaction approximately doubled the number of panicles per plant. In field 3 seed production appeared to be more affected within than outside tufts, but this is probably an artifact arising from inexperienced personnel making the distinction between the two categories. As opposed to field 5, the number of seeds per panicle varied inversely with panicle number on fields 3 and 4. Thousand seed weight seemed to be re-

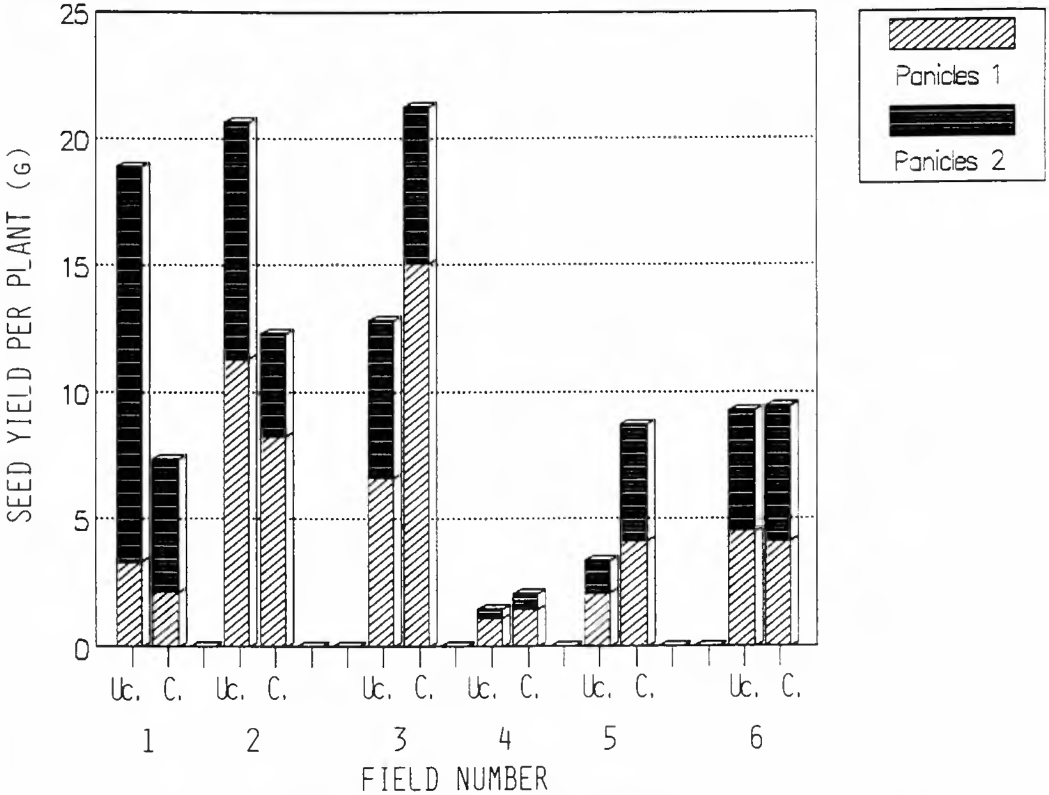

Figure 4. Seed yield (100% purity; 14% water content) of panicles within (panicles 1) and outside (panicles 2) tufts as influenced by soil compaction on six experimental fields. Means of five ecotypes. Uc. = uncompacted, C. = compacted

Table 11. Number of panicles per plant, seed number per panicle and thousand seed weight (mg) as related to uncompacted (Uc.) and compacted (C.) plots on different soil types. Means of five ecotypes

	Panicle number			Seeds per panicle			Thousand seed weight		
Field	Uc.	C.	Sign.	Uc.	C.	Sign.	Uc.	C.	Sign.
				Loamy sand / sandy loam					
1	210.9	83.1	***	233	224	ns	339	336	ns
2	227.7	123.6	*	255	287	ns	324	332	ns
				Silt loam / silty clay loam					
3	137.7	282.7	*	296	222	**	341	327	ns
4	20.9	32.9	ns	152	138	ns	330	332	ns
5	59.8	121.6	*	175	235	ns	259	261	ns
				Loam					
6	107.9	125.5	ns	247	219	ns	338	328	ns

Table 12. Seed yield per plant (SY g; 100% purity; 14% water content), number of panicles within tufts (PNi), number of panicles outside tufts (PNo), total panicle number (PNt), number of seeds per panicle (SN), thousand seed weight (TSW mg), speed of germination (SG %) and germination capacity (GC %) in five ecotypes. Means of two compaction treatments and six experimental fields (two fields for SG and GC)

Ecotype	SY	PNi	PNo	PNt	SN	TSW	SG	GC
'Leikra'	6.22	38.5	35.8	74.3	269	249	60.7	70.3
'Lavang'	5.02	45.4	77.3	122.7	123	267	70.7	80.0
'Foss'	12.81	61.9	61.5	123.4	259	367	73.7	86.3
'Sunnvollen'	21.54	118.1	116.4	234.5	224	387	69.3	86.6
'Herøya'	7.58	48.9	35.5	84.4	244	334	60.9	77.4
Sign.	***	**	**	**	***	***	ns	***
$LSD_{0.05}$	7.03	39.0	46.5	74.6	45	28	-	2.4

latively unaffected by compaction treatments.

On the intermediate textured soil in field 6, panicle number was slightly higher after compaction, but this was compensated by the other yield components, making any difference barely detectable with respect to seed yield.

Germination was unaffected by compaction treatments.

'Sunnvollen' was clearly superior to the other ecotypes when number of panicles and seed yield were concerned (Table 12). 'Lavang' and 'Foss' were almost equally ranked with respect to panicle number, but because 'Lavang' had less than half as many seeds per inflorescence and a much lower seed weight, the seed yield was significantly higher in 'Foss'. The lowest panicle number and thousand seed weight, but the highest number of seeds per panicle, were found in 'Leikra'.

Although there was a clear tendency, no significant difference was found between ecotypes as to germination after ten days. At the end of the test period, germination capacities were significantly higher for 'Foss' and 'Sunnvollen' than for 'Lavang', 'Herøya' and, in particular, 'Leikra'. Germination capacity was more clearly related to thousand seed weight than was speed of germination ($r = 0.69^{***}$ and $r = 0.26$ns, respectively).

For all yield components great discrepancies were found between fields as to the response to compaction in various ecotypes. On average, there was a slight tendency for 'Sunnvollen' and, to a lesser extent, 'Herøya' to be more sensitive to dense soils than 'Leikra', 'Lavang' and 'Foss', but this was hardly enough to consider as a general trend.

DISCUSSION

Soil compactibility

From a Swedish investigation, Eriksson et al. (1974) concluded that the water content was the factor most essential for the compactibility of the surface layer of agricultural soils. Next in order of ranking were number of passages and tractor weight and wheel characteristics. The results from field 4 clearly prove the kinds of disastrous effects tillage and compaction of heavy soils at too high a water content may have on plant growth and yield. Growth failed in both uncompacted and compacted plots; in the former because of unfavourable aggregate size and poor root-soil contact, in the latter probably because of the great mechanical impedance encountered by plant roots and rhizomes.

According to Bertilsson (1971) and Hillel (1982), soil compactibility reaches its maximum at an intermediate water content. Below this level the obtainable bulk density increases with increased soil wetness, mainly because water acts as a lubricant, reducing internal friction between soil particles. Beyond the optimum, as the soil approaches the saturation point, compactibility is reduced through lack of air-filled porosity, or - on fine-textured soils - air bubbles may be occluded within the soil and therefore unable to escape. This theory has considerable relevance to the results for field 5, in which the soil was probably on the dry side of the optimum at the compaction in June 1988 and on the wet side two months later. In the latter case a resiliency of the soil was actually reported by the tractor driver. For this field hardly any effect of compaction on bulk density or total porosity was detectable (Table 4, Fig. 1).

Bulk density

Petelkau (1984, 1986) considers that root proliferation is likely to be restricted by bulk densities beyond 1.52 and 1.40 kg dm^{-3} on sandy loams and silty clay loams, respectively. Thus, high density may be an explanation for growth being hampered by compaction in field 1. In general, however, the adoption of the bulk density criterion requires a correction for soil organic matter content (Table 1). For example, the difference in bulk density between uncompacted plots in fields 4 and 5, which had a fairly similar textural composition, can primarily be ascribed to a higher humus content in the former field (Table 1). For the same reason, a density of 1.42 kg dm^{-3} does not necessarily indicate an unfavourable soil structure in field 6, as this soil contained only 2.7% organic matter. Based on 26 samples from Norwegian clay soils (>10-12% clay, depending on silt content), Riley (1983b) calculated that the bulk density decreased by 0.09 kg dm^{-3} per percentage unit increase in organic matter content.

Soil strength

Many workers consider that soil strength, measured using a penetrometer, is a more relevant criterion of plant root growth than bulk density (Drew & Goss 1973, Taylor 1974, Gooderham 1977, Ehlers et al. 1983). For example, Taylor & Gardner (1963) obtained a correlation as close as $r = -0.96$ between penetration resistance and cotton taproot growth in soil cylinders. Besides bulk density, soil water content was the major factor affecting soil strength, and thereby root penetration. From other experiments Taylor & Ratliff (1969) and Barley et al. (1965) concluded that soil water potential rarely affects root growth directly, but rather through the greater penetration resistance encountered in dry soils. This view has later found physiological support (Greacen & Oh 1972).

The influence of soil water content on penetrometer readings is evident from Table 3. For example, the consistent increase in resistance from the first to the second year in field 1 can best be explained by the lower water content at the latter measurement. In field 6 penetrometer readings probably overestimated soil loosening during winter.

The fundamental justification for relating root growth to penetration resistance is the fact that root tips are unable to penetrate pores of less than their own thickness, normally in the range 100-800 um (Wiersum 1957). Though the actual limit was later modified to mean the diameter of the stele rather than of the entire root (Scholefield & Hall 1985), it seems quite obvious that roots have to create their own path through the soil by displacement of soil particles (Aubertin & Kardos 1965). However, unlike a rigid metal penetrometer forcing its way along a straight line, plant roots are flexible and benefit from cracks and planes of weakness in the soil (Stolzy & Barley 1968). Slime secretion may reduce or eliminate soil-root friction, and water absorption may provide shrinkage cracks and fissures. Moreover, the combination of axial and radial pressures exerted by roots is a more efficient way of penetrating the soil than the unidirectional movement of a cone penetrometer. For all these reasons, cone penetrometers commonly measure soil strength values two to eight times greater than those encountered by plant roots (Eriksson et al. 1974, Whiteley et al. 1981).

It has been reported that penetrometer values from 0.8 to 5.0 MPa completely inhibit root elongation (Greacen et al. 1969). The great variation in estimated values can be explained to some extent by differences in penetrometer techniques. Gooderham (1976) obtained very close correlation between penetrometer readings in the field (13 mm probe) and those obtained with laboratory equipment (1 mm probe) in undisturbed soil cores. Nevertheless, the latter values were 2.4 times those measured directly in the field. Also Dexter & Tanner (1973) proved an inverse relationship between probe diameter and the calculated soil strength values. In the present investigation, smaller probes were often used on compacted than on uncompacted plots; hence the effect of compaction on mechanical impedance might be somewhat overestimated in Table 3.

The relevance of the penetrometer method is also affected by penetration rate and the shape of the probe. Voorhees et al. (1975) found that a 10° probe more closely resembled the tapered tip of a plant root than a 60° probe. This is in good agreement with the theory propounded by Whiteley et al. (1981), who calculated that the pressure required to expand a spherical cavity (like a blunt penetrometer probe) would be 2-5 times that required for a cylindrical cavity (like a root tip or a strongly tapered probe). According to Voorhees et al. (1975), the error caused by great cone angles will be more accentuated on cohesive than on granular soils. It might therefore well be that the soil strength values given in Table 3 are more relevant to plant growth on the loamy sand/sandy loam than on the silty (clay) loams. On uniform, sandy soils in Australia, wheat yields were found to decrease linearly with penetration resistances (30° cone angle) beyond 1.0 MPa (Henderson 1989).

There appears to be little information available on the pressures exerted by rhizomes when penetrating the soil. Fisher (1964) noted that rhizomes have a constant diameter and are therefore unable to widen openings by lateral expansion. On the other hand, rhizomes take advantage of their sharply pointed cataphyll which, acording to observations from gardeners, green managers etc., is able to penetrate even woody roots or asphalt (Petersen 1981). Nevertheless, the general picture will probably be that rhizome extension, but not necessarily formation, is more sensitive to mechanical impedance than root growth, mainly because of the greater diameter and rigidity of the rhizomes. The results from field 6, in which compaction enhanced tillering and dry matter production, but reduced plant diameter, substantiate this conclusion.

Gas exchange

Besides mechanical impedance, restricted soil aeration is a factor commonly associated with soil compaction. In order to provide sufficient gas exchange even after heavy rainfalls, 10% (v/v) is usually reckoned to be a minimum value of coarse air-filled pores (Soane et al. 1981, Boone 1988, Håkansson et al. 1988). This limit can only serve as a rough guideline, however, since gas exchange at the plant root level also depends on the tortuosity and continuity of the pore system. Air permeability might therefore be a better indication of the soil aeration status (Hillel 1982).

In the present material, air-filled porosities considerably below the 10% limit were assessed in soil cores from compacted plots in fields 3, 4 and 6 (Fig. 1), and especially in the case of field 3, air permeability was also very low (Table 4). For this field, however, the representativeness of the small soil cylinders may be questioned, as a great number of cracks and fissures were observed, particularly in the dry year of 1989, and these were avoided at sampling. Jong et al. (1983) and Heinonen (1986) have earlier documented that surface cracks are very efficient in improving gas diffusion, and Boone (1986) highlighted spatial variability as an essential factor with regard to soil aeration and rootability. In an earlier Norwegian experiment (Gaheen & Njøs 1978), the area of surface cracks was significantly increased by soil compaction; this is consistent with observations in field 3 and may partly explain why compaction enhanced plant growth.

Whereas the convective flow of gases in the soil, as measured by air permeability, depends on pore-size distribution, gas diffusion is better correlated to total porosity (Hillel 1982, Boone et al. 1986). Greenwood (1969) in fact calculated that many small pores would be more effective than a few large pores in providing oxygen to plant roots, given that the total pore area was the same. In concurrence with this, Eavis (1972) found that a greater air-filled porosity was required at a low bulk density than at a high bulk density. Other workers have also calculated that gas diffusion will seldom be limiting for plant growth, even after compaction (Tackett & Pearson 1964, Aura 1983). This must be even more so in scattered plant stands, as in the present experiment. And, should the external gas diffusion nevertheless become limiting, there is the possibility that plants can provide their roots with oxygen by means of internal transport (Grable 1966, Greenwood 1969). Root porosities as great as 23% have indeed been reported from compaction/irrigation experiments with smooth meadow grass (Agnew & Carrow 1985).

Plant growth will always be related to soil compactness by an optimum curve (Rosenberg 1964, Eavis 1972). Since compaction increases unsaturated hydraulic conductivity, the optimum degree of compactness (Eriksson et al. 1974) will generally be higher in dry than in wet years (Riley 1983a, Håkansson et al. 1988). Both at Landvik and at Hellerud/Leirsund, however, the precipitation for May-September exceeded the normal level by 20-30% in 1987 as well as in 1988, and although May-July 1989 was rather dry at both locations, results had hardly been markedly different in a wetter year. On the other hand, it seems clear that poor soil-root contact on loose soils may have restricted absorption of water and nutrients, even in wet years. In earlier Norwegian investigations, poor yields of cereals have indeed been associated with excess soil loosening (Njøs 1962, Eggum 1972, Magnus 1980).

Ecotypes/cultivars for compact soils

In light of its extensive use on football grounds and other sports fields, the concept of breeding compaction-tolerant smooth meadow grass cultivars seems very attractive. A first step would be to elucidate the genetical variability in this character. It is then remarkable that 'Sunnvollen' tended to be more vulnerable to compaction than 'Herøya', despite the latter being collected from a much looser soil. This can partly be explained by the great amount of gravel and small stones in the soil native to 'Sunnvollen'; these particles have probably provided pores and channels for root and rhizome extension and have therefore biased the penetrometer readings. Moreover, since the main effect of compaction differed so fundamentally between soil groups, not a lot of emphasis can be attached to the rather vague interactions presented in Table 8. It may be interesting to note that for field 1 - the only field where both vegetative growth and generative growth were severely impaired by compaction - 'Herøya' was in fact relatively most impaired by compaction as regards dry matter production and seed yield, and it ranked second (after 'Sunnvollen') as regards plant diameter. However, owing to their rather tuft-like growth habit, neither of these ecotypes seems well adapted for turf, and, if one were to start breeding for compaction tolerance, then collection and screening of far more ecotypes would be needed. Possibly, a ranking of already existing cultivars - as in the study by Shearman & Watkins (1985) - would be more efficient, at least in the short term.

Seed production

The seed production analysis confirmed the general opinion that panicle number is the most important yield component (Langer 1980). However, since correlations between the components were not significantly negative (Table 10), competition must have been rather low in the scattered plant stands.

Based on the vegetative development in the year of establishment, the difference in seed yields obtained at Landvik and Leirsund/Hellerud was remarkably high. Whilst, on average for fields, the panicle numbers recorded at Leirsund/Hellerud were quite similar to the numbers of tillers counted in the previous autumn, panicle numbers were considerably higher than tiller numbers at Landvik, notably for the fields established in 1988. This indicates that growth at Landvik - unlike Leirsund/Hellerud - proceeded for much longer than tiller countings, which were carried out in the first part of October. The great difference in the mean temperature for October-November, especially in 1988 (5.5 and 0°C at Kjevik and Gardermoen, close to Landvik and Leirsund/Hellerud, respectively) strongly supports this conclusion. Moreover, the high organic matter content of the soils at Landvik has probably supplied nitrogen in this period.

Thousand seed weights obtained at Hellerud in 1989 (field 5) were notably lower than those for the remaining fields. In spite of the fact that rainfall in the period 29 May to 16 July 1989 was greater at Hellerud than at Landvik (87 and 66 mm at Gardermoen and Kjevik, respectively) this probably indicates that water was more severely lacking on the heavy soil at the former location. From Fig. 1 it is evident that a high proportion of the soil water content in field 5 was kept in pores < 0.2 µm, unavailable to plant roots.

Compared with Denmark and Sweden, seed yields of smooth meadow grass are very poor in Norway, less than 200 kg ha^{-1} on average (Statens frøkontroll 1987b, 1988). This can partly be explained by adverse climatic conditions and lack of experience, but this report - as well as an earlier one (Aamlid 1990b) - also suggests that the two Norwegian cultivars 'Leikra' and 'Lavang' do not have a very high seed production potential. For 'Leikra' this can mainly be ascribed to a poor tillering capacity (Aamlid 1990a). 'Lavang', on the other hand, tillers profusely, but since its differentiation of inflorescences starts as early as September (Rognli & Staver 1979), tillers formed in autumn may either become unreproductive or develop only small panicles in the subsequent year. Furthermore, since both 'Leikra' and 'Lavang' are light-seeded, a considerable portion of the gross yield is often lost when cleaning the seed or in the standard blowing procedure.

It is to be hoped that more attention will be paid to seed production characteristics in current Norwegian breeding programme for smooth meadow grass.

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Vegetative and reproductive growth of *Poa pratensis* L. as influenced by soil pH

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Two ecotypes of *Poa pratensis* L. collected at pH 4.5 ('Rønholt') or 7.4 ('Herøya') and typical genotypes of cvs. 'Leikra' and 'Lavang' were grown in pot and field experiments. At $Ca(NO_3)_2$, $Ca(H_2PO_4)$ and K_2SO_4 inputs equivalent to 240 kg N, 60 kg P and 240 kg K ha^{-1}, growth was not affected by pH in the range 4.6-7.1, but failed completely at pH 3.5. When inputs were reduced to 0-100 kg N, 10 kg P and 50 kg K ha^{-1}, tillering and dry matter accumulation were greatest at pH 5.7 in 'Herøya' and at pH 7.1 in the other ecotypes. Growth of roots and rhizomes was more impaired by low pH than was growth of tillers. Plant height was, and dry matter accumulation tended to be, more favourably affected at low rates of nitrogen than at high rates. In the field experiment, pH elevation from 5.5 to 6.6 caused a greater increase in vegetative growth than in seed yield. It is concluded that 'Rønholt' and 'Herøya' were not particularly well adapted to acid and neutral/alkaline soils, respectively.

Key words: Acidification, adaptation, aluminium, calcium, ecotypes, liming, mineralization, nitrification, seed production, yield components.

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Smooth meadow grass (*Poa pratensis* L.) is one of the major species in amenity grasslands throughout the cool temperate climates of the world (Beard 1973, Håbjørg 1988). It generally amounts to 40 to 60 weight per cent of turfgrass seed mixtures, but it is frequently sown as a monoculture as well, notably in sports fields. In Scandinavia more erect and higher yielding cultivars are also often incorporated in seed mixtures for permanent meadows and pastures, particularly in the North.

In the literature, smooth meadow grass is commonly considered to make high demands on the soil reaction value (e.g. Jetne 1981, Håbjørg 1988). At pH-values below 5.5, different species (e.g. *Festuca* spp., *Agrostis* spp.) will usually compete better for soil nutrients giving rise to undesirable botanical compositions. The result will be less persistence and durability in turfgrass areas and decreasing yields in fodder production.

Soil acidification has increased considerably with increasing use of commercial fertilizers. Most important is the nitrification of ammonia. Although some protons are neutralized - by exchanged OH^- or HCO_3^- when NO_3^- is adsorbed by the plant roots, the maintenance of a stable pH requires 2 kg CaO per kg nitrogen in NH_4^+ fertilizers (Nömmik 1966).

Acid precipitation may also contribute to soil acidification. While water containing only CO_2 has a pH value of 5.6, the annual average of the Norwegian precipitation ranges from 4.8 in the northwest to 4.2 on the south coast (Statens forurensningstilsyn 1987). Occasionally it may even fall below 3.5 in industrial areas. Still, the exact contribution of acid rain to the total soil acidification remains a matter of controversy (Last et al. 1980).

A number of workers have reported better botanical composition and higher grass yields when lime has been added (e.g. Pestalozzi 1970, Hovde 1973). Heavy liming is rather expensive, however, and the effect of surface applications on pH in grasslands may often be limited to the 5 cm topsoil layer (Hovde 1973, Håland 1984, Murray & Foy 1980). A steep pH gradient through the soil profile may restrict rooting depth and render the plants more susceptible to drought, nutrient deficiency, and winterkill (Palazzo & Duell 1974, Reid et al. 1969). Furthermore, in many sports fields the soil is composed of nearly pure sand, and since the cation exchange capacity is very low, the added calcium and magnesium compounds may be leached within a few months (Håbjørg 1977).

Instead of changing the soil reaction to fit the desired plants, a greater tolerance to acid soils could be incorporated into the plant material. Since aluminium toxicity is the major reason for poor growth at pH values below 5.0 on mineral soils, tolerance to this element has received most attention. Differential tolerance between cultivars has been found in many species including barley, wheat, rice, lucern and perennial ryegrass (Foy 1974b). In a comparison of 35 cultivars of smooth meadow grass, there was hardly any difference in dry weight accumulation at pH 5.7, but at pH 5.0 the most tolerant cultivar yielded twelve times more dry matter than its most vulnerable counterpart (Murray & Foy 1978).

The objective of the work reported here was to examine whether a differential tolerance to acid soils exists among Norwegian ecotypes and commercial cultivars of smooth meadow grass and, if so, whether such a tolerance can be related to vegetative and reproductive growth habits.

MATERIALS AND METHODS

Plant material

In autumn 1986 ten ecotypes of smooth meadow grass were collected from permanent grasslands in the Skien region, approximately 180 km southwest of Oslo. Two of the localities, 'Rønholt' and 'Herøya' were very different with respect to soil pH (Table 1). In addition, one typical genotype of each of two commercial cultivars, 'Leikra' and 'Lavang', were selected by breeders. Until the start of the various experiments, the genotypes were propagated vegetatively under non-inductive conditions.

Table 1. Bulk density, loss on ignition, $pH(H_2O)$, P-AL, K-AL, $K\text{-}HNO_3$ and Mg-AL in the soil from which 'Rønholt' and 'Herøya' were collected

	Bulk denisty kg dm^{-3}	Ignition loss %	pH (H_20)	P-AL	K-AL	$K\text{-}HNO_3$	Mg-AL
				mg (100g)$^{-1}$			
Rønholt	0.87	9.1	4.5	2	20	36	3
Herøya	0.87	10.4	7.4	1	9	58	17

Pot experiment 1

Sieved sandy soil (2.2 kg dry weight) was filled into tight 2.5 dm^3 plastic pots. pH was adjusted to four different levels by incubation of diluted H_2SO_4 or pure $CaCO_3$ (Table 2). Distilled water was added to 60% of field capacity at free drainage; pots were covered with plastic film and placed at 15°C.

Four weeks after incubation plants of the four ecotypes, each consisting of 2-6 tillers, were cut to 12 cm height and transplanted into the pots. Fertilizer solutions were added as follows:

240 kg N ha^{-1} equivalent to 0.211 g pot^{-1} in $Ca(NO_3)_2 \cdot 4\,H_2O$
60 kg P ha^{-1} equivalent to 0.053 g pot^{-1} in $Ca(H_2PO_4)_2 \cdot H_2O$
240 kg K ha^{-1} equivalent to 0.211 g pot^{-1} in K_2SO_4

The plants were sorted into three replicates in accordance with their size and placed in greenhouse compartments at 15-18°C temperature. Since the experiment was carried out during the winter, fluorescent light (Philips TL 33, 25 Wm^{-2}, 400-700 nm) was supplied for 18 hours per day in addition to natural daylight. Throughout the experiment, distilled water was added twice av week up to 60% of field capacity.

Five weeks after establishment, plant height was measured and the plants cut to 10 cm. At the termination of the experiment three weeks later the following plant characters were recorded:

1. Plant height (mm).
2. Tillers within tufts (no).
3. Tillers from rhizomes (no).
4. Total number of rhizomes (primary + secondary (Moser et al. 1968)).
5. Dry weight of tillers within tufts (mg).
6. Dry weight of tillers from rhizomes (mg).
7. Dry weight of rhizomes (mg).
8. Dry weight of roots (mg).

Pot experiment 2

The main changes compared with the previous experiment were: (i) the lowest pH level was abandoned, (ii) the pH-levels were slightly adjusted (Table 2), (iii) the levels of phosphorus and potassium were reduced to the equivalents of 10 and 50 kg ha^{-1}, respectively, (iv) nitrogen fertilization was included as a factor in the experiment with the following levels:

X. 0 kg N ha^{-1}
Y. 50 kg N ha^{-1}
Z. 100 kg N ha^{-1}

Table 2. Quantities of 97% H_2SO_4 or pure $CaCO_3$ added and pH values obtained after three and eight weeks in pot experiments 1 and 2. Means of four ecotypes and, in pot experiment 2, of three nitrogen levels

pH-level	Mg ha^{-1}		pH value		
	H_2SO_4	$CaCO_3$	3 wk	8 wk	Mean
		Pot experiment 1			
I	7.50	-	3.43	3.51	3.5
II	1.75	-	4.47	4.75	4.6
III	-	-	5.11	5.42	5.3
IV		4.50	6.98	7.14	7.1
		Pot experiment 2			
I	1.00	-	4.42	4.66	4.5
II	-	0.50	5.56	5.88	5.7
III	-	4.00	7.03	7.17	7.1

The strong reduction in nutrient application was caused by a considerable discrepancy between the results of pot experiment 1 and the preliminary findings in the field experiment. A hypothesis was set forward that the adverse effects of low pH could be offset by increased nitrogen application.

In addition to the characters recorded in the previous experiment, anthocyanin colouring on leaf sheaths and blades was estimated (scale 0-5, 5 is most). According to Nittler & Kenny (1971) this is a good indication of calcium deficiency in some cultivars of smooth meadow grass.

Field experiment

In April/May 1987 three different pH levels (Table 3) were established by addition of either lime or sulphuric acid to sandy soils at Landvik (280 km southwest of Oslo) and Leirsund (30 km northeast of Oslo). Details on soil texture, chemical analyses and amounts of lime and acid applied have been presented elsewhere (soils 1 and 3 according to Aamlid 1990b). Fertilization prior to planting was 40 kg N ha^{-1} in compound fertilizer NPK 16-7-12.

Table 3. Soil reaction values obtained at the different pH levels in field experiments at Landvik and Leirsund. Means of samples taken in July and October 1987 and May and October 1988

	pH level		
	I	II	III
Landvik	4.4	5.7	6.7
Leirsund	4.7	5.3	6.4
Mean	4.6	5.5	6.6

On 12 June (Landvik) and 2 July (Leirsund) 1987, plants of the four ecotypes, similar in size to those used in the pot experiments, were transplanted into the fields. In order to prevent any mingling of rhizomes from different plants, both rows and plants were spaced at 1 m distances. Weeds were controlled by herbicides (mainly propachlor) and hand removal. The experimental design was a split plot with six replicates, and three plants of each ecotype were randomized into the main (pH) plots.

Owing to the unexpectedly low pH values prevailing on the acid plots at Leirsund in summer 1987 (Aamlid 1990b), some plants died within a few weeks after transplantation. On 12 August, therefore, 6 plants of 'Leikra', 6 plants of 'Lavang', 3 plants of 'Rønholt' and 8 plants of 'Herøya' were replaced by new ones. At Landvik, no such replacement was necessary.

In October 1987 plants from three replicates at both locations were excavated and brought into the laboratory. Apart from dry weight of roots, the same recordings were made as in pot experiment 1. In the remaining three replicates plants were not cut or fertilized in autumn, but 30 kg N ha^{-1} was applied in compound fertilizer NPK 14-6-16 in spring 1988.

After heading in the middle of May, diameter per plant was measured as the greatest distance between inflorescences from rhizomes. Panicles within and outside tufts were counted and harvested in the period 13-18 July at Landvik and 20-22 July at Leirsund. Seed stalks were cut 1 cm below the lowest node of the panicles, and the weight of inflorescences per plant was recorded. Threshing was done by hand and most of the chaff and light seeds were removed by a laboratory cleaner. After a new weighing, a sample of 0.5 g was put into the seed blower and the fraction of pure seed determined. Thousand seed weight and water content were recorded in accordance with official rules (Statens frøkontroll 1987a).

Statistical methods

Experimental data were subjected to standard statistical procedures. In earlier reports significant location·ecotype interactions have been documented for smooth meadow grass (Håbjørg 1979a, 1979b); hence, it was considered justifiable to use replicates within locations as the error term when analyzing data from the field experiment. In this report $P \leq 0.001$, $0.001 < P \leq 0.01$ and $0.01 < P \leq 0.05$ have been denoted by ***, ** and *, respectively.

RESULTS

Pot experiment 1

Though there was a tendency for 'Lavang' and 'Rønholt' to survive longer than 'Leikra' and 'Herøya', growth of all ecotypes could be disregarded at the lowest pH value in pot experiment 1 (Fig. 1). Within the pH range 4.6 - 7.1, soil reaction had no significant impact on

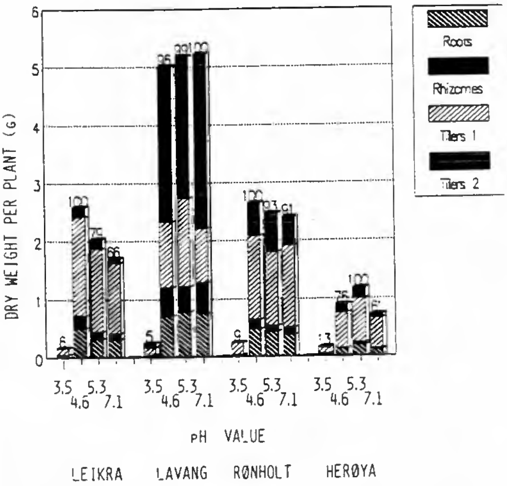

Figure 1. Effect of soil pH on dry weight of roots, rhizomes and tillers within (tillers 1) and tillers outside (tillers 2) tufts in four ecotypes in pot experiment 1. Numbers above bars denote relative dry matter yields

plant height, tillering, rhizome formation or dry matter accumulation. Actually, the highest dry matter yield seemed to be achieved at pH 4.6 in 'Leikra' and 'Rønholt' and at pH 5.3 in 'Herøya', whilst it was fairly unaffected in 'Lavang'. Significant effects of ecotype were found in all characters studied. Because of vigorous rhizome formation and a high proportion of the rhizomes emerging rapidly, total tiller number was two to seven times higher in 'Lavang' than in the other ecotypes at the end of the experiment (Table 4). On defoliation after five weeks, equal plant heights were assessed in 'Leikra' and 'Lavang', but three weeks later 'Lavang' was superior also in this respect. By contrast, 'Herøya' grew poorly under all conditions.

Pot experiment 2

Plant height

pH had no significant impact on height at the first cut, but regrowth during the next 3 weeks was clearly augmented by the second pH increment, especially at low nitrogen inputs (Fig. 2). At the end of

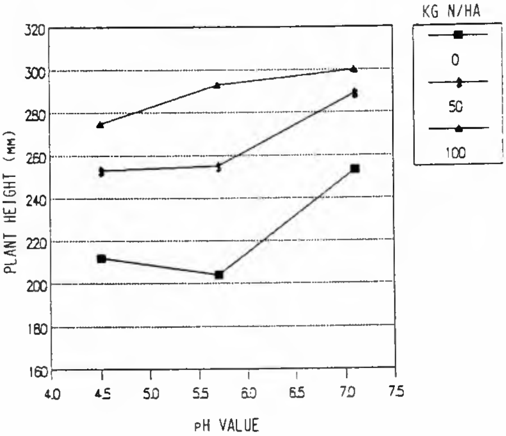

Figure 2. Plant height after eight weeks as affected by soil pH at three levels of nitrogen application. Means of four ecotypes in pot experiment 2

Table 4. Plant height after five and eight weeks, total rhizome number per plant and number of tillers within and outside tufts after eight weeks in four ecotypes of smooth meadow grass. Means of 4 pH levels in pot experiment 1

	Plant height, mm		Rhizomes no	Tillers, no		
	5 weeks	8 weeks		Within tufts	Outside tufts	Total
'Leikra'	319	353	9.8	10.5	4.4	14.9
'Lavang'	320	389	58.0	13.9	54.4	68.3
'Rønholt'	293	317	13.0	14.9	12.8	27.7
'Herøya'	203	220	5.6	6.3	3.3	9.6
Sign.	***	***	***	**	***	***
$LSD_{0.05}$	17	24	8.6	5.0	8.0	8.9

the experiment, the average heights of the ecotypes were as follows ($LSD_{0.05} = 11$):

'Leikra'	'Lavang'	'Rønholt'	'Herøya'
303	235	254	245

Numbers of tillers and rhizomes

pH elevation strongly enhanced rhizome formation and tillering. Although the pH·ecotype interaction was highly significant, no striking difference could be seen between ecotypes as to the relative response in rhizome formation (Fig. 3). On the contrary, 'Herøya' was the only ecotype which developed the highest tiller number at the intermediate pH level (Fig. 4). The pH·nitrogen interaction was not significant for either number of rhizomes or tillers.

Dry matter production

With the exception of 'Herøya' which attained the highest total dry weight at the intermediate pH level, dry matter accumulation was generally stimulated by high soil reaction values (Fig. 5). The effect was less pronounced in 'Rønholt' than in 'Leikra' and 'Lavang'. In the 'Lavang' ecotype in particular dry weight of roots showed a dramatic response to improvement in soil reaction. Since the

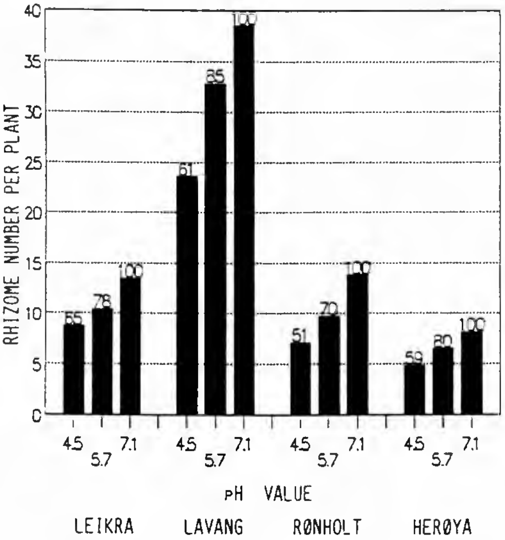

Figure 3. Effect of soil pH on number of rhizomes in four ecotypes. Means of four ecotypes in pot experiment 2. Numbers above bars denote relative rhizome numbers

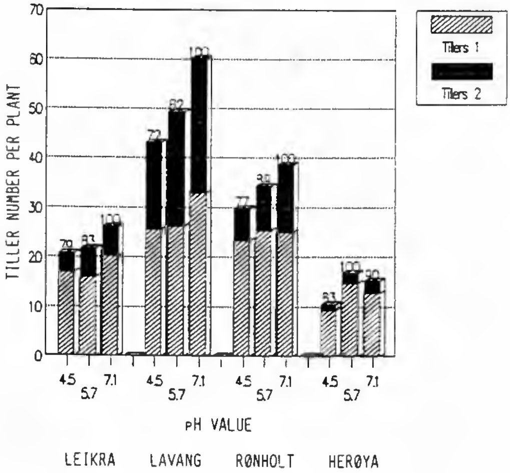

Figure 4. Effect of pH value on number of tillers within (tillers 1) and outside (tillers 2) tufts in four ecotypes. Means of three nitrogen levels in pot experiment 2. Numbers above bars denote relative tillering

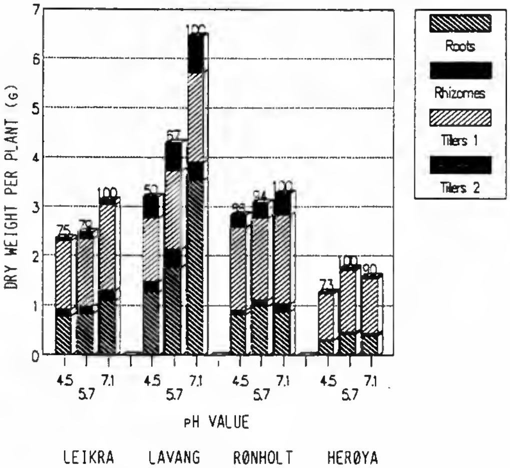

Figure 5. Effect of pH value on dry weight of roots, rhizomes and tillers within (tillers 1) and outside (tillers 2) tufts in four ecotypes. Means of three nitrogen levels, pot experiment 2. Numbers above bars denote relative dry matter accumulation

increase in tiller dry weight was not of the same magnitude, the top/(root + rhizome) ratio fell from from 1.25 at pH 4.5 to1.00 at pH 5.7 and only 0.69 at pH 7.1. A less pronounced drop in the top/(root + rhizome) ratio at increased pH levels was detected in 'Leikra' and 'Herøya'.

Although the pH-nitrogen interaction was not significant ($P = 0.11$), a diminishing response to pH elevation could generally be recorded only at the highest nitrogen input (Fig. 6). A separate analysis conducted for 'Herøya' revealed that dry weight of this ecotype was highest at the intermediate pH level only when nitrogen was applied at rates of 50 or 100 kg ha^{-1} (Fig. 7). At the zero nitrogen treatment, the highest pH level was most favourable, as in the other ecotypes.

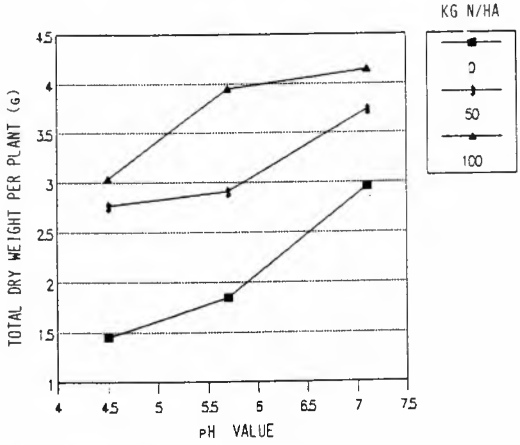

Figure 6. Effect of soil pH on dry weight accumulation at different levels of nitrogen application. Means of four ecotypes, pot experiment 2

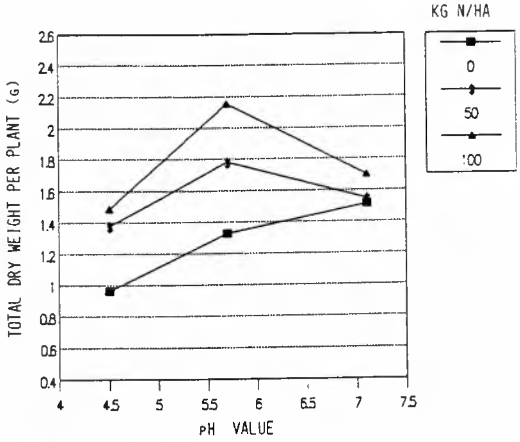

Figure 7. Dry weight of 'Herøya' in pot experiment 2 as influenced by soil pH at different levels of nitrogen application

Anthocyanin colouring

While 'Leikra' retained its light green appearance regardless of treatments, anthocyanin colouring of leaf sheaths and blades was quite pronounced in 'Rønholt' and in fact severe in 'Herøya'. Though there were some irregular responses in all ecotypes except 'Lavang', the plants generally became greener and healthier when pH was raised from 4.5 to 5.7 (Fig. 8) and additional nitrogen applied (data not shown).

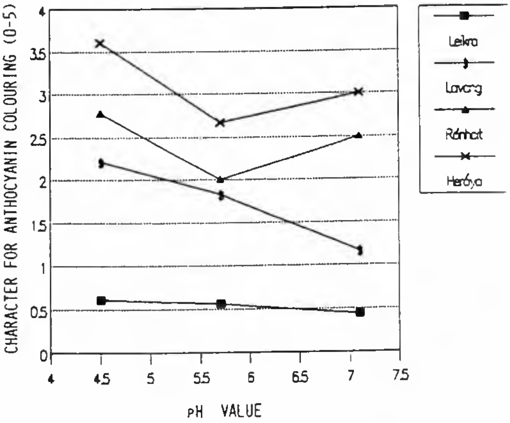

Figure 8. Effect of soil pH on anthocyanin colouring of leaf sheaths in four ecotypes as determined on a relative scale from 0 to 5 (5 indicates most anthocyanin colour). Means of three levels of nitrogen, pot experiment 2

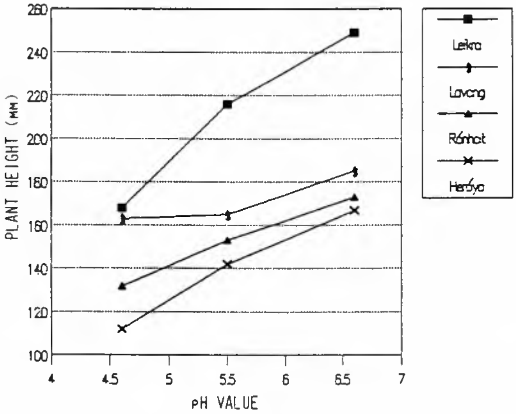

Figure 9. Effect of soil pH on plant height of four ecotypes. Means of two locations

Field experiment

Vegetative growth 1987

Plant height

pH elevation generally increased height growth (Fig. 9). The differences between ecotypes were highly significant, mostly reflecting those reported from pot experiment 2. Neither the main effect of location nor the location-ecotype interaction was significant.

Rhizome number

Whilst the average number of rhizomes was calculated to 100.1 at Landvik, only 40.0 rhizomes were formed per plant at Leirsund. 'Lavang' usually formed three to four times as many rhizomes as the other ecotypes, and since the absolute difference between the two locations was greatest in this cultivar, the location-ecotype interaction was also highly significant (Table 5). However, on a relative scale, the difference between locations was of the same magnitude in all ecotypes.

Neutralization of soil acidity generally seemed ($P=0.06$) to stimulate rhizome formation (Fig. 10). 'Lavang' as the only ecotype was hardly retarded in growth as pH dropped from 5.5 to 4.6; on the other hand, its rhizome number almost doubled when pH was raised from 5.5 to 6.6. The relative response to higher pH values was most pronounced in 'Herøya'; approximately nine times as pH increased from 4.6 to 6.6.

Tiller number

Whilst tillering within tufts only differed slightly between the two locations, average tiller number outside tufts was more

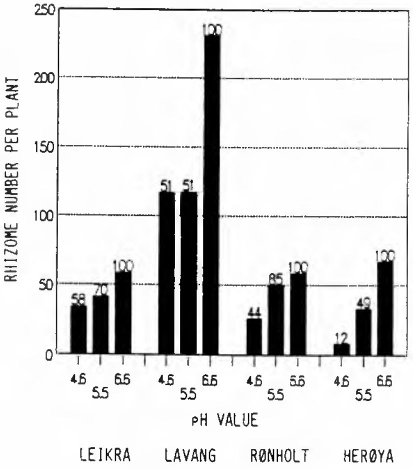

Figure 10. Effect of soil pH on number of rhizomes per plant in four ecotypes. Means of two locations. Numbers above bars denote relative rhizome numbers

Table 5. Total number of rhizomes per plant in four ecotypes at two locations. Means of three pH values

	'Leikra'	'Lavang'	'Rønholt'	'Herøya'	Mean **
Landvik	61.5	226.2	62.6	50.1	100.1
Leirsund	27.3	84.2	26.7	21.8	40.0
Mean ***($LSD_{0.05}=12.0$)	44.4	155.2	44.7	35.9	
Significance of interaction: ***	($LSD_{0.05}=17.0$)				

than twice as high at Landvik as at Leirsund. However, the difference between locations in total tiller number varied between ecotypes, the growing conditions at Landvik being comparatively less favourable for 'Leikra' than for 'Herøya', 'Rønholt' and - notably - 'Lavang' (Table 6).

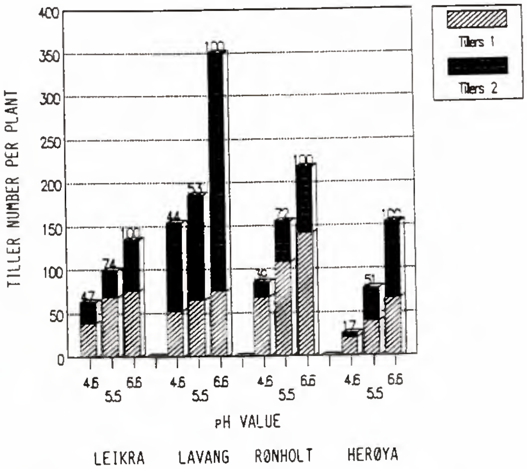

Figure 11. Effect of soil pH on number of tillers within (tillers 1) and outside (tillers 2) tufts in four ecotypes. Means of two locations. Numbers above bars denote relative tillering

Total tiller number increased significantly when pH value was raised from the lowest to the highest level (Fig. 11). As for number of rhizomes, 'Lavang' exhibited the strongest absolute increase in the 5.5-6.6 interval, while the greatest relative increase throughout the pH range was recorded in 'Herøya'. In all ecotypes tiller formation from rhizomes was more affected by pH than that within tufts.

Dry weight

Dry weight of tillers outside tufts was significantly higher and dry weights of rhizomes tended ($P=0.054$) to be higher at Landvik than at Leirsund. 'Leikra' and, to a certain extent, 'Herøya' were less affected by location than 'Lavang' and 'Rønholt' (Table 7).

Dry matter accumulation was clearly stimulated by elevated pH values in all ecotypes (Fig. 12). Though 'Herøya' appeared to be relatively more impaired by the lowest pH value than the other ecotypes, no significant pH-ecotype interaction could be detected.

Table 6. Total tiller number per plant in four ecotypes and at two locations. Means of three pH levels

	'Leikra'	'Lavang'	'Rønholt'	'Herøya'	Mean
					*
Landvik	108.1	307.7	188.0	102.7	176.6
Leirsund	90.4	152.1	117.3	68.4	107.1
Mean *** ($LSD_{0.05}=17.9$)	99.2	229.9	152.7	85.6	
Significance of interaction: ***	($LSD_{0.05}=25.3$)				

Table 7. Dry weight per plant (except roots; g) in four ecotypes and at two locations. Means of three pH levels

	'Leikra'	'Lavang'	'Rønholt'	'Herøya'	Mean
					ns ($P=0.09$)
Landvik	13.65	22.47	18.09	7.21	15.36
Leirsund	13.28	13.66	9.05	5.64	10.41
Mean *** ($LSD_{0.05}=3.14$)	13.47	18.07	13.57	6.43	
Significance of interaction: ***	($LSD_{0.05}=4.47$)				

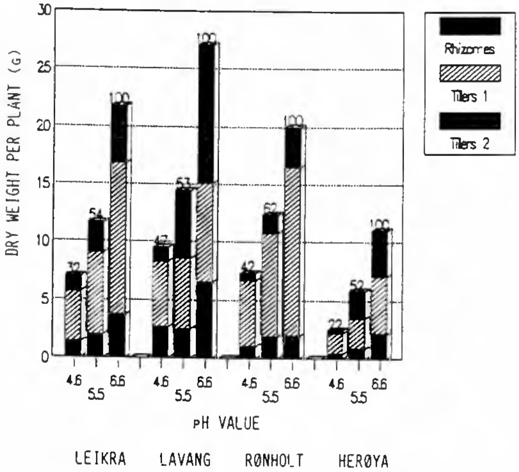

Figure 12. Dry weight of rhizomes and tillers within (tillers 1) and outside (tillers 2) tufts of four ecotypes as influenced by soil pH. Means of two locations. Numbers above bars denote relative dry matter accumulation

Seed production 1988

Regression analysis of seed yield (SY g; 100% purity; 14% water content) on weight of inflorescences before threshing (IW g) revealed that the proportion of seeds in the gross weight was clearly lower in 'Lavang' than in the other ecotypes:

'Leikra' : SY = -0.017 + 0.596 · IW (r^2 = 0.93)
'Lavang' : SY = 0.034 + 0.444 · IW (r^2 = 0.96)
'Rønholt' : SY = 0.120 + 0.561 · IW (r^2 = 0.97)
'Herøya' : SY = 0.010 + 0.603 · IW (r^2 = 0.98)

Panicle number was always the most important yield component, explaining 69-93% of the variation in seed yield depending on ecotype. However, since the intercorrelation between panicle number per plant and seed number per panicle was generally low (Table 8), the latter component also contributed significantly to the explanation of variation in seed yield in all ecotypes (Table 9). Due to intercorrelation with preceding variab-

Table 8. Simple correlation coefficients among seed yield (SY) per plant and its components: panicle number per plant (PN), seed number per panicle (SN) and thousand seed weight (TSW) in four ecotypes

	PN	SN	TSW	PN	SN	TSW
		'Leikra'			'Lavang'	
SY	0.83***	0.41ns	0.23ns	0.84***	0.30ns	-0.01ns
PN		-0.02ns	-0.01ns		-0.15ns	-0.35ns
SN			0.49*			0.55*
		'Rønholt'			'Herøya'	
SY	0.96***	0.42ns	0.26ns	0.97***	-0.26ns	-0.71*
PN		0.20ns	0.31ns		-0.44ns	-0.69**
SN			-0.04ns			0.02ns

Table 9. Intercept and regression coefficients with significance levels in the full model of the contributions to seed yield per plant (g; 100% purity; 14% water content) in four ecotypes by the components: panicle number per plant (PN), seed number per panicle (SN) and thousand seed weight (TSW mg) when included in this order in the model

	'Leikra'	'Lavang'	'Rønholt'	'Herøya'
Intercept	-5.172	-7.979	-5.513	-13.550
PN	0.0741***	0.0393***	0.0686***	0.0774***
SN	0.0144***	0.0352***	0.0580***	0.0436*
TSW	0.0048ns	0.0110ns	-0.0131ns	0.0080ns

les, thousand seed weight did not contribute significantly in the multiple regression on seed yield.

The total number of panicles per plant was significantly higher in 'Lavang' and 'Rønholt' than in the other ecotypes (Table 10). 'Rønholt' also developed the heaviest seeds and achieved the highest seed yield per plant. 'Lavang' was clearly inferior in seed number per panicle; hence, its total seed yield was of the same size as that recorded for 'Leikra'. 'Herøya' ranked as intermediate with respect to all yield components and attained the second highest seed yield per plant.

In sharp contrast with 'Rønholt' and 'Herøya' which achieved two to three times higher seed yields at Landvik than at Leirsund, 'Leikra' actually performed slightly better at the latter location (Table 11). For 'Lavang', a scarcity of panicles at Leirsund was compensated by many seeds per panicle and a high thousand seed weight; thus, for this ecotype there was only a minor difference between the two locations as to seed yield per plant.

Higher soil reaction values increased seed yield significantly. Consistent with the component analysis cited above, the effect could mainly be ascribed to a more vigorous formation of panicles as the pH value increased (Table 12). On the other hand, the average number of seeds per

Table 10. Seed yield per plant (SY g; 100% purity; 14% water content), panicle number within tufts (PNi), panicle number outside tufts (PNo), total panicle number per plant (PNt), seed number per panicle (SN) and thousand seed weight (TSW mg) in four ecotypes. Means of two locations and three pH values

Ecotype'	SY	PNi	PNo	PNt	SN	TSW
'Leikra'	7.11	40.8	37.9	78.6	365	249
'Lavang'	7.23	33.9	127.4	161.3	159	297
'Rønholt'	14.51	95.6	92.7	188.3	206	355
'Herøya'	9.33	43.5	66.2	109.6	240	336
Sign.	***	***	***	***	***	***
$LSD_{0.05}$	2.31	12.0	31.8	36.4	68	22

Table 11. Seed yield per plant (g; 100% purity; 14% water content) of four ecotypes at two locations. Means of three pH levels

	'Leikra'	'Lavang'	'Rønholt'	'Herøya'
Landvik	6.45	7.60	21.21	13.48
Leirsund	7.77	6.85	7.81	5.18
Significance of interaction: ***	($LSD_{0.05} = 3.27$)			

Table 12. Effect of pH value on seed yield per plant (SY g; 100% purity; 14% water content), panicle number within tufts (PNi), panicle number outside tufts (PNo), total panicle number per plant (PNt), seed number per panicle (SN) and thousand seed weight (TSW mg). Means of two locations and four ecotypes

pH value	SY	PNi	PNo	PNt	SN	TSW
4.5	2.12	16.2	20.9	37.1	200	299
5.4	11.38	61.1	81.9	142.9	282	317
6.4	15.13	83.0	140.4	223.4	246	311
Sign.	**	***	**	***	**	ns
$LSD_{0.05}$	4.86	18.2	44.1	58.2	32	16

panicle was influenced favourably by the intermediate pH level.

The pH-ecotype interaction was highly significant as regards seed yield. This could chiefly be ascribed to a stronger response to pH elevation in 'Rønholt' and 'Herøya' than in the other two ecotypes (Fig. 13). Whereas 'Rønholt' showed the greatest yield increase due to the first pH increment, 'Herøya' was most responsive in the second interval.

In all ecotypes there was an increased contribution to seed yield by panicles outside tufts as soil acidity was relieved. This shift in importance was mainly reflected in the number of panicles of the two categories per se, but there was also a tendency for number of seeds per panicle outside tufts to be favoured by high pH levels as compared with the corresponding character of panicles within tufts (Table 13). On the other hand, no consistent difference between the two panicle categories was evident with respect to thousand seed weight.

Table 13. Effect of soil pH on seed number per panicle inside and outside tufts. Means of two locations and four ecotypes

	pH value			
	4.6	5.5	6.6	Mean
Within tufts	221	271	229	240
Outside tufts	171	299	265	245

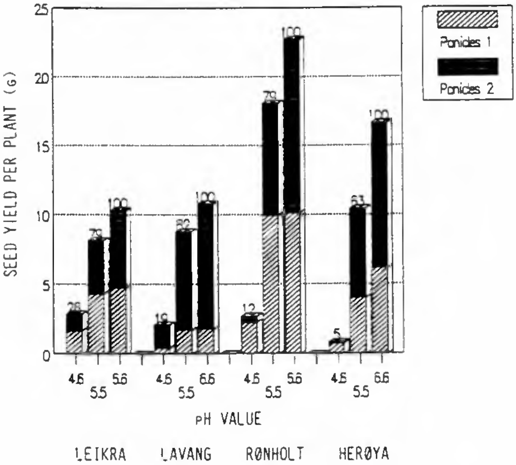

Figure 13. Seed yield (100% purity; 14% water content) of panicles within (panicles 1) and outside (panicles 2) tufts in four ecotypes grown at three pH levels. Means of two locations

DISCUSSION

Aluminium toxicity

Despite the fact that the pH value is by far the most commonly used indicator of soil acidity, it is widely accepted that the concentration of protons per se is generally not the detrimental factor in acid soils. Numerous experiments have demonstrated that plant growth in nutrient solutions is not significantly affected by pH if sufficient calcium is available and toxic ions such as a aluminium and manganese are not present (Kamprath & Foy 1985, Marschner 1986). Admittedly, the competitive effect of H^+ on absorption of base cations will increase when solutions become more acid, but until pH falls below approximately 4.0, plant membranes are seldom injured and leakage of cell constituents does not take place (Moore 1974).

Although the high proton concentration might have contributed to the growth failure at pH 3.5 in pot experiment 1 (Fig. 1), increased solubility of aluminium is definitely the most probable explanation for the poor growth at pH values below 5.0 in most of the present material. The pH value below which Al becomes soluble in toxic concentrations varies among soils (Foy 1974b), however, pH 5.0 is often considered to be an approximate threshold value (Kamprath & Foy 1985). Whilst Al^{3+} is predominating at pH below 4, hydroxyaluminium ions, such as $Al(OH)^{2+}$, and $Al(OH)_2{}^+$ are more prevalent in the 4.0 - 5.0 interval. Most results point to the trivalent ion as the most toxic species (Marschner 1986), but there are also indications that $Al(OH)^{2+}$ may be even more harmful (Moore 1974).

Root growth is generally regarded as

the most sensitive indicator of Al toxicity. Probably as a result of inhibited cell division, roots become brown, stubby and thickened (Foy 1974b). Consequently, absorption of water and nutrients, notably phosphate, will be impaired. In pot experiment 2 low pH values hampered growth of not only roots, but also rhizomes more than growth of tillers (Fig. 5); hence the top/(root + rhizome) ratio was highest at the lowest pH level in three out of four ecotypes. Similar results have been obtained with *Poa trivialis* L. (Nieuwenhuizen et al. 1985).

The damage caused by aluminium depends on the consentration of other ions in the soil solution. Abundant supplies of phosphate can precipitate and thus detoxify Al both in the soil solution and in plant roots (Foy 1974b, 1988). However, in interpreting the unexpectedly vigorous growth at pH 4.6 in pot experiment 1 (Fig. 1), it is probably more appropriate to consider the high amounts of calcium added in $Ca(NO_3)_2$ and $Ca(H_2PO_4)_2$. Ca^{2+} is known to stabilize cell walls and protect membranes against disruption and leakage (Foy 1974a). Since the two ions compete for the same negative charges on the root surface, high Ca concentrations will to a great extent alleviate the negative effects of Al (Marschner 1986). An antagonistic relationship between Ca^{2+} and H^+ has also been documented, and results cited in Moore (1974) and Kamprath & Foy (1985) indicate that the optimum Ca concentration for plant growth is higher at low than at high pH values. Although anthocyanin colouring is a general indicator of phosphorus deficiency, the pronounced reddish or purple colour at the lowest pH and nitrogen levels in pot experiment 2 (Fig. 8) may suggest a lack of Ca under these conditions (Nittler & Kenny 1971). Unfortunately, no accurate recordings were made of anthocyanin colouring in pot experiment 1, but there was a general impression that it was less marked than in the later experiment.

pH·nitrogen interactions

Since phosphorus and nitrogen were both applied in forms containing large amounts of calcium, the impacts of pH in the pot experiments were regrettably confounded by the effects of this element. This complicates interpretation of the results, notably for the pH range 4.5-5.5. Although there are some indications that abundant nitrogen fertilization might mitigate the harmful effects of pH values below 5.0 (Whinham & Beaverstock 1985), it seems improbable that a high consentration of NO_3^- exclusively should have been able to prevent toxic effects of Al and cause optimum growth at pH 4.6 in pot experiment 1. This conclusion is substantiated by the fact that Curtin & Smillie (1986) obtained very little growth of Italian ryegrass (*Lolium multiflorum* Lam.) in a strongly acid soil (pH 4.2) even when NH_4NO_3 was added at a quantity corresponding to 375 kg N ha^{-1}. By contrast, they recorded a significant nitrogen response in bentgrass (*Agrostis capillaris* L.). The latter species is known to be very tolerant to acid soils (Foy 1974b), so there is little doubt that smooth meadow grass is more like ryegrass in this respect.

In pot experiment 2 and also in the field experiment pH elevation augmented growth far beyond the limit normally associated with Al toxicity. The major reason for this stimulation was probably increased microbiological activity with an accompanying release of nutrients, mainly nitrogen. According to Scheffer & Schachtschabel (1984), ammonification of nitrogen from soil organic matter is only weakly influenced by soil pH in the interval 5.2-7.8; on the other hand the subsequent nitrification is maximal in a narrower pH interval from 6.0 to 8.0. This is supported by soil analyses from experiments adjacent to those described here, in which the content of NO_3^- tended to increase after pH elevation (Aamlid 1990b).

Because of the much longer period of growth, the effect of pH value on nitrogen availability might be more pronounced in the field than in the pot experiments. In particular at Landvik, where the soil originally had a fairly high organic matter content (Aamlid 1990b), pH elevation from 5.5 to 6.6 strongly enhanced plant growth. In pot experiment 2, 'Leikra' and 'Lavang' also tended to respond more to the second than to the first pH increment, but no such tendency could be detected in 'Rønholt' and certainly not in 'Herøya' (Fig. 4 and 5). In the pH interval from 5.5 to 7, the Al-Ca antagonism is not likely to be confounded with the effect of nitrogen; therefore, it is noteworthy that the pH response curves for plant height and total dry weight in pot experiment 2 seemed to flatten out only at the highest nitrogen input (Fig. 2 and 6). A similar relationship between liming and nitrogen application has been documented in field experiments with cereals (Lyngstad 1986).

Seed production

The number of panicles per plant - and thus the seed yield (Fig. 13) - was relatively more surpressed on the most acid plots than the corresponding number of tillers recorded the previous autumn. This must be due to many weak tillers either not passing the juvenile stage in autumn or not being able to develop inflorescences in spring, probably attributable to limited supply of nutrients. On the other hand, the nitrogen mineralization promoted by the second pH increment was clearly more advantageous to vegetative growth than to seed yield. This is in good agreement with results from Oregon, USA, where a pH value not higher than 5.8 is recommended for seed production of smooth meadow grass (Youngberg 1980). Such a recommendation might well be correct for sown stands also in Norway (Aamlid 1990c), but evidently, the optimum pH value is higher in open, transplanted stands like in the present ones, in which competition was not so severe.

From a study on the relationship between vegetative and reproductive growth of spaced plants of smooth meadow grass, Wijk (1985) reported correlation coefficients of 0.52 and 0.76 (two different years) between number of vegetative tillers in March and number of inflorescences in June. However, since tiller number was negatively correlated with number of germinating seeds per panicle and thousand seed weight, no significant relationship existed between tiller number in March and seed yield in June. To a certain extent, this seems compatible with the present reduction in average size of inflorescences upon pH elevation (Table 12). More surprisingly, owing to strong negative intercorrelations between the seed yield components, Wijk (1985) found no significant relationship between panicle number and seed yield per plant either. This result is in clear contradiction to those presented here (Tables 8 and 9) and in many other reports (for a review, see Langer 1980) in which panicle number has been shown to exert the dominating influence on seed yield.

Though its vegetative production was clearly inferior at all pH levels, 'Herøya' had a growth habit quite similar to 'Rønholt'. It is noteworthy that both these ecotypes were better seed producers than the two cultivars commercially available in Norway (Table 10). This could partly be ascribed to a higher thousand seed weight, but more important was that a greater proportion of the tillers formed in autumn produced seeds in the following summer. At the two higher pH levels at Landvik, the number of panicles in 'Rønholt' and 'Herøya' was in fact considerably higher than the number of tillers recorded in October the previous year. This suggests that 'Rønholt' and 'Herøya' continued to produce tillers later in autumn than 'Leikra' and 'Lavang' and/or that the juvenile stage had a shorter duration in the former two ecotypes.

According to official Norwegian seed statistics, 'Lavang' normally produces seed yields clearly superior to those of 'Leikra' (Statens frøkontroll 1987b, 1988). To a certain extent this might be explained by inadequate production techniques for 'Leikra' (G.H. Jonassen pers. comm.); nevertheless the seed yields of 'Lavang' in this investigation were remarkably poor. From other trials (Håbjørg 1979b, Nordestgaard 1983) it is well established that heading, flowering and seed maturation occur two to seven days earlier in North Norwegian than in South Norwegian cultivars of smooth meadow grass. Since harvest date was the same for all ecotypes in the present experiment, it might well be that more seed shattered before harvest in 'Lavang' than in the other ecotypes. Such an explanation is not consistent with the general experience that smooth meadow grass has a good seed retention capability (Jonassen 1978), but it is supported by the comparatively low number of seeds per panicle in this ecotype (Table 10) and by its low regression coefficient between weight of unthreshed mass and pure seed yield.

Adaptation to climate and soil

The general superiority of both vegetative growth and seed production at Landvik as compared with Leirsund can partly be attributed to a high water table and flooding at the latter location (Aamlid 1990b). However, there is little doubt that differences in weather have to be considered as well. Unlike the other ecotypes, 'Leikra' performed quite well at Leirsund as compared with Landvik. Consistent with an earlier phytotron experiment (Aamlid 1990a), the more continental type of climate at Leirsund - in particular the greater difference between day and night temperatures - was probably advantageous to 'Leikra'. To a certain extent this temperature variation also explains why rhizome formation, which is known to benefit from high temperatures both day and night (Aamlid 1990a), was relatively more hampered than tillering at Leirsund as compared with Landvik (Tables 5 and 6).

On the basis of the low pH prevailing at the locality from which it was collected, it was hypothesized that 'Rønholt' would be relatively less impaired by acid soils than the other ecotypes. In the rather comprehensive material presented, there are only three indications which offer some support to this hypothesis: (i) in the strongly acid soil (pH 3.5) in pot experiment 1, most plants of 'Rønholt' and 'Lavang' survived some weeks longer than those of 'Leikra' and 'Herøya'; (ii) on the most acid plots at Leirsund, the number of dead plants which had to be replaced six weeks after planting was somewhat lower in 'Rønholt' than in the other ecotypes; (iii) in pot experiment 2, total dry matter accumulation was less hampered by low pH values in 'Rønholt' than in the other ecotypes (Fig. 5).

Despite these indications, the material as a whole far from proves the existence of any specific aluminium or acid soil tolerance in 'Rønholt'. As opposed to acid-tolerant smooth meadow grass cultivars mentioned by Murray & Foy (1980), dry matter accumulation in 'Rønholt' was clearly stimulated by alleviation of soil acidity, and the response was even more pronounced with respect to seed production the subsequent year.

For 'Herøya' the picture is somewhat more complicated. This ecotype was collected from a heavily polluted area, quite adjacent to metallurgic industry. Unfortunately, no micronutrient analysis was conducted on soil samples from the locality, but it will be expected that this soil - in spite of its high pH value - contained high amounts of plant available iron, manganese, zinc and perhaps copper as well. By contrast, the sandy soil from Landvik used in the pot experiments might well have become deficient in one or more of these elements when limed to pH values above 6.5. In addition, the high amounts of Ca^{2+} added in $CaCO_3$ have probably depressed the uptake of other cations; this also accounts for the negative effects of liming on 'Herøya' in pot experiment 2 only when $Ca(NO_3)_2$ was applied (Fig. 7). The antagonistic relationship between Ca and micronutrient cations also offers a plausible explanation for the negative effects of liming on three out of four ecotypes in pot experiment 1. Reduced Mn content in leaves of smooth meadow grass at pH values above 4.8 has earlier been reported earlier by Palazzo & Duell (1974), although these workers were not able to detect any visible deficiency symptoms even at pH 7.4.

As opposed to the pot experiments, 'Herøya' indeed showed the strongest relative response to pH elevation in the field trial. Apparently, soil reaction values close to 6.5 did not impose any severe micronutrient deficiency under these conditions. Possibly an extensive root penetration has rendered the plants capable of extraxting micronutrients from deeper soil horizons. From a study on the growth of various grasses and legumes in pot and field experiments, Hojito et al. (1985) concluded that the nature of the root system should be taken into consideration when ranking species according to acid soil tolerance.

To draw a tentative conclusion, it cannot be taken for granted that ecotypes of smooth meadow grass growing in soils with extreme pH values are genetically adapted to these conditions. Due to apomixis, the natural selection process will probably be much slower in *Poa* than in for example *Festuca* and *Agrostis*. In particular the latter genus is known to possess the potential to adapt very quickly to extreme edaphic conditions (Gundersen 1988).

Instead of the long and apparently labourious way of breeding special acid-tolerant cultivars of smooth meadow grass, a more direct approach would probably be to test the inherent tolerance of cultivars which are already certified. As demonstrated by Palazzo & Duell (1974) and Murray & Foy (1978, 1980) a great variation is likely to exist, in spite of the fact that new cultivars are not generally bred with acid tolerance in mind.

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Technical note: On spectral calibration of Kodak grey cards in red and near-IR bands

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Kodak grey cards (KGCs) are widely used standard reflectivity panels in field spectroscopical studies supporting environmental satellite remote sensing. The reflectance properties of five KGCs sampled from one single batch have been measured. The mean reflectances within AVHRR bands 1 and 2 were calculated using the spectral response curves of these two channels and the results have been compared with data from other recent studies. The great differences which were found between them were explained partly by variations in the actual wavelengths covered by the different spectrometers and partly by the various experimental designs used. The major reason for these differences, however, is concluded to be the factual spectral differences between cards. For field spectroscopical studies aiming at comparisons between channels or with data collected in other studies, it is recommended that only cards from one single batch be used and that representative reflectance values be determined by means of a spectrometer with an integrating sphere and a specular reflectance trap.

Key words: Field spectroscopy, remote sensing, reference cards.

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Field spectroscopy supporting satellite remote sensing

Within the framework of satellite remote sensing, the utilization of ground reference data is a prerequisite for obtaining valid results (Dozier & Strahler 1983). Field spectroscopical measurements can play several roles in this context (Milton 1987). Radiometric data collected by spectroradiometers or multiband radiometers can be used for direct calibration of satellite-borne measurements, but careful attention must be paid to variations in the spectral and spatial properties of the field- and satellite-borne instruments and the differences in atmospheric path and measurement geometry (Duggin & Philipson 1985). Field-collected radiometric data have also proven to be useful for modelling purposes through the testing of different kinds of models. The now widely applied NOAA AVHRR-driven herbaceous biomass monitoring technique using the Normalized Difference Vegetation Index was founded on modelling studies using field spectroscopy (see e.g. Tucker 1979). A third function of field spectroscopy is a predictive one, e.g. for defining the optimum satellite sensor or bands for a given task or for defining the optimal period of the year for acquiring satellite data.

The two approaches two field spectroscopy

In order to obtain reflectance values of objects located in the field, represented by the bidirectional reflectance factors (BRF), two principally different approaches can be applied. BRF refers to the geometrical measurement configuration, with both the energy source (sun) and sensor set in a certain position (defined by two angles) in relation to the target measured (Silva 1978). These approaches have been named "cos- conical" and "bi-conical", respectively (Milton 1987). In the cos-conical approach two sensors are applied simultaneously, the one being an apertured radiometer measuring the upwelling radiance from the object studied, and the other measuring the downwelling radiance from the sun (irradiance) within the same wavelengths. The two radiometers have to be spectrally intercalibrated. The bi-conical approach involves the use of one apertured radiometer by which the upwelling radiance is sequentially measured from the object and from a standard reflectivity panel with known reflectivity. For a comprehensive discussion of the advantages/disadvantages of the two approaches, refer to Duggin & Cunia (1983) and Milton (1987).

Kodak grey cards as standard reflectivity panels

Kodak Grey cards (KGCs), commonly called Kodak neutral test cards, were - and still are - manufactured as reference cards for photographical purposes and not for field spectroscopical utilization. Despite this, they have been widely applied as reflectance standards in field spectroscopical studies as well (see e.g. Williamson 1989; Milton 1989). Their main advantages compared with other commonly used reflectance standards, such as barium sulphate, $BaSO_4$, used by e.g. Batista and Rudorff (1990), or Halon resin, are:

(i) low cost,
(ii) easy availability, and
(iii) spectral similarity to many real world objects and land cover types.

On the other hand, their disadvantages are:

(i) unspecified angular properties (non-Lambertian),
(ii) uncalibrated wavelength-dependent reflectance values from the manufacturer, even though the reflectance is specified at 18% for visible wavelengths, and
(iii) rather limited maximum size (20 cm x 25 cm), which may cause problems when using radiometers with a 10 - 20 ° instantaneous field-of-view. This requires a short distance between radiometer and the card, which could readily cast a shadow onto the card from the radiometer.

OBJECTIVES

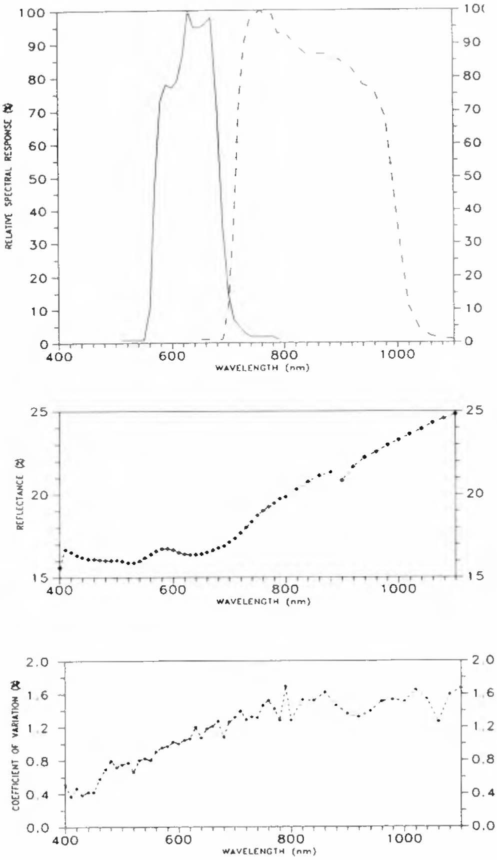
The main objective of the study was to determine representative reflectance values within wavelengths of channels 1 and 2 for the NASA Goddard Space Flight Center (GSFC) Mark II hand-held radiometer for a batch of KGCs used at Centre de Suivi Ecologique (Center for Ecological Monitoring), Senegal. Cards from the same batch were used during two bi-conical field spectroscopical measurement campaigns of burnt savanna areas carried out in December 1988 - January 1989 and November - December 1989 in Western Senegal (Langaas 1989; Langaas and Kane 1991).

The results obtained in this study would also render possible comparison with values found in other recent studies of KGCs; notably Palmer (1982), Milton (1989) and Philipson et al. (1989).

EXPERIMENTAL PROCEDURE

The measurements were carried out in a laboratory context using a Perkin-Elmer Lambda 9 UV/VIS/NIR spectrometer with a 60 mm integrating sphere (Liekmeier, undated). The sphere had a white inside coating and had been corrected to 100% reflectance a few weeks before this study using pressed $BaSO_4$ powder which had been absolutely calibrated by the Eastman Kodak Laboratory. The instrument was also calibrated to 0% reflectance through correction for dark currents. The spectrometer covers the spectral range 300 - 2500 nm, of which the range 300 - 885 nm uses a photomultiplicator while the 890 - 2500 nm spectral region employs a lead-sulphide, PbS, detector. Samples, 5 cm x 5 cm, cut out from the centre of five randomly selected unused KGCs of standard size, 20 cm x 25 cm, were employed. These cards were taken from several KGCs bought December 1988. They were all assumed to come from the same production batch; this was borne out by there being little variation in wavelength-dependent intercard reflectance (see Fig. 3). The samples covered a small hole in the sphere where they were hit by the light beams at an incidence angle of 8 ° from a stable light source. The effect of specular reflection of the non-Lambertian KGCs was further reduced. The outgoing reflected light with the same angle of incidence as the light beam was directed through a small hole in the sphere and is thus not included in the integrated hemispherical reflectance values. The small angle of 8 ° is in accordance with the recommendations of the CIE (1986), in that the angle of incidence radiation should be less than 10 ° for colour measurements. The spectral region 300 - 2500 nm was measured. Bandwidths of 2 nm were applied for the region 300 - 885 nm, and some larger bandwidths - up to 20 nm - for wavelengths above 885 nm.

It was intended that the wavelength-dependent reflectance values obtained with the Perkin-Elmer spectrometer should be weighted with the spectral responsivity of the radiometer used in the field to obtain as correct values as possible. The exact spectral responsivities of the NASA GSFC Mark II bands 1 and 2 were not available. The reflectances of the KGCs within the NASA GSFC Mark II bands 1 and 2 were calculated instead by applying the pre-launch spectral responsivity curves of NOAA-7 AVHRR channels 1 and 2 as given by Kidwell (1986) and shown in Figure 1, since the field radiometer was intended for comparison with and validation of data from this sensor (Tucker et al. 1980).



RESULTS AND DISCUSSION

The mean reflectances were 16.6% and 20.6% for the wavebands defined by the spectral responsivity curves for NOAA-7 AVHRR channels 1 and 2, respectively. Average spectral reflectances for the range 400 - 1100 nm are given in Figure 2. The local minimum found at around 900 nm is a function of instrument voltage instability when changing between detectors.

Reflectance properties of KGCs have been examined by others earlier; the values found in some of these studies are summarized in Table 1. Noteworthy from this table are the considerable differences in the reflectances obtained within the two bands. The ranges in the red band and the near-IR band were 5.8% and 7.7%, respectively. The fact that the radiometers used in the various experiments covered slightly different regions of the spectrum can partly explain the differences between the extremes found in these studies. However, the rather strong autocorrelation in reflectances between neighbouring wavelengths does not give credence to this being the principal cause of the dissimilarity. A more feasible explanation for the considerable variety of reflectance values obtained in the two bands is more likely to be found in the differences in the experimental design for the various studies and the absolute calibration of the instrument(s) used.

Inconsistency in reflectivity characteristics between KGCs has been documented in earlier studies, particularly between cards from different production batches. Milton (1989) applied a Spectron SE590 spectroradiometer to measure the reflective properties of KGCs which had undergone different kinds of treatments. The exact geometrical measurement configuration he applied was not specified, but it was bidirectional and thus gave bidirectional reflectance factors. Coefficients of variations (CVs) of up to 15% were found in near-IR wavelengths for 10 unused KGCs from different batches. For the red band (≈ Landsat TM channel 3) a range of 16.0 - 20.79% between the least and most reflective cards was found, while for the near-IR band (≈ Landsat TM channel 4) the range was 17.21 - 25.86%. Cards from the same batch had less variation, only reaching a maximum CV of 2% within the 400 - 1100 nm range.

Table 1. Summary of reflectances at red and near-IR wavelengths from some recent studies

Reference	N[1]	Red band (nm) BRF/Reflectance (%)	Near-IR band (nm) BRF/Reflectance (%)
Palmer (1982)		597 - 690	752 - 1027
	4	22.4[2]	28.3[2]
Milton (1989)		630 - 690	760 - 900
	24	18.9[2]	23.2[2]
	10	16.5 - 20.8[3]	17.2 - 25.9[3]
Philipson et al. (1989)		630 - 690	760 - 900
	1	21.6[4]	26.4[4]
This study (1990)		572 - 673	715 - 988
	5	16.6[2]	20.6[2]

[1] Number of sample cards measured.
[2] Average BRF/reflectance value from centre of cards from same batch.
[3] Maximum range of reflectance values for cards of different batches.
[4] Average values from measurements of the four quadrants of a single card. Three replicates.

Philipson et al. (1989) applied a cos-conical field spectroscopic measurement approach (see e.g. Duggin 1980) with two EXOTECH 100AXM+T radiometers; one apertured radiometer measured the upwelling radiance from horizontally placed KGCs on the rooftop of a building, while another measured the downwelling irradiation onto a KGC using a hemispherically integrating cosine receptor. In this study intracard variations in particular were examined by measuring the four quadrants of a standard KGC, and goniometric properties were examined by comparing BRFs measured at several azimuth angles about a perpendicular to the plane of the standard.

Palmer (1982) performed his calibration in a laboratory environment. Light beams from a tungsten halogen lamp were let through a baffle and the KGCs and the reference material; pressed Halon G-80 powder, with an assumed reflectivity of 99% within the whole range of wavelengths covered, was placed perpendicularly on the light beams. The reflected light from the KGC and the Halon G-80 was measured sequentially by a Radiometrics RMR-10 radiometer at an angle of 30 ° to the incident light beam.

In the present study a spectrometer with an integrating sphere with calibrated reflectance properties was utilized. This enabled estimation of the hemispherical reflectance of the cards. A specular reflectance trap was used to exclude the specular component of the hemispherical reflectance at the reflective angle equal to incident angle. This was considered to be a methodological refinement since the cards were intended for BRF estimations and the inclusion of the specular component would provide a higher value than those that would be obtained for all BRFs with a reflectance angle that differed from the angle of incidence.

The distinct differences found in experimental schemes with regard to considerations like measurement environment (outdoor vs. laboratory), selection of instrument, calibration of instrument and geometrical configuration for the four studies discussed underline the problem of (lack of) standarization.

The main cause of the wide differences can, however, be attributed to the genuine and considerable spectral differences in the KGCs measured. The range of spectral values found by Milton (1989) for new cards from separate production batches is the strongest confirmation of this. As previously pointed out, these cards were originally intended by the manufacturer for photographic applications which do not require the high level of precision required by physical measurement exercises using field spectroscopy.

SUMMARY AND CONCLUSIONS

The hemispherical reflectances (excluding specular reflective components) of five KGCs have been measured for the spectral region 300 - 2500 nm using a 0 - 100% reflectance calibrated spectrometer with integrating sphere and specular reflective trap. Reflectances within NOAA-7 AVHRR channels 1 and 2 were calculated by spectral weighting using the known pre-launch spectral responsivity curves for the two channels. The sample mean values for channels 1 and 2 were 16.6% and 20.6%, respectively.

These results were compared to values of red and near-IR reflectances (or BRFs) obtained in other studies of KGCs. The reasons for the large differences between the extreme minimum and extreme maximum values found for red and near-IR bands were discussed. Differences in the exact band locations and in the experimental design in particular with respect to features like measurement environment (outdoor vs. laboratory), selection of instrument, calibration of instrument and geometrical configuration are all factors which contribute towards these differences. Factual differences between cards are considered to be the primary cause, however.

This implies that if KGCs are used as standard reference card in field spectroscopical studies and if a comparison of the BRFs obtained for the different spectral regions is wanted and/or a comparison with data acquired in other studies, then only cards from the same batch should be used and at least a sample of these should be calibrated to obtain representative spectral reflectances for the cards used within the bands measured by the field radiometer.

If available, it is suggested that this calibration is carried out using a spectrometer with an integrating sphere and specular reflectance trap. The specular reflectance trap enables exclusion of a strongly unrepresentative BRF value which should also be avoided in the field. The integrating sphere ensures that the remaining anisotropic properties are "smoothed" and that a representative BRF will be found.

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