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Assessment of available zinc for rice in soils of the Tabora region, Tanzania

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Msolla, M.M., J.M.R. Semoka & B.R. Singh 1994. Assessment of available zinc for rice in soils of the Tabora region, Tanzania. *Norwegian Journal of Agricultural Sciences* 8: 1-12. ISSN 0801-5341.

Four Zn extractants, EDTA-(NH₄)₂CO₃, DTPA, HCl and EDTA, were screened for suitability in assessing the available Zn status of rice-growing areas of the Tabora region in Tanzania. Rice response to Zn application was evaluated in a glasshouse experiment and in three field trials. Zinc sulphate was applied in the glasshouse experiment while ZnSO₄ and ZnO were tested in the field trials. Extractable Zn in the potted soils was also determined at the end of the experiment. In addition the Zn status of 32 soils in major rice growing areas was assessed. EDTA-(NH₄)₂CO₃ and DTPA-extractable Zn levels in the soil were significantly correlated with rice dry matter yield from the glasshouse experiment and gave critical Zn deficiency levels of 0.86 and 1.10 mg kg⁻¹, respectively. Correlation coefficients for EDTA and HCl extractable Zn versus dry matter yield were not found to be significant. At the end of the experiment it was found that in all treatments where Zn was applied DTPA extractable Zn was more than three times the critical level established in this study. Zinc deficiency which was found to be a widespread problem in rice-growing areas of the Tabora region, covering 66% of the areas, was corrected by application of either ZnSO₄ or ZnO. The optimum rate of application was 10 kg ha⁻¹. We recommend the use of DTPA for assessing the available Zn status in these soils.

Key words: Critical Zn deficiency level, DTPA-extractable Zn, EDTA, EDTA-(NH₄)₂CO₃, HCl, rice, Tanzania

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Zinc deficiency is a widespread problem in rice-growing areas. De Datta (1981) ranks Zn deficiency as the third most serious nutritional problem limiting paddy yield world-wide while in the Philippines it is rated as the second most serious nutritional disorder (Ponnamperuma 1977). In Tanzania, earlier studies on zinc examined the response of wheat to Zn application in soils of the Mbeya district (Kamasho & Singh 1982) and response of maize to Zn application (Nzabhayanga & Mkeni 1989; Mkangwa 1992), but hardly any research has been carried out on assessment of Zn status of soil in the rice-growing areas of Tanzania.

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Rice is an important food crop in Tanzania, but a large proportion of the rice consumed is still imported although there are many areas in the country where high yields could be produced. It is therefore important to investigate ways of intensifying production with a view to reducing or eliminating importations. Previous studies focusing on determining responses of rice to N,P and K fertilizers resulted in fertilizer recommendations for many of the ricegrowing areas in Tanzania (Samki & Harrop 1984). The recommended rates have been tested in several sites in the Tabora region but only small increases in paddy were obtained (Msolla, 1986, unpublished data). In some cases symptoms typical of Zn deficiency, e.g. bronzing of leaves and death of seedlings in the early stages of growth, were observed. This led us to suspect that Zn deficiency was probably responsible for limited yield.

A number of extractants have been utilized to evaluate plant available zinc in soils (Wear & Evans 1968, Lindsay & Norvell 1978; Sillanpää 1982) and the success of an extractant was often related to crop and soil conditions.

The objectives of this study were: (i) to identify a suitable Zn extractant for soils of the Tabora region and to establish a critical Zn deficiency level; (ii) to determine the response of rice to Zn application, and (iii) to assess the Zn status of soil in the major rice growing areas in this region.

MATERIALS AND METHODS

Ten soils were selected from the major rice-growing areas in the region. The soils were analysed for soil pH, organic carbon, Bray 1 extractable P and cation exchange capacity following the procedures described by Page et al. (1982). Particle size distribution was determined using the hydrometer method (Day 1965). The water content of the soils at field capacity was determined as described by Savage (1978). The soils have been classified according to the soil taxonomy system by Acres (1983). Data for these properties for the 10 soils used for the glasshouse study and their classification are presented in Table 1.

Table 1. Physical and chemical characteristics of the soils used for pot experiment

Site name	Classification (Great group)	Texture Class*	pH	Organic carbon %	Available P(ppm)	CEC c mol kg ⁻¹
Membe	Eutrotox	S	8.2	0.42	9.12	4.57
Mwamapuli	Propaquent	SCL	6.8	0.62	18.25	20.37
Ndembezi	Propaquent	SCL	6.2	0.66	14.04	13.34
Mwamala	Eutrotox	SL	5.6	0.48	12.63	7.30
Mwalala	Propaquent	SL	6.6	0.22	18.25	7.43
Lugubu	Pelludert	SC	6.7	1.00	26.66	14.88
Ikindwa	Eutrotox	SL	7.1	1.08	14.04	7.88
Chamwabo	Eutrotox	S	7.4	0.46	12.63	2.79
Itunda	Eutrotox	CL	6.2	1.04	12.63	15.65
Malolo	Eutrotox	SCL	7.3	1.20	11.93	15.76
Mean			7.4	0.72	15.02	10.95

* S = Sand; SCL = Sand clay loam; SL = Sandy loam, CL = Clay loam

Extractable Zn was extracted by four methods, namely; 0.005M DTPA at pH 7.3 (Lindsay & Norvell 1978), 0.1M EDTA-(NH₄)₂CO₃ at pH 8.6 (Trierweiler & Lindsay 1969), 0.05M EDTA adjusted to pH 7.0 with NH₄OH (Viro 1955) and 0.1M HCl (Wear & Evans 1968). Zinc contents in all the aliquots was determined by atomic absorption spectrophotometry.

Glasshouse experiment

Ten soils collected from the sampling sites listed in Table 1 were used in the study. Airdried soil was ground and sieved through an 8 mesh and 4 kg was packed into 6-L plastic pots. Three rates of Zn, viz., 0, 5, and 10 mg kg⁻¹, were tested and replicated three times. Zinc was thoroughly mixed with soil as zinc sulphate (ZnSO₄). Phosphorus from calcium monophosphate, K from K₂SO₄ and Cu from CuSO₄.5H₂O were applied in all the pots at rates of 15, 15 and 2.5 mg kg⁻¹, respectively. Analytical reagents were used in all cases to minimize contamination.

The soils were moistened to field capacity, and equilibrated for two days, after which 15 pregerminated seeds were sown in each pot. Seedlings were thinned to ten plants, fourteen days after planting (DAP). The potted soils were flooded and the first N dose of 25 mg N kg⁻¹ was applied. The second equivalent amount of N was applied 35 DAP. The plants were grown for 56 days and the shoots were harvested by cutting at one centimetre above the soil surface. Shoots were washed in detergent solution and rinsed in deionized water and dried at 70°C for 48 h. Samples were then weighed and ground using a cyclone sample mill with stainless steel blades and sieved through a 1 mm sieve. Samples of plant material were digested by the modified H₂SO₄-HClO₄ digestion method of Cresser & Parsons (1979) and digests were made to volume with deionized water. Zinc in the digests was determined by atomic absorption spectrophotometry.

Soil samples were taken from the potted soils after harvest, air dried, ground to < 2 mm and analysed for DTPA extractable Zn.

Field experiment

Two sites with low extractable Zn, namely Mwamapuli in the Igunga district and Ikindwa in the Nzega district, were selected for field experiments. At Mwamapuli two experiments on adjacent locations, hereafter referred to as Mwamapuli A and B, were conducted in successive years. Thus, results of three field experiments are reported.

Each site was ploughed, harrowed and levelled. Experimental plots were demarcated, each being 24 m² and bunds were built around each plot to control water movement from one plot to another. Phosphorus and potassium were applied to all plots at the rate of 30 kg ha⁻¹ each. The sources of the nutrients were triple superphosphate for P and muriate of potash for K. Five treatments, viz., a control and Zn rates of 10 and 20 kg ha⁻¹ applied either as zinc sulphate or zinc oxide, were tested on each site. The treatments were arranged in a randomized block design and replicated three times. All fertilizers were broadcasted and incorporated into the soil.

The plots were flooded and rice seedlings (variety Afaa Mwanza) raised in a nursery for three weeks were transplanted. The intra-row and inter-row spacings were 20 cm x 20 cm giving 600 plants per plot. Nitrogen was applied at the rate of 80 kg N ha⁻¹ as ammonium sulphate in two equal splits. The first half was applied two weeks after transplanting and the second at 40 days after transplanting (about panicle initiation stage).

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Weeds were controlled by pulling them out by hand. There was no serious pest attack or disease incidence and thus no control measures were used. An adequate water level in the plots was maintained throughout the growing period from rainfall and supplementary irrigation when necessary. At maturity the crop was harvested by hand, threshed and grain yield was measured and expressed in Mg per hectare at 14% moisture.

Soil Zn status

To assess the Zn status of major ricegrowing areas, 22 soil samples were collected in addition to the 10 soils used in the glasshouse study and analysed for extractable Zn content using 0.005M DTPA. DTPA was preferred because, in addition to the results reported in this study, it is already adopted for Cu in other parts of Tanzania based on the results of Kamasho & Singh (1982). This extractant was also found to give the highest correlation between soil zinc and zinc concentration in maize plants grown in the acid soils of northern Zambia(Banda & Singh 1989). The sampled areas represent about 80% of the rice-growing areas of the Tabora region.

Data analysis

The MSTAT statistical package was used for analysis of variance and comparison of means of data from both pot and field experiments. The critical Zn deficiency level was determined by both the graphical and the statistical methods of Cate & Nelson (Cate & Nelson 1965, 1971). Percentage yield was calculated as:

$$\frac{\text{Yield of treatment without Zn}}{\text{Highest yield}} \times 100$$

RESULTS AND DISCUSSION

Extractable Zn

Zinc concentrations by the four extractants are presented in Table 2. The average amounts of Zn extracted by the extractants were in the order: EDTA-(NH₄)₂CO₃ < 0.005 M DTPA < 0.1 M HCl < 0.01 M EDTA pH 7.0. Sedberry et al. (1979) found the ranking of the extractants to be: DTPA < IN NH₄OAc pH 4.8 < EDTA-(NH₄)₂CO₃ < EDTA + 1N NH₄OAc < 0.1N HCl. For salt-affected soils in India, Singh & Takkar (1981) observed the order to be: double acid < DTPA < EDTA-(NH₄)₂CO₃ < 0.005 MEDTA. The double acid extractant extracted the smallest amount of Zn, probably because of partial neutralization by calcium carbonate. The soils used in this study were non-saline and non-calcareous (Msolla 1992) thus enabling 0.1N HCl to extract relatively more Zn.

Correlation coefficients were calculated between soil pH, organic carbon and clay content of the soils with extractable Zn by each of the extractants tested (Table 3). Only 0.1N HCl extractable Zn was significantly correlated with organic carbon content($r = 0.671$ at $P = <0.05$). The rest of the correlation coefficients were non-significant. Martens (1968) also found that Zn extracted by 0.1N HCl, 1.0N HCl and 2 N MgCl₂ from 14 acid soils was not significantly correlated with soil pH, organic matter and clay content.

Osiname et al. (1973b), on the other hand, found that Zn extracted by 0.1N HCl, 1.0N HCl, EDTA-(NH₄)₂CO₃ and DTPA was significantly correlated with soil pH and silt + clay but only that extracted by 0.1N HCl and DTPA was significantly correlated with organic matter.

Table 2. Zinc extracted by four extractants from unfertilized soils used for pot experiment

Site name	EDTA-(NH ₄) ₂ CO ₃ (0.1M)	0.005M DTPA	0.1M HCl	0.05M EDTA (pH 7.0)
mg kg ⁻¹				
Membe	0.64	0.65	0.63	6.24
Mwamapuli	0.58	0.95	1.58	6.64
Ndembezi	1.18	2.10	1.13	2.82
Mwamala	0.80	0.75	2.00	2.44
Mwalala	0.70	1.10	1.55	3.32
Lugubu	0.70	0.90	2.13	3.40
Ikindwa	0.64	0.70	2.00	2.52
Chamwabo	0.42	0.50	0.88	3.80
Itunda	0.52	1.00	1.88	4.20
Malolo	0.86	0.80	2.25	5.32
Mean	0.70	0.95	1.60	4.07

Table 3. Correlation coefficients between extractable Zn by different extractants and selected soil properties

	DTPA	EDTA-(NH ₄) ₂ CO ₃	0.1NHCl	EDTApH7.0
Soil pH	-0.444ns	-0.289ns	-0.457ns	0.419ns
O.C.	-0.037ns	0.075ns	0.671*	0.021ns
Silt	0.598ns	0.173ns	0.163ns	-0.239ns
Clay	0.34ns	0.186ns	0.54ns	0.113ns
Silt + clay	0.477ns	0.210ns	0.507ns	0.006ns

* Significant at $P < 0.05$; ns = nonsignificant.

Haq and Miller (1972) reported that extractable Zn by EDTA-(NH₄)₂CO₃, DTPA, EDDHA and double acid was significantly correlated with organic matter but not with clay content. EDDHA and double acid extractable Zn gave negative and significant correlations with soil pH but Zn extracted by EDTA-(NH₄)₂CO₃ and DTPA was not significantly correlated with this parameter. Whereas extractable Zn in a particular soil decreases as pH increases, the relationship between the two parameters in many soils is not always consistently predictable.

The effects of Zn application on rice DM yield in 10 soils from the Igunga and Nzega districts are indicated in Table 4. Zinc application increased dry matter yields in nine soils out of 10. In soils responsive to Zn, both Zn application levels, i.e. 5 and 10 mg kg⁻¹, gave positive responses, although in five soils the relative response from the higher rate was

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lower than that from the lower rate. This suggests that higher rates of Zn may increase yields further.

Table 4. Effect of zinc application on dry matter and percentage yield in 10 soils from the Tabora region

Site name	Dry matter yield (g/pot)			Percentage change in DM yield		Percentage yield
	0 mg kg ⁻¹	5 mg kg ⁻¹	10 mg kg ⁻¹	0 and 5 mg kg ⁻¹	5 and 10 mg kg ⁻¹	
Membe	12.98	14.49	16.51	11.89	13.94	79
Mwamapuli	15.78	17.33	19.91	9.75	14.89	70
Ndembezi	20.11	20.07	19.95	-0.20	-0.60	100
Mwamala	16.94	18.67	20.74	10.21	11.08	82
Mwalala	17.98	18.97	21.06	5.51	11.02	85
Lugubu	16.11	18.54	18.74	15.02	1.07	86
Ikindwa	13.45	14.81	15.98	10.11	7.90	84
Chamwabo	12.11	15.75	16.71	30.05	6.09	72
Itunda	17.19	18.97	20.04	10.35	5.64	86
Malolo	16.75	18.21	19.00	8.70	4.33	88
Mean	15.94x	17.60y	18.73z	11.14		7.54

Mean dry matter yields in the same row followed by different letters are significantly different at $P < 0.05$ by the Duncan's multiple range test

The soil which did not respond to Zn application had the highest EDTA-(NH₄)₂CO₃ - and DTPA - extractable Zn, suggesting relatively high Zn availability. Also, the differences in Zn levels extracted by the different extractants were smallest in this soil. The zinc concentration in shoots can be seen in given Table 5. Rice response (percentage yield) was related to Zn concentration in shoots ($r = 0.80^{**}$, $P < 0.01$). All soils which responded to Zn application had plant Zn concentration values < 32 ppm in the control treatment. Generally, the lower the Zn concentration the greater was the response to applied Zn. Plants grown in Ndembezi soil had $32 \mu\text{g Zn g}^{-1}$ in the shoots and did not respond to Zn application. Table 4 also gives the percentage yield data, which ranged from 72 to 100. The response data indicated that the soil Zn levels ranged from low to high.

Critical Zn deficiency level

Plots of soil test values versus percentage yield and R^2 values for the four extractants can be seen in Fig. 1. The EDTA-(NH₄)₂CO₃ method gave the highest R^2 value of 0.63 which was associated with a critical Zn deficiency level of 0.86 mg kg^{-1} . This critical level is close to that of 1.18 mg kg^{-1} reported for soils of India (Sakal et al.1984). The DTPA method was second with a maximum R^2 value of 0.61 and a critical Zn deficiency level of 1.10 mg kg^{-1} . In addition, Zn extracted by DTPA and EDTA -(NH₄)₂CO₃ was significantly correlated with Zn uptake by rice plants ($r = 0.82$ at $P < 0.01$ for DTPA-Zn and $r = 0.68$ at $P < 0.05$ for EDTA (NH₄)₂CO₃ -Zn). These results suggest that either of these two methods could be used for Zn extraction in the soils tested.

Table 5. Effect of zinc application on shoot zinc concentration and zinc uptake

Site name	Zinc concentration (ppm) at			Mean concentration (ppm)	Zinc uptake (ug/pot) at			Mean uptake (ug/pot)
	0 ppm	5 ppm	10 ppm		0 ppm	5 ppm	10 ppm	
Membe	16.00	28.00	29.00	24.3 ^d	204.31	373.10	481.98	444.06 ^f
Mwamapuli	19.00	34.00	59.00	37.3 ^{nh}	244.54	694.20	977.00	638.88 ^{cd}
Ndembezi	32.00	45.00	52.00	43.0 ^a	671.26	879.10	1023.10	857.82 ^a
Mwamala	20.00	31.00	40.00	30.3 ^{cd}	338.00	825.80	946.70	703.51 ^{bc}
Mwalala	27.00	40.00	48.00	38.3 ^{nh}	488.47	729.80	1054.90	557.53 ^b
Lugubu	26.00	37.00	47.00	36.7 ^{nh}	467.93	800.20	1010.90	708.10 ^{bc}
Ikindwa	19.00	38.00	47.00	34.7 ^{bc}	253.70	402.40	670.41	442.17 ^f
Chamabo	16.00	24.00	36.00	25.3 ^d	190.02	512.00	630.16	444.06 ^f
Itunda	32.00	42.00	58.00	44.0 ^a	644.53	807.50	1050.60	834.21 ^a
Malalo	27.00	39.00	51.00	39.0 ^{nh}	364.09	434.80	874.60	557.83 ^p
Means	23.40 ^a	35.80 ^y	46.72 ^z		386.69 ^q	645.89 ^r	872.13 ^s	

* Means in the same column or row followed by the same letter are not significantly different ($P \leq 0.05$) using the Duncan's multiple range test. The respective LSD's are 6.14 and 3.56 ppm for the (a-c) and (x-z) letters respectively and 100.22 and 59.33 ug/pot for the (A-E) and (c-g) letters respectively

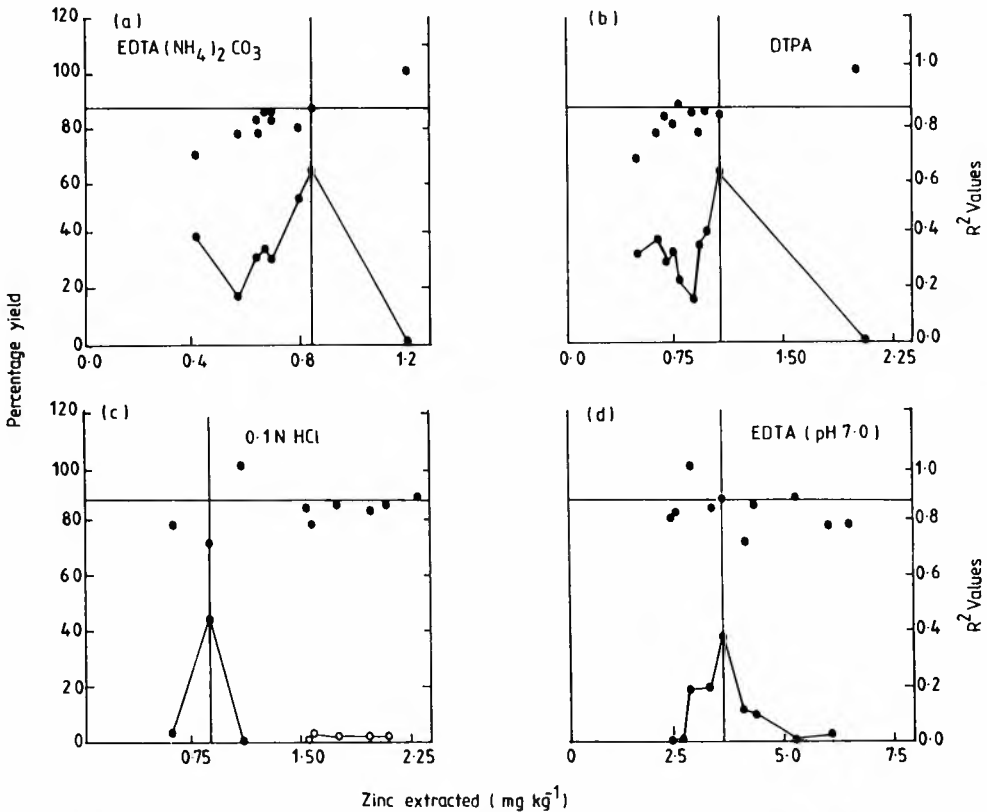


Fig. 1. Extractable Zn by different extractants in relation to R² values and yield response to applied Zn: (a) EDTA (NH₄)₂CO₃ (R² = 0.63 at P < 0.05) (b) DTPA (R² = 0.61 at P < 0.05) (c) HCl (R² = 0.41 ns) (d) EDTA pH 7.0 (R² = 0.38 ns)

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HCl (0.1M) and EDTA(pH 7.0) gave much lower and non-significant R^2 values, indicating poor correlation between Zn extracted and percentage dry matter yield. HCl proved unsuitable for these soils probably because most of the soils in this study were slightly acid to alkaline. This extractant is known to be suitable for Zn extraction in acid soils (Osiname et al. 1973a; Nelson et al. 1959). Nelson et al. (1959) showed that in order to improve the predictability of the HCl extractant for plant available Zn in calcareous soils, titratable alkalinity had to be taken into account.

Extractable Zn after harvest

Extractable Zn in the soils used for the pot study was determined after termination of the experiment (Table 6). Extractable Zn ranged from 0.31 to 1.52, 3.39 to 5.70, and from 7.27 to 10.11 mg Zn kg⁻¹ soil at the application rates of 0, 5, and 10 mg kg⁻¹ soil, respectively. In the control soils cultivated without Zn fertilization only one soil had an extractable Zn value above the critical level established in this study. In all cases where Zn was applied, extractable Zn values were much higher than the critical level. These observations suggest that one application may suffice for more than one crop. This is in agreement with studies reported elsewhere. Boawn et al. (1960) reported that where Zn was applied at a rate of 18 kg ha⁻¹ to a fine sandy loam soil, approximately 35% of it was still extractable with 0.2N HCl five years after incorporation. Brown et al. (1964) found that a rate of 2.5 mg Zn kg⁻¹ was adequate for up to seven successive crops of sweet corn under greenhouse conditions.

Table 6. DTPA extractable Zn at the beginning and after termination of glasshouse experiment at different rates of Zn applied

Site name	Residual Zn at different rates of Zn application			
	Initial DTPA Zn	0 mg kg ⁻¹	5 mg kg ⁻¹	10 mg kg ⁻¹
		Mg kg ⁻¹		
Membe	0.65	0.41	3.57	7.35
Mwamapuli	0.95	0.67	4.26	7.99
Ndembezi	2.10	1.52	5.70	10.11
Mwamala	0.75	0.47	4.01	7.27
Mwalala	1.10	0.63	4.52	7.59
Lugubu	0.90	0.61	4.15	7.72
Ikindwa	0.70	0.38	3.39	7.50
Chamwabo	0.50	0.31	3.88	7.49
Itunda	1.00	0.71	4.39	8.16
Malolo	0.80	0.58	4.09	7.78
	0.95	0.63	4.2	7.9

Field experiments

Results from field experiments conducted on three sites which tested low in DTPA extractable Zn are presented in Table 7. Zinc application increased paddy yields at all trial

sites. At the two locations in Mwamapuli the highest yield was obtained with 20 kg Zn ha⁻¹ for both ZnSO₄ and ZnO. At Ikindwa, on the other hand, paddy yield at the 20kg Zn ha⁻¹ rate was not significantly different from that at 10kg Zn rate. The trend observed at Ikindwa suggests that the 10 kg rate was probably optimum for this site.

Table 7. Paddy yields at Ikindwa and Mwamapuli as affected by rates and sources of zinc

Site name	ZnSO ₄ (kg ha ⁻¹)			ZnO(kg ha ⁻¹)	
	0	10	20	10	20
Mg ha ⁻¹					
Ikindwa	1.10c	1.90b	2.10ab	2.20ab	2.50a
Mwamapuli A	2.90c	4.20b	4.80a	4.50b	4.90a
Mwamapuli B	3.10c	4.96b	5.63ab	5.27ab	6.07a

A and B represent the two locations where experiments were conducted in Mwamapuli village. Mean yields in the same row followed by the same letter are not significantly different at $P < 0.05$

Paddy yields at Mwamapuli were much higher than those at Ikindwa. This was attributed to more favourable soil properties in the former site, e.g. heavier texture, higher content of exchangeable bases and CEC than in the latter site (Table 1).

The effectiveness of the two Zn sources tested differed slightly but not significantly. ZnO gave slightly higher yields than ZnSO₄. This could perhaps be due to lower leaching losses since dissolution of ZnO occurs slowly.

Soil Zn status.

The DTPA extractable Zn status of rice-growing areas of the Tabora region can be seen in Table 8, and it is evident that Zn deficiency occurs extensively in that region. Zn deficiency is therefore a major factor limiting rice production in the Tabora region.

Table 8. Soil fertility categories and available Zn status of rice growing soils in Tabora Region

Fertility category	Extractable Zn (mg kg ⁻¹)		
	Critical level	Range	Percentage of sampled soils
Deficient	< 1.10	0.50-1.10	66
Adequate	> 1.10	1.15-2.70	34

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Effects of added compost and farmyard manure on P release from Minjingu phosphate rock and its uptake by maize

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Incubation and glasshouse experiments were carried out to evaluate the effects of compost and farmyard manure (FYM) on the release and plant availability of P from Minjingu phosphate rock (Minjingu PR) when applied to an Ultisol. Treatments in the incubation study were Minjingu PR (400 mg P/kg soil) applied alone and in combination with compost or FYM at 2.5 g/kg each. Treated soils were brought to field capacity and allowed to incubate for up to 90 days. Samples were taken at regular intervals and analysed for extractable P, exchangeable Ca, pH and exchangeable Al. The results showed that the organic materials, particularly FYM, considerably enhanced the dissolution of Minjingu PR in the experimental soil. At 60 days, excluding the P contribution of the organic materials, Minjingu PR with compost had released 58 mg P/kg, and Minjingu PR with FYM, 74 mg P/kg compared with a release of only 45 mg P/kg soil when Minjingu PR was applied alone. Treatments in the pot study comprised a control, 40 mg P/kg as triple super-phosphate TSP; 20, 60 and 100 mg P/ha as Minjingu PR; and combinations of FYM and compost at 2.5 and 5 g/kg with 40 mg P/kg Minjingu PR. Maize dry matter (DM) yield, P and Ca uptake were determined after six weeks of growth. TSP (20 mg P/kg) significantly increased DM yield and P uptake, indicating that the test soil required supplemental P. Minjingu PR at the same rate also increased DM yields but to a lesser extent than TSP. Comparable yields with TSP were only obtained when Minjingu PR was applied at three times the rate of TSP. Application of Minjingu PR with compost increased extractable P but DM yield and P uptake were depressed, possibly as a result of microbial immobilization of the released P. By contrast, FYM (2.5 g/kg) application significantly enhanced the agronomic effectiveness of Minjingu PR as reflected by increased DM yield and P uptake. This was attributed to the effect of FYM to enhance the dissolution of Minjingu PR and to minimize subsequent fixation of the released P.

Key words: Compost, farmyard manure, maize, P release, P uptake, rock phosphate, Tanzania.

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Phosphorus deficiency is a major constraint to crop production in many areas of Tanzania, especially those with highly weathered soils. Triple superphosphate (TSP) is the recommended P fertilizer for these soils but its use is limited by its high cost and sometimes inadequate supply. The use of ground phosphate rock (PR) as an alternative to the more expensive conventional fertilizers has been the subject of many studies. Results of many of these studies indicate that PRs are more effective in acidic soils low in P (Khasawneh & Doll 1978; Hammond et al. 1986).

Minjingu PR located near Lake Manyara in Arusha, Tanzania has received considerable research attention (Patel 1975; Ngatunga & Deckers 1984; Mnkeni et al. 1991). Results of some of the studies indicated that TSP was superior to Minjingu PR in the year of application, but Minjingu PR had a better residual effect (Patel 1975). The good residual effect of Minjingu PR is encouraging, but, the utility of this P source would be greater if ways could be found of increasing its effectiveness in the year of application.

Work carried out elsewhere indicates that organic materials could enhance crop utilization of P from PRs (Welte 1978; El-Banna et al. 1978; Chakraborty 1982; Dhar & Singh 1982). Chakraborty (1982) reported increased extractable P in all plots which received Purulia PR in conjunction with farm-yard manure (FYM) while Dhar & Singh (1982) working with wheat observed higher yields in plots receiving Purulia PR with compost. These experiences suggest that coapplication of Minjingu PR with organic materials such as FYM and compost could enhance its agronomic effectiveness. Manure which could be put to such use is abundant in Tanzania, its production being estimated at 11 million metric tons per year (Kyomo & Chagula 1983).

In view of the foregoing, this study was carried out to evaluate the effects of FYM and compost in solubilizing P from Minjingu PR and its subsequent effect on maize growth and P uptake.

MATERIALS AND METHODS

The experimental soil was collected from the Magadu area of the Sokoine University of Agriculture (SUA) farm, situated at 6°51'S and 37°39'E at an altitude of approximately 550 m a.s.l. The soil was classified as a Typic Paleustult following the Soil Taxonomy System (Soil Survey Staff 1975). Selected properties of the soil are presented in Table 1. Samples were collected from an 0-15 cm depth, composted and air-dried. Samples for laboratory analysis and incubation studies were ground to pass through a 2 mm sieve, while soil used for the pot experiment was ground to pass through an 8 mm sieve.

Minjingu PR and TSP (20% P) were used as sources of phosphorus. The chemical composition of Minjingu PR can be seen in Table 2. Farmyard manure (FYM) and compost, collected from the university farm, were the organic materials used. Their respective chemical properties are presented in Table 3.

Table 1. Some physico-chemical properties of individual profile horizons

Horizon Depth (cm)	Particle size analysis (%)			Bray 1P mgP/k g	pH 1:2 (0.0 1M CaCl ₂)	OC Total (%)	N (%)	Exchangeable cations						
	Sand	Silt	Clay					Ca	Mg	Na	K	H	Al	CEC
	----- cmol(p ⁺) kg ⁻¹ -----													
Ap (0-10)	55	26	19	5.61	4.4	1.20	0.11	1.61	1.30	0.04	0.70	0.50	1.40	6.63
Abt (10-26)	53	9	38	4.21	4.4	0.86	0.10	1.12	0.90	0.05	0.30	0.39	3.62	6.75
Bt ₁ (26-43)	43	7	50	2.81	4.3	0.24	0.08	0.84	0.90	0.18	0.30	0.20	6.80	8.51
Bt ₂ (43-110)	41	3	56	2.81	4.3	0.24	0.80	0.48	0.30	0.40	0.28	0.80	6.80	8.24
Bt ₃ (+ 110)	37	5	58	2.81	4.2	0.17	0.08	0.22	0.18	0.55	0.24	0.22	8.00	8.16

OC = organic carbon; CEC = cation exchange capacity

Table 2. Concentration of major elements in Minjingu PR as determined by X-ray fluorescence

Major constituent	SiO ₂	Al ₂ O ₃	Fe ₂ O ₃	MgO	CaO	Na ₂ O	K ₂ O	TiO ₂	MnO	P ₂ O ₅
	----- percent -----									
Concentration	11.17	1.28	0.58	1.64	50.72	0.54	0.62	0.02	0.03	30.63

Table 3. Some chemical properties of the organic materials used in the experiment (on oven dry basis)

Organic material	Concentration in percent					
	OC	Total N	Total P	C:N:P	Total Ca	Total K
FYM	28.47	2.68	0.48	46:5:1	0.54	2.70
Compost	10.21	0.70	0.06	170:12:1	0.45	0.65

OC = organic carbon; FYM = Farmyard manure

Soil pH was electrometrically determined in 0.01M CaCl₂ (1:1) (McLean 1965), organic carbon by the wet combustion method (Nelson & Sommers 1982) and total nitrogen by the micro-Kjeldahl digestion method (Bremner & Mylvaney 1982). Extractable P was determined by the Bray and Kurtz No. 1 method (Bray & Kurtz 1945) but colour development was done by the ascorbic acid-molybdate blue method as described by Watanabe & Olsen (1965). Cation exchange capacity was determined by the ammonium

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acetate saturation method (Chapman 1965). Sodium and K were determined by flame photometry, while Ca and Mg were measured by atomic absorption spectrophotometry in the ammonium acetate leachate. Particle size distribution was analysed following the Bouyocous hydrometer method as described by Dewis & Freitas (1970). Exchangeable Al was determined by the KCl method as described by McLean (1965). These properties are summarized in Table 1.

Incubation study

In the incubation study, two sets of experiments were carried out simultaneously. One set was used to investigate the effects of organic materials on P release from Minjingu PR while the second set was used to monitor the effects of the same treatments on selected soil properties. The treatments consisted of a control and 400 mg P/kg soil (as Minjingu PR) applied singly and in combination with 2.5 g/kg compost or FYM.

In the first set, 20 g soil samples were weighed into 250-ml plastic containers and mixed with compost, FYM and Minjingu PR as per treatments above. The soils and incorporated materials were moistened to approximately field capacity and incubated at 25°C for 0, 7, 14, 30, and 90 days. Each treatment was replicated three times. Distilled water was added periodically to maintain the samples at approximately field capacity. At the end of each incubation period a complete set of treatments was withdrawn from the incubator for P extraction and analysis by the Bray 1 procedure (Bray & Kurtz 1945).

In the second set, 400 g soil samples weighed into 500- ml plastic containers were used. Treatments were applied as in the first set and similar incubation conditions were maintained. At the end of each incubation period samples were taken from the different treatments and analysed for pH, exchangeable Ca and Al following procedures described earlier.

Glasshouse study

Treatments in the glasshouse study also included combinations of P sources with and without compost or FYM. The P sources and organic materials were thoroughly mixed with 2 kg soil samples contained in 3-l plastic pots. Treatments were replicated four times and arranged in a randomized design. Five maize seeds (*Zea mays l. var. Ilonga composite*) were drilled in each pot and thinned to two plants per pot one week after emergence. Nitrogen (20 mg kg⁻¹) was applied as ammonium sulphate two weeks after germination. Moisture in the pots was maintained at approximately field capacity throughout the growing period.

The crop was harvested after five weeks of growth by cutting above-ground portions of the plants at soil level. The plants were then washed with distilled water, dried at 65°C to constant weight, and DM yields determined. The dry samples were ground to pass through a 1 mm sieve and subsamples dry ashed for tissue P and Ca analysis following the method described by the AOAC (1970). The data obtained were analysed using the complete randomized design model as described by Steel & Torrie (1980).

RESULTS AND DISCUSSION

Incubation study

The effects of the different treatments on extractable P are summarized in Fig. 1. Notable increases in extractable P were observed on the compost and FYM-treated samples, suggesting that the organic P of the materials underwent mineralization and released some P (Fig. 1). After 90 days of incubation, FYM-treated samples had released more P than the compost-treated samples. This apparent difference in the effects of the two organic materials reflected the differences in their initial total P content, whereby the P content in FYM (Table 3) was many times higher than that in the compost. Minjingu PR applied alone underwent considerable dissolution in the soil. Extractable P values increased with incubation time and attained a peak after 60 days at which time it had released 45 mg P/kg soil (Fig. 1). The substantial dissolution of Minjingu PR in the soil could be attributed to the soil's acidic nature, low extractable P, and low exchangeable Ca (Table 1). It is widely reported that the dissolution of PR increases with increasing acidity in soils and, accordingly, the effectivity of PR is higher in acid soils (Khaswneh & Doll 1978; Hammond et al. 1986).

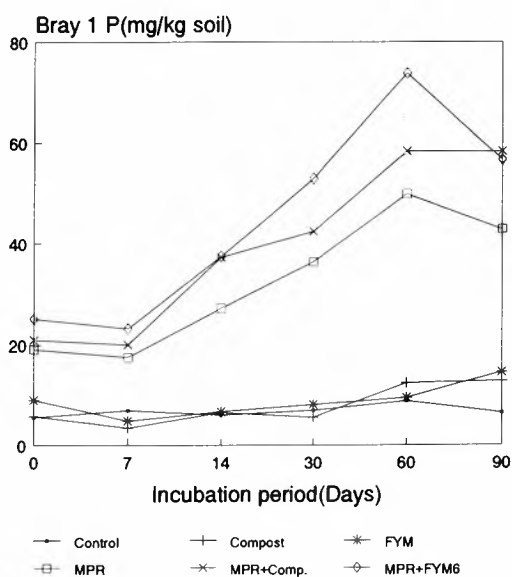


Fig. 1. Changes in Bray 1 P with incubation time in a Paleustult treated with 400 mg P/kg as Minjingu phosphate rock (MPR) alone and in combination with 2.5 g/kg compost (CO) or farmyard manure (FYM)

Coapplication of Minjingu PR with FYM and compost resulted in enhanced P release from the PR, generally reaching a peak value after 60 days of incubation (Fig. 1). The magnitude of increase observed at each incubation period was far greater than could be ascribed to the P released from the mineralization of organic P contained in the FYM and compost. The increased release of P could be attributed to enhanced dissolution of the PR due to presence of the organic acids released during the decomposition of organic materials. These results concur to some extent with those of Chakraborty (1982) who observed increased citrate extractable P in field plots in which Purulia PR was applied in combination with FYM.

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This effect has also been reported by Alexander (1977) and Jaggi (1986) who attributed it to accelerated weathering of the PR caused by organic acids produced during the microbial decomposition of the organic materials. These acids solubilize PR by removing its Ca through chelation reactions.

Generally, FYM enhanced the dissolution of Minjingu PR more than compost. FYM contained a C:N ratio of about 10:1 as compared with about 15:1 in the compost (Table 3), which could have resulted in a higher rate of decomposition of FYM and release of organic acids. Organic acids are reported to solubilize PR as observed by Alexander (1977).

In addition to P release, the dissolution of Minjingu PR released considerable amounts of Ca into the soil (Table 4). Exchangeable Ca increased from 1.87 cmol/kg at the beginning of incubation to 2.55 cmol/kg at 60 days. The increases in exchangeable Ca were accompanied by small but consistent increases in soil pH (data not presented) and decreases in exchangeable Al (Table 5). This could have been due to a liming effect of PR or precipitation of Al by P (Munns 1965) released from PR or P retention by soil colloid by legand(OH⁻) exchange. Hammond (1978) reported similar results when working with North Carolina PR on an acid soil.

Table 4. Effect of incubating Minjingu phosphate rock (MPR) with and without compost (CO) or farmyard manure (FYM) on exchangeable Ca (cmol kg⁻¹)

Incubation period (d)	Control	CO	FYM	MPR (400 mg/kg soil)	CO + MPR	FYM + MPR	LSD (5%)
--- 2.5 g kg ----							
7	1.65	1.74	1.96	2.08	2.11	2.08	ns
14	1.85	1.80	1.94	2.30	2.33	2.41	0.24
30	1.77	1.78	1.90	2.46	2.45	2.58	0.13
60	1.85	1.88	1.99	2.55	2.65	2.69	0.12
90	1.78	1.83	1.87	2.39	2.44	2.46	0.02

NS = Non-significant; LSD - Least significant difference

Table 5. Effect of incubating Minjingu phosphate rock (MPR) with and without compost (CO) or farmyard (FYM) on exchangeable Al (cmol kg⁻¹)

Incubation period (d)	CO	FYM	MPR (400 mg)/kg soil	CO + MPR	FYM + MPR	LSD (5%)	
Control							
----- 2.5 g/kg ----							
0	1.23	1.15	1.10	0.97	0.92	0.97	NS
7	1.23	1.03	0.93	0.57	0.60	0.64	0.10
14	1.20	0.97	0.88	0.51	0.42	0.37	0.13
30	1.27	0.95	0.85	0.30	0.34	0.34	0.32
60	1.25	0.97	0.82	0.10	0.10	0.10	0.12
90	1.23	0.90	0.75	0.10	0.10	0.10	0.08

NS = Non-significant; LSD = Least significant difference

Application of either compost or FYM in combination with Minjingu PR resulted in even larger increases in exchangeable Ca. Greater increases were again associated with the FYM treatment consistent with the already noted effect of this treatment on the dissolution of the PR. Corresponding decreases in exchangeable Al were observed when Minjingu PR was coapplied with the organic materials.

The increase in extractable P observed throughout the incubation period when Minjingu PR was applied alone confirmed the potential usefulness of this material as a source of P for plants reported earlier by Mnkeni et al. (1991). The further increase in extractable P observed when Minjingu PR was applied in conjunction with organic materials implied that coapplication with these organic materials may further enhance the agronomic effectiveness of Minjingu PR. This prompted a need for agronomic evaluation of these potential effects in a glasshouse study.

Glasshouse study

In the glasshouse experiment, Minjingu PR was again applied alone and in combination with compost or FYM. The results obtained are summarized in Table 6. Application of TSP at 20 mg P/kg increased DM yield and P uptake significantly over the control, indicating that the experimental soil needed supplemental P. This was consistent with soil test results (Table 1) which showed the soil to be deficient in P.

Application of 20 mg P/kg as Minjingu PR resulted in a significant but smaller growth response compared to the equivalent amount of P applied as TSP. A larger and significant increase in DM yield and P uptake was, however, observed when the rate of Minjingu PR application was trebled to 60 mg P/kg. Increasing the rate to 100 mg P/kg resulted in only marginal increases in yield and P uptake, indicating that a plateau had been reached with respect to these two variables. However, with Ca uptake a plateau was not reached as a significant increase in Ca uptake was still obtained at the 100 mg P/kg rate of Minjingu PR application.

The observed response to added Minjingu PR demonstrated that the P released during its dissolution is taken up and utilized by maize plants. The better performance of Minjingu PR when applied at 60 mg/kg was related to increased extractable P which resulted in a greater P uptake (Table 6). Thus, the inability of Minjingu PR to produce a comparable response to TSP at 20 mg P/kg could be attributed to a slow rate of release of plant available P such that the P demand by maize plants was not met. However, the good response observed when the PR was applied at 60 mg P/kg suggests that this constraint could be compensated for by applying the PR at a higher rate than that of TSP.

Application of Minjingu PR (20 mg P/kg) in combination with compost depressed DM yields and P uptake relative to those obtained with Minjingu PR alone. This was surprising in that the same treatments had a positive effect on P extracted from the potted soils after harvest (Table 6). It is possible that the wide C:N:P ratio of the compost caused immobilization of available P by soil microbes, thereby interfering with its uptake by plants.

In contrast to compost, the combination of Minjingu PR with FYM at both 2.5 and 5 g/kg resulted in significant increases in both yield and P uptake when compared to treatments which received FYM and Minjingu PR separately. This was in line with the incubation study results which revealed that FYM promoted greater solubilization of P from

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Minjingu PR than compost. This effect was also reflected in the extractable P levels observed in the potted soils after harvest (Table 6).

Table 6. Effects of applying TSP and Minjingu PR (MPR) alone and in combination with compost (CO) or farmyard manure (FYM) on maize DM yield, P and Ca uptake, and extractable P after harvest

Treatment	DM yield (g/pot)	P uptake (mg/pot)	Ca uptake (mg/pot)	Extractable P after harvest (mg/pot)
Control	2.37 f	3.17 b	88.6 ef	5.0 e
TSP (20 mg/P/kg)	5.23 b	6.58 a	97.5 e	8.7 cd
MPR (20 mgP/kg)	4.47 d	4.05 ab	94.4 e	8.6 cd
MPR (60 mgP/kg)	5.95 a	6.42 a	126.6 bc	12.8 a
MPR (100 mg P/kg)	5.97 a	6.77 a	151.7 a	13.5 a
CO (2.5 g/kg)	3.88 gf	2.99 b	78.8 ef	5.0 e
CO (2.5 g/kg) + MPR (20 mg P/kg)	4.27 de	3.63 ab	95.0 e	12.5 a
CO (5g/kg)	3.68 g	2.29 b	72.6 f	4.6 e
CO (5 g/kg) + MPR (20 mg P/kg)	4.10 ef	3.08 b	99.5 de	9.5 bc
FYM (2.5 g/kg)	4.76 c	4.02 ab	96.5 e	5.6 e
FYM (2.5 g/kg + MPR (20 mg P/KG)	5.44 b	6.03 a	141.2 ab	13.5 a
FYM (5 G/KG)	5.37 b	5.39 ab	118.3 cd	7.8 b
FYM (5 g/kg) + MPR (20 mgP/kg)	5.66 b	6.32 a	142.6 a	13.5 b
F - ratio	86.7**	5.51**	16.2**	49.56**
CV (%)	4	28	12	10

Means within the same column followed by the same letter are not significantly different at $P = 0.05$ according to Duncan's New Multiple Range Test;

** : significant at 0.01 probability level

The FYM could also have contributed to the enhanced agronomic effectiveness of the PR through its documented ability to reduce P fixation in soils (Mnkeni & MacKenzie 1985, 1988). Apparently, although chemical P fixation in soils increases PR dissolution, the same also decreases the plant availability of P from PR (Chien et al. 1980; MacKay et al. 1986; Syers & MacKay, 1986). Thus, by decreasing P fixation, FYM could have increased the availability of P released from PR dissolution.

CONCLUSION

Minjingu PR released sufficient amounts of P to influence maize yields and P uptake in the experimental soil, though not to the same extent as TSP. For effectiveness comparable with that of TSP, PR needed to be applied at about three times the TSP rate. Coapplication with FYM increased the P release and agronomic effectiveness of Minjingu PR. The compost

used in this study also increased P release from Minjingu PR but had a negative effect on its agronomic effectiveness, possibly because it encouraged microbial immobilization of the released P due to its wide C:N:P ratio.

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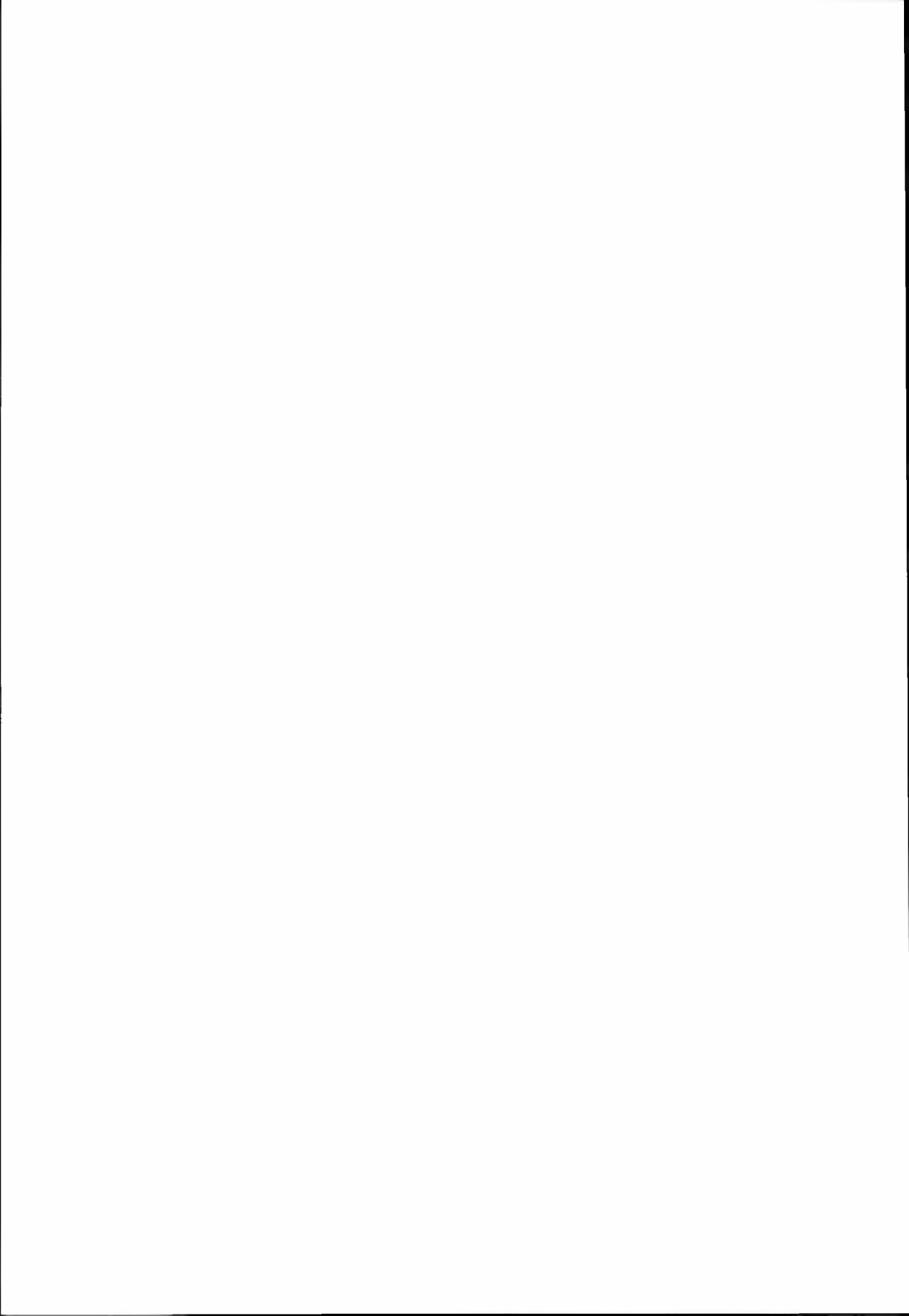
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The influence of wind on plant development and physiology: a review

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Wind has an influence on plant development and physiology through leaf temperature, water and CO₂ diffusion, and through mechanical disturbance. Plants are shaped and may be injured by the wind. As climatic factors interact with one another, and with the nutrient status, plants for shelter belts should be evaluated under multiple stresses. Wind tolerance is genetically based and may be improved by means of selection and breeding. Adaptation of plants at a site also depends on photoperiodic responses and tolerance to diseases and pests in the prevailing environment. Further research should focus on identifying plant characteristics that can be used as markers for wind tolerance as this would simplify a selection programme for wind tolerance in trees for shelter belts.

Key words: Anatomy, morphology, physiology, plants, wind

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Wind is a major factor in the climate of Norway. Even though gale force winds are infrequent, the consequences of wind can be severe (Allen 1992). However, the daily wind status of a site is usually more important in the development and physiology of plants.

The effects of wind on plants were classified as mechanical damage, physiological response, anatomical adaptations and morphological changes (Wade & Hewson 1979). However, it is difficult to establish a direct link between the cause and effect of wind on plants, especially at the physiological level (Davis & Norman 1988). Low temperatures, salt damage to plant tissues, and increased deposits of pollutants often accompany strong winds (Grace 1977), and can also have an influence on plant development.

Unequal heating of ocean and land masses with an expected rise in global temperatures and the heavier level of precipitation in northern areas may cause an increase in wind and gale frequencies (Walsh 1993), thus enhancing the importance of shelter belts (NLVF 1992). Selection for wind-tolerant plants can improve the establishment of high quality shelter belts. Such a selection programme would benefit from knowledge of the relationship between wind tolerance, morphology, anatomy and physiology of the plants.

This review examines the effects of wind on the development and physiology of plants. Previous reviews, with varying emphasis (Grace 1977; Wade & Hewson 1979; Nobel 1981; Biddington 1985; MacKerron & Waister 1985; McNaughton 1986; Gardingen

& Grace 1991), were partly used as a basis for the present paper. The documentation of physiological wind responses in plants points towards the possibility of using the plant characteristics in selection programmes for wind tolerance.

TRANSPIRATION

In the transpiration process, water is transferred to the atmosphere in exchange for CO₂. Water loss is therefore a necessary price to pay for carbon fixation. The boundary layer comprises the zone of air close to the surface of an object (about 1 mm thick). The driving force of the diffusion of water vapour from the leaf to the atmosphere is proportional to the vapour pressure gradient between the boundary layer and the atmosphere (McNaughton 1986). The difference in temperature between leaf and atmosphere, which is influenced by wind, is therefore important. The air around plants may have a higher or a lower vapour pressure than the boundary layer (McNaughton 1986), and therefore a clear-cut effect of wind on humidity diffusion from plants cannot be found. Dixon & Grace (1984) observed a concurrent reduction in the leaf-air vapour pressure difference in experiments with wind-exposed young trees.

The boundary layer of quiet air represents an insulating layer, with a resistance to transfer of water and heat between the plants and the atmosphere. The water store of the plant tissues covers only 1-2 h of maximal transpiration, and long before this reservoir is exhausted, the plants close the stomata (Judd & McAneney 1984). The water transfer from the plant to the atmosphere by evaporation is highly energy demanding:

$$E_t = \mu M$$

where E_t = transpiration energy, μ = latent evaporation heat per unit mass of water, M = mass of water transpired. This energy loss from the leaves results in a decrease in the temperature of the plant.

The main resistance to CO₂, heat and water exchange between the plant and the atmosphere can be found in the mesophyll of the leaves, the stomata, the cuticle and the boundary layer. The wind directly affects only the resistance of the boundary layer, which is small compared with the resistance of the leaf (Gardingen & Grace 1991). Resistance of the stomata dominates other factors in the water diffusion, since the function of the stomata is to control this diffusion.

The combination of strong wind and drought may cause excessive cuticular water loss from the plants. In response to a wind velocity of 3.5 m s⁻¹, Grace (1974) observed, first, a decrease in the transpiration rate. There was, however, an increase over the next two days in both day- and nighttime transpiration, probably caused by increased surface damage to the leaves from movement and collisions between leaves within the canopy. Damage to the epidermis may also induce damage to cells adjacent to the stomata, which thus may lose part of their function as a result of reduced turgor pressure. In consequence, both cuticular and stomatal transpiration may increase (MacKerron 1976; Grace 1977). Leaf surface damage was also observed in response to wind in *Pinus sylvestris* and *Picea sitchensis* (Gardingen & Grace 1991). Transpiration increased at high wind velocity in *Festuca*

arundinacea, when the plants were exposed to phosphorus depletion (Grace et al. 1982; Pitcairn & Grace 1982). There may have been an effect of nutrient deficiency on the types of tissues formed in the leaves, which thus increased the susceptibility to wind damage (Pitcairn & Grace 1982). Cuticular water loss is of little importance unless the plants are at the wilting point, the cuticle is damaged, or is poorly developed.

The effects of the wind may in some cases, but not all, appear through water relations (Davis & Norman 1988, McNaughton 1986). However, wind usually exacerbates the effects of water stress (Grace & Russel 1982).

PHOTOSYNTHESIS

Photosynthesis includes many climate-dependent processes. For instance, the water balance of the plants determines CO₂ diffusion through the stomata. Other processes in the incorporation of carbon to sugars are also strongly affected by the temperature of the leaves, stems and roots.

A large leaf has a thicker boundary layer with higher resistance to energy and water transfer than a smaller leaf. Weather conditions, therefore, affect the small leaves to a greater extent than large leaves (McNaughton 1986). The temperature of small leaves is close to that of the ambient air, while the large leaves may have a temperature several degrees higher during the day, and cooler during the night. Mechanical damage occurs more frequently in large leaves than in small leaves.

The boundary layer is thicker around leaf surfaces with hairs and wrinkles compared with smooth leaves. The edge effect increases the coupling of the leaf temperature to that of the atmosphere (Gardingen & Grace 1991).

The solar radiation energy (E_r) is absorbed by plants and the ground as heat, and only a small fraction is utilized by the plants for photosynthesis. Wind creates a convective mass and energy flux (E_c), which transports humidity and heat away from the plant environment. The radiation energy, convective energy flux, and the energy of the transpiration flux rate (E_t) are the three most important factors in the energy budget of plant organs:

$$E_r = E_c + E_t$$

The coupling of ambient and leaf temperature is highest in turbulent air, and lowest where there is little air movement (McNaughton 1986). Solitary and tall plants are therefore closely coupled to the ambient weather conditions, whereas short plants, and those in a dense canopy may have microclimatic conditions significantly different from the macroclimate. Thus, individual plants may function as mutual shelters, those on the windward side of a canopy creating shelter for those on the leeward side. The "wave-regeneration" phenomenon in forest stands is characterized by a regeneration zone and a die-back zone in the plant stand making up "waves" in the landscape (Robertson 1987). The function of the observed wave regeneration in forest stands may be a consequence of the dynamics within a plant stand described above. Plants with a high temperature demand may thus survive in a cool climate (Grace 1977).

The effect of wind on photosynthesis per se may be small even though the wind may

reduce the boundary layer and increase CO₂ availability to the plants. However, the boundary layer resistance is very small compared with the other kinds of resistance in CO₂ diffusion (Grace 1977). Caldwell (1970) observed a rapid and strong reduction of photosynthesis in *Rhododendron* at high wind velocity. In contrast, there was a weak response in *Pinus cembra*, which is far better adapted to a windy environment. Farquhar et al. (1987) concluded that the genetic control of stomatal conductance is strong.

In *Sorghum*, net photosynthesis in undamaged tissues increased by 48-85% after neighbouring tissues were damaged by wind and sandblast (Armbrust 1982). Thus, increased photosynthesis in undamaged tissues may in some plants compensate for tissue lost after wind damage. Wind-resistant plants may, however, also conduct photosynthesis in conditions of high wind velocities (Caldwell 1970).

In conifers, which photosynthesize in the winter, strong wind and drought may reduce the stored reserves and thus reduce the growth potential of the plants (Grace 1977).

In soybean, light penetration was deeper in sheltered rather than in exposed canopies, thus enhancing photosynthesis and production of dry matter (Ogbuehi & Brandle 1981).

RESPIRATION

The respiratory processes are greatly affected by the temperature and water balance of the plants. In a study by Todd et al. (1972), the respiration in nine species increased by 20-40% in response to a wind velocity of 7.2 m s⁻¹. There was a significant increase in respiration even though movement of the leaves by wind was prevented. An increase in respiration may be the cause of reduced yield in wind-exposed plants, although the wind often leads to an immediate decrease in leaf temperature, which reduces respiration. However, an increase in respiration can be expected if damage from wind has to be repaired or compensated for.

PLANT STRUCTURE AND ANATOMY

The wind causes a physical strain on the plant structures. A plant moves in the wind like a pendulum, with the fixed point at ground level. The drag force from the wind on plants depends on the wind, the total leaf area of the plant and the interference from wind gusts and other trees (Milne 1990, 1992). Movement in the plant and the wind gusts in the same phase may cause a much greater strain on the plants than from the wind alone. It has therefore been difficult to evaluate the critical wind velocity that causes up-rooting or snap-off.

Plants have a plastic phenotype enabling adaptation to environmental conditions. This is particularly important in trees, since such flexibility protects against large environmental changes during their long life span (Thompson 1991; Libby 1992).

In *Acer pseudoplatanus* (Wilson 1984) and in strawberry (MacKerron 1976), wind caused damage in cuticula and leaf cells. Wilson (1984) suggested that leaves affected by wind were more susceptible to nutrition loss and pathogens, as leaf wetness was enhanced by the wind. Rain, combined with wind enhances the erosion of waxes from the leaves

(Baker & Hunt 1986). Other species (*Picea sitchensis*) are perhaps less sensitive to rough treatment (Gardingen & Grace 1991). The number of lesions, the total leaf surface conductance, and the uptake of radio-labelled SO_4^{2-} increased with increasing abrasions in leaves of *Fagus silvatica* (Hoad et al. 1992). The cuticle and epidermis cells of leaves of *Picea sitchensis* and *Pinus sylvestris* were damaged by a wind velocity of 11 m s^{-1} in wind tunnel experiments (Gardingen et al. 1991).

The formation of compression wood on the leeward side in conifers and tension wood on the windward side of deciduous trees is a well-known response to wind (Wade & Hewson 1979; Wilson & Archer 1979). Differential wood deposition on the leeward and windward sides of the trunks is caused by changes in the cell morphology (Wade & Hewson 1979) and may be mediated through hormones (Wilson & Archer 1979; Nobel 1981). The strength of the stems in trees seems to be regulated by varying the rate of cell production (Wilson & Archer 1979).

The structure of trees is adapted to minimize support costs (Wilson & Archer 1979; Cannell & Morgan 1989). These costs may differ in trees subjected to a windy environment, compared with those in a calmer environment. The shape of tree crowns will vary accordingly.

The stability of trees depends on the soil, the root system and the forces acting on the tree-soil system (Coutts 1986). Sitka spruces planted near the stumps of earlier growing trees were less stable than plants on soil free from stumps. This should influence the choice of method in the establishment and re-establishment of windbreaks and forests (Prest et al. 1991; Quine et al. 1991).

Wind from mainly one direction shapes the plants (Nobel 1981; Yoshino 1973), and trees with asymmetric crowns, flag trees, may be good indicators of the local prevailing wind direction (Holroyd 1970). Flagging may be induced by the difference in temperatures of the windward and leeward sides of the trees (Grace 1977). However, salt spray may also cause deformations in the trunks and crowns of trees (Wade & Hewson 1979). Persistent and moderately strong winds cause more deformations than gale force and infrequent winds (Robertson 1987). The wind may lead to deformation of the tree trunk by torsion. This can cause splitting of the trunk if the plants are subjected to a strong wind from the opposite direction to that which originally shaped the plants (Mattheck 1992).

The effect of the physical strain caused by wind on plant morphology is similar to that observed after touching and moving plants (Biddington 1985; Biddington & Dearman 1985). The flexibility of bean plants was enhanced after rubbing the plants compared with plants that were untouched (Jaffe et al. 1984). *Pinus radiata* plants that were prevented from swaying became more elongated and had thinner stems than trees that were allowed to sway (Jacobs 1954). Broccoli transplants were similarly affected when subjected to wind, brushing or water stress, especially so in one of three years (Latimer 1990). This probably illustrates the variation in conditions between years and the difficulty in evaluating the effect of each growth factor in a set of factors in field experiments. The root growth may also be affected by the movement of the above-ground plant parts (Whitehead & Luti 1962; Coutts 1986), and pathogens entering through wounds may destroy the plants.

Elongation, number of nodes and chlorophyll content were affected in tomato plants subjected to mechanical stimulation (Mitchell et al. 1975). In *Phaseolus vulgaris* the decrease in elongation and the increase in radial growth were accompanied by an increase

in ethylene production. Both root- and top-growth were reduced by the mechanical manipulation of the plants (Huberman & Jaffe 1981). Wind reduced elongation in *Pinus contorta* (Rees & Grace 1980), and the effects were the same as those from shaking the trees. Wind is probably strong enough to induce such effects under most climatic conditions (Grace 1977).

The effect of wind alone gave a 20% reduction in leaf extension, and the combination of wind and phosphorus depletion reduced the leaf extension by 40% in *Festuca arundinacea* (Pitcairn & Grace 1982). In *Festuca arundinacea* and *Lolium perenne*, an increase in wind speed from 1 to 7.4 m s⁻¹ reduced the leaf area by 24%. Photosynthesis was not affected and neither ethylene production nor drought stress was observed, indicating mechanical rather than physiological strain as a cause of the effect (Russel & Grace 1978). A reduction in leaf area resulted from reduced cell expansion and not from altered cell number. Needles of coniferous trees on the leeward side were twice as long as those on the windward side (Wade & Hewson 1979). In *Acer pseudoplatanus*, the most damaged leaves were those with the smallest leaf area. Injured leaves could not expand to full size, and the most severely damaged ones were prematurely lost (Rushton & Toner 1989). Wilson (1980) observed increasing leaf damage with increasing wind velocity, the youngest leaves being most affected. Physical damage and physiological damage in plants are thus coupled.

Many plants are sensitive to any change in the position of the meristems. There seems to be a balance in plants between height growth and the growth of the branches (Grace 1977). The flexibility of this balance may be characteristic of genotypes of plants and therefore renders plants resistant or susceptible to wind effects. Plant movements may be sensed by a not yet described plant sensor (Gardingen & Grace 1991), or by the position of the apex in relation to the vertical. Plant movements may induce changes in hormone concentration or distribution.

Beyl & Mitchell (1983) found reduced gibberellin content in mechanically manipulated sunflower plants, and an increase in ABA content of the leaves. Epinasty, increased stem thickness and the production of ethylene have been observed in response to mechanical stimulation of plant parts, and the phyto-hormone auxin may be an important factor together with ethylene (Jaffe 1980).

SELECTION FOR WIND RESISTANCE

There may well be plant features that relieve the strain from wind more in the wind-resistant plants than in the those susceptible to wind. Plant structure, the composition and amount of cuticula, wrinkles, hairs and the lobe characteristics of the leaves and physiological traits may be adaptations to wind in resistant plant genotypes. Such characteristics may, when identified, be used in the selection of wind-resistant plants.

Climate-adapted plants should be made more available for use in shelter belts. Traditionally, selection of plants for shelter belts has been made through observations of plants in established shelter belts (Groven 1983, 1985), but only a few selection programmes of this kind have been conducted (Cunningham 1988). The lack of emphasis on selection for wind resistance in trees, and the low level of production of special plants

for shelter belts may be due to high costs and a limited market (Hollowell & Porterfield 1986; Cunningham 1988). Progeny tests in Denmark have revealed that the seed source is important for wind tolerance in trees (Brander 1993), thus indicating the wide genetic variation among populations. A cheap alternative to elaborate selection programmes is the use of local seed sources and seed harvested from superior trees. However, this method may be time-consuming because detailed seed source descriptions are necessary, and reliable results from observations in the offspring can only be made several years after planting. Cunningham (1988) emphasizes the multitude of stresses often imposed on the plants in shelter belts, and the importance of selection for stresses other than from wind. Grace (pers. comm.) estimated the heritability of wind tolerance in a grass species of 0.2, whereas that of *Pinus caribaea* var. *hondurensis* was as low as 0.08 (Woolaston et al. 1990). The physiological plasticity of trees may be greater than in grasses, however (Libby 1992).

CONCLUSIONS

Height is an important feature in trees used for shelter belts. Shrubs may have other selection criteria, for example branching and the ability to compete with weeds. Photoperiod adaptation and resistance to pests and diseases are also very important.

In an environment with a variable coastal climate it seems important to maintain large genetic diversity. This implies emphasis on seed propagation and, when clones are used, several clones in each shelter belt.

The leaf temperature and water use are related in complex ways. In arid regions and during dry seasons the effect of shelter on the water use efficiency (WUE) may be the single most important factor. In other regions, or at differing times of the year, the effect on temperature may be equally or more important for plant growth and development. However, the effects of wind on plants depend on many interacting factors in the physical environment of the plants, as well as the physiological responses in the plants. Future research in this area should focus on mechanisms of wind tolerance. A selection method using small seedlings would speed up the selection process for climate-adapted plants. Knowledge about responses in the plants may become the basis for selection of wind-tolerant plants.

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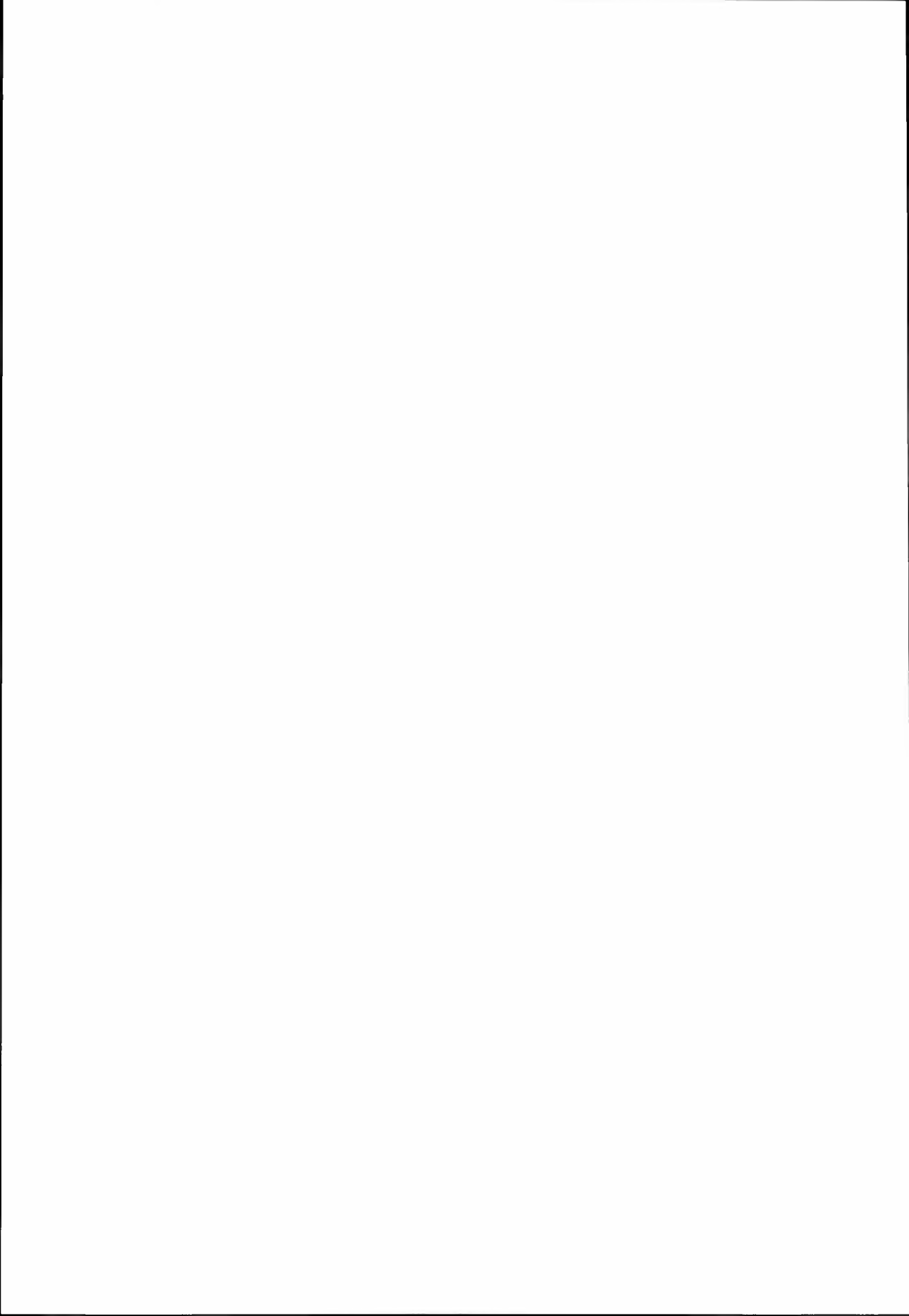
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Measuring and mapping crop loss with 35 and 70 mm aerial photography

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Small hand-held cameras were used to photograph two sites affected by excessive fertilization. Crop loss was measured and mapped off the oblique aerial photography using a standard digitizing tablet. Accuracy of the 1:7000 scale 70 mm photograph was 0.33 m; accuracy of the 1:11000 scale 35 mm imagery was 2 m. Accuracy difference was attributed primarily to different photo scales and the quality of ground control. Digital elevation models (DEMs) supplied the elevation data for monoscopic measurements. Different DEMs were tested: a DEM created from control points captured off a 1:5000 scale map, a DEM created from elevation contours transferred from a 1:1000 scale map, and a DEM created from stereoscopic photography. The simple mapping procedures did not require photogrammetric skill or training, and took about one hour per site. Provided a suitable scale map is available for control purposes, this straightforward technique enables agronomists to measure directly off a single small-format photograph with a standard digitizing tablet.

Key words: Aerial photography, crop loss, fertilization, mapping.

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Although excessive fertilization can reduce potential crop yields, the actual loss for a given site is difficult to determine before harvest. Since lodging is easily seen from the air, one can use a variety of remote sensing tools to measure crop loss. Practically speaking, however, small-format (35 and 70 mm) aerial photography appears to be the most suitable for surveying small areas (< 100 ha). Although satellite imagery covers a vast amount of land, it lacks suitable ground resolution (at best 9 X 9 m pixel resolution) and requires sophisticated equipment and specialized training to make area measurements. Conventional large format (23 X 23 cm) aerial photography provides high resolution and accuracy for photogrammetric purposes; however, the aerial surveys are expensive (minimum NOK 8000 per mission). Small-format aerial photography provides reliable measurements, and is cost-effective for mapping small areas (Warner 1989). Moreover, agronomists can conduct their own aerial surveys with standard cameras; and use the photography for digital mapping and measuring with basic office equipment.

The application of small-format aerial photography for photogrammetry is well documented. In recent years, JORDFORSK has paid particular attention to innovative applications of hand-held (oblique) photography for agronomists and natural resource specialists (Warner & Carson 1992a; Warner 1993). This study illustrates two methods of mapping and measuring crop areas off an oblique photograph, using a standard digitizing tablet.

Capturing measurements off a single photo is based upon transforming photo coordinates into ground coordinates. The process is entirely analytical: objects on the photograph are digitized and through conventional photogrammetric equations these (x, y) photo coordinates are transformed into familiar (X, Y, Z) Cartesian coordinates. The heart of the operation – transforming photo coordinates to ground coordinates – is based upon knowing the camera's geometry, position and angular orientation (relative to the ground) at the moment of exposure.

In order to measure the location of objects on a single photo, their elevations must be known. Elevation is usually determined by linking the photograph to a digital elevation model (DEM). The DEM can be constructed in three ways: (1) generated internally from control points, which are known ground coordinates used to level the scale the photograph, (2) imported from an external source, e.g., an existing DEM from mapping authorities, or (3) created from photogrammetric height measurements, which are made from two overlapping photographs. The following two studies examine the practical aspects of using these different DEMs for computing crop areas.

MATERIALS AND METHODS

Two croplands in Ås, Norway were selected for mapping and measuring. Both were photographed in late August 1993 using small hand-held cameras from a light aircraft (Cessna 172). The primary advantage of using a hand-held camera – rather than one vertically mounted camera on the outside of the aircraft – is that the photographer can ensure that the area of interest is properly framed (i.e. fully covered). In addition, the photographer has immediate camera access for loading film and adjusting the aperture. Exposure is normally set on a priority shutter speed of 1/500 sec.

Another advantage of hand-held photography is that two overlapping exposures, taken from distant exposure stations, can cover the *entire* area of interest and be used for making height measurements. The method is quite simple: oblique photographs are taken as the aircraft circles the area of interest. This type of photography can provide a high level of photogrammetric accuracy by enabling a large *base:height* ratio to be achieved – a favourable geometric condition for mapping photography (Wolf 1974). Moreover, the technique provides almost 100% overlap between exposures; a factor which can reduce the amount of ground control required in mapping projects. Finally, this method of photography produces a large photo scale, thus increasing photogrammetric accuracy. The reason being that if the area were photographed along a straight flight path, with standard 60% endlap – as in conventional large-format aerial photography – the flying height of the camera could be higher than if it were circled (Fig. 1). Note: as flying height increases, photo scale decreases, thus photo measurement accuracy decreases.

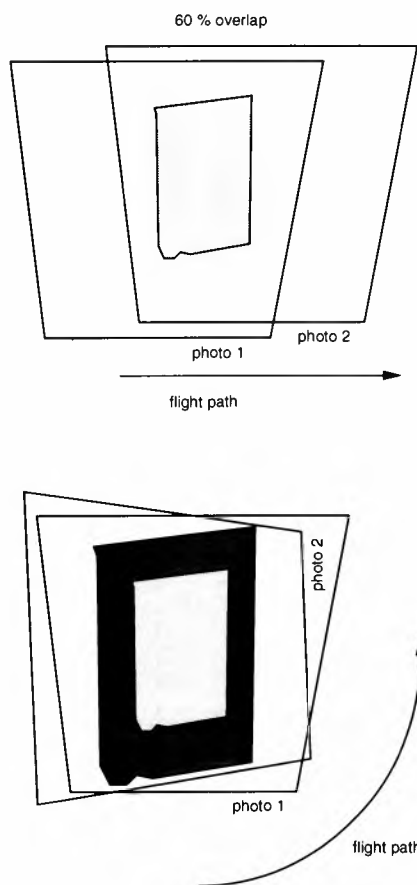


Fig. 1. Oblique overlap photography along a straight flight path (top) and a circling flight path (bottom). Dark shaded area (bottom) shows increased photo scale

There were similarities and differences in the two case studies. Both sites had similar landscape characteristics: 150 X 250 m with >5% slope. They were photographed from the left-hand side of the aircraft under similar conditions: flying height about 400 m (above ground level) with the camera tilted about 45° (upward from vertical). Standard (non-metric) cameras were used: a 35 mm fitted with a 35 mm lens and a 70 mm (645 format) fitted with 75 mm lens, and area measurements were made from single enlargements, using a standard digitizing tablet (details of the photo measurement system which drove the digitizing tablet and computed the photogrammetric solutions are detailed by Warner & Carson (1992b)). Of particular interest are the two principle differences between the case studies: (1) the source and quality of ground control, and (2) the techniques used to generate DEMs.

Case 1

Since a DEM of the site did not exist – and a DEM created from a few control points would not characterize the undulating landscape – a DEM was generated from numerous

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height measurements captured off two overlapping photos (Figs. 2 and 3). Although the overlapping photos could not be viewed in true stereo fashion, they are referred to as a *stereo model* in this paper.



Fig. 2. Case 1, left photograph for 35 mm stereo model



Fig. 3. Case 1, right photo for 35 mm stereo model

In principle, if one knows the (X,Y,Z) ground coordinates of six well-distributed points in the stereo model (i.e. *control points*), it is possible to determine the angular orientations of the camera at the amount of exposure; and from this information it is possible to determine the X,Y,Z location of any object in the model. This is accomplished by measuring *parallax*, i.e. the change in appearance of an object as the viewpoint is shifted (Wolf 1974). With that explanation in mind, let us examine the actual procedures.

Two 35 mm diapositives were enlarged to A4 format via a colour laser copier (Canon CLC200). Copying costs are 25% of the conventional photographic enlargement; moreover, unlike conventional enlargement methods, image deformation is relatively small (Warner & Andersen 1992). The enlargements were taped on a standard digitizing tablet, and oriented following the traditional photogrammetric procedures of interior, relative and absolute orientation, explained as follows:

First, the frame corner of each photograph was digitized. *Interior orientation* transformed the digitizer's coordinates to the photo measurement system, and accounted for any scale change.

Next, 12 control points were collected off a 1:5000 scale topographic map. The procedure was straightforward. First, the map was taped next to a photograph, and four map-reference coordinates were recorded. Then a control point (e.g. a building corner) was digitized on the photograph, then on the map, followed by typing in the elevation of the point. After this was repeated for every control point, the control point file was saved. The entire operation took about 20 minutes.

The second orientation, *relative orientation*, determined the position and angular orientation of one photograph with respect to the other. This simple procedure consisted of merely digitizing a control point of the left photograph followed by digitizing the same point on the right photograph. In addition to the control points, four pass points were collected (objects without known ground coordinates). Any detail on the photographs can serve as a pass point, but pass points should be well distributed across the model. After measuring the 16 points, the relative accuracy of model measurements was computed by a standard photogrammetric solution (Schut). Specifically, the accuracy of measuring any object on the stereo model was 35 μm at image scale.

The final orientation, *absolute orientation*, scaled and levelled the stereo model to the ground (based upon control point data) and determined the expected accuracy of points measured on the model: 1.90 m in X-direction, 3.38 m in Y-direction, and 1.47 m in elevation (Z). In oblique imagery, measurements in the Y-direction are generally worse than those in X or Z, because the tilted camera creates considerable scale variation along the Y-axis (foreground to background).

Since the 1:5000 scale map showed a 15 m elevation difference across the 150 X 250 m field, it was assumed that a DEM created from a few control points would be inadequate. It was necessary, therefore, to generate a detailed DEM by measuring the elevation of numerous objects off the stereo model. The following question naturally arose: "How much *better* is a DEM created from the stereo model than one created from control points?" In order to address this question 18 elevations computed from (i) the DEM based upon control points and (ii) from the stereo model were compared.

First, transparent overlays were placed on top of both the right and left photos. Then three contour interval lines were visually transferred (85 m, 90 m, and 95 m elevation)

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from 1:5000 scale map onto the photographs. Along each line six object points were selected (annotated). With the measurement system in monoscopic mode, 18 points were recorded, and the DEM (created from control points) issued elevation values. This was done for both the left photo (Fig. 4) and right photo (Fig. 5). Finally, without the assistance of a DEM the elevation of each annotated point on the stereo model was measured. This was accomplished by switching the measurement system into stereo-mode and merely digitizing an annotated point on the left photo, followed by recording the same point on the right photo. Object height was computed (in near-real time) from the parallax measurement.

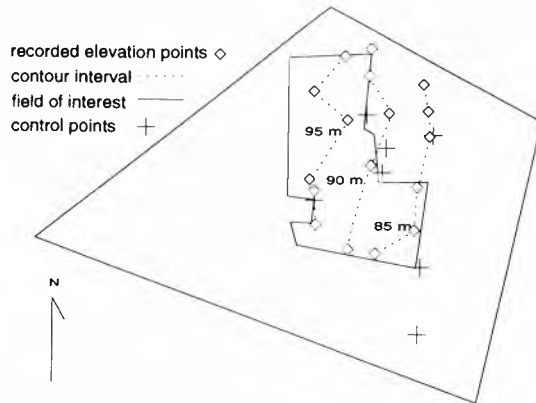


Fig. 4. Map projection of elevation contours superimposed on right photo area

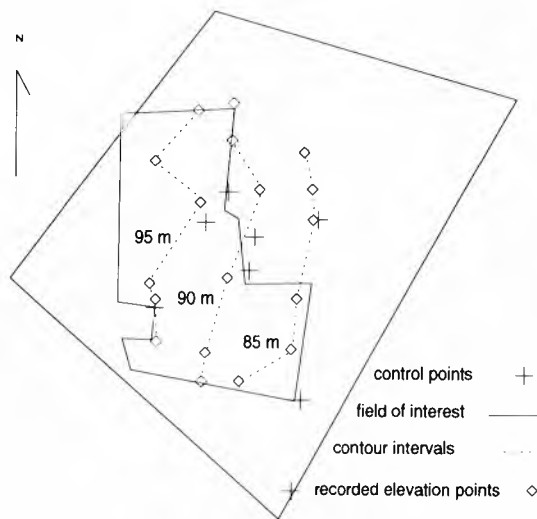


Fig. 5. Map projection of elevation contours superimposed on right photo area

A statistical t-test showed that in all cases there was no significant difference between elevations of identical points recorded on the left and right photos, using the control point DEM. There was, however, a significant difference (98%) between elevations recorded using the control point DEM and elevations recorded from the stereo model. For the 80 m and 95 m contour intervals, there was a significant difference (98%) between map elevations and elevations recorded off a single photo; however, there was no significant difference between map elevations and stereoscopic height measurements. For the 90 m contour, the situation was reversed. This error can probably be explained by the mis-location of the 90 m contour line on the transparent overlays, rather than erroneous parallax measurements.

After determining that the stereo height measurements were significantly more accurate than the control point DEM, the 18 points were exported to Golden Software's Surfer program (Version 4.0), gridded to 10 m cells, and a DEM was generated using the inverse distance (power of 2) algorithm. With the 18-point DEM on the file, the right photo was selected for monoplotted. The cursor was set on continuous mode (1 mm at enlarged photo scale, or approximately 1.5 m on the ground), the field border digitized, and its area recorded: 28,478 m². The areas (polygons) of standing grain were then digitized and summed: 20,718 m², 73% of the crop area. For geo-referencing purposes buildings and roads were digitized, the data exported to a simple mapping program (Golden Software's MapViewer), and a map issued (Fig. 6). Total mapping time was about one hour.

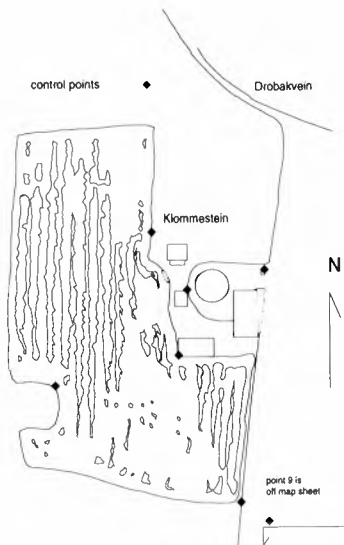


Fig. 6. Case site map made from 1:10 400 original photo scale

Case 2

In this example a detailed DEM was generated by digitizing contour intervals superimposed on a single photograph. This technique was developed for two reasons. First, one cannot assume that every photograph will have a suitable, overlapping partner to make a stereo

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model. If the angular orientations of the two photographs are too large or too small, relative orientation will not provide reliable results. Second, even if a suitable stereo model exists, there are circumstances when it is difficult to identify corresponding objects on two photographs. For instance, if a field is blanketed with an evenly grown crop, it is virtually impossible to digitize the same point on both photographs. This is especially true when working with oblique photographs taken from distance exposure stations.

Digitizing map (elevation) contours superimposed on a photo was straightforward and took less than one hour, including photo orientation. The 70 mm negative (6 X 4.5 mm format) was enlarged to A4 format with a conventional optical enlarger. The print was oriented as described in Case 1 (Fig. 7); of course, relative orientation was omitted because only one photograph was used. Eight control points were captured off a 1:1000 scale map, using the same technique as that described in Case 1. The large-scale map's point location accuracy (0.1 m) produced excellent control data; which in turn generated a relatively high order of precision for the small-format imagery. Objects measured off the image were accurate to within 0.33 m.

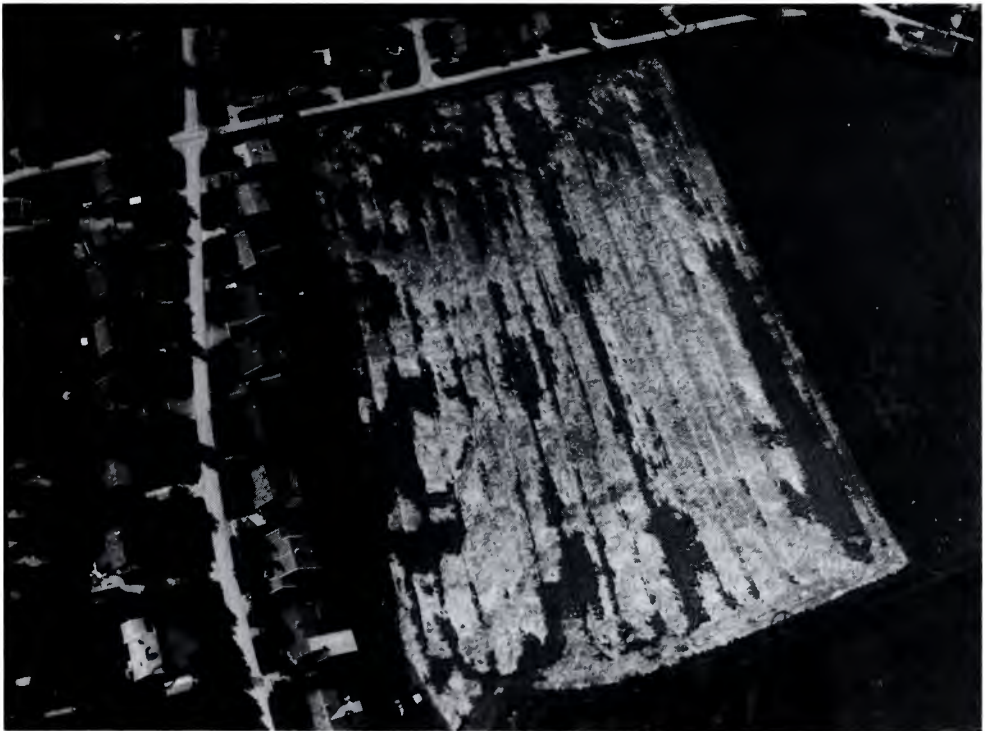


Fig. 7. 70 mm (645 format) of Case 2 site, 1:7000 original scale photo

To digitize the map's elevation contours, a transparent overlay was placed upon the single photo and the contour lines annotated by aligning features. For example, contour interval 95 (m) began at control point 8 and arched towards control point 2 (Fig. 8). The elevation was registered for recorded points at a prescribed value, e.g., "Z=95 m", the digitizer's cursor was set in continuous mode (1 mm), then a contour line was digitized. The data were exported to Surfer, gridded to 10 m cells, and a DEM was generated using the inverse distance (power of 2) algorithm.

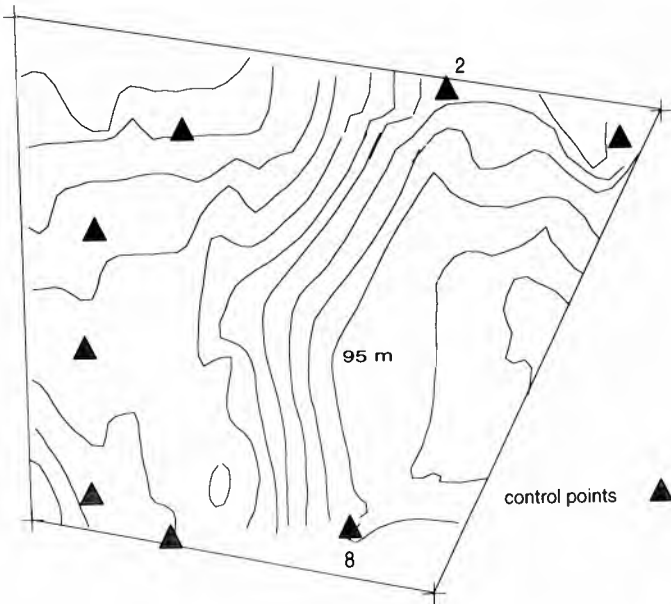


Fig. 8. Map projection of elevation contours superimposed on 70 mm photo

After the DEM was tied to the photo, the entire field (35,910 m²) was digitized, after which the plots (polygons) of standing grain were digitized and their areas tallied: 12,741 m², about 35% of the total crop area. Digitizing time was about 45 minutes. For reference purposes, control points and neighbouring streets were digitized, the data exported to MapViewer and a map issued (Fig. 9).

CONCLUSIONS

The influence of a DEM on single-photo measurements should be emphasized. Since terrain relief displaces objects on an aerial photograph – especially on oblique! – one must know the elevation difference across the image before selecting a DEM. Only by knowing the nature of the landscape can one judge what kind of DEM is required. Generally speaking, if the landscape is relative flat a DEM created from control points is probably acceptable.

Or if the landscape has moderate terrain relief and the photography is near-vertical, a control point DEM will more than likely suffice. If, however, there is considerable terrain relief – particularly when using oblique photography – one should use a DEM with numerous, reasonably accurate elevations.

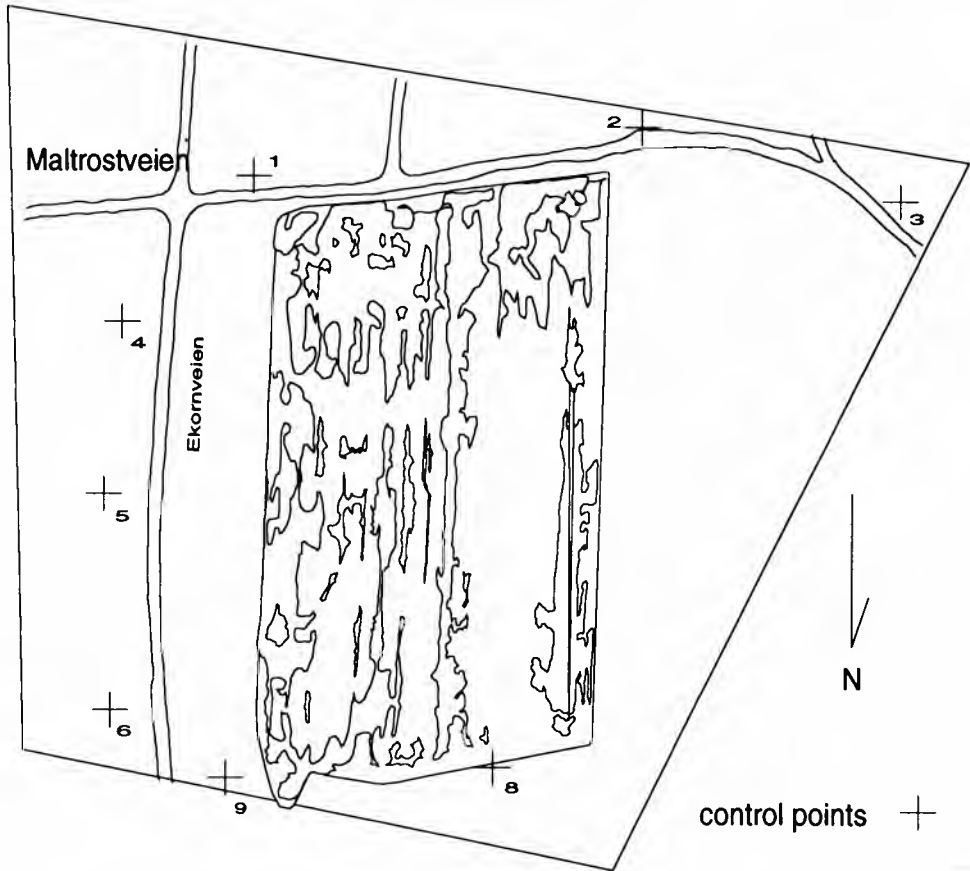


Fig. 9. Case 2 site map made from 1:7000 original photo scale

It should be noted that the amount of elevation data does not necessarily indicate the DEM's quality. For instance, in both cases presented the DEM seemed adequate; however, in Case 1 only 18 data points were used, whereas in Case 2 there were 3688 elevation points (although a third of the points were outside the crop area). Thus a distinction must be made between DEM accuracy and DEM representation. Accuracy is the extent to which an estimated value (in this case Z determination) approaches the *true* value, i.e. the degree to which it is free from bias. Representation, however, is similar to precision: it refers to the spread of measurements (in this case, the spatial distribution of measurements), whether or

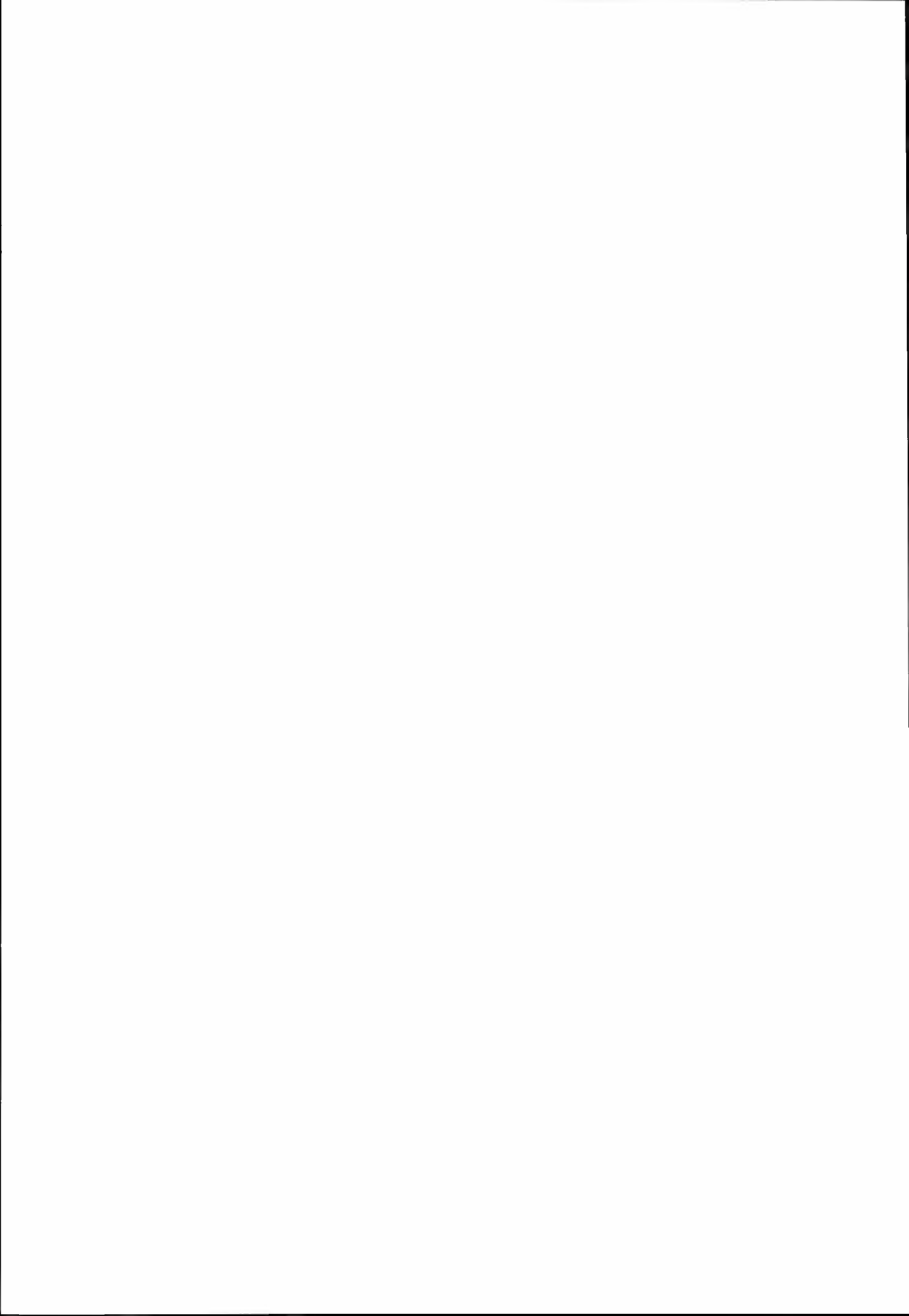
not the values approximate truth. For example, if an area is flat, then three true-height values would yield an accurate DEM, yet one might argue the representation is poor. However, if the area is steeply undulating, then many, properly distributed height values would yield a representative DEM; though its accuracy would remain questionable.

The issue of photo measurement accuracy must also be addressed. In Case 1 the expected ground location accuracy was about 2 m, whereas in Case 2 the accuracy was about 0.33 m. Although different cameras and film were used, and different techniques enlarged the original imagery, the (one order of magnitude) accuracy difference is primarily attributed to photo scale and the quality of ground control. In Case 2, the original photo scale was nearly twice as large as that in Case 1 (1:7000 versus 1:10,400). Moreover, the control points for Case 2 came from a 1:1000 scale map, whereas Case 1 relied upon control points from a 1:5000 scale map.

All things considered, hand-held small-format aerial photography appears to be a suitable tool for agronomists who wish to measure crop area. Provided topographic maps and original imagery are at suitable scales, imagery from a small, non-metric camera can provide reliable measurements with reasonable accuracy.

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Chemical amelioration of polluted soils

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A variety of potential chemical ameliorators were tested in laboratory experiments for the restoration of podzolic soils polluted by copper, nickel and sulphur. The problem of such polluted soils is widespread in the Kola region of northern Russia. Humic acids, fused phosphate, decarbonized calcite, lime, silica gel and peat were all tested as chemical ameliorants, and of these the most effective were decarbonized calcite and peat. The addition of 200-300 g/m² decarbonized calcite or 8000 g/m² peat resulted in a significant decline in nickel, copper and sulphur output from the soil.

Key words: Chemical amelioration, heavy metals, soil pollution, sulphur.

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In studies of soil pollution considerable attention is presently focused on the ecological effects of contamination, whereas much less effort has been directed toward investigating the restoration of these polluted soils (de Haan et al. 1986; Bisessar 1989; Choi & Lee 1990; Evdokimova & Mozgova 1992). Heavy metal pollution of sandy soils can readily result in serious contamination of groundwater and nearby streams because of low buffering capacity and little water filtration (Bruemmer et al. 1986). Protection of adjacent water bodies could be achieved through chemical alteration of the soil, resulting in increased binding of heavy metals and sulphur. We tested a variety of chemicals for this purpose using a sandy soil polluted by copper, nickel and sulphur.

MATERIALS AND METHODS

For our investigation we used the plough horizon of a cultivated haplocryod (Soil Survey Staff 1992) with a loamy sandy texture and a clay content of 2%. The pH (H₂O) of this soil was 5.8, CEC (NH₄ acetate method) was 9.2 meq/100g. The total content of carbon was about 2%, the proportion of humic and fulvic acids was 0.4 (Pereverzev 1987). Cylindrical plastic columns (1661 cm³, diameter 9.2 cm, height 25 cm) of the soil, artificially polluted by CuSO₄ (1.93 kg/m²) and NiSO₄ (2.02 kg/m²) were studied in the laboratory. CuSO₄ and

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NiSO₄ were mixed with the upper 15 cm of soil. Various chemical ameliorators were added (in the same way as the pollutants) to the soil columns and the soils were watered with distilled water every 10 days (100 mm precipitation) during the 30-day experiment. Water passing through the soil column (eluate) was collected over 1-2 days after each watering session.

The pH values of the solution were measured by a pH glass electrode method and the Cu and Ni concentrations were measured by atomic absorption spectrophotometry (AAS) in air-acetylene flame - Perkin-Elmer 2380. The AAS was used according to the producer's manual (1976). The analysis of sulphate content was carried out by means of liquid-chromatography (Water 431 Millipor).

The following ameliorators were tested:

1. Humic acids (HA), extracted from the soil (plough horizon of cultivated podzol) by 0.1N NaOH and precipitated from this solution by 1N H₂SO₄; cleaned with 1% solution of HCl+HF; dried at a temperature of 60°C. The extraction method was described by Orlov & Grishina (1981). Testing amounts - 12.5, 25.0, 50.0 and 100.0 g/m².
2. Fused phosphate (FP), the product of a local plant - Kovdor Mining Concentrating Combine. The composition of fused phosphate was the following: P₂O₅ - 19.5, MgO - 16.9, CaO - 34.8, SiO₂ - 24.3%. Testing amounts - 120, 160 and 310 g/m².
3. Decarbonized calcite (DC) produced by exposing CaCO₃ to a temperature of 400°C for five hours (Paus & Klyuchnikova 1986). Testing amounts - 15, 75, 150, 380 and 750 g/m².
4. CaCO₃ (further - "lime") - 15, 150 and 750 g/m².
5. Peat: botanical composition - 40% sphagnum, 40% wood residues, 20% herbaceous residues; pH (KCl) was about 4, CEC - 98 meq/100g. Testing amounts - 1000, 8000 and 12000 g/m².
6. Silica gel - 150, 750 and 1500 g/m².

It was supposed that soil organic matter (in our case - humic acids and peat) and silica gel have a high cation exchange capacity and would therefore be able to absorb the contaminants. Fused phosphate produced by a local plant was studied earlier as a soil fertilizer and it was thought that this material could be examined as an ameliorator on account of the high concentrations of those elements that could have some influence on the soil pH. Lime was studied earlier for ameliorating soils polluted by heavy metals (Bisessar 1989; Evdokimova & Mozgova 1992). Paus & Klyuchnikova (1986) referred to the application of decarbonized calcite as a good sorbent for industrial purposes and this prompted us to try this substance in our experiment and compare it with the effect of lime. In order to find the lowest application rates of ameliorators a wide range was tested. For HA, peat and lime the traditional rates for fertilizing soils with these substances was adhered to, and for DC the dosages were the same as those for lime.

RESULTS AND DISCUSSION

Without amelioration (control), there was a considerable leaching of nickel (about 20% of the added amount) and sulphur (10%) from the soils, whereas copper loss was negligible. The addition of silica gel played a major role in reducing the leaching of Cu and Ni, but had no effect on SO₄ (See Fig. 1a). Humic acids and fused phosphate had only a negligible

effect on loss of these pollutants (Fig. 1b, 1c).

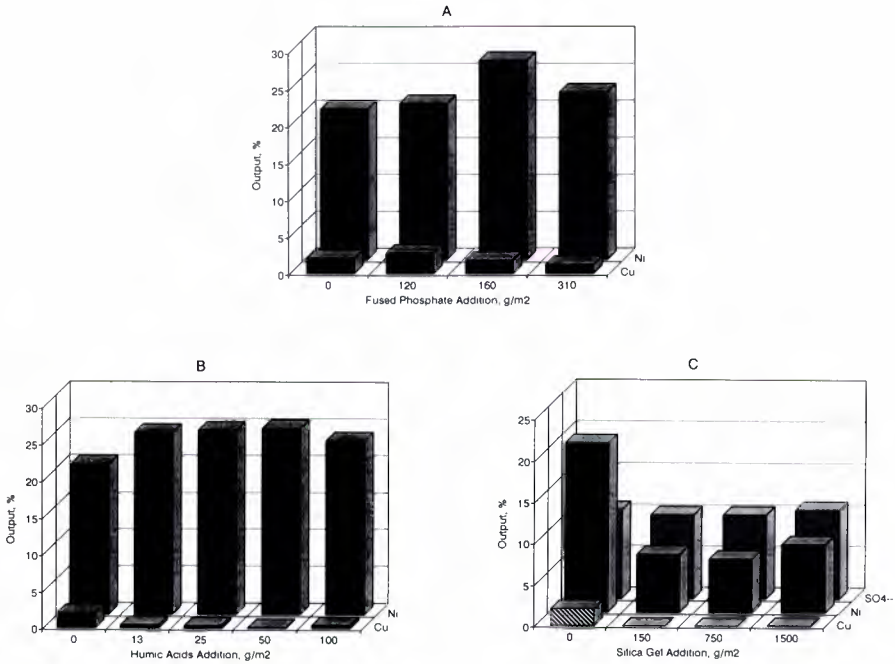


Fig. 1. Influence of addition of silica gel (A), fused phosphate (B) and humic acids (C) on element output (as a percentage of the amount of element added)

Lime and decarbonized calcite (DC) were both very effective in reducing output of Cu, Ni and sulphur (Figs. 2a and 2b). The greatest reduction in output of the pollutants resulted from the smallest addition of lime and DC (150 g/m²), which indeed caused a pronounced increase in pH (Figs. 3a and 3b).

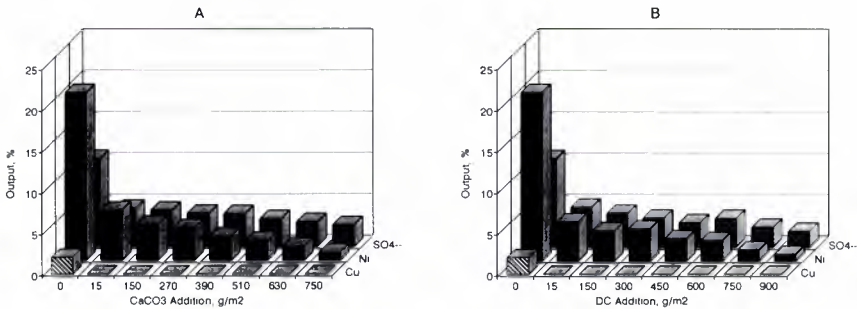


Fig. 2. Influence of addition of CaCO₃ (A) and decarbonized calcite (B) on element output (as percentage of the amount of element added)

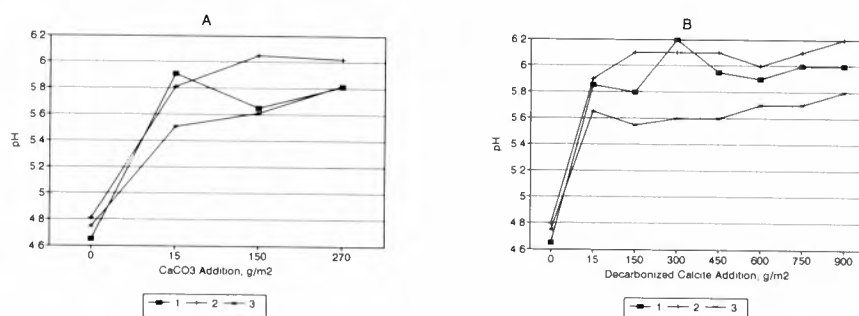


Fig. 3. Influence of addition of CaCO₃ (A) and decarbonized calcite (B) on pH of soil solution: 1, 2, 3 - first, second and third 10-day periods respectively

It is known that pH in soils plays an important role in the immobilization of heavy metals in soils; metal adsorption increases with increasing soil pH (Schnitzer & Skinner 1962; Bruemmer et al. 1986). The addition of lime and DC (Figs. 3a and 3b) has an influence on soil pH and, as a result, on metal immobilization. The increased adsorption of SO₄ could be caused by precipitation of CaSO₄.

Paus & Klyuchnikova (1986) found the occurrence of polyradical surfaces on DC, formed as a result of the exposure of natural Ca-carbonate to high temperatures. CaCO₃ was transformed to the considerably stable, free-radical form Ca'-O', which was proved by the electron-paramagnetic resonance spectrum analysis. Thus, DC can play a role in radical polymerization reactions. Moreover, the biradical nature of DC promotes the attachment of both cations and anions, increasing its ability to bind Cu, Ni and SO₄ in the soil. Thus, it can be assumed that the effect of lime on metal adsorption was an indirect one, but the effect of DC was direct.

Peat application was also very effective (Fig. 4). An application of 8000 g/m² was enough to decrease nickel and sulphur outputs from about 20% to 4% and from 10% to 2% respectively. A high organic matter content (total content of carbon was 45.6%) and subsequently a high ion exchange capacity of peat are probably responsible for this phenomenon. Functional groups of soil organic matter can form stable complexes with cations (Schnitzer & Skinner 1962, 1966), and can also play a major role in binding anions (Gobran & Nilsson 1988; Vance & David 1992; Gobran & Tipping 1993). In this connection the inactivity of humic acids in our experiment (Fig. 1c) was caused by changes in their structure during extraction from the soil. Unfortunately we failed to carry out the analyses of sulphur content in the experiment with application of HA and therefore the effects of HA and peat cannot be compared. The slower binding of Ni in comparison with Cu can be explained by the lower ionic potential of Ni (Pauli 1974). Schnitzer & Skinner (1966) suggested the following order of stabilities of complexes formed between soil fulvic acids and divalent metal ions at pH 5.0: Cu > Pb > Fe > Ni > Mn = Co > Ca > Zn > Mg. The stable complexes formed between humic acids and Cu were noted by Stevenson et al. (1993), who studied the stability constants of these complexes. In an earlier work Stevenson (1976) demonstrated that HA-Cu complexes are more stable than HA-Cd complexes (Cd also has lower ionic potential than Cu).

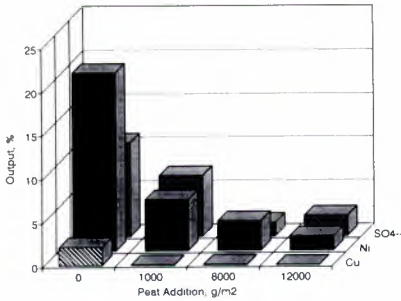


Fig. 4. Influence of addition of peat on element output (as a percentage of the amount of elements added)

CONCLUSION

Decarbonized calcite, lime and peat were the most effective ameliorators in holding Cu, Ni and sulphur in sandy podzolic soils. Most of this effect was achieved with the smallest additions of these chemicals. Before making any recommendations for the practical application of the ameliorators on polluted areas, the results of our experiment should be tested under field conditions.

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Effects of herring scraps feeding on body fat composition, growth and fur quality in silver foxes

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A study was carried out to evaluate herring scraps as a feed ingredient for silver foxes, focusing in particular on alterations in fatty acid composition of body fat which could be due to impaired fat metabolism. Frozen-stored and acid-preserved herring scraps accounted for 0, 20 and 30% of the diets in the growing-furring period. It was found that acid-preserved herring scraps as feed resulted in better fat quality than the frozen-stored scraps, possibly because of a more thorough blending of the antioxidant into the material. The dietary fatty acid composition was reflected in the subcutaneous fat of the animals. Liver fat was less affected by dietary fat, and independent of dietary fat source, high percentages of 20:4 n6 (arachidonic acid) and of 22:6 n3 (docosahexaenoic acid) were detected in the liver fat. Liver vitamin E content was not affected by the diets. General health status, measured as mortality rate and growth performance, was satisfactory in all dietary groups. Fur characteristics were not significantly influenced by the herring scraps diets.

Key words: Body fat, fish oil, foxes, vitamin E.

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In foxes, dietary marine oils have led to pathological changes in organ tissues and accumulation of n3 fatty acids in the liver (Rouvinen 1991). Herring (*Clupea harengus*) has a substantial fat content, and a high dietary level of herring scraps may be a potential cause of fat metabolic disorders. Diets based mainly on herring by-products have been reported as a risk factor for vitamin deficiencies, growth impairment, poor fur quality and deaths in silver foxes (Høie & Rimeslåtten 1951). The severe health problems pointed to in the latter study were probably related to oxidation of the highly unsaturated fat and a subsequent vitamin E deficiency.

In a previous study, Ahlstrøm & Skrede (1993) found that in comparison to a conventional diet, a diet containing 25% frozen-stored herring scraps produced higher body weight gain and a slightly improved fur quality in silver foxes. The purpose of the present experiment was to study the effect of high levels of herring scraps in silver fox diets, with

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the main emphasis on possible changes in fatty acid composition in body tissues which could indicate malfunctions in fatty acid metabolism.

MATERIALS AND METHODS

Animals and diets

The experiment, which was carried out at the Department of Animal Science, Agricultural University of Norway, began on 12 July and ended at pelting time in late November. The experimental groups comprised 20 silver foxes each, 10 males and 10 females. Two animals of different sex were kept in each cage. The amounts of herring scraps in the experimental diets were:

Diet 1. Control (no herring scraps)

Diet 2. 20% frozen-stored herring scraps

Diet 3. 30% herring scraps (15% frozen-stored + 15% acid-preserved)

The diet composition is presented in Table 1. In the experimental diets, protein and fat in herring scraps replaced coalfish scraps, lard and soybean oil in the control diet.

Table 1. Composition of diets (percent)

Ingredients	Control	Herring scraps	
		20%	30%
Herring scraps, frozen	-	20.0	15.0
Herring scraps, acid-pres.	-	-	15.0
Cod scrap	12.0	12.0	12.0
Coalfish scrap	20.3	6.6	-
Slaughterhouse offal	10.0	10.0	10.0
Blood	8.0	8.0	8.0
Precooked wheat/oats ¹⁾	7.0	7.0	7.0
Precooked corn	5.1	5.1	5.1
Fish meal	6.0	6.0	6.0
Lard	3.0	3.0	2.1
Soybean oil	3.4	0.6	-
Vitamin mixture ²⁾	1.0	1.0	1.0
Hemax ³⁾	0.2	0.2	0.2
Water	24.0	20.5	18.6

¹⁾ Containing 70% wheat and 30% oats.

²⁾ Containing grass meal (50%) and brewers' yeast (50%) fortified with the following vitamins per 100 g: Vitamin A, 30000 I.U.; vitamin D₃, 3000 I.U.; DL- α -tocopherol acetate, 300 mg; thiamine, 180 mg; riboflavine, 18 mg; niacin, 15 mg; Ca-pantothenate, 15 mg; pyridoxine-HCl, 30 mg; folic acid, 1.5 mg; biotin, 0.15 mg; B₁₂, 0.09 mg.

³⁾ Product of Peter Møller A/S, Oslo, containing ferric glutamate at 20 mg Fe/g.

Frozen and acid-preserved herring scraps were supplied by R. Domstein & Co., Måløy.

The supplier added 200-300 mg/kg ethoxyquin to the herring scraps as an antioxidant. The frozen herring scraps were stored at -20°C. For acid preservation, 2.5% formic acid was used. The acid-preserved herring scraps were stored in 30 L airtight plastic containers at room temperature.

Feed was prepared three times weekly and kept in a refrigerator. *Ad libitum* feeding and watering were adopted. Rejected feed was collected daily and recorded on a group basis. Samples of feed ingredients and diets were taken four times during the experiment and stored at -20°C pending analysis.

Growth and fur quality

The animals were weighed at the start of the experiment, on 12 July, and on 15 September, and the final body weight was recorded at the beginning of the pelting season, on 27 November. Fur characteristics were evaluated on dried skins by the staff of the fur farm at the Department of Animal Science as described by Ahlstrøm & Skrede (1993).

Analyses of feed

Proximate composition, free fatty acids (FFA), peroxide and anisidine values of the herring scraps and the experimental feeds were assayed at the laboratory of The Norwegian Fur Breeders' Association. Dry matter was determined by drying at 104°C for 4 h after pre-drying at 70°C for 12 h. Ash was determined by drying at 550°C for 12 h. Crude fat was assayed by extraction with diethyl ether, and crude protein as Kjeldahl-N x 6.25. Free fatty acids (FFA) were isolated in a neutral solution of ethanol/carbontetrachloride and titrated with sodium hydroxide to the neutral point (Welch 1976).

Anisidine value was assayed by mixing 0.1 g fat with 9.9 ml hexane. Absorbance at 350 nm (A₂) was measured. Anisidine reagent (0.5 ml) was added to the mixture (2.5 ml) and incubated for ten minutes at room temperature followed by absorbance reading at 350 nm (A₁). Anisidine value = 100(1.2 · A₁-A₂). Hexane was used as a blank in the assay. Peroxide value was determined according to the method of AOAC (1980).

Fatty acid composition of feed and herring scraps was assayed at the Department of Animal Science. Samples were treated with hydrochloric acid prior to extraction of lipids by chloroform:methanol 2:1 (Folch & al. 1956). Fatty acids were methylated by methanol in sulphuric acid (Welch 1976), and the methylesters were separated and quantified by gas-liquid chromatography. Calculation of dietary metabolizable energy (ME) contents was based on composition of the feed ingredients, estimated digestibility coefficients and the following values of ME (kJ/g): protein (N x 6.25), 18.8 kJ; fat, 39.8 kJ; carbohydrate, 17.6 kJ (Enggaard Hansen et al. 1991).

Tissue analyses

At pelting, immediately after killing, liver and subcutaneous fat were collected from two males and two females in each group for fatty acid analysis. The tissue samples were cooled with ice and stored at -70°C pending analysis. Fatty acid composition of liver and body fat was determined as described above. The vitamin E content was determined according to the method by McMurray & Rice (1983). The columns were products of Brownlee Lab, precolumn: RP-18 Newguard 7 μ 15x3.2 mm, the main column: Spheri-5 RP- 5 μ 100x4.6 mm. The mobile phase was methanol/water (97/3). Detection was at 294

nm, and an external standard was used for quantification.

Statistics

The differences among means were tested statistically by analysis of variance (SAS Institute, 1985). The effects of diet and body fat type (subcutaneous fat or liver fat) within diet were tested. The models were: $Y_i = \mu + a_i + \epsilon_i$ where Y_i = the i .th observation, μ = general mean, a_i = fixed effect of diet or fixed effect of body fat type and ϵ_i = random effect.

RESULTS

Feed composition

The ME content was slightly higher in the herring scraps diets, while the energy distribution was quite similar among the diets (Table 2). The average fat and protein contents in herring scraps were 15.8% and 15.3% in the frozen-stored, and 20.8% and 14.0% in the acid-preserved type. Fat originating from herring scraps accounted for 38% and 67% of the total fat content in diets containing 20 and 30% herring scraps, respectively.

Table 2. Content of metabolizable energy (ME) and energy distribution in the diets

	Control	Herring scraps	
		20%	30% ¹⁾
MJ/kg	6.9	7.0	7.4
From protein (%)	33.2	35.4	34.1
From fat (%)	48.8	46.9	49.3
From carbohydrate (%)	18.0	17.7	16.6

¹⁾ 20% = frozen-stored herring scraps, 30% = 15% frozen-stored + 15% acid-preserved herring scraps

The FFA content in the herring scraps increased during the experiment, from 2.4 to 6.6% in frozen-stored scraps and from 9.3 to 10.3% in acid preserved scraps. Analysis of peroxide and anisidin values revealed variable results, but there was a tendency towards increased values during the experimental period. A marked difference between the two types of herring by-products was that the acid-preserved type had a lower peroxide value (maximum: 6.6 mEq O₂/kg fat) and anisidine value (maximum: 11.2). Analysis of the frozen-stored herring scraps disclosed a maximum peroxide value of 63.1 mEq O₂/kg fat and a maximum anisidine value of 52.4. The pH of the acid-preserved herring scraps was stable at 4.2 throughout the experiment.

The FFA percentage in the diets tended to increase throughout the experimental period. The control diet reached a maximum of 8.5%, while both treatment diets reached 11.3% FFA at the most. Peroxide values and anisidine values of the diets tended to increase with the amount of herring scraps included and also with storage time. In October the peroxide

values were 58, 78, 262, and the anisidine values 45, 75 and 238, respectively, in increasing order with respect to the content of herring scraps.

Fatty acid composition of herring scraps

The fatty acid analysis of the herring scraps (Table 3) revealed that among the saturated fatty acids, C14:0 (myristic acid) and C16:0 (palmitic acid) predominated, and C18:0 (stearic acid) was scarce. The monounsaturated fatty acids constituted the largest group, with C18:1 n9 (oleic acid), C20:1 n9 (gadoleic acid) and C22:1 n11 (cetoleic acid) as the most abundant. The main polyunsaturated n3 fatty acids were C18:4 n3 (octadecatetraenoic acid), C20:5 n3 (eicosapentaenoic acid) and C22:6 n3 (docosahexaenoic acid). The fatty acid composition differed somewhat between the frozen-stored and the acid-preserved herring scraps. In particular, the contents of C20 + C22 n3 fatty acids were higher in the acid-preserved type (Table 3).

Table 3. Fatty acid composition of herring scraps and experimental diets (percent). Average and standard deviation of four samples. Standard deviation in parentheses

	Herring scraps		Diets		
	Frozen-stored	Acid preserved	Control	Herring scraps	
				20% ¹⁾	30%
C14:0	8.7 (0.5)	8.4 (0.4)	2.2c (0.8)	4.3b (0.8)	5.7a (1.1)
C16:1 n7	5.9 (0.6)	5.5 (0.2)	1.2c (0.3)	2.7b (0.3)	3.5a (0.3)
C16:0	14.1 (0.3)	13.5 (0.3)	18.5 (4.5)	18.8 (2.8)	18.8 (0.9)
C18:4 n3	3.2 (0.3)	3.6 (0.1)	0.4c (0.3)	1.1b (0.2)	1.7a (0.1)
C18:3 n3	0.9 (0.1)	1.4 (0.1)	6.9a (3.6)	1.7b (0.8)	1.0b (0.1)
C18:2 n6	1.4 (0.1)	1.5 (0.1)	22.3 (14.1)	13.1 (9.6)	7.1 (5.9)
C18:1 n7	-	-	0.9 (0.8)	1.4 (0.2)	1.2 (0.4)
C18:1 n9/n11	8.8 (1.1)	9.7 (1.3)	21.7 (4.6)	20.1 (0.6)	13.9 (4.7)
C18:0	1.8 (0.8)	1.2 (0.1)	15.5 (6.5)	13.1 (4.6)	13.3 (2.2)
C20:5 n3	9.1 (1.2)	6.7 (0.4)	1.2c (0.2)	3.7b (0.5)	6.4a (1.4)
C20:4 n6	0.3 (<0.1)	0.2 (<0.1)	0.2 (0.1)	0.1 (<0.1)	0.1 (<0.1)
C20:1 n9	10.8 (1.6)	12.5 (0.2)	3.5b (0.1)	9.7a (0.6)	11.3a (0.8)
C22:6 n3	8.0 (1.1)	7.4 (0.5)	1.6c (0.2)	3.3b (0.5)	4.6a (0.2)
C22:1 n9/n11	15.3 (4.1)	19.7 (1.1)	1.6b (0.3)	6.2a (0.9)	6.7a (2.1)
Saturated	24.6 (0.5)	23.1 (0.5)	36.2 (4.7)	36.2 (4.8)	37.8 (6.7)
Monounsaturated	40.8 (4.8)	47.4 (1.1)	28.9b (3.8)	40.1a (2.8)	36.6a (4.7)
Polyunsaturated	22.9 (0.9)	20.8 (1.1)	32.6 (8.9)	23.0 (9.3)	20.9 (5.0)
C20 + C22	43.5 (4.0)	46.5 (9.1)	8.1c (0.5)	23.0b (0.9)	29.1a (0.8)
n3	21.2 (1.1)	19.1 (0.8)	10.1 (1.5)	9.8 (1.1)	13.7 (1.5)
n6	1.7 (<0.1)	1.7 (<0.1)	22.5a (5.5)	13.2ab (4.8)	7.2b (6.8)

¹⁾ 20% = frozen-stored herring scraps. 30% = 15% frozen-stored + 15% acid preserved herring scraps. Different letters within rows among diets indicate significant differences (p < 0.05)

Fatty acid composition of diets

The fatty acid profile of herring scraps was clearly reflected in the diets (Table 3), particularly by the increasing amounts of C20 and C22 fatty acids and the decreased level

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of C18:2 n6 and C18:3 n3 in comparison to the control diet. The content of some of the fatty acids, particularly C18:2 n6, which is abundant in soybean oil, revealed considerable variation between samples within diet. No systematic time dependent variations were observed, however.

Animal studies

Subcutaneous fat

The differences in dietary fatty acid composition were to a large extent maintained in the fatty acid composition of subcutaneous body fat (Table 4). However, subcutaneous fat revealed a higher level of monounsaturated fatty acids (C16:1 n7, C18:1 n9), and a lower level of saturated and polyunsaturated fatty acids compared with dietary fat. In addition, a reduction in the long-chained fatty acids (C20 + C22) was observed.

Table 4. Fatty acid composition of silver fox subcutaneous fat and liver fat (percent) and p-values indicating differences in fatty acid concentration in subcutaneous fat and liver fat of animals within diet. Average of four animals

	Subcutaneous fat			Liver fat			p-values, effects of body fat type		
	Control	Herring scraps		Control	Herring scraps		Control	Herring scraps	
		20%	30% ¹⁾		20%	30%		20%	30%
C14:0	3.5c	5.9b	6.9a	1.1	2.2	3.0	0.001	0.001	0.001
C16:1 n7	5.6b	7.7a	8.2a	1.5	2.8	3.3	0.001	0.001	0.001
C16:0	18.1c	20.0a	19.2b	20.3	24.6	27.8	0.37	0.11	0.04
C18:4 n3	0.1c	0.7b	0.8a	0.3	0.2	0.3	0.05	0.002	0.001
C18:3 n3	1.8a	1.0b	0.8b	0.6	0.5	0.4	0.001	0.001	0.02
C18:2 n6	20.1a	8.7b	5.3c	19.8a	16.2ab	12.8b	0.83	0.001	0.001
C18:1 n7	1.6b	1.8a	1.9a	2.1b	2.5a	2.5a	0.004	0.001	0.001
C18:1 n9/n11	31.7a	29.1b	27.3c	9.7	13.7	16.3	0.001	0.01	0.003
C18:0	8.5a	7.1b	6.0c	24.6	19.1	16.2	0.003	0.04	0.03
C20:5 n3	0.3b	0.9a	1.0a	2.4	2.7	2.8	0.014	0.17	0.05
C20:4 n6	0.1	0.1	0.1	7.0	4.0	2.8	0.001	0.007	0.01
C20:1 n9	1.2c	3.6b	5.7a	0.3b	0.6ab	1.1a	0.001	0.001	0.001
C22:6 n3	0.9b	2.0a	2.4a	6.7	7.1	5.5	0.003	0.14	0.17
C22:1 n9/n11	0.8c	3.0b	5.4a	-	0.2	0.4	-	0.002	0.001
Saturated	30.1b	33.0a	32.1a	46.0	45.9	47.0	0.001	0.001	0.001
Monounsaturated	40.9c	45.2b	48.5a	13.6	19.8	23.6	0.001	0.002	0.001
Polyunsaturated	23.3a	13.4b	10.4c	36.8a	30.7ab	24.6bc	0.001	0.004	0.008
C20 + C22	3.3b	9.6b	14.6a	16.4	14.6	12.6	0.002	0.46	0.21
n3	3.1b	4.7a	5.0a	10.0	10.2	9.0	0.004	0.39	0.50
n6	20.2a	8.8b	5.4c	26.8a	20.2b	15.6c	0.002	0.001	0.002

¹⁾ 20% = frozen-stored herring scraps. 30% = 15% frozen-stored + 15% acid-preserved herring scraps. Different letters within rows among subcutaneous and liver fat indicate significant differences ($p < 0.05$)

Liver fat

The fatty acid composition of the liver was less influenced by dietary fatty acid composition than the subcutaneous fat (Table 4). However, some effects were observed, especially in

the percentage of C18:2 n6 and C20:1 n9. In comparison to dietary and subcutaneous fat, the polyunsaturated fatty acids were more abundant in the liver, demonstrated by higher levels of C20:4 n6 and C22:6 n3. This was most pronounced in animals fed the control diet. Furthermore, the liver fat was more saturated than dietary and subcutaneous fats due to larger amounts of C18:0.

Vitamin E

The average liver vitamin E content was found to be 29.0 µg/g in the control group, 34.0 µg/g in the group receiving 20% herring scraps, and 34.8 µg/g in the group receiving 30% herring scraps. This would indicate an equal vitamin E status in all groups, independent of dietary composition.

Growth and fur quality

The animals in the experiment revealed normal growth, and there were only minor differences between groups. However, the herring scraps groups seemed to have a slightly improved growth performance compared to the control group (Fig. 1). The feed consumption data revealed that the herring products caused no problems as regards palatability. The average daily consumption of metabolizable energy was 3.1 MJ in the control group and 3.3 and 3.4 MJ in groups fed 20 and 30% herring scraps, respectively. Generally, the foxes were in a good healthy condition and no mortality occurred.

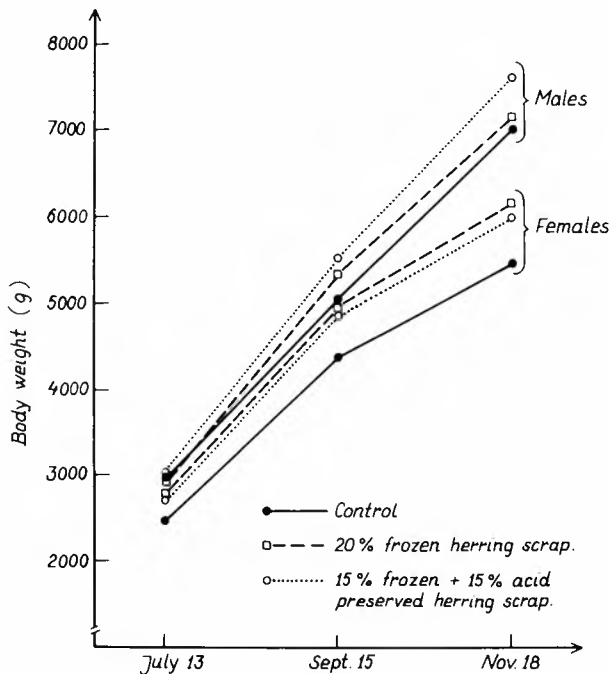


Fig. 1. The effect of herring scrap feeding on body weight gain in silver foxes

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The evaluation of the silver fox skins revealed only minor differences between groups (Table 5). In addition to the general evaluation of guard fur and underfur colour, a thorough examination of the frequency of brown guard hairs was carried out. Some hairs of a brownish colour were discovered in six skins in the control group, the corresponding figures for animals fed 20 and 30% herring scraps being two and one, respectively. With one exception, skins with some brown-coloured hairs originated from three different litters, each with at least two affected skins.

Table 5. Evaluation of silver fox skins. Average with standard deviation in parentheses

	Control		Herring scraps			
			20% ²⁾		30%	
Number of skins	16		16		17	
Skin length, (cm)	99.7	(6.1)	102.5	(4.0)	102.9	(5.7)
Dry skin weight, (g)	503.1b	(51.9)	548.6a	(33.5)	574.2a	(91.0)
Density ¹⁾	5.6	(0.9)	5.7	(1.0)	5.9	(1.3)
Texture ¹⁾	5.7	(0.9)	6.0	(0.8)	5.4	(1.0)
Cover ¹⁾	5.5	(0.8)	6.1	(1.1)	5.6	(1.6)
Colour guard fur ¹⁾	5.7	(0.7)	5.3	(1.0)	5.4	(1.5)
Colour underfur ¹⁾	4.9	(1.0)	4.9	(0.8)	5.0	(1.0)
Hair quality ¹⁾	5.6	(1.0)	5.9	(1.2)	5.6	(0.8)
General impression ¹⁾	5.5b	(0.8)	6.2a	(1.1)	5.3b	(0.9)

¹⁾ Subjectively graded from 1 (poorest) to 10 (best).

²⁾ 20% = 20% frozen-stored herring scraps. 30% = 15% frozen-stored + 15% acid-preserved herring scraps. Different letters within a row indicate significant differences ($p < 0.05$)

The fur parameter "general impression" was significantly improved in the group fed 20% herring scraps compared to the other groups ($p < 0.05$). Hair quality, texture and covering were also slightly improved in this group, though no significant differences were found.

DISCUSSION

The chemical composition of the frozen-stored herring scraps used in the present experiment was fairly similar to that reported earlier by Skrede (1986) and Ahlström & Skrede (1993). The acid-preserved herring scraps had a somewhat higher fat content, but this was still within the normal range found in whole herring (Lambertsen 1973).

Peroxide and anisidine values of frozen-stored and acid-preserved herring scraps differed substantially. This was possibly related to the liquid consistency of the acid-preserved herring scraps allowing a better blending of the antioxidant into the material and to the airtight storage, thus preventing fat oxidation more effectively than in the frozen-stored herring scraps. The fat quality of the frozen-stored herring scraps used in this investigation might be questionable on the basis of the peroxide (63.1 mEq O₂/kg fat) and anisidine values (52.4) obtained. However, the fat oxidation products did not seem to influence the health status of the animals in our study. Rouvinen (1987) reported poor

health conditions and an increase in mortality rate in mink fed 20% frozen-stored herring scraps. The peroxide value of the herring scraps was, however, 160 mEq O₂/kg, which is considerably higher than the values observed in the present experiment. In an experiment with mink, which lasted for eight weeks during the late growth period, Engberg et al. (1993) found that feed with a peroxide value of 473 meq O₂/kg fat did not affect growth rate and health conditions provided there was a sufficient vitamin E supply. The highest peroxide value, 262 meq O₂/kg fat, in the diet containing 30% herring scraps in the present experiment was below this level.

The higher FFA content in the acid-preserved herring scraps compared with that in the frozen-stored scraps, was probably caused by enzymatic hydrolysis which can occur after acid preservation (Austreng et al. 1979). Furthermore, formic acid has been reported to be more lipolytic than other preservative acids (Austreng et al. 1979).

The variation in fatty acid composition within diets could be due to inhomogeneous samples. This was particularly expressed in the content of C18:2 n₆, which mainly originated from soybean oil. The fluidity of the soybean oil has probably to some extent complicated the sampling. Nevertheless, the average value for C18:2 n₆ in the four samples was not far from what could be expected from the diet formula.

The fats of the herring scraps influenced the tissue fatty acid composition in this study. This supports results from other investigations with silver foxes, blue foxes and mink fed fish-based diets (Skrede & Gulbrandsen 1985; Rouvinen & Kiiskinen 1989; Rouvinen 1991). Rouvinen (1991) found an increase in n₃ fatty acids in the liver of silver foxes fed a fish-based diet containing about 20% Baltic herring and 4% capelin oil, and suggested an impairment of fat metabolism attributable to marine fat. In contrast to the experiment by Rouvinen (1991), the diets in the present study were not strictly based on either fish fat or land animal fat.

Biochemical studies of the cellular fat metabolism of the silver fox have not yet been performed. Metabolic studies in the rat have shown that the initial chain-shortening of C20:5 n₃ and C22:6 n₃ largely takes place in the peroxisomes (Hagve & Christophersen 1986). The results of the present experiment can not clarify the ability of silver foxes to metabolize C20:5 n₃ and C22:6 n₃ in the same way, but the fatty acid analysis of the liver revealed that the content of these fatty acids was fairly similar and independent of the dietary level. Neat et al. (1981) showed that in rats the ability of the liver cells to chain-shorten C22:1 n₉ was highly correlated to their capacity for peroxisomal β-oxidation. The low amounts of C20:1 n₉ and C22:1 n₉/n₁₁ at the expense of an increased level of C18:1 n₉ in the liver in the present experiment may suggest a chain-shortening activity in silver foxes.

The alteration of the fatty acid composition in total lipids from the diet to the liver in the present experiment was probably also due to the influence of the liver phospholipids, which in land animals are dominated by C20:4 n₆ and C22:6 n₃ (Norum et al. 1989), with C20:4 n₆ found more frequently in the phosphatidylcholine and C22:6 n₃ in the phosphatidylethanolamine. In rats, Gudbjarnason & Oskardottir (1977) demonstrated that feeding of 10% cod liver oil, with a high content of C20:5 n₃ and C22:6 n₃, led to a higher level of these acids in phospholipids and neutral fat of the heart at the expense of C18:2 n₆ and C20:4 n₆. In the liver phosphatidylethanolamine of mink, Skrede & Gulbrandsen (1985) observed the same effect after feeding different levels of capelin oil.

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The results of the total liver fatty acid composition in the present study showed a similar reduction in n6 fatty acids, but no further increase in n3. However, it is evident that the liver fat content in mink is about 2.5 times higher than that in silver foxes (Rouvinen et al. 1989, Rouvinen 1991). This may influence the effect of the phospholipid fraction on the total liver fatty acid composition.

Vitamin E is as an antioxidant protecting tissue membranes against oxidating substances. Deficiency of vitamin E has been reported to occur in fur animals after feeding high levels of marine oils, causing yellow fat disease, muscular degeneration and death (Høie & Rimeslåtten 1951; Ender & Helgebostad 1975). Polyunsaturated fatty acids in marine oils are susceptible to auto-oxidation and diets rich in these oils require increased amounts of vitamin E to give protection against lipid oxidation (Harris & Embee 1963). The requirement of vitamin E is found to be 1.57 mg/MJ ME (Stowe & Whitehair 1963) + 0.6/g polyunsaturated fatty acids (Harris & Embee 1963). The diets in the present study had an average energy content of 7.0 MJ ME/kg feed and the concentration of polyunsaturated fatty acids was about 30% of the fat which give 25 g/kg fresh feed. The requirement would be about $1.57 \text{ mg} \cdot 7.0 \text{ MJ} + 0.6 \text{ mg} \cdot 25 \text{ g} = 26.0 \text{ mg}$ vitamin E/kg fresh feed. Thus the supplemented level of 30 mg vitamin E/kg fresh feed should be sufficient. This is supported by the liver vitamin E values obtained, and the fact that no deficiency symptoms developed.

The tendency for higher final body weights for the animals fed herring scraps in the present experiment could have been caused by higher dietary energy concentrations compared to the control diet. Previous studies (Skrede 1986; Ahlstrøm & Skrede 1993) have also revealed improved growth rate in silver foxes fed herring scraps diets. Rouvinen et al. (1991) reported that there were minor differences in silver fox growth when a fish-based diet was fed compared to a diet based on slaughterhouse offal.

The individual fur characteristics revealed no consistent effect of the herring scraps diets compared to the control diet. Nevertheless, the 20% herring scraps diet supported a significantly improved "general impression" of the fur. Rouvinen et al. (1991) reported that the fur quality characteristics of silver foxes were improved after feeding a fish-based diet. The only exception was that the colour purity appeared to be negatively influenced by the extensive fish fat feeding. In mink, Hillemann & Mejbörn (1983) found a positive effect of C18:2 n6 on fur quality and recommended that the dietary fat should contain at least 20% C18:2 n6 to ensure high fur quality. In the present investigation the fur parameters did not differ significantly with dietary C18:2 n6 levels varying from 22 to 7%. This may possibly indicate that the level of C18:2 n6 in all diets covered the requirement in silver foxes.

CONCLUSIONS

The results of the present study suggest that as much as 30% of herring scraps may be included in diets for silver foxes without any negative effects on growth performances or general health status. No changes in the fatty acid composition of subcutaneous or liver fat were observed which could indicate impaired fat metabolism. In addition, our results indicate that fur quality may be slightly improved by use of moderate levels of herring scraps in the diets.

ACKNOWLEDGEMENTS

The staff of the fur animal farm at the Department of Animal Science is acknowledged for their skilful help in the performance of the experiment. We thank Áshild Longva at the Department for her work with the fatty acid analysis, and Egil Kjos and the co-workers at the laboratory of The Norwegian Fur Breeders' Association for their great help with the chemical analyses.

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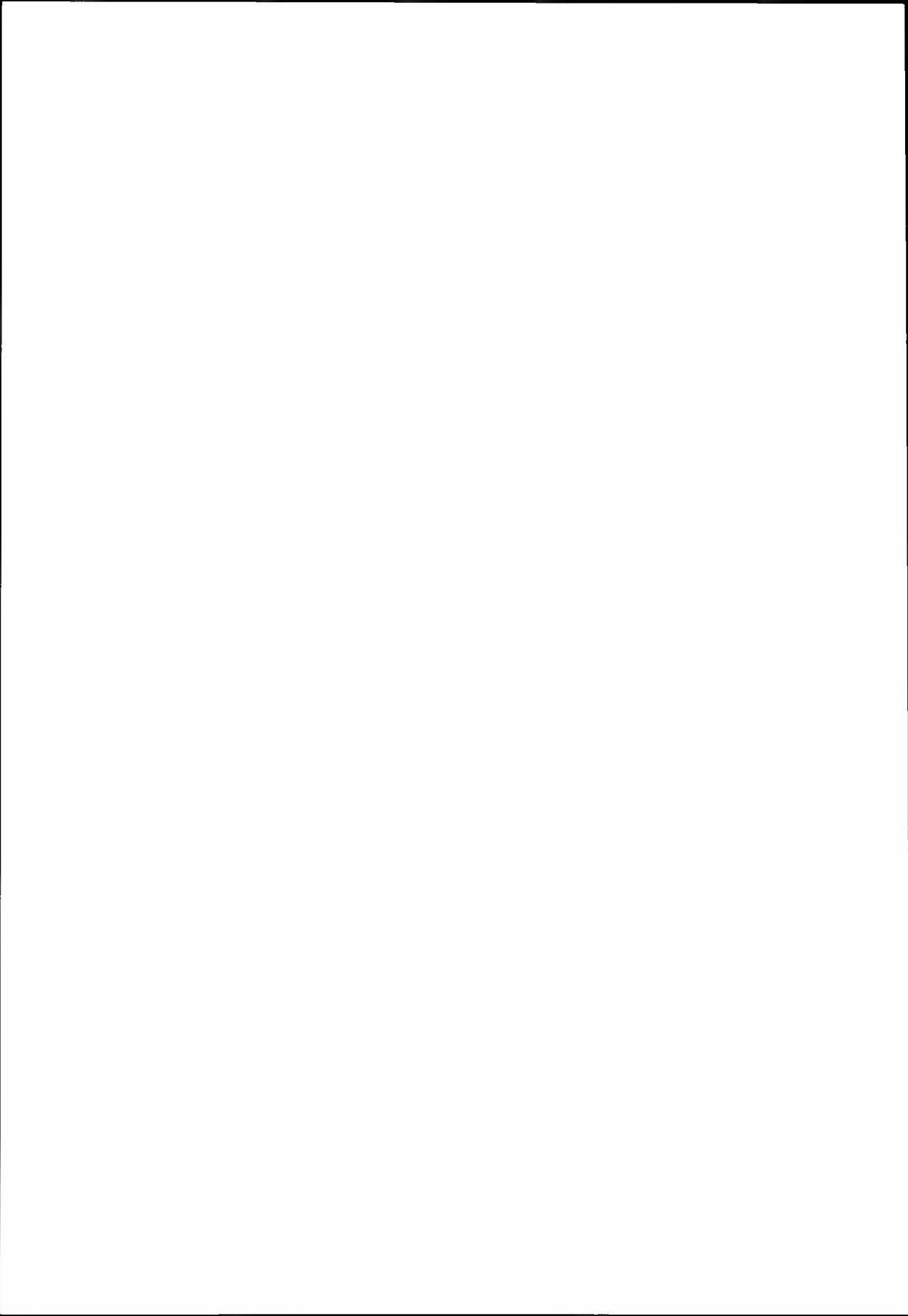
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Effects of tree density on productivity and fruit quality of 'Red Gravenstein' on rootstocks M9 and M26 in a single-row system

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Ystaas, J., O. Hovland & A. Kvåle 1994. Effects of tree density on productivity and fruit quality of 'Red Gravenstein' on rootstocks M9 and M26 in a single-row system. *Norwegian Journal of Agricultural Sciences* 8: 69-74. ISSN 0801-5341.

In a single row system of a high density apple orchard the performance of 'Red Gravenstein' on rootstocks M9 and M26 at density 890 - 2660 trees/ha was assessed over 10 years. It was found that tree vigour was affected by rootstocks, but tree density had no influence on tree size as measured by trunk girth. Cumulative yield per tree over the first eight cropping years was affected by tree density; the lowest tree density producing the highest crop on both rootstocks. The highest cumulative yield/ha was produced on M9 at density 2000 trees/ha, outyielding 'Red Gravenstein' on M26 at density 1270 trees/ha by 56%. Important components of fruit quality were not affected by tree density. High density orchards of 'Red Gravenstein' are most likely to be successful on rootstock M9 at density 2000 trees/ha under Norwegian growing conditions.

Key words: Apple, components of fruit quality, planting system, yield, yield efficiency.

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'Red Gravenstein' is a vigorous cultivar (Stedje & Skard 1947). In intensive planting systems production of 'Red Gravenstein' has been successful when dwarfing rootstocks have been used in single- or double-row systems (Ystaas & Kvåle 1989). Early and high yields of apple orchards are strongly influenced by tree density (Christensen 1979; Wertheim 1985), because the total dry matter production which sets the limit to potential fruit yield depends on light interception by the fruit trees (Jackson 1978).

In a single-row system of a high density apple orchard wide alleyways represent inefficient land use, because light interception is reduced due to reduction in tree numbers. Under Norwegian growing conditions where many orchards are located on steep hillsides a row distance of 4.0-4.5 m is required to operate an orchard tractor safely. This raises the question of whether increasing the tree number by reducing the within-row distance possibly can compensate for the inefficient wide alleyways in a single row intensive planting system. This study is an assessment of the performance of 'Red Gravenstein' on rootstocks M9 and M26 in a single-row system within the density of 2000-2660 trees/ha (M9) and 890-1270 trees/ha (M26) over ten years (1983-92).

MATERIALS AND METHODS

Two field trials with 'Red Gravenstein' on rootstocks M9 and M26 in a single-row planting system were conducted in the experimental orchard of Ullensvang Research Station, Lofthus, at 60° North, over ten years (1983-92).

'Red Gravenstein' on M9 had a between-row distance of 4 m, while the within-row distances were (a) 0.94 m (2660 trees/ha), (b) 1.10 m (2270 trees/ha), (c) 1.25 m (2000 trees/ha). The between-row distance of 'Red Gravenstein' on M26 was 4.5 m. The within-row distances included (a) 1.75 m (1270 trees/ha), (b) 2.0 m (1110 trees/ha), (c) 2.5 m (890 trees/ha).

The experimental design was randomized blocks with five replicates in the trial on M9 and three replicates in the trial on M26. In both experiments there were five trees in each plot. 'Quinte' and 'Summerred' on M26 were used as guard trees and pollinizers.

The experimental trees were planted in spring 1983 as maidens without feathers. The trees were raised with a central leader and trained as free spindle for the initial three years. Later, the trees were transformed to slender spindle and trained according to Wertheim (1968). All trees on M9 were staked, while the trees on M26 were supported by a string at the top and slender bamboo canes. Tree height was kept at 2.5 m by pruning.

The soil was a loamy sand with 4.5% organic matter. Soil management combined frequently mown grass in the alleyways with 1-m-wide herbicide strips along tree rows. Drip irrigation was provided. Fertilizer application was monitored by chemical leaf and soil analysis. Fruit thinning was done by hand whenever necessary.

Trunk girth measurement was taken 25 cm above the graft union. Yield was recorded for the whole experimental plot consisting of five trees. Fruit weight was determined on a representative sample of 100 apples per plot. Random samples of 20 apples from each plot were kept in cold storage at 4°C for 4-5 weeks until fruit quality examinations took place. Sensoric analysis by a panel of five trained judges was carried out on ground colour (scores 1-9), surface red colour (scores 1-9) and flavour (scores 1-9). The content of soluble solids was measured using an Atago digital refractometer. Titratable acidity was determined by titrating diluted juice samples to pH 8.1 with 0.1N NaOH and calculated as a percentage of malic acid on a fresh weight basis.

RESULTS AND DISCUSSION

Tree vigour, as measured by trunk girth, was not significantly affected by tree density (Fig. 1 and 2). In a comprehensive study with 'James Grieve' and 'Spartan' on rootstocks M9 and M26, Christensen (1979) found that growth was restricted at higher densities than 1000 trees per ha. At the end of the experimental period (10 years), however, a strong influence on tree size by rootstocks was found (Tables 1 and 2); 'Red Gravenstein' on M26 gave more vigorous trees than 'Red Gravenstein' on M9. This observation is in accordance with recent results of Scandinavian rootstock studies (Callesen 1989; Ystaas & Frøyenes 1993).

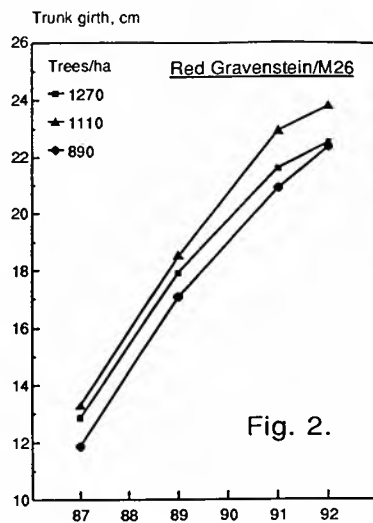
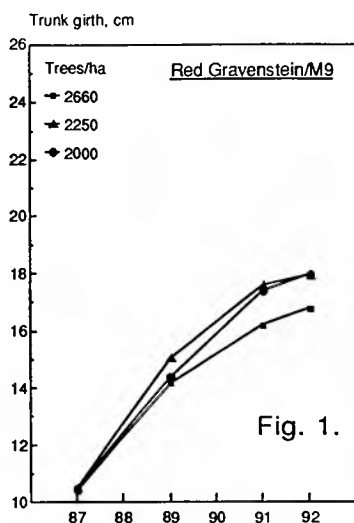


Fig. 1-2. Trunk girth of 'Red Gravenstein' on rootstocks M9 and M26 as affected by tree density in a single-row system over 8 cropping years. Vertical bars represent LSD, $P=0.05$

Table 1. Effects of different tree densities on trunk girth, cumulative yield and yield efficiency of 'Red Gravenstein' on M9 over 10 years

Spacing m	Tree density trees/ha	Trunk girth (1992) cm	Cumulative yield kg/tree	Cumulative yield tons/ha	Yield efficiency kg/cm ²
4 x 0.94	2660	16.8	35.1	93.4	1.56
4 x 1.10	2270	18.0	40.5	91.0	1.56
4 x 1.25	2000	18.0	49.7	99.4	1.95
LSD ($P=0.05$)		NS	7.0	NS	0.38

Table 2. Effects of different tree densities on trunk girth, cumulative yield and yield efficiency of 'Red Gravenstein' on M26 over 10 years

Spacing m	Tree density trees/ha	Trunk girth (1992) cm	Cumulative yield kg/tree	Cumulative yield tons/ha	Yield efficiency kg/cm ²
4.5 x 1.75	1270	22.5	50.3	63.9	1.26
4.5 x 2.00	1110	23.8	54.3	60.2	1.20
4.5 x 2.50	940	22.4	59.7	53.1	1.57
LSD ($P=0.05$)		NS	6.0	6.8	NS

The experimental trees were weak at planting and the first crop was delayed by one or two years compared with high quality trees (Fig. 3 and 4). Yield per tree over the first eight cropping years was found to be significantly affected by tree density (Tables 1 and 2); the lowest tree density producing the highest crop on both rootstocks. This finding is in accordance with the results reported by Christensen (1979) and Wertheim (1985). In terms of yield per ha, it was found that the largest crop was produced at the lowest tree density (2000 trees/ha) for 'Red Gravenstein' on M9. Although the difference in cumulative yield per ha is not significant, the trees representing the lowest density (2000 trees/ha) had the highest yield efficiency; indicating that tree density higher than 2000 trees/ha may imply negative effects of shading and severe competition for water and nutrients. 'Red Gravenstein' on M26 at lower densities obtained, however, the highest cumulative yield per ha at the highest density (1270 trees/ha) (Table 2). This result is in accordance with the general trend reported by Christensen (1979) and Wertheim (1985) of an increase in yield per ha when tree number is increased at low tree density. The main reason for the improved productivity of the apple orchard is a higher level of light interception at higher tree density (Jackson 1978).

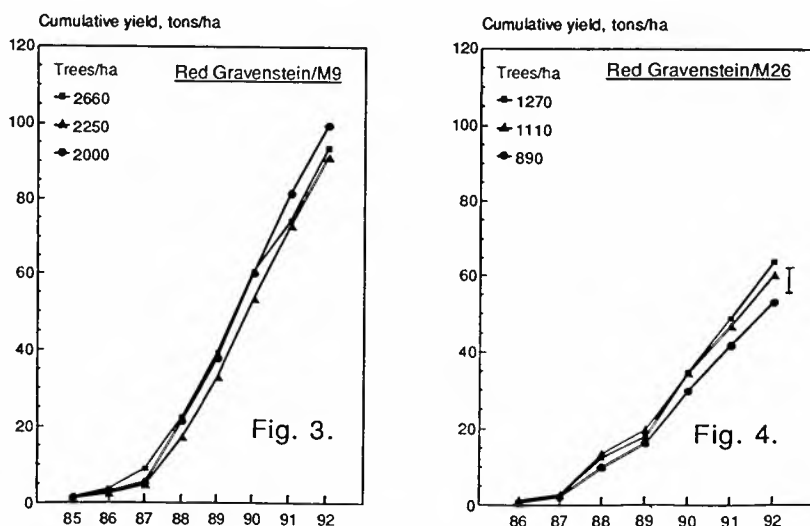


Fig. 3-4. Cumulative yield of 'Red Gravenstein' on rootstocks M9 and M26 as affected by tree density in a single row system over 8 cropping years. Vertical bars represent LSD, $P=0.05$

Biological growth control of tree vigour by dwarfing rootstocks is a prerequisite for successful high density apple orchards (Wertheim 1989). This effect is clearly demonstrated in the present study where 'Red Gravenstein' on M9 at density 2000 trees/ha outyielded 'Red Gravenstein' on M26 at density 1270 trees/ha by 56% over 10 years from planting (Fig. 3 and 4, Tables 1 and 2).

Important components of fruit quality such as fruit weight, soluble solids, titratable acid, ground colour, red surface colour and flavour were not influenced by tree density (Tables 3 and 4) within the range tested. The fruit quality met the quality standards of

apples grown in a northern climate (Kvåle 1973; Vangdal 1985). Working with 'Golden Delicious' and 'Karmijn de Sonnaville' under Dutch growing conditions, Wertheim (1985) did not find any effect of increased tree density on sugar or acid content nor on taste or storage behaviour of the fruits.

Table 3. Effects of tree density on components of fruit quality of 'Red Gravenstein' apples on M9

Tree density trees/ha	Fruit weight g	Soluble solids %	Titrateable acid %	Flavour ¹⁾ scores 1 - 9	Ground ²⁾ colour scores 1-9	Red surface ³⁾ colour scores 1-9
2660	164	11.8	0.77	5.5	5.7	5.4
2270	169	11.8	0.78	5.5	5.6	5.5
2000	169	11.8	0.79	5.6	5.8	5.8
LSD (P=0.05)	NS	NS	NS	NS	NS	NS

¹⁾Flavour scores 1-9, where 1=very poor, 3=poor, 5=medium; acceptable, 7=good, 9=excellent

²⁾Ground colour scores 1-9, where 1=dark green and 9=bright yellow

³⁾Surface red colour scores 1-9, where 1=without any red colour and 9=whole surface red

Table 4. Effects of tree density on components of fruit quality of 'Red Gravenstein' apples on M26

Tree density trees/ha	Fruit weight g	Soluble solids %	Titrateable acid %	Flavour ¹⁾ scores 1 - 9	Ground ²⁾ colour scores 1-9	Red surface ³⁾ colour scores 1-9
1270	169	11.4	0.71	6.0	6.5	5.8
1110	181	11.4	0.70	6.1	6.5	6.1
940	172	11.5	0.69	6.0	6.5	5.7
LSD (P=0.05)	NS	NS	NS	NS	NS	NS

¹⁾ Flavour scores 1-9, where 1=very poor, 3=poor, 5=medium; acceptable, 7=good, 9=excellent

²⁾ Ground colour scores 1-9, where 1=dark green and 9=bright yellow

³⁾ Surface red colour scores 1-9, where 1 = without any red colour and 9 = whole surface red

CONCLUSION

High density orchards of 'Red Gravenstein' are most likely to be successful on rootstock M9, giving satisfactory control of tree vigour. In a single-row system with 4-m-wide alleyways, within-row distance of 1.25 m providing a density of 2000 trees/ha gave the highest yield within the range of tree density tested.

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A comparison between meadow fescue and timothy silage

2. *In vivo* digestibility experiments including studies on *in sacco* degradation and rumen fermentation in sheep fed silage alone or different silage:concentrate ratios

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Johansen, A. 1994. A comparison between meadow fescue and timothy silage 2. *In vivo* digestibility experiments including studies on *in sacco* degradation and rumen fermentation in sheep fed silage alone or different silage:concentrate ratios. Norwegian Journal of Agricultural Sciences 8:75-90. ISSN 0801-5341.

Meadow fescue (MF) and timothy (T) silage was evaluated in four *in vivo* digestibility experiments with sheep. In three experiments silage was fed alone and organic matter digestibility (OMD) was significantly higher for MF (73.5%) than for T (72.1%). In the fourth experiment 30% and 60% concentrates (on dry matter (DM) basis) were supplied to the silages and studies on *in sacco* degradability and rumen fermentation were included. The effective protein degradability was slightly, but significantly higher for T than for MF. No significant difference in DM degradability was found. Ration OMD increased and crude fibre digestibility (CFD) decreased with increasing concentrate level. At 60% concentrates no difference in OMD between the two silage rations was found. CFD decreased to a slightly greater extent for T than for MF rations, probably due to a more depressed rumen pH. The rumen proportion of acetic + butyric acid over propionic acid tended to be lower with MF than with T.

Key words: Concentrates, digestibility, *Festuca pratensis*, *Phleum pratense*, rations, rumen fermentation, silage, sheep

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In Norway timothy (*Phleum pratense* L.) and meadow fescue (*Festuca pratensis* Huds.) are the most important grass species sown for forage. However, relatively little information about the ensilability of meadow fescue and the feeding value of the resulting silage is available. As a part of an experimental series to examine the quality of meadow fescue silage three feeding experiments with dairy cows were conducted at Bodin Gård, close to Vågønes Research Station, Bodø (67°17'N) during the years 1987-90 (Johansen & Nordang 1994). Each of the feeding experiments was followed by *in vivo* digestibility experiments

with sheep fed silage sampled throughout the production experiment. From the digestion coefficients energy and protein values of the silage were estimated.

However, it is well known that concentrate supplements may alter the digestibility of the ration (Huhtanen 1991). Organic matter (OM) digestibility of the total ration usually increases with an increasing concentrate ratio but several researchers have shown that the digestibility of the roughage component is depressed (Ekern 1972, Bøe 1989a, Huhtanen 1991). Furthermore, variations in rumen degradation and fermentation may cause differences in energy and protein utilisation that cannot be identified from *in vivo* digestibility measurements. To evaluate these effects a supporting digestibility experiment was conducted, in which sheep were offered diets with varying silage:concentrate ratios. In addition, the *in sacco* degradation of the feeds included in the diets and variation in rumen fermentation between morning and afternoon was studied. The present article details both the standard *in vivo* digestibility experiments and the additional investigations.

MATERIALS AND METHODS

Feeds

Three digestibility experiments (Expts. 1-3) with sheep were conducted at Vågønes Research Station, and a fourth (Expt. 4) was conducted at the Department of Animal Science, Agricultural University of Norway (AUN), Ås. The following feeds were offered the animals:

Expt. 1 (Vågønes):	Meadow fescue and timothy silage harvested in 1987
Expt. 2 (Vågønes):	Meadow fescue and timothy silage harvested in 1988
Expt. 3 (Vågønes):	Meadow fescue and timothy silage harvested in 1989
Expt. 4 (AUN):	Meadow fescue and timothy silage harvested in 1989 supplied by two concentrate mixtures.

All silages were made from a first cut of meadow fescue (cv. Salten) and timothy (cv. Bodin). The grass species were direct cut using a flail harvester one to two weeks after start of heading. Meadow fescue used in Expts. 2, 3 and 4 was at a slightly later stage in morphological development than the timothy. Dates of harvest, dry matter yield, botanical composition of the swards and the chemical composition of the fresh grass are given by Johansen & Nordang (1994). In Expt. 1 formic acid (85%) was used as an additive, while formic acid (64%) plus ammonia (6%) was used in the later experiments. The grass species were ensiled separately in wooden tower silos at Bodin Gård for use in feeding experiments with dairy cows (Johansen & Nordang 1994). The concentrates used in Expt. 4 were the commercial mixtures Kunøtt A (Mix A) and Kunøtt C (Mix C), produced by Felleskjøpet Trondheim. The declared amounts of digestible crude protein (DCP) were 12.5% and 32%, respectively.

The silages used in Expts. 1-3 were sampled throughout the dairy cow experiments. At the end of each feeding experiment the samples were chopped and mixed to produce one test feed. All feeds used in Expt. 4 were collected at the end of the last dairy cow experiment. Thus, silages used in Expts. 3 and 4 were from the same origin. Daily rations

for the digestibility trials were prepared and kept frozen until two days before use. After being frozen rations for Expt. 4 were brought to AUN. During preparation a representative sample from each of the feeds was frozen and retained for chemical analyses. A sample of each feed used in Expt. 4 was taken for *in sacco* measurements. At AUN the samples of silages to be incubated in nylon bags were freeze-dried (-60°C) and concentrates oven-dried at 45°C for 24 h. The dried feeds were milled through a 1.6 mm screen and representative samples for chemical analyses were taken.

Animals and experimental design

The sheep were of varying age (2-7 years) and liveweight (65-90 kg). In Expts. 1-3 a total of four wethers were used for each silage which was fed without concentrate supplement. In Expt. 4 four diets were tested in which the two silages were combined with two concentrate levels. The ratios of silage to concentrates were 70:30 and 40:60 on dry matter (DM) basis and the diets were planned to comply with rations in the dairy cow experiments (Johansen & Nordang 1994). The experiment was planned according to a 4x4 Latin square design using four wethers fitted with permanent rumen cannulae. However, only two rams and one wether were available at the start of the experiment. Because of this, one diet was fed to all three animals at one time. The diets were fed in a random order during four periods.

In all experiments each period lasted 21 days comprising 11 days of adaptation followed by 10 days of total faeces collection. Daily faecal output was recorded and retained frozen until the end of each experiment. Representative samples were ground for chemical analyses. The sheep were fed at approximately maintenance level and offered the feeds in two equal portions at 7:30 and 14:30 h. In Expt. 4 the concentrates were offered about 20 minutes before the silage. The daily amounts of silage and concentrates offered are shown in Table 1. The animals which were kept in digestibility cages had free access to water.

Table 1. Daily amounts of silage and concentrate DM (g) offered to the animals in Expts. 1, 2, 3 and 4. Silage:concentrate ratio on dry matter (DM) basis

Silage:concentrate ratio	Expts. 1-3	Expt. 4	
	100:0	70:30	40:60
Silage, g DM	930	650	350
Mix A, g DM	0	247	432
Mix C, g DM	0	10	50

In Expt. 4 *in sacco* measurements were conducted during the last 13 days of each period. The bags used had an inner size of 7 x 14 cm and was made of nylon cloth with a pore size of 36 μm . In each period all the three feeds included in the diet (either meadow fescue or timothy silage and the concentrates) were tested in separate bags. All incubations started at 07:00 h and lasted for 0, 2, 4, 8, 16, 24, 48 and 72 (silage only) hours. Within animal and incubation time 3 to 6 replicates of each of the feeds were incubated, with increasing number of bags with increasing incubation time. Maximum nine bags were placed in the

rumen at each time and each bag contained two grams dry matter. After the incubation nylon bags were gently rinsed in cold tap water and thereafter washed in cold water for about half an hour, using a washing machine. In order to determine the water soluble part of the feeds three replicates that had not been incubated in the rumen followed the same washing procedure (0 h incubation). After being dried at 45°C for at least 48 hours the bags were weighed and residuals of the different feeds within incubation time and animal were pooled and retained for chemical analyses.

At the final day of each period in Expt. 4 ten rumen fluid samples were collected between 07:00 h and 19:30 h. The samples were taken through the rumen cannula using a vacuum pump and pH was measured immediately. After being strained through a double layer of cheese cloth, 10 ml of fluid were preserved with 0.5 ml of 50% formic acid and stored at 5°C until analysis of volatile fatty acids (VFA) and ammonia-N. During the *in sacco* measurements and collection of rumen fluid there were problems with the one wether. The dry matter content of the rumen digesta seemed quite low and the production of fermentation gasses caused leakage when opening the rumen cannula. However, no relationship between the condition in the rumen and the different diets were observed.

Chemical analyses, calculations and statistical methods

Chemical analyses of the feeds, nylon bag residuals and faeces were carried out at Holt Research Station, Tromsø. Feeds and faeces were analysed for DM, crude protein (CP, calculated as Kjeldahl-N·6.25), ash, ether extract and crude fibre (CF). Also neutral detergent fibre (NDF), acid detergent fibre (ADF) and lignin (ADL) were analysed, except for Expt. 1. Analyses of water soluble carbohydrates (WSC), ammonia-N, true protein, VFA, lactic acid and ethanol were taken for the silages. Nylon bag residues were analysed for DM and CP. The methods used when analysing DM, ash, ether extract, CP, true protein, WSC, ammonia-N and CF are described by AOAC (1980). Pedersen & Lysnes (1991) described the method of gas chromatography used when analysing the organic acids and ethanol. The methods developed by Van Soest (1963a,b) were used for NDF, ADF and ADL. Rumen fluid samples were analysed at Department of Animal Science, AUN. Ammonia-N was determined by the automated colorimetric indophenol reaction (Logsdon 1960) and VFA by gas chromatography.

Silage DM was corrected for losses of volatile substances, assuming that 80% of VFA and 100% of the ethanol are lost during oven drying at 103-105°C. Digestion coefficients for the concentrate mixtures were computed from the ingredient composition, using the digestion coefficients of Sundstøl *et al.* (1986). In Expt. 4 digestion coefficients for the silages were calculated by difference. Rumen degradation constants were calculated using the Non-linear Least Squares procedure (SAS 1987) from the equation (1) of Ørskov & McDonald (1979):

$$p = a + b(1 - e^{-ct}) \quad (1)$$

where

- p = actual degradation after time t
- a = the soluble fraction, intercept of the degradation curve
- b = the insoluble, degradable fraction
- c = rate constant of degradation

The degradation constants were used to calculate the effective protein degradation (EPD) and the effective dry matter degradation (EDD). DM disappearance after 48 hours (DMD48) was calculated from equation (1). EPD and EDD were computed using the equation (2) of Ørskov & McDonald (1979):

$$\text{EPD or EDD} = a + bc/(c + k) \quad (2)$$

where k = rumen outflow rate. Two rumen outflow rates were used; 3 % or 8 % per hour which corresponds to a low and high feeding level, respectively.

All statistical analyses were carried out using the General Linear Models procedure described by SAS (1987). For data from Expts. 1-3 the following model was used:

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

where

Y_{ij} = digestion coefficient

μ = general mean

α_i = effect of the i -th silage (i = meadow fescue, timothy)

β_j = effect of the j -th experiment (j = 1, 2, 3)

$(\alpha\beta)_{ij}$ = effect of the interaction between silage and experiment

e_{ij} = random error

In addition, data from each of the Expts. 1-3 were tested separately. The data from Expt. 4 was examined using an analysis of variance, including the effects of silage, concentrate ratio, animal and the interactions between silage and concentrate ratio and between silage and animals. Other interactions were omitted from the model.

RESULTS

Composition of the feeds

The mean contents of CP and CF were slightly higher for meadow fescue silage than for timothy silage (Table 2). In Expts. 2 and 3 contents of NDF, ADF and ADL were higher for timothy than for meadow fescue silage, but in Expt. 4 analyses of CF and cell wall constituents corresponded well. Silages used in Expts. 3 and 4 had a somewhat higher amount of CP and CF than silages used in the previous experiments. The mean content of WSC and the total amount of organic acids (VFA and lactic acid) were higher for meadow fescue silage than for timothy silage. The difference in the concentration of ammonia-N was variable while true protein tended to be lower for meadow fescue than for timothy silage. The chemical analyses of the concentrate mixtures (Table 3) corresponded relatively well with that calculated from the ingredient composition.

80 *A comparison between meadow fescue and timothy silage*

Table 2. Chemical composition of the silage

	Expt. 1		Expt. 2		Expt. 3		Expt. 4	
	Meadow fescue	Timothy	Meadow fescue	Timothy	Meadow fescue	Timothy	Meadow fescue	Timothy
Dry matter, %	24.8	26.4	25.9	24.3	23.3	21.7	23.6	20.7
<u>In % of dry matter:</u>								
Crude protein	11.1	10.2	10.6	11.8	13.4	12.1	13.0	13.0
Ether extract	3.8	3.8	3.6	4.2	6.0	5.1	5.9	5.8
Crude fibre	36.2	34.8	36.3	35.8	38.2	37.8	38.1	36.3
N-free extracts	42.5	46.0	42.5	42.4	36.0	39.0	36.6	39.6
Ash	6.4	5.3	7.0	5.8	6.4	6.0	6.4	5.3
NDF ¹⁾	-	-	61.8	62.1	64.0	65.9	66.1	64.9
ADF	-	-	36.7	37.5	38.6	39.2	40.7	38.8
ADL	-	-	2.3	2.9	2.2	2.8	2.5	2.4
WSC ²⁾	4.4	3.0	4.8	3.8	2.2	2.3	2.1	1.9
Organic acids	9.9	8.6	10.0	10.8	10.9	8.0	11.1	8.8
Ammonia-N in % of total N	5.7	6.7	10.0	8.9	10.8	14.5	13.1	10.2
True protein in % of CP	55.2	57.9	46.6	54.1	44.5	45.3	40.1	36.6

¹⁾ NDF = neutral detergent fibre, ADF = acid detergent fibre, ADL = lignin

²⁾ WSC = water soluble carbohydrates

Table 3. Ingredient and chemical composition of the concentrate mixtures used in Expt. 4. Calculated digestion coefficients (%) in parenthesis

	Mix A	Mix C
<u>Ingredient composition (%):</u>		
Ground barley	22.9	
Ground oat	20.3	
Wheat bran	7.0	25.0
Durra (Sorghum)	20.0	
Rapeseed meal, extr.	10.0	17.9
Guar meal	5.5	15.0
Soybean meal	3.7	10.3
Fish meal		20.0
Molasses	7.0	4.0
Maize		1.5
Hydrogenated marine fat	1.2	2.6
Minerals, vitamins, etc.	2.4	3.7
<u>Chemical composition (%):</u>		
Dry matter	88.1	89.6
Organic matter	82.1 (81.9)	79.6 (80.8)
Crude protein	16.8 (81.2)	35.5 (88.1)
Ether extract	4.1 (79.8)	7.1 (82.3)
Crude fibre	5.6 (37.7)	7.0 (44.4)
N-free extracts	55.6 (87.3)	29.7 (80.2)
Ash	6.0	10.0

***In vivo* digestibility**

Results from standard digestibility experiments at Vågønes (Expt. 1-3) show that digestion coefficients of DM, OM, CF and NDF were higher for meadow fescue silage than for timothy silage (Table 4). A similar tendency was seen for ether extract and ADF. The ranking between silages according to CP digestibility was variable. In general, the digestibility was higher for silage used in Expt. 3 than in the previous experiments. It should also be noted that the digestibility for ADF was higher than that for NDF. When the data from each experiment was analysed separately the only statistically significant differences found were those for CP digestibility in Expts. 1 and 2 and for ether extract and ADF in Expt. 3.

Table 4. Digestion coefficients (%) for meadow fescue and timothy silage in Expts. 1-3

	Expt. 1		Expt. 2		Expt. 3		SEM	Sign. of effects ¹⁾		
	Meadow fescue	Timothy	Meadow fescue	Timothy	Meadow fescue	Timothy		S	E	SxE
Dry matter	72.7	70.9	72.1	70.6	75.8	74.8	1.9	+	**	NS
Organic matter	73.8	71.8	72.8	71.6	77.1	75.9	1.9	+	***	NS
Crude protein	71.3	67.4	68.2	71.5	71.7	70.1	2.5	NS	NS	*
Ether extract	69.9	72.4	77.4	75.0	82.0	77.5	1.8	+	***	**
Crude fibre	77.1	74.4	75.2	73.2	84.2	82.2	1.8	**	***	NS
N-free extracts	71.9	70.7	71.6	69.9	70.8	71.3	2.3	NS	NS	NS
NDF	-	-	71.8	69.6	79.6	78.1	1.5	*	***	NS
ADF	-	-	73.6	73.4	83.1	81.4	1.5	NS	***	NS

¹⁾ S=silage, E=experiment, SxE=interaction, SEM=standard error of means, Statistical differences are given as: +=p<0.1, *=p<0.05, **=p<0.01, ***=p<0.001, NS=not significant, Other abbreviations; see Table 2

Due to problems with the analytical procedures at the laboratory analyses of cell wall constituents in faeces from Expt. 4 were not reliable and, digestion coefficients for these fractions were not calculated. The only significant difference between silage rations in Expt. 4 was the higher CF digestibility for meadow fescue rations than for timothy rations (Table 5). At the low concentrate level (30%) digestion coefficients for DM and OM were slightly higher for the ration based on meadow fescue than for that based on timothy silage. No clear differences were seen at the high concentrate level (60%). In general, the OM digestibility of the rations increased by increasing the concentrate level and to a slightly greater extent for timothy rations than for meadow fescue rations. However, digestibility of CF was found to decrease.

The digestion coefficients for CF calculated by difference in Expt. 4 were significantly higher for meadow fescue silage than for timothy silage. For both silages the digestibility of CF and ether extract was relatively high. Ether extract and NFE digestibilities increased significantly with the concentrate ratio while CP digestibility decreased. For most of the components significant differences between animals were found, with the wether usually showing a higher digestibility than the two rams. However, no changes in the ranking of the silages were seen by omitting the wether from the computations.

82 *A comparison between meadow fescue and timothy silage*

Table 5. Digestion coefficients (%) for the total ration and for the silage in diets with different silage:concentrate ratios (Expt.4)

Silage:Concentrates	Meadow fescue		Timothy		SEM	Silage	Sign. of effects ¹⁾	
	70:30	40:60	70:30	40:60			Conc. ratio	Silage x Conc. ratio
<u>Total ration:</u>								
Dry matter	77.0	78.7	76.7	79.1	1.43	NS	+	NS
Organic matter	79.4	81.4	78.3	81.3	1.42	NS	*	NS
Crude protein	75.2	76.2	75.3	78.5	2.04	NS	NS	NS
Ether extract	84.0	87.2	81.9	87.0	1.34	NS	**	NS
Crude fibre	80.0	77.2	76.6	71.4	2.42	*	*	NS
N-free extract	79.8	84.3	79.9	85.2	1.27	NS	**	NS
<u>Silage:</u>								
Organic matter	78.3	80.4	76.7	80.0	2.72	NS	NS	NS
Crude protein	71.4	62.5	71.1	69.0	5.29	NS	NS	NS
Ether extract	85.2	95.2	82.5	95.6	2.16	NS	***	NS
Crude fibre	82.7	85.8	79.4	79.9	2.89	*	NS	NS
N-free extract	75.1	78.7	75.3	81.5	3.03	NS	*	NS

¹⁾ See Table 4

***In sacco* degradation**

Results from the *in sacco* measurements in Expt. 4 are shown in Table 6. The calculated intercepts of the degradation curves of DM and protein (a) were nearly equal to the water soluble fractions obtained from bags which were washed without first being incubated. The soluble fraction of DM was significantly higher for meadow fescue silage than for timothy silage ($p=0.004$). No significant difference in degradation of the insoluble fraction (b) was found between the two silages. At the low concentrate level the rate of DM degradation (c) was lower for meadow fescue than for timothy silage, but at high concentrate level this trend was reversed. The mean disappearance of DM after 48 hours incubation (DMD48) was 74.5 and 71.8 for meadow fescue and timothy silage, respectively. Also the effective DM degradation (EDD) tended to be higher for meadow fescue, but none of the differences were statistically significant. The DM degradation tended to be depressed by increasing concentrate ratio, but only statistically significant for EDD. No significant interactions were found.

The soluble protein fraction was significantly higher for meadow fescue than for timothy silage and depressed to a greater extent by increasing concentrate level. However, the degradation of the insoluble protein fraction and the rate constant of degradation were both significantly higher for timothy silage. The effective degradability of protein (EPD) was slightly, but significantly, higher for timothy than for meadow fescue silage. Moreover, EPD for meadow fescue was more depressed by increasing the concentrate ratio than that for timothy. Statistically significant differences between the animals were found for most of the variables analysed. As for the *in vivo* digestibility, *in sacco* measurements in the wether tended to be inconsistent with the two rams.

Table 6. Degradation constants (a, b, c)¹⁾, dry matter disappearance after 48 h incubation (DMD48) and effective degradability of dry matter (EDD) and crude protein (EPD) for silages incubated in sheep fed diets with different silage:concentrate ratios

Silage:Concentrates	Meadow fescue		Timothy		SEM	Sign. of effects		
	70:30	40:60	70:30	40:60		Silage	Conc. ratio	Silage x Conc. ratio
Dry matter:								
a (%)	28.1	26.4	23.1	22.7	1.22	**	NS	NS
b (%)	61.7	49.4	55.2	54.5	5.98	NS	NS	NS
c (%)	3.92	4.59	5.74	4.04	1.07	NS	NS	NS
DMD48 (%)	78.0	70.9	74.5	69.1	5.94	NS	NS	NS
EDD (% , k=0.03)	61.7	56.7	59.1	53.9	3.71	NS	+	NS
EDD (% , k=0.08)	47.7	44.7	45.9	41.1	2.39	NS	*	NS
Crude protein:								
a (%)	68.4	66.4	64.1	65.3	0.74	**	NS	*
b (%)	18.3	17.5	22.5	19.5	1.72	*	+	NS
c (%)	9.53	9.24	13.76	17.02	4.05	*	NS	NS
EPD (% , k=0.03)	82.0	79.5	82.5	81.3	0.86	+	*	NS
EPD (% , k=0.08)	78.1	75.7	78.3	77.9	0.63	*	*	*

¹⁾ a = soluble fraction, b = insoluble, degradable fraction, c = rate constant of degradation, k = rumen outflow rate (% per hour), EDD and EPD = $a + bc/(c+k)$, Other abbreviations; see Table 4

The degradability of the concentrate mixtures was slightly depressed by increasing the concentrate:silage ratio, but no statistically significant effect of the varying diets was found. The mean values (over all four rations) are presented in Table 7. Generally, differences in DM degradation were small. The soluble protein fraction (a) was higher for Mix C than for Mix A while the opposite relationship was seen at fraction b. DMD48 and the effective degradability of both DM and protein was slightly higher for Mix A than for Mix C.

Table 7. Degradation constants (a, b, c), effective degradability of dry matter and protein and dry matter disappearance after 48 h (DMD48) for concentrate mixtures

	Dry matter		Crude protein	
	Mix A	Mix C	Mix A	Mix C
a (%)	43.8	41.6	32.6	38.3
b (%)	40.0	39.2	51.9	41.1
c (%)	15.3	14.4	16.2	15.1
dg _{k=3}	76.2	73.6	68.6	66.2
dg _{k=8}	68.6	66.2	65.2	64.7
DMD48	83.5	80.7		

¹⁾ dg = EDD and EPD for dry matter and protein, respectively
Other abbreviations; see Table 6

Rumen fermentation studies in Expt. 4

Results from the studies on rumen fermentation are shown in Figure 1. At the low concentrate level no clear difference in rumen pH between the two silage rations was seen. At the high concentrate level pH was higher with meadow fescue than with timothy silage. The latter had a minimum pH of 5.94 after the second meal (15:15 h) and was still below 6.2 at 19:30 h.

Differences in total VFA concentration were variable. Regarding the proportion between the different rumen acids, both minimum and maximum values of the ratio between acetic (C2) + butyric (C4) over propionic (C3) acid appeared to be more extreme for meadow fescue than for timothy silage. The minimum (C2+C4):C3 ratios were found relatively short time after feeding, mainly caused by an increased proportion of propionic acid. The maximum concentration of ammonia-N was found somewhat later. At low concentrate level no clear difference between the two silages was seen. At high concentrate level a higher concentration of ammonia-N was found with meadow fescue silage than with timothy silage.

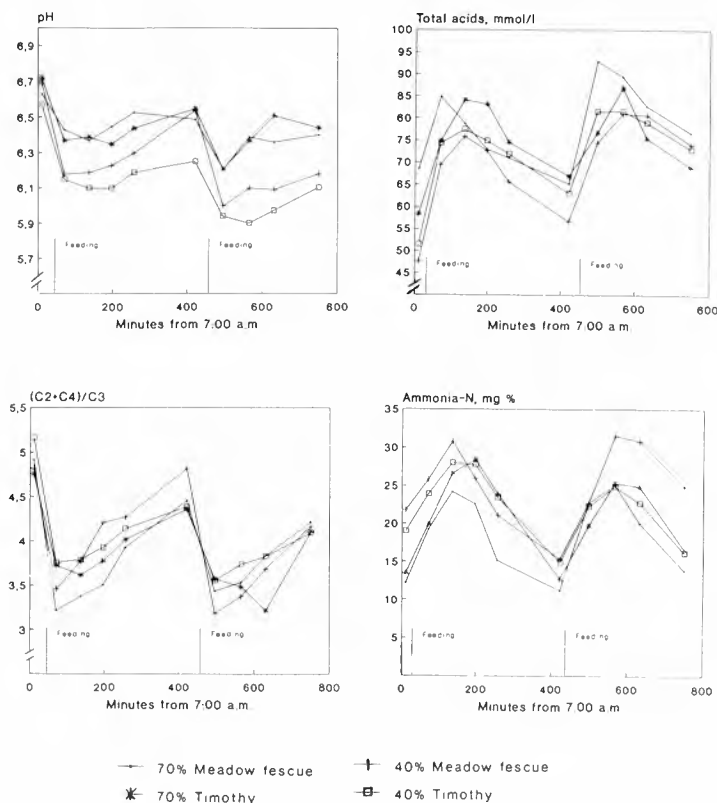


Figure 1. Diurnal variations of rumen pH, total concentration of VFA (total acids), ratio between acetic and butyric acid over propionic acid ((C2+C4):C3) and concentration of ammonia-N. Measurements in sheep fed meadow fescue and timothy silage with two levels of concentrates supplied (30% and 60% on dry matter basis).

DISCUSSION

In general, differences in chemical composition between the two silages were small. This was in good agreement with results from feeding experiments with bulls (Johansen & Nordang 1993). The inconsistency in the relationship between the different fibre analyses (CF versus cell wall constituents) was probably due to heterogeneity of the silage. The main differences between the two silages were the somewhat poorer fermentation quality, the higher OM digestibility and the higher fraction of soluble DM and CP for meadow fescue than for timothy silage. Because silages used in Expts. 3 and 4 were from the same origin and differences between the samples were small, a comparison of the results from the two experiments was most adequate. In the following *in vivo* and *in sacco* results will be discussed. Differences in fermentation quality, which might be due to a higher buffering capacity of meadow fescue than of timothy grass, is discussed by Johansen & Nordang (1993, 1994).

***In vivo* digestibility**

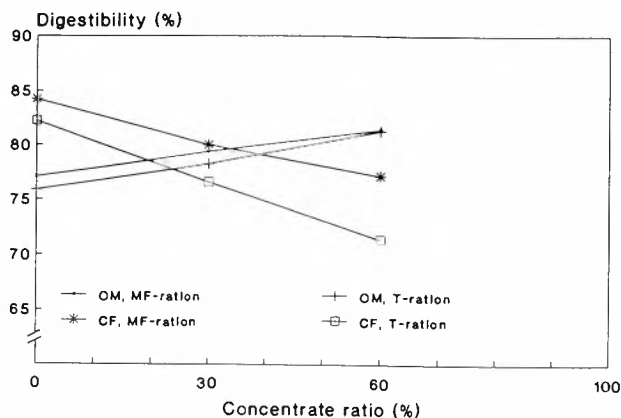
In previous investigations higher *in vitro* digestibility for meadow fescue grass than for timothy grass harvested at the same morphological stage has been found (Demarquilly & Weiss 1970, Demarquilly & Jarrige 1974, Schjelderup 1980). Although meadow fescue was at a more advanced morphological stage at harvest than timothy in two of the present experiments, *in vivo* OM and DM digestibility was significantly higher of meadow fescue than of timothy silage. This was in good agreement with results from experiments with bulls (Johansen & Nordang 1993). Among the different digestion coefficients that of CF showed the most striking difference between meadow fescue and timothy silage. The digestion coefficients of CF and cell wall constituents corresponded well but the higher digestibility of ADF than of NDF was surprising because most other reports show the opposite relationship. The lower digestibility of timothy silage might partly be explained by differences in rumen fermentation and pH. Unfortunately the animals used in Expts. 1-3 were not fitted with rumen cannulae and therefore no rumen studies were included.

Several researchers have found an increase in OM digestibility and a fall or steady state for CF and NDF when silage is supplemented by concentrates (Ekern 1972, Thomas et al. 1980, Hole 1985, Bøe 1989a). In Figure 2 results from Expt. 3 and Expt. 4 are combined to show OM and CF digestibility for silage rations with 0, 30 and 60% concentrates. The figure confirms the trend of interaction between concentrate levels and silages which was seen in Expt. 4. Thus, although OM digestibility was higher for meadow fescue silage than for timothy fed alone, no difference was seen for diets including 60% concentrates.

The increased proportion of concentrates tended to depress CF digestibility more for the timothy rations than for meadow fescue rations. The degradation of fibre has usually its optimum in the pH range 6.2-7.0 (Dixon 1985). At rumen pH below 6.0-6.1 the cellulase activity is negligible and hence also the degradation of fibres (Mould & Ørskov 1984). Istasse & Ørskov (1983) found that the degradability of hay was highly correlated to the summated depression below pH=6. In these studies the fall in rumen pH after feeding was more pronounced and lasted for a longer period for timothy silage than for meadow fescue silage. The differences in rumen pH between the two silage rations may be

explained by a higher buffering capacity of meadow fescue silage than of timothy silage. This theory is mainly attributed to the higher concentration of organic acids in the silage and the higher concentration of ammonia-N in the rumen fluid. The relationship between organic acids and the buffering capacity is described by McDonald et al. (1991) and the effect of the concentration of ammonia-N in the rumen fluid has been discussed by Briggs et al. (1957) and Tyrrell (1980).

Figure 2. Organic matter (OM) and crude fibre (CF) digestibility for rations with different concentrate:silage ratios. Values obtained from Expts. 3 and 4. (MF = meadow fescue silage, T = timothy silage)



Among several, Bøe (1989a) and Huhtanen (1991) have reported a depressed digestibility of grass silage by supplying concentrates to the ration. In the present computations the opposite relationship was found. Computing the digestibility of a feed in a mixed ration by difference is based on the assumption that no interactions between the basal ration and the experimental feed occurs. In many circumstances this assumption is not valid. Moreover, by decreasing the proportion of the experimental feed in the diet the error introduced by a possible false value for the basal ration increases. It was speculated whether the digestion coefficients for the concentrates were actually higher than calculated. By extrapolating the curves in Figure 2 to 100% concentrates gives OM and CF digestibilities of approximately 83% and 67%, respectively. The calculated values for Mix A were 81.9% and 37.7%. Considering these possible errors it was considered that estimates for silage digestibility in Expt. 4 not were adequate.

***In sacco* degradation**

The higher soluble DM and CP fraction for meadow fescue silage than for timothy silage obtained from nylon bag incubations corresponded well with the higher concentration of organic acids, WSC and ammonia-N for meadow fescue silage. Generally, the proportion of soluble protein was in good agreement with results from other recent *in sacco* experiments with grass silage (Johansen 1988, Tuori et al. 1992, Kjos 1992 unpublished).

The proportion of soluble nutrients has limited influence on the potential and effective degradability of silages, which mainly depend upon the proportion of the insoluble degradable fraction (b), the rate of degradation (c) and the rumen outflow rate (k). The inconsistent relationship between the two silages with respect to the DM degradation rate

partly explain why no statistically significant differences in DM degradability were found. Moreover, the higher rate of degradation of the insoluble CP fraction caused that EPD became higher for timothy than for meadow fescue. The mean EPD was 81,9% and 80,8% for timothy and meadow fescue silage, respectively. Although this difference was statistically significant it is considered to have minor effect for the protein values calculated according to the AAT-system (Harstad 1992, Harstad & Volden 1992). What concerns the concentrates, EPD was higher for Mix A than for Mix C, but the difference was less than might be expected considering that fish meal accounted for 20% of the ingredients in Mix C. According to Mehrez et al. (1980) EPD of fish meal is highly dependent of the quality and treatment of the meal. This indicates that the fish meal used in Mix C had a relatively high EPD.

It was clearly shown that the silage degradability decreased with increasing rumen outflow. Rumen outflow will usually increase with the feeding level which is itself often associated with increased concentrate levels. In this experiment differences in the feeding level were relatively small but other factors such as pH and more readily available energy sources may explain the depressed degradability of the silages with increasing concentrate level. The rumen degradabilities of the concentrates tested were less affected by changes in the diet than those of meadow fescue and timothy silage. This is probably because sugars and starches, which are the main carbohydrate sources in the concentrates, are degraded by most of the rumen bacteria present under a wide range of rumen pH. The degradation of starch and other easily fermentable carbohydrates usually increases the proportion of propionic acid in the rumen, which is often found by increasing the amounts of concentrates in the diet. In Expt. 4 no such effect was found.

Many researchers have found a high correlation between the DMD48 and *in vivo* OM digestibility of the feed (Sauvant et al. 1985) although Bøe (1989b) showed that this correlation greatly dependent on the feeding level. In Expt. 4 the depressed DMD48 with increasing concentrate level contradicted the computed OM digestibility for the silages. This was considered to support the conclusion made that the difference method not was useable to estimate the OM digestibility of the silages. On the other hand, the fact that no significant differences in DMD48 were found between the two silages was in good agreement with the negligible differences in OM digestibility of the rations at high concentrate levels.

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Further studies on the effects of ozone concentration on growth of subalpine plant species

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The effects of three ozone concentrations (15, 43 and 78 nmol mol⁻¹ in 8 h day⁻¹) on growth of 13 subalpine plant species were studied over a period of 40-56 days in growth chambers installed in a greenhouse. Seeds from one geographic location of each species were usually included. For *Agrostis tenuis* and *Trifolium pratense* seeds from two and four locations, respectively, were used. The dry weight of *Carex atrofusca*, *Comarum palustre* and *Trifolium pratense* was negatively affected by concentrations at 43 nmol mol⁻¹ O₃, but the other species were unaffected. In addition to these three species, there was a decrease in the dry weight of *Erigeron borealis* at the highest O₃ concentration. Leaf injuries caused by 43 nmol mol⁻¹ O₃ were observed in *Trifolium pratense* but not in the other species. At the highest O₃ concentration, leaf injuries were observed also in *Astragalus frigidus*, *Carex atrofusca*, *Comarum palustre*, *Erigeron borealis*, *Eriophorum angustifolium*, *Festuca pratensis*, *Geranium sylvaticum*, *Melica nutans* and *Vaccinium myrtillus*. No effect of O₃ at all was found in *Gnaphalium norvegicum*, *Juniperus communis* and *Thalictrum alpinum*. Similar O₃ effects were observed in the two localities of *Agrostis tenuis*. The percentage leaf area with O₃ injury symptoms in *Trifolium pratense* varied slightly between the localities, while the dry weight was affected to the same extent.

Key words: Growth, leaf injury, ozone, subalpine plants.

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A study of the O₃ sensitivity of a range of subalpine plant species has been carried out in Norway during the past few years as part of the national work on "Critical levels" (Mortensen & Nilsen 1992; Mortensen 1993). It was found that the growth rate of very few of the species investigated was negatively affected by realistic O₃ doses, i.e. 40-50 nmol mol⁻¹ in 8 h day⁻¹, over a period of some weeks (Pedersen & Semb 1990). Of some 40 wild plant species so far investigated in Norway, *Phleum commutatum* has proved to be the most O₃-sensitive species (Mortensen 1993) followed by *Phleum pratense* (Mortensen 1992) and *Betula pubescens* (Mortensen & Skre 1990). So far, only relatively few of the subalpine

plant species have been studied with respect to O₃ sensitivity. The objective of this work has been to identify some of the most O₃-sensitive wild plant species, primarily from among the most common subalpine plant species in Norway. By observing the vitality/injury symptoms of these sensitive species in nature it is thought that an indication of O₃ stress on vegetation might be detected. The aim of the present work was therefore to try to identify some additional species which could be useful as indicators of O₃ stress.

MATERIAL AND METHODS

Seeds were harvested at an altitude of 900-1150 m above sea level (a.s.l.) in the Jotunheimen district (61.5°N, 8.5°E) during the autumn of 1992. After drying, the seeds were stored at 4°C. The species included were: *Astragalus frigidus* (L.) A. Gray, *Carex atrofusca* Schkuhr, *Comarum palustre* L., *Erigeron borealis* (Vierh.) Simm., *Eriophorum angustifolium* Honck., *Geranium sylvaticum* L., *Gnaphalium norvegicum* Gunn., *Juniperus communis* L., *Melica nutans* L., *Thalictrum alpinum* L. and *Vaccinium myrtillus* L.. Seeds of two localities of *Agrostis tenuis* Sibth., from the Nordic Gene Bank, NGB no. 2866 (61°N, 9.5°E) and no. 2867 (62.5°N, 11°E) from 680 m a.s.l. were included. Seeds of four localities of *Trifolium pratense* L. were also included: NGB no. 1574 (62.5°N, 11.5°E), no. 1583 (61°N, 9.5°E), no. 1637 (60°N, 8.5°E) and no. 6733 (60°N, 9°E) from 750-805 m a.s.l..

The seeds were sown in January 1993 in a greenhouse compartment. The seeds of *Agrostis tenuis*, *Trifolium pratense* and *Phleum pratense* L. (cv. Forus), however, were sown in the middle of March. *Phleum pratense* was included for reference since in an earlier study it was found that this species is relatively O₃ sensitive (Mortensen 1992). On 14 April seedlings of all species were potted in a mixture of standard fertilized peat (Floralux, Nittedal industrier Ltd., Norway) and 25% perlite in 1 l pots, three seedlings per pot. On 16 April five pots (in a few cases three pots) of each species were placed in each of six growth chambers described earlier by Mortensen & Nilsen (1992). The pots were watered regularly with a complete nutrient solution in order to maintain the electrical conductivity at about 2.0 mS cm⁻¹ (Mortensen 1992).

Three O₃ concentrations were established, two chambers per concentration (Table 1): 15, 43 and 78 nmol mol⁻¹ given 8 h day⁻¹ (10.00-18.00 h). Ozone was generated from dry air using a high-voltage generator (Nomizon, Normiljø Ltd., Sweden). The effect of O₃ produced by the air has recently been compared with the effect of the same level of O₃ produced by oxygen on *Phleum pratense*, (Mortensen 1994). The two treatments caused the same amount of foliar injury, and it was concluded that no toxic by-products were produced by the generator when air was used instead of oxygen. The O₃ concentration was measured twice an hour by a scanner switching the air flows from the chambers sequentially to an O₃ analyser (Monitor Labs. Inc., Model 8810). Supplementary light was given at a level of 150 μmol m⁻² s⁻¹ during 20 h day⁻¹ (11 mol m⁻² day⁻¹) by means of high pressure sodium lamps (SON XL-T). The light was measured by means of a Lambda LI-185B instrument with quantum sensor (400-700 nm). The contribution of daylight inside the chambers was, on average, 20 mol m⁻² day⁻¹. This value was based on measurements taken at the Meteorological Station at Særheim, which were reduced by 50% due to the reduction in light

caused by the greenhouse and growth chamber constructions. The total number of photosynthetic active photons inside the chambers was therefore $31 \text{ mol m}^{-2} \text{ day}^{-1}$, which is somewhat lower than the natural light conditions in May-July ($40\text{-}50 \text{ mol m}^{-2} \text{ day}^{-1}$) in Norway. The air temperature was $15/10^\circ\text{C}$ at 12/12 h intervals, and the relative humidity 85-90% (Table 1).

Table 1. Climatic conditions in the six growth chambers during the experiment. The daily period is divided into the O_3 exposure period (10.00-18.00 h) and the remaining part of the day (18.00-08.00 h) without additional O_3

Chamber no.	O_3 conc. (nmol mol^{-1})		Air temperature ($^\circ\text{C}$)			% relative humidity
	10-18 h	18-10h	08-20 h	20-08 h	Mean	
1	77 ± 11	22 ± 6	15.0	10.5	12.8	87 ± 6
2	15 ± 9	14 ± 8	14.6	10.0	12.3	93 ± 9
3	43 ± 8	21 ± 6	14.2	9.9	12.1	84 ± 7
4	78 ± 11	21 ± 6	15.1	10.1	12.6	87 ± 6
5	42 ± 9	21 ± 6	14.8	10.1	12.5	88 ± 6
6	14 ± 9	14 ± 8	15.5	10.9	13.2	90 ± 6

Trifolium pratense was harvested after 40 days, and the other species after 53-56 days (8-11 June 1993). At the end of the experiment plant fresh and dry weights (the roots not included), and percentage leaf injury (of the total leaf area) were recorded. The injury was visually determined at intervals of 10% on individual plants. In *Trifolium pratense* also plant height, and leaf area and dry weight of 30 leaves per chamber were recorded. All data were subjected to an analysis of variance with chambers as replicates.

RESULTS

The dry weight of *Carex atrofusca*, *Comarum palustre* and *Trifolium pratense* decreased when the O_3 concentration increased from 15 to 43 nmol mol^{-1} , while the other species were unaffected (Tables 2 and 3). It was found that these three species were more affected by O_3 than the reference species *Phleum pratense*. In addition to these species, the dry weight of *Erigeron borealis* was decreased at $78 \text{ nmol mol}^{-1} \text{ O}_3$, while the other species remained unaffected. *Trifolium pratense* was the only species in which leaf injuries developed when the O_3 concentration was increased from 15 to 43 nmol mol^{-1} , while all species except *Gnaphalium norvegicum*, *Juniperus communis* and *Thalictrum alpinum* developed injury at 78 nmol mol^{-1} . The visible injury symptoms, which varied between the species included chlorosis, necrosis, bronzing, and white, brown and red spots (Table 2). The injuries in *Trifolium* included bronzing, brown spots and leaf wilting (necrosis), usually starting at the leaf margins. The four localities of *Trifolium* responded similarly to O_3 exposure, except with respect to the amount of leaf injury, which was lower in one of the localities at $43 \text{ nmol mol}^{-1} \text{ O}_3$ compared with that in the other localities (Fig. 1).

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Table 2. The effect of O₃ concentration on growth and leaf injury of different plant species. The dry weight at start of the experiment is given in parentheses. Values followed by different letters within each column and species are significantly different according to Duncan's multiple range test at p < 0.05 level

Species	O ₃ conc. (nmol mol ⁻¹)	Dry wt. (g plant ⁻¹)	% dry of fresh wt.	% leaf injury	Injury symptoms
<i>Agrostis</i>	15	4.0a	23.6a	2b	Chlorosis/necrosis of oldest leaves
<i>tenuis</i> NGB 2866	43	4.1a	21.7a	2b	
(0.024 g)	78	4.0a	22.5a	17a	
<i>Agrostis</i>	15	4.3a	21.9a	2b	Chlorosis/necrosis of oldest leaves
<i>tenuis</i> NGB 2867	43	4.4a	21.2a	2b	
(0.017 g)	78	4.4a	20.7a	17a	
<i>Astragalus</i>	15	0.085a	19.8b	0b	Bronzing and bleaching
<i>frigidus</i>	43	0.051a	19.8b	0b	
(0.009 g)	78	0.046a	21.6a	60a	
<i>Carex</i>	15	0.63a	18.2a	0b	Brown spots/necrosis developing from leaf tip
<i>atrofusca</i>	43	0.37b	17.5a	4b	
(0.004 g)	78	0.34b	18.7a	86a	
<i>Comarum</i>	15	2.37a	22.8a	0b	White spots
<i>palustre</i>	43	1.65b	22.6a	2b	
(0.018 g)	78	1.31b	22.4a	18a	
<i>Erigeron</i>	15	1.31a	14.7a	0b	Slight bronzing
<i>borealis</i>	43	1.20ab	14.9a	0b	
(0.017 g)	78	1.02b	15.3a	2a	
<i>Eriophorum</i>	15	0.21a	19.9a	0b	Slight bronzing
<i>angustifolium</i>	43	0.16a	20.1a	0b	
(0.005 g)	78	0.20a	20.9a	9a	
<i>Geranium</i>	15	2.46a	27.2a	0b	Brown spots
<i>sylvaticum</i>	43	2.08a	27.0ab	3b	
	78	2.15a	25.1b	48a	
<i>Gnaphalium</i>	15	1.82a	15.7a	0a	None
<i>norvegicum</i>	43	1.64a	14.5a	0a	
(0.023 g)	78	1.51a	15.5a	0a	
<i>Juniperus</i>	15	0.33a	27.4a	0a	None
<i>communis</i>	43	0.32a	28.0a	0a	
	78	0.31a	27.9a	0a	
<i>Melica</i>	15	2.32a	25.7a	0b	White and brown spots/necrosis developing from leaf tip
<i>nutans</i>	43	2.15a	24.8b	0b	
(0.023 g)	78	2.06a	24.7b	10a	
<i>Thalictrum</i>	15	0.025a	36.0a	0a	None
<i>alpinum</i>	43	0.019a	29.5a	0a	
	78	0.018a	34.9a	0a	
<i>Vaccinium</i>	15	0.64a	38.6a	0b	Red-brown spots
<i>myrtillus</i>	43	0.52a	42.2a	0b	
	78	0.69a	39.3a	17a	
Reference species:					
<i>Phleum</i>	15	7.2a	21.5a	0b	Chlorosis/necrosis of oldest leaves
<i>pratense</i> 'Forus'	43	7.1a	20.9a	10b	
(0.009 g)	78	4.6b	21.1a	67a	

Table 3. Effect of O₃ concentration on growth and leaf injury of four localities (NGB no.) of *Trifolium pratense*. Significance level: ns, not significant; *, p < 0.05; **, p < 0.01; ***, p < 0.001

	Dry wt. (g pot ⁻¹)	% dry of fresh w.	Leaf area (cm leaf ⁻¹)	Leaf dry wt. (mg leaf ⁻¹)	SLA (cm ² g ⁻¹)	Plant height (cm)	% leaf injury
<u>O₃ conc. (nmol mol⁻¹):</u>							
15	6.51a	13.1ab	11.4a	35a	328a	21.3a	0a
43	5.17b	12.8b	9.9b	30b	329a	18.4b	24b
78	4.36c	13.8a	6.3c	23c	280b	17.2c	77a
<u>Locality:</u>							
NGB 1583	6.32a	13.6a	9.8a	34a	289c	20.9a	36a
NGB 1637	6.04a	13.4ab	9.3ab	30b	313b	19.6b	37a
NGB 6733	5.20b	13.3ab	9.1bc	29b	309bc	18.0c	30a
NGB 1574	3.81c	12.7b	8.6c	25c	339a	17.1d	31a
d.f.							
O ₃	2	***	*	***	***	***	***
Locality (L)	3	***	ns	*	***	**	**
O ₃ x L	6	ns	ns	ns	ns	ns	**

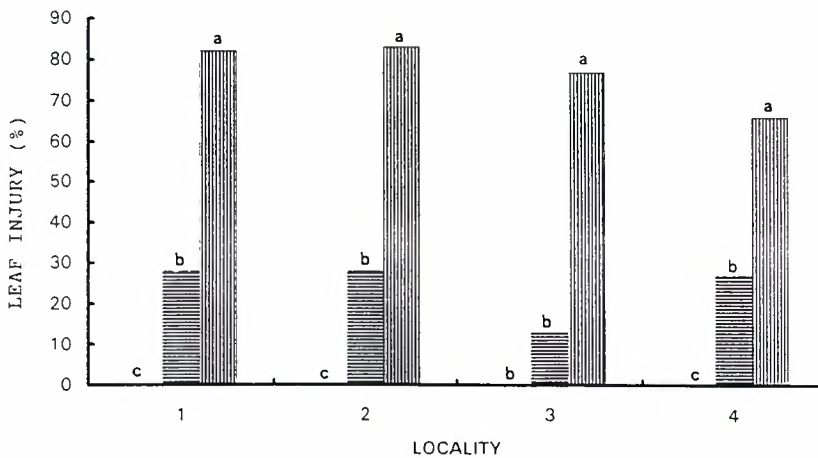


Fig. 1. Percentage leaf area with injury symptoms at 15 (■), 43 (▨) and 78 nmol mol⁻¹ (□) O₃ in four localities of *Trifolium pratense*, including NGB no. 1583 (1), no. 1637 (2), no. 6733 (3) and no. 1574 (4). For further information see Material and Methods. Different letters at the top of the columns within each locality indicate that the values are significantly different according to Duncan's multiple range test at p < 0.05

DISCUSSION

As in previous studies with subalpine plants, a wide variation in the O₃ sensitivity between species was found (Mortensen & Nilsen 1992; Mortensen 1993). At concentrations which frequently occur in nature in Norway (40-50 nmol mol⁻¹), three out of 13 species were

affected with respect to dry weight reductions. Only in *Trifolium pratense* were the dry weight reductions accompanied by visible symptoms of injury. This species should therefore be an interesting indicator plant for O₃ stress on vegetation since the injury symptoms also seemed to be relatively O₃ specific. This species has also previously been shown to be relatively sensitive to O₃ (Ashmore 1984; Kohut et al. 1988; Mortensen 1992). In the present experiment the reference species, *Phleum pratense*, was less sensitive to O₃ than *Trifolium pratense*, which concurs with the findings of Kohut et al. (1988). Although some variations in the amount of O₃-induced leaf injury between the four clover localities were found, all localities were relatively O₃ sensitive. It is well documented that the O₃ sensitivity between different varieties/populations of a species can vary considerably (Kress et al. 1982; Reiling & Davison 1992; Guzy & Heath 1993).

Foliar injuries occurred in most of the species at the highest level of O₃. However, in most cases this effect was not accompanied by a reduction in dry weight. In a previous study nine out of 19 species developed leaf injuries at 40-53 nmol mol⁻¹ during 8 h day⁻¹ for 1-3 months, but dry weight reduction was found in only one species (Mortensen 1993). In his review article Tingey (1985) summarized that foliar injury may or may not cause a reduction of growth and yield in different species. As shown with *Carex atrofusca* and *Comarum palustre* in the present study, growth reductions may indeed take place without foliar injury.

In the study of O₃ effects on wild plant species in Norway, about 50 species have so far been investigated (Mortensen & Nilsen 1992; Mortensen 1993). Of these species the dry weights of *Phleum commutatum*, *Betula pubescens* and *Plantago lanceolata* from previous studies, and *Trifolium pratense*, *Carex atrofusca* and *Comarum palustre* from the present study are likely to be negatively affected by levels of O₃ (40-50 nmol mol⁻¹) which occur periodically in Norway (Pedersen & Semb 1990). Slight foliar injury, however, occurred in one-third of all species studied. The extent of O₃ injury may be modified by the environmental factors in the field. Therefore, care should be taken when the results from growth chamber experiments are transferred to the field situation.

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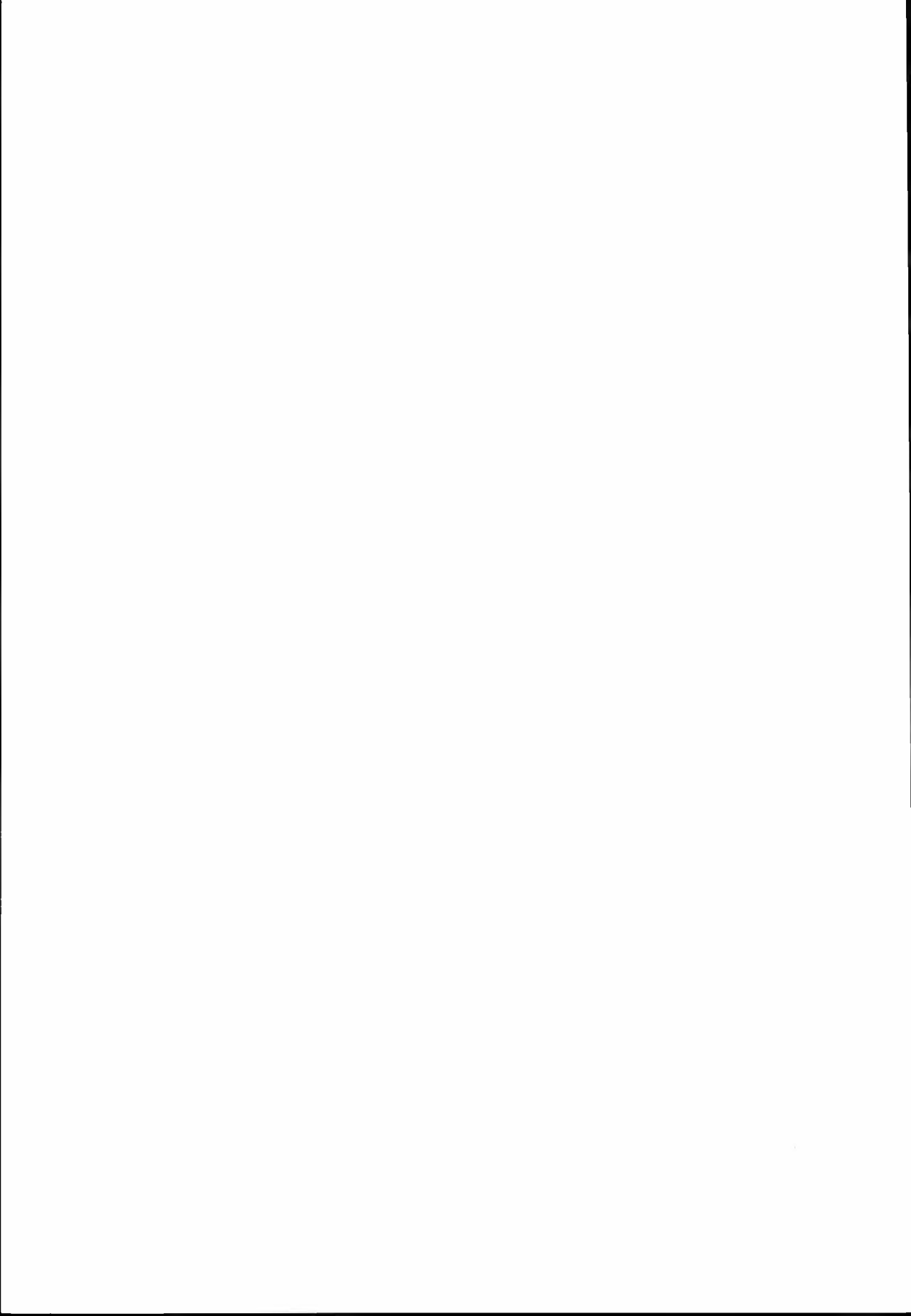
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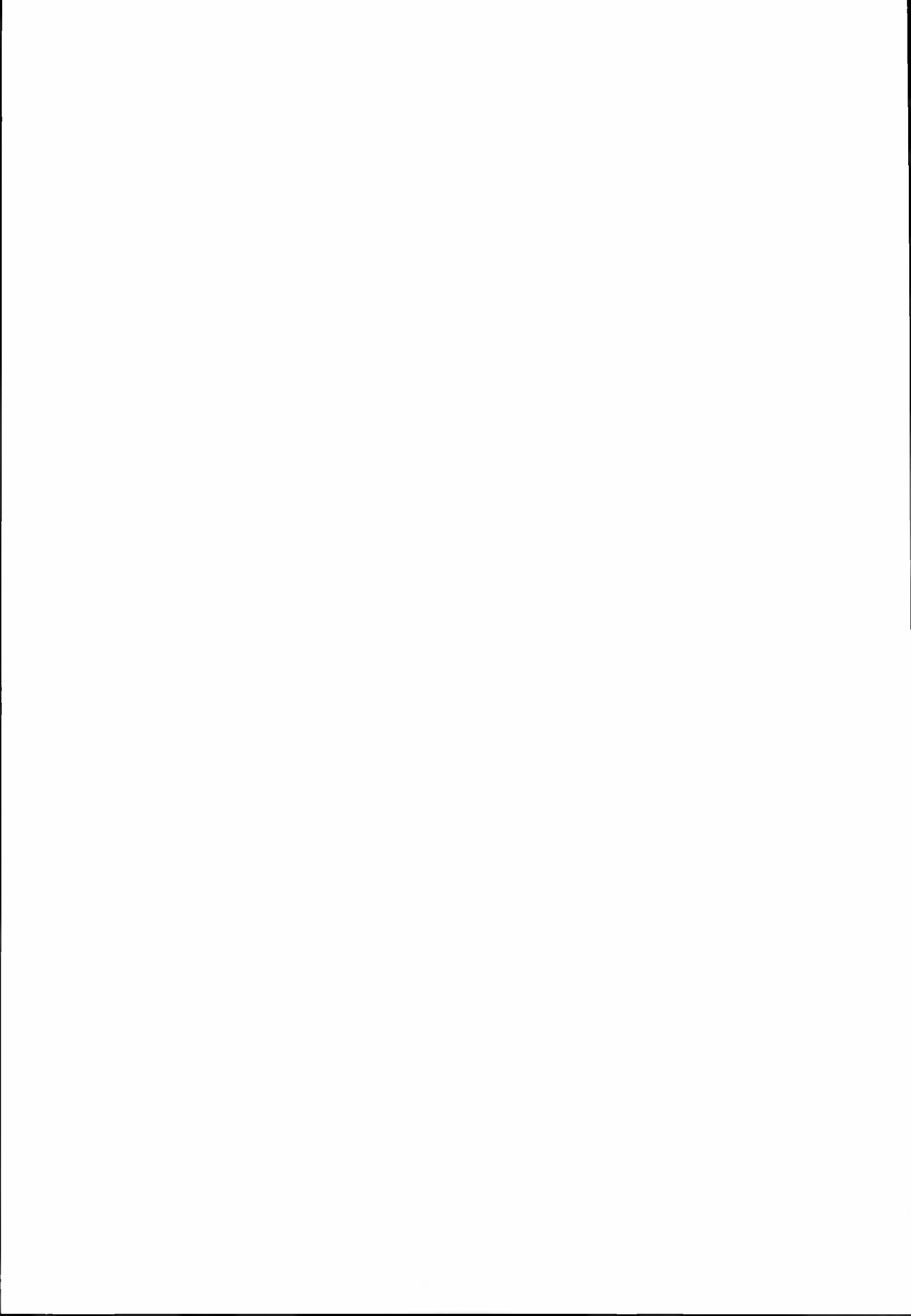
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