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The drawing on the cover is from Kjell Aukrust's *«Guttene på broen»*.

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Effects of different environments and selection for persistency in laying hens

III. Genetic and phenotypic parameters of egg production traits

LUN JUN MOU
Agricultural University of Norway, Department of Animal Science, Ås, Norway

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The heritabilities of egg production traits, the genetic and phenotypic correlations between different traits and between the part-record and the complete record were investigated in the present study. In general, the heritabilities estimated from sire components of variance were lower than those from dam components except for egg weight (EW) and body weight (BW). The heritability of age at sexual maturity (SM) was about 0.50. BW is a relatively high heritable trait and the estimated heritability for BW at different ages was about 0.65 from sire components and about 0.40 from dam components. Egg number (EN), percent egg production (PE) and egg mass (EM) had very similar estimated heritabilities. The sire component heritabilities for EN, PE and EM were around 0.20 for the different early part-records (e.g. up to 42, 50 or 58 weeks) and about 0.15 for the whole or residual records, while the corresponding figures were about 0.50 and 0.40 from the dam components. The estimated heritabilities for EW were about 0.60 and 0.23 from sire and dam components, respectively.

The genetic correlations were estimated from sire components of variance. For most of the traits studied, the genetic correlations estimated in different control periods were very close for each pair of traits. SM was found to be positively correlated with all the traits except early part EN, correlations being from low to moderate. The correlations of BW with all other traits were from low to moderate. PE was found to be both higher and more positively correlated with EM and lower and less negatively correlated with EW than EN. From the same early part-period, PE was found to be more highly correlated, genetically and phenotypically, with EN, PE and EM recorded at 70, 88 weeks, R1 and R2 period than EN. It is suggested that PE might be a better selection criterion for improving egg production than EN.

Key words: Correlation, egg production, heritability, laying hens, persistency, selection.

Lun Jun Mou, Department of Animal Science, Macdonald College of McGill University, 21, 111 Lakeshore Road, Ste. Anne de Bellevue, P.Q, Canada H9X 1C0.

The prediction of breeding value plays an important role in genetic improvement programmes. Prediction of individual breeding value, even in its simplest form, relies on the knowledge of the additive genetic and phenotypic variances of the traits concerned. However, the variances are not known in all situations. To predict breeding value for a particular situation, one is faced with the prospect of either using estimates based on past experience or, preferably, estimating the variance in the best manner possible from the same set of data on which the selection is to be based and applying the estimates in stead of the true parameters to the construction of selection indexes or to the newer mixed model procedure.

Practically all selection in egg-laying breeds today is carried out on an annual cycle. This takes into consideration the genetic advantage from the shorter generation interval and has the practical convenience of the operations of caging, selection, mating, hatching etc., always occurring at the same time each year. In order to achieve an annual cycle, the early part-record of egg production at the age of about 40 weeks has been used to evaluate individual breeding value. The genetic improvement in the early part-record has been achieved and so has annual egg production (Kolstad 1983, Maijala 1984). Some researchers, however, have noticed that the genetic gain of annual egg production has been slowed down after several generations of selection on the basis of the early record (Morris 1963, 1964, Gowe & Strain 1963, Gowe 1974). One reason is probably due to the fact that the stocks, having undergone selection based on part-records for a number of generations, may not exhibit strong positive genetic correlation between part and whole production (Singh et al. 1985). Bohren (1970) stated that, theoretically, the genetic correlation between part and whole egg production may change from positive to negative, although there is no clear evidence that this has actually happened in any population.

Another reason may be that exclusive reliance on the early part-record may only decrease age of sexual maturity at the expense of persistency. A number of investigations have been performed to compare the efficiency of selection on early part-record and residual record (Singh et al. 1985, Chhikara et al. 1985).

The objective of the present paper is to study the relationship between the part and whole egg production record and between early part and different residual records. The genetic and phenotypic correlations among several traits of egg production will be estimated to provide a reasonable selection method to improve egg production persistency.

MATERIALS AND METHODS

An experiment was started in 1986 at the Agricultural University of Norway with the aim of improving egg production persistency through selection on the basis of the early part-record and of the prolonged production record. The background and general outline of the experiment and the traits of interest have been discussed by Kolstad & Mou (1990) and Mou & Katle (1990).

The data used for estimating parameters were extracted from the second generation of the unselected base population established in 1986. There were 2448 pullets housed in two production environments when 16 weeks old. Only hens with complete records were used for the estimation of parameters.

The traits included in the analyses are summarized in Table 1. The same statistical model was used for all the traits analysed:

$$Y = Xb + W_1s + W_2d + e$$

Abbreviations used in this work: BW = body weight, EM = egg mass, EN = egg number, EW = egg weight, PE = percent egg production, R1 = first residual period, R2 = second residual period, SM = age at sexual maturity.

Table 1. Summary of the traits investigated

Control period	Trait					
	SM	BW	EN	PE	EW	EM
1st day of lay	SM					
At 42 weeks		BW_{42}	EN_{42}	PE_{42}	EW_{42}	EM_{42}
» 50 »		BW_{54}[1)]	EN_{50}	PE_{50}	EW_{50}	EM_{50}
» 58 »			EN_{58}	PE_{58}	EW_{58}	EM_{58}
» 70 »		BW_{70}	EN_{70}	PE_{70}	EW_{70}	EM_{70}
» 88 »		BW_{88}	EN_{88}	PE_{88}	EW_{88}	EM_{88}
42 - 70 »			EN_{R1}	PE_{R1}	EW_{R1}	EM_{R1}
71 - 88 »			EN_{R2}	PE_{R2}	EW_{R2}	EM_{R2}

1). BW_{54} was taken at 54 weeks instead of 50 weeks of age.

Where Y is a vector of observations, b is the vector of fixed effect, here it stands for housing effect (only one fixed effect involved), s and d are two random factors (sire and dam within sire), e is the residual random error and X, W, and W_2 denote the incidence matrices for b, s and d, respectively.

Some assumptions were made as follows:

$E(Y) = Xb$, $E(s) = 0$, $E(d) = 0$, $E(e) = 0$, $Var(s) = I\sigma^2_s$, $Var(d) = I\sigma^2_d$, $Var(e) = I\sigma^2_e$, $Cov(s, d) = 0$, $Cov(s, e) = 0$, and $Cov(d, e) = 0$.

An ANOVA table (as Table 2) was used for calculating the different variance components. The interpretation of the observational components of variance in the above sib analysis is summarized in Table 3.

Both sire and dam components contain one-quarter of the additive genetic variation. The dam component also contains one-quarter of the dominance variance and the common environment variance. The heritabilities and genetic correlations were estimated from sire, dam and combined sire and dam components of variances and covariances using Harvey's LSMLMW programme (Harvey 1987). The formulae used for calculating the parameters and their standard errors were given by Harvey (1987).

Table 2. The ANOVA table used for the hypothesis testing and estimation of variance components

Source	Sum of squares[1)]	E(MS)
Sire	R(μ,s,H)-R(μ,H)	$\sigma^2_e + k_2\sigma_d^2 + k_3\sigma_s^2$
Dam:sire	R(μ,s,d,H)-R(μ,s,H)	$\sigma^2_e + k_1\sigma_d^2$
Housing	$\hat{B}'Z^{-1}\hat{B}$(adj. for s d effects)	$\sigma^2_e + Q(H)$
Progeny	y'y -R(μ,s,d,H)	σ^2_e

1) H = effect of housing system.
$\hat{B}'$ = a row vector of soultion for the effect of housing system.
Z = a square segment of the inverse of the least-squares coefficient matrix for a particular set of effects.
R( ) = reduction in sum of squares from fitting models containing different parameters.

Table 3. Observational components and their interpretation

Observational components		Covariance and causal components estimated
Total:	$\sigma^2_T = \sigma^2_s + \sigma^2_d + \sigma^2_e = V_P$	$= V_A + V_D + V_{Ec} + V_{Ew}$
Sires:	$\sigma^2_s = Cov_{HS}$	$= 1/4V_A$
Dams:	$\sigma^2_d = Cov_{(FS)} - Cov_{(HS)}$	$= 1/4V_A + 1/4V_D + V_{Ec}$
Progeny:	$\sigma^2_e = V_P - Cov_{(FS)}$	$= 1/2V_A + 3/4V_D + V_{Ew}$
Sires + dams:	$\sigma^2_s + \sigma^2_d = Cov_{(FS)}$	$= 1/2V_A + 1/4V_D + V_{Ec}$

RESULTS

Population mean and variation

Table 4 gives the sample means and standard deviations for the traits studied. The age at sexual maturity was 147.4 days with a standard deviation of 8.4 days. Body weights at 42, 54, 70 and 88 weeks of age were not particularly different from each other, which means that body weight in the whole production period changed very little with time.

Table 4. Means and standard deviations of the traits of concern

Length of record time	Trait				
	BW(g)	EN	PE(%)	EW(g)	EM(kg)
To 42 weeks	2079±173	116.3±11.2	79.2±6.9	55.1±2.7	6.49±0.65
» 50 »		155.3±14.7	76.6±7.0	56.9±2.7	8.83±0.85
» 58 »	2090±203[1)]	193.1±19.5	74.6±7.4	58.2±2.7	11.24±1.15
» 70 »	2073±203	246.3±27.7	71.8±8.0	59.5±2.7	14.68±1.69
» 88 »	2108±230	309.0±40.8	65.7±8.6	60.9±2.9	18.70±2.53
42-70 »		130.2±20.8	66.4±10.6	63.0±2.9	8.19±1.28
71-88 »		62.9±18.3	49.8±14.5	63.7±3.0	4.03±1.20

1) BW was measured at 54 weeks instead of 58 weeks of age.

The numbers of eggs laid in the early part-period (until 42 weeks), the first residual period (42-70 weeks) and the second residual period (71-88 weeks) were 116.3, 130.2 and 62.9, respectively. The cumulative egg numbers to 70 and 88 weeks of age were 246.5 and 309.3. The results from the present study are not very different from the previous reports for this breed.

PE from sexual maturity to 42, 50, 58, 70 and 80 weeks of age decreased with increased control time. The individual egg production of hens was very poor after 70 weeks of age.

Average EW showed a stable increase throughout the period. The average EW in the early part-period (EW_{42}) was about 8 g lighter than that in the first residual period (EW_{R1}) and about 9 g lighter than that in the second (EW_{R2}).

EM is a synthetic trait made up of two component traits, EN and EW. EM was used to measure the total productivity of the hens. As seen in Table 4, EM from SM to 42, 50, 58, 70 and 88 weeks were 6.5, 8.8, 11.2, 14.7 and 18.7 kg, respectively.

It can be seen from Table 4 that EN, PE and EM in the residual periods showed much more variation than the same trait in the early part-periods.

Table 5. Heritability estimates and their standard error for all traits of interest

Trait	h^2_S	h^2_D	h^2_{S+D}
BW_{42}	.65 ± .12	.48 ± .11	.57 ± .06
BW_{54}	.59 ± .11	.36 ± .10	.48 ± .05
BW_{70}	.68 ± .11	.34 ± .10	.47 ± .05
BW_{88}	.46 ± .10	.12 ± .10	.29 ± .05
SM	.50 ± .10	.46 ± .11	.48 ± .05
EN_{42}	.23 ± .07	.54 ± .11	.38 ± .05
EN_{50}	.21 ± .07	.54 ± .11	.37 ± .05
EN_{58}	.20 ± .07	.55 ± .11	.37 ± .05
EN_{70}	.16 ± .07	.54 ± .11	.35 ± .05
EN_{88}	.15 ± .07	.41 ± .11	.28 ± .05
EN_{R1}	.14 ± .06	.45 ± .11	.30 ± .05
EN_{R2}	.18 ± .07	.11 ± .11	.14 ± .04
PE_{42}	.20 ± .07	.47 ± .11	.33 ± .05
PE_{50}	.24 ± .07	.49 ± .11	.36 ± .05
PE_{58}	.23 ± .07	.52 ± .11	.38 ± .05
PE_{70}	.19 ± .07	.51 ± .11	.35 ± .05
PE_{88}	.18 ± .07	.38 ± .10	.28 ± .05
PE_{R1}	.14 ± .06	.45 ± .11	.30 ± .05
PE_{R2}	.18 ± .07	.11 ± .11	.14 ± .05
EW_{42}	.52 ± .10	.21 ± .10	.37 ± .05
EW_{50}	.57 ± .10	.21 ± .10	.39 ± .05
EW_{58}	.62 ± .11	.28 ± .10	.44 ± .05
EW_{70}	.62 ± .11	.23 ± .10	.43 ± .05
EW_{88}	.60 ± .11	.23 ± .10	.40 ± .05
EW_{R1}	.59 ± .11	.24 ± .10	.41 ± .05
EW_{R2}	.54 ± .11	.24 ± .10	.39 ± .05
EM_{42}	.21 ± .07	.34 ± .10	.28 ± .05
EM_{50}	.23 ± .07	.38 ± .10	.31 ± .05
EM_{58}	.22 ± .07	.43 ± .11	.33 ± .05
EM_{70}	.16 ± .07	.48 ± .11	.32 ± .05
EM_{88}	.15 ± .06	.38 ± .10	.27 ± .05
EM_{R1}	.15 ± .06	.45 ± .10	.30 ± .05
EM_{R2}	.18 ± .07	.11 ± .10	.15 ± .04

Heritability

The heritability estimates for all the traits recorded are given in Table 5. All of them were significantly different from zero except the estimates for BW_{88}, EN_{R2}, PE_{R2} and EM_{R2} computed from dam components of variance.

SM High heritability estimates of SM are very often reported (e.g. 0.54 by Flock 1977, 0.42 by Kinney 1969, 0.44 by Kolstad 1972 and 0.49 by Chhikara et al. 1985). The heritability estimates in the present study (0.50, 0.46 and 0.48 for the sire, dam and sire plus dam components of variance, respectively) are therefore in agreement with those found in the literature.

BW As shown in most scientific papers, BW is a highly heritable trait. Our estimates are coincident with the reports in the literature. The heritabilities calculated from the dam components of variances are generally low compared with those from the sire components of variances for this traits (Table 5). Although the body weight at different ages did not dif-

fer very much, the estimates of heritability of BW decreased with age.

EN The heritability estimates for EN appeared to decrease as the control time progressed, although the decrease was not very pronounced. The heritability estimates for EN_{42}, EN_{50} and EN_{58} were found to be slightly higher than those for EN_{70} and EN_{88}. The estimated heritabilities of EN_{R1} and EN_{R2} from sire components were roughly the same as the estimates for EN_{70} and EN_{88}, while the estimate for EN_{R2} from the dam component was much lower than those for EN_{70}, EN_{88} and EN_{R1} (Table 5). With one exception (EN_{R2}), heritability estimates of EN at different ages from sire components are generally lower than those from dam components.

PE To some extent PE measures the same character as EN. It was, therefore, assumed that the heritability estimates for PE at the various control times should not be markedly different from those for EN at the same length of control time. The heritability estimates for PE from the sire components were somewhat lower than those from the dam components (Table 5).

EW Unlike EN and PE, the heritabilities for EW in different periods estimated from sire components were consistently higher than those from dam components. The estimates of heritability from sire components for EW at different periods ranged from 0.42 to 0.63, while those from dam components ranged from 0.21 to 0.25.

EM EM is a synthetic trait which contains the variation both from EN and EW. From the present study, it seems that EM is influenced more by EN than by EW. The heritability estimates for EM at the various periods were consistent with those estimates for EN (Table 5).

Genetic and phenotypic correlations

Only the correlations estimated from the sire components of variances will be presented and discussed. First, the correlations for the same trait measured at different ages are considered. Then, the correlations between different traits at certain ages are discussed.

The correlation of the same trait measured at different ages

As given in Table 6, the BW at different ages were highly correlated, both genetically and phenotypically.

The genetic and phenotypic correlations between EN at the different control times are given in Table 7. Both genetic and phenotypic correlations showed the

Table 6. Genetic correlation (above diagonal) and phenotypic correlation (below diagonal) between body weight at different ages

Trait	1	2	3	4
1. BW_{42}		.85	.95	.90
2. BW_{54}	.83		.97	.90
3. BW_{70}	.76	.79		1.00
4. BW_{88}	.67	.67	.72	

Table 7. Genetic correlation (above diagonal) and phenotypic correlation (below diagonal) between egg numbers at different ages

Trait	1	2	3	4	5	6	7
1. EN_{42}		.95	.87	.74	.40	.36	-.12
2. EN_{50}	.94		.98	.89	.56	.59	-.12
3. EN_{58}	.85	.95		.97	.72	.76	.08
4. EN_{70}	.73	.85	.94		.89	.90	.42
5. EN_{88}	.60	.73	.82	.92		.94	.90
6. EN_{R1}	.44	.63	.80	.93	.90		.67
7. EN_{R2}	.22	.30	.39	.52	.81	.57	

same pattern. The further apart the two control periods from each other, the lower the correlation between the EN in the two periods.

The genetic and phenotypic correlations between the early part-records (EN_{42}, EN_{50} and EN_{58}) and the annual record (EN_{70}) were high, and showed an increasing tendency with increasing length of the part control. This means that the accuracy of prediction of EN_{70} using part-record will increase as the control time is prolonged. The part-whole correlations of EN_{42}, EN_{50} and EN_{58} with EN_{88} were lower than those between the early part-records with EN_{70}. The EN in the first residual period (EN_{R1}) was not highly correlated with EN_{42}, but with EN_{58}, EN_{70} and EN_{88}. EN_{R2} was found to be negatively correlated with EN_{42} and EN_{50} genetically, although the correlations were low (approx. -0.10). The genetic correlation between EN_{R2} and EN_{58} was close to zero (0.08).

Table 8. Genetic correlation (above diagonal) and phenotypic correlation (below diagonal) between percent egg production at different ages

Trait	1	2	3	4	5	6	7
1. PE_{42}		.99	.98	.92	.69	.76	.13
2. PE_{50}	.93		.99	.94	.72	.82	.09
3. PE_{58}	.84	.95		.98	.81	.89	.23
4. PE_{70}	.72	.85	.94		.92	.96	.49
5. PE_{88}	.59	.72	.82	.92		.96	.81
6. PE_{R1}	.44	.65	.81	.94	.90		.66
7. PE_{R2}	.23	.32	.41	.53	.82	.57	

As can be seen in Table 8, all the correlations among the PE at different control periods were positive. Compared with the early part-record of EN, the early part-record of PE (PE_{42}, PE_{50} and PE_{58}) showed high part-whole correlation with PE_{70} and PE_{88}. For a single trait prediction, PE_{42}, PE_{50} and PE_{58} were equally good for predicting PE_{70} because of high genetic correlation among PE_{42}, PE_{50}, PE_{58} and PE_{70}. The PE in the first residual period (PE_{R1}) was also highly correlated with the early part-records (PE_{42}, PE_{50} and PE_{58}) genetically.

From the present data it can be concluded that the correlations (genetic and phenotypic) between PE_{R2} and the early part-records (PE_{42}, PE_{50} and PE_{58}) are very low, indicating that PE_{R2} cannot be sufficiently improved by selection on early part-record.

Average EW at different control periods was highly correlated, both genetically and phenotypically. The genetic correlation among average EW at different control periods ranged from 0.82 to 0.99, and the corresponding phenotypic correlations from0.52 to 0.97 (Table 9).

Although the variation in EM included the variation both from EN and EW, the patterns of the correlations among EM in the different control periods appeared to be the same as those for EN in different control periods. In general, there were high part-whole genetic and phenotypic correlations among EM in different control periods (Table 10). The only exception was for EM_{R2}, which was negatively related genetically with EM_{42} and EM_{50}. The genetic correlation between EM_{R2} and EM_{58} was negligible ($r_G = 0.06$).

Table 9. Genetic correlation (above diagonal) and phenotypic correlation (below diagonal) between egg weight at different ages

Trait	1	2	3	4	5	6	7
1. EW_{42}		.99	.98	.94	.92	.85	.82
2. EW_{50}	.97		.99	.97	.95	.89	.89
3. EW_{58}	.94	.98		.99	.98	.94	.93
4. EW_{70}	.88	.94	.98		.99	.98	.92
5. EW_{88}	.81	.88	.92	.97		.98	.96
6. EW_{R1}	.66	.78	.86	.93	.93		.93
7. EW_{R2}	.52	.74	.81	.72	.87	.76	

Table 10. Genetic correlation (above diagonal) and phenotypic correlation (below diagonal) between egg mass at different ages

Trait	1	2	3	4	5	6	7
1. EM_{42}		.98	.91	.82	.87	.44	-.15
2. EM_{50}	.94		.97	.91	.97	.67	-.11
3. EM_{58}	.86	.95		.98	1.00	.80	.06
4. EM_{70}	.72	.83	.93		1.00	.91	.34
5. EM_{88}	.57	.68	.79	.91		.92	.77
6. EM_{R1}	.43	.61	.78	.94	.89		.57
7. EM_{R2}	.15	.26	.35	.49	.81	.54	

Comparison of the correlations between traits at different ages

In Tables 11 and 12 the genetic and phenotypic correlations between different traits in the same control period are presented. The genetic correlation between SM and EN varied from -0.51 at 42 weeks of age to 0.42 in the R1 period. SM was

Table 11. Genetic correlation between different traits at the same age

Trait	Age (weeks)[1)]						
	42	50	58	70	88	R1	R2
SM with							
EN	-.51	-.24	-.07	.08	.26	.42	.33
PE	.24	.29	.32	.36	.42	.42	.33
EW	.38	.36	.35	.34	.35	.25	.37
Em	-.24	.04	.19	.34	.50	.60	.42
EN with							
PE	.87	.86	.92	.96	.98	1.00	1.00
EW	-.38	-.32	-.33	-.41	-.37	-.43	-.26
EM	.72	.70	.72	.69	.76	.79	.95
PE with							
EW	-.13	-.13	-.18	-.29	-.28	-.39	-.33
EM	.72	.75	.75	.74	.81	.79	.95
EW with							
EM	.36	.46	.44	.38	.32	.25	-.03

1). R1 = First residual period
R2 = Second residual period

Table 12. Phenotypic correlation between different traits at the same age

Trait	Age (weeks)[1)]						
	42	50	58	70	88	R1	R2
SM with							
EN	-.41	-.33	-.27	-.20	-.13	-.04	.00
PE	.08	.01	-.02	-.03	-.02	-.04	.00
EW	.25	.23	.22	.20	.18	.08	.09
EM	-.30	-.21	-.17	-.13	-.07	-.01	-.02
EN with							
PE	.88	.94	.97	.99	.99	1.00	1.00
EW	-.20	-.21	-.21	-.24	-.22	-.23	-.15
EM	.89	.88	.90	.92	.94	.95	.98
PE with							
EW	-.07	-.13	-.16	-.21	-.20	-.23	-.15
EM	.81	.86	.89	.92	.94	.95	.98
EW with							
EM	.25	.28	.24	.15	.12	.08	.03

1). R1 = First residual period
R2 = Second residual period

negatively correlated with EN_{42}, EN_{50} and EN_{58}, but positively with EN_{70}, EN_{88}, EN_{R1} and EN_{R2}. It should be pointed out that the high negative genetic correlation between SM and EN_{42} is reasonable because the length of the control period up to 42 weeks of age is strongly dependent on age at sexual maturity. This dependency will be weakened as the length of the control period increases.

The genetic correlation between SM and PE was positive and showed an increasing trend as the length of the control period increased. The genetic correlation between SM and EW changed very little with age (ranging from 0.25 to 0.38). The genetic correlation between SM and BW was not high (around 0.20). The genetic correlations between SM and EM showed a trend similar to the correlations between SM and EN, which were from moderate negative to strong positive.

EN was highly correlated with PE, both genetically and phenotypically, in all periods (from 0.87 to 1.00), but negatively correlated with EW. The genetic correlation between EN and EW was about -0.4, while the phenotypic correlation was about -0.2. EN was found to be very little correlated with BW. EN and EM, on the contrary, were highly correlated, both genetically and phenotypically.

Compared with EN, PE was less negatively correlated with EW, especially in the early part control period. The genetic correlation between PE and EW in the early period was about -0.15, but increased to -0.39 in the first residual period, while the corresponding phenotypic correlations between PE and EW were lower. PE was found to be slightly more highly correlated with BW than EN in the early periods. The genetic and phenotypic correlations between PE and EM were very high, especially in the second residual period. In the same period, the correlation between PE and EM was nearly the same as that between EN and EM.

EW was positively correlated with BW, although the correlation was not very high ($r_G = 0.18 - 0.34$, $r_P = 0.22 - 0.28$). The genetic correlation between EW and EM was moderate except for that

between EW_{R2} and EM_{R2}, which was close to zero. BW and EM were found to be positively correlated, genetically and phenotypically. The genetic correlation of these two traits ranged from 0.19 to 0.41, while the phenotypic correlation ranged from 0.02 to 0.20.

Comparison of part-whole correlations for the different early part criteria

For the purpose of convenience, the traits recorded at 70 weeks, 88 weeks, R1 and R2 periods are called target traits which will be improved. The correlations between early part EN, PE and EM with different target traits are presented in Table 13. Generally, the correlation between early part-record and the target trait increased as length of the early part-record increased. The target traits recorded at 70 weeks of age (EN_{70}, PE_{70} or EM_{70}) had the highest correlation with the early part-record, while the target traits recorded in the R2 period (EN_{R2}, PE_{R2} or EM_{R2}) had the lowest correlation with the early part-record - even negative correlation appeared.

For the same early part-period, PE was found to be more highly correlated with target traits than EN or EM if the target traits were EN or PE. However, the early EM had a higher correlation

Table 13. Part-whole and part-residual correlations for traits of special interest

	At 42 weeks			At 50 weeks			At 58 weeks		
	EN_{42}	PE_{42}	EM42	EN_{50}	PE_{50}	EM_{50}	EN_{58}	PE_{58}	EM_{58}
r_G:									
EN_{70}	.74	.91	.55	.89	.92	.61	.97	.95	.66
EN_{88}	.40	.67	.21	.56	.69	.30	.72	.79	.42
EN_{R1}	.36	.76	.25	.59	.82	.45	.76	.89	.57
EN_{R2}	-.12	.13	-.25	-.12	.09	-.24	.08	.23	-.08
PE_{70}	.54	.92	.44	.76	.94	.57	.88	.98	.67
PE_{88}	.30	.67	.18	.50	.72	.31	.68	.81	.45
PE_{R1}	.36	.76	.25	.59	.84	.45	.76	.89	.57
PE_{R2}	-.12	.13	-.25	-.13	.09	-.24	.08	.23	-.08
EM_{70}	.40	.73	.82	.60	.77	.91	.68	.74	.98
EM_{88}	.11	.53	.87	.31	.57	.97	.48	.64	1.00
EM_{R1}	.13	.64	.44	.36	.68	.67	.52	.73	.80
EM_{R2}	-.19	.13	-.15	-.19	.07	-.11	.02	.20	.06
r_P:									
EN_{70}	.73	.69	.64	.85	.83	.73	.94	.93	.83
EN_{88}	.60	.58	.73	.72	.69	.82	.82	.82	.71
EN_{R1}	.44	.45	.37	.63	.65	.54	.80	.81	.70
EN_{R2}	.22	.23	.15	.30	.32	.23	.39	.41	.32
PE_{70}	.67	.72	.59	.81	.85	.71	.92	.94	.82
PE_{88}	.56	.59	.48	.69	.72	.59	.80	.82	.70
PE_{R1}	.44	.44	.37	.63	.65	.54	.80	.81	.70
PE_{R2}	-.22	.23	.15	.30	.32	.23	.39	.41	.32
EM_{70}	.64	.63	.72	.77	.77	.83	.87	.87	.93
EM_{88}	.52	.53	.57	.65	.66	.68	.75	.76	.79
EM_{R1}	.39	.41	.43	.59	.61	.61	.75	.77	.78
EM_{R2}	.19	.21	.15	.27	.30	.26	.36	.38	.35

with EM_{70}, EM_{88}, EM_{R1} and EM_{R2} than the early EN or early PE did. In fact, EN_{R2}, PE_{R2} or EM_{R2} were scarcely improved through indirect selection of either of the early recorded traits because none of the early recorded traits was highly correlated with EN_{R2}, PE_{R2} or EM_{R2} (Table 13).

DISCUSSION

Until recently, the estimation of variance-covariance components from animal breeding data has relied almost exclusively on Henderson's (1953) methods for unbalanced mixed models. Method 3, especially, has been widely used, greatly aided by the availability of a 'general purpose' computer program tailored towards the estimation of genetic parameters (Harvey 1975). Interest has grown in Maximum Likelihood (ML) and related procedures which yield estimators with more desirable properties (Harville 1977). The restricted maximum likelihood, developed by Patterson & Thompson (1971), has become accepted as the preferred method of estimating variance-covariance components in animal breeding. The minimum norm quadratic unbiased estimation (MINQUE) of variance-covariances was suggested by Rao (1971). Kennedy (1981) has summarized the properties of these four different procedures (ANOVA, ML, REML and MINQUE) and discussed their advantages and disadvantages.

Meyer (1986) presented a computing strategy for estimating variance-covariance components by REML when only one random factor (sires) was included in the model.

Colleau et al. (1989) compared the REML estimates of genetic parameters with Henderson's method 3 for the type traits of Normande cattle breed. It has been found that the difference between Henderson's method 3 and REML estimates and their sampling errors were very small (Colleau et al. 1989). For the balanced data, Henderson's method 3 and REML yield the same estimators (Kennedy 1981). Although ML, REML and MINQUE procedures are available in some general statistical computer package (e.g. procedure VARCOMP in SAS), these are often not suitable for the analysis of large data sets from animal breeding programmes.

The complicated algorithm and considerable computational demand of REML has restricted its applications, especially for multivariate analysis or models with more than one random factor. The data from poultry breeding is relatively balanced compared with the data from other livestock. Taking both accuracy of estimating and computational demand into account, Henderson's method 3 is more practical than the other methods (REML, ML, etc.) and therefore was used in the present study to estimate the variance-covariance components.

The housing effect was not significant for all the traits studied except EN_{42} and EM_{42}. Therefore, no correction has been made for the housing effect. The second residual period (R2 period, from 70 to 88 weeks of age) was used in this study to check the egg production persistency after the ordinal production period. It was found that the percent production in R2 was very low (lower than 50%) and there were large variations in PE_{R2}, indicating that there is no economic advantage in keeping hens for such a very long period unless the production persistency can be improved.

As shown in Table 5, BW and EW were highly inheritable, and the heritability estimates for these traits did not change very much from period to period. The heritability estimates for EN, PE and EM in the various periods were very close. In general, the heritability estimates for EN, PE and EM in the earlier part periods (at 42, 50 and 58 weeks) were slightly higher than those at 70 weeks, 88 weeks, and in the R1 and R2 periods. The recorded heritability estimates of egg production (EN or PE) varied, depen-

ding on the population from which the estimates were calculated. The recorded heritability estimates for EN in the early part-period (about 40 weeks of age) ranged from 0.20 to 0.60 (Kinney 1969, Kolstad 1972, Kolstad 1980, Foster 1981 and Chhikara et al. 1985). The heritability estimate for this trait in the present study was within this range. The recorded heritability estimate for annual egg production (usually EN till 500 days of age) was lower than that for early part production, most of which were between 0.1 and 0.2 from sire component of variance (Bohren et al. 1970, Gowe et al. 1973, Emsly et al. 1977 and Chhikara et al. 1985). Our results are in good agreement with those reports. There are a few reports on heritability estimates for EM. According to Waring et al. (1962), Kolstad (1979) and Jain & Roberts (1980), the heritability estimates for EM at different ages were quite close to that for egg number. A similar result was obtained from the present study.

Generally, the heritability estimates from sire component of variance were lower than those from dam component of variance for the same trait in this study. The dam component of variance, in addition to containing a quarter of the additive genetic variance, also contains a quarter of dominance variance and whole maternal environmental effect, so it is reasonable that the dam component of variance was larger than the sire component of variance. EW seemed to be an exception - the heritability estimate of this trait from sire component was higher than that from the dam component. A satisfactory explanation for this needs more information.

Both the genetic (r_G) and the phenotypic (r_P) correlations between part-record and full record for the same trait were high, while the corresponding genetic and phenotypic correlations between part and residual record were relatively lower. It was observed that the part-full correlation increased as duration of the part-record increased, and that the correlation (both r_G and r_P) between the measures in two adjacent periods was higher than that in two remote periods. The higher part-full genetic correlation as increased duration of the part-record suggested that to use a longer part-record would increase selection efficiency provided that the generation interval could be kept the same. This is specially true when the early part EN is used as a selection criterion. It is worth noting that the genetic correlations between the measurements (EN, PE and EM) in the R2 period and in earlier part-periods (42, 50 and 58 weeks of age) were very low or even negative, which indicates that selection on the early part-record could not sufficiently improve the production in the R2 period regardless of whether EN_{R2}, PE_{R2} or EM_{R2} was chosen to be improved. One of the purposes of this experiment was to explore the method of improving egg production after the normal production period (R2 period). From the result of the present study, this seemed not to be very promising because of the low genetic correlation.

The genetic correlation between SM and EN varied depending on the duration of the record time for EN. As reported in the literature, there was high negative genetic correlation between SM and EN_{42} (-0.51). So selection based on EN_{42} can lead to a decrease in SM. This is a desirable change only if the age at sexual maturity is not early. The genetic correlation between SM and EN_{70} was very low (0.08), indicating that the hens with earlier sexual maturity will not necessarily give higher annual production. The only explanation for this is probably that the hens which started to lay earlier had lower persistency in the later period of production. The situation was quite different concerning the genetic correlation between SM and PE. These two traits had moderate positive correlation no matter which production period was considered.

EW was found to be negatively correlated with EN and PE of early part, full and residual production. This is in agree-

ment with the results reported by Abplanalp (1951), Jerome et al. (1956), Waring et al. (1962) and Jain & Roberts (1980). The negative genetic correlation between EW and EN was higher than that between EW and PE, indicating that selection based on early EN would decrease EW more than would selection on early PE. Considering the negative genetic correlation between EW and EN or PE, Waring et al. (1962), Bo' ren (1970) and Jain & Roberts (198(suggested using EM as a selection criterion.

The genetic correlation between EM and EN or PE at different record time was about 0.80, which was twice as high as that between EM and EW. This indicates that EM was more influenced by EN and PE than by EW. A similar result was also reported by Kolstad (1980) and Jain & Roberts (1980).

Early part-record of egg production (EN or PE) has commonly been used in egg layer breeding to improve annual production under two conditions: (1) high genetic correlation between part and full production; (2) shorter generation interval. There is no doubt about the effectiveness of selection for the early part-record. However, no direct comparison of realized genetic gains in annual EN or annual PE from selection based on early part EN and on early part PE are available. Most comparisons have been based on the relevant genetic parameter estimates. Fairfull & Gowe (1990) found, according to their long-term selection results, that the "early-EN-selected" strains had greater gain in early EN than the "early-PE- selected" strains and vice versa. They also found that the "early-EN-selected" strains had increasingly earlier SM but showed no significant improvement in PE from the same long-term selection during 1971-1980, while two of the "early-PE-selected" strains had significantly later SM and, therefore, the early EN in these strains did not change significantly despite the improvement in early PE (Gowe & Fairfull 1980, 1986). According to the results in the present study, early PE was correlated more highly with EN_{70}, EN_{88}, EN_{R1}, PE_{70}, PE_{88}, PE_{R1}, EM_{70}, EM_{88} and EM_{R1} than early EN. This suggests that early PE could be a better selection criterion for improving annual or residual part production. After analysing the result from a 5-generation selection experiment, Flock (1977) found that early rate of production could be a better predictor of total EN because of its higher correlation with production in the residual period. The genetic correlations of EM_{70}, EM_{88}, and EM_{R1} with early EM were found to be higher than those with early part EN or early part PE. As duration of the part-record increased, the genetic correlation between early EN and whole or residual EN, PE and EM increased dramatically. However, the genetic correlation of early PE with whole or residual EN, PE and EM did not increase greatly as length of the part-record increased (Table 13).

SUMMARY

1. The heritability estimates for SM, BW and EW were very high (0.50-0.70), while those for EN, PE and EM were relatively lower (0.14-0.24). In the same period, the heritability estimates for EN, PE and EM were almost the same. As the duration of the period increased, the heritability estimates of EN, PE and EM tended to decrease slightly.

2. The heritability estimate from the sire component of variance was always lower than that from the dam component of variance for all the traits except EW and BW.

3. In most situations, if not all, the genetic correlations were higher than the phenotypic correlations. The genetic and phenotypic correlation between the measures of BW during different periods was very high (r_P: 0.67-0.83, r_G: 0.8-1.0). For EW measured in the different periods, the genetic correlation ranged from 0.82 to 0.99 and the phenotypic ones from 0.66

to 0.98. The genetic correlation between part and full record for EN, PE and EM showed the same increased trend with increased duration of the part record. The genetic correlation between part and full record was higher than that between part and residual record for the same trait. There was very low or even negative correlation between early part and the second residual record, which indicates that egg production in the second residual period cannot be sufficiently improved by selection based on early part record. Compared with EN and EM, PE showed higher part-full and part- residual correlation, both genetic and phenotypic.

4. With the exception of the correlation between SM and EN, the genetic and phenotypic correlation for each pair of traits did not change greatly from period to period. In particular, the correlations between SM and PE, SM and EW, EN and PE, EN and EM and PE and EM were identical from period to period.

5. For single trait prediction, the early part-record of PE could be the best predictor of the full or residual record of EN and PE, while the early part-record of EM could be the best predictor of the full or residual record of EM. The accuracy of prediction for the full or residual record from early part-record will increase as the length of the part-record is increased.

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Effects of different environments and selection for persistency in laying hens

IV. Efficiency of different alternative selection methods for improving egg production persistency

LUN JUN MOU & NILS KOLSTAD
Agricultural University of Norway, Department of Animal Science, Ås, Norway

Mou. L.J. & N. Kolstad 1990. Effects of different environments and selection for persistency in laying hens. IV. Efficiency of different alternative selection methods for improving egg production persistency. Norwegian Journal of Agricultural Sciences 4: 289–303. ISSN 0801-5341.

In this study, different alternative selection methods for improving egg production persistency in laying hens were explored. A selection index was constructed for improving egg production using percent egg production or egg mass instead of egg number. It was shown that it is possible to use the different traits in the index and in the aggregate genotype. The selection efficiency can be greatly increased by extending the conventional early part-record to 58 weeks of age without increasing generation interval where percent egg production and egg weight are concerned in the indexes and aggregate genotypes. Effects of relative economic values, family size and excluding different sources of information on selection efficiency are also discussed.

Key words: Egg production, laying hens, persistency, selection efficiency, selection index.

Lun Jun Mou, Department of Animal Science, Macdonald College of McGill University, 21, 111 Lakeshore Road, Ste. Anne de Bellevue, P.Q, Canada H9X 1C0.

For some time now significant genetic improvement has been obtained in egg production, and it seems likely that this improvement will continue because of the still appreciable genetic variation in most of the traits of economic importance. According to Kolstad (1983), the annual genetic gain for Norwegian Leghorn was 0.31 g for egg weight (EW), 1.41 for egg number (EN) and 0.17 kg for egg mass (EM) to 500 days of age. The genetic gains for age at sexual maturity (SM) and body weight (BW) were -1.31 days and 12.2 g, respectively. Maijala (1984), on reviewing the recent reports on genetic progress in egg production, found that, on average, number of eggs per hen had increased by two eggs, hen-day egg production by 1%, EM by 0.2 kg per hen per year, while SM decreased by one day a

Abbreviations used in this work: BW = body weight, EM = egg mass, EN = egg number, EW = egg weight, PE = percent egg production, R1 = residual period, SM = age at sexual maturity.

year. Kashyap et al. (1981) reported that average annual genetic gain was 2.9 eggs per hen housed to 72 weeks of age and 0.5% hen-day egg production.

Egg production to a certain age can be measured as (1) number of eggs, (2) percent egg production (PE) or rate of lay, and (3) egg mass, which is the product of egg number and egg weight. The selection for egg production is almost exclusively based on the early part-record in order to keep a one-year generation interval.

The importance of a short generation interval in poultry breeding to maximize genetic improvement per unit of time was emphasized some time ago by Dickerson & Hazel (1944). Dempster & Lerner (1947) proposed use of the early partial egg record as a selection criterion for improving annual production. The hypothesis was made that maximum gain in annual egg production per unit of time could be made by selecting on the basis of partial egg records. The loss in accuracy with selection based on the part-time records was shown to be more than compensated for by the advantage of a shorter generation interval. Further confirmation of higher relative selection efficiency by using part-time records was presented by Lerner & Cruden (1948), Maddison (1954) and Morris (1956), based on parameter estimates from different populations. The reports from Erasmus (1962) and Van Vleck & Doolittle (1964) also provided additional support for the hypothesis. The result was that selection on the basis of part-time records became widely accepted.

Serious doubts as to the validity of using part-time records to improve annual production were raised by Morris (1963, 1964), Gowe & Strain (1963), Gowe (1970) and Gowe (1974), based on their long-term selection experiments. According to these reports, selection based on early part-records might not necessarily lead to improvement in total egg production. Exclusive reliance on early part-records may only decrease SM at the expense of production persistency.

There are a number of reports dealing with the relative efficiency of different selection criteria, but unfortunately, the comparisons are almost entirely based on single trait selection, not on a multi-trait selection index which is commonly used in poultry breeding today.

The objectives of the present study are: (1) to explore the alternative selection methods for improving egg production persistency using selection index theory, (2) to compare the efficiency of different selection methods, and (3) to devise a practical selection procedure for improving egg production persistency.

MATERIAL AND METHODS

A population of egg layers was established at the Department of Animal Science, Agricultural University of Norway, for a selection experiment to improve egg production persistency (Kolstad & Mou 1990). The data used in the present study were from the second generation of that parent population. The routine management, recording system and estimation of parameters are described in detail by Kolstad & Mou (1990), Mou & Katle (1990) and Mou (1990).

Egg production persistency may be defined as the average weekly or monthly egg production after the peak production, or the number of weeks in production until the flock has to be replaced at, say, 60% production (Flock 1980). In the present study the production persistency is defined as either PE up to 70 or 88 weeks of age, or PE in the residual period (from 42 to 70 weeks of age). High production in the later production period implies high persistency. The percent production is measured on an individual level and can be used as a selection criterion.

The general selection index (I) and the aggregate genotype or net merit (H) are defined as follows:

$$I = \sum_{i=1}^{m} b_i x_i = b'x \qquad (1)$$

$$H = \sum_{i=1}^{n} v_i y_i = v'y \qquad (2)$$

where

$x = (x_1\ x_2 \ldots\ x_m)$ = a row vector of m known phenotypic values

$y = (y_1\ y_2 \ldots\ y_n)$ = a row vector of n unknown genotypic values

$b' = (b_1\ b_2 \ldots\ b_m)$ = a row vector of m partial regression coefficients to be computed

$v' = (v_1\ v_2 \ldots\ v_n)$ = a row vector of n known relative economic values for the traits involved

The following relationships exist from the above definition:

$$\sigma^2_I = b'Pb \qquad (3)$$

$$\sigma^2_H = v'Cv \qquad (4)$$

$$\sigma_{IH} = b'Gv \qquad (5)$$

where:

P is an m x m matrix of phenotypic variance-covariances between m traits in I,

C is an n x n matrix of genotypic variance-covariances between n traits in H and

G is an m x n matrix of genotypic covariances between m traits in I and n traits in H.

When the same traits are included in I and H, C and G are identical. Note that the number of traits (m) in I could be equal to, greater than or smaller than the number of traits (n) in H. Even totally different traits can be involved in I and H if the correlations are known among these traits. The index coefficients, i.e. the b vector needed to construct the selection index, are derived such that the correlation between I and H is a maximum or that $\Sigma(H-I)^2$ is a minimum. The following system equation is used for the solution of b:

$$Pb = Gv \quad \text{or}$$
$$b = P^{-1}Gv \qquad (6)$$

The selection index used in poultry breeding for female and male candidates can be written as follows:

$$I\,♀♀ = b'x = \sum_{i=1}^{m} [b_{i1}(P_{i1} - P_i) + b_{i2}(P_{i2} - P_i) + b_{i3}(P_{i3} - P_i)] \qquad (7)$$

$$I\,♂♂ = b'x = \sum_{i=1}^{m} [b_{i2}(P_{i2} - P_i) + b_{i3}(P_{i3} - P_i)] \qquad (8)$$

where:

m is the number of traits,

b_{ij} is the partial regression coefficient of the *ith* trait on the index for female and male, respectively ($i = 1, 2, \ldots, m$; $j = 1, 2, 3$ for ♀♀ or $j = 2,3$ for ♂♂),

P_{i1} is a female breeding candidate's phenotypic value for the *ith* trait,

P_{i2} is average phenotypic values for the *ith* trait of full-sisters of a female or male breeding candidate, respectively,

P_{i3} is average phenotypic values for the *ith* trait of half-sisters of a female or male breeding candidate, respectively, and

P_i is the population mean for the *ith* trait.

When selection is based on I, the genetic gain of the aggregate genotype (ΔH) is

$$\Delta H = b_{HI}(\bar{I}_S - \bar{I}_\mu) \qquad (9)$$

$$= r_{IH}\, i\, \sigma_H \qquad (10)$$

where $\bar{I}_S$ and $\bar{I}_\mu$ are the mean index values of the selected individuals and the whole population, respectively, and i is

the selection intensity (i.e. $i = (\bar{I}_S - \bar{I}_\mu)/\sigma_I$).

The genetic gain in H is proportional to r_{IH}. The genetic gain in the *ith* trait in H due to selection based on I is:

$$\Delta G_i = g_i' b(i/\sigma_I) \qquad (11)$$

where g_i' is the *ith* row of the genotypic variance-covariance matrix G.

The most useful measure of the efficiency of the index is the correlation between the index (I) and the aggregate genotype (H), r_{IH}, since the total genetic gain is directly proportional to this correlation. The relative importance of each trait in the index can, therefore, be measured by the reduction in r_{IH} which would result from omitting that particular trait from the index. If the trait contributes little to the efficiency, it may be deleted from the index even if it is a trait of economic importance.

In the present study, early part-records of PE up to 42, 50 or 58 weeks of age were used in the index to compare the relative selection efficiency, while the record up to 70, 88 weeks of age or the record in the residual period (42-70 weeks) were included in the different aggregate genotypes (Fig. 1). Owing to the negative correlation between PE and EW, early part-records of EM were also used to compare the relative selection efficiency.

Six different indices were developed which could be divided into two groups according to similar component traits. Group A includes I_1, I_2 and I_3, in which PE and EW are concerned in addition to SM and BW, while Group B includes I_4, I_5 and I_6, in which EM is concerned in addition to SM and BW. Six aggregate genotypes are also grouped correspondingly. Each index can be used for improving each of the six different aggregate genotypes, so there are $6 \times 6 = 36$ different combinations of selection indices and aggregate genotypes. All selection

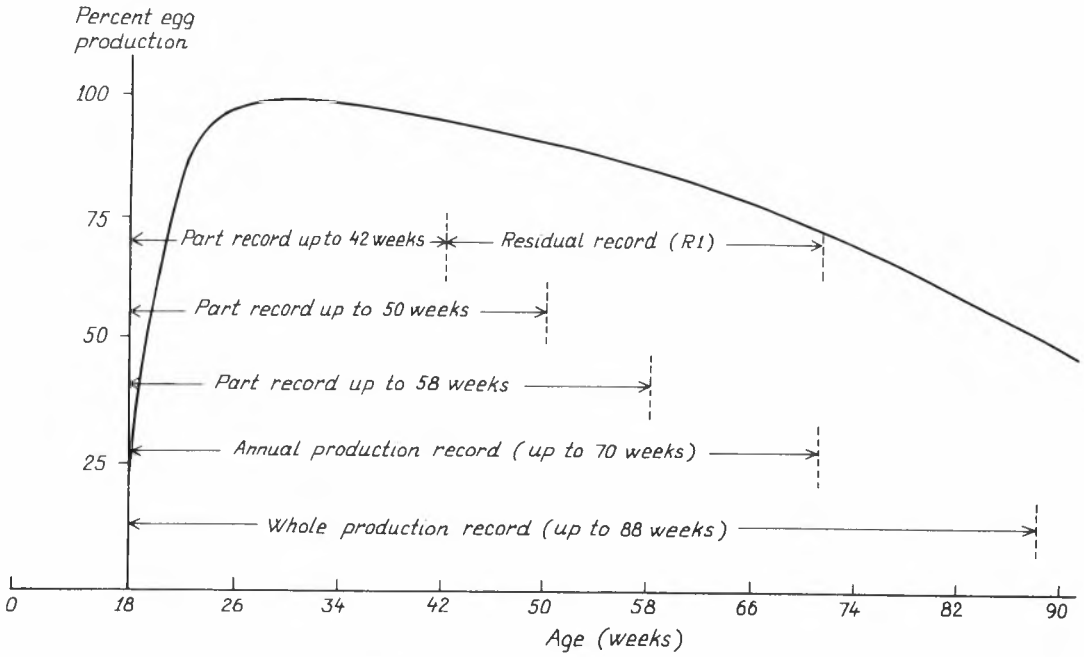

Fig. 1 Graphical demonstration of the alternative selection criteria

Table 1. Definition of different indices and aggregate genotypes

Group	Index	Traits included 1), 2)				
A	I_1	SM	BW_{42}	EW_{42}	PE_{42}	
A	I_2	SM	BW_{42}	EW_{42}	PE_{50}	
A	I_3	SM	BW_{42}	EW_{42}	PE_{58}	
B	I_4	SM	BW_{42}	EM_{42}		
B	I_5	SM	BW_{42}	EM_{55}		
B	I_6	SM	BW_{42}	EM_{58}		
	Aggregate genotype					
A	H_1	SM	BW_{42}	EW_{42}	PE_{70}	
A	H_2	SM	BW_{42}	EW_{42}	PE_{88}	
A	H_3	SM	BW_{42}	EW_{42}	PE_{42}	PE_{R1}
B	H_4	SM	BW_{42}	EM_{70}		
B	H_5	SM	BW_{42}	EM_{88}		
B	H_6	SM	BW_{42}	EM_{42}	EM_{R1}	

1). SM = Age at sexual maturity (days)
BW = Body weight taken at 42 weeks of age (hg)
EW = Egg weight at 42 weeks of age (g)
EM = Egg mass (kg)
PE = Percent egg production
2). The subscripts denote the age in weeks, and R1 means the first residual period (42-70 weeks).

indices and aggregate genotypes are listed in Table 1 together with the traits included in each case.

The performance of the breeding candidate, its full-sib mean performance and its half-sib mean performance are used in the selection index. This may be referred to as a family selection index. For example, a female index I_1 and H_1 can be written as follows:

$$\begin{aligned} I_1 = b'x = {} & b_1SM_i + b_2BW_{42i} \\ & + b_3EW_{42i} + b_4PE_{42i} \\ & + b_5SM_f + b_6BW_{42f} \\ & + b_7EW_{42f} + b_8PE_{42f} \\ & + b_9SM_h + b_{10}BW_{42h} \\ & + b_{11}EW_{42h} + b_{12}PE_{42h} \end{aligned} \quad (12)$$

$$\begin{aligned} H_1 = v'y = {} & v_1SM_G + v_2BW_{G42} \\ & + v_3EW_{G42} + v_4PE_{G70} \end{aligned} \quad (13)$$

where subscripts i, f and h denote individual, full-sib and half-sib records, expressed as the deviation from the population mean, v_1, v_2, v_3 and v_4 are relative economic values and subscript G denotes genotypic value. The male index is similar to the female one except that there is no individual own record.

Cunningham's (1968) program SELIND, with some modification (Pettersen & Sehested 1985), was used for computing the general index and reduced index with the excluding model. The family size used was 4 and 24 for full-sib and half-sib families, respectively. The relative economic values for each trait were calculated according to the price in 1989 using the method described by Kolstad (1975). The correlation between index and aggregate genotype (r_{IH}) and the genetic gain for each trait (ΔGi) were used as criteria for evaluating the selection indices. The selection intensity (i) used in calculating the expected genetic gains was 1.4. In the calculation processes, different economic values were tried in order to balance the gain of each component trait.

The relative selection efficiency (RE)

of two selection indices was measured by the ratio of the genetic gains in H (ΔH) achieved by using the different indices, a and b, using the following formula:

$$RE = \Delta H^a / \Delta H^b = (r^a_{IH} \; i \; \sigma_H)/(r^b_{IH} \; i \; \sigma_H) = r^a_{IH}/r^b_{IH} \quad (14)$$

where ΔH^a and ΔH^b are the genetic gain of H by using index a or b, r^a_{IH} and r^b_{IH} are correlations between index a or b and H, and the other symbols used are as defined before.

RESULTS

The genetic and phenotypic parameters used to compute the b-values were estimated from the present population (Mou 1990). Heritabilities, genetic and phenotypic standard deviations and relative economic values are listed in Table 2 and genetic and phenotypic correlations in Table 3.

Table 2. Heritabilities, genetic and phenotypic standard deviations, and relative economic values

Trait	h^2	σ_P	σ_G	v
SM, days	0.50	8.4	5.94	-0.50
BW_{42}, hg	0.65	1.7	1.37	-0.50
EW_{42}, g	0.53	2.7	1.97	1.50
PE_{42}, %	0.20	6.9	3.09	0.40
PE_{50}, "	0.24	7.0	3.43	-----
PE_{58}, "	0.23	7.4	3.55	-----
PE_{70}, "	0.19	8.0	3.48	1.00
PE_{88}, "	0.18	8.6	3.65	1.40
PE_{RI}, "	0.14	10.6	3.97	0.60
EM_{42}, kg	0.21	0.7	0.32	4.50
EM_{50}, "	0.23	0.9	0.43	-----
EM_{58}, "	0.22	1.2	0.56	-----
EM_{70}, "	0.16	1.7	0.68	4.50
EM_{88}, "	0.15	2.5	0.97	4.50
EM_{RI}, "	0.15	1.3	0.50	4.50

Table 3. Genetic (above diagonal) and phenotypic correlations (below diagonal) used in the construction of the indices

Trait	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1. SM, days		0.26	0.38	0.24	0.29	0.32	0.36	0.42	0.42	-0.24	0.04	0.19	0.34	0.50	0.60
2. BW_{42}, hg	0.09		0.27	0.25	0.27	0.30	0.27	0.18	0.27	0.29	0.30	0.37	0.38	0.29	0.40
3. EW_{42}, g	0.25	0.26		-0.13	0.09	0.10	-0.11	-0.13	-0.10	0.36	0.14	0.13	0.51	0.42	0.47
4. PE_{42}, %	0.10	0.09	-0.08		0.99	0.98	0.92	0.69	0.76	0.72	0.70	0.75	0.73	0.53	0.64
5. PE_{50}, "	0.01	0.11	0.11	0.93		0.99	0.94	0.72	0.82	0.62	0.75	0.77	0.77	0.57	0.68
6. PE_{58}, "	-0.02	0.11	0.11	0.84	0.95		0.98	0.81	0.89	0.56	0.66	0.75	0.77	0.64	0.73
7. PE_{70}, "	-0.03	0.10	-0.14	0.72	0.85	0.94		0.92	0.96	0.44	0.57	0.67	0.74	0.73	0.65
8. PE_{88}, "	-0.02	0.08	-0.15	0.59	0.72	0.82	0.92		0.96	0.18	0.31	0.45	0.59	0.81	0.80
9. PE_{RI}, "	-0.04	0.09	-0.13	0.44	0.65	0.81	0.94	0.90		0.25	0.45	0.57	0.67	0.78	0.79
10. EM_{42}, kg	-0.29	0.17	0.14	0.81	0.78	0.71	0.59	0.48	0.37		0.98	0.91	0.82	0.87	0.44
11. EM_{50}, "	-0.21	0.20	0.20	0.78	0.86	0.81	0.71	0.59	0.70	0.94		0.97	0.91	0.97	0.67
12. EM_{58}, "	-0.17	0.21	0.21	0.73	0.84	0.89	0.82	0.70	0.70	0.86	0.95		0.98	1.00	0.80
13. EM_{70}, "	-0.12	0.19	0.15	0.63	0.77	0.87	0.92	0.80	0.88	0.72	0.83	0.93		1.00	0.91
14. EM_{88}, "	-0.07	0.16	0.16	0.53	0.66	0.76	0.86	0.94	0.85	0.57	0.68	0.79	0.91		0.92
15. EM_{RI}, "	-0.01	0.16	0.08	0.41	0.61	0.77	0.89	0.85	0.95	0.43	0.61	0.78	0.94	0.89	

The correlations between index and aggregate genotype, r_{IH}

The correlations between different indices and their aggregate genotypes are listed in Table 4. In general, the correlations are high. Most of the correlation

Table 4. Correlations between different indices and alternative aggregate genotypes

Index	Aggregate genotype					
	H_1	H_2	H_3	H_4	H_5	H_6
Group A:						
I_1	0.628	0.577	0.578	0.629	0.501	0.633
I_2	0.683	0.623	0.652	0.633	0.544	0.646
I_3	0.731	0.681	0.708	0.610	0.559	0.653
Group B:						
I_4	0.655	0.592	0.612	0.640	0.753	0.614
I_5	0.594	0.612	0.586	0.652	0.750	0.659
I_6	0.467	0.557	0.595	0.661	0.730	0.683

coefficients are about 0.65. Two points are worth noting from the results in Table 4. First, for the indices in Group A, the correlation between the indices and the aggregate genotypes increases with prolongation of the part-record. The same conclusion cannot be drawn for the indices in Group B. Secondly, the indices in Group A have, as expected, higher correlation with H_1, H_2 and H_3 than with H_4, H_5 and H_6 and vice versa for the indices in Group B.

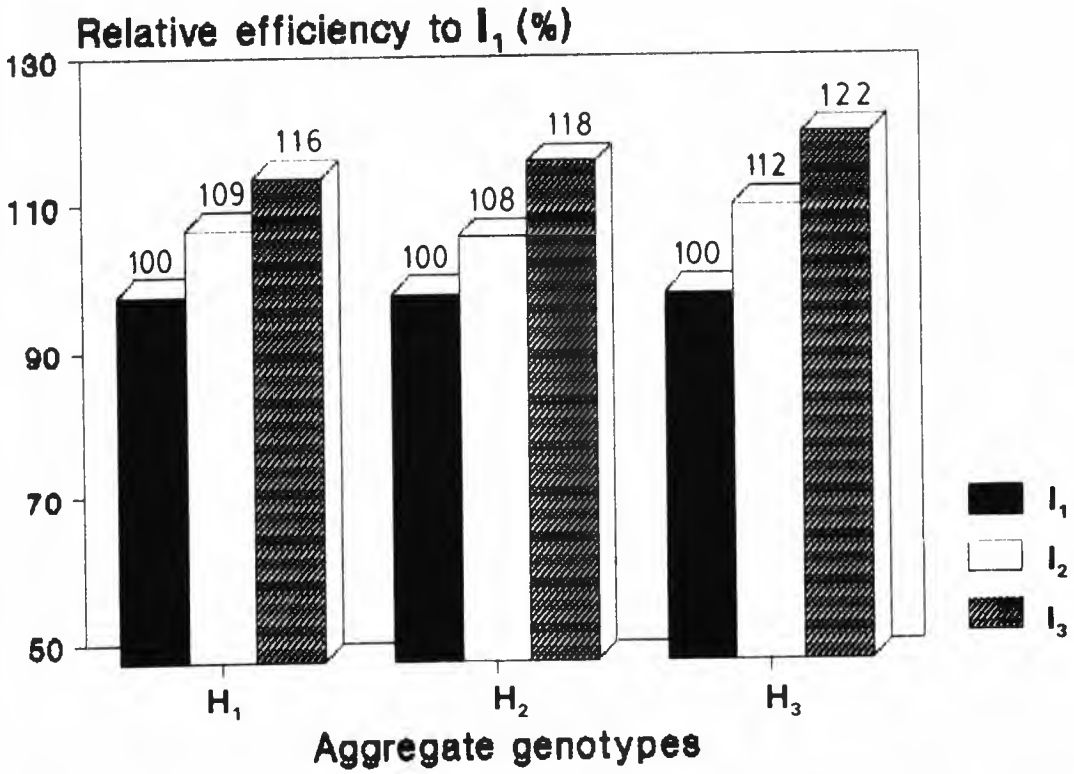

Fig. 2. Relative selection efficiency of I_1, I_2 and I_3 for improving different aggregate genotypes.

Table 5. Expected genetic gains of different aggregate genotypes and their component traits when PE and EW are intended to be improved

Aggr. gent.[1)]	ΔH NOK	Expected gain of each trait (ΔGi) SM days	BW_{42} hg	EW_{42} g	PE_{70} %	PE_{88} %	PE_{42} %	PE_{R1} %
From female index I_3:								
H_1	2.95	-0.81	0.17	0.92	1.25			
H_2	3.08	1.30	0.22	0.72		1.98		
H_3	2.87	-0.74	0.18	0.95			1.08	1.29
From male index I_1:								
H_1	2.20	-1.03	0.11	0.71	0.67			
H_2	1.88	0.52	0.14	0.66		0.88		
H_3	2.21	-1.26	0.08	0.69			0.23	0.81
Total:								
H_1	2.58	-0.92	0.14	0.82	0.96			
H_2	2.48	0.91	0.18	0.69		1.43		
H_3	2.54	-1.00	0.13	0.82			0.66	1.05

1). Aggr. gent. = Aggregate genotype

Comparison of the selection efficiency when PE and EW are intended to be improved

Taking the selection efficiency of I_1 as 100%, the relative efficiencies of the different indices in Group A are shown in Fig. 2. Compared with I_1, I_3 is 16%, 18% and 22% more effective in improving H_1, H_2 and H_3, respectively.

In the last three lines in Table 5, total genetic gain for the different aggregate genotypes and their component traits is the average genetic gain from selection of males (by using I_1) and females (by using I_3). For one round of selection, SM will decrease by about one day for H_1 and H_3 and will increase by about one day for H_2. BW will increase slightly in all three aggregate genotypes (about 15 g). The genetic gain of EW in H_2 is a little lower than that in H_1 and H_3, but this will be compensated by the higher genetic gain in percent production.

As seen from Table 5, the total expected genetic gain of H_1 and H_3 and the corresponding component traits do not differ greatly, indicating that whether or not the annual production (PE_{70}) is divided into two parts, PE_{42} and PE_{R1}, it does not affect the expected total genetic gain and the genetic gain of each component trait.

If the aggregate genotype includes PE_{88} instead of PE_{70}, the total genetic gain will be larger, but this genetic gain would certainly take a longer time to realize. It should be pointed out that the expected gain for SM is positive in H_2, that is, SM will increase. It has been found that decreasing the positive change in SM by giving higher negative economic value to this trait will slow down the genetic gain for EW and PE. The compromise is to maximize the genetic gain for EW and PE while controlling the positive change in SM within an acceptable range.

In order to maintain a one-year generation interval, the males have to be evaluated by using male index I_1. The genetic gains from selection of males are lower compared with those from selection of females, partly because the earlier part-record (up to 42 weeks) is used, and partly because the males do not have

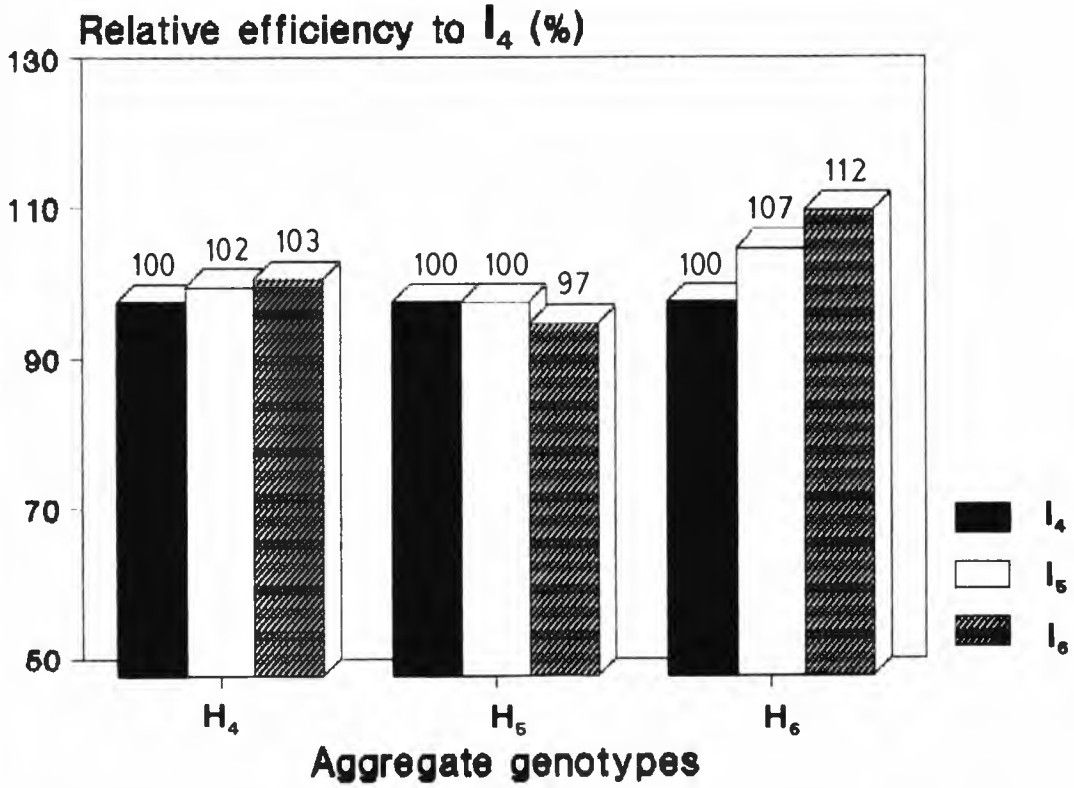

Fig. 3. Relative selection efficiency of I_4, I_5 and I_6 for improving different aggregate genotypes.

their own records and the evaluation of their breeding values is entirely reliant on their sibs' records.

To make the genetic gains of PE and EW in H_1, H_2 and H_3 comparable with the genetic gains of EM in H_4, H_5 and H_6, the genetic gains of PE and EW in H_1, H_2 and H_3 were converted into the corresponding gains of EM. The converted genetic gains of EM for one round of selection are 467, 564 and 456 g for H_1, H_2 and H_3, respectively. When judged by unit of time the converted expected genetic gain of EM in H_2 was not as high as that in H_1 and H_3.

Comparison of the selection efficiency when EM is intended to be improved

The comparison of the selection efficiencies of the different indices in Group B is shown in Fig. 3, taking the selection efficiency of I_4 as 100%. Unlike the indices in Group A, an increase in length of the early part-record did not lead to a proportional increase in the selection efficiency. In improving H_4 and H_5, the efficiencies of three indices (I_4, I_5 and I_6) were very similar, but in improving H_6, I_6 is still 12% more effective than I_4.

For this group of indices, the economic advantage of prolonging the early part-record was not as significant as for the indices in Group A. So, it was decided to use index I_4 for improving H_4, H_5 and H_6. The expected genetic gains for the different aggregate genotypes and their component traits are presented in Table 6. The total gain is the mean of the genetic gain from the selection of females and males equally weighed.

In order to improve the aggregate genotypes H_4 and H_6, the genetic gain of

Table 6. Expected genetic gains of different aggregate genotypes and their component traits when EM is intended to be improved

Aggr. gent.[1]	ΔH NOK	Expected gain of each trait (ΔGi) SM days	BW_{42} hg	EM_{70} kg	EM_{88} kg	EM_{42} kg	EM_{R1} kg
From female index I_4:							
H_4	2.23	-0.51	0.16	0.49			
H_5	3.84	1.88	0.20		0.96		
H_6	2.13	-0.60	0.30			0.22	0.26
From male index I_4:							
H_4	1.90	-0.47	0.11	0.42			
H_5	3.25	1.32	0.12		0.80		
H_6	1.80	-0.56	0.21			0.22	0.18
Total:							
H_4	2.07	-0.49	0.14	0.46			
H_5	3.55	1.60	0.16		0.88		
H_6	1.97	-0.58	0.26			0.22	0.22

1). Aggr. gent. = Aggregate genotype

SM was about -0.5 days per generation, which is desirable. BW increased slightly. The genetic gain of EM was about 500 g per generation. The genetic gain of H_5 was much higher than H_4 and H_6 (Table 6). The genetic gain of EM_{88} in this aggregate genotype was close to 900 g per generation. However, SM would increase by 1.5 days per generation.

Effect of change in relative economic values on selection efficiency

To test the effect of the changes in relative economic value on selection efficien-

Table 7. Effects of change in economic values on σ_H and r_{IH}

Relative economic values SM	BW_{42}	EW_{42}	PE_{70}	σ_I	σ_H	r_{IH}
0.00	-0.16	1.38	1.00	2.75	4.09	0.67
-0.10	»	»	»	2.69	3.80	0.71
-0.25	»	»	»	2.32	3.51	0.66
-0.50	»	»	»	2.12	3.50	0.61
-1.00	»	»	»	3.29	5.01	0.66
0.00	-0.10	»	»	3.03	4.12	0.74
»	-0.20	»	»	2.98	4.07	0.73
»	-0.50	»	»	2.84	3.95	0.72
»	-1.00	»	»	2.69	3.84	0.70
»	-1.50	»	»	2.66	3.86	0.69
»	-2.00	»	»	2.74	3.96	0.69
»	-0.10	0.50	»	2.44	3.47	0.70
»	»	1.00	»	2.71	3.76	0.72
»	»	1.50	»	3.15	4.26	0.74
»	»	»	0.50	2.48	3.21	0.77
»	»	»	1.50	4.09	5.67	0.72
»	»	»	2.00	5.15	7.21	0.71

cy (based on r_{IH}), I_3 and H_1 were used in the simulation. In Table 7, different sets of relative economic values have been tried. The general conclusion is that changing the relative economic values in a certain range does not greatly affect the correlation between index and aggregate genotype, but it does affect the variance of index and aggregate genotype. If higher negative economic weight is given to SM and BW, r_{IH} will decrease slightly.

Taking σ_H, r_{IH} and percent gain of each component trait into account, the following relative economic values were chosen:

Trait	Relative economic value
SM	-0.50
BW_{42}	-0.50
EW_{42}	1.50
PE_{42}	0.40
PE_{R1}	0.60
PE_{70}	1.00
PE_{88}	1.40
EM_{42}	4.50
EM_{R1}	4.50
EM_{70}	4.50
EM_{88}	4.50

Effect of family size on selection efficiency

Family size will influence the selection efficiency. In order to find the sufficient number of families and sufficient number of individuals in each family, different family sizes were tried using I_3 and H_1. It was found that selection efficiency increased as the family size increased until the family size reached 10 full-sib families of 10 full sibs each. No further increase in selection efficiency was obtained after that point. Taking the selection efficiency of 10 full-sib families of 10 full sibs each as 100%, the relative selection efficiencies for various family sizes are shown in Figs. 4 and 5.

The number of full sibs in each full-sib family is more important than numbers of full-sib families for the female index (Fig. 4). Even with two full-sib families of two full sibs in each family, the relative efficiency is still 93% (Fig. 4). Increasing the number of full-sib families does not increase the selection efficiency as greatly as increasing the number of birds in each full-sib family. Actually, when the total of members in each full-

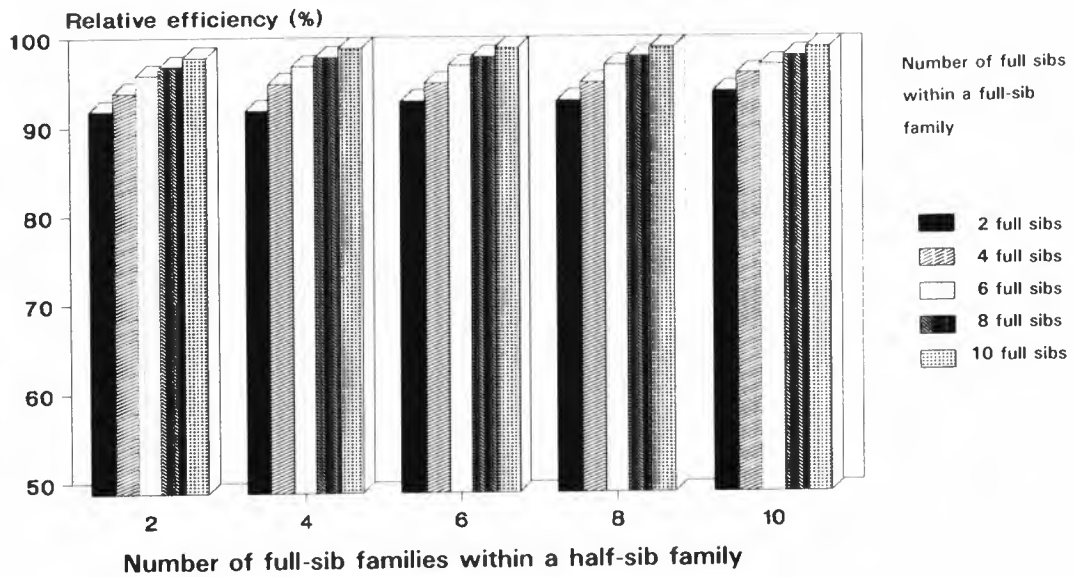

Fig. 4. Relative selection efficiency of various full-sib and half-sib family sizes to 10 full-sib families of 10 full sibs each (female index)

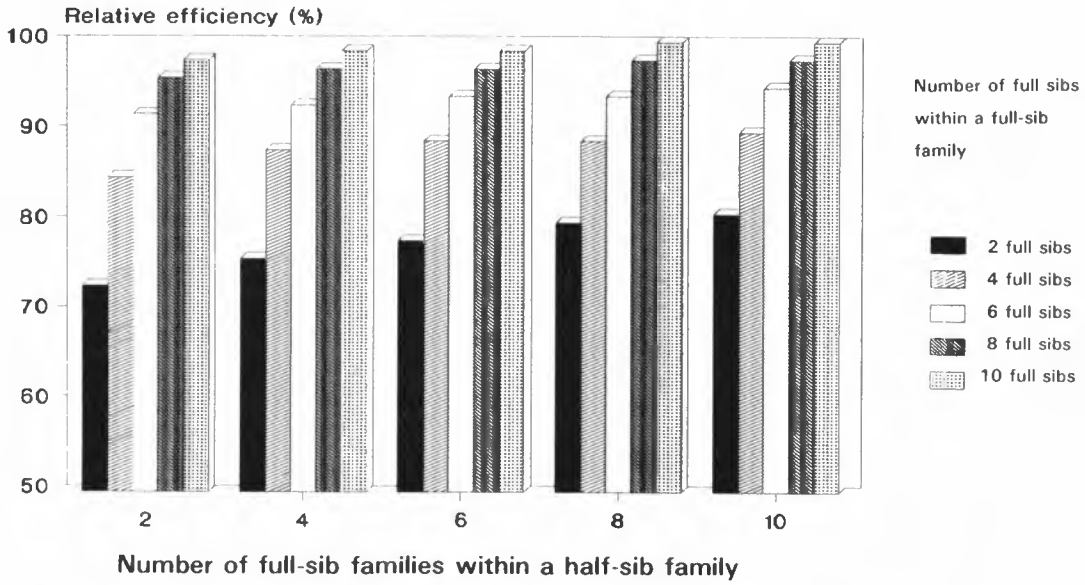

Fig. 5. Relative selection efficiency of various full-sib and half-sib family sizes to 10 full-sib families of 10 full sibs each (male index)

sib family is equal to or more than six, increasing the number of full-sib families gives very little change in the selection efficiency (Fig. 4). So, a sufficient number of full-sib families seems to be four and the number of birds in each full-sib family to be six (i.e. 4 X 6 = 24 is sufficient in a half-sib family, on average).

The rate of increasing selection efficiency by increasing family size is relatively higher for the male index than that for the female index. With two full-sib families of two full sibs each, the efficiency is only 73%. Eight full-sib families of eight full sibs each appeared to be sufficient for the male index (Fig. 5).

Effect of excluding some sources of information on selection efficiency

The relative selection efficiencies for the different reduced indices are given in Table 8. The efficiency of the full index (I_{i+f+h}, index in which individual record, full-sib means and half-sib means are included) is assumed to be 100%. Excluding the half-sib mean performance from I_{i+f+h} only decreases the efficiency by 2% and excluding the full-sib mean performance decreases the efficiency by 4%. If the individual record is used solely, selection efficiency is just 90%. The selection efficiency of the index including only full- and half-sib mean performance (I_{f+h}) is 74%, while the efficiencies of the index only including full-sib or half-sib mean performances alone are 68% and

Table 8. Comparison of the relative efficiencies of indices when different sources of information are omitted

Index [1]	σ_I	σ_H	r_{IH}	RE (%) [2]
I_{i+f+h}	3.15	4.26	0.74	100
I_{i+f}	3.08	4.26	0.72	98
I_{f+h}	3.01	4.26	0.71	96
I_i	2.84	4.26	0.67	90
I_f	2.13	4.26	0.50	68
I_h	1.75	4.26	0.41	55
I_{f+h}	2.33	4.26	0.55	74

1) Subscripts i, f and h in the index denote individual record, full-sib mean performance and half-sib mean performance, respectively.
2) RE = Relative efficiency

55%, respectively. Generally, individual, full-sib and half-sib records are obtained simultaneously, so I_{i+f+h} is preferable. However, for the selection of males, only I_{f+h} can be used, and the efficiency is just 3/4 compared with I_{i+f+h}.

DISCUSSION

In current poultry selection programmes, the early part-records of EN up to about 40 weeks of age are used in the selection index. Early PE was found to be more closely correlated genetically with production persistency or total EN up to 70 or 88 weeks than was early EN (Bohren 1970, Flock 1977, 1980, Foster 1981, Mou 1991). Gowe & Fairfull (1984) reported that the part-record PE (to 273 days) selection was more effective in improving full-record EN (to 497 days), full-record PE and residual-record PE than the part-record EN (to 273 days) selection, and that selection for EN reduced sexual maturity much more than selection for PE. Traditionally, the selection index includes SM, BW_{40}, EW_{38} and EN_{42}. It might place too much emphasis on the early sexual maturity in such an index because EN_{42} is also greatly dependent on SM. It is preferable to use part-record PE as a selection criterion to improve annual production.

Practically all selection programmes in egg production are carried out on an annual cycle owing to the practical convenience of the operation. The accuracy of predicting whole egg production from part-records is greatly dependent upon the part-whole genetic correlation. As reported in other literature, the part-whole genetic correlation increases as duration of the part-record increases. Use of multi-stage selection or retrospective selection to improve annual egg production is reported in several papers. Singh & Mohanty (1985) reported that the genetic correlation between residual and whole production was higher than that between early part and whole production. They found that selection efficiency could be greatly increased by retrospectively selecting more hens than were needed as parents based on part-records and subsequently rejecting the excess progeny on the complete annual production records, as compared with selection based on part-records alone.

In the present study, if I_3 is used in a selection programme instead of I_1, the total improvement in H_1 and H_3 will increase by about one-sixth and one-fifth, respectively. Obviously, I_3 should be used where PE and EW are concerned in addition to SM and BW. Using index I_1 for males and I_3 for females, the expected genetic gain of SM, EW and PE_{70} in H_1 for one round of selection will be -0.9 days, 0.8 g and 0.96%, respectively. The results presented in this study are similar to the report by Flock (1980), in which an annual progress of 1.2% in rate of lay and -0.8 days in SM were achieved in the Lohmann Cuxhaven Leghorn breeding programme for the period from 1965 to 1971. Even though the expected gain of PE_{88} in H_2 in the present study is high, the increase in SM could be a serious drawback. Dividing the annual record (PE_{70}) into two parts, PE_{42} and PE_{R1}, does not seem to increase the genetic gain of annual production.

In this study, it was found that the selection efficiency could be greatly increased by using the part-record PE up to 58 weeks of age instead of to 42 weeks of age. To maintain a one-year generation interval, the selection could be arranged as follows: (1) selecting males on their sibs' part-record up to 42 weeks (using male index I_1); (2) mating all hens at the same time as the selection based on early record at 42 weeks of age; (3) keeping the part-record up to 58 weeks of age; (4) selecting the progeny based on dams' performance at 58 weeks (using female index I_3). The first batch of chickens can be hatched when the hens are about 52 weeks of age, which makes a generation interval of around one year.

Since percent production is negative-

ly correlated with EW (both phenotypically and genetically), it was suggested that EM might be a better selection criterion (Waring et al. 1962, Hicks 1963, Bohren 1970, Renganathan et al. 1979). It was found in the present study that extending the part-record from 42 to 58 weeks does not increase the selection efficiency significantly when EM is included in an index instead of PE and EW. So the conventional part-records to 42 weeks were used to predict the expected genetic gain. Compared with other reported results (i.e. Maijala 1984), the expected genetic gain of EM seems to be very high when the indices in Group B are used. In particular, when H_5 is used, the expected gain of EM_{88} could be about 900 g per generation. However, one-and-a-half days increase in SM in H_5 is undesirable. SM would increase in this aggregate genotype possibly because of the very high positive genetic correlation between SM and EM_{88}. As mentioned earlier, the positive increase in SM could be slowed down by giving higher negative economic value to this trait, but the total genetic gain and the genetic gain of EM_{88} would then be lower. Although it is not known how well the realized genetic gains will match with the expected ones, this may be an excellent opportunity for the poultry breeders to reconsider their selection programmes.

In conclusion, the following are summarized:

1. The early part-record of PE and EM can be used in the indices for efficiently improving either the annual production or the prolonged production up to 88 weeks of age.

2. Extending the early part-record from 42 to 58 weeks of age will greatly increase the genetic gain without increasing the generation interval when PE and EW are considered in addition to SM and BW in the indices and the aggregates.

3. When EM is used instead of PE and EW in the index, extending the part-record from 42 to 58 weeks of age will not bring further advantages for improving either the annual or the prolonged EM up to 88 weeks of age.

4. Although changing the relative economic values in a certain range did not greatly affect the selection efficiency and total genetic gain, the genetic gains of the component traits might vary substantially depending on the relative economic values used.

5. A sufficient number of full-sib families in each half-sib family would seem to be four and the number of individuals in each full-sib family to be six for the female index. The corresponding figures for the male index are eight and eight.

6. Excluding full-sib or half-sib means from a full index, I_{i+f+h}, will not decrease the selection efficiency greatly. The selection efficiency of an index including only full-sib and half-sib means is just 74% of a full index.

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Evaluation of the feeding value of fresh forages, silage and hay using near infrared reflectance analysis (NIR)

I. A comparison of different methods for predicting the nutritive value

NILS PETTER KJOS
Agricultural University of Norway, Department of Animal Science, Ås, Norway

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Various Norwegian meadow crops were harvested at different cuts and preserved as fresh herbage, silage and hay. The chemical composition and nutritive value of the samples were determined by wet chemistry, *in vitro* or *in vivo* procedures and near infrared reflectance analyses (NIR). The regressions of *in vivo* organic matter digestibility (OMD) on different measurements of the nutritive value were calculated. The best agreements were found between *in vivo* OMD and *in vitro* digestibility of dry matter (IVDMD), the combination of crude protein (CP), acid detergent fibre (ADF) and lignin (ADL), and the combination of ADF and ADL. The NIR-predicted ADF content also gave a good agreement. Netural detergent fibre (NDF) in addition to ADF and ADL gave no further improvements in the regressions. The NIR-predicted values for CP, digestible crude protein (DCP), crude fibre (CF) and IVDMD were in less agreement with *in vivo* OMD than the values determined according to traditional analytical methods. For NDF and ADF, the situation was the opposite. When good laboratory routines exist, NIR-predicted values are expected to be slightly less correlated with digestibility than the values determined according to wet chemistry.

Key words: Chemical composition, feeding value, fresh herbage, hay, *in vivo* digestibility, *in vitro* DMD, meadow crops, near infrared reflectance analysis, silage.

Nils Petter Kjos, Agricultural University of Norway, Department of Animal Science, P.O. Box 25, N-1432 Ås-NLH, Norway

A good knowledge of the nutritive value of forages is important in both research and advisory work. One of the most common procedures for evaluating the nutritive value of feedstuffs is the determination of *in vivo* digestibility. Since this

method is both expensive and laborious, however, simpler and more rapid techniques for forage evaluation are being developed. Amongst these are methods relating to chemical composition (crude protein (CP), crude fibre (CF), forage fibre analysis according to van Soest), different microbial methods (ruminal *in vitro* procedures, enzymatic techniques), and physical methods (near infrared reflectance spectroscopy (NIR), nuclear magnetic resonance spectroscopy). Degradation characteristics obtained by means of nylon bags incubated in the rumen *(in sacco)* is also an interesting method.

In advisory work it is of great importance to obtain the results of the analyses quickly. In such situations NIR has given promising results for predicting the nutritive value of forages, with the best results for chemical composition.

In this study, the predictions of the *in vivo* organic matter digestibility (OMD) of fresh herbage, silage and hay made from different chemical constituents, ruminal *in vitro* procedures or NIR were compared using regressions of the actual data obtained from *in vivo* experiments on the different estimates.

MATERIALS AND METHODS

Forage samples

In 1985 and 1986, samples of the most common meadow crops taken from different locations in Norway were collected. The different crops were grown in pure cultures and were harvested at different maturity stages. The majority of the samples were harvested one week prior to heading (early cut), or at flowering (late cut). The average time-lag between early and late cut was 34 days. In addition there were some samples harvested at heading (normal cut), and some samples of regrowth (second cut). The crops were preserved in three different ways: as frozen fresh herbage, as silage and as barn-dried hay. The different forage samples, irrespective of location and year of harvest, are given in Table 1.

Chemical analysis

Dry matter (DM), ash, CP, ether extract (EE), CF and N-free extracts (NFE) were determined according to the Weende method (A.O.A.C. 1980). Neutral detergent fibre (NDF), acid detergent fibre (ADF) and lignin (ADL) were determined according to Goering & Van Soest (1970). *In vivo* digestibility of the different nutrients was determined in digestibility experiments with sheep from which digestible crude protein (DCP), fattening feed unit (FU) and metabolizable energy (ME) were calculated. For the calculations of FU, crude fibre deductions of 1.0 kcal/g for fresh herbage and 1.5 kcal/g for hay were used. FU in silage was calculated using the value number of 0.80. ME was calculated according to the equation

$$ME\ (kJ/kg\ DM) = 15.9 \times DXP + 37.7 \times DXL + 13.8 \times DXF + 14.6 \times DXX$$

where DXP, DXL, DXF and DXX indicate content of digestible CP, EE, CF and NFE, respectively (van der Honing et al. (1977). The *in vitro* digestibility of dry matter (IVDMD) was determined according to the method described by Tilley & Terry (1963). All analyses were run in duplicate, and the results are given as mean values.

NIR analysis

The NIR analyses for CP, DCP, CF, IVDMD and FU were carried out using a Technicon 500 monocromator, with separate broad-based calibration equations for fresh herbage, silage and hay. These equations are described by Kjos (1990). Samples for these NIR analyses were dried at 60°C and milled through a 1.0 mm aperture screen in a Christy & Norris hammermill. NIR analyses of NDF and ADF were performed by means of a Neotec 6350 monocromator at Pennsylvania State University, USA, using a broad-based calibration equation

Table 1. Chemical composition of the material in this study

		Dry matter	Ash	Crude protein	Ether extract	Crude fibre	N-free extracts	NDF	ADF	ADL	n
		%	% of dry matter								
FRESH HERBAGE											
Meadow grass	Early cut	18.5	9.5	29.2	3.3	22.7	35.3	54.2	23.9	11.7	2
(Poa pratensis)	Normal cut	16.6	7.2	18.7	3.6	30.7	39.8	51.5	28.4	13.8	1
	Late cut	23.8	7.3	13.1	2.6	35.0	42.0	67.4	37.8	12.9	2
Meadow fescue	Early cut	16.5	10.8	23.0	3.5	25.2	37.6	47.2	27.5	11.1	3
(Festuca pratensis)	Normal cut	16.5	11.0	15.9	2.8	32.6	37.7	64.9	37.5	10.1	2
	Late cut	25.2	8.0	12.0	2.2	33.4	44.4	64.4	37.0	12.0	2
	Second cut	16.9	12.4	14.8	3.6	29.0	40.2	57.9	35.0	10.5	1
Cocksfoot	Early cut	16.7	11.4	28.1	3.6	22.2	34.7	56.6	22.7	12.5	1
(Dactylis glomerata)	Late cut	17.4	6.9	13.2	2.3	37.4	40.2	65.0	38.2	15.3	1
Smooth bromegrass	Early cut	15.1	10.4	25.7	3.0	26.1	34.8	60.4	30.3	8.5	2
(Bromus inermis)	Late cut	30.9	6.4	9.6	2.6	32.3	49.1	62.0	36.3	12.0	2
Timothy	Early cut	18.1	8.9	21.7	3.1	23.9	42.4	61.1	29.2	11.1	2
(Phleum pratense)	Normal cut	17.5	5.7	12.0	2.3	37.1	42.9	74.8	41.1	12.9	1
	Late cut	27.6	6.7	9.8	2.4	34.6	46.5	66.9	37.8	15.7	2
	Second cut	11.5	9.6	22.6	4.3	29.6	33.9	61.7	32.8	9.2	1
Rye grass	Early cut	15.1	11.0	35.5	5.4	17.4	30.7	43.6	23.4	11.1	2
(Lolium perenne)	Late cut	18.6	5.7	11.1	3.3	32.9	47.0	61.5	36.6	13.4	2
Red clover	Early cut	14.2	14.9	26.2	3.5	17.0	38.4	40.1	25.7	12.4	2
(Trifolium pratense)	Late cut	18.5	9.8	19.1	2.7	25.5	42.9	49.0	33.0	21.0	2
Meadow fescue/	Early cut	19.1	9.4	17.8	3.1	27.8	41.9	57.7	30.2	9.4	1
Timothy	Normal cut	15.1	8.6	17.2	2.6	35.8	35.8	71.9	41.3	12.2	1
	Second cut	16.1	15.5	16.1	3.1	28.0	37.3	60.4	36.6	12.9	1
SILAGE											
Meadow grass	Early cut	18.6	9.2	23.2	8.4	23.2	36.0	40.0	26.9	9.7	2
	Normal cut	21.4	8.9	16.8	5.1	30.4	38.8	52.1	31.1	9.8	1
	Late cut	25.0	7.1	9.5	4.0	33.6	45.8	65.4	38.3	12.4	2
Meadow fescue	Early cut	17.0	10.0	23.4	9.2	24.3	33.1	42.7	26.9	8.3	3
	Late cut	22.5	8.1	10.8	3.4	34.4	43.3	62.8	38.3	12.1	3
Cocksfoot	Early cut	19.4	10.8	24.2	6.2	23.7	35.1	42.6	27.4	9.5	1
	Late cut	18.5	5.9	12.5	4.9	36.2	40.5	64.0	39.7	13.3	1
Smooth bromegrass	Early cut	17.3	10.2	21.9	6.4	28.6	32.9	48.9	32.1	7.9	2
	Late cut	27.6	6.5	9.5	3.2	33.7	47.1	62.0	37.8	15.1	2
Timothy	Early cut	19.0	10.5	20.0	6.4	23.7	39.4	46.7	30.6	9.2	3
	Normal cut	20.4	6.9	10.8	3.9	34.3	44.1	62.6	36.2	9.0	1
	Late cut	24.1	6.6	8.1	3.2	38.0	44.2	72.5	43.9	16.6	3
Rye grass	Early cut	16.7	11.0	29.0	12.1	20.2	27.7	35.9	25.6	9.9	2
	Late cut	18.4	5.7	10.3	4.1	35.7	44.2	63.6	39.7	12.9	2

Table 1. Chemical composition of the material in this study

		Dry matter	Ash	Crude protein	Ether extract	Crude fibre	N-free extracts	NDF	ADF	ADL	n
		%	% of dry matter								
Red clover	Early cut	19.4	13.9	21.6	5.9	19.0	39.6	34.6	28.7	12.2	2
	Late cut	19.7	8.4	15.9	4.0	27.5	44.2	47.4	36.5	16.8	2
HAY											
Meadow grass	Early cut	88.7	8.6	22.9	3.4	23.8	41.3	55.1	25.9	13.5	2
	Late cut	88.2	6.7	11.1	2.2	36.0	44.0	71.4	38.7	17.4	2
Meadow fescue	Early cut	84.5	10.6	23.7	3.7	25.1	36.9	54.8	26.7	11.4	2
	Late cut	84.4	7.9	10.5	1.9	36.7	43.0	68.9	38.5	12.1	2
Cocksfoot	Early cut	90.3	10.2	27.2	4.1	23.6	34.9	52.5	26.2	10.4	1
	Late cut	87.7	7.3	10.7	2.3	36.0	43.7	69.8	40.9	13.7	1
Smooth bromegrass	Early cut	85.6	9.9	21.1	3.3	29.8	35.9	61.3	31.2	10.4	2
	Late cut	88.1	5.8	7.6	1.8	34.4	50.4	66.5	39.2	15.9	2
Timothy	Early cut	87.7	8.7	19.7	3.0	27.8	40.8	60.8	30.9	12.9	2
	Normal cut	87.8	6.9	14.2	2.9	30.8	45.2	64.1	33.6	14.2	1
	Late cut	89.1	6.4	8.7	2.2	36.1	46.6	68.3	38.2	16.1	2
Rye grass	Early cut	85.8	12.4	31.7	2.9	19.5	33.5	56.1	22.8	9.0	2
	Late cut	80.8	5.9	9.1	1.8	36.9	46.3	74.0	41.6	12.9	2
Red clover	Early cut	89.2	11.7	23.9	2.8	20.8	40.8	35.1	24.2	17.8	1
	Late cut	88.9	9.0	15.8	2.2	27.3	45.7	46.4	33.5	18.6	2

for fresh herbage, silage and hay. The samples analysed in the USA were milled through a 1.0 mm aperture screen by a Cyclotec cyclone mill.

Statistical analysis

The statistical analyses were carried out using linear regressions. Different chemical, enzymatic and physical parameters were used as independent variables, and they were regressed on *in vivo* OMD. The determination coefficients between different constituents in the fresh herbage samples and the corresponding constituents in the silage and hay samples (R^2) were also calculated. The residual standard deviation (RSD), calculated as a residual mean square error (RMSE) in SAS (1982), was used to compare the differences between the dependent and independent variables. The coefficients of variance (CV) were also calculated.

RESULTS

Chemical composition and nutritive value

The results of the chemical analyses for the different qualities of the forage samples, irrespective of location and year of harvest, are given in Table 1. The corresponding feed evaluation values, including the digestibility values, are given in Table 2. The NIR-predicted values are given in Table 3. No indications of effect of year or location of harvest could be found, and therefore the mean values for the different maturity stages of each species are given in these tables.

As expected, the early-cut samples had high nutritive values, with rye grass as the best. The contents of CP and DCP in the early-cut samples were remarkably high, particularly for the samples of fresh herbage. The early-cut red clover samples had a relatively low nutritive value, and the content of ADL was high.

Table 2. Digestibilities of the different chemical components and some quality measurements derived from these

		In vitro DM digestibility	*In vivo* digestibility: Organic matter	Crude protein	Ether extract	Crude fibre	N free extract	Digestible crude protein	ME[1]	FU[2]
		%	%					g/kg DM		
FRESH HERBAGE										
Meadow grass	Early cut	77.2	82.7	85.0	53.9	88.8	79.5	248	11.5	93.8
	Normal cut	68.0	70.2	75.3	65.0	75.6	64.0	141	10.1	76.5
	Late cut	58.7	60.1	65.1	53.4	62.5	56.7	87	8.4	59.6
Meadow fescue	Early cut	78.0	80.5	80.2	58.6	87.6	77.4	185	11.0	88.5
	Normal cut	69.8	73.8	73.9	58.7	81.5	68.0	117	9.9	75.5
	Late cut	61.2	58.1	59.6	37.2	58.6	56.7	72	7.8	55.8
	Second cut	68.1	73.1	65.2	63.4	85.4	68.0	97	9.8	76.3
Cocksfoot	Early cut	79.8	78.7	84.5	46.9	85.5	73.1	237	10.7	86.8
	Late cut	61.2	62.6	70.8	34.9	63.9	60.3	93	8.6	61.0
Smooth bromegrass	Early cut	74.0	76.6	77.6	49.3	84.5	73.3	199	10.5	85.1
	Late cut	61.4	59.5	56.5	47.8	56.2	62.8	54	8.4	61.3
Timothy	Early cut	70.7	72.9	75.8	46.5	74.9	72.2	164	10.1	81.2
	Normal cut	62.3	68.4	67.6	44.5	76.8	62.7	81	9.5	70.5
	Late cut	63.5	62.0	62.7	42.4	62.4	62.6	61	8.6	62.6
	Second cut	72.6	79.3	80.9	51.4	88.3	73.9	183	11.0	86.1
Rye grass	Early cut	76.2	83.4	85.4	70.0	87.5	81.5	303	12.6	103.9
	Late cut	65.0	66.7	62.0	70.9	69.4	65.4	69	9.6	72.5
Red clover	Early cut	66.2	76.3	80.7	65.3	68.8	77.5	212	10.2	84.0
	Late cut	64.4	64.9	68.6	56.6	52.0	71.9	131	9.0	69.4
Meadow fescue/ Timothy	Early cut	74.4	75.1	71.4	59.0	83.9	72.1	127	10.4	81.9
	Normal cut	67.2	73.7	76.2	61.6	82.3	64.8	131	10.2	75.7
	Second cut	63.5	70.2	58.7	55.0	84.9	65.4	95	9.0	69.4
SILAGE										
Meadow grass	Early cut	72.8	82.5	81.0	83.8	89.1	77.3	188	12.7	84.6
	Normal cut	68.5	74.7	78.3	75.0	79.6	69.2	131	10.8	77.1
	Late cut	48.9	59.8	58.4	67.6	61.1	58.1	56	8.7	63.3
Meadow fescue	Early cut	74.3	83.6	83.7	84.3	91.7	75.9	196	12.9	85.0
	Late cut	62.7	60.8	59.3	67.1	64.8	57.2	65	8.6	63.5
Cocksfoot	Early cut	74.2	82.2	82.0	77.7	89.4	78.4	198	11.9	82.8
	Late cut	60.4	57.9	67.6	69.5	58.7	52.7	84	8.7	61.8
Smooth bromegrass	Early cut	68.6	76.0	79.2	75.7	87.3	64.3	174	11.1	77.2
	Late cut	58.7	55.4	56.6	59.5	53.1	55.5	55	8.0	59.0
Timothy	Early cut	71.4	78.7	78.4	75.2	82.8	77.6	157	11.4	79.5
	Normal cut	68.4	69.8	61.2	64.9	76.1	67.4	66	10.0	73.9
	Late cut	55.1	55.1	58.5	52.0	55.7	53.9	47	7.8	58.6
Rye grass	Early cut	72.5	82.2	82.4	88.6	92.4	71.5	238	13.3	82.3
	Late cut	64.3	65.8	60.5	76.9	69.5	62.8	62	9.7	70.7

Table 2. Digestibilities of the different chemical components and some quality measurements derived from these

		In vitro DM digestibility	*In vivo* digestibility: Organic matter	Crude protein	Ether extract	Crude fibre	N free extract	Digestible crude protein	ME[1]	FU[2]
		%	%					g/kg DM		
Red clover	Early cut	60.6	66.8	75.3	79.0	67.1	60.2	163	9.6	65.0
	Late cut	59.3	62.5	64.6	76.2	44.6	71.2	103	9.1	64.9
HAY										
Meadow grass	Early cut	78.2	79.8	80.2	55.5	84.5	79.0	184	11.2	83.8
	Late cut	56.8	57.9	63.1	38.2	61.8	53.8	71	8.0	45.3
Meadow fescue	Early cut	78.0	80.3	79.5	53.8	86.8	78.2	189	11.0	81.2
	Late cut	57.5	63.1	62.8	40.7	66.8	60.8	66	8.6	50.3
Cocksfoot	Early cut	75.0	77.6	83.0	54.3	84.7	71.4	226	10.8	79.5
	Late cut	63.0	62.9	64.5	37.6	66.5	60.8	69	8.6	51.2
Smooth bromegrass	Early cut	72.3	78.0	76.8	52.2	84.9	75.2	162	10.7	74.6
	Late cut	60.2	61.5	51.0	39.3	61.1	64.1	38	8.5	52.3
Timothy	Early cut	72.3	74.6	78.9	44.1	77.0	73.0	155	10.3	72.7
	Normal cut	70.0	73.2	72.4	48.6	78.9	71.1	103	10.2	70.5
	Late cut	59.3	63.5	63.7	35.0	63.8	64.6	55	8.8	52.8
Rye grass	Early cut	80.4	79.5	80.2	51.4	93.1	73.2	254	10.7	82.2
	Late cut	62.7	59.5	42.6	46.2	67.2	57.1	39	8.2	47.4
Red clover	Early cut	66.1	71.9	82.7	45.9	58.7	74.1	198	9.7	72.1
	Late cut	61.8	66.5	71.4	54.0	47.6	76.6	113	9.2	62.6

1) ME MJ/kg DM
2) FU - FU/100 kg DM

This may be partly attributable to some contamination in the red clover samples, as a result of some straw being left in the field from the previous growth season. The timothy samples also had a relatively low nutritive value.

The decrease in the nutritive value with delayed time of harvest was notable, with the highest decrease observed for rye grass, and to a lesser extent for cocksfoot and meadow fescue. The highest values for the late-cut samples were observed for red clover, especially in content of CP and DCP. The nutritive value for the late-cut rye grass samples was also relatively high.

Some correlations between content of nutrients and the nutritive value of fresh herbage, silage or hay are given in Table 4. The correlations between *in vivo* OMD and the content of fibrous constituents were all negative, while CP was positively correlated with *in vivo* OMD. The nutritive value was strongly correlated with *in vivo* OMD. The correlations between the content of ADL and the other fibrous constituents were low, except for the silage samples. The CF content showed good positive correlation with NDF and ADF.

In vivo OMD regressed on chemical composition

In Table 5 the *in vivo* OMD of fresh herbage, silage and hay is regressed on the content of different chemical consti-

Table 3. NIR-predicted composition and feeding value of the forages

		Crude protein	Crude fibre	NDF	ADF	Digestible crude protein	*In vitro* DM digestibility	Fattening feed unit
		% of DM				g/kg DM	%	FU/100kg DM
FRESH HERBAGE								
Meadow grass	Early cut	24.6	-	47.6	29.7	178	79.6	-
	Normal cut	16.1	-	58.3	37.7	105	70.4	-
	Late cut	12.1	-	59.4	42.5	70	61.2	-
Meadow fescue	Early cut	20.2	-	51.3	32.1	140	78.1	-
	Normal cut	13.6	-	60.4	39.7	83	66.7	-
	Late cut	10.7	-	58.9	41.8	59	61.5	-
	Second cut	13.3	-	52.7	36.5	80	67.5	-
Cocksfoot	Early cut	26.0	-	47.2	30.2	190	80.2	-
	Late cut	11.0	-	63.6	41.6	61	63.4	-
Smooth bromegrass	Early cut	22.7	-	51.6	34.1	163	68.6	-
	Late cut	10.0	-	57.6	41.8	53	60.2	-
Timothy	Early cut	19.2	-	55.9	35.4	132	74.4	-
	Normal cut	10.1	-	70.6	43.1	53	59.2	-
	Late cut	8.8	-	65.0	42.9	42	62.5	-
	Second cut	17.8	-	60.5	35.0	120	75.2	-
Rye grass	Early cut	28.6	-	26.6	44.2	214	83.8	-
	Late cut	8.0	-	40.6	60.7	36	65.0	-
Red clover	Early cut	25.3	-	41.3	34.5	185	71.9	-
	Late cut	15.7	-	46.5	41.6	101	70.3	-
Meadow fescue/ Timothy	Early cut	16.4	-	55.6	36.2	107	74.9	-
	Normal cut	13.3	-	63.8	41.6	81	62.8	-
	Second cut	15.4	-	56.0	37.5	99	64.1	-
SILAGE								
Meadow grass	Early cut	21.6	-	23.2	24.1	173	-	86.9
	Normal cut	15.4	-	39.1	31.4	115	-	79.7
	Late cut	11.2	-	50.1	40.0	76	-	73.2
Meadow fescue	Early cut	21.2	-	37.2	28.9	167	-	85.6
	Late cut	11.3	-	46.9	38.7	77	-	78.8
Cocksfoot	Early cut	24.0	-	34.8	24.3	189	-	86.7
	Late cut	13.2	-	59.4	42.0	89	-	89.3
Smooth bromegrass	Early cut	19.7	-	41.9	33.4	154	-	77.5
	Late cut	9.4	-	51.6	40.5	59	-	77.1
Timothy	Early cut	19.7	-	39.5	31.8	153	-	83.4
	Normal cut	11.3	-	58.1	39.9	74	-	74.5
	Late cut	9.5	-	55.6	40.5	60	-	68.1
Rye grass	Early cut	26.1	-	27.0	31.0	211	-	89.0
	Late cut	10.1	-	32.0	37.1	65	-	73.5

Table 3. NIR-predicted composition and feeding value of the forages

		Crude protein	Crude fibre	NDF	ADF	Digestible crude protein	*In vitro* DM digestibility	Fattening feed unit
		% of DM				g/kg DM	%	FU/100kg DM
Red clover	Early cut	23.1	-	30.6	23.8	177	-	67.7
	Late cut	15.3	-	54.6	38.6	103	-	72.5
HAY								
Meadow grass	Early cut	18.8	25.8	51.2	28.8	162	-	75.0
	Late cut	11.2	37.7	63.6	40.5	80	-	60.2
Meadow fescue	Early cut	19.9	24.8	49.6	28.4	167	-	76.4
	Late cut	11.0	40.3	68.4	42.5	78	-	58.3
Cocksfoot	Early cut	26.4	22.3	49.5	26.4	222	-	83.4
	Late cut	11.7	37.5	66.0	41.6	85	-	65.3
Smooth bromegrass	Early cut	23.4	28.3	53.6	32.2	186	-	81.0
	Late cut	8.0	38.5	61.0	39.1	49	-	59.8
Timothy	Early cut	18.5	28.6	53.2	33.6	137	-	69.4
	Normal cut	13.5	32.1	62.1	35.8	96	-	64.2
	Late cut	7.9	39.4	66.9	40.3	52	-	59.8
Rye grass	Early cut	27.5	17.5	49.8	27.7	253	-	85.5
	Late cut	9.0	40.0	67.4	42.2	49	-	57.2
Red clover	Early cut	26.1	15.9	39.5	29.4	223	-	76.1
	Late cut	13.6	25.8	45.9	35.2	118	-	73.4

Table 4. Correlations relating *in vivo* organic matter digestibility, crude fibre or lignin content to the content of some nutrients and energy values of fresh herbage, silage and hay

		Correlation coefficients		
		Fresh herbage (n=36)	Silage (n=32)	Hay (n=26)
In vivo OM digestibility	Crude protein	0.85	0.82	0.84
	Crude fibre	-0.67	-0.72	-0.83
	NDF	-0.52	-0.76	-0.61
	ADF	-0.73	-0.86	-0.89
	Lignin	-0.48	-0.82	-0.49
	ME	0.95	0.97	0.99
	Fattening feed unit	0.96	0.98	0.99
	IVDMD	0.98	0.98	0.99
Crude fibre	NDF	0.81	0.95	0.83
	ADF	0.91	0.91	0.96
	Lignin	0.09	0.54	0.25
Lignin	NDF	-0.03	0.54	-0.09
	ADF	0.17	0.70	0.36

Table 5. Regressions of *in vivo* OM digestibility (y) on different chemical constituents (x) in fresh herbage, silage and hay. Units as in Table 1

	Constituents			Regressions[1] Intercept	b_1	b_2	b_3	R^2	RSD	CV
FRESH HERBAGE (n=36)	Crude protein	Lignin		63.2	0.88	-0.71		0.78	4.01	5.63
	Crude protein	ADF	Lignin	68.3	0.81	-0.11	-0.72	0.79	4.06	5.70
	Crude protein	Crude fibre	Lignin	62.0	0.90	0.03	-0.70	0.78	4.07	5.71
	Crude protein			52.9	0.96			0.73	4.47	6.26
	ADF	Lignin		115.5	-0.98	-1.01		0.67	4.99	7.00
	NDF	ADF	Lignin	116.6	-0.05	-0.92	-1.03	0.67	5.06	7.10
	Crude fibre	Lignin		110.2	-0.86	-1.16		0.63	5.27	7.40
	ADF			105.9	-1.07			0.54	5.79	8.11
	NDF	ADF		104.5	0.08	-1.16		0.54	5.85	8.21
	Crude fibre			97.2	-0.91			0.45	6.30	8.84
	NDF			98.5	-0.47			0.27	7.28	10.21
SILAGE (n=32)	Crude protein	ADF	Lignin	100.9	0.41	-0.64	-1.42	0.85	4.52	6.51
	ADF	Lignin		120.8	-0.99	-1.53		0.83	4.73	6.80
	NDF	ADF	Lignin	120.0	-0.08	-0.82	-1.60	0.83	4.79	6.91
	Crude protein	Lignin		77.1	0.78	-1.78		0.82	4.90	7.06
	Crude protein	Crude fibre	Lignin	86.2	0.61	-0.22	-1.77	0.82	4.91	7.07
	Crude fibre	Lignin		113.4	-0.65	-2.16		0.78	5.34	7.69
	NDF	ADF		124.0	0.26	-2.02		0.75	5.76	8.30
	ADF			121.3	-1.53			0.74	5.79	8.34
	Crude protein			47.8	1.30			0.67	6.46	9.31
	NDF			105.3	-0.68			0.58	7.33	10.55
	Crude fibre			104.2	-1.20			0.52	7.79	11.22
HAY (n=26)	Crude protein	ADF	Lignin	141.0	-0.48	-1.59	-0.78	0.84	3.68	5.27
	ADF	Lignin		113.1	-1.10	-0.50		0.83	3.75	5.38
	NDF	ADF	Lignin	111.7	0.04	-1.16	-0.44	0.83	3.83	5.49
	NDF	ADF		105.4	0.18	-1.40		0.81	3.89	5.58
	ADF			109.2	-1.19			0.80	3.97	5.70
	Crude fibre	Lignin		112.7	-1.07	-1.81		0.77	4.28	6.13
	Crude protein	Crude fibre	Lignin	125.5	-0.21	-1.29	-0.99	0.78	4.35	6.24
	Crude protein			54.0	0.93			0.70	4.80	6.88
	Crude protein	Lignin		55.6	0.91	-0.09		0.70	4.90	7.02
	Crude fibre			104.8	-1.17			0.69	4.91	7.03
	NDF			102.3				0.37	6.97	9.99

[1] $y = \text{intercept} + b_1x_1 + b_2x_2 + b_3x_3$.
All regressions were statistically significant ($p < 0.001$), except for NDF in the fresh herbage samples which were significant ($p < 0.01$).

Table 6. Regressions of *in vivo* OM digestibility (y) on IVDMD, alone or in combination with chemical constituents (x) of fresh herbage, silage and hay. Units as in Tables 1 and 2

	Constituents		Regressions[1] Intercept	b_1	b_2	R^2	RSD	CV
FRESH HERBAGE	IVDMD		-6.8	1.14		0.79	3.93	5.51
(n=36)	IVDMD	Crude protein	12.3	0.73	0.47	0.86	3.27	4.59
	IVDMD	Crude fibre	8.9	1.00	-0.22	0.80	3.84	5.39
	IVDMD	NDF	5.3	1.06	-0.11	0.80	3.87	5.42
	IVDMD	ADF	5.2	1.03	-0.15	0.79	3.95	5.54
SILAGE	IVDMD		-4.2	1.14		0.70	6.11	8.81
(n=32)	IVDMD	Crude protein	10.6	0.71	0.74	0.83	4.74	6.83
	IVDMD	ADF	62.6	0.59	-0.93	0.81	4.99	7.19
	IVDMD	NDF	34.2	0.81	-0.33	0.78	5.34	7.69
	IVDMD	Crude fibre	29.9	0.86	-0.56	0.78	5.41	7.80
HAY	IVDMD		6.1	0.94		0.89	2.95	4.23
(n=26)	IVDMD	ADF	40.4	0.66	-0.45	0.92	2.53	3.62
	IVDMD	NDF	22.8	0.85	-0.17	0.92	2.61	3.74
	IVDMD	Crude fibre	23.4	0.80	-0.25	0.90	2.87	4.12
	IVDMD	Crude protein	12.0	0.81	-0.17	0.89	2.92	4.19

[1] $y = \text{intercept} + b_1x_1 + b_2x_2$
All regressions were statistically significant ($p < 0.001$).

tuents. The lowest RSD was obtained for a multiple regression consisting of CP, ADF and ADL. This combination of constituents was better than the combination of NDF, ADF and ADL, especially for the fresh herbage samples. CP therefore seems to fit well in combination with ADF and ADL. CP and ADF were the best single predictors, while NDF and CF gave the highest RSD. ADL in addition to ADF produced a clear improvement in the predictions, while the addition of NDF gave no such improvement. A combination of CF and ADL resulted in a lower RSD for the regressions than ADF.

In vivo OMD regressed on IVDMD

The regressions of *in vivo* OMD on IVDMD, alone or in combination with some chemical components, are given in Table 6. Compared with the results from Table 5, both the fresh herbage samples and hay samples gave a lower RSD when *in vivo* OMD was regressed on IVDMD. For the silage samples, IVDMD predicted *in vivo* OMD with a lower RSD than was predicted with CP, NDF and CF, respectively, but the RSD values were higher than observed for the multiple regression of CP, NDF and CF. For IVDMD combined with some of the chemical components, R^2 was increased. For silage, R^2 was increased from 0.70 to 0.83 when CP was included. ADF, NDF and CF also contributed positively, but to a lesser extent. For fresh herbage, the inclusion of CP increased R^2 from 0.79 to 0.86. Here CF, NDF and ADF had only minor effects. When NDF or ADF was included in the hay sample regression, R^2 increased from 0.89 to 0.92. CP and CF had almost no effect on this regression. The regressions were best for the hay samples, followed by the fresh herbage samples, with the lowest values for the silage samples.

In vivo OMD of fresh herbage, silage or hay regressed on NIR estimated values

In Table 7 the *in vivo* OMD of fresh herbage, silage and hay is regressed on chemical composition, IVDMD or FU, all estimated by NIR. Here ADF and NDF to-

Table 7. Regressions of *in vivo* OM digestibility (y) on NIR-predicted values (x) for fresh herbage, silage and hay. Units as in Table 3

	Constituents		Regressions[1] Intercept	b_1	b_2	b_3	R^2	RSD	CV
FRESH HERBAGE	NDF	ADF	122.6	0.17	-1.63		0.78	4.09	5.7
(n=36)	ADF		125.3	-1.45			0.77	4.13	5.7
	Crude protein	ADF	113.7	0.19	-1.23		0.77	4.16	5.8
	IVDMD		7.3	0.92			0.68	4.85	6.8
	Crude protein		53.4	1.08			0.68	4.85	6.8
	NDF		106.3	-0.64			0.31	7.07	9.9
SILAGE	NDF	ADF	124.2	0.35	-2.03		0.78	5.41	7.8
(n=32)	Crude protein	ADF	104.5	0.37	-1.20		0.75	5.76	8.2
	ADF		121.1	-1.51			0.74	5.76	8.2
	Fattening feed unit		-36.2	1.36			0.73	5.82	8.3
	Crude protein		44.9	1.50			0.64	6.72	9.6
	NDF		94.6	-0.60			0.37	8.91	12.8
HAY	NDF	ADF	113.8	0.31	-1.75		0.85	3.42	4.9
(n=26)	Crude protein	ADF Crude fibre	112.9	0.22	-1.76	0.50	0.86	3.49	5.0
	ADF	Crude fibre	122.4	-1.82	0.37		0.85	3.51	5.0
	ADF		117.1	-1.35			0.83	3.63	5.2
	Crude protein	ADF	115.5	0.03	-1.32		0.83	3.71	5.3
	Fattening feed unit		19.9	0.72			0.69	4.87	6.9
	Crude fibre		95.5	-0.84			0.62	5.42	7.7
	Crude protein		54.7	0.94			0.59	5.64	8.0
	NDF		109.3	-0.70			0.50	6.18	8.8

[1] $y = \text{intercept} + b_1x_1 + b_2x_2 + b_3x_3$.
All regressions were statistically significant ($p<0.001$).

gether gave the lowest RSD values. ADF alone resulted in slightly poorer regressions. CF combined with ADF gave a small positive effect compared with ADF alone (only for hay samples), while CP gave no improvements when combined with ADF. The poorest regressions of *in vivo* OMD on the actual NIR-estimated values were observed for CP, CF and especially NDF. Compared with traditional methods, the NIR-predicted values for IVDMD or CP resulted in higher RSD values for the *in vivo* OMD regressions. For ADF or NDF and ADF together, the NIR-predicted values gave lower RSD values however. *in vivo* OMD regressed on these gave nearly as low an RSD value as the best regressions given in Table 5. The regressions seemed to be poorest for the silage samples.

The conformity between chemically determined and NIR-predicted values is discussed by Kjos (1990).

In vivo OMD of silage or hay regressed on fresh herbage

In Table 8, the *in vivo* OMD of silage or hay is regressed on chemical composition and IVDMD in the fresh herbage samples. The best regressions here were obtained for IVDMD, *in vivo* OMD and NIR-predicted content of ADF. On the other hand, *in vivo* OMD of silage and hay was regressed poorly on the content of CF or NDF in the fresh herbage. No significant effects were observed when the chemical constituents in question were combined with ADL, compared with the regressions on these constituents alone.

NIR-predicted ADF content was bet-

Table 8. Regressions of *in vivo* OM digestibility (y) of silage and hay on different parameters for the nutritive values of fresh herbage

Constituents in fresh herbage			SILAGE (n=27) R^2	SILAGE (n=27) RSD	HAY (n=26) R^2	HAY (n=26) RSD
Chemically determined						
IVDMD			0.81	4.83	0.77	4.20
In vivo OM digestibility			0.79	5.10	0.73	4.58
NDF	ADF		0.73	5.93	0.73	4.68
NDF	ADF	Lignin	0.73	6.03	0.73	4.77
Crude protein	ADF	Lignin	0.71	6.27	0.73	4.74
Digestible crude protein			0.71	6.06	0.69	4.90
Crude protein			0.69	6.18	0.70	4.84
ADF	Lignin		0.66	6.67	0.71	4.80
ADF			0.63	6.82	0.70	4.78
Crude fibre	Lignin		0.54	7.78	0.66	5.21
Crude fibre			0.46	8.22	0.62	5.42
NDF			0.18	10.15	0.30	7.36
NIR-predicted						
ADF			0.79	5.10	0.71	4.73
IVDMD			0.75	5.63	0.70	4.82
Digestible crude protein			0.63	6.84	0.67	5.06
Crude protein			0.63	6.84	0.67	5.06

All regressions were statistically significant ($p<0.001$), except for NDF which was significant ($p<0.01$) for hay and ($p<0.05$) for silage.

ter related to *in vivo* OMD than traditionally determined ADF content. For IVDMD, and also content of CP and DCP, the traditionally determined values were best.

RSD values for *in vivo* OMD of the hay samples were generally lower than values for the silage samples. For the fresh herbage parameters which gave the best regressions (IVDMD, *in vivo* OMD, NIR-estimated ADF), R^2 was higher for the silage samples than for the hay samples. The parameters which resulted in the poorest regressions (NIR-estimated CP and DCP, laboratory-determined CF and NDF) had the highest R^2 for the hay samples.

DISCUSSION

Chemical composition and nutritive value

The early-cut herbage samples had a protein content more than twice that of the late-cut samples. These high contents of CP and DCP are somewhat misleading, however, since a considerable part of CP in the early-cut samples comprises NPN (non-protein N). The CP and DCP values in the early-cut samples therefore overestimate their protein value. The contents of fibrous constituents (CF, NDF, ADF, ADL) are remarkably higher in the late-cut samples, because of their higher degree of maturity.

Table 4 indicates that CP and ADF are better correlated with *in vivo* OMD than CF, NDF and ADL. ADF gives better estimates of the lignocellulose content of the samples than CF and NDF, and is therefore expected to correlate better with digestibility. Moreover, the relatively low correlation observed for ADL in the fresh herbage and hay samples indicates that the ADL content does not give a good indication of the nutritive va-

Table 9. Some of the best regressions of *in vivo* OM digestibility (y) for the corresponding samples of fresh herbage, silage and hay

			Fresh herbage n = 26		Silage n = 26		Hay n = 26	
			RSD	R^2	RSD	R^2	RSD	R^2
Chemically determined								
Crude protein	ADF	Lignin	3.65	0.87	3.32	0.92	3.68	0.84
NDF	ADF	Lignin	3.99	0.85	3.36	0.91	3.83	0.83
NDF	ADF		4.62	0.79	4.50	0.85	3.89	0.81
ADF			4.65	0.77	4.40	0.85	3.97	0.80
Crude protein			4.07	0.82	6.01	0.71	4.80	0.70
In vitro digestibility								
IVDMD			4.09	0.82	6.35	0.69	2.94	0.89
NIR-predicted								
Crude protein	ADF	Crude fibre	-	-	-	-	3.49	0.86
NDF	ADF		3.69	0.87	5.12	0.80	3.42	0.85
ADF			3.53	0.87	5.18	0.79	3.63	0.83
Crude protein			4.44	0.79	6.18	0.70	5.64	0.59
IVDMD			4.90	0.75	-	-	-	-
Predicted from the fresh herbage samples								
In vivo OM digestibility			-	-	4.39	0.85	4.58	0.73
IVDMD			-	-	4.83	0.83	4.20	0.77
Crude protein	ADF	Lignin	-	-	5.19	0.81	4.74	0.73
NDF	ADF	Lignin	-	-	5.20	0.81	4.77	0.73
NDF	ADF		-	-	5.20	0.80	4.68	0.73
ADF			-	-	5.45	0.77	4.78	0.70
Crude protein			-	-	5.62	0.75	4.84	0.70
NIR-predicted	ADF		-	-	4.54	0.84	4.73	0.71
NIR-predicted	IVDMD		-	-	5.28	0.78	4.82	0.70

lue, although it represents the least digestible constituent. The contents of NDF, ADF and CF were also poorly correlated with the ADL content. The digestibility of ADL shows considerable variation caused by species of grasses (Minson 1982), and legumes have a higher digestibility of ADL than the grass species. This may contribute to the relatively low correlations observed for ADL.

Prediction of in vivo OMD from chemical analyses, IVDMD or NIR analyses

In Table 9, RSD and R^2 values for some of the best regressions of *in vivo* OMD for the corresponding samples of fresh herbage, silage and hay are given. The listed regressions are chosen from Tables 5, 6 and 7. These results, together with the results from the tables in question, are used to evaluate the different predictors.

For fresh herbage and hay, IVDMD showed the best agreement with *in vivo* OMD. The relatively low values observed for IVDMD in the fresh herbage samples were caused by one outlier. When this sample was omitted, R^2 values increased from 0.82 to 0.87. In Table 6, IVDMD gave the best agreement with *in vivo* OMD, even when the outlier was included. Multiple regressions including CP, ADF and ADL also showed good correlation with *in vivo* OMD. Slightly lower correlations were obtained with NIR-predicted ADF. Including the NIR-predicted content of NDF, CF or CP in addition to ADF gave no significant improvement in the correlations. The traditionally determined detergent constituents (NDF, ADF and ADL) were in less agreement with *in vivo* OMD relative to NIR-predicted ADF. The chemically de-

termined forage fibre analyses were carried out by unskilled personnel, because of a relatively low number of samples for such analyses being run at our department. Therefore, NIR-predicted values for the content of NDF and ADF may give better results than chemically determined values if the calibration equations are based on carefully performed chemical analyses. For CP and IVDMD, NIR-predicted values showed poorer correlation to *in vivo* OMD than the traditionally determined values.

For the silage samples, the multiple regression including CP, ADF and ADL was the best. Multiple regressions including traditionally determined NDF, ADF and ADL, or NIR-predicted NDF and ADF, also showed good correlations with *in vivo* OMD. Traditionally determined CP was better at predicting *in vivo* OMD than NIR-predicted CP.

For fresh herbage, silage and hay, removal of NDF from the regressions which also included ADF hardly affected the correlations. The ranking of the single predictors, with IVDMD as the best (except for the silage samples), followed by CP, ADF, CF, NDF and ADL, is mainly in accordance with that reported by, among others, Witt & Nørgaard Pedersen (1974), McLeod & Minson (1976), Minson (1982), Murray (1986) and Coelho et al. (1988). Several of these authors, however, report somewhat better correlations between *in vivo* OMD and ADL content. Combinations of components often increase the accuracy of the predictions, as observed in this study for some of the fibrous components (ADF, CF or ADL), and CP combined with fibrous components. Lindberg & Lindgren (1988) reported that fibre analysis may be insufficient for predicting digestibility in samples of second cut, since the digestibility of such samples is poorly correlated with the fibre content.

A combination of IVDMD and chemical components may give improved accuracy when predicting *in vivo* OMD, as indicated in Table 6. For the samples of fresh herbage and silage, which had lower R^2 values than the hay samples, CP combined with IVDMD resulted in considerably improved predictions. Wainman et al. (1984), too, have reported a positive effect of combining *in vitro* digestibility with chemical components when predicting the feeding value of forages.

In vivo OMD can be predicted by NIR with a varying degree of accuracy. Norris et al. (1976) and Murray (1986) reported R^2 values of 0.78 and 0.82, respectively, while Winch & Major (1981) reported an R^2 value of 0.46. A high degree of accuracy during calibration is necessary to achieve good predictions of the digestibility. In this study, no NIR calibrations for *in vivo* OMD were available. Therefore, the chemical components predicted by NIR were used as the basis for NIR estimation of *in vivo* OMD. In general, NIR predicts chemical composition with a higher degree of accuracy than it predicts the more complex measurements such as digestibility. Such an indirect prediction of *in vivo* OMD may therefore be just as good as a direct determination. A calibration equation for chemical components is also easier to make than calibrations for animal responses, because larger calibration sets can be obtained without being dependent on digestibility trials. This was also shown by the results obtained for NIR-predicted ADF content in this study, and it indicates that the NIR technique can perform as efficiently as the traditional methods in determining *in vivo* OMD.

A method not included in this study is the one involving rumen degradability, determined by nylon bags incubated in the rumen (Ørskov & McDonald, 1979). Ørskov et al. (1987) and Lindberg & Lindgren (1988) reported R^2 values for the relationship between rumen degradability and *in vivo* digestibility of 0.79 and 0.92, respectively.

Prediction of in vivo OMD in silage or hay from values obtained on fresh herbage samples

The regressions of *in vivo* OMD for silage or hay on values in the corresponding fresh herbage samples are given in Table 9.

The best predictions of *in vivo* OMD in hay were made from data obtained for the hay samples themselves. The R^2 value for *in vivo* OMD in hay predicted from IVDMD in the fresh herbage samples was 0.77 compared with 0.89 when predicted from IVDMD in the hay samples. Only CP in the fresh herbage gave the same R^2 value (0.70) as CP in the hay samples.

For the silage samples, too, the best predictions of *in vivo* OMD were made from data obtained for the silage samples themselves. As an example, the R^2 for *in vivo* OMD in silage predicted from a combination of CP, ADF and ADL in the fresh herbage samples was 0.81 compared with 0.92 when predicted from the corresponding combination in the silage samples. Compared with the results for the hay samples, predictions from data obtained on fresh herbage samples gave better results.

The correlation between *in vivo* OMD in fresh herbage and silage was higher than the correlation for fresh herbage and hay, and this may explain some of the poorer *in vivo* OMD predictions obtained from the hay samples. However, results for fresh herbage may give useful predictions of the nutritive value in the preserved herbage.

SUMMARY

1. Chemical composition and nutritive value of samples of fresh herbage, silage and hay were determined by wet chemistry, by *in vivo* or *in vitro* procedures and by near infrared reflectance analysis (NIR). The samples were harvested at different maturity stages.

2. The early-cut samples had a higher content of CP and DCP, and a lower content of CF, NDF, ADF and ADL than the late-cut samples. *In vivo* OMD and IVDMD were also higher for the early-cut samples. In general, CP and ADF had better correlation with *in vivo* OMD than CF, NDF and ADL.

3. Good agreements were found between *in vivo* OMD and IVDMD, and *in vivo* OMD and the combination of CP, ADF and ADL. ADF and ADL taken together also corresponded well with *in vivo* OMD. NDF in addition to ADF and ADL gave no further improvements. When single chemical components were used as predictors, the best agreements with *in vivo* OMD were found for CP and ADF.

4. Chemical composition and nutritive value of fresh herbage may give useful information about *in vivo* OMD of the corresponding silage and hay samples. There was a better correlation between fresh herbage and silage than between fresh herbage and hay. The best information, however, is provided by the silage or hay samples themselves.

5. NIR-predicted values were slightly less in agreement with *in vivo* OMD than the chemically determined values, with the exception of NDF and ADF. NIR-predicted values may provide useful information about the nutritive value of forages.

6. The good agreement between *in vivo* OMD and NIR-predicted NDF and ADF values compared with chemically determined values indicates that when good routines do not exist for analyses of particular constituents, NIR may be an alternative. The calibration equations for such constituents must be very good, however. For constituents where good analyti-

cal routines do exist, the wet chemistry methods are assumed to give more accurate results.

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Evaluation of the feeding value of fresh forages, silage and hay using near infrared reflectance analysis (NIR)

II. Effects of drying procedure, type of mill and particle size

NILS PETTER KJOS
Agricultural University of Norway, Department of Animal Science, Ås, Norway

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Crude protein (CP), digestible crude protein (DCP), *in vitro* dry matter digestibility (IVDMD) and fattening feed units (FU) in samples of fresh herbage or silage were determined by traditional methods or by near infrared reflectance (NIR) analysis. The samples for NIR analysis were dried using six different drying procedures and ground using three different mills each fitted with two different aperture screens (0.75- 0.80 mm and 1.00 mm). The NIR predictions for samples dried or ground using different procedures were compared with the traditionally determined values by regression. For samples dried at 50°C, 60°C or 70°C there were no differences in the accuracy of the NIR predictions. Samples dried at 80°C or freeze-dried samples gave different NIR predictions. The two aperture screen sizes used here both gave NIR predictions with the same degree of accuracy when used on the same type of mill. Samples prepared by means of different mills were predicted with different levels of accuracy. In general, the same preparation procedures should be used for calibration samples and test samples.

Key words: Drying procedures, feeding value, fresh herbage, grinding procedures, near infrared reflectance analysis, sample preparation, silage.

Nils Petter Kjos, Agricultural University of Norway, Department of Animal Science, P.O. Box 25, N-1432 Ås-NLH, Norway

Near infrared reflectance analysis (NIR) is a method involving the absorption of near infrared light (1100-2500 nm) in organic compounds. The method is based on the fact that each of the major chemical components in forages has specific absorption characteristics which are a result of the heat-induced asymmetric stretching vibrations of hydrogen bonds in the functional groups of molecules (Marten et al. 1985). The method can be used for predicting the content of diffe-

rent components in forage samples, and this is achieved through calibration equations made for each component of interest.

NIR is a rapid method, and no chemicals are required. The sample preparation involves drying and grinding and can be carried out using different procedures. If a commercial NIR laboratory receives samples which are prepared somewhere else, there is a possibility that these samples may be prepared by somewhat different procedures, thus giving divergent results. The following study was carried out to test the effect of sample preparation on the accuracy of the NIR predictions.

MATERIALS AND METHODS

Forage samples

From a set of forage samples harvested in 1985 at different maturity stages (Kjos 1990a), six of fresh herbage and five of silage were randomly chosen. These samples are shown in Tables 1 and 2. The material was unprepared when sampled.

Chemical analyses

Crude protein (CP) and digestible crude protein (DCP) were determined according to the Weende method (A.O.A.C. 1980). Fattening feed unit (FU) was calculated on the basis of digestibility experiments with sheep. *In vitro* dry matter digestibility (IVDMD) was determined in accordance with Tilley & Terry (1963). All analyses were run in duplicate, and the results are given as the mean values.

Table 1. Crude protein (% of dry matter), digestible crude protein (g/kg dry matter) and *in vitro* DM digestibility in the six samples of fresh herbage

Forage sample		Maturity stage	Crude protein	Digestible crude protein	*In vitro* DM digestibility
Rye grass	*(Lolium perenne)*	Early cut	34.0	289	75.8
Smooth bromegrass	*(Bromus inermis)*	Early cut	25.2	195	74.9
Meadow grass	*(Poa pratensis)*	Normal cut	18.7	141	68.0
Meadow fescue	*(Festuca pratensis)*	Second cut	14.8	97	68.1
Timothy	*(Phleum pratense)*	Normal cut	12.0	81	62.3
Meadow grass	*(Poa pratensis)*	Late cut	15.3	110	59.0
MEAN			20.0	152	68.0

Table 2. Fattening feed unit per 100 kg dry matter in the five samples of silage

Forage sample		Maturity stage	Fattening feed unit
Rye grass	*(Lolium perenne)*	Early cut	84.8
Meadow fescue	*(Festuca pratensis)*	Early cut	83.8
Cocksfoot	*(Dactylis glomerata)*	Early cut	82.8
Meadow grass	*(Poa pratensis)*	Late cut	63.6
Timothy	*(Phleum pratense)*	Late cut	52.8
MEAN			73.6

Preparation of the NIR samples

Each of the forage samples was divided into six subsamples for different drying procedures. After drying, each of these

Table 3. Preparation of the NIR samples in this experiment

DRYING PROCEDURE	GRINDING PROCEDURE	
1. Oven-dried 50°C, 48 hours	1. Retsch cutting mill; 0.75 mm sieve	(R 0.75)
2. Oven-dried 60°C, 24 hours	2. Retsch cutting mill; 1.00 mm sieve	(R 1.00)
3. Oven-dried 60°C, 48 hours	3. Christy & Norris hammer mill; 0.8 mm sieve	(HM 0.80)
4. Oven-dried 70°C, 24 hours	4. Christy & Norris hammer mill; 1.00 mm sieve	(HM 1.00)
5. Oven-dried 80°C, 24 hours	5. Tecator cyclone mill; 0.75 mm sieve	(CM 0.75)
6. Freeze-dried	6. Tecator cyclone mill; 1.00 mm sieve	(CM 1.00)

subsamples was ground on one of three different mills, each equipped with two different sieves. Thus, each forage sample gave a total of thirty-six subsamples with different preparations (cf. Table 3).

NIR analyses

The NIR analyses of these samples were conducted at a forage laboratory, «Grovfôrlaboratoriet», which is run by the National Association of Milk Producers in Norway (NML). The samples were scanned using a Technicon 500 monocromator connected to a Hewlett Packard HP 1000 computer. Absorbances (log 1/R) were measured for every 4th nm in the actual wavelength range and the NIR spectrum for each sample was stored on floppy-disks. The samples were run in duplicate.

The nutritive value of each sample was estimated from the NIR spectra, by means of calibration equations developed and used by the forage laboratory. The calibration samples were oven-dried at 60°C and ground with a Retsch mill or hammer mill. CP, DCP and IVDMD in the dried fresh herbage samples were estimated using the equation «GRA 7», while FU was estimated using the equation «SUR 7». Both equations are described by Kjos (1990b).

Statistical analyses

The chemically determined (LAB) values were compared with the NIR-predicted (NIR) values and this comparison was made for each of the drying procedures and each of the grinding procedures, respectively. The results are given as the average difference between LAB and NIR values (BIAS), standard error of prediction (SEP), mean corrected standard error of prediction (SEP(C)), and the determination coefficient between LAB and NIR values (R^2). SEP was calculated as the square root of the residual mean square, and SEP(C) was calculated according to the equation

$$SEP(C) = 1/(n-1)\sqrt{[\Sigma(LAB_i - NIR_i - BIAS)^2]}$$

where n = number of samples, LAB_i = chemically determined value and NIR_i = NIR-predicted value of the i-th sample. SEP, SEP(C), and R^2 are measurements of the relation between the LAB and the NIR values for the different sets of samples. The NIR predictions obtained for the different preparation procedures were also compared, and the results are given as the mean corrected standard error of difference (SED(C)).

No significant effects of the NIR duplicates were found, so the mean values for each NIR sample were used in the statistical tests of the effect of preparation procedures. These tests were carried out according to a 6 x 6 x 6 factorial design for the fresh herbage samples, and a 5 x 6 x 6 factorial design for the silage samples. The tests were described by the model

$$Y_{ijk} = \mu + a_i + b_j + c_k + (ab)_{ij} + (bc)_{jk} + (ac)_{ik}$$

i = 1-6 for fresh herbage
i = 1-5 for silage
j = 1-6
k = 1-6

where Y_{ijk} = mean of the NIR-estimated values
μ = overall mean effect
a_i = effect of forage sample
b_j = effect of drying procedure

c_k = effect of grinding procedure and $(ab)_{ij}$, $(bc)_{jk}$, and $(ac)_{ik}$ = effects of the respective two-factor interactions.

This was a mixed model with forage sample as a random effect, and drying procedure together with grinding proce-

Table 4. Effect of drying procedure on the NIR predictions of crude protein (CP), digestible crude protein (DCP) and *in vitro* DM digestibility (IVDMD) in the dried fresh herbage samples. Accuracy of the predictions for the different sets, n = 36

		MEAN	SD	BIAS	Standard error of prediction (SEP)	Mean corrected standard error of prediction SEP(C))	R^2
LAB-determined CP (% in DM)		20.0	7.6				
NIR-predicted CP (% in DM)	50°C, 48 h	18.3[b]	6.5	1.7	2.59	2.01	0.94
	60°C, 24 h	18.1[a]	6.6	1.9	2.77	2.02	0.94
	60°C, 48 h	18.2[ab]	6.7	1.8	2.64	1.95	0.94
	70°C, 24 h	18.1[a]	6.7	1.9	2.71	1.93	0.94
	80°C, 24 h	18.8	6.9	1.2	2.54	2.24	0.91
	Freeze-dried	17.7	5.9	2.3	3.25	2.29	0.95
LAB-determined DCP (g/kg DM)		152	72				
NIR-predicted DCP (g/kg DM)	50°C, 48 h	124[b]	56	27.5	36.66	24.55	0.92
	60°C, 24 h	122[a]	57	29.7	38.27	24.47	0.91
	60°C, 48 h	123[ab]	58	28.8	37.19	23.92	0.92
	70°C, 24 h	122[a]	58	29.8	37.83	23.64	0.92
	80°C, 24 h	128	60	23.9	34.95	25.90	0.88
	Freeze-dried	119	51	33.3	42.76	27.24	0.93
LAB-determined IVDMD (%)		68.0	6.2				
NIR-predicted IVDMD (%)	50°C, 48 h	67.8[a]	7.8	0.3	4.39	4.44	0.68
	60°C, 24 h	67.8[a]	7.9	0.3	4.44	4.50	0.67
	60°C, 48 h	67.4[a]	8.0	0.6	4.51	4.53	0.68
	70°C, 24 h	67.4[a]	8.1	0.6	4.71	4.73	0.67
	80°C, 24 h	66.5	8.1	1.5	5.29	5.14	0.59
	Freeze-dried	68.8	8.0	-0.8	4.67	4.67	0.66

a, b - Mean values with the same superscripts are not significantly different ($p < 0.05$).

Table 5. Effect of drying procedure on the NIR predictions of fattening feed units per 100 kg DM (FU) in the silage samples. Accuracy of the predictions for the different sets, n = 30

		MEAN	SD	BIAS	Standard error of prediction (SEP)	Mean corrected standard error of prediction SEP(C))	R^2
LAB-determined FU		73.6	13.2				
NIR-predicted FU	50°C, 48 h	81.3[a]	7.7	-7.7	10.10	6.62	0.88
	60°C, 24 h	80.7[a]	7.8	-7.2	9.83	6.86	0.84
	60°C, 48 h	80.7[a]	7.2	-7.1	9.82	6.91	0.89
	70°C, 24 h	80.4[a]	7.1	-6.9	9.64	6.84	0.90
	80°C, 24 h	81.7[a]	8.2	-8.0	10.53	7.03	0.81
	Freeze-dried	80.3[a]	7.5	-6.8	9.60	6.93	0.85

a, b - Mean values with the same superscripts are not signficantly different ($p < 0.05$).

dure as fixed effects. Therefore the effect of forage sample and the effects of the interactions had to be tested against the error term, while the two fixed effects had to be tested against the interaction between forage sample and drying procedure, carried out by PROC GLM in SAS (1982).

RESULTS

Some data for each of the forage samples are already given in Tables 1 and 2.

Effects of drying procedure

The mean values and standard deviation for the NIR predictions of samples prepared by the different drying procedures are given in Tables 4 and 5. These tables show the accuracy of the NIR predictions.

The effects of drying procedures were significant for CP ($p<0.05$), DCP ($p<0.05$) and IVDMD ($p<0.01$) in the fresh herbage samples, but not for FU in the silage samples.

As given in Table 4, the NIR predictions of the fresh herbage samples dried at 80°C differed from the predictions made on the freeze-dried samples ($p<0.001$). Both of these preparation procedures also gave predictions that differed from the NIR predictions obtained on samples dried at 50°C to 70°C ($p<0.001$). For IVDMD, there was no significant difference between the predictions made on the four sets of samples dried at 50°C to 70°C, while there was a slight difference between predictions made on samples dried at 50°C and samples dried at 60°C or 70°C for CP and DCP ($p<0.001$). Compared with the samples dried at 50°C to 70°C, those dried at 80°C had higher estimates of CP and DCP, while the estimates of IVDMD were lower. For the freeze-dried samples, the situation was the opposite. The accuracy of the predictions made on the samples dried at 50°C, 60°C and 70°C, respectively, was of a similar level, while samples dried at 80°C or freeze-dried samples were predicted with a lower level of accuracy for CP and DCP. For IVDMD, the freeze-dried samples were predicted with a relatively good degree of accuracy.

In spite of there being no significant effect of the drying procedure on the prediction of FU in the silage samples, there was a clear tendency toward this. The samples oven-dried at 80°C had the highest estimates (see Table 5). These samples also had the lowest level of accuracy of the predictions.

The correlations between LAB values and NIR-predicted values for the freeze-dried samples were at least as good as those for the oven-dried samples. For CP and DCP, the freeze-dried samples gave NIR predictions with lower values compared with corresponding oven-dried samples. The freeze-dried samples had a stronger green colour than the oven-dried samples, and this might have influenced the NIR spectra. In general, the absor-

Table 6. Comparison of NIR predictions of the fresh herbage samples prepared by different drying procedures (x and y), given as mean corrected standard error of difference (SED(C))

Drying procedure x	y	Crude protein SED(C)	Digestible crude protein SED(C)	*In vitro* DM digestibility SED(C)
50°C, 48 h	60/70°C	0.56	4.85	1.30
50°C, 48 h	80°C, 24 h	0.84	7.27	2.10
50°C, 48 h	Freeze-dried	1.04	9.11	1.78
60/70°C	80°C, 24 h	0.74	6.45	1.71
60/70°C	Freeze-dried	1.14	9.94	1.61
80°C, 24 h	Freeze-dried	1.41	12.39	1.96

Table 7. Effect of grinding procedure on the NIR predictions of crude protein (CP), digestible crude protein (DCP) and *in vitro* DM digestibility (IVDMD) in the dried fresh herbage samples. Accuracy of the predictions for the different sets, n = 36

			MEAN	SD	BIAS	Standard error of prediction (SEP)	Mean corrected standard error of prediction SEP(C))	R^2
LAB-determined CP (% in DM)			20.0	7.6				
NIR-predicted CP (% in DM)	R;	0.75	18.6[c]	6.5	1.4	2.63	2.28	0.92
	R;	1.00	18.7[c]	6.5	1.3	2.59	2.27	0.92
	HM;	0.80	17.8[a]	6.9	2.2	2.88	1.88	0.94
	HM;	1.00	17.8[ad]	6.9	2.2	2.81	1.81	0.95
	CM;	0.75	18.2[b]	6.4	1.9	2.79	2.12	0.94
	CM;	1.00	18.0[bd]	6.3	2.0	2.83	2.05	0.95
LAB-determined DCP (g/kg DM)			152	72				
NIR-predicted DCP (g/kg DM)	R;	0.75	127[c]	55	25.0	36.40	26.83	0.90
	R;	1.00	127[c]	56	24.5	35.83	26.51	0.90
	HM;	0.80	120[a]	59	32.2	39.40	23.00	0.92
	HM;	1.00	120[ad]	60	31.8	38.75	22.46	0.92
	CM;	0.75	123[b]	55	29.2	38.51	25.50	0.91
	CM;	1.00	122[bd]	54	30.2	39.05	25.12	0.92
LAB-determined IVDMD (%)			68.0	6.2				
NIR-predicted IVDMD (%)	R;	0.75	68.6[c]	7.7	-0.6	4.40	4.42	0.67
	R;	1.00	68.6[c]	7.6	-0.6	4.54	4.57	0.64
	HM;	0.80	67.5[b]	8.4	0.5	5.00	5.04	0.65
	HM;	1.00	67.5[b]	8.6	0.5	5.04	5.09	0.65
	CM;	0.75	66.7[a]	7.7	1.3	4.48	4.34	0.68
	CM;	1.00	66.7[a]	7.8	1.3	4.58	4.44	0.67

Abbrevations for grinding procedure, see Table 1.
a, b, c, d - Mean values with the same superscripts are not sigificantly different ($p < 0.05$).

Table 8. Effect of grinding procedure on the NIR predictions of fattening feed units per 100 kg DM (FU) in the silage samples. Accuracy of the predictions for the different sets, n = 30

			MEAN	SD	BIAS	Standard error of prediction (SEP)	Mean corrected standard error of prediction SEP(C))	R^2
LAB-determined FU			73.6	13.2				
NIR-predicted FU	R;	0.75	80.6[a]	7.2	-7.1	9.75	6.85	0.89
	R;	1.00	80.5[a]	7.2	-6.9	9.73	6.94	0.88
	HM;	0.80	81.5[a]	8.2	-8.0	9.99	6.16	0.89
	HM;	1.00	81.4[a]	8.2	-7.9	9.94	6.18	0.88
	CM;	0.75	80.3[a]	7.3	-6.8	10.11	7.66	0.77
	CM;	1.00	80.8[a]	7.3	-7.1	10.03	7.25	0.85

Abbrevations for grinding procedures, see Table 1.
a - Mean values with the same superscript are not signficantly different ($p < 0.05$).

bances (log 1/R) were lower for the freeze-dried samples.

In Table 6, the fresh herbage sample sets, which had significantly different NIR predictions for the drying procedures, are compared. The table shows that for CP and DCP, the freeze-dried samples had the highest SED(C) values when they were compared with the other samples, which indicates that the freeze-dried samples had the most divergent predictions. In the comparisons where samples dried at 80°C were included, the SED(C) values were high too. This was also the case for the IVDMD predictions, but here the highest (SED(C) values were found for the samples dried at 80°C.

When a comparison was made of predictions of FU based on silage samples dried in different ways, it was difficult to find any clear effect.

Effects of grinding procedure

The mean values and the standard deviations of the NIR-estimated values for each of the six grinding procedures are given in Tables 7 and 8. The accuracy of the predictions is also indicated in these tables.

The effects of grinding procedure on the NIR-predicted values were significant for CP, DCP and IVDMD in the dried fresh herbage samples ($p < 0.001$), but not for FU in the dried silage samples.

As indicated in Table 7, the predictions for the dried fresh herbage samples prepared on different mills were different. The Retsch-milled samples had NIR predictions with the highest value, while the estimates of CP and DCP in the hammer-milled samples had the lowest values. For IVDMD, estimates with the lowest value were found for the cyclone-milled samples. The smallest differences were found between samples ground with the hammer mill and the cyclone mill. There was no significant difference between the NIR-estimated values for samples of different particle size within mills. The level of accuracy of the predicitons obtained by the individual mills was different, but there was no effect of particle size within mills. For CP and DCP, the best predictions were obtained with hammer-milled samples, while the Retsch-milled samples seemed to have the lowest level of accuracy. For IVDMD, the highest level of accuracy was obtained with the cyclone-milled samples.

There was no significant difference between the predictions of FU based on the silage samples prepared by different grinding procedures. However, there was a tendency towards a greater correspondence between actual and predicted values for samples of different particle size ground on the same type of mill, than for samples ground on different mills. The accuracy of the FU predictions was lowest for the cyclone-milled samples (cf. Table 8).

In Table 9, a comparison of the predictions obtained for samples ground by means of the different mills is presented. This table shows that SED(C) was highest between samples ground with the

Table 9. Comparison of NIR predictions for the fresh herbage and silage sample sets prepared by different mills (x and y), given as mean corrected standard error of difference (SED(C))

Mill type		FRESH HERBAGE			SILAGE
		Crude protein	Digestible crude protein	*In vitro* DM digestiblity	Fattening feed unit
x	y	SED(C)	SED(C)	SED(C)	SED(C)
Retsch mill	Hammer mill	0.75	6.47	1.29	1.40
Retsch mill	Cyclone mill	0.73	6.30	1.32	1.40
Hammer mill	Cyclone mill	0.94	8.11	1.65	1.68

hammer mill and the cyclone mill, while SED(C) values between samples ground with the Retsch mill and the hammer mill, and the Retsch mill and the cyclone mill were of about the same magnitude.

Correspondence between actual and predicted values

The correspondence between LAB-determined and NIR-predicted values is discussed by Kjos (1990b).

DISCUSSION

Effects of drying procedure

The results indicate that the predictions made for the samples dried at 80°C or freeze-dried were different from the predictions for the other samples. These other samples, dried at 50°C to 70°C, had similar predictions, and drying at these temperatures is most frequently reported in the literature, among others by Marten et al. (1985).

For fresh herbage, the best correlation between chemically determined and NIR-estimated values was obtained with freeze-dried samples, but there was a higher BIAS effect than for the other sample sets. Freeze-drying is a gentle drying method, and the freeze-dried samples had a darker green colour than the corresponding oven-dried samples. Marum et al. (1979) reported that samples with a different colour, caused by different drying methods, can result in changes in the spectral properties of the samples. Blosser et al. (1988) reported that when equations developed on oven-dried samples were used to predict freeze-dried samples, the accuracy of the predictions was reduced appreciably. They also reported that the drying method did not alter the accuracy of the NIR predictions when the calibration sets were prepared in the same way as the prediction sets. On the other hand, the samples dried at 80°C showed the lowest correlations between chemically determined and NIR-estimated values. When samples are dried at a high temperature, their chemical properties are altered, thus probably giving different absorption characteristics for these samples compared with samples dried at lower temperatures. An example of such an alteration is the reaction between protein and reducing sugars (Maillard reaction).

When silage samples are oven-dried, some of the dry matter is lost as volatile fatty acids (VFA). Freeze-drying gives a reduced loss of VFA from the silage samples, and it is therefore expected that oven-dried and freeze-dried silage samples will not be predicted with the same accuracy. However, there is no clear indication of this in the results from this study.

The samples included in the calibrations were oven-dried at 60°C, and it is expected that samples dried in the same way as the calibration samples will also give the most accurate predictions. However, the samples dried at temperatures from 50°C to 70°C were predicted with a similar accuracy, and drying at these temperatures therefore seemed to have a relatively small effect on the results of the NIR predictions made by the equations used in this study.

Effects of grinding procedure

Particle size. For samples ground with the same type of mill, but with different sieves, there was no significant difference between the NIR predictions. The differences were somewhat greater for the cyclone mill compared with the other two mills. The SED(C) values for these differences were lower than the SED(C) values between the parallels in this study, indicating that both the 0.75 mm and the 1.00 mm aperture size can be used without having any effect on the predictions obtained from the equations used here. According to Norris et al. (1976), the degree of accuracy of the NIR predictions is higher for samples with a smaller particle size, but within the actual range for each type of mill in this study the effect of particle size is small.

Type of mill. For the fresh herbage

samples there was a significant difference between NIR predictions obtained on samples prepared on the different mills. The different mill types in this study gave samples with a different particle size distribution, in spite of the same aperture size. The difference in particle size distribution was determined by visual investigation. This difference will have an influence on the absorption of near infrared light in the samples as a result of light scatter (Shenk et al. 1979). The Retsch mill gave the coarsest and less homogeneous samples, while the finest particles were obtained with the cyclone mill. The heterogenous particle size of the Retsch-milled samples resulted in a lower R^2 value and a higher systematic difference between predictions of these samples and samples ground on the other two mill types. The calibration equations were made from samples ground with a Christy & Norris hammer mill or a Retsch mill. Winch & Major (1981) showed that the best NIR predictions can be expected when the calibrations are made on samples with the same particle size, i.e. ground on the same type of mill as the samples to be predicted, and that finely ground samples gave the greatest degree of accuracy. In the study by Blosser et al. (1988), NIR predictions based on an equation developed on samples ground with a Christy & Norris mill were compared with predictions from an equation developed on samples ground with a cyclone mill, and they found no difference in the predictions attributable to grinding procedure. However, the general recommendation is that samples for NIR analysis should be ground in a cyclone mill (Marten et al. 1985).

In this study, as indicated in Tables 7 and 8, there were no great differences in the accuracy of the NIR predictions made on either hammer-milled samples or on cyclone-milled samples. On the other hand, Table 9 indicates that the SED(C) value was lower between predictions of samples ground with the hammer mill and the Retsch mill than between predictions of samples ground by the hammer mill and the cyclone mill. This indicated that, apart from the BIAS effect found for each mill type, the sample sets from the Retsch mill and the hammer mill gave equal predictions. One reason for this might be that both samples ground with the Retsch mill and the hammer mill are included in the calibration equation.

When samples are ground with the cyclone mill, the moisture content in the samples is reduced because of increased temperature and airflow through the mill. This will normally result in a higher content of dry matter in the cyclone-milled samples. In this study, no such effect was found (Kjos 1990b). However, the higher SED(C) levels observed between the predictions of samples from the hammer mill and the cyclone mill indicate a difference in the absorption characteristics of the samples from these mills.

It can be concluded from this study that the same type of mill should be used for grinding the calibration samples and the prediction samples. If the same samples are ground with different types of mill at different laboratories, then samples ground by the same mill types should also be included when calibrating the equipment.

The effect of mill type is also discussed in another study, in which the accuracy of the NIR predictions by the equations used in this study is also discussed (Kjos 1990b).

SUMMARY

1. Crude protein (CP), digestible crude protein (DCP), *in vitro* DMD (IVDMD) and fattening feed unit (FU) were determined in some samples of fresh herbage and silage. CP, DCP, IVDMD and FU in these samples were also predicted by NIR, using NIR equations made from samples dried at 60°C and milled with a cutting mill or a hammer mill. The ef-

fects of drying and grinding procedures on the NIR predictions were studied.

2. The samples for NIR analyses were oven-dried using five different procedures (50°C, 48 h; 60°C, 24 h; 60°C, 48 h; 70°C, 24 h; 80°C, 24 h) or freeze-dried (-50°C to -60°C). The dried samples were ground using three different mills (Retsch cutting mill, Christy & Norris hammer mill or Tecator cyclone mill), and two different aperture screens (0.75 - 0.80 mm and 1.00 mm) were used on each mill.

3. There was no effect on the degree of accuracy of the NIR predictions by drying at temperatures from 50°C to 70°C. The different accuracy levels observed for samples dried at 80°C or the freeze-dried samples were probably caused by altered absorption characteristics for these samples. Samples dried in these ways should therefore be avoided if no such samples are included in the NIR equations. Any of the drying temperatures, 50°C, 60°C or 70°C, can be used successfully in sample preparation for the equations studied here.

4. There was no effect on the accuracy of the NIR predictions when the two different aperture screens were used on the same type of mill. For the different mills, however, there was an effect on the accuracy of the NIR predictions. The cyclone mill have a more homogeneous particle size, while the least homogeneous samples were obtained by the Retsch mill. The best results are expected when calibration samples and test samples are prepared on the same type of mill.

5 In general, samples for NIR analysis should be prepared using the same procedures as used for the calibration samples. Samples with a homogeneous particle size distribution are expected to give the most accurate NIR predictions.

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Effects of ozone on *Triticum aestivum* L. at two temperature and water regimes

LEIV M. MORTENSEN
Agricultural University of Norway, Department of Horticulture, Ås, Norway

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The effects of O_3 concentrations (3 and 85 nll^{-1}) on *Triticum aestivum* L. were studied at two temperature (14 and 22°C) and two water levels (low and high). Top and root dry weights were similarly decreased by high O_3 concentration at all treatments. Moderate drought conditions (low water) decreased the top but not the root dry weight. Increases in temperature decreased root weight while top weight remained unaffected. The wilting of leaves was enhanced as the O_3 concentration or temperature increased or the water level decreased.

Key words: Growth, O_3 concentration, temperature, *Triticum aestivum*, water level.

Leiv M. Mortensen, Agricultural University of Norway, Department of Horticulture, P.O. Box 22, N-1432 Ås-NLH, Norway.

Soil moisture is an important factor controlling plant growth. Drought causes stomata closure and decreased uptake of CO_2 (Schulze 1986). With a reduced stomatal aperture, the uptake of ozone in plants is also likely to be reduced. Accordingly it has been found that under conditions of water stress the yields of alfalfa (Temple et al. 1988) and of pinto beans (Tingey et al. 1982) were less reduced than under well-watered conditions. However, results from the NCLAN programme indicate that the drought stress has to be relatively severe before crop yield response to ozone is affected (Heagle 1989).

In this paper the effects of soil moisture and air temperature on the response of wheat plants to ozone have been studied. This study is a continuation of earlier studies on the influence of climatic factors such as light, air humidity and CO_2 levels on the O_3 sensitivy of wheat (Mortensen 1990a, 1990b). The temperature is also of particular interest since most ozone experiments are carried out in warmer climatic conditions than those in Norway (Mortensen 1989). A better understanding of possible O_3 x temperature interactions will help us to interpret results from other countries in relation to Norwegian conditions.

MATERIALS AND METHODS

Seeds of *Triticum aestivum* L., the spring wheat cultivar Runar, were sown on 27 November in vermiculite (grade 1) in 11 cm pots (0.45 l volume). The temperature

was 16°C and the photosynthetic photon flux density (PPFD) 140 µmol m^{-2} s^{-1} was provided by fluorescent tubes (Philips TL 33RS) 24 h day^{-1}. On 22 December, 14 pots, each containing two seedlings, were placed in each of eight growth chambers (inside a greenhouse compartment) previously decribed by Mortensen (1982).

Two O_3 concentrations were established, one without O_3 enrichment (3 nll^{-1}) and one with O_3 enrichment (85 nll^{-1}) for 7 h day^{-1} (09.00-16.00 h). Ozone was generated from air using a high-voltage O_3 generator (Nomizon, Nordmiljø ab, Sweden). The O_3 concentration was measured in each chamber twice per hour by means of a scanner which switched air flows from the chambers sequentially to an O_3 analyser (Model 1008 AH, Dasibi Environmental Corp.). The mean and maximum concentrations during the 7-h O_3 application period and the rest of the diurnal period were recorded separately by a datalogger. The daily maximum O_3 concentration was 10-20% higher than the mean concentration. The concentrations of nitrogen oxides (NO_x) were measured by means of a Monitor Labs. Inc. (Model 8840) analyser. The NO_x concentration at the high O_3 treatment was 5-10 nll^{-1}, which originated partly from the O_3 generator (50%) and partly from the outside air.

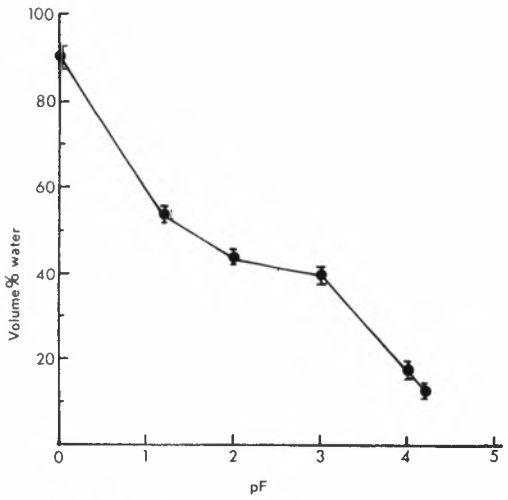

Figure 1. The relationship between volume % water and water potential (pF values) of vermiculite (grade 1)

Two temperature levels were established, 14 and 22°C. Supplementary light was provided by means of fluorescent tubes (Philips TL 33RS) placed at the top of the chambers, 250 µmol m^{-2} s^{-1} PPFD for 24 h day^{-1}. The light was measured with a Lambda LI-185B instrument with quantum sensor (400-700 nm) at top of the plants. The pots in each chamber were divided into two groups of seven pots each. One group of pots was given a high watering level, the other group was watered less frequently in order to introduce a moderate water stress situation which did not cause wilting of the leaves. In practice, the high watering level pots were allowed to decrease in water content from field capacity to about 50% of field capasity. The other pots were moderately watered, the water content varying from 15 to 50% of field capacity. This was done by weighing the pots. A retention curve of vermiculite was measured at the Institute of Soil Science, Agricultural University of Norway, Ås (Figure 1). On the basis of the calculated volume % water it was found that the water potential in high watering level pots varied between about 0 and -1 bar, and in the low watering level pots between about -1 and -10 bar.

The plants were watered with a complete nutrient solution consisting of (mg l^{-1}): N, 158; P, 32; K, 209; Ca, 103; Mg, 35; S, 32; Fe, 1.8; Mn, 0.8; Zn, 0.16; Cu, 0.11; B, 0.16; Mo, 0.03 - giving an electrical conductivity of 1.8 mS cm^{-1}. During the experiments conductivity in the pots was between 1.5 and 2.5 mS cm^{-1}. Growing wheat in vermiculite is likely to cause cupper deficiency, probabely as a result of high zinc content, so the plants were sprayed with 0.5% cupper lime.

The environmental conditions of the chambers are summarized in Table 1. On termination of the experiment (13 Janua-

Table 1. Environmental conditions during the experimental period in the different replicates and treatments. Mean values with standard deviations are given

Replicate no.	Temperature (°C)	%RH	O_3 conc. (nll^{-1}) 09.00-16.00 h	16.00-09.00 h
1	14.4±0.6	79±6	3±2	4±2
2	14.3±0.5	81±5	3±2	4±2
1	14.1±0.4	84±5	84±20	4±3
2	14.0±0.3	83±3	85±17	4±2
1	22.0±0.5	85±4	3±2	3±2
2	21.9±0.4	88±5	2±1	3±1
1	22.0±0.5	84±3	87±16	4±2
2	22.0±0.4	86±3	86±14	3±1

ry 1988) top fresh weight, top and root dry weight, total number of leaves and number of leaves wilted, number of shoots and the highest shoot per pot were all recorded. All recordings were subjected to analysis of variance according to a split-plot design.

RESULTS

Increasing the O_3 concentration decreased the top dry weight by 21 to 34% at the different temperature and water treatments, and no significant interactions between O_3 and the treatments were found (Tables 2 and 3). Decreasing the water level decreased top dry weight by 7-22% at the different treatments, while temperature had no effect. At time of harvest the flag leaf was visible at 22°C but not at 14°C. The root dry weight decreased by 38 to 53% in the different treatments as the O_3 concentration increased. Raising the temperature decreased the mean root weight from 2.71 to 1.79 g (i.e. by 34%) and total dry weight by an average of 15%. The increase in top:root ratio caused by O_3 was not significant because of variation in the plant material. Raising the temperature from 14 to 22°C increased the mean top:root ratio from 1.3 to 2.0.

Table 2. Variance ratios (F) and significance levels for the different variables in spring wheat. The errors a and b mean squares are given. Significance levels: *, $P<0.05$, **, $P<0.01$, ***, $P<0.001$

		Dry weights (g)								
	Df	Top	Root	Total	Top:Root	% d.w. of fresh	Total no. leaves	% wilted leaves	No. of shoot	Height
Replicate	1	6.25	1.26	3.14	1.51	0.072	6.01	0.38	0.54	0.51
O_3	1	26.1*	28.7*	91.9**	3.15	3.31	19.9*	11.3*	19.0*	4.28
Temp. (T)	1	0.03	13.5*	13.0*	10.4*	2.49	2.98	23.1*	0.09	33.9*
O_3 x T	1	0.23	1.08	0.82	0.33	0.054	0.79	2.52	0.98	0.51
Error a	3	0.12	1.71	1.73	2.50	12.6	11.5	17.7	4.80	28.0
Water (W)	1	23.5**	0.79	0.38	12.8*	112***	1.73	20.6*	57.6**	15.4*
O_3xW	1	2.68	0.13	0.77	0.65	7.32	1.95	24.7**	6.41	2.51
TxW	1	0.24	0.16	0.32	1.86	3.91	3.10	12.5*	0.03	1.08
O_3xTxW	1	1.72	0.08	0.02	0.15	0.075	0.08	4.02	0.27	0.73
Error b	4	0.50	5.28	5.08	1.30	1.98	45.7	98.3	7.43	86.3

Table 3. The effect of 3 and 85 nl l^{-1} O_3 on growth of spring wheat at different temperature and water levels. Mean values (±SE) are given

Temperature (°C)	Water level	n	Top		Dry weights (g) Root		Total		Top:root		% d.w. of fresh		Total no. of leaves		% wilted leaves		No. of shoots		Height (cm)	
			3	85	3	85	3	85	3	85	3	85	3	85	3	85	3	85	3	85
14°C	low	14	3.46 ±0.6	2.47 ±0.08	3.46 ±0.34	2.16 ±0.15	6.92 ±0.38	4.63 ±0.18	1.00 ±0.10	1.14 ±0.08	18.5 ±0.5	16.7 ±0.4	26.4 ±1.1	26.7 ±0.8	8.7 ±2.1	33.8 ±1.5	5.4 ±0.3	5.1 ±0.5	74.5 ±1.0	77.1 ±1.1
	high	14	4.21 ±0.19	3.14 ±0.15	3.53 ±0.33	1.67 ±0.10	7.74 ±0.49	4.81 ±0.21	1.19 ±0.12	1.88 ±0.12	15.5 ±0.3	15.1 ±0.3	32.5 ±1.3	28.1 ±0.8	1.2 ±0.6	37.5 ±1.5	10.3 ±0.5	7.9 ±0.4	80.9 ±1.2	80.9 ±1.2
22	low	14	3.39 ±0.08	2.69 ±0.16	2.59 ±0.30	1.56 ±0.21	5.98 ±0.37	4.25 ±0.34	1.31 ±0.15	1.72 ±0.26	20.3 ±0.3	18.1 ±0.4	30.7 ±1.3	28.7 ±1.2	35.1 ±2.7	44.8 ±1.8	5.4 ±0.3	4.7 ±0.2	76.3 ±1.4	83.4 ±2.3
	high	14	4.37 ±0.26	2.88 ±0.22	2.06 ±0.29	0.96 ±0.11	6.43 ±0.52	3.85 ±0.30	2.12 ±0.22	3.00 ±0.24	16.1 ±0.4	15.5 ±0.2	31.6 ±1.0	26.7 ±1.9	6.9 ±0.8	42.7 ±1.9	10.9 ±0.7	7.1 ±0.8	89.3 ±2.5	87.8 ±1.9

Increasing the water level increased the top:root ratio from 1.3 to 2.1. The percentage of dry weight decreased as the watering level increased.

High O_3 concentration decreased the total number of leaves and substantially increased the percentage of wilted leaves. Lowering the water level caused significant leaf wilting at low O_3 concentration at 22°C but not at 14°C. This was probably due to a higher water consumption by the plants at high temperature and a faster drying out of the pots. At high O_3 concentration the percentage of wilted leaves varied from 34 to 44% with the highest values at 22°C. The number of shoots per pot was reduced by high O_3 concentration and reduced watering.

Raising the temperature or the water level increased plant height. The results indicated that high O_3 concentrations increased the height at a low but not at high watering level, however, the interaction was not significant.

DISCUSSION

The total dry weight was not significantly influenced by the water level while the top:root ratio was strongly affected. This indicates that the moisture stress was high enough to influence the assimilate partitioning (more root relative to top growth) but not high enough to cause stomata closure or reduced photosynthesis. In conditions of moderate stress the influence of ozone exposure was similar to that in well-watered conditions, probably because the rate of ozone absorption was little affected by the extent of water stress. The present findings are in agreement with those indicated by Heagle (1989), namely, that the water stress must be severe before the O_3 effect is influenced. Higher PPFD levels than used in the present experiment would probably have resulted in increased transpiration rates, loss of turgor pressure and stomatal closure, at similar water potentials in the pots.

Raschke (1975) concluded that the stomatal aperture follows the temperature curve of CO_2 assimilation. In the present experiment the top dry weight was similar at 14 and 22°C while total dry weight was about 15% higher at 14°C. A higher total weight at 14°C can be explained by the higher rate of leaf wilting (ageing) at 22°C, or by the relatively low PPFD which probably caused a decrease in the optimal temperature for growth. At least the difference in dry weight production between the two temperature levels was not large, which indicates similar leaf diffusion resistance and ozone absorption rates at the two temperatures. If this is the case, small differences in ozone sensitivity between temperatures, as found in the present experiment, could be expected. However, varying temperatures during exposure and pre-exposure periods have been shown to influence the ozone sensitivity of plants in different species (Wilhour 1970; Davis & Wood 1973; Dunning et al. 1974; Dunning & Heck 1977). The results also indicate that the effect of temperature on the physiology and/or morphology of plants may affect the influence of ozone.

It is well known that water stress stimulates the endogenous ethylene production of plants (McMichael et al. 1972, Guinn 1976, Wright 1980). At a leaf water potential of -8 to -10 bars caused by water stress, the ethylene production increased rapidly in wheat plants (Wright 1977). Mehlhorn & Wellburn (1987) found that ethylene-producing pea plants were much more sensitive to ozone than plants which did not produce ethylene. Stomatal closure and reduced ozone uptake must then be the reason for there being no increase in the ozone injury under water stress conditions.

The results from our experimental series with wheat indicate that air humidity and light strongly modify the effects of ozone, while temperature and soil moisture, at least within certain ranges have minor influence (Mortensen 1990a, 1990b). Moreover, the future atmospheric increase in CO_2 concentrations most probably will decrease the effect of certain ozone doses (Mortensen 1990a).

ACKNOWLEDGEMENTS

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The effects of low O_3 concentrations on growth of *Triticum aestivum* L. at different light and air humidity levels

LEIV M. MORTENSEN
Agricultural University of Norway, Department of Horticulture, Ås, Norway

Mortensen, L.M. 1990. The effects of low O_3 concentrations on growth of *Triticum aestivum* L. at different light and air humidity levels. Norwegian Journal of Agricultural Sciences 4: 337–342. ISSN 0801-5341.

The effects of four ozone (O_3) concentrations (6, 33, 66 and 101 nll^{-1}), 6 h per day, on growth of *Triticum aestivum* L. were studied in growth chambers. Four different combinations of photosynthetic photon flux densities (PPFD) and relative air humidities (RH) were established: 85/65, 85/90, 220/65 and 220 µmol m^{-2} s^{-1} PPFD/ 90% RH. At high RH O_3 concentrations above 33 nll^{-1}, at low RH concentrations above 66 nll^{-1} decreased the shoot dry weight. The per cent or absolute effect of the highest O_3 concentration on shoot weight increased as the RH increased, and the percentage effect of O_3 increased by lowering the PPFD. The root dry weight generally decreased at O_3 concentrations above 33 nll^{-1}. The shoot:root dry weight ratio generally increased with increasing O_3 concentrations above 33 nll^{-1}. Plant height was little affected by the O_3 concentrations at high PPFD, but was significantly reduced by the highest O_3 concentrations at low PPFD. The percentage of wilted leaves increased almost linearly with increasing O_3 concentrations, and to a greater extent at low PPFD and/or high RH than at high PPFD and/or low RH.

Key words: Air humidity, growth, ozone, photon flux density (PPFD), *Triticum aestivum*.

Leiv M. Mortensen, Agricultural University of Norway, Department of Horticulture, P.O. Box 22, N-1432 Ås-NLH, Norway.

High O_3 concentrations occur over wide geographical areas including the United States and Europe (Jacobson 1982; Derwent & Kay 1987). Relatively high concentrations (> 50 nll^{-1}) have also been measured at several sites in Scandinavia at latitudes ranging from 58 to 70°N (Hoem et al. 1989). The background concentration during summer is about 20-30 nll^{-1}. The climatic conditions vary considerably between the different regions, and interactions between O_3 and climate are therefore of great interest. It is known from previous studies that the effect of O_3 may be modified by climatic factors such as light, temperature and air humidity (Heck et al. 1965; MacDowall 1965; Otto & Daines 1969; Davis & Wood 1973; Dunning & Heck 1973, 1977; Mortensen 1989, 1990). Most studies, however, have been performed at very high O_3 concentrations, and often only the amount of leaf injury has been recorded. In the present work the effects of low

O_3 concentrations on the shoot and root growth of *Triticum aestivum* have been studied at different light and air humidity levels.

MATERIALS AND METHODS

Seeds of *Triticum aestivum* L. cv. Runar (spring wheat) were sown in vermiculite (grade 1) in 110 mm pots (0.45 l volume) - two seedlings per pot were grown. After 18 days pots were distributed into eight growth chambers described by Mortensen (1982), and kept in a greenhouse compartment. In the first experiment a supplementary light level of 220 µmol m^{-2} s^{-1} photosynthetic photon flux density (PPFD) was provided by means of fluorescent tubes on top of the chambers (Philips TL 33RS). Each chamber contained 8 pots in the first experiment. In the second experiment two PPFD levels (85 and 220 µmol m^{-2} s^{-1}) were applied in each chamber by placing the plants on shelves inside each chamber. Each chamber contained 16 pots divided between the two PPFD levels. The light was measured at the top of the plants using a Lambda LI-185B instrument with a quantum sensor (400-700 nm). In both experiments a relative air humidity (RH) of $65 \pm 10\%$ was established in one half of the chambers, and $90 \pm 5\%$ in the other half. The mean air temperature was at 17.0 ± 0.5°C in all chambers.

The O_3 gas was generated from air by a high-voltage ozone generator (Nomizon, Nordmiljø ab, Sweden). The O_3 concentration was measured twice per hour in each chamber by means of a scanner switching air flows from the chambers to an ozone analyser (Model 1008 AH, Dasibi Environmental Corp.). The mean concentrations with standard deviations throughout the O_3 exposure period and the rest of the day were calculated. Four O_3 concentrations were established in Experiment 1: 5 ± 1, 30 ± 7, 60 ± 9 and 94 ± 15 nll^{-1}, and four in Experiment 2: 6 ± 1, 33 ± 6, 66 ± 14 and 101 ± 20 nll^{-1}, 6 h per day. The O_3 concentrations for the remaining 18 h of the day were 4 ± 1 and 5 ± 1 nll^{-1} in the first and second experiment, respectively. The concentration of nitrogen oxides (NO_x) was measured by means of a Monitor Labs. Inc. (Model 8840) analyzer. The NO_x concentration at the highest O_3 concentration was 5-10 nll^{-1}, which originated partly from the ozone generator and partly from the outside air. In Norway, the NO_x concentration is seldom above a few nll^{-1} in the countryside (Joranger et al. 1986). In a short test the effect of O_3 produced by air was compared with O_3 produced by oxygen at similar concentrations. No differences in leaf injury developed between these two treatments. Any interacting effect between O_3 and NO_x could therefore be excluded.

The plants were watered with a complete nutrient solution consisting of (mg l^{-1}):

N	P	K	Ca	Mg	S	Fe	Mn
158	32	209	103	35	32	1.8	0.8
Zn	Cu	B	Mo				
0.16	0.11	0.16	0.03				

which gave an electrical conductivity of 1.8 mS cm^{-1}.

The first experiment was carried out from 28 January and the second from 2 March, both lasting 21 days. The photosynthetic active radiation (PAR) contributed to the chambers by daylight averaged 3 and 6 mol m^{-2} day^{-1} (corresponding to 35 and 70 µmol m^{-2} s^{-1} for a 24 h photoperiod) in the first and second experiment, respectively (data obtained from the Department of Physics and Meteorology, Ås). This was about 50% of the outside radiation and was due to shading of the greenhouse and the growth chamber constructions.

At termination of the experiments shoot fresh weight, shoot and root dry weight, plant height measured to top of the longest leaf, total number of tillers and leaves and number of wilted leaves per pot were recorded. Because of the dif-

ferent light levels in the two experiments the results are given separately, and presented as means with standard errors.

RESULTS

The effect of increasing O_3 concentrations on shoot dry weight varied with the different light and humidity treatments (Fig. 1). In both experiments ozone reduced the dry weight more at high than at low RH. As found in the second experiment this was the case both at low and high PPFD. In general O_3 concentrations between 30 and 60 nll^{-1} reduced the dry weight at high RH while higher O_3 concentrations were needed to reduce the weight at low RH. In absolute values the effect of O_3 was similar at low and high PPFD. The percentage reduction of shoot dry weight by increasing the O_3 concentration from 6 to 101 nll^{-1} was about 35% at high and about 60% at low PPFD. The shoot dry weight in the first experiment was much lower than in the second because of considerable lower levels of daylight.

The root dry weight generally decreased at O_3 concentrations higher than about 30 nll^{-1} (Fig. 2). The effect of O_3

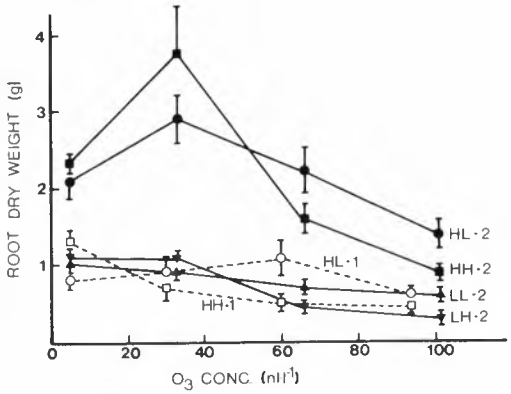

Figure 2. The effect of O_3 concentration on root dry weight of wheat at different PPFD and RH levels. See Fig. 1 text

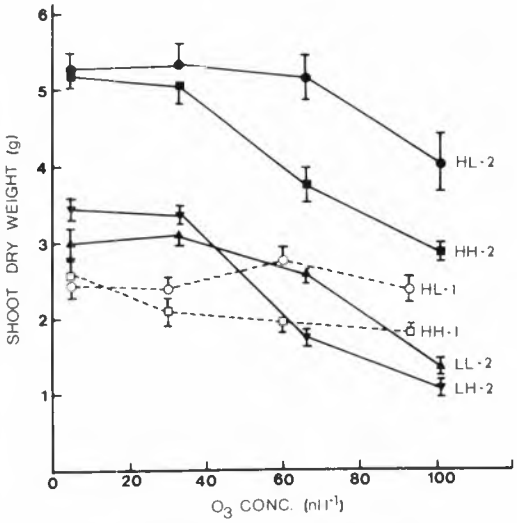

Figure 1. The effect of O_3 concentration on shoot dry weight of wheat per pot at different photosynthetic photon flux densitiy (PPFD) and relative humidity of the air (RH). First letter represents PPFD level, L = low (85 µmol m^{-2} s^{-1}) or H = high (220 µmol m^{-2} s^{-1}). The second letter represents RH level, L = low (65%) or H = high (90%). The numbers represent the first or second experiment

increased as the RH was raised. Between 5 and 30 nll^{-1} the effect of O_3 on root weight varied between the different climate conditions and the two experiments. In the second experiment the root weight was increased by O_3 when the plants were grown at high PPFD while O_3 had no or a negative effect in this interval in the other treatments.

The shoot:root dry weight ratio generally increased as the O_3 concentration was increased (Fig. 3). In the second experiment, however, increasing the O_3 concentration from 6 to 33 nll^{-1} at high PPFD decreased the shoot:root ratio. At low PPFD in Experiment 2 the highest O_3 concentration reduced the shoot:root ratio.

The effect of O_3 concentration on plant height at high PPFD was small, but a substantial decrease in plant height took place with increasing concentrations at low PPFD (Fig. 4). The number of tillers per pot was significantly decreased by increasing the O_3 con-

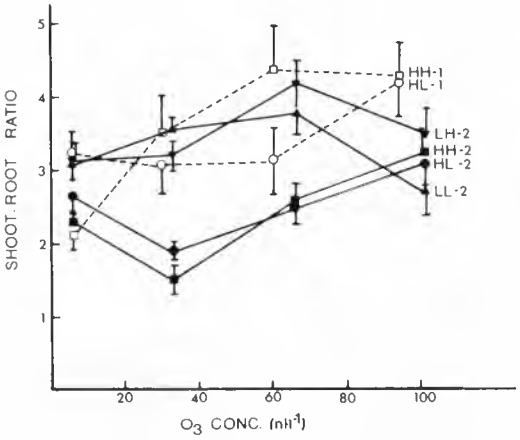

Figure 3. The effect of O_3 concentration on shoot:root dry weight ratio of wheat at different PPFD and RH levels. See Fig. 1 text

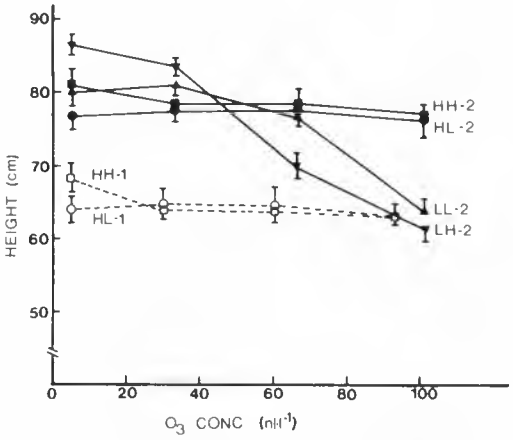

Figure 4. The effect of O_3 concentration on plant height of wheat at different PPFD and RH levels. See Fig. 1 text

centration and the more so at high compared with low RH and at low compared to high PPFD (Fig. 5). At the high PPFD/low RH combination the effect of O_3 on the number was insignificant while at the low PPFD/high RH combination the reduction was about 70%. The effect of O_3 on number of leaves was comparable with the effect on number of tillers, and the results are not presented. Chlorosis, necrosis and leaf wilting caused by

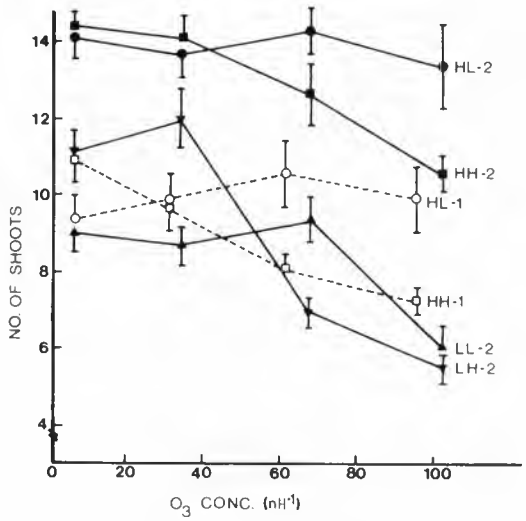

Figure 5. The effect of O_3 concentration on number of shoots per pot at different PPFD and RH levels. See Fig. 1 text

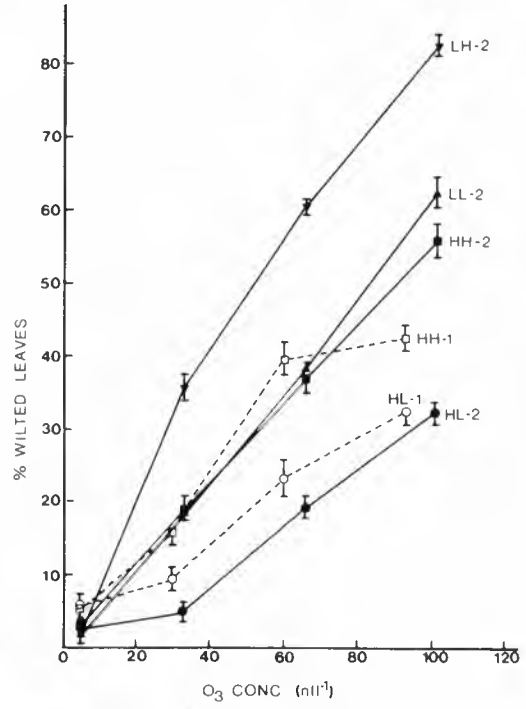

Figure 6. The effect of O_3 concentration on the percentage of wilted leaves per pot, at different PPFD and RH levels. See Fig. 1 text

O_3 occurred as the leaves aged. The percentage wilted of total number of leaves increased linearly with the O_3 concentration (Fig. 6). The effect, however, was much stronger at low PPFD and/or high RH compared with high PPFD and/or low RH.

DISCUSSION

The interacting effects between O_3 and PPFD and RH on growth of wheat plants at relatively low O_3 concentrations are consistent with results recently found in shoot growth of wheat at high O_3 concentrations (Mortensen 1990). The increased negative effect of O_3 on plant growth at high compared with low RH has been shown to be caused by an increased stomatal aperture and uptake of O_3 (McLaughlin & Taylor 1981). Probably as a result of increased absorption of O_3 the threshold concentration for reduction of shoot dry weight decreased as RH increased from 65 to 90%. Decreasing the PPFD level caused an increase in the percentage negative effect of O_3 on shoot and root dry weights. No clear decrease in the threshold concentration for reduced dry weights at decreasing PPFD was found. However, this was very clear with respect to plant height. The decreased sensitivity to O_3 at high compared with low PPFD may be related to a higher content of ascorbic acid in the leaves (Aaberg 1958; Grimstad 1982), which may neutralize the O_3 absorbed through the stomata (Chameides 1989).

Increasing the O_3 concentrations generally increased the shoot:root ratio in accordance with what is usually found in ozone experiments (Cooley & Manning 1988; Mansfield et al. 1988). It is difficult to explain why the shoot:root ratio decreased at high PPFD by increasing the O_3 concentration from 6 to 33 nll^{-1} in the second experiment. However, few experiments which have included analysis of the shoot:root dry weight ratio seem to have included so low O_3 concentrations. The reduced shoot:root ratio at the highest O_3 concentrations at low PPFD in the second experiment can be explained by excessive leaf wilting in these treatments.

The North American research on wheat in open-top chambers indicates that this species is relatively tolerant to ozone, although significant cultivar differences can occur (Heck et al., 1983, 1984). However, in an experiment with wheat in Switzerland the yield was already decreased at 35 nll^{-1} O_3 (Fuhrer et al. 1988). In a Danish experiment some growth parameters in spring wheat were affected at 50 nll^{-1} (Johnsen et al. 1988). As shown in the present results, variations in climate, such as light and air humidity, may well account for the differences in threshold concentrations for reduced growth and yield. For this reason it is important to relate any effect of O_3 on plants to the prevailing climatic conditions in order to understand the variations in results found in different experiments and countries.

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Effects of ozone on growth of *Triticum aestivum* L. at different light, air humidity and CO_2 levels

LEIV M. MORTENSEN
Agricultural University of Norway, Department of Horticulture, Ås, Norway

Mortensen, L.M., 1990. Effects of ozone on growth of *Triticum aestivum* L. at different light, air humidity and CO_2 levels. Norwegian Journal of Agricultural Sciences 4: 343–348. ISSN 0801-5341.

The effects of ozone on the growth of *Triticum aestivum* L. were studied at different light, air humidity and CO_2 levels in growth chambers. Increasing the ozone concentration from <10 to 100-125 nll^{-1} (6 h day^{-1}) when the plants were grown at 100 µmol m^{-2}s^{-1} photosynthetic photon flux density (PPFD) and 90% air humidity (RH) significantly decreased top dry weight and plant height and increased the percentage of wilted leaves. The effects of ozone decreased when PPFD was increased to 200 and 350 µmolm^{-2}s^{-1} or the RH was decreased from 90 to 60%. The effects of ozone on top dry weight, plant height and percentage of wilted leaves were decreased when plants were grown at 700-800 µll^{-1} CO_2 compared to 300-345 µll^{-1}.

Key words: Air humidity, CO_2, light, ozone, *Triticum aestivum*.

Leiv M. Mortensen, Agricultural University of Norway, Department of Horticulture, P.O. Box 22, N-1432 Ås-NLH, Norway.

It is well known that environmental conditions such as light, air humidity and temperature can have an influence on the effects of different air pollutants on plants (Juhren et al. 1957; MacDowall 1965; McLaughlin & Taylor 1981; Freer-Smith 1985; Mansfield et al. 1986; Mortensen 1986, 1989). It is therefore important to take into account the variation in weather conditions which exists in different geographical regions and over time when evaluating the effect of ozone on plants. Likewise, in order to be able to relate results from growth chamber experiments to the open field it is important to know how the climatic conditions in controlled growth chamber experiments influence the results of ozone fumigation.

A few experiments have been conducted on the effects of ozone on plants in different climatic conditions (Mortensen 1989). In most of these studies, however, only the degree of leaf injury has been reported and not the growth effects. In the present work the influence of light and air humidity on the effects of ozone on growth of spring wheat has been studied. Furthermore, the effects of ozone at high CO_2 concentrations have been studied in order to obtain some information

on how the atmospheric increase in CO_2 content (Idso 1989) can influence the effect of this pollutant.

MATERIALS AND METHODS

Experiment 1:
Seeds of *Triticum aestivum* L. cv. Runar (spring wheat) were sown in 90 mm pots (0.25 l volume) filled with limed (1 kg m^{-3}) and fertilized sphagnum peat moss. Two seedlings per pot were grown. After 2-3 weeks 24 pots were placed in each of eight growth chambers inside a greenhouse compartment (Mortensen 1982). Supplementary light was provided by means of fluorescent tubes (Philips TL 33 RS) mounted at the top of the chambers. The plants were subjected to 100, 200 and 350 µmol m^{-2} s^{-1} photosynthetic photon flux density (PPFD) measured at the top of the plants. The different light levels were obtained by placing the plants at shelves at different heights within each chamber. The light was measured using a Lambda LI-185B instrument with quantum sensor. The photoperiod was 18 h day^{-1}. The air temperature was maintained at 20.0±0.5°C. Two relative air humidities (RH), 60±5% and 90±5%, corresponding to a water vapour deficit of 940 and 230 Pa respectively, were established.

Two ozone concentrations were given, one without (<10 nll^{-1}) and one with enrichment (100-125 nll^{-1}) for 6 h day^{-1} (10.00-16.00 h). The ozone gas was generated by a high-voltage ozone generator (Nomizon, Nordmiljø ab, Sweden) using air. The ozone concentration in each chamber was measured three times an hour using a scanner switching air flows from the chambers to an ozone analyser (Model 1008 AH, Dasibi Environmental Corp.). The concentration of nitrogen oxides (NO_x) was measured by means of a Monitor Labs. Inc. (Model 8840) analyser. The NO_x concentration at the high ozone level was 5 - 10 nll^{-1}, which originated partly from the ozone generator and partly from the outside air. The general NO_x concentration in Norway is seldom above 2 - 3 nll^{-1} (Joranger et al. 1986).

The plants were watered with a complete nutrient solution (two or three times a week) consisting of (mg l^{-1}):

N	P	K	Ca	Mg	S	Fe	Mn
158	32	209	103	35	32	1.8	0.8

Zn	Cu	B	Mo
0.16	0.11	0.16	0.03

This gave an electrical conductivity of 1.8 mS cm^{-1}.

The same set of treatments were given in two separate chambers. Two experiments with the same design were carried out, the first from 12 February until 5 March (21 days), the second from 7 March until 24 March (17 days), 1987. Altogether this gave four replicates of each treatment. The mean daylight radiation was 4 and 6 mol m^{-2} day^{-1} (62 and 93 µmol m^{-2} s^{-1} as means for an 18 h day^{-1} photoperiod) in the two experiments respectively (data obtained from the Department of Physics and Meteorology, Ås). At the end of the experiments, plant height, fresh and dry weights of shoots, total number of leaves and wilted leaves were recorded. All data were subjected to a an analysis of variance according to a split-plot design.

Experiment 2:
Three-week old wheat seedlings were planted in 110 mm pots (0.45 l volume) in vermiculite (grade 1), two seedlings per pot. Vermiculite was used so that the root dry weights could be included in the measurements. Eight pots were placed in each of eight growth chambers. Two ozone concentrations were established, one without (<10 nll^{-1}) and one with enrichment (mean concentration 65 nll^{-1}, and daily maximum concentration 90 nll^{-1}) for 7 h day^{-1} (08.00-15.00 h) were established. Two CO_2 concentrations, 300-345 and 700-800 $µll^{-1}$, were given at both ozone levels. The experiment included

two replicates of the four treatments. The air temperature was 20.0±0.5°C and humidity 80±5% RH. The experiment was carried out in the period from 7 to 20 April, 1988. The mean PPFD inside the chambers was 15 mol m^{-2} day^{-1} which was 50 % of the outside radiation (data from Department of Physics and Meteorology, Ås). No supplementary light was given in this experiment because of high natural irradiation.

At termination of the experiment top fresh and top and root dry weights, total number of leaves and number of wilted leaves, number of shoots and plant height were recorded.

RESULTS

Top dry weight was decreased by high ozone concentration, and significant interactions were found between ozone and RH and ozone and PPFD (Tables 1 and 2). Increasing the ozone concentration decreased the dry weight at 60% RH by 8%, and 35% at 90% RH, as an average. Increasing the ozone concentration at 100, 200 and 350 µmol m^{-2} s^{-1} decreased the dry weight by 35, 24 and 11%, respectively. At high RH, plant height was significantly decreased by ozone at the lowest PPFD and increased at the highest PPFD. At low RH, plant height was slightly decreased by ozone at the lowest PPFD and increased at the highest PPFD. Total number of leaves was only slightly influenced by the ozone concentration. Increasing the ozone concentration caused wilting of the leaves, and the effect increased as the RH increased or the PPFD decreased (Tables 1 and 2). Increasing the PPFD at high ozone levels decreased the percentage of wilted leaves,while increasing the PPFD at low ozone levels increased the wilting. The latter effect was probably due to the faster growth and development and therefore earlier senescence of leaves at high PPFD compared with low PPFD.

Significant interactions between ozone and CO_2 concentrations were found in top dry weight, percentage of dry matter, percentage of total number of leaves wilted and on plant height (Tables 3 and 4). While ozone decreased the total dry weight by 53% at normal CO_2, it was decreased by 28% at high CO_2 (Table 3). No significant effect of ozone and CO_2 was found on the top/root ratio. Enriching the air with CO_2 reduced the leaf wilting caused by ozone. Plant height

Table 1. Effects of ozone, photosynthetic photon flux density (PPFD) and relative humidity (RH) on vegetative growth (mean values with ±SE based on single pots in parantheses) of *Triticum aestivum* grown for 21 and 17 days in replicated experiments. Two ozone concentrations (nll ^{1}) were applied

PPFD (µmol $m^{-2}s^{-1}$)	%RH	Dry weight (g)		Plant height (cm)		Total no. of leaves		% wilted leaves	
		<10	100-125	<10	100-125	<10	100-125	<10	100-125
100	60	1.95	1.57	77.8	76.3	22.4	21.2	2.1	34.3
		(0.09)	(0.09)	(1.2)	(1.6)	(0.5)	(0.7)	(0.7)	(1.4)
	90	1.87	0.88	80.6	69.6	20.9	15.5	3.2	53.6
		(0.09)	(0.07)	(1.4)	(1.6)	(0.8)	(0.8)	(0.8)	(2.0)
200	60	2.39	2.23	68.8	66.9	23.9	23.7	9.8	26.3
		(0.09)	(0.10)	(1.2)	(1.2)	(0.7)	(0.6)	(2.3)	(1.4)
	90	2.84	1.72	71.2	71.9	23.9	21.2	11.9	36.1
		(0.13)	(0.08)	(1.0)	(1.1)	(0.7)	(0.7)	(1.8)	(1.5)
350	60	2.64	2.62	57.2	59.5	24.9	24.8	15.4	22.9
		(0.10)	(0.11)	(1.0)	(1.2)	(1.0)	(1.0)	(2.8)	(1.6)
	90	2.87	2.30	61.0	66.0	24.5	26.0	21.6	37.4
		(0.12)	(0.11)	(0.8)	(1.4)	(0.8)	(0.8)	(3.1)	(1.7)

Table 2. Variance ratios (F) and significance levels of main effects and interactions between ozone (O_3), PPFD and RH on vegetative growth of *Triticum aestivum*. Significance levels; °, $P<0.10$; *, $P<0.05$**; $P<0.01$; ***, $P<0.001$. MS error a and b are given on separate lines

	Df	Dry weight	% dry matter	Plant Height	No. of leaves	% wilted leaves
Replicate	3	17.3***	3.74	11.2**	0.22	2.67
O_3	1	46.7***	0.017	1.28	6.13*	95.9***
RH	1	3.69	0.001	6.92*	7.00*	12.6**
O_3*RH	1	19.8**	0.444	0.700	2.28	5.22*
MS error a	9	0.599	54.0	75.9	30.0	598
PPFD	2	180***	59.6***	144***	15.3***	2.05
O_3*PPFD	2	7.33**	2.76	15.6***	2.37	42.2***
RH*PPFD	2	6.58**	0.025	8.88**	2.39	1.13
O_3*RH*PPFD	2	2.01	1.66	7.45**	1.29	1.60
MS error b	24	0.202	29.7	51.7	53.8	176

Table 3. Effects of O_3 and CO_2 concentration on vegetative growth (mean values with ±SE in parantheses) of *Triticum aestivum*

CO_2 conc. ($\mu l\,l^{-1}$)	O_3 conc. ($nl\,l^{-1}$)	Dry weight (g pot^{-1}) Top	Root	Total	Top/root	% dry matter	Total no.of leaves	% wilted leaves	No.of shoots	Plant height (cm)
300-345	<10	3.18	0.84	4.01	3.94	11.0	39.4	5.1	10.4	75.3
		(0.17)	(0.06)	(0.22)	(0.20)	(0.13)	(1.9)	(0.7)	(0.5)	(0.7)
	65-75	1.49	0.42	1.90	3.62	15.5	39.4	77.2	6.5	64.6
		(0.05)	(0.02)	(0.06)	(0.16)	(0.16)	(0.6)	(0.7)	(0.2)	(1.0)
700-800	<10	3.54	1.11	4.65	3.23	11.2	40.7	4.9	11.4	74.7
		(0.20)	(0.07)	(0.25)	(0.13)	(0.10)	(1.5)	(0.7)	(0.5)	(0.9)
	65-75	2.62	0.71	3.33	3.68	13.4	33.9	63.8	9.1	74.4
		(0.18)	(0.04)	(0.21)	(0.13)	(0.17)	(1.8)	(1.4)	(0.6)	(1.0)

Table 4. Variance ratios (F) and significance levels of main effects and interaction between O_3 and CO_2 concentration on vegetative growth of *Triticum aestivum*. For significance levels see Table 2 text

	Df	Dry weight Top	Root	Total	Top/root	% dry matter	Total no. of leaves	% wilted leaves	No. of shoots	Plant height
O_3	1	227***	35.7**	125***	0.12	146***	53.2**	2748***	42.7**	45.3**
CO_2	1	75.0**	16.8*	45.2**	3.04	11.0*	8.21*	29.3**	14.2*	22.9**
O_3*CO_2	1	20.1*	0.02	6.74°	4.25	16.6*	3.49	27.7**	3.18	41.7**
MS residual error	4	0.12	0.08	0.38	0.55	1.16	25.2	25.0	3.58	10.5

was significantly decreased by ozone at normal CO_2 but not at high CO_2.

DISCUSSION

Decreased sensitivity to ozone at higher PPFD is in accordance with previous observations on beans where the pre-treatment PPFD affected the amount of leaf damage (Heck & Dunning 1967; Dunning & Heck 1973, 1977). Similar interactive effects of PPFD and air pollution on plant growth have been found with nitrogen oxides in tomato (Mortensen 1986), sulphur dioxide in timothy grass (Mansfield et al. 1986) and a mixture of these two gases in birch plants (Freer-Smith, 1985). The reduced effect of ozone on plants grown at high compared with low PPFD may be associated with changes in the membrane structures of the cells including lipid components and sulphhydryl linkages (Dunning & Heck 1977). Increasing the light level can also cause an increase in the ascorbic acid content of the leaves (Aaberg 1958; Grimstad 1982), which could neutralize the ozone gas taken up through the stomata (Chameides 1989). It has been reported that high light levels during exposure to ozone will increase the absorption and injurious effect of ozone because of an increased stomatal aperture (Heck et al. 1965; Dunning & Heck 1977). However, good light conditions during growth in the present experiment obviously increased the tolerance to ozone.

Air humidity affects stomatal aperture and the uptake of ozone (McLaughlin & Taylor 1981; Jensen & Roberts 1986). The present results are in accordance with previous observations that incresed air humidity during exposure increases the ozone sensitivity of beans, tobacco, pine and ash (Otto & Daines 1969; Wilhour 1970; Davis & Wood 1973). Although the effect of pre-treatment RH seems to be of less importance, RH may in some cases cause changes in plant growth and morphogenesis, which again will influence the ozone sensitivity of the plant (Mortensen 1989).

It is well known that the CO_2 concentration in the air controls the stomatal aperture and thereby the gas exchange between leaf and air (Pearcy & Bjørkman 1983). Increasing the concentration causes a reduction in the aperture and consequently also a reduction in pollutant uptake. This is in agreement with the decreased effect of ozone on plant growth at high CO_2 concentrations found in the present investigation. Similar results have been obtained with tobacco plants exposed to ozone at normal and high CO_2 concentrations while no interactive effect between CO_2 and ozone has been found with pinto beans (Heck & Dunning 1967). Increasing the CO_2 concentration has been found to significantly increase the ascorbic acid content of tomato leaves (Madsen 1971). It is possible that this effect of CO_2 contributes to a reduced effect of ozone at high CO_2 concentrations. The control of CO_2 concentration is obviously very important in any air pollution study. In controlled environment chambers the concentration will readily drop below normal because of CO_2 consumption by the plants. The yearly increase in CO_2 concentration exceeds 1 $\mu l l^{-1}$ (Idso 1989) and in future experiments with ozone this should be taken into account. The magnitude of stomatal response to CO_2 concentration varies greatly among species (Pearcy & Bjørkman 1983) and this will probably cause different responses regarding the ozone/CO_2 interactions.

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Progeny testing in *Syringa*

JOHANNA L.F. ERSTAD & OLE BILLING HANSEN
Agricultural University of Norway, Department of Horticulture, Ås, Norway

Erstad J.L.F. & O.B.Hansen, 1990. Progeny testing in *Syringa*. Norwegian Journal of Agricultural Sciences 4: 349–355. ISSN 0801-5341.

Half–sib families of *Syringa josikaea* Jacq. f.ex. Rchb. and *S. reflexa* Schneid. were studied during five growing seasons. Selected mother plants from a Fenno–Scandinavian collection were compared with regard to reproductive capacity and ornamental characters in their offspring. Even between these selected individuals large differences occurred. In each species superior families were found. Their mother plants with good general combining ability were selected for seed production.

Key words: Half–sib family selection, reproductive capacity, *Syringa josikaea*, *Syringa reflexa*.

Johanna L.F. Erstad, Agricultural University of Norway, Department of Horticulture, P.O. Box 22, N–1432 Ås–NLH, Norway.

Syringa josikaea Jacq. f.ex. Rchb. and *S. reflexa* Schneid. are widely grown in Norway. Both species can be grown far north into the Arctic Circle, where they still react adequately to the climatic circumstances.

Until now, both species have mainly been propagated vegetatively, because of their great variability in height, shape and flower colour. Four new clones of *S. josikaea* have been released in Norway recently (Kjær, 1987). Leaf mosaic, possibly due to virus infection, is a problem, especially in *S. josikaea*. Some of the new clones are also affected. The symptoms in *S. josikaea* differ from those in *S. vulgaris*, where a nematode transmitted virus has been detected (Cooper, 1975).

The purpose of the experiment was to find mother plants which give hardy, homogeneous offspring with a high ornamental value after generative propagation in order to reduce production costs in the nursery. Lilacs can easily be propagated generatively. Junttila (1971a) has described the collecting and sowing of seeds of lilacs in the Nordic countries.

In 1973 seeds were collected from carefully selected mother plants in Fenno–Scandinavia (Junttila, 1974). The offspring was planted in the nursery of the Agricultural University of Norway and a second selection of promising mother plants was made in 1983. The present report deals with the progeny testing of these 2nd generation mother plants.

MATERIALS AND METHODS

For both species 15 mother plants remained after selection for disease resistance and general impression in the collection

of Fenno–Scandinavian offspring in 1983. Seeds were extracted and sown in three replications of 50 seeds from each plant. They were then submitted to 6 weeks cold–moist pretreatment at 3°C. Germination at 18–20°C was registered 6 weeks after the end of the pretreatment. The seed trays, after transplanting the seedlings, were then submitted to 4 weeks additional cold–moist treatment. A final score for germination % was made 4 weeks after the end of this period.

Seeds from one *S. josikaea* and two *S. reflexa* plants germinated poorly. Because of this the three families were omitted from the field experiment. One family of *S. reflexa* showed few of the characteristics of the species, which also applied to the mother plant on closer inspection. This family was not included in the calculations.

Twenty–five plants of each of the remaining 14 and 12 half–sib (HS) families of *S. josikaea* and *S. reflexa*, respectively, were planted in single rows in the field. The following characters were studied: establishment (% surviving plants in each family after one year in the field), leaf mosaic (percentage of affected plants), bush–shape (scale 1–9 where 1 = flat, 5 = round, 9 = columnar), general impression (scale 1–9), annual height 1985–1987, and flowering. Flowering was observed for the first time in 1987, and the percentage of flowering plants was registered as well as flower bud colour (scale 1–3; 1 = lilac, 2 = intermediate, 3 = pink) and colour intensity (scale 1–4). In 1988 almost all plants flowered and, in addition to colour and colour intensity, richness of flowering (scale 1–9) was scored. For all scalar characters «1» described the least desirable.

Statistical analysis: For each species, an analysis of variance was carried out for the germination percentage. Family means for establishment and leaf mosaic were compared with a X^2-test. Field characters were analyzed for variance between families. For characters measured several times, both within and between family variance were studied in a nested model. Significant differences between families were estimated with the Ryan–Einot–Gabriel–Welsh multiple F–test (REGWF) at the 5%–level (SAS Institute, 1987).

Table 1. Germination after 6 + 4 weeks cold–moist pretreatment, field establishment and reproductive capacity (plants per 100 seeds) in 15 half–sib families of *Syringa josikaea*. Means with different letters are significantly different according to REGWF (P = 0.05)

FAMILY	GERMINATION (%)	ESTABLISHMENT (%)	REPRODUCTIVE CAPACITY
1	75abc	68d	51fg
2	75abc	96ab	72bcd
3	58c	52f	30ij
4	62c	88bc	55ef
5	77abc	100a	77bc
6	78abc	56e	44gh
7	75abc	32g	24j
8	73abc	92abc	67cd
9	67bc	52f	35hi
10	62c	84c	52fg
11	89ab	100a	89a
12	85ab	92abc	78b
13	91a	88bc	80ab
14	67bc	96ab	64de
15	15d	–	–
Mean	74	78	58

RESULTS

Syringa josikaea

Germination after the first cold–moist pretreatment averaged 63% for all families. After the second pretreatment the average germination increased to 74% (Table 1). In three families (nos. 7, 10 and 15) the germination percentage increased by more than 25% from the first to the second germination period.

Establishment varied from 32% to 100% with an average of 78% (Table 1). Differences between families were very significant ($P < 0.01$). *Reproductive capacity*, i.e. the percentage of seeds resulting in viable plants, was calculated as: % germination * % establishment. On average, about 60 plants grew from 100 seeds (Table 1). Differences between families were very significant ($P < 0.01$).

Leaf mosaic. Each year about one month after the beginning of the growing season some of the plants showed discolouring of the leaves, resembling virus infection. The symptoms intensified during summer and the plants became stunted. On average, almost 28% of the plants showed symptoms, the differences between families were very significant ($P < 0.01$). Family 5 was the only family without symptoms (Table 2).

Bush–shape varied from round (5.0, family 7) to some more oval (6.7, family 4); the differences were very significant (Table 2).The average scores for *general impression* were rather low (3.8 – 5.9), mainly because of the occurrence of leaf mosaic (Table 2). The differences between families were significant.

Height. No significant differences between plants within families were observed. However, significant differences were found between families. Two overlapping groups could be distinguished, families 1 and 5 being highest and family 7 lowest (data not shown).

Flowering. Differences between families for the number of flowering plants were significant (Table 3). A few families had only lilac flower buds (average = 1.0), but most of the families showed some variation in colour (average > 1.0) (Table 3). The within family variance was not significant for colour intensity. However, between families significant differences were found, family 9 showing the most intense colour and family 1 the

Table 2. Family means for the occurrence of leaf mosaic (mean with 95% confidence interval = 28 ± 9), bush shape and general impression in 14 half–sib families of *Syringa josikaea*. Means with different letters are significantly different according to REGWF (P = 0.05)

FAMILY	LEAF MOSAIC (%)	BUSH SHAPE (1–9)	GENERAL IMPRESSION (1–9)
1	18	6.5a	5.4ab
2	25	6.4a	5.7a
3	23	6.6a	4.9abc
4	41	6.7a	4.9abc
5	0	6.4a	5.9a
6	79	6.6a	4.1bc
7	25	5.0b	3.8c
8	44	6.1ab	5.7a
9	31	6.0ab	5.3ab
10	14	6.4a	5.0abc
11	32	6.0ab	5.4ab
12	9	6.4a	5.7a
13	27	6.0ab	4.9abc
14	21	6.4a	5.4ab

Table 3. Percent flowering plants, flower colour, colour intensity and richness of flowering in 14 half–sib families of *Syringa josikaea*. Means with different letters are significantly different according to REGWF (P = 0.05)

FAMILY	% FLOWERING IN 1987	COLOUR (1–3)	COLOUR INTENSITY (1–4)	RICHNESS OF FLOWERING (1–9)
1	24bc	1.0	2.3c	1.6de
2	42abc	1.0	3.0abc	7.2a
3	62ab	1.5	2.8abc	5.3abc
4	54ab	1.3	3.1abc	4.3abcde
5	84a	1.2	3.0abc	6.0ab
6	0c	2.2	2.8abc	1.2e
7	38abc	1.4	3.0abc	2.5cde
8	39abc	1.0	2.7abc	4.0abcde
9	62ab	1.1	3.3a	5.4abc
10	71ab	1.1	2.7abc	2.8bcde
11	64ab	1.2	3.1abc	4.6abcde
12	26bc	1.2	2.5abc	4.9abcd
13	46abc	1.6	2.3bc	3.5bcde
14	46abc	1.6	3.3ab	2.7bcde

least intense (Table 3). For the richness of flowering in 1988 significant differences were found between families (Table 3). Family 6 still had the lowest percentage of flowering plants and only a few trusses per plant. Family 2 showed the greatest richness in flowering.

Syringa reflexa

Germination after the first cold–moist pretreatment averaged 40%. After the second period the average germination increased to 54% (Table 4). In three families (nos. 2, 8 and 10) more than 1/3 of the seeds germinated after the second cold–moist pretreatment.

Establishment was generally better than for *S. josikaea* (Table 5). Differences between families were not significant. Differences in *reproductive capacity*, how-

Table 4. Germination after 6 + 4 weeks cold–moist pretreatment, field establishment and reproductive capacity (plants per 100 seeds) in 14 half–sib families of *Syringa reflexa*. Means with different letters are significantly different according to REGWF (P = 0.05)

FAMILY	GERMINATION (%)	ESTABLISHMENT (%)	REPRODUCTIVE CAPACITY
1	59ab	100	59ab
2	59ab	96	57ab
4	51ab	96	49ab
5	59ab	100	59ab
6	81a	100	81a
7	65ab	100	65ab
8	22b	–	–
9	32ab	100	32b
10	47ab	96	45ab
11	80a	96	77a
12	43ab	100	43ab
13	48ab	100	48ab
14	56ab	92	52ab
15	50ab	–	–
Mean	54	98	56

ever, were very significant ($P < 0.01$) (Table 4).

Leaf mosaic was not very serious in *S. reflexa*. Most families were unaffected, and each of the affected families had only a few plants showing symptoms (Table 5). Still, the differences between families were very significant ($P < 0.01$).

Bush–shape varied from 6.2 (family 9) to 7.1 (family 5). The differences between families were not significant (data not shown).

General impression varied from 4.5 to 5.8, significant differences between families were found (Table 5).

Height. No significant differences were found either within or between families (data not shown). Average height in 1986 was a good predictor for flowering in 1987. Non–flowering plants averaged 57 cm, flowering plants 70 cm.

Flowering In 1987 22–72% of the plants flowered (Table 5). The differences between families were significant. All families showed pink flower buds (data not shown). Colour intensity on average was less than in *S. josikaea* (Table 6). There were no significant differences between plants within families. However, significant differences were found between families. Richness of flowering in 1988 varied from 0 to 5.0 (Table 6).

Table 5. Family means for occurrence of leaf mosaic (mean with 95% confidence interval = 3 ± 3) and general impression in 12 half–sib families of *Syringa reflexa*. Means with different letters are significantly different according to REGWF ($P = 0.05$)

FAMILY	LEAF MOSAIC (%)	GENERAL IMPRESSION (1–9)
1	0	5.7ab
2	0	5.3abc
4	0	4.5d
5	0	4.9bcd
6	4	5.4abc
7	0	5.2abc
9	16	5.2abcd
10	12	4.8cd
11	4	4.7cd
12	0	5.7ab
13	0	5.3abc
14	0	5.8a

Some of the plants (especially from family 14) that had flowered in 1987 did not flower in 1988. Differences between families were very significant.

DISCUSSION

Although the plants from the Fenno–Scandinavian collection were cultivated,

Table 6. Percent flowering plants, flower colour intensity, and richness of flowering in 12 half–sib families of *Syringa reflexa*. Means with different letters are significantly different according to REGWF ($P = 0.05$)

FAMILY	% FLOWERING IN 1987 (0–1)	COLOUR INTENSITY (1–4)	RICHNESS OF FLOWERING (1–9)
1	72a	2.34a	4.4a
2	58ab	2.11a	4.2ab
4	54ab	2.35a	2.9abcd
5	68a	2.04a	4.0ab
6	48ab	1.94a	5.0a
7	68a	1.98a	2.4bcd
9	60ab	2.26a	1.7def
10	67a	1.71ab	0.7ef
11	62a	1.94a	1.0def
12	32ab	1.50ab	2.3cde
13	68a	1.90a	3.8abc
14	22b	0.90b	0 f

selected specimens, they showed considerable genetic variation (Junttila, 1974). The second generation, which is described here, was obtained after open pollination of 30 individuals remaining after natural and artificial selection.For wild species Cooper (1963) found that plants in a local population may be phenotypically alike, but will show considerable variation when moved to another environment, adaptation showing polygenic inheritance. In other introduced ornamental species the gene pool was more limited, such that homogeneous offspring could be obtained after one generation (Erstad & Hansen, 1990).

Selection of the mother plants must be based on the performance of the offspring. Both field characters and reproductive capacity must be considered.

Germination differed significantly between HS families in both species. This was also observed in selected mother plants of other species (Erstad & Hansen, 1990). Since all seeds were collected at Ås they had had the same environmental conditions during dormancy induction. In some families the germination percentage increased significantly with increasing cold–moist pretreatment, suggesting genetic differences in dormancy or in the response to the pretreatment. Ease of germination should be considered important for selecting easily produced garden ornamentals.

Germination was generally lower for *S. reflexa* than for *S. josikaea*, reflecting the more pronounced dormancy in *S. reflexa* as observed by Junttila (1971b). In spite of a better establishment for *S. reflexa*, its reproductive capacity in this experiment was lower than for *S. josikaea*. Both germination and establishment are important factors for economy in production of garden plants. If the establishment percentage generally varies as much as the findings for *Syringa* indicate, this character is much underestimated in most breeding programmes.

The occurrence of leaf mosaic reduces the ornamental value of the plants considerably. Therefore, the selection of mother plants with homogeneous, symptomless offspring is of great interest. In both 1987 and 1988 attempts were made to identify a pathogen but without result. Whether the cause is pathogenic or some genetic/physiological aberration, the affected plants are not saleable. There seemed to be a genetic factor involved because some families were more affected than others.

In *S. josikaea* mosaic occurrence must be given much negative emphasis, and family 5 is the only family in this progeny test worth considering for further selection. Early flowering is also important to the nursery and family 5 does well in this respect. Family 5 was also among the best for all other characters observed, although correlations between shape, height and general impression and leaf mosaic can be expected. In family 5 some plants with a deviating, intermediate flower colour were observed, but otherwise all characteristics of *S. josikaea* were present. Since the mother plants of both species were growing in the same field, some interspecific crossing may have occurred (Pringle, 1977). The within family variance was not significant for those characters in which this could be studied, so the offspring can be considered homogeneous. Family 5 then seems to fulfil important criteria for selection and should be tried out on a larger scale. The mother plant originated from seed collected in Gävle (Sweden) (cf. Junttila, 1974) and has been described with dark lilac buds (Njálsson, unpublished). Njálsson has studied the rooting potential of semi–hardwood cuttings from the selected plants. Depending on the season, no. 5 gave 5–40% rooting, which was low compared with other *S. josikaea* genotypes.

In *S. reflexa* family 1 is superior when considering all characters studied. Families 5, 7 and 6 may also be considered in that order. Family 6, of course, is interesting because of its high reproductive capacity. The mother plant of family

no. 1 resp. 5, 6, and 7 originated from seed collected in Trondheim (Norway), Lepaa (Finland), and from two collections in Kuopio (Finland) (cf. Junttila 1974). None of these mother plants produced any plantlets from semi–hardwood cuttings (Njálsson, unpublished). So, in both species a valuable contribution can be expected from generatively propagated selections in addition to vegetatively propagated ones.

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Propagating *Cupressus macrocarpa* Hartw. 'Goldcrest' from cuttings

OLE BILLING HANSEN
Agricultural University of Norway, Department of Horticulture, Ås, Norway

Hansen, O.B. 1990. Propagating *Cupressus macrocarpa* Hartw. 'Goldcrest' from cuttings. Norwegian Journal of Agricultural Sciences 4: 357–361. ISSN 0801-5341.

A two–year study of rooting in the ornamental *Cupressus macrocarpa* Hartw. 'Goldcrest' showed that cuttings between 7 and 20 cm in length rooted equally well in spring. Large cuttings (13–20 cm) produced a greater number of roots than small cuttings (7–13 cm), except when they suffered under high temperatures or low light conditions. Cuttings with a base of brown, second–year growth rooted just as easily as cuttings with only first–year growth. There was 18% rooting of cuttings in which the base was wounded and 34% in those in which it was not wounded. Cuttings with the basal swelling intact did not root as well as cuttings without the swelling (58% vs 72%). Cuttings treated with root–promoting substances (IBA–talc 1.0–2.0% a.i.) produced higher rooting percentages (83–88) and a greater number of roots in each cutting (3.9) compared with non–treated cuttings (30% and 2.7 roots). Cuttings obtained in March rooted better (85%) than those taken in July (26%) or October (1%).

Key words: *Cupressus macrocarpa*, cuttings, propagation.

Ole Billing Hansen, Agricultural University of Norway, Department of Horticulture, P.O. Box 22, N–1432 Ås-NLH, Norway.

Cupressus macrocarpa Hartw. 'Goldcrest' is an ornamental conifer with light green foliage and upright growth habit. In Scandinavia it is grown indoors only and is sold in many different sizes and shapes. Importation of the plant has shown a steady increase during the 1980s. While in 1987 the total number of imported plants was 19,000, in 1988 it was 60,000 (Importsentralen for gartneriartikler 1989). Although reliable methods for propagation by cuttings could reduce the need for this importation, *Cupressus macrocarpa* is considered fairly difficult to propagate by this method. Hartmann and Kester (1983) suggest that the cuttings be taken during the winter months and recommend auxin treatment to aid rooting.

This study was undertaken to examine the effects of time of year for obtaining cuttings, their length and constitution, wounding, and of the application of root–promoting substances on the rooting of *C. macrocarpa* 'Goldcrest' cuttings.

MATERIALS AND METHODS

Two–year–old, 30–40 cm long rooted cuttings of *Cupressus macrocarpa* 'Gold-

crest' were obtained in the fall of 1986 and overwintered at about 5°C in a greenhouse. On 20 February 1987 the plants were placed at about a 15°C day temperature and a 10°C night temperature for use as stock plants. The average temperature increased steadily throughout the summer, then declined. Cuttings were obtained from these stock plants for three factorially designed experiments.

Experiment 1
Cuttings of two lengths (7–13 cm and 13–20 cm) (Fig. 1) were obtained on 14 March 1987 by cutting as closely as possible to the central stem, thus including the basal swelling. Most of the cuttings had bases of brown, second–year growth. The wet cutting bases were treated in a root–promoting substance containing indole butyric acid (IBA) – Rhizopon AA in two concentrations, 1.0 and 2.0% active ingredients. These two treatments were compared with a 24 h soak in 50 and 100 mgl^{-1} of the potassium salt of indole butyric acid (K–IBA). Each treatment consisted of three replications of five cuttings each (small cuttings) and five replications of five cuttings each (large cuttings). Equal numbers of both cutting lengths were kept as untreated controls.

Experiment 2
Cuttings obtained on 4 July and of the same two lengths as in Experiment 1 were divided into two separate groups, those in group 1 being wounded by longitudinal removal of two 1 cm slices of bark on opposite sides at the base of each cutting. The bases of the cuttings were then dipped in Rhizopon AA at concentrations of 1.0, 2.0 and 4.0% a.i. Each combination of treatments consisted of two replications of ten cuttings each.

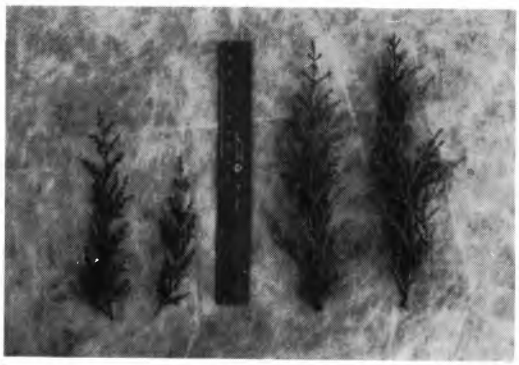

Figure 1. Small (left) and large (right) cuttings of *Cupressus macrocarpa* 'Goldcrest'. Ruler is 17 cm

Experiment 3
Cuttings obtained 9 October of the same two lengths as in Experiments 1 and 2 were divided into two groups: group 1 being cut as close as possible to the central stem, i.e. with the basal swelling as in Experiments 1 and 2. The cuttings in group 2 were taken randomly within the lateral shoot, i.e. without the swelling. The cutting bases were treated in the same concentrations of root–promoting substance as in Experiment 2. Each combination was repeated twice with 10 cuttings each.

Experiment 4
A new group of 30–40 cm stock plants was obtained in February 1988. These plants grew in a heated greenhouse until cuttings were taken on 10 April and 14 May. Cuttings obtained from lateral shoots were included in a factorially designed experiment of three cutting lengths: 7–10 cm, 10–13 cm and 13–16 cm. These were compared with 13–16 cm laterals with 0.5–2.0 cm brown base. The bases of the cuttings were treated in 1.0% or 2.0% Rhizopon AA or 100 or 200 mgl^{-1} K–IBA. Each combination of treatments was repeated twice with 10 cuttings.

Experiment 5
Cuttings 10–13 cm long were obtained on 10 June and included in a factorial experiment. They were of two kinds; with and without basal swelling, as described in Experiment 3. They were treated in 1.0% or 2.0% Rhizopon AA. Each combination of treatments was repeated four times with 10 cuttings.

The cuttings were inserted in dibbled holes in a medium containing fertilized peat and perlite (1v:1v) in 37x23 cm flats. Cuttings were rooted under a «fog» regime produced by ultrasonic nozzles (Sonicore). Bottom heat was maintained at 22–24°C except in hot periods when the air temperature exceeded the temperature intended for the rooting medium. The average minimum air temperature was about 15°C and the average daily maximum about 25°C.

Rooting was scored after 12 to 15 weeks. In experiments 3 and 5 rooting was scored twice; after 12 and 24 weeks. The rooting percentages and the number of roots emerging from each cutting and exceeding 5 mm were recorded.

The results were analysed statistically by using a standard F–test procedure for unbalanced designs. The models include all main effects and all two–way interactions and were found to be significant at the 1.0% level. Differences between levels of each main effect were tested in accordance with the REGWQ multiple comparison procedure (SAS Institute 1982). In the tables, means that are not significantly different are followed by the same letter or letters. All the presented results are significant at least at the 5% level.

Figure 2. Rooting in small (left) and large (right) cuttings of *Cupressus macrocarpa* 'Goldcrest'. Ruler is 17 cm

RESULTS

Both large and small cuttings rooted equally well in spring (57% in Experiment 1), but the larger cuttings produced 3.9 roots per cutting while the smaller cuttings produced only 2.7 roots. The root system of the large cuttings was more extensive than that of the small cuttings (Fig. 2). In the October experiment (Exp. 3) small cuttings rooted better (31%) than large cuttings (18%). Usually the large cuttings produced callus but no roots, even after 24 weeks in the propagation chamber.

Cutting length seemed to have just as much of an impact on rooting as whether the base was green (current year's growth) or brown (previous year's growth) (Table 1). This was, at least, true for cuttings rooting under summer conditions.

Leaving the basal swelling on each cutting did not promote rooting. In Experiment 5, 58% of the cuttings with basal swelling rooted while 72% of the cuttings without swelling rooted.

Table 1. Effect of cutting length and state of cutting base on the rooting % at two sticking dates in *Cupressus macrocarpa* 'Goldcrest' (Exp. 4)

Cutting category	10 April	14 May
7–10 cm green base	26a	31a
10–13 cm —	26a	15b
13–16 cm —	37a	13b
13–16 cm brown base	45a	13b

Table 2. Effect of cutting length and wounding on rooting % of *Cupressus macrocarpa* 'Goldcrest' (Exp. 2)

Cutting length	Control	Wounded	Average
Small (7–13 cm)	22ab	3b	12
Large (13–20 cm)	45a	32a	38
Average	34	18	

Wounding the base of each cutting had a negative effect on the rooting percentage (Table 2). Wounding the smaller cuttings was especially harmful.

Cuttings of *Cupressus macrocarpa* 'Goldcrest' benefited from auxin treatment (Table 3). Treatments in 1.0% and 2.0% IBA–talc were very successful, producing more than 80% rooting and a greater number of roots per cutting compared with control cuttings and cuttings treated for 24 h in 50–100 mgl^{-1} K–IBA. Treatment in 2.0% IBA–talc hastened rooting compared to 1.0% IBA–talc. After 12 weeks the rooting percentages in Experiment 5 were 78 and 52 for 2.0 and 1.0%, respectively, while after 24 weeks they were 84–90 for both IBA concentrations. Cuttings treated in 4.0% IBA–talc showed no significant improvement in rooting compared with those treated in 1.0 and 2.0% (Exp. 2).

Table 3. Effect of treatment with root promoting substances – IBA–talc (Rhizopon AA) and dissolved potassium salt IBA (K–IBA) on rooting of *Cupressus macrocarpa* 'Goldcrest' (Exp.1)

	Rooting %	No. of roots
Control	30c	2.7b
1.0 % IBA–talc	83a	3.9a
2.0 % IBA–talc	88a	3.9a
50 mgl^{-1} K–IBA	53b	2.2b
100 mgl^{-1} K–IBA	60b	2.2b

The effect of time of sticking could be examined by comparing the rooting of equally treated cuttings from Experiments 1–3, namely cuttings of lengths 7–13 cm and 13–20 cm treated in 1.0% or 2.0% IBA–talc. The cuttings rooted best in spring (Table 4). Autumn cuttings hardly rooted at all, while 20–30% of the summer cuttings rooted. In 1988 differences were found between sticking dates 10 April, 14 May and 10 June, the average rooting percentages being 31, 16 and 52, respectively.

Table 4. Effect of sticking month and cutting length on the rooting % in cuttings of *Cupressus macrocarpa* 'Goldcrest' (Exp. 1–3). N.S. = not significant

	Cutting length (cm)		
	7–13	13–20	Average
March	84	87	85a
July	23	30	26b
October	3	0	1c
	37 N.S.	39 N.S.	

DISCUSSION

Although golden forms of *Cupressus macrocarpa* have a poor rooting reputation (Halliwell & Larkbey 1974), juvenile forms are easily propagated. Stock plants therefore should be kept young and vigorous (as in our experiments) starting with 30–40 cm stock plants.

Large cuttings (13–20 cm) produced a greater number of roots and a more extensive root system than smaller cuttings (7–13 cm). If the environmental conditions in the propagation chamber are sufficient to keep the cuttings turgid, a large cutting will supply the base with more carbohydrates than a small cutting; making possible a greater number of roots. However, when environmental conditions are suboptimal, the large cuttings suffer more readily than smaller ones. This may explain why our large cuttings did not root as well in autumn and winter.

Soft tips are suggested as better cutting material than shoots where the base

has hardened (Clark 1971). In our experiments both cutting categories rooted well (Table 1).

Keeping the basal swelled portion within laterals intact on the cuttings was detrimental to rooting. This negative effect may have been caused by larger wound surfaces promoting infections and resulting in many dead cuttings.

Wounding the base of the cutting has proved to be promotive for rooting in many species (e.g. *Ilex*, *Rhododendron*). Indeed, when using *Cupressus* cuttings of older wood, wounding may be necessary for successful rooting (McDaniels & Meade 1963, Macdonald 1986). However, it proved harmful for rooting of the fairly small cuttings in our experiments.

Root promoting substances are necessary for successful rooting in *Cupressus macrocarpa* (cf. Clark 1971). Concentrations of 1.0 and 2.0% a.i. IBA–talc were most successful. Dipping the base of each cutting in the talc formulation of IBA is a crude way of applying the root promoting substances. It was noted that most of the cutting bases died and that roots emerged from swellings 1.0–3.0 cm from the cutting base. Swelling or callusing in the lower part of the cutting always occurred on rooted cuttings.

Cupressus cuttings root most readily in spring. Many conifers propagate best in early spring when vegetative growth is about to resume (Hovind 1984). Winter cuttings are recommended by McDaniel & Meade (1963) and Hartmann & Kester (1983). As the growing season progresses the rooting potential decreases. High temperatures in summer readily cause wilting; this was one probable cause of the inconsistency in rooting in 1988 (Experiments 4 and 5). In the autumn and winter light intensity is low and successful cutting propagation probably demands supplemental lighting. High light intensity seems to be very important for successful rooting in many «Aurea»–type cultivars (Clark 1971, Halliwell & Larkbey 1974). Too low irradiation probably caused poor rooting in the October sticking.

CONCLUSION

For *Cupressus macrocarpa* 'Goldcrest' the most successful rooting was achieved in spring and subsequent to treatments with root–promoting substances, i.e. 1.0–2.0% IBA–talc. Cutting lengths of 7–20 cm were successful; the larger cuttings producing a greater number of roots and potentially quicker growth of the young plants.

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The effects of three tillage systems combined with different compaction and mulching treatments on soil temperature and soil thermal properties

TROND BØRRESEN and ARNOR NJØS
Agricultural University of Norway, Department of Soil Sciences, Section of Soil Fertility and Management, Ås, Norway

Børresen, T. and A. Njøs, 1990. The effects of three tillage systems combined with different compaction and mulching treatments on soil temperature and soil thermal properties. Norwegian Journal of Agricultural Sciences 4: 363–371. ISSN 0801-5341.

Soil temperature was measured in a field experiment involving three tillage systems - conventional tillage, reduced tillage and direct drilling - combined with compaction and mulching treatments. Soil temperature was measured periodically at different soil depths over two growing seasons. Thermal conductivity and other soil thermal properties were calculated.

The influence of the different tillage systems on the mean soil temperature was only slight. Soil compaction with tractor wheels increased the mean temperature at 6 and 24 cm depths. Mulching with 4000 kg straw per ha reduced the mean temperature in May by 2.5, 1.9, 1.4°C at 2, 6 and 24 cm depths, respectively.

Direct drilling reduced the maximum and raised the minimum temperature at 2 and 6 cm depths, as compared with conventional tillage. Compaction with tractor wheels and rolling the seedbed with a Cambridge roller resulted in higher minimum and lower maximum temperatures, except at 24 cm depth, where the maximum temperature was increased. Mulching lowered the maximum soil temperature in May by 7.7, 4.9 and 1.8°C at 2, 6 and 24 cm depths, respectively. The minimum temperature was increased as a result of mulching by 1.3 and 0.3°C at 2 and 6 cm depths, but was decreased at 24 cm depths.

The thermal properties of the soil were influenced by the different tillage systems in the 2-6 cm soil layer. Soil compaction by tractor wheels and mulching caused changes in these properties down to 24 cm depth. Direct drilling increased the volumetric heat capacity, thermal conductivity and thermal diffusivity in the 2-6 cm soil layer as compared with the other treatments.

Heat capacity, thermal conductivity and thermal diffusivity down to 24 cm were all higher in soil covered by plant residues than in bare soil. The compaction treatment produced the same effect, with the exception of the volumetric heat capacity in the 6-24 cm layer. Rolling after sowing in conventionally tilled soil, changed the soil thermal properties to a lesser extent than compaction by tractor wheels.

Key words: ploughless tillage, soil temperature, soil thermal properties.

Trond Børresen. Agricultural University of Norway, Department of Soil Sciences, P.O.Box 28, N-1432 Ås-NLH, Norway

Tillage influences soil temperature by altering soil thermal properties, the surface configuration and surface residue cover. Van Duin (1956) has discussed the theoretical implications of tillage on soil thermal properties. He found that decreasing soil porosity or increasing soil water content increased thermal conductivity and that soil heat flux was reduced by loosening the surface soil layer. Allmaras et al. (1977) found that thermal conductivity increased with increasing intensity of secondary tillage after ploughing. Potter et al. (1985) have reported higher thermal conductivity in the non-tillage system than in the conventionally tilled system.

Thermal diffusivity was higher in non-tilled than in conventionally tilled soil (Hay et al. 1978, Carter & Rennie 1985, Johnson & Lowery 1985, Potter et al. 1985). Johnson & Lowery (1985) found a higher volumetric heat capacity in non-tilled than in tilled soil. Non-tilled soils have been reported to exhibit lower daily maximum temperatures than tilled soils (Lal 1974, Mock & Erbach 1977, Gauer et al. 1982). The conclusion drawn from many of the experiments concerning soil temperature and tillage systems has been that surface residue cover is the most important factor affecting soil temperature (Griffith et al. 1973, Carter & Rennie 1985, Potter et al. 1985, Unger 1978). Von Hoyningen-Huene (1971) determined the reflection from fresh straw as being twice the value of bare soil.

Soil temperature, thermal properties and energy balance can be expected to change when the soil is compacted (Willis & Raney 1971, Voorhees 1976). Rolling the soil after sowing raised the soil temperature in the seedbed (Njøs 1965; Chirkov 1979).

In Norway most of the small grain production is carried out with conventional tillage systems, but recently there has been some adoption of new tillage systems. It is important to understand the effect of tillage on the physical properties and processes occurring in the soil. Njøs (1977), Riley (1983, 1984, 1985), Marti (1984) and Ekeberg et al. (1985) have published results on yields, soil physical and chemical properties with different tillage systems in Norway. There have been no investigations concerning the effects of tillage systems on soil temperature and soil thermal properties in Norway. The objective of this study was to compare the effect of different soil treatments on soil temperature, soil thermal properties and yield.

MATERIALS AND METHODS

The study was conducted during the summer seasons of 1983 and 1984 at the Agricultural University of Norway, Ås, 59°40'N and 10°46'E, altitude approximately 70 m above sea level. The area has been under cultivation for some time, the recent 25 years under grain farming. In 1969 the site was tile drained by means of plastic pipes spaced at 7 m intervals at a depth of 0.8 m.

The experiment was carried out on a

Table 1. Physical soil analysis of the experimental site

Horizon	Depth cm	Particle size distribution (% w/w)			Ignition loss (% w/w)	Bulk density (kg m^{-3})	Water (% v/v)	
		sand	silt	clay			pF2	pF4.2
Ap	0 - 24	28	45	27	8.4	1290	40	16
Bg1	24 - 35	8	71	21	10.0	1590	33	15
Bg2	35 - 50	45	29	26	3.9	1500	29	13
2BC	50 - 100	74	18	8	2.8	1670	28	10

clay loam (0-24 cm depth) overlying a silt loam (24-35 cm depth). According to the USDA SOIL TAXONOMY (1974) the soil can be tentatively classified as a typic haplaquept. The physical properties of the soil are given in Table 1.

The climate of the frost free-season is characterized by a cold early spring, a pre-summer drought, and a wet autumn from around 10 September. The frost generally does not penetrate deeper than 0.5 m.

The three tillage systems were combined with different compaction and mulching treatments. The mulching treatment was carried out in 1984 only.

Tillage treatments

Conventional tillage: Ploughing (20 cm) in autumn followed by harrowing before sowing in spring.

Reduced tillage: No ploughing, but with harrowing (5-7 cm) in spring.

Direct drilling: No tillage.

Compaction treatments

No compaction: No compaction after sowing.

Rolling: Rolling with a Cambridge roller (700 kg, 2.3 m width).

Compaction: One pass, wheel by wheel with a tractor weighing 25 kN, the inflation pressure of the tractor tyres was 250 kPa for the front wheels and 90 kPa for the rear wheels.

Mulching treatments

Without straw: Bare soil surface.

With straw: 4000 kg ha^{-1} dry straw (15% water).

The soil temperature was measured hourly by means of thermocouples (copper-constantan) at 2, 6 and 24 cm depths in bare soil. The results in this report include the measurements from the May period over two years.

The volumetric heat capacity (C) of the soil was determined by summing the product of the volume fractions (f) and volumetric heat capacities of the soil constituents as given by equation 1 (Hillel 1980):

$$C = f_m C_m + f_o C_o + f_w C_w \qquad (1)$$

where the subscripts m, o and w represent soil minerals, organic matter and water, respectively. C_m, C_o, C_w were obtained from Hillel (1980). The f_m, f_o, f_w coefficients in equation 1 were obtained from soil tests for organic matter (Tinsley 1950) moisture determinations (de Boodt 1967), material volume and bulk density (von Nitzsch 1936, Torstensson & Eriksson 1936).

The soil thermal diffusivity (D) was calculated using the amplitude of the maximum and minimum temperatures over 2 to 6 and 6 to 24 cm soil depths and the following formula (Taylor & Ashcroft 1972):

$$D = \pi (Z_2 - Z_1)^2 / t \ln(A_1/A_2) \qquad (2)$$

where D is the thermal diffusivity ($m^2 s^{-1}$); t is the period of the temperature wave (s); Z_2 and Z_1 are the depths for the highest and lowest soil temperatures, respectively; and A_1 and A_2 represent the amplitudes of the diurnal temperature (°C) wave at depths Z_1 and Z_2 respectively.

Thermal conductivity (k) was calculated from equation 3 (Hillel 1980):

$$k = DC \qquad (3)$$

where D is thermal diffusivity and C is volumetric heat capacity.

RESULTS AND DISCUSSION

Soil thermal properties

Tillage systems

The effects of tillage systems on soil thermal properties for the horizons 2-6 and 6-24 cm are shown in Table 2. In the 2-6 cm layer the effect of tillage treatments was statistically significant.

Soil thermal diffusivity was lower for

Table 2. Soil thermal properties for three tillage systems, average for compaction treatments in 1983 and 1984

Depth	Tillage	Thermal diffusivity ($10^{-7}m^2s^{-1}$)	Vol. heat capacity ($MJm^{-3}K^{-1}$)	Thermal conductivity ($10^{-1}Wm^{-1}K^{-1}$)
2-6 cm	Conventional	3.4	1.95	6.6
	Reduced	2.3	1.94	4.6
	Direct drillig	3.8	2.13	8.2
	LSD-5%/sl	0.9*	0.09**	1.7**
6-24 cm	Conventional	3.7	2.44	9.1
	Reduced	3.9	2.41	9.6
	Direct drilling	4.0	2.45	9.7
	LSD-5%/sl	ns	ns	ns

sl = significance level
ns = not significant

reduced tillage than for the other tillage treatments (Table 2). This may have been because of the coarse seedbed structure created by reduced tillage in this experiment. The directdrilled soil showed the highest value for thermal diffusivity at both 2-6 and 6-24 cm depths. This effect of direct drilling is also reported by Hay et al. (1978), Carter & Rennie (1985), Johnson & Lowery (1985) and Potter et al. (1985). This soil had a higher bulk density and lower air content at pF2 than the soil in the other treatments.

The volumetric heat capacity in the 2 - 6 cm depth was significantly higher for the direct drilling treatment than for the other two treatments (Table 2). Higher bulk density and higher water content of the soil tend to give such results.

The heat conductivity of the soil was lowest for reduced tillage and highest for direct drilling (Table 2). Potter et al. (1985) showed that thermal conductivity was 20% higher in the non-tillage system as compared to the conventionally tilled system at all soil water contents.

Compaction

Traffic compaction of the seedbed after sowing using a tractor weighing 25 kN changed the soil thermal properties in the 2-6 and 6-24 cm layers (Table 3). Thermal diffusivity and thermal conductivity were increased by 70-80% by com-

Table 3. Soil thermal properties for different compaction, average for tillage systems in 1983 and 1984

Depth	Compaction	Thermal diffusivity ($10^{-7}m^2s^{-1}$)	Vol. heat capacity ($MJm^{-3}K^{-1}$)	Thermal conductivity ($10^{-1}Wm^{-1}K^{-1}$)
2-6 cm	Uncompacted	2.4	1.88	4.5
	Compacted	4.0	2.14	8.5
	LSD-5%/sl	0.9*	0.15**	1.7**
6-24 cm	Uncompacted	3.7	2.42	8.9
	Compacted	4.1	2.45	10.0
	LSD-5%/sl	0.1**	ns	0.4**

Compacted = compacted by tractor wheels

paction at the 2-6 cm depth. The effect of compaction was significant with higher temperatures at the 6 and 24 cm depths for these properties.

The volumetric heat capacity was higher after compaction than without compaction, but only in the 2-6 cm layer (Table 3). This was probably the result of the higher bulk density caused by compaction.

For conventionally tilled soil, rolling was compared with the other compaction treatments (Table 4). The results showed that in ploughed soil the effect of the compaction treatments was limited to the upper 2 - 6 cm layer. Rolling less of an effect on the soil thermal properties than compaction by tractor wheels.

Mulching

Management of the plant residues is important, especially in non-tillage systems. In this experiment a straw cover of 4000 kg ha^{-1} influenced the soil thermal properties to a greater extent than the tillage and compaction treatments (Table 5). Thermal diffusivity, volumetric heat capacity and thermal conductivity showed increased values under the straw cover as compared with bare soil. This is due to the higher soil water content in a mulched soil. The effect of mulching was statistically significant at the 2-6 and 6-24 cm layers.

Table 4. Soil thermal properties for different compaction of a conventionally tilled soil in 1983 and 1984

Depth	Compaction	Thermal diffusivity ($10^{-7}m^2s^{-1}$)	Vol. heat capacity ($MJm^{-3}K^{-1}$)	Thermal conductivity ($10^{-1}Wm^{-1}K^{-1}$)
2-6 cm	Uncompacted	2.6	1.81	4.6
	Rolled	2.9	1.99	5.8
	Compacted	4.2	2.10	8.7
	LSD-5%/sl	0.7**	0.13**	1.4**
6-24 cm	Uncompacted	3.7	2.44	9.0
	Rolled	4.3	2.48	10.2
	Compacted	3.7	2.45	9.1
	LSD-5%/sl	ns	ns	ns

Compacted = compacted by tractor wheels

Table 5. Soil thermal properties for different mulching; average for tillage systems and compaction in 1983 and 1984

Depth	Mulching	Thermal diffusivity ($10^{-7}m^2s^{-1}$)	Vol. heat capacity ($MJm^{-3}K^{-1}$)	Thermal conductivity ($10^{-1}Wm^{-1}K^{-1}$)
2-6 cm	Without	2.9	1.88	5.6
	With	4.7	2.19	10.6
	LSD-5%/sl	0.8*	0.10**	2.2**
6-24 cm	Without	3.8	2.31	8.7
	With	4.5	2.44	11.0
	LSD-5%/sl	0.5*	0.10*	1.4**

Table 6. Soil temperature (°C) for different tillage systems; average for compaction treatments in May 1983 and 1984

Depth	Tillage	Mean	Maximum	Minimum	Amplitude
2 cm	Conventional	11.9	18.1	7.2	10.9
	Reduced	12.2	18.5	7.0	11.0
	Direct drilling	12.0	17.0	8.0	9.1
	LSD-5%/sl	0.1***	0.4***	0.2**	0.7***
6 cm	Conventional	11.5	15.1	8.2	6.8
	Reduced	11.7	14.9	8.8	6.2
	Direct drilling	11.5	14.6	8.7	5.9
	LSD-5%/sl	0.1***	0.3***	0.2***	0.5**
24 cm	Conventional	10.0	10.5	9.2	1.3
	Reduced	10.3	10.8	9.7	1.1
	Direct drilling	10.0	10.5	9.4	1.1
	LSD-5%/sl	0.1***	0.2***	0.1***	0.1***

Soil temperature

Tillage systems

The mean temperature at 2, 6 and 24 cm depths did not differ between conventionally tilled soil and direct-drilled soil (Table 6). However, reduced tillage resulted in a higher mean temperature than that of the other two tillage treatments. One reason for this might be less reflection of solar energy from these plots.

Maximum and minimum soil temperatures are much more influenced by tillage treatments than the average soil temperature (Table 6). The amplitudes indicated that the fluctuations are greater for conventional tillage than for the other tillage treatments (Table 6).

Compaction

At a 2 cm depth compaction with tractor wheels after sowing non influence on the mean temperature (Table 7). The maximum temperature at this depth was decreased by compaction and the minimum temperature was increased. At the 6 and 24 cm depths the mean temperature increased after compaction. This indicates that more of the heat is tran-

Table 7. Soil temperature (°C) for different compaction, average for tillage systems (May 1983 and 1984)

Depth	Compaction	Mean	Maximum	Minimum	Amplitude
2 cm	Uncompacted	12.0	18.2	7.3	10.9
	Compacted	12.1	17.5	7.8	9.7
	LSD-5%/sl	ns	0.3***	0.1**	0.4***
6 cm	Uncompacted	11.4	14.7	8.4	6.3
	Compacted	11.7	15.7	8.7	6.3
	LSD-5%/sl	0.1***	0.2***	0.1***	ns
24 cm	Uncompacted	9.9	10.4	9.3	1.1
	Compacted	10.3	10.8	9.5	1.2
	LSD-5%/sl	0.1***	0.1***	0.1***	0.1***

Compacted = compacted by tractor wheels

Table 8. Soil temperature (°C) for different compaction of conventionally tilled soil; average for May 1983 and 1984

Depth	Compaction	Mean	Maximum	Minimum	Amplitude
2 cm	Uncompacted	12.0	18.7	6.8	11.9
	Rolled	11.9	17.9	7.2	10.7
	Compacted	11.9	17.4	7.5	9.9
	LSD-5%/sl	ns	0.8***	0.3**	0.9***
6 cm	Uncompacted	11.5	15.2	8.1	7.1
	Rolled	11.4	14.8	8.3	6.5
	Compacted	11.5	14.9	8.4	6.5
	LSD-5%/sl	ns	ns	0.2**	0.5*
24 cm	Uncompacted	9.9	10.4	9.1	1.3
	Rolled	10.1	10.6	9.3	1.3
	Compacted	10.0	10.6	9.3	1.3
	LSD-5%/sl	ns	0.1*	0.2**	ns

Table 9. Soil temperature (°C) for different mulching; average for tillage systems and compaction (May 1983 and 1984)

Depth	Mulching	Mean	Maximum	Minimum	Amplitude
2 cm	Without	13.1	20.2	7.6	12.6
	With	10.6	12.5	8.9	3.5
	LSD-5%/sl	0.2***	0.5***	0.3***	0.7***
6 cm	Without	12.5	16.6	8.9	7.7
	With	10.4	11.7	9.2	2.5
	LSD-5%/sl	0.2***	0.4***	0.2***	0.4***
24 cm	Without	10.7	11.3	9.8	1.5
	With	9.3	9.5	8.9	0.7
	LSD-5%/sl	0.2***	0.1***	0.1***	0.1***

sported down to this depth in compacted as compared with loose soil.

Table 8 gives the results of different compaction of conventionally tilled soil. After ploughing (each year) there was no difference in the average soil temperature at 2, 6 and 24 cm depths. However, the temperature range was influenced by the compaction treatments, especially at 2 and 6 cm depths. Rolling, and especially compaction by tractor wheels, decreased the diurnal temperature variation.

Mulching

The experiment showed that straw cover lowered the mean soil temperature at all three depths by 2.5, 2.1 and 1.4°C, respectively (Table 9). The maximum soil temperature at these depths was reduced much more. At the 24 cm depth there was also a reduction in the minimum temperature. The results for the soil thermal properties showed higher values when the soil was covered with straw as compared with bare soil. Together, these results indicated a higher reflection of solar energy from the straw-covered surface than from the bare soil.

CONCLUSIONS

The results of this study showed that direct drilling reduced soil temperature in the upper layers (0-24 cm) in the early growing season, particularly when the straw was left on the surface. In practice the surface will be clean only after ploughing (conventional tillage). After direct drilling there will be some surface residue, depending on the management of the straw. In this experiment the effect of the straw cover was greater than the effect of compaction and tillage systems. This was true of the soil temperature as well as of the soil thermal properties.

Over the two years there were no significant differences in yields for the tillage systems and compaction treatments (Børresen 1986). However, it was observed that the germination was one or two days delayed when the grain was direct drilled as compared with sowing after conventional tillage.

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Comparative Performance of North European and North American Strains of Reed Canary Grass in Alaska

Performance of reed canary grass

LESLIE J. KLEBESADEL & STEPHEN M. DOFING[1]
University of Alaska Fairbanks, Agricultural and Forestry Experiment Station, 533 E. Fireweed, Palmer, Alaska 99645.

[1] Corresponding author. Agricultural and Forestry Experiment Station, 533 E. Fireweed, Palmer, Alaska 99645.

Leslie J. Klebesadel & Stephen M. Dofing[1]. Comparative Performance of North European and North American Strains of Reed Canary Grass in Alaska. Performance of reed canary grass. Norwegian Journal of Agricultural Sciences 4: 373–387. ISSN

The objective of this study was to compare reed canary grass *(Phalaris arundinacea L.)* strains that are adapted to extreme northern latitudes in Europe with North American cultivars that frequently sustain severe winter injury or total winterkill in southcentral Alaska. The strains Rovik and Hansvoll latitudes from 69° to 70° N. in Norway were markedly superior in winter survival to ten North American cultivars in four experiments, and were found to be more winterhardy than nine other north European accessions from latitudes 55° to 60° N. in two experiments. All accessions from Norway, the Soviet Union and Sweden surpassed the strains from Denmark and North America in winter survival. Seeding-year forage yields of the Norwegian strains were lower than those of the ten North American cultivars. In second and third year forage production, Rovik surpassed Hansvoll but yielded less than many of the compared non-*Phalaris* grasses. Nonetheless, the considerably more winter-hardy Norwegian strains identify a previously unrealized reservoir of winter-hardy reed canary grass germ-plasm for use in Alaska.

Key words: *Phalaris arundinacea* L., reed canary grass, winter survival.

Reed canary grass (*Phalaris arundinacea* L.), a tall-growing, cool-season, leafy, sod-forming, perennial is indigenous to North America, Europe and Asia (Hanson 1972; Hulten 1968; Marten 1985; Smith 1981). Wherever it has become adapted, it produces high yields of forage on fertile soils and serves as pasture, hay and silage (Decker et al. 1967; Marten 1985; Smith 1981).

The species has a very extensive root system and is very drought tolerant in deep soils (Marten 1985; Smith 1981), but its natural habitat is poorly drained and low to wet areas that are subject to occasional flooding. Therefore, unlike most other forage species, reed canary grass thrives on lowland soils; moreover, it is more tolerant of mild to moderate soil acidity than most other cultivated grasses. Because of

its rhizomatous nature, reed canary grass is also valued as an effective soil binder for erosion control in waterways and gullies (Hanson 1972; Marten 1985; Smith 1981). These characteristics suggest that reed canary grass should be useful on the vast areas of soil in Alaska that tend to be poorly drained and/or moderately acidic.

However, the marginal to poor winter-hardiness of all reed canary grass strains evaluated previously in Alaska has been a deterrent to significant use of the species in this state. Irwin (1945) summarized early experimental evaluations of many grasses in Alaska during the period 1898 to 1945 at seven widely dispersed experimental stations ranging from 57° to 65.5° N. Lat. Earliest plantings of reed canary grass were recorded in 1905 at Kenai and in 1906 at the Rampart station on the Yukon River in interior Alaska. These were the only recorded evaluations of the species at those stations and both plantings suffered winterkill in the first winter.

Only six other experimental trials were planted with this grass in Alaska prior to 1945; those were between 1932 and 1940 at the Matanuska and Fairbanks stations and winterkill was usually complete during the first or second winters. Sources of seed and latitudinal adaptation of reed canary grass strains used in those early trials are not known with certainty; however, they were probably obtained through US Department of Agriculture sources in eastern USA or through commercial channels in the Pacific Northwest states.

From 1945 to 1984, Alaska Experimental Station records show seed importations for trials of several reed canary grass cultivars as well as non-cultivar commercial seed from the conterminous states and Canada. All of those cultivars and strains from the northern states or southern Canadian provinces have generally performed poorly in southcentral Alaska, usually succumbing to winterkill during the first or second winter (unpublished information, Alaska Agricultural and Forestry Experimental Station). There is a tendency toward somewhat better winter survival of North American reed canary grass on Alaska's more southern and coastal Kenai Peninsula, where winter stresses are somewhat milder than in the Matanuska Valley (Klebesadel 1983).

Occasional roadside patches of introduced reed canary grass occur in agricultural areas of Alaska (Hulten 1968; Porsild & Cody 1980) where the canary grass has escaped from earlier cultivation attempts. Though persistent in this non-stressful habitat, grass grown in croplands from seed collected from roadside stands is exposed to greater winter stresses and has winterkilled (unpublished information, Alaska Agricultural and Forestry Experimental Station).

The northwestern limits of the native range of reed canary grass in North America apparently reach coastal, southeastern Alaska (Hulten 1968; Porsild & Cody 1980). However, ecotypes from areas of such modest winter stress undoubtedly would not be winter-hardy in this area (Klebesadel 1985b).

The range of reed canary grass extends much farther north in Europe than in North America (Hulten 1968). The study of several other forage species in Alaska (Klebesadel 1984, 1985a, 1985b; Klebesadel et al. 1964; Klebesadel & Helm 1986) has demonstrated that cultivars and strains from northernmost origins are the most winter-hardy in this area, especially those origins characterized by severe winter conditions.

Accordingly, contacts were established to secure the seed of north European reed canary grass strains for evaluation in Alaska. Two of the strains obtained, Rovik and Hansvoll have been adapted in northern Norway at latitudes 69° to 70° N, north of the Arctic Circle. The seed of these strains and of nine other numbered accessions from between 55° and 60° N. in Denmark, Sweden and the Soviet Union was obtained for evaluation. Those and most of the currently available cultivars of reed canary grass from North America (Hanson 1972) were compared with other winter-hardy, non-*Phalaris* grass cultivars at the University of Alaska's Matanuska Research Farm (61.6° N) in southcentral Alaska.

Table 1. Percent age winter survival of 14 reed canary grass strains from diverse latitudinal origins and eight winter-hardy control grasses grown as individual plants in rows in an exposed location at the Matanuska Research Farm (61.6°N). Experiment 1; planted 31 May 1984.

Source	Strain	Latitudinal adaptation or origin	1985		1986	
			Winter survival	Vigour rating[1]	Winter survival[2]	Vigour rating[1]
Reed canary grass:		°N	%		%	
Norway	Rovik	69–70	99 a[3]	5.4 f	98 a	3.4
	Hansvoll	69–70	94 b	5.5 f	100 a	3.0
Canada	Common	44–52	6 cde	9.0 g	0	–
	Castor	44–52	1 e	9.8 i	0	–
	Grove	44–52	1 e	9.8 i	0	–
	Frontier	44–52	0	–	–	–
USA	Vantage	41–44	9 c	9.2 gh	0	–
	Venture	41–44	7 cd	9.2 gh	0	–
	Ioreed	41–44	5 cde	9.2 gh	0	–
	MN-76	43–48	2 de	9.7 hi	0	–
	Palaton	41–44	2 de	9.3 ghi	0	–
	Flare	41–44	1 e	9.8 i	0	–
	Rise	41–52	0	–	–	–
	Superior	42–46	0	–	–	–
Other grasses:						
Norway	Engmo timothy	69–70	100 a	3.6 de	100 a	3.1
	Lavang Kentucky bluegrass	69–70	100 a	2.5 b	100 a	1–2[4]
Alaska	Polar bromegrass	61.6	100 a	1.8 a	100 a	1–2[4]
	Arctared red fescue	61.6	100 a	2.2 ab	100 a	1.8
	Nugget Kentucky bluegrass	61.6	100 a	3.1 cd	100 a	2.2
Canada	Dormie Kentucky bluegrass[5]	69	98 a	2.6 bc	100 a	1–2[4]
USA	Manchar bromegrass	43–47	98 a	4.0 e	100 a	1–2[4]
	Garrison creeping foxtail	45–52	99 a	3.3 d	100 a	1–5[4]

[1]) Means of ratings of all living plants: 1 = excellent survival and vigour, 9 = barely alive (some means exceed 9.0 as a result of total winterkill in some replicates).

[2]) Percentage survival in 1986 of plants alive in 1985.

[3]) Within each column, means not followed by a common letter are significantly different (5 % level) using Duncan's Multiple Range Test.

[4]) Rating of individual plants no longer possible; adjacent plants had coalesced because of active vegetative spread; values shown are estimated range of vigour ratings.

[5]) Selected in Canada from germ plasm orginating in the Murmansk region of the USSR (69°N).

MATERIALS AND METHODS

In spring 1984 four field experiments were established in Knik silt loam (coarse-silty over sandy or sandy-skeletal, mixed, non-acid Typic Cryorthent). Commercial fertilizer which was disked into each ploughed seedbed before planting, supplied nitrogen (N), phosphorus (P) and potassium (K) at 34, 63 and 60 kg/ha, respectively. Randomized complete block experimental designs were used in all trials. A pre-emergence application of dinitro-o-sec-butylphenol (dinoseb) in water solution was sprayed onto each seedbed one to three days after planting in order to control broadleaf weeds.

Experiment 1: On 31 May 1984, 14 reed canary grass strains and eight control grasses listed in Table 1 were seeded at light rates in rows 7.6 m long and 0.46 m apart with six replications. When the seedlings were 5 to 8 cm tall they were thinned by hand to leave individual seedlings about 20 to 30 cm apart. Aerial growth on all plants was mowed and removed on 5 October 1984 and on 21 October 1985, leaving a 5 cm stubble to prevent uneven snow retention on the rows during the winter. On 30 April 1985 and on 13 May 1986 the entire experiment was top-dressed with commercial fertilizer that supplied N, P and K at 34, 63 and 60 kg/ha, respectively. When the growth of surviving plants was well underway in 1985 and 1986, living and dead plants were counted in each row to determine the percentage of winter survival, and each living plant was rated for vigour.

Experiment 2: On 5 June 1984, 22 reed canary grass strains were solid-seeded in rows 3.6 m long and 0.46 m apart with two replications. This test took place in an exposed field area which was subject to wind removal of insulating snow cover and, therefore, exposure to maximum winter stress; the strains used and the results are reported under «exposed site» in the text and in Table 2. Aerial growth on all rows was clipped and removed on 9 October 1984 and 16 October 1985 leaving a 5 cm stubble. Top-dressings of commercial fertilizer in the springs of 1985 and 1986 were applied on the same dates and at the same rates as in Experiment 1. In spring 1985 all rows were rated for estimated percentage of winter survival; in spring 1986 all rows were rated for estimated percentage of full original stand.

Experiment 3: On 7 June 1984 the same 22 strains as used in Experiment 2 were solid-seeded in rows 3.6 m long and 0.61 m apart with two replications in a less exposed field site. This experiment (referred to as «protected site» in the text and in Table 2) was in the lee of a wooded tract and consequently was not subject to wind removal of snow cover during winter. Top-dressings of commercial fertilizer in the springs of 1985 and 1986 were applied on the same dates and at the same rates as in Experiment 1. Each row was rated in spring 1985 and spring 1986, as were the rows in Experiment 2.

Experiment 4: On 24 May 1984, 12 reed canary grass strains were broadcast-seeded in plots 5.5 m long and 1.5 m wide with four replications. Eighteen northern-adapted non-*Phalaris* grass cultivars listed in Table 3 were planted for winter-hardiness and forage-production comparisons; cultivar or common names appear in Table 3. Non-*Phalaris* species included in this test and seeding rates in kg per ha were (some of these species were also included in Experiment 1): Kentucky bluegrass (*Poa pratensis* L) = 29, timothy (*Phleum pratense* L) = 9, meadow fescue (*Festuca elatior* L) = 25, red fescue (*F. rubra* L) = 29, orchard grass (*Dactylis glomerata* L.) = 25, creeping foxtail (*Alopecurus arundinaceus* Poir.) = 25, quack grass (*Agropyron repens* (L.) Beauv.) = 28, pumpelly bromegrass (*Bromus pumpellianus* Scribn.) = 25, and smooth bromegrass (*B. inermis* Leyss.) = 25. 'Polar' bromegrass is predominantly of hybrid origin between smooth and pumpelly bromegrasses. All broadcast-seeded plots of reed canary grass were planted at 20 kg/ha.

All plots were harvested for seeding-year forage yields on 26 September 1984. On 30 April 1985 and 13 May 1986, commercial fertilizer top-dressed uniformly on all plots supplied N, P and K at 141, 47 and 45 kg/ha, respectively. Shortly after first cut forage harvests in 1985 and 1986, ammonium nitrate top-dressed uni-

Table 2. Visual estimates of comparative winter survival and stand filling among reed canary grass strains from diverse latitudinal and geographic origins grown in solid-seeded rows in exposed and protected field sites at the Matanuska Research Farm (61.6°N). Experiments 2 and 3; planted 5 and 7 June 1984, respectively.

Source	Strain	Latitudinal adaptation or origin	Exposed site		Protected site: Ice-covered replicate		Protected site: Replicate not ice-covered	
			Winter 1984-85	19 June 1986	Winter 1984–85	19 June 1986	Winter 1984–85	19 June 1986
		°N	% Winter survival	% of original stand	% Winter survival	% of original stand	% Winter survival	% of original stand
Norway	Rovik	69-70	89 a[1]	98 a	95	100	100	100
	Hansvoll	69-70	83 a	95 a	95	100	100	100
USSR	PI-369291	55. 3	20 b	80 ab	40	85	95	100
	PI-345662	59. 9	20 b	85 a	40	85	90	95
	PI-209979	(?)	13 bc	58 bc	35	90	90	100
	PI-369292	55. 3	8 bc	13 e	25	80	70	80
	PI-406316	59. 9	6 c	20 de	10	45	70	90
Sweden	PI-235547	59. 9	6 c	40 cd	35	95	70	90
Denmark	PI-234694	55. 7	1 c	4 e	2	5	65	90
	PI-235551	55. 1	0	–	10	30	55	95
	PI-234697	60. 4	0	–	2	5	25	70
Canada	Castor	44-52	2 c	2 e	5	15	70	90
	Grove	44-52	1 c	1 e	5	10	60	90
	Frontier	44-52	0	–	1	2	65	90
USA	Rise	41-52	1 c	3 e	20	50	95	95
	Palaton	41-44	1 c	0	10	5	90	95
	Venture	41-44	1 c	0	25	10	75	80
	Vantage	41-44	1 c	1 e	10	15	85	95
	Ioreed	41-44	1 c	1 e	10	20	80	95
	Flare	41-44	1 c	1 e	5	5	75	80
	MN-76	43-48	0	–	0	–	15	40
	Superior	42-46	0	–	0	–	1	5

[1]) Within each column, means not followed by a common letter are significantly different (5 % level) using Duncan's Multiple Range Test.

Table 3. Seeding-year and subsequent oven-dry forage yields over two years of 12 reed canary grass strains from various world sources, and 18 northern-adapted non-Phalaris grasses at the Matanuska Research Farm. Experiment 4; broadcast-seeded plots planted 24 May 1984.

Source	Strain	1984	1985			1986			Three-year total
		26 Sep	9 July	11 Sep	Total	30 June	10 Sep	Total	
Reed canary grass					Kg per hectare				
Norway	Rovik	3077 i-l[1]	2269 g	1662 de	3931 g	2291 def	3549 d	5480 e	12848 g
	Hansvoll	1707 m	898 h	1145 ef	2044 h	898 g	2493 e	3392 f	7143 hi
Canada	Frontier	5975 abc	Tr[2]	Tr	Tr	(WK)[3] - -	- -	- -	5975 ijk
	Castor	5346 b-e (WK)	- -	- -	- -	- -	- -	- -	5346 ijk
	Grove	4582 d-g (WK)	- -	- -	- -	- -	- -	- -	4582 jk
USA	Palaton	6806 a	Tr	Tr	Tr	(WK) - -	- -	- -	6806 hi
	Venture	6312 ab	Tr	Tr	Tr	(WK) - -	- -	- -	6312 hij
	Ioreed	5795 abc	Tr	Tr	Tr	(WK) - -	- -	- -	5795 ijk
	Vantage	5728 abc	Tr	Tr	Tr	(WK) - -	- -	- -	5728 ijk
	Rise	5548 bcd	Tr	Tr	Tr	(WK) - -	- -	- -	5548 ijk
	Flare	5166 c-f	Tr	Tr	Tr	(WK) - -	- -	- -	5166 ijk
	MN-76	4043 f-i (WK)	- -	- -	- -	- -	- -	- -	4178 jk
Other grasses:									
Norway	Lavang Kentucky bluegrass	2358 lm	5818 a	2021 cd	7839 a	5413 a	2403 e	7818 ab	18015 a-d
	Lofar bromegrass	4223 e-i	4829 b	1999 cd	6828 abc	3167 c	4178 a-d	7345 a-d	18397 abc
	Engmo timothy	4605 d-g	2605 fg	1864 cd	4470 fg	2381 def	4313 a-d	6694 b-e	15769 ef
	Salten meadow fescue	3886 g-k	1055 h	3235 a	4290 g	Tr	Tr	Tr	8176 h
	Salten II meadow fescue	2357 h-l	1302 h	2650 b	3953 g	Tr	Tr	Tr	7210 hi
	Hattny orchard grass	3818 g-k	Tr	943 f	943 i	(WK) - -	- -	- -	4762 jk
	Hattfjeldal orchard grass	4043 f-j	Tr	292 g	292 i	(WK) - -	- -	- -	4335 jk
Iceland	Adda timothy	4335 e-h	2695 fg	1841 cd	4537 fg	2628 cde	4402 a-d	7031 cde	15903 def

Alaska	Arctared red fescue	2718 klm	4852 b	2426 bc	7278 ab	3953 b	3661 cd	7615 ab	17610 a-e
	Polar bromegrass	4245 e-i	4829 b	1954 cd	6783 abc	3908 b	4425 a-d	8333 a	19363 a
	Nugget Kentucky bluegrass	2740 klm	3032 efg	6312 a	6312 bc	2942 cd	4492 abc	7435 abc	16487 cde
	Pumpelly bromegrass[4]	4312 e-h	3864 cd	2336 bc	6199 bcd	2740 cde	4020 bcd	6761 b-e	17274 a-e
	Quack grass[5]	3774 g-k	3549 cde	1572 de	5121 d-g	2605 cde	4649 ab	7255 a-d	16151 de
Canada	Commercial bromegrass	4425 e-h	4650 b	1976 cd	6626 bc	2650 cde	5031 a	7682 ab	18734 ab
	Carlton bromegrass	3234 g-j	4133 bc	1864 cd	6199 cde	2538 cde	4649 ab	7188 a-d	17162 b-e
USA	Manchar bromegrass	3481 g-k	3729 cde	1954 cd	5683 c-f	2111 ef	4649 ab	6761 b-e	15926 cde
	Signal bromegrass	5616 bcd	3189 def	1662 de	4852 efg	1752 f	4380 a-d	6132 de	16600 b-e
	Garrison creeping foxtail	2987 jkl	2448 fg	2223 bcd	4672 fg	2021 ef	4312 a-d	6334 cde	13994 fg

[1]) Within each column, means not followed by a common letter are significantly different (5 % level) using Duncan's Multiple Range Test.
[2]) Trace amount of herbage inadequate for harvestable yield.
[3]) No further yields; stand winterkilled completely.
[4]) Composited line representing several indigenous Alaskan collections.
[5]) Grown from seed collected from a local, naturalized population.

formly on all plots supplied N at 95 kg/ha. Forage harvests took place on 9 July and 11 September 1985, and on 30 June and 10 September 1986. Harvest procedures were as described previously (Klebesadel 1985a). All yields are reported on the oven-dry basis (60°C).

RESULTS AND DISCUSSION

All the grasses established well in all the experiments with the single exception of the less vigorous and fewer seedlings per row of the US cultivar Superior in Experiments 2 and 3. Although a heavy seeding rate was used for the low germination seed lot this did not adequately compensate by producing a full stand. In addition a curious anomaly was noted in the differential reaction among reed canary grass strains to the pre-emergence herbicide used. Dinoseb has been used without injury on North American strains of reed canary grass in past years, and none of the strains showed injury in the 1984 plantings. In contrast, there was very obvious herbicidal injury to the Norwegian reed canary grass strains Rovik and Hansvoll. Many of the earliest seedlings whitened and died, and stands from later germinating seeds were very slow to establish. These effects were more apparent in the broadcast plots (Experiment 4) than in the row seedings (Experiments 1, 2 and 3).

Experiment 1: Reed Canary grass Strains and Other Grasses as Individual Plants in Rows

The exposed location and short stubble left in the autumns of 1984 and 1985 in this experiment ensured maximum exposure of plant crowns to winter stresses. When winter survival counts were taken in late May 1985, all North American strains of reed canary grass were rated as 100 % winterkilled. Very slow recovery of a few plants during the growing season, however, prompted second counts and those data appear in Table 1. Despite some late-appearing growth on a few plants, winter survival of all North American strains of reed canary grass was very poor (mean = 3 %). Moreover, ratings of plant vigour were also much poorer than in the other grasses compared, which was due to

severe winter injury (Table 1). None of the plants of the 12 North American strains of reed canary grass survived the 1985–86 winter.

Rovik and Hansvoll reed canary grass from northern Norway survived both winters markedly better (94 % to 100 %) than the North American strains (Table 1). In spring 1985 the vigour ratings of Rovik and Hansvoll plants were somewhere between those of the non-hardy reed canary grass strains and the more winter hardy non-*Phalaris* grasses indicating some winter injury to the Norwegian reed canary grass strains. The two Norwegian strains rated somewhat better in vigour in spring 1986 than in spring 1985, as the second winter (1985–86) was slightly less stressful on plants. All of the non-*Phalaris* grasses showed excellent winter survival and sustained little injury during both winters, as was indicated by the good vigour ratings.

Although no survival or vigour ratings were recorded in spring 1987, virtually all of the Rovik and Hansvoll plants appeared to have survived the third winter.

Experiments 2 and 3: Reed Canary Grass Strains in Rows in Exposed vs. Protected Field Sites

The range in percentage of winter survival among the 22 strains of reed canary grass in solid-seeded rows was great, and survival was markedly influenced by the field location of the experiments which in turn influenced the exposure of the plants to winter stresses (Table 2). Winter survival again was related generally to the latitudinal origins of the strains. The two Norwegian strains from extreme northern origins were much superior to all other entries from more southerly sources, with the greatest differences occurring where exposure increased the severity of winter stresses.

In the exposed-site experiment, estimates of percentage of winter survival of North American cultivars were 2 % or less. Similarly, winter survival of accessions from Denmark was very poor. Even though those three strains derived from more northerly latitudes (55° to 60° N.) than the North American strains, winter stresses in Denmark are apparently too mild for high levels of winter-hardiness to be conferred on strains originating there. The single accession from Sweden was generally similar in hardiness to the three least hardy accessions from the USSR. These results parallel the generally poor winter survival noted previously in southcentral Alaska of Swedish cultivars of Kentucky bluegrass, red fescue, meadow fescue and timothy (Klebesadel 1984, 1985a; Klebesadel et al. 1964; Klebesadel & Helm 1986).

A greater range in percentage of winter survival was seen in accessions from the USSR. The least hardy strain survived at 6 % and the two most winter-hardy were rated at 20 % survival in spring 1985; the latter two were significantly less winter-hardy than the two Norwegian strains, but survived significantly better than the other 18 strains from Europe and North America. With recovery during 1985, and a somewhat less severe subsequent winter (1985–86), the same two USSR strains were rated as 80 % and 85 % of full stands in spring 1986 (Table 2). The superior survival of some USSR strains over those from similar latitudes in Denmark and Sweden is probably due to more severe winter stresses being prevalent in the more continental origins of the USSR strains. Nonetheless, the USSR accessions, originating from between 55° and 60° N. were generally somewhat inferior in winter survival to the more northern-adapted Rovik and Hansvoll from 69° to 70° N. in Norway.

The protected-site experiment was adjacent to a wooded tract and leeward of strong winter winds. Therefore some snow cover protected the grass rows for part of the winter, providing considerably more protection from cold stress than in the exposed site and resulting in generally better winter survival (Table 2). However, an unforeseen difference in winter conditions occurred during the protected-site experiment. One replicate was slightly and uniformly better drained than the other. When mild temperatures thawed the snow during the winter of 1984–85, it refroze as a layer of ice 5 to 10 cm thick on the poorly drained replicate and remained there for over two months («ice-covered» in Table 2).

A similar ice covering did not occur during the winter of 1985–86.

Although winter survival of most grasses was better in both replicates of the protected-site experiment than in the exposed-site experiment, survival in the spring of 1985 was much poorer in the ice-covered replicate than in the one that had not been subjected to ice coverage. In the latter replicate, several of the North American, Danish and Swedish cultivars and accessions survived with relatively minor winter injury.

A comparison of the 1984–85 winter survival percentages recorded in spring 1985, and the percentage of original full stand recorded in June 1986 (Table 2) in the exposed site and in the ice-covered replicate, reveals that severely injured stands have a marked ability to recover. This was more true of the moderately injured USSR and Swedish strains than the more severely injured and less winter-hardy North American cultivars.

Experiment 4: Reed Canary Grass Strains and Other Grasses in Broadcast-Seeded Plots for Forage Production

During the seeding year (1984) forage yields were favoured by well-distributed precipitation that was above normal in each of the months from April through August. In contrast, precipitation in 1985 and 1986 was below normal in four of those five months in both years. The April through August precipitation totalled 21.9 cm in 1984, 2.0 cm above normal; for the same period in 1985, rainfall was 4.9 cm below normal and, in 1986, 2.7 cm below normal.

Seeding-year forage yields of all 12 North American cultivars of reed canary-grass were excellent and generally higher than the forage yields of most of the other 18 grasses compared (Table 3). In contrast, the two most northerly adapted reed canary-grass strains from Norway were among the lowest-yielding entries in the seeding year. To some extent, the lower yields of Rovik and Hansvoll were due to slower establishment owing to herbicidal injury effects but, in addition, they were of considerably shorter height in the seeding year than the North American strains of reed canary grass.

At harvest in late September, seeding-year height of all North American cultivars was 76 to 91 cm. In contrast, Rovik was 56 to 66 cm tall while Hansvoll plants, with least culm elongation and the highest proportion of lax leaf growth of all reed canary grasses, were only 25 to 30 cm tall. Foliage of Rovik plants in late September, unlike all other reed canary-grass strains, showed some bleaching or yellowing. Similar colour change has been noted near onset of winter in leaves of very winter-hardy, northern-adapted red fescue strains at this location (Klebesadel 1985a; Klebesadel et al. 1964).

During the 1984–85 winter, all of the North American strains of reed canary grass were so severely injured that none recovered sufficiently to produce measurable yields in 1985. Other severely injured grasses were Hansvoll reed canary grass and two meadow fescue and two orchard grass cultivars, all from Norway; however, all five recovered sufficiently to produce harvestable yields in 1985. Although Rovik sustained some winter injury, it significantly surpassed Hansvoll in the first cut and in total forage yield in 1985, and in both cuts and in total yield in 1986 (Table 3). Rovik produced significantly less than 10 other non-*Phalaris* grasses in the first cut in 1985. In the second cut, Rovik ranked 14th out of the 30 grasses compared, but yielded significantly less than only four of the other grasses. In total yields of 1985, Rovik ranked 16th but yielded significantly less than only eight of the other grasses. In 1986, only four grasses yielded significantly more forage than Rovik in the first cut, and only five surpassed it by a significant margin in the second cut.

In general forage yields in 1986 for most of the very winter-hardy, non-*Phalaris* grasses were not greatly different from those in 1985. However, the more marginally winter-hardy grasses, such as the two reed canary-grass strains from northern Norway and the timothy cultivars Engmo from Norway and Adda from Iceland, benefited from the milder 1985–86 winter and averaged over 50 % greater production in 1986 than in 1985.

The seven bromegrass strains were all included in the 11 highest-yielding grasses in the 3-year totals. The least winter-hardy grasses in the experiment were the 10 North American reed canary grass cultivars, the two Norwegian orchard grass cultivars, and the two Norwegian meadow fescue cultivars; hence, all were low in the 3-year total yields.

In 1985, most grasses produced more forage in the first cut than in the second; in 1986 the reverse was true. The higher first-cut yields in 1985 are believed to be partly due to a later first cut date, and partly to a carryover effect of abundant moisture during 1984. Moreover, despite otherwise limited precipitation during 1986, over ten cm of rainfall in July helped to increase second cut yields that year.

The below normal precipitation in 1985 and 1986 undoubtedly suppressed forage yields of all grasses in both years, the first cut more than the second cut in 1986. The above normal precipitation in 1984, and the below normal precipitation in 1985 and 1986, tend to distort forage yield comparisons in the 3-year totals (Table 3); the 10 non-hardy reed canary grass cultivars are somewhat disproportionately favoured by the uneven moisture supply over the three years.

CONCLUSIONS

The results reported here provide the informational basis for wider utilization of this species in Alaska.

In these trials the generally good performance of reed canary grass strains from northern Norway reveals that there are levels of winter-hardiness within this species that are considerably superior to the inadequate levels found in the more southern-adapted North American strains.

Although Rovik and Hansvoll are less winter-hardy than several of the cultivars compared in other species, both were markedly hardier than any of the 10 North American reed canary grass strains and several of the other comparable accessions from northern Europe. These results parallel and reinforce earlier findings within other species (Klebesadel 1984, 1985a, 1985b,; Klebesadel et al. 1964; Klebesadel & Helm 1986) confirming that the best winter survival in Alaska is achieved with ecotypes from far northern origins, especially from northern areas where winter stresses are relatively severe.

In Europe the species occurs in Norwegian, Swedish and Finnish Lapland (Alway 1931; Hulten 1968) and on the Kola Peninsula of the USSR at 66° to 70° N. (Hulten 1968). These areas are considerably north of the North American origins of reed canary grass strains that have been non-hardy in this area of Alaska. A greater representation of germ-plasm from the northernmost portions of the range of the species in both hemispheres should be sought and evaluated in Alaska.

The observed capacity of several strains that had sustained considerable winter injury to recover and fill decimated stands reveals a valuable characteristic in reed canary grass. Stands estimated at only 10 % to 40 % winter survival in Experiments 2 and 3 were seen to revive and thicken to much fuller stands during one year of recuperation. Whether utilized for forage or for soil stabilization, recovery and filling of injured, thinned stands by the rapid spread of rhizomes is a desirable attribute that can circumvent the need to till and replant.

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Content

Statens fagtjeneste for landbruket, Moerveien 12, 1430 Ås, Norge
Norwegian Agricultural Advisory Centre, Moerveien 12, 1430 Ås, Norway

Indre Smaalenenes Trykkeri A/S, Mysen