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The influence of feed and water withdrawal time on post mortem biochemical changes and meat tenderness in broilers

Starvation and broiler quality

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The effect of feed and water withdrawal time (6, 12, 18, 24 and 30 hours) on post mortem changes in breast muscles and quality of broiler meat was evaluated. Glycogen content and R value in breast muscles were not influenced by feed and water withdrawal time. However, there was a significant difference in latic acid concentration between broilers starved for 6 hours and those starved for 12 hours. The initial pH and tenderness of the breast muscles decreased significantly after 12 hours feed and water withdrawal. The opposite effect was observed for thigh meat. The most tender thigh meat was found in broilers starved for 30 hours. The feed and water withdrawal time did not influence roast losses.

Key words: Broiler, post mortem changes, starvation time, tenderness.

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Very little work has been reported on the effect of preslaughter fasting on early post mortem metabolism and subsequent meat characteristics. However, the influence of fasting in depleting the glycogen reserve in muscles has been known since the work of Bernard in 1877 (Lawrie 1974). Later, Bate-Smith & Bendall (1949) observed that a 48–72 hours fast decreased the glycogen content in rabbit psoas muscle and raised the ultimate pH. Pingel & Schneider (1987) found a significantly higher pH value in the breast muscle of geese with long starvation, which could point to the fact that glycogen stores were partially used up at the time of slaughter. Pingel & Schneider related lower grill losses to the higher ultimate pH-value but they did not find any significant differences for pH values and grill losses in the thigh muscle.

Warriss et al. (1988), on the other hand, reported that although feed withdrawal had no effect on glycogen concentration in the breast muscle of broiler chickens the glycogen concentration was significantly reduced in the thigh muscle after 12 hours. Ultimate pH was elevated only in the thigh muscle. Also, Ngoka et al. (1982) found that there was no influence of feed withdrawal (15 hours) on glycogen content, initial pH or cooking loss in breast muscle in turkey. However, fasting caused a significant increase in the final pH as compared with the group fed ad libitum. The latter group also had an insignificantly higher shear value than the unfed group.

However, Farr et al. (1983) reported increased toughness (higher shear value) with increasing feed withdrawal time in the breast meat of broiler chickens, but they observed the reverse effect in the thigh meat.

Ehinger (1977) was unable to show the effect of fasting on cooking loss and shear value of broiler chicken breast meat, but he found that

the values for both parameters in thigh meat first decreased after 24 hours of fasting and then increased after 48 hours.

Early post mortem changes are perhaps the most important factors affecting subsequent poultry meat tenderness. Since the rate of onset of rigor mortis is a reflection of the rate of post mortem glycolysis, many of the investigations have attempted to establish a relationship between biochemical changes to glycolysis and tenderness of poultry meat. De Fremery & Pool (1959, 1960), reporting on post mortem changes in chicken breast muscle, found that an accelerated onset of rigor mortis resulted in a more rapid loss of glycogen with a subsequent increase in muscle toughness. The concluded later (De Fremery & Pool 1963) that an increased rate of post mortem glycolysis resulted in tougher poultry meat and that an increase in the rate of lactic acid formation was a decisive factor. Khan & Nakamura (1970) also reported a causative role of lactate in toughness of breast muscle. Stewart et al. (1984) found that pH decline and muscle tenderness were parallel functions of the post mortem glycolysis and rigor mortis processes but were not necessarily related in a cause effect relationship. The divergent results from the influence of fasting on tenderness of poultry meat as well as the lack of information about the relationship between fasting and onset of rigor mortis were the reason for undertaking this study. Thus, in this experiment, an effort was made to evaluate the effect of varying feed and water withdrawal time on certain biochemical and technological characteristics of broiler chicken muscles.

MATERIAL AND METHODS

Commercial broiler chickens of mixed sex were reared on litter in pens in the Experimental Broiler House at the department. From two flocks each containing 600 birds, 75 broiler chickens were chosen at random. They were 38 days old at the start of the experiment. For each withdrawal period, 15 birds were tagged individually and put into transportation crates. They were held without feed and water for 6, 12, 18, 24 and 30 hours respectively prior to slaughter. The birds were slaughtered in a commercial processing plant situated about 50 km from the department. They were electrically stunned, standard cut, bled, scalded and mechanically plucked. About 15 minutes after the blood vessels were cut, the pH of the breast muscles was recorded using a digital Altotest 2 pHMeter equipped with an Ingold insertion probe electrode. At the same time, approximately 10 g samples of Pectoralis major were taken and frozen immediately in liquid nitrogen for R value, glycogen and L lactic acid determination. They were then transported to the laboratory and stored at ÷ 70°C until needed. Frozen muscle samples (Pectoralis major) were extracted with perchloric acid, without prior thawing, in accordance with the procedure described by Dalrymple & Hamm (1973). The concentration of glycogen, L lactic acid and so-called R value were determined in this extract.

Glycogen was determined by the enzymatic method of Dalrymple & Hamm (1973). It was hydrolysed by amyloglucosidase (Boehinger, Mannheim) and estimated as glucose using glucose, 6 phosphate dehydrogenase and hexokinase (Boehinger, Mannheim). L lactic acid was determined by the enzymatic method using commercially available reagents (Boehinger, Mannheim). The R value (the ratio of inosine to adenine nucleotides) was determined according to Honikel & Fischer (1977).

The eviscerated and chilled carcasses were packed in plastic bags and stored in the freezer at ÷ 20°C until they were analysed. Before the analyses, the carcasses were kept for 48 hours at 4°C.

Each half of the 15 carcasses per treatment was packed in a plastic baking bag and roasted in a convection oven at 175°C to an internal temperature of 90°C. The halved carcasses were weighed before and after heating and roast losses (%) were calculated.

The roasted breast and thigh meat were ground separately in a meat grinder (4 mm holes). Samples of 40 g were placed in a Kramer shear-cell (6.5 × 6.5) and sheared by 10 blades

mounted on an Instron (TM-SM) at a crosshead speed of 100 mm/min. The shear values measured from the peak force were expressed as kg force per 1 g sample.

The data was analysed by the Statistical Analysis System (SAS Institute Inc., Carry NC, 1985) and Duncan's multiple range test was applied to determine differences between means.

RESULTS AND DISCUSSION

Biochemical changes in the breast muscles

The pH values, glycogen and lactic acid concentration and ratio of inosine to adenine nucleotides (R value) are presented in Table 1. All these biochemical parameters characterize development of rigor mortis.

The initial pH of breast muscles monitored 15 minutes after death averaged 5.9 and ranged from 5.59 to 6.16. A variance analysis revealed that starvation had a significant influence on pH value. The initial pH of broiler chickens starved for 6 and 12 hours was significantly higher than the pH of the other groups. No significant differences through starvation were detected for initial pH between 18 and 30 hours.

This is contrary to the data of Pingel & Schneider (1987), who found significantly higher initial pH values in breast muscle of geese after 48 hours starvation (6.16) versus 8 hours starvation (6.02).

It is important to emphasize that the decline of pH in breast muscles was very fast in al experimental groups (Table 1). The low pH exhibited by chicken breast muscle testifies to accelerated post mortem alternation in these muscles.

Kijowski et al. (1982), recording pH in breast muscle at different times after slaughter, found an average pH value measured 15 minutes post mortem was 6.14. Lyon et al. (1983) noted that initial pH measured 20 minutes post mortem was 6.3. Stewart et al. (1983) reported that the initial pH of intact breast muscles was 6.4. In another experiment, Lyon et al. (1984) showed that the initial pH of broiler breast muscles measured within 20 minutes post mortem was 6.1. These authors suggested that antemortem stress could influence initial pH values and subsequent rate of pH decline. Davidek & Velisek (1973) comparing the effects of extreme, moderate and absence of struggle on the biochemical change in breast muscle noted

Table 1. Effect of feed and water withdrawal time on biochemical changes in broiler chicken breast muscle measured 15 minutes after slaughtering.

Withdrawal time (hours)	pH	R value (250/260 nm)	Glycogen as µMol glucose/g fresh muscle	Lactic acid µMol/g fresh muscle
6	6.02a	1.07	12.82	77.32c
12	5.96a	1.13	12.94	90.65a
18	5.82b	1.11	13.35	78.23bc
24	5.81b	1.11	13.29	89.82ab
30	5.79b	1.13	11.89	86.37abc
F value	9.47***	0.50	0.37	2.61*
R^2 value	0.35	0.03	0.02	0.14

Each value is the mean of 15 observations
a–c: Means within each column followed by the same letter are not significantly different ($p>0.05$)
***: ($p\leq0.001$)
* : ($p\leq0.05$)

pH values of 5.90, 6.50 and 7.15 respectively 15 minutes after death.

It appears that the differences in the initial pH values between birds within one group could possibly have been due to differences in antemortem stress and may have been caused by differences in reaction of the live brid to handling, holding times and other stress factors.

The development of rigor mortis is closely related to the pH value because the hydrogen ions generated in muscles come from hydrolysis of ATP (Hultin 1985). The onset of rigor mortis occurs when the post mortem pH decreases to around 5.9 and the R value (IMP/ATP ratio) reaches a level of around 1,1 (Honikel & Fischer 1977). According to previously published values (Khan & Frey 1971; Davidek & Velisek 1973), the R value indicates the onset of rigor mortis at values between 75 and 85 % loss of ATP in muscle.

The R value in breast muscles of experimental broiler chickens indicated that conversion of ATP to IMP was very rapid and not affected by starvation time. It is noteworthy that all mean R values were higher than 1.1 except for the group starved 6 hours, which also showed a pH value of 6.02. It would appear from this data that the muscles of chickens from this group (6 hours) were still in a prerigor state, while those from the remaining groups indicated the onset of rigor mortis just 15 minutes after slaughtering. This difference has not been statistically confirmed, mainly on account of the great scattering of individual data (0.91–1.40). It could be explained by the different responses of the birds to stress factors.

The time from death to onset of rigor mortis in poultry muscle has been reported to vary from as early as 10 to 30 minutes post mortem (Khan 1974) or as late as 5 to 7 hours post mortem (Khan 1971). Some of these reported differences in the time of onset of rigor mortis were probably due to the various types of birds used in the experiments and slaughter conditions.

Glycogen content in breast muscles 15 minutes post mortem varied widely from 4.79 µMol/g to 33.98 µMol/g between birds and averaged 13.10. In a living state, glycogen concentration in breast muscles is about 0.5 %, i.e. 27.68 µMol. A comparison of the average values of glycogen between the experimental groups did not show any significant dependency on the duration of the feed and water withdrawal.

The results of the present study concur with the findings of Ngoka et al. (1982), who did not find any effect of feed withdrawal on glycogen content in turkey breast muscle. More recently, also Warriss et al. (1988) ascertained no influence of feed withdrawal on glycogen concentration in chicken breast muscle. According to McCormick et al. (1979), starvation resulted in a metabolic shift from a predominantly carbohydrate metabolism towards increased fat catabolism. They assumed that the fasted chickens utilized fatty acids predominantly as an energy source. This could explain the lack of differences between experimental groups in glycogen content.

The wide variation of glycogen content in breast muscle was reflected in the greatly differentiated values of lactic acid. Consentration of lactic acid ranged from 51.87 µMol/g to 109.96 µMol/g between birds and averaged 83.92 µMol/g.

Khan & Nakamura (1970), reporting lactic acid contents in breast muscle immediately after slaughter, showed 38 µMol/g in chickens with minimum struggle and 86 µMol/g with unrestricted struggle. The findings of Grey et al (1974) support the results mentioned above: 44.0 ± 23 µMol/g lactic acid in breast muscle from restricted-struggle birds and 60.01 µMol/g from unrestricted birds. McGinnis et al. (1989) found 29.2 µMol/g in breast muscle of unoperated (control) broiler chickens immediately post mortem. Grey & Jones (1977) reported a value of 65 (46–85) µMol/g 11 minutes after slaughter. However, Kijowski et al. (1982) ascertained 16.92 µMol/g in the breast muscle of commercially slaughtered broiler chickens 15 minutes post mortem.

In the present study, the lowest mean values of lactic acid were obtained from birds starved 6 hours (72.32 µMol/g) and the highest (90.65 µ

Mol/g) from birds starved 12 hours. The average values of these experimental groups were significantly different ($p<0.05$). However, there was no effect of starvation time on lactic acid content in breast muscles of birds held without food and water 18–30 hours. In the normal resting muscle, there should be a relatively low level of lactic acid. However, when birds struggle extensively before death, much lactate can be produced and for the most part this is present in the muscle post mortem. Moreover, there may be a substantial amount of lactate present at all times because the breast muscle fibres are predominantly fast-twitch glycolitic muscle (Addis, 1986).

On the basis of results presented in Table 1, it is not possible to postulate that feed and water withdrawal time was of great consequence in the biochemical change in breast muscle. It would appear that detection of the effect of starvation on biochemical alternation was hindered by the wide individual variability of the birds. On the other land, our findings showed an accelerated glycolysis and rapid onset of rigor mortis in the breast muscles of experimental chickens. The fast accumulation of lactic acid in combination with rising R value and rapid declining pH indicated the accelerated biochemical processes. Since the broiler chickens were killed is a commercial slaughter house, it is difficult to ascertain which stress factor was decisive in post mortem muscle alteration. A well recognized response to stress is increased glycogenolysis and lipolysis but not all animals react in the same way or to the same degree to any one of these stresses.

Technological characteristics of broiler chicken meat

The investigation of the thawed carcasses included the measurements of pH values in meat slurry, roast losses and shear force values. The mean values of the examined parameters from each starvation treatment together with results of variance analysis are presented in Table 2.

The pH of the breast meat slurry showed the same tendency as pH values recorded 15 minutes after slaughter. The significantly highest values (5.93) were in the meat from birds starved 6 hours and 12 hours. The lowest pH value (5.82) was determined in meat slurry from broiler chickens starved 30 hours. The pH of thigh meat was also significantly influenced by starvation time but the opposite effect was observed. The significantly highest values (6.63) were measured in thigh meat from chickens held without food and water for 24 and 30 hours. Generally, pH of thigh meat showed higher values than breast meat.

Warriss et al. (1988) found that breast meat in birds starved for 36 hours had a final pH slightly but significantly lower compared with the fed control group and the final pH in thigh meat was elevated compared to the fed groups. The PH values reached maximum after 18 hours starvation and then started to decrease.

Ngoka et al. (1982) reported the increasing of the final pH value of 0.06 units in turkey breast muscle starved for 15 hours as compared to the fed ad libitum group.

Food and water withdrawal time did not affect roast losses. This is consistent with the findings of Ehinger (1977) and Ngoka et al. (1982), who did not find any effects of starvation on cooking loss of breast meat.

A comparison of shear values indicated that tenderness of breast meat was influenced by starvation time. Breast meat from birds starved 18 hours and over required more force to shear meat (less tender) than birds starved for less than 18 hours. The highest shear force value (3.69 kg/g) was noted for the 30 hour feed and water withdrawal, whilst the lowest value was recorded for the 6 hour starvation. Shear force in thigh meat had a tendency to rise up to 18 hours, achieving its highest value (1.80 kg/g) at this point with a subsequent decrease. Food and water withdrawal for 30 hours resulted in the lowest shear value (1.60 kg/g) and was significantly different from the shear values of 18 and 24 hour starvation treatments.

It is noteworthy that shear force values of breast meat were always higher than those of thigh meat. This can be attributed to higher pH value (Table 2) and a greater fat content in thigh meat than in breast meat.

Table 2. Effect of feed and water withdrawal time on roast loss, pH and tenderness of broiler chicken meat measured after thawing.

Withdrawal time (hours)	Roast loss (%)	Breast meat		Thigh meat	
		pH	Shear value (kg/g)	pH	Shear value (kg/g)
6	23.4	5.93a	3.03b	6.57ab	1.66ab
12	23.4	5.93a	3.22b	6.55b	1.69ab
18	25.1	5.85b	3.54a	6.55b	1.80a
24	24.2	5.84b	3.59a	6.63a	1.79a
30	23.6	5.82b	3.69a	6.63a	1.60b
F value	0.90	4.33*	7.34***	3.19*	3.30*
R^2 value	0.05	0.20	0.30	0.15	0.16

Each value is the mean of 15 observations.
a–b: Means within each column followed by the same letter are not significantly different ($p>0.05$)
***: ($p\leq0.001$)
* : ($p\leq0.05$)

Similar results were obtained by Farr et al. (1983), who showed increased toughness in breast meat of broiler chickens with increasing length of withdrawal time (6.5 kg/g after 10 hours starvation versus 7.0 kg/g after 25 hours). The reverse was observed in thigh meat, where a shear force of 6.1 kg/g after 10 hours starvation was registered versus 5.5 kg/g after 25 hours. On the other hand, Ngoka et al. (1982) reported the decreasing tendency of shear value in breast meat of turkey starved for 15 hours prior to slaughter as compared to a fed ad libitum group. Ehinger (1977), investigating the influence of starvation and transport on technological characteristics of broiler chickens, could not show any effect of starvation on shear value of breast meat but noted increased tenderness in thigh meat after 24 hours of starvation and a decreasing of tenderness after 48 hours.

Based on the results obtained in this study, a feed and water withdrawal time of no longer than 12 hours is suggested. After this time, tenderness, which is one of the most important characteristics of broiler meat, undergoes unfavourable changes. This is probably related to the rapid decrease of initial pH, which is a reliable and sensitive indicator of the rate and extent of early post mortem biochemical alternation.

SUMMARY

This study was designed to determine the effect of feed and water withdrawal time (6, 12, 18, 24 and 30 hours) on biochemical changes in breast muscles and tenderness of breast and thigh roast in broilers.

Seventy-five unsexed broiler chickens which were 38 days old were used in the experiment. Fifteen broilers for each starvation treatment were slaughtered in a commercial processing plant. The pH in the breast muscles was recorded fifteen minutes after killing. Simultaneously, samples of the breast muscles were taken and frozen in liquid nitrogen for R value, glycogen and lactic acid analyses. Thawed carcasses were used to evaluate meat loss, final pH and shear value of breast and thigh meat.

Feed and water withdrawal time did not affect the glycogen content and R value in the breast muscles. Lactic acid concentration was lowest (77.32 uMol/g) in the breast muscles of birds starved for 6 hours while the highest value

(90.65 uMol/g) was exhibited in broilers starved for 12 hours. The initial pH in the breast muscles decreased significantly after 12 hours feed and water withdrawal. The fast accumulation of lactic acid, high R values (about 1.1) and rapid drop in the initial pH indicated an accelerated biochemical process. Tenderness of breast meat was influenced by starvation time; shear value of breast meat was lowest (3.03 kg/g) after 6 hours starvation and increased significantly after 12 hours. Thigh meat showed the reverse effect. The lowest shear value (1.60 kg/g) was noted for broilers starved for 30 hours. Thigh meat required considerably slighter shear force than breast meat. Roast loses were not affected by feed and water withdrawal time.

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The influence of starvation time on carcass yield and proximate meat composition of broilers

Starvation on yield and composition

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The purpose of the present experiment was to study the effect of various lengths of starvation period on live weight losses of broiler chickens, oven-ready yield of carcasses and proximate composition of breast and thigh meat. One hundred and fifty broiler chickens were randomly selected into five groups and held in transportation crates without feed and water for 6, 12, 18, 24, 30 hours prior to slaughter. Feed and water withdrawal resulted in live weight losses, the rate of losses decreasing, however, with increasing withdrawal time. Oven-ready yield based on initial weight was unaffected by up to 12 hours of starvation but decreased significantly thereafter. Starvation of more than 12 hours had no significant effect on yield calculated on the basis of preslaughter weight. The extended starvation time resulted in a decreased fat content and increased protein content in both breast and thigh meat. However, moisture was reduced significantly only in breast meat.

Key words: Chickens, composition, starvation, yield.

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Proper starvation of poultry is necessary to improve the sanitary conditions during processing operations. During this period, the alimentary tract is emptied non-digested feed components, products of metabolic processes and numerours bacteria. Moreover, the full digestive tract is more difficult to remove and susceptible to breakage during automatic evisceration. Soiling may result in contamination of the carcass.

It is well known that fasting causes live weight shrinkage in broilers. The weight loss increases linearly with the time of starvation after a 4–6 hours period of feed and water withdrawal (Wabeck 1972; Veerkamp 1978; Summers & Leeson 1981; Chen et al. 1983), the live weight shrinkages of broilers varying between 0.06 % and 0.51 % per hour. Veerkamp (1978) reported that weight losses were mainly caused by the losses of edible parts (0.24 % per hour). He concluded that weight losses per hour of fasting had been lower in an earlier period.

The duration of fasting time is one of the factors affecting eviscerated carvass yield and process profitability in the slaughterhouse. Considerable research has been done in this area and the reports generally indicate that extended withdrawal periods of feed or feed and water tend to reduce poultry yield through increased live shrinkage. Individual experiments diverge in relation to the fasting time required before there is a reduction in eviscerated carcass yield.

Some authors have reported no yield losses with up to 16 hours of fasting (Smidt et al. 1964; Summers & Leeson 1979), whereas others have shown a tendency towards yield loss with increased withdrawal time when calculations were based on initial weight (Wabeck 1972; Veerkamp 1986).

No influence of fasting time was found by

Veerkamp (1986) when the carcass yield was calculated as a percentage of live weight immediately prior to slaughter. An opposite trend was observed by Wabeck (1972), who reported an increase in carcass yield (based on pre-slaughter weight) with extended starvation. Smidt et al. (1964) found a tendency towards an increase in carcass yield up to 12 hours with a decrease thereafter.

Drop in yield is probably due to an increased metabolic breakdown of tissue (Smidt et al. 1964; Wabeck 1972). Salmon (1979) has postulated that with extended withdrawal time body tissue is metabolized to provide nutrients and energy and that this has resulted in lower carcass weight and yield. However, Ang & Hamm (1985) did not find any influence of prolonged starvation on proximate composition, vitamins and mineral contents in breast muscle except protein.

Industrial practice of feed and water withdrawal varies from flock to flock according to whether the flock is collected during the day or night. Thus, birds may be processed over a wide range of fasting periods, inducing higher yield losses.

With these factors in mind, the present experiment was designed to measure the effect of varying periods of fasting (from 6 to 30 hours) prior to slaughter on live weight shrinkage, carcass yield and proximate meat composition.

MATERIALS AND METHODS

Broiler chickens used in this study were 39 days old and of mixed sex from one commercial strain. Thay were reared on litter in pens under continuous lighting in the Experimental Broiler House at the Department of Animal Science. Birds received the finishing diet (see Table 1) during the last two weeks prior to the experiment. On hundred and fifty broiler chickens were chosen at random from two flocks containing 600 birds. They were weighed individually at the start of feed and water withdrawal (the initial weight), tagged and placed in transportation crates. They were held without feed and water for periods of 6, 12, 18, 24 and 30 hours prior to slaughter. The thirty broilers for each withdrawal period were weighed directly before killing. The chickens were slaughtered in a commercial processing plant about 50 km from the Broiler House. Loss of live weight (%) was calculated on the basis of initial weight and weight immediately prior to killing. The broiler carcasses were weighed after evisceration and dripping. Oven-ready yield (%) was calculated, based on the initial weight prior to water and feed withdrawals as well on the weight before killing. Chilled carcasses were packed in plastic bags and stored at ÷ 20°C until they were analysed. The carcasses were kept for 24 hours at 4°C before analysis. The contents of dry matter, protein and fat were estimated in breast and thigh meat.

Samples of 5 g were dried at 115°C to a constant weight for 16 hours. Protein contents (%) were estimated in accordance with the Kjeldahl micro method modified according to Tingwall

Table 1. Composition of diet %

	%
Soyabean meal	13.4
Wheat	12.5
Oats	15.0
Corn	12.5
Barley	19.9
Animal fat	3.7
Soyabean oil	0.3
Wheat bran	8.4
Herring meal	5.6
Meat and bone meal	3.5
Mineral mix	1.8
Methionine	0.6
Vitamins	0.5
Pellet binder	2.0
Sugar	0.1
β-glukanaze in sugar	0.2
ME (MJ/kg)	12.1
Dig. protein (%)	16.0

(1978) and the amount of fat determined by Foss-Let (AOAC 1980). The data was analysed using the general linear model, regression and correlation procedures of the Statistical Analysis System (SAS 1985). Treatment means were separated by the Duncan multiple range test.

RESULTS AND DISCUSSION

The live weight losses of birds during fasting and oven-ready yield of carcasses based on initial live weight and preslaughter weight are presented in Table 2. The losses were significantly influenced by the length of feed and water withdrawal time. They increased almost linearly during starvation and were described with the following equation:

$$\text{Live weight losses, \%} = 0.287 \cdot \text{hours} + 1.691 \quad (R^2 = 0.83)$$

The coefficient describing the weight losses per hour as a percentage of initial live weight in the experiments of other authors has varied from 0.06 to 0.51 % per hour (Veerkamp 1986).

The experimental broiler chickens lost 0.52 % of their live weight per hour during the first 6 hours. After this period, weight losses decreased with increasing withdrawal time and were 0.42, 0.41, 0.37 and 0.33 % per hour for periods 6–12, 12–18, 18–24 and 24–30 hours respectively.

The intensive shrinkage of live weight in the first period of fasting was due to emptying of the digestive tract.

Progressive decrease in alimentary canal contents resulted in a reduction in the rate of weight losses. However, the permanent shrinkage of broilers' live weight could not be accounted for only by the emptying of the alimentary canal.

Veerkamp (1978) reported that the weight of the contents in the alimentary canal decreased rapidly during the initial hours of fasting but that losses were negligible after this period. Therefore, the shrinkage of live weight during prolonged fasting was the consequence of body mass losses.

This was reflected in carcass yields calculated on the basis of initial live weight and oven-ready weight. Data showed no loss in carcass yields up to and including 12 hours fasting, after which time the yields were significantly

Table 2. The effect of feed and water withdrawal time on live weight losses and oven-ready yield of broiler chickens

Withdrawal time	Initial weight	Live weight losses	Oven-ready yield based on initial weight	Oven-ready yield based on preslaughter weight
hr	g	%	%	%
6	1382	3.2 e	57.0 a	58.9 b
12	1403	5.0 d	57.3 a	60.3 a
18	1399	7.4 c	55.9 b	60.4 a
24	1386	8.8 b	54.6 c	59.9 a
30	1462	9.9 a	54.5 c	60.5 a
F value	1.06	205.22***	17.23***	6.95***
R^2 value	0.04	0.85	0.37	0.19

Each value is the mean of 30 observations

a–e: Means within each column followed by the same letter are not significantly different ($p \geq 0.05$).

***: $p \leq 0.001$.

reduced. After 18 hours of water and feed withdrawal the yield was 1.4 % lower in comparison with the yield after 12 hours. Extension of the fasting period to 30 hours gave a yield decrease of 1.4 % during the extended period.

Smidt et al. (1964) reported that there was no significant loss in carcass yield during fasting periods of 16 hours or less. The yield was significantly reduced when the fasting period was 24 hours or longer. Similar reports were made by Summers & Leeson (1979), who indicated no yield losses with up to 16 hours of fasting. On the contrary, Wabeck (1972) and Veerkamp (1978, 1986) reported that carcass yield showed a permanent decreasing tendency with increased withdrawal time.

Carcass yield calculated on the basis of preslaughter weight increased significantly after 12 hours of fasting and then remained almost at the same level. Lower yields obtained after 6 hours starvation in relation to 12 hours starvation were due to continuous emptying of the digestive tract during these 6 hours. Yields were more constant during the next period (12–30 hours) because they included losses due to shrinkage in both preslaughter and oven-ready weights. This conslusion is supported by estimates of correlation coefficients. Yield expressed as a percentage of initial weight was inversely correlated with loss of live weight fragment (r= -64) to (r= 0.22). The results obtained indicated that carcass yield is dependent not only on withdrawal time but particularly on when the bird is weighed. Birds weighed just prior to slaughter show greater yields than birds weighed at the beginning of starvation.

Table 3 gives the mean proximate composition of breast and thigh meat from broiler chickens slaughtered after various periods of water and feed withdrawal.

The extended fasting resulted in dehydration in breast meat. The content of water in breast meat after 24 hours was about 0.6 % lower in relation to broiler chickens starved 6 hours. Simultaneously, the protein content of this meat was significantly greater. The amount of fat was significantly reduced after 30 hours starvation. No change was recorded in moisture in thigh meat during starvation. However, water and feed withdrawal significantly affected protein and fat contents. Broiler chickens starved for 30 hours had most of the original protein

Table 3. The effect of feed and water withdrawal time on proximate composition of breast and thigh meat of chicken carcasses.

With drawal time /hrs)	Breast meat			Thigh meat		
	Protein %	Fat %	Moisture %	Protein %	Fat %	Moisture %
6	21.92 b	1.70 a	74.08 a	17.48 c	7.77 a	73.12
12	21.88 b	1.52 ab	74.10 a	17.40 c	7.75 a	72.91
18	22.31 ab	1.44 ab	74.01 a	18.26 b	7.43 a	72.81
24	22.66 a	1.71 a	73.42 b	18.72 ab	8.02 a	72.47
30	22.85 a	1.19 b	73.41 b	18.87 a	5.98 b	72.70
F value	4.66**	3.75**	4.76**	12.23***	5.17**	2.31
R^2 value	0.22	0.19	0.22	0.43	0.24	0.12

Each value is the mean of 15 observations
a–c: Means within each column followed by the same letter are not significantly different ($p \geq 0.05$)
***: $p \leq 0.001$
** : $p \leq 0.01$

content and also less fat in thigh meat. This partly agrees with the results of Ang & Hamm (1985), who reported a significantly higher percentage of protein in the breast meat after 20 hours and 32 hours fasting compared with 8 hours fasting. However, they did not find any change in the fat and moisture content of breast meat during the broiler starvation.

Based on the results of the present experiment, the following conclusion can be drawn. Extension of feed and water withdrawal for more than 12 hours may cause reducation in oven-ready yield and changes in the proximate composition of broiler chicken meat.

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Russian Satellite Imagery of Norway - An Accuracy Investigation of KFA-1000

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The planimetric accuracy of a Russian KFA-1000 image covering parts of southern Norway is examined using a camera calibration procedure. The results indicate a two-dimensional accuracy of less than 9.0 m, and the investigated image has a slightly oblique geometry caused by an omega tilt of 10 gons. The suitability and accuracy of different types of check points are also discussed.

Key words: Camera calibration, geometric accuracy, remote sensing, satellite mapping.

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V/O Sojuzkarta is a foreign trade association of the Russian geodesy and cartography administration. Since the 1960s it has been offering satellite products and services to socialist and developing countries throughout the world, and continues to do so today even to non-socialist countries.

One of the most interesting products from a satellite mapping point of view, is the images from the KFA-1000 camera with image scale of aprroximately 1:250000 and a given resolution of 5-10 m (Piskulin 1989).

Figure 1 shows some specifications of the different Sojuzkarta products.

Our KFA-1000 image proved to have a scale of 1:350000 and a correspondingly greater survey height than the table indicates.

A comparative study of different satelliteborne cartographic sensors carried out by the University of Hannover (Konecny et al. 1988) examined the metric camera (MC), the large format camera (LFC), SPOT and the Russian KATE-200 and KFA-1000.

The main aim of the study was to test the possibilities of image orientation by aerial triangulation, coordinate determination and topographic data extraction with these images. The results indicate that there is a somewhat greater degree of completeness with the KFA-1000

Camera type Type of survey	Survey height (km)	Survey scale	Number of zone	Spectral range (mm)	Film format size (mm)	Covered square (km)	Film's overlap (per cent)	Resolution (m)
KATE—200 Polyzonal	~250	~1:1250000	3	500–600 600–700 700–900	180 × 180	220 × 220	60	15–30
MKF—6 Polyzonal	~300	~1:2500000	6	460–500 500–560 580–620 640–680 700–740 780–860	56 × 81	140 × 200	20 60 80	20
KATE—140 Only visible zone	~250	~1:1750000	1	500–700	180 × 180	310 × 310	20 60 80	60
KFA—1000 Colour spectrozonal	~250	~1:250000	1	570–670 670–800	300 × 300	75 × 75	60	5–10

Figure 1. Products offered by Sojuzkarta (Piskulin 1989).

images than with the multispectral SPOT images. Although the resolution of the KFA-1000 images seems to be slightly better than SPOT results, the panchromatic SPOT has a better height accuracy than the KFA-1000, according to the German comparison.

The Agricultural University of Norway's Department of Surveying acquired a KFA-1000 image covering parts of southern Norway for accuracy examination. This image has also been the subject of comparative investigations with SPOT images (Dick 1989).

Since just one image of the area was available, the geometric study was reduced to being a two-dimensional one (Figure 2).

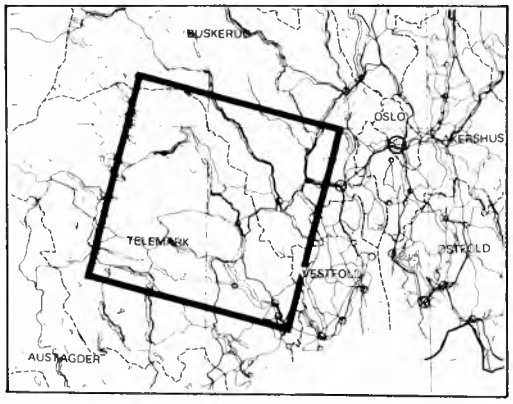

Figure 2. Area covered by the KFA-1000 image

ACCURACY TEST

Background

Different approaches can be taken when carrying out an accuracy test on single space or aerial photographs. Since no height information can be obtained from the image, the ground truth must be reduced to any map projection system before comparison can be made.

Satellite images in digital form can be delivered in different stages of geometrical correction. Images from photographic sensors have the 'original' geometry, and corrections must be taken into consideration before further use of the image can be made.

The check points to be used in the test can be sorted in various ways, some of them (model points) to determine the model, others (check points) to estimate the accuracy. (Sharpe & Wiebe 1988).

Another approach is to use all the points as model points and then later as check points. At least when no group of points is more reliable or accurate than another, this seems to be as appropriate a method as any other.

Test procedure

Selection of check points

A total of 130 check points were chosen for the accuracy test. Some of the criteria for point selection are listed below:

- Points had to be identifiable on the paper copy in the scale 1:100000.
- Objects with the best possible contrasting features were preferable. In the test area small lakes surrounded by light (dry) boggy vegetation were well suited.
- The position had to be unique on the map, with no changeable details, e.g. arable land.
- The object had to be symmetrical in shape. (Large buildings were not used because of vertical extension and disturbing shadow.)
- The object had to be as small as possible.

By using computer-assisted methods like pattern recognition in the measurements, other types of points (and requirements) could probably have been used without any loss of accuracy (Table 1).

Coordinate determination of check points

Planimetric coordinates are taken from map series in 1:5000 or reduced scale 1:10000 or 1:20000 for some of the points. The coordinates are given with 5 m

Table 1. Distribution of the 110 check points on different feature classes

Lakes	44	(also small islands)
Roads	33	(road intersections)
Bridges	21	(centre of bridge or pier)
Rivers	8	(outlet or intersection)
Others	4	(e.g. vegetation border)
Total	110	

resolution in the NGO system (Transverse Mercator) zones II and III. All points are transformed to zone II before further calculations.

Height values for correction and calculation are taken from given elevations (lakes) or contours.

Image measurement of check points

There was no available photogrammetric instrument in Norway of sufficient accuracy that could be used because of the large format of the image (30x30cm). Ways of overcoming the problems included:

- Making a photographic reproduction of the image in suitable pieces, measuring with traditional instruments and joining the pieces together before calculation. Disadvantage: Lack of control in the tranformation because of to few fiducials.

- Shipping the image to a foreign institution which has an instrument with image carriers of sufficient size. Disadvantage: Greater possibility of identification errors by the operator because of 'unknown' check points.

The solution decided upon was to adapt a three-axial calibration instrument at the research centre (SINTEF) in Trondheim. With 8x magnifying optics and a calibrated spatial accuracy of 1µm, the instrument seemed to match the task.

Out of the 130 pre-selected check points, 110 were measured on the image in addition to the five fiducial marks. Because of limited time for taking the measurements, not all the points were measured twice as planned. The fiducials were measured three times: at the start, in the middle and at the end of the sequence. This turned out to be very important since a mysterious shift in the coordinate system occurred in the measurements. Since the shift was constant throughout the whole image, we could estimate the size from the additional fiducial measurements. The time of the shift was found by including the points, one by one, in the later calculations and terminating when the residuals of the last point were higher than 'normal'.

Correction and estimation

The image coordinates were corrected with reference to the earth's curvature by using the terrain height and position in the image of the check points.

The accuracy estimation was carried out using camera calibration procedures. Input data required were 3D terrain coordinates and image coordinates of all the check points in addition to image coordinates of the fiducials. The number of unknown parameters in the estimation was selected and successive iterations performed.

The theory of bundle adjustment and a least squares element method are used in the calculations. The parameters can be given different weights to provide special results, i.e. 'freezing' the camera constant value (Andersen 1989).

Gross error detection

Points with large residuals were checked manually to find possible digitizing or typing errors before any rejection from the further calculation. A total of 17 out of 110 points were rejected because of large residuals and their distribution between the different feature classes is given in Table 2.

Table 2. Distribution of rejected points

Feature class	Number of check points	Rejected points	Percentage of rejection in each class
Roads	33	8	24
Bridges	21	3	14
Lakes	44	4	9
Rivers	8	0	0
Others	4	2	50
All	110	17	15

CAMERA CALIBRATION RESULTS - KFA 1000

Coordinates of the projection center (in metres)
and rotations (in gons).
Below: mean errors in same units.

XO	YO	ZO	FI	OMEGA	KAPPA
198518.750	-13276.903	350128.094	-0.1722	-9.5432	-15.0215
148.333	145.714	47.180	0.0268	0.0264	0.0022

Calibration parameters:

Focal length: F=1015.330

Radial distortion:	dR=-0.57803E+01*R		(R in mm, dR in mykron)
Radial distortion:	dR= 0.22926E-03*R**3	+- 0.15E-04*R**3	(R in mm, dR in mykron)
Radial distortion:	dR= 0.10032E-08*R**5	+- 0.47E-09*R**5	(R in mm, dR in mykron)
Film distortion:	dX=+0.980394781*X	+- 0.084457*X	(X in mm, dX in mykron)
Film distortion:	dX=-0.174375147*Y	+- 0.069851*Y	(Y in mm, dX in mykron)
Film distortion:	dX= 0.004273811*X*Y	+- 0.000599*X*Y	(X,Y in mm, dX in mykron)
Film distortion:	dY=-0.000215480*X*Y	+- 0.000621*X*Y	(X,Y in mm, dY in mykron)
Film distortion:	dY=-0.004236376*X*X	+- 0.000425*X*X	(X in mm, dY in mykron)

Distortion curve:
(positive value of dR means off-center distortion)

R (mm)	dR (mykron)
0.0	0.0 +- 0.0
10.0	-57.6 +- 0.0
20.0	-113.8 +- 0.1
30.0	-167.2 +- 0.4
40.0	-216.4 +- 0.9
50.0	-260.0 +- 1.7
60.0	-296.5 +- 2.8
70.0	-324.3 +- 4.2
80.0	-341.8 +- 6.0
90.0	-347.2 +- 8.0
100.0	-338.7 +- 10.1
110.0	-314.5 +- 12.2
120.0	-272.5 +- 14.1
130.0	-210.5 +- 15.7
140.0	-126.2 +- 16.6
150.0	-17.1 +- 16.9
160.0	119.4 +- 16.8
170.0	286.1 +- 17.4
180.0	486.1 +- 21.3
190.0	722.6 +- 30.6
200.0	999.0 +- 46.3

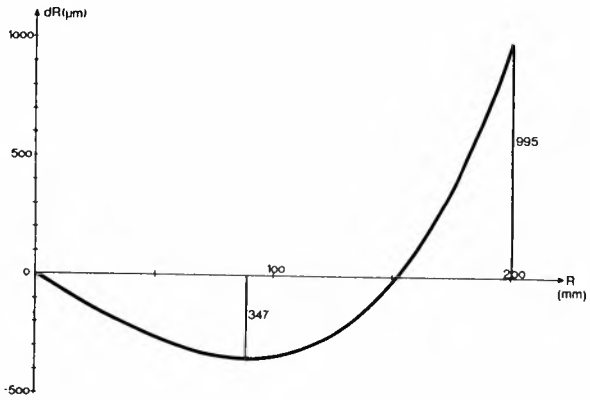

Figure 3. Camera calibration results

RESULTS

Camera calibration

The accuracy test was carried out using camera calibration routines and in addition to the point accuracy results inner orientation data of the KFA-1000 were estimated.

Two essential results were :

- Values of up to 990 microns for the radial lens distortion.
- Deviation of 9.5 gons from the vertical axis perpendicular to the flight direction (Omega rotation).

Both these effects have to be considered during further use of the images by including corrections or standard photogrammetric treatment.

The camera calibration results are given in figure 3.

Geometric accuracy

The residuals of the control points result

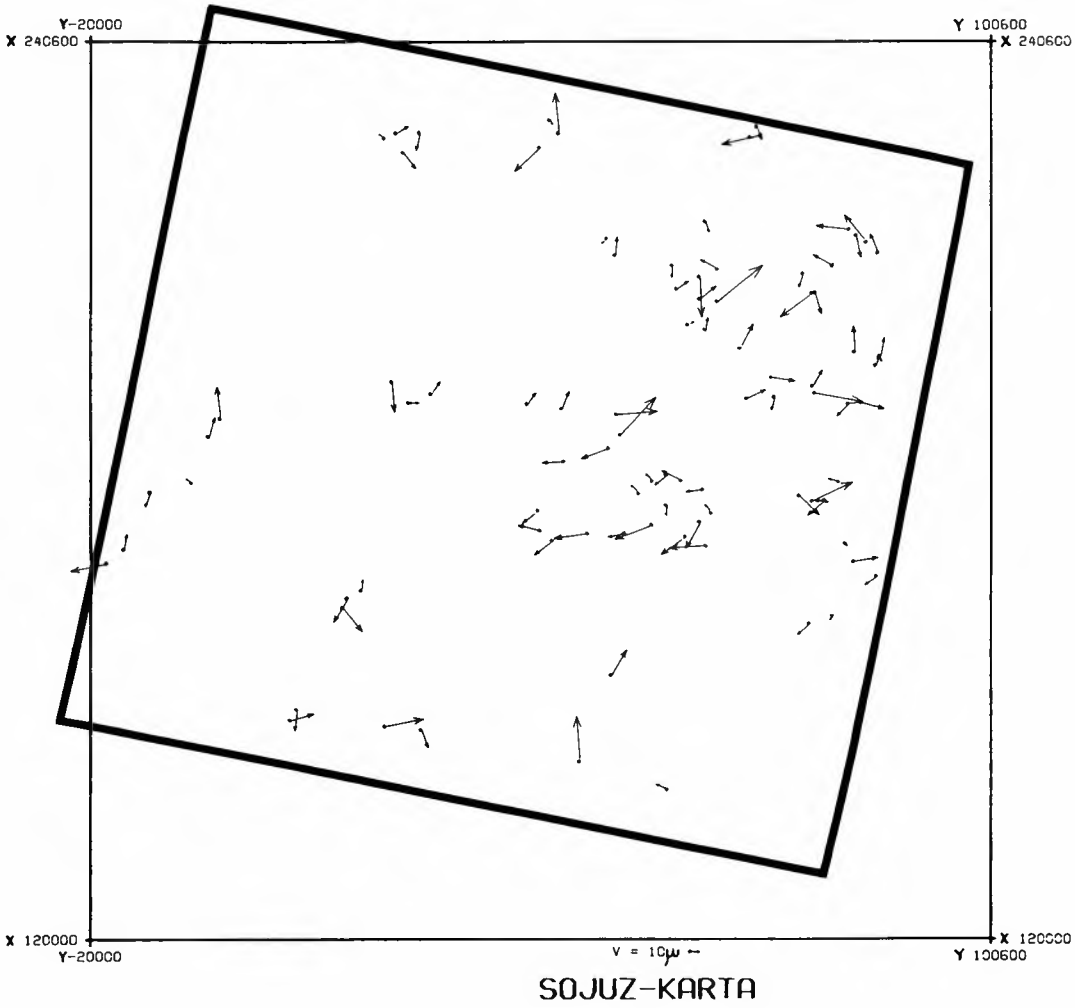

Figure 4. Residuals and distribution of the check points

from a least squares estimation of the camera calibration. All the points are given equal weight, independent of feature class.

Residual sizes and distribution in the image are shown in figure 4 and check points from all feature classes are included.

The check points were divided into groups depending on feature classes, and residuals were estimated for each group. The results were more or less as expected in accordance with size, shape and type of objects selected as check points. The differences between the groups were not considerable, however (figure 5).

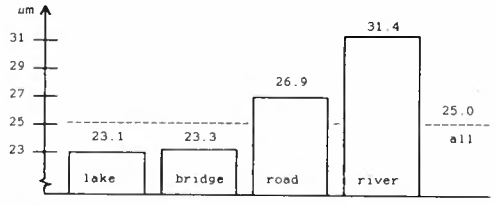

Figure 5. Mean planimetric (two-dimensional) errors of the check points

In the test, many sources of error affected the overall accuracy results. The measured error, e_{meas}, can include the map error, e_{map}, the digitizing error, e_{dig}, and the actual image error, e_{image}. If we consider these errors to be independent, they can be combined in the following way:

$$e_{meas}^2 = e_{image}^2 + e_{map}^2 + e_{dig}^2$$

The digitizing error indicates the accuracy with which the image measurements are performed. Additional measurements of the fiducial marks were the basis for our estimation and therefore the results also show the repetition accuracy.

A two-dimensional error of 25 µm was the result of our measurements. This seems to be too high and may have been caused by some inconvenient functioning of the joystick steering the digitizer instrument.

The check point coordinates taken from topographic maps scaled at 1:5000 are said to have a mean error of ± 0.25mm in map scale or approximately 3.5 µm in image scale. In the reduced scale, 1:20000, the corresponding error is 14 µm. From the number of points in the different scales, the one-dimensional map error is estimated to be 6 µm and $e_{map} = 9$ µm.

From the error sizes above, the mean image error, e_{image}, is estimated to be 12 µm, which is far less than the measured error. The contribution of other errors, in this case the digitizing error in particular, overshadows the 'real' image error.

CONCLUSION

The accuracy test results from this investigation indicate that the Russian KFA-1000 images from Sojuzkarta have planimetric characteristics similar to those of panchromatic SPOT images shown in other tests. A two-dimensional mean error of 25 µm was the overall result. In applications where the 'original' 30x30 cm image can be used directly or in scanned, digital form, the KFA-1000image will be an alternative or supplement to SPOT.

The rather oblique geometry and the size of the radial distortion of the image, however, call for a photogrammetric treatment to maintain accuracy.

In the investigation the accuracy and reliability of the different feature types selected as check points were determined. As might be expected with two IR sensible channels, 'waterfeatures' were the best for identification and measuring. Small, circular lakes surrounded by light (dry) vegetation together with bridges gave the best results, while asymmetric and often indistinct crossroads were less accurate as check points.

Since only one image was available

in this investigation, the stereoscopic (3D) properties of KFA-1000 must await a later investigation.

Along with the results from the study of the image quality and information content (Dick 1989), the results indicate that the KFA-1000 images represent an interesting supplement in satellite mapping projects.

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Polycross Progenies in Cocksfoot (*Dactylis Glomerata* L.) Grown under Variable Environmental Conditions

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The paper reports on the results of a series of field experiments in which the mixed progenies from 9 polycross (Pc) fields, 62 half sib (HS) families and 5 control populations were grown in four blocks at each of three locations. Observations were carried out over two or three years. The most important results may be summarized as follows:

1. Significant and sizeable genetic variation was observed between mixed Pc progenies and HS families for dry matter (DM) yield, in vitro digestibility and crude protein content of the fodder, and in winter survival. Strong interactions were found between populations or families over years and locations. The second order interactions, population/family x location x year were particularly strong for DM yield as well as for the quality characters. By means of ecovalence (EV) estimates the differences in yield stability could to some extent be traced back to the origin and prehistory of the materials.
2. Genotypic correlations approximately equal to 0.7 were found at all locations between winter survival and DM yield in the first cut, showing that about 50% of the variation in yield can be accounted for by the variation in winter survival.
3. The correlations between frost tolerance and resistance to two fungal diseases determined in the laboratory on one hand, and winter survival and DM yield in the field on the other, were in general low, although significant in some cases. A low ($r = -0.259$) but significantly negative correlation between winter survival at Ås in South Norway and Alta in North Norway demonstrates how difficult it is to simulate field conditions in the laboratory.
4. There was a tendency towards negative genotypic correlations between DM yield on the one hand and in vitro digestibility and protein content on the other. Comparisons of mixed Pc progeny means do, however, indicate that yield and the two quality characters are relatively easy to combine.

Key words: Cocksfoot, polycross progenies

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Previous investigations have shown that there is great genetic variation between and within local populations of cocksfoot from various parts of our country (Larsen 1978, 1979, Honne 1979). In the experiments reported so far, the initial materi-

als comprised random samples of clones laid out in field experiments at one location (Honne 1979), or similar clones tested for characters associated with winter hardiness under laboratory conditions (Larsen 1978, 1979). Based on the results from variability experiments with 200 clones from each of three local populations, Honne conducted a selection procedure for high and low yield, intercrossing the selected clones and laying out a seed-sown field experiment which included selected and non-selected populations. Aastveit (1985) continued this experiment over a period of nine years. In one of the populations there was an average response to selection of about 9% for high dry matter (DM) yield as compared with the nonselected population. In the other populations the selection responses in both directions were negligible.

Based on the results from experiments with clones and a reciprocal hybrid between two populations a number of polycross (Pc) fields were established and seed harvested during the years 1979-81. In 1982 a series of field experiments were laid out at three locations in which, in addition to the dominating market varieties, progenies from 10 Pc fields were included along with some nonselected and selected populations. In this paper the results from this series of experiments are presented.

MATERIAL AND METHODS

The material included in the Pc fields came originally from three local Norwegian populations, namely Leikund, Hattfjelldal and Holt, and from the Danish variety (Unke). The origins of these populations are as follows:

Leikund: Local population from the Valdres valley in South Norway, 61°07'N, about 525 m a.s.l. Leikund has been a dominating market variety until 1982.

Hattfjelldal: Local population from Hattfjelldal in mid-Norway,65°30'N, about 235 m a.s.l. Market variety since 1976.

Holt: Local population from Tromsø in North-Norway, 68°57' N, about 25 m a.s.l.

Unke: Breeding variety from the former Pajbjergfonden, Børkop, Denmark, 55°30'N. (Honne 1979).

Table 1 surveys the materials in each of the 10 Pc fields and the progenies included in the experimental series. The clones in Pc fields 6/79 and 7/79 had been selected in three generations for high frost tolerance in the laboratory (cf. Larsen 1983). The selection of clones for high or low yield was based on data from replicated variability experiments with 200 clones from plants selected at random within each population. As can be seen from Table 1, Pc fields 18/80 and 19/80 contained full-sib (FS) families from reciprocal pair crosses between Hattfjelldal and Leikund. Families from reciprocal crosses were included because Honne (pers. comm.) at that time had found some evidence of cytoplasmic effects.

All the Pc fields were laid out in accordance with the design suggested by Olesen & Olesen (1973). In order to obtain enough seed from the various families the Pc fields were seed harvested over two years. Since the clones in most of the Pc fields varied significantly in respect of seed production, mixed progenies were produced by mixing equal weights from each family.

If all the individual families from the 10 Pc fields had been included, the entries would have been too large to handle. For this reason and also because of insufficient seed from some families, the number of entries was restricted to mixed progenies from 9 Pc fields and in addition 62 HS families, two of the original populations (Leikund and Hattfjell-

Table 1. Survey of the polycross fields

Polycross	Material in the polycross	Progenies included in the present exp. series
6/79	22 clones from Hattfjelldal selected over 3 generations for high frost tolerance	Mixed progeny + 22 HS families
7/79	22 clones from Unke selected over 3 generation for high frost tolerance	Mixed progeny
14/79	22 clones from Leikund selected for low yield	Mixed progeny
15/79	22 clones from Leikund selected for high yield	Mixed progeny
30/79	22 clones selected for high yield in Leikund and Hattfjelldal	Mixed progeny + 13 HS families
16/80	22 clones from Holt selected for high yield	6 HS families
8/80	22 clones from plants of Leikund, selected in a 4th year ley, at Skagahøgdi 1150 m a.s.l.	Mixed progeny + 20 HS families
17/80	22 clones from Hatt-fjelldal selected for high yield	Mixed progeny + one HS family
18/80	22 FS families from pair crosses between Leikund (♀♀) and Hattfjelldal (♂♂)	Mixed progeny
19/80	22 FS families from pair crosses between Hattfjelldal (♀♀) and Leikund (♂♂)	Mixed progeny

dal), the varieties Apelsvoll and Frode, and the breeding population Hatney.

The individual experiments in the series were laid out at the following locations:

Agricultural University, Ås in south east Norway, 59°40'N, about 100 m a.s.l.

Vågønes Research Station near Bodø in mid-Norway, 67°17'N, about 20 m a.s.l.

Holt Research Station, Section Alta, 69°57'N, about 10 m a.s.l.

The experimental design comprised special types of incomplete blocks described by Aastveit (1977). Each of the four complete replications at each location was divided into four groups, each containing 19 families or populations and in addition two control populations, which in this case comprised the market varieties Apelsvoll and Hattfjelldal. The allocation of entries to groups, the distribution within groups and the distribution of groups within replication were all at random. For the Ås experiment the fertilizers N, P and K were applied at

rates of 12.0, 2.9 and 5.5 kg/decare (1 decare = 1/10 ha), respectively, at the time of sowing and this was repeated annually in the spring. Additional N, P and K at rates of 10.0, 2.9 and 4.6 kg/decare, respectively, were applied after the first cut. In the case of three cuts, rates of 8.0, 1.9 and 3.6 kg/decare, respectively, were applied after the second cut. Approximately the same amounts of fertilizer were applied at the other two locations in the spring and after the first cut. The sizes of the machine sown plots were 9.5, 12.0 and 8.25 m^2 at Ås, Vågønes and Alta respectively. At all locations, sowing at a rate of 2 kg/decare took place in the middle of May 1982.

All trials were harvested at the beginning of panicle emergence (cut 1). The second cut was taken 40 days after the first one, and in the case of a third cut (Ås, 1984) again 40 days later. All experiments were harvested twice in 1983. The Ås experiment should have been harvested three times each year, but due to draught only two cuts were taken in 1983. In the third year (1985) only the Alta experiment was harvested, and then only once (cut 1). At harvest, samples of about 1 kg from each plot were weighed raw, dried at 60°C for 72 hours and weighed again for determination of the DM percentage. The same samples were used for determination of quality. For the Ås experiment, in vitro digestibility of dry matter (IVDDM%) was determined at the Vågønes Research Station according to a slightly modified Tilley & Terry (1963) method. In addition, samples from all plots in all experiments and cuts were subjected to NIRR analyses of digestibility and crude protein of the DM at the Løken Research Station according to the method described by Aastveit & Marum (1989). Only the NIRR results are presented in this paper.

Winter survival was determined visually by judging the percentage of cover on each plot in the autumn and spring about one month after growth had started. Start of growth in the spring and growth cessation in the autumn were also determined by visual inspection of each plot. Frost tolerance, as well as resistance to snow mold (*Fusarium nivale*) and *Typhula ishikariensis*, was measured in the laboratory by A.M. Tronsmo in the Institute of Plant Pathology by application of methods described by her (Tronsmo 1985, 1988a, b). Frost tolerance in the laboratory was also determined by Tronsmo using methods described by Larsen (1978) and Tronsmo (1985,1988a, b).

STATISTICAL

Since repeated observations were made on the same plots over years in all the individual experiments, years are considered as a fixed factor in a split plot analysis (Steel & Torrie,1980, Nguyen & Sleper 1983, Rognli, 1987). Expected mean squares are based on a random effect model for replication (R) and entries (G = families or populations), while years are fixed effects. In series of field experiments it is quite usual to consider the effect of location as random, too. In this case, however, we have chosen to consider location effects as fixed, since the locations were chosen along a latitude gradient in order to investigate adaptability of the material within a great range of environmental conditions. Random or fixed in this connection may have consequences for the analysis of stability and establishment of potential synthetic varieties. The interaction between family or population with average performance of location over years can be considered as predictable, while the interaction between family or population over years within locations is random (cf. Lin & Binns 1988).

Our data were first analysed according to the model

$$X_{ijkl} = \mu + G_i + R_{l(k)} + L_k + (GL)_{ik} + (GR)_{il(k)} + Y_j + (YL)_{jk} + (YR)_{jl(k)} + (GY)_{ij} + (GLY)_{ijk} + e_{ijkl} \quad (1)$$

where μ is the general mean, and G, R, L and Y designate effects of family or population, replication, location and year, respectively. The first two effects are supposed to be random variables with zero expectation and variances σ^2_G and σ^2_R. The effects (GL), (GR), (YL), (YR), (GY) and (GLY) designate effects of interactions while (e) indicates unexplained deviations. These effects are also supposed to be independent random variables with expectation equal to 0 and variances σ^2_{GL}, σ^2_{GR}, σ^2_{YL}, σ^2_{YR}, σ^2_{GY}, σ^2_{GLY} and σ^2_e, respectively. Since a great three-factor interactions (GLY) occured for most of the characters studied, the individual experiments have also been analysed by means of the same model, but excluding location effects and their interactions. The various variance components are tested for significance by appropriate linear combinations of mean squares. Covariance components have been estimated by means of the same model. In order to estimate the stability of the various families and populations, ecovalence (EV_i) is used.

RESULTS

All families and populations

The data over all locations and two years are complete for DM-yield, IVDDM% (NIRR) and percentage of crude protein (NIRR). For DM yield in particular the quality of the three experiments was quite different, as illustrated by the estimated coefficients of variation (CV) presented in Table 2. An unweighted analysis of variance of all families and populations over all locations and two years resulted in a highly significant three-factor interaction for all characters analysed over all locations (Table 3). In spite of great interaction effects significant overall entry effects were also obtained for all characters with the exception of DM yield in the first cut.

Table 4 presents the overall location means for each year. The table shows that the number of days to panicle emergence increased with latitude, while the DM yield, at least in total, was reduced. It is remarkable, however, how high the yields of cocksfoot were in Alta, which is close to the 70th latitude. In the second year the DM yields in Alta were almost the same in the first and second cuts as

Table 2. Coefficient of variation at each location for the most important characters (two years)

Character		Location		
		Ås	Vågønes	Alta
DM yield	cut 1	9.15	22.80	21.16
	cut 2	6.59	11.11	13.62
	Total	4.83	13.81	15.41
IVDDM% Lab,	cut 1	1.45	-	-
» »	cut 2	1.65	-	-
IVDDM% NIRR,	cut 1	1.37	1.45	1.35
» »	cut 2	1.33	1.58	1.83
Crude protein,	cut 1	5.00	7.75	8.99
» »	cut 2	6.06	6.29	7.34
Winter survival		10.85[1)]	31.00[1)]	41.02[2)]

[1)] Second year. [2)] Third year

Table 3. Significance level of some variance ratios for all items and over all locations and two years

Source of variation	DM yield			IVDDM% NIRR		Protein% NIRR	
	Cut 1	Cut 2	Total	Cut 1	Cut 2	Cut 1	Cut 2
Locations (L)	***	***	***	***	***	***	***
Entries (G)	ns	**	*	***	***	*	*
Years (Y)	***	***	***	***	***	***	***
L x Year	***	***	***	***	***	***	***
G x Location	*	ns	ns	ns	ns	ns	ns
G x Year	**	***	**	ns	ns	ns	**
G x L x Y	***	***	***	***	***	***	***

ns = not significant at the 5% level
* $0.01 < P < 0.05$
** $0.001 < P < 0.01$
*** $P < 0.001$

Table 4. Location means of all families and populations

Character	Ås		Vågønes		Alta		
	1983	1984	1983	1984	1983	1984	1985
Panicle emergence (days after April 30)	31.9	30.4	40.0	-	71.4	47.3	40.1
DM (kg/decare)							
Cut 1	514	511	397	139	366	501	377
Cut 2	311	390	258	347	194	368	-
Total	825	1236	655	486	560	869	-
Winter survival (%)	100	95.1	98.1	69.2	-	-	64.3
IVDDM% (NIRR)							
Cut 1	73.7	74.8	76.5	76.3	76.3	72.5	-
Cut 2	72.7	75.4	66.8	71.9	75.1	72.8	-
Protein% (NIRR)							
Cut 1	13.9	17.6	16.5	19.0	15.7	15.2	-
Cut 2	14.3	16.5	13.2	12.4	12.3	15.3	-

those in Ås. The superiority of Ås as compared with Alta for total yield in 1984 was mainly due to an extended growing season in Ås and therefore a third cut. Table 4 shows that the crude protein content of DM and the IVDDM% varied considerably between locations, years and cuts. There was, however, no clear cline variation of these characters with latitude.

Table 4 also gives the overall means for winter survival in the spring in the second year of harvest for the experiments in Ås and Bodø, and for the third harvest year in Alta. Unfortunately, winter survival was not observed in Alta in 1983 and 1984. What can be said is that the stand in Alta was good after the first two winters. In order to get a better test for winter hardiness the experi-

mental field in Alta was not ploughed in the autumn of 1984. Instead, the stand of each plot was evaluated in the autumn of 1984 and in the spring of 1985. As shown later the variation in winter survival became large in 1985.

Stability in DM yield of all families and populations has been studied by estimation of EV values over locations and two years (Table 5). Among the five control populations Leikund came out with the lowest EV for DM yield in the first cut as well as in total DM yield and may therefore be regarded as the most stable among the control populations. On the other hand, Apelsvoll had the highest EV values. Among the mixed Pc progenies 6/79 and 7/79 were the most stable. The clones in these polycrosses were selected for high frost tolerance within the populations Leikund and Unke, respectively (Table 1). The clones in the polycrosses 14/79, 15/79, 30/79 and 8/80 were all selected from Leikund. It should be observed that the mixed progenies from all these polycrosses were more unstable than the nonselected Leikund population. Highly significant genotype- environment interactions were also found for HS families within the same populations, and from Table 5 it can be seen that great ranges in stability among HS families from the same polycrosses were observed.

Mixed Pc progenies and varieties

Tables 6 and 7 present the means of DM and quality averaged over two years for the mixed Pc progenies and the five control populations. The experimental errors at Vågønes were considerable, therefore only the variance ratio for crude protein between items became significant. At Ås highly significant item- year interactions were obtained for DM yield in the second cut and in total. As a result of these interactions, the average differences between items were not significant. The item variance ratios for DM

Table 5. Stability of DM yield in cut 1 and in total over three locations and two years. Ecovalence estimates (EV)

Population/variety	Cut 1		Total	
	Average (EV)	Range	Average (EV)	Range
Control populations				
Leikund	644		176	
Hattfjelldal	775		284	
Apelsvoll	1063		315	
Hatney	747		256	
Frode	819		204	
Pc progenies				
6/79 mixed prog.	661		263	
6/79 22 HS families	743	520-1027	292	223-379
7/79 mixed prog.	497		187	
8/80 » «	840		262	
8/80 20 HS families	830	646-1026	251	126-338
14/79 mixed prog.	731		265	
15/79 » «	879		283	
17/80 » «	693		207	
18/80 » »	849		282	
19/80 » «	975		378	
30/79 » «	834		275	
30/79 13 HS families	887	715-1159	287	184-360

Table 6. Dry matter (DM) yield in kg per decare of nine mixed polycross (Pc) progenies and five populations/varieties at three locations and in total averaged over two years

Pc progeny/population	Ås			Vågønes			Alta			Average		
	Cut 1	Cut 2	Total	Cut 1	Cut 2	Total	Cut 1	Cut 2	Total	Cut 1	Cut 2	Total
Pc 6/79 Mixed	534	332	1022	333	330	663	465	288	753	444	317	813
Pc 7/79 «	441	310	903	273	313	586	339	258	597	351	294	695
Pc 8/80 «	507	356	1030	261	298	559	373	285	658	380	313	749
Pc 14/79 «	517	336	1009	279	293	572	386	244	630	394	291	737
Pc 15/79 «	503	369	1048	241	306	547	460	326	786	401	334	794
Pc 17/80 «	477	345	987	268	303	571	410	281	691	385	310	750
Pc 18/80 «	536	352	1056	270	286	556	457	271	728	421	303	780
Pc 19/80 «	534	349	1053	239	301	540	432	330	762	402	327	785
Pc 30/79 «	525	360	1059	278	311	589	383	298	681	395	323	776
Leikund, commercial	540	320	1026	321	308	626	464	309	773	441	312	802
Hattfjelldal, «	559	339	1061	297	329	626	433	290	723	430	319	803
Apelsvoll, «	574	340	1089	274	304	578	409	277	686	418	307	779
Hatney	501	351	1014	285	288	573	463	260	723	416	299	770
Frode, «	471	368	1014	310	335	645	305	276	581	362	326	747
Significance levels:												
Pc progeny/population (G)	***	ns	ns	ns	ns	ns	*	ns	**	***	***	***
G x year (Y)	ns	**	**	ns	ns	ns	ns	*	ns	ns	ns	ns
G x Location (L)										ns	ns	ns
G x L x Y										ns	ns	ns
L.s.d. (0.05)	26						71		52	39	18	45

Tabell 7. Percentage in vitro digestability (IVDDM%) and crude protein content of nine mixed Pc progenies and five populations/varieties averaged over 2 years (NIRR data)

Pc progeny/population	Ås				Vågønes				Alta				Average			
	IVDDM%		Protein%		IVDDM%		Protein%		IVDDM%		Protein%		IVDDM%		Protein%	
	Cut 1	Cut 2	Cut 1	Cut 2	Cut 1	Cut 2	Cut 1	Cut 2	Cut 1	Cut 2	Cut 1	Cut 2	Cut 1	Cut 2	Cut 1	Cut 2
Pc 6/79 Mixed	73.9	74.3	15.0	15.1	75.6	68.9	17.9	12.9	72.9	73.4	14.4	13.2	74.3	72.2	15.9	13.7
Pc 7/79 «	73.2	74.8	15.4	16.1	76.1	69.2	17.0	12.3	75.6	73.7	15.2	13.7	74.9	72.4	15.9	14.1
Pc 8/80 «	74.3	73.5	17.2	16.1	77.0	69.7	17.8	13.0	73.6	74.4	16.0	14.2	75.0	72.4	17.0	14.4
Pc 14/79 «	73.4	74.3	15.8	16.1	76.0	68.8	17.6	12.9	71.1	73.8	14.6	13.5	73.8	72.3	16.2	14.2
Pc 15/79 «	73.8	74.9	16.0	16.2	77.1	70.3	18.9	13.0	73.6	74.2	15.1	13.3	74.9	73.1	16.7	14.2
Pc 17/80 «	75.1	74.3	15.8	15.4	76.0	69.0	17.5	12.7	74.5	74.8	15.7	14.0	75.2	72.7	16.3	14.0
Pc 18/80 «	73.7	73.8	16.1	16.4	76.3	69.4	17.6	12.7	74.7	73.9	15.0	13.7	74.9	72.3	16.2	14.3
Pc 19/80 «	74.0	73.0	16.0	15.5	75.9	69.6	19.1	13.4	75.0	73.7	15.9	13.5	75.0	72.1	17.1	14.1
Pc 30/79 «	74.3	74.5	15.6	15.8	76.2	69.0	17.2	12.7	72.8	73.2	15.7	13.2	74.6	72.2	16.2	13.9
Leikund, commercial	73.5	74.8	15.3	15.6	75.7	69.4	16.6	13.6	74.3	74.3	16.4	15.1	74.5	72.9	16.1	14.8
Hattfjelldal, «	74.0	73.2	15.4	15.4	75.8	69.5	17.3	12.3	73.5	74.0	15.4	13.9	74.5	72.2	16.1	13.9
Apelsvoll, «	73.1	74.3	15.5	15.6	76.3	69.6	17.5	13.4	73.7	74.0	15.2	13.1	74.4	72.6	16.1	14.0
Hatney, «	75.2	73.6	15.5	15.3	75.6	69.3	17.2	12.8	74.3	73.5	14.4	13.5	75.0	72.1	15.8	13.9
Frode, «	74.2	74.8	15.5	15.7	77.2	70.6	17.2	13.0	74.9	74.2	16.0	13.8	75.5	73.2	16.3	14.2
Significance levels:																
Pc progeny/population (G)	**	**	**	ns	ns	ns	ns	**	**	ns	ns	**	ns	ns	**	ns
G x year (Y)	ns	ns	ns	ns	ns	ns	ns	ns	ns	**	ns	ns	ns	ns	ns	ns
G x Location (L)													ns	ns	ns	ns
G x L x Y													***	***	**	**
L. s. d. (0.05)	0.5	0.5	0.4					0.4	0.7			0.5			0.3	

yield in the first cut, IVDDM% in both cuts and crude protein content in the first cut were highly significant, however. For DM yields in the Ås experiment none of the Pc mixed progenies exceeded the market variety Apelsvoll, which is the leading market variety in this region of the country. Although statistically significant, the differences between items for quality were relatively small.

Highly significant and relatively large differences were found between items for DM yield in Alta (Table 6). The varieties Apelsvoll and Frode are quite clearly not adapted to the growing conditions in the North. Clone selection for low (14/79) and high (15/79) yield in the Leikund population has led to a significant difference between the two Pc mixed progenies when grown under conditions of hard winter stress in Alta.

On average over all locations the mixed progeny from Pc 6/79 gave the highest DM yield, although not significantly higher than that of Hattfjelldal, the variety from which the clones in Pc 6/79 were selected. As already shown (Table 5), Pc 6/79 (mixed) also seems to possess high developmental stability. High developmental stability was found for Pc 7/79 (mixed), too, but this population is quite inferior in average DM yield (Table 6). There was no significant difference between the mixed Pc progenies from reciprocal FS families (18/80 and 19/80).

The HS-families

From the Pc 6/79 all HS families were included in this series of experiments. Originally the plan was to include also all the 22 families from Pc 8/80. However, two of the clones in this cross failed to produce enough seed, therefore only 20 families were included. In addition, the series comprised 13 HS families from Pc 30/79 and one HS family from Pc 17/80. The data from Pc 6/79 and 8/80 were subjected to separate analyses of variance. Interactions between HS families and years and between HS families and

Table 8. Means and ranges of HS families or populations averaged over two years

			Total DM Yield		IVDDM% (NIRR)				Protein % (NIRR)			
					Cut 1		Cut 2		Cut 1		Cut 2	
Location	Population	N	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range
Ås	Pc 6/79	22	995	924-1065	74.0	73.2-74.8	73.5	72.8-74.3	15.7	14.9-16.1	15.2	14.5-15.9
	Pc 8/80	20	1036	952-1101	74.4	73.6-75.2	74.1	72.7-75.1	15.8	14.9-16.6	15.4	14.6-16.7
	Pc 30/79	13	1074	1016-1151	74.2	72.9-74.9	74.4	73.6-75.2	15.6	15.1-16.2	15.2	14.6-16.0
	All items	76	1030	902-1165	74.2	72.9-75.6	74.0	72.7-75.5	15.7	14.9-16.6	15.4	14.5-16.7
Alta	Pc 6/79	22	746	641-841	73.3	71.7-74.4	73.7	72.3-74.3	15.0	14.1-15.6	13.8	13.0-14.5
	Pc 8/80	20	711	580-844	74.7	73.4-75.8	74.1	72.8-75.1	15.5	14.4-17.4	13.8	12.9-14.3
	Pc 30/79	13	704	637-777	74.3	72.2-75.3	74.0	73.1-75.8	15.6	14.9-16.3	13.8	12.8-14.5
	All items	76	715	580-844	74.0	72.2-75.8	74.0	73.1-75.8	15.4	14.1-17.4	13.8	12.8-15.1
Vågønes	Pc 6/79	22	543	498-602	76.2	75.4-77.4	69.2	68.1-70.2	17.9	16.8-19.5	12.8	11.4-14.2
	Pc 8/80	20	578	512-623	76.6	75.9-77.2	69.3	68.7-70.1	17.7	16.1-18.8	13.0	11.5-14.1
	Pc 30/79	13	579	515-607	76.4	75.9-77.4	69.6	69.2-70.2	17.7	16.4-18.1	12.5	11.7-13.6
	All items	76	569	498-663	76.4	75.4-77.4	69.3	68.1-71.0	17.7	16.1-19.5	12.8	11.4-14.2

locations were very pronounced for the families in Pc 8/80, showing that genetic variation in developmental stability also exists within the local populations. Table 8 shows the means and ranges of HS families from three Pc-fields for total DM-yield, IVDDM% and crude protein content. All populations and families are included in the table for comparisons.

As can be seen from Table 8, some HS families gave the highest yields in Ås as well as in Alta. Families HS-14 from Pc 6/79, and HS-29, HS-30, HS-36 and HS-40 from Pc 8/80 also gave the highest average yields obtained in this series, all populations and families taken into account.

Winter survival

Winter survival was observed in both years at Ås and Vågønes, but only in the third year in Alta. Coverage percentages in the spring of the three years were as follows:

	1st year	2nd year	3rd year
Ås	100	95	-
Vågønes	98	69	-
Alta	-	-	64

Significant differences between families and populations were found at Ås and Alta. Owing to high error, no significant difference between items could be found at Vågønes. As can be seen from Table 9 most of the populations and families had satisfactory winter survival in Ås, with the exception of some of the HS families from Pc 6/79. In Alta, on the other hand, the best winter survival was found among the HS families from Pc 6/79. The factors determining winter survival in Alta and Ås would therefore seem to be different. For all families and populations there was a significant negative correlation between winter survival in Ås and Alta ($r = -0{,}259$, $p < 0.05$). Even for the HS-families from Pc 6/79 this correlation was negative ($r = -0.29$), but did not reach the 5% level of significance. Winter survival was not significantly correlated with stability as measured by the ecovalence.

Genotypic correlations between characters

Genotypic correlations were estimated between all characters measured or scored in each of the two years and at each location. Some of the most important correlations are presented in table 10. The correlations are based on all

Table 9. Distribution of HS families from Pc field 6/79, Pc field 8/80 and three varieties for winter survival in Ås and Alta

Winter survival (% Family/variety	20	30	40	50	60	70	80	90	N	Mean
Ås, year 2.										
Pc 6/79, HS families					1	3	5	13	22	90
Pc 8/80, HS families									20	98
Leikund								1	1	98
Hattfjelldal								1	1	100
Apelsvoll								1	1	99
Alta, year 3:										
Pc 6/79, HS families				3	6	9	3	1	22	75
Pc 8/80, HS families	1	3	1	2	6	3	4		20	65
Leikund						1			1	72
Hattfjelldal					1				1	66
Apelsvoll				1					1	59

Table 10. Some genotypic correlation coefficients (rg)

Characters	Ås		Vågønes		Alta		
	1983	1984	1983	1984	1983	1984	1985
DM yield cut 1 vs.							
- DM yield cut 2	0.02	0.26	0.32	0.49	0.37	0.18	-
- Earliness	- 0.13	- 0.42	- 0.20	-	-0.32	- 0.28	- 0.22
- IVDDM%	0.02	- 0.20	- 0.23	- 0.15	0.07	- 0.35	-
- Protein%	- 0.21	- 0.39	- 0.07	- 0.66	- 0.38	- 0.65	-
- Winter survival	-	0.67	0.05	0.70	-	-	0.67
DM yield, cut 2 vs.							
- Earliness	- 0.19	0.09	- 0.20	-	0.10	0.12	-
- Wintersurvival		0.21	0.04	0.38	-	-	-
IVDDM% vs. protein%	- 0.05	0.34	0.20	0.14	0.19	0.36	-
Winter survival vs.							
- Earliness	-	- 0.24	0.08	-	-	-	- 0.18

76 families and populations included in this series. It is not easy to find good estimates of the standard errors of genetic correlation coefficients. Significance levels are therefore left out in Table 10. Where the coefficients are 0.3-0.4 or higher, there is good reason to regard them as being of considerable significance.

Table 10 shows that with two exceptions there was a positive genotypic correlation between DM yield in the first and second cuts. The correlation between DM yield in the first cut and earliness, measured as days to panicle emergence, was negative in all cases. In nearly all cases IVDDM% and percentage of crude protein were negatively correlated with DM yield, showing that high quality was generally associated with low yield. These correlations were highest for protein content. High genotypic correlations were obtained in the second and third years of ley between winter survival and DM yield. Based on the genotypic correlation coefficients nearly half of the variation in DM yield in the first cut the second and third years of ley could be attributed to variation in winter survival. Most of the other correlations given in Table 10 are low and inconsistent over years and locations.

Correlations between laboratory tests and field observations

All 76 families and populations included in this series of field experiments were tested in the laboratory for frost tolerance and resistance to two fungi. Freezing tolerance was tested at two temperatures, -10 and -11°C, and the fungi tested were *Fusarium nivale* (S1) and *Typhula ishikariensis* (S2). Table 11 shows the correlations between laboratory tests on the one hand and DM yield and winter survival in the field on the other. The table shows that significant, relatively low but rather consistent correlations were obtained between freezing tolerance on one hand and DM yield and winter survival on the other in both Ås and Alta. In Ås significant but small correlations were also observed between *F. nivale* resistance in the laboratory and field observations of yield and winter survival. The lack of significant correlations for the Vågønes experiment may be due to insignificant genetic variation for yield as well as for winter survival.

Table 11. Phenotypic correlations between laboratory tests and field observations

	Field				
	DM yield in first cut			Winter survival	
Laboratory	Year 1	Year 2	Year 3	Year 2	Year 3
Trial 1 (Ås)					
Freezing tolerance					
T10	0.25*	0.25*		0.33*	
T11	0.03	0.45**		0.41**	
Fungi resistance					
S1	0.15	0.28*		0.27*	
S2	0.20	0.06		0.01	
Trial 3 (Vågønes)					
Freezing tolerance					
T10	0.03	0.21		0.11	
T11	0.07	0.14		0.07	
Fungi resistance					
S1	0.13	-0.05		0.01	
S2	0.19	-0.00		0.04	
Trial 2 (Alta)					
Freezing tolerance					
T10	0.39**	0.49**	0.21		0.32*
T11	0.15	0.41**	0.12		0.18
Fungi resistance					
S1	0.00	-0.15	-0.12		-0.19
S2	0.22	0.11	0.02		-0.05

Discussion and conclusions

Cocksfoot or orchard grass, as it is also called, belongs to the polyploid complex in the genus *Dactylis* (Stebbins 1956). Based on extensive cytological studies, Müntzing (1937), and later on Myers (1941) found *Dactylis glomerata* to be an autotetraploid species. The polyploid species of *Dactylis* have a wide natural distribution in western Asia, Europe and northern Africa compared with the diploid *Dactylis* species (Stebbins 1956). According to Stebbins the northern border for the natural distribution of the tetraplaid *D. glomerata* in Norway is around the 67th latitude, which means close to the Vågønes Research Station, where one of the experiments in the present series was located.

The clones in 8 of the 10 polycrosses reported upon here came from two local populations, Leikund and Hattfjelldal. The latter one originates from a valley in mid-Norway, while the other (Leikund) originates from a valley at a fairly high altitude in South-Norway (Table 1). Honne (1979) has shown in field experiments with clones that there is great genetic variation within both populations for yield, earliness and other quantitative characters. The present series of experiments with mixed progenies from nine Pc fields, HS families

from some of the polycrosses and five control populations, has first of all demonstrated strong interactions between families and populations over years and locations. In particular, the three-factor interaction between family or populations with year and locations was strong for yield as well as for quality characters. Genotype-environment interactions of this kind seem to be quite common in cocksfoot (Breese 1969, Gray 1982). By means of EV estimates great differences in stability between varieties, mixed Pc progenies and HS families within polycrosses, have been demonstrated (Table 5). Among the control populations the variety Leikund had the highest stability. The variety Hattfjelldal and the selected population Hatney also had high stability, while the variety Apelsvoll proved to be rather unstable. Among the mixed Pc progenies, 6/79 and 7/79 had the highest stability. Since the clones in Pc 6/79 came from Hattfjelldal, this result was not unexpected. What was unexpected, however, was the high stability of mixed Pc 7/79, since the clones in Pc 7/79 came from the Danish variety Unke, which under Norwegian growing conditions has proved to be a poor adapter. There is therefore good reason to believe that the high stability of the Pc 7/79 mixed progeny is due to selection for high frost tolerance in the laboratory over three generations (Larsen 1983). The yield level of the Pc 7/79 mixed progeny, however, was very low compared with that of the other mixed Pc progenies and control populations (Table 6). The other mixed Pc progeny that came from clones also strictly selected for frost tolerance in the laboratory, Pc 6/79, was considerably more stable than Hattfjelldal, which is the origin of Pc 6/79. It is noteworthy that the mixed progeny of Pc 6/79 gave the highest DM yield averaged over two years and all locations, although this superiority as compared to the other items was not significant (Table 6).

The mixed progenies from both Pc 14/79 and 15/79, derived all their clones from the variety Leikund. In the former the clones had been selected for low raw matter yield, while in the other case the clones were selected for high RM yield. Table 6 shows that this selection has resulted in a significant difference in RM-yield over locations and years. A comparison with the performance of Leikund shows that the response tended toward low yield.

Winter survival is important in cocksfoot, in the southern lowlands as well as at higher latitudes and in the highlands. At all three locations genotypic correlations of approximately 0.7 were found between winter survival and DM yield in the first cut (Table 10), showing that about 50% of the variation in DM yield can be accounted for by the variation in winter survival. The correlations between characters determined in the laboratory and winter survival in the field were in general fairly low, as can be seen from Table 11. Based on the HS-families from Pc 6/79 and Pc 8/80 Tronsmo (1988a,b) found narrow sense heritability estimates ranging from 0.55 to 0.72 for frost tolerance and from 0.33 to 0.61 for the two fungal diseases *Fusarium nivale* and *Typhula ishikariensis*. Despite these relatively high narrow sense heritabilities, the correlations between resistance to the two diseases in the laboratory on the one hand and winter survival and DM yield in the first cut on the other were slightly significant in only one case each (Table 11). The corresponding correlations between frost tolerance in the laboratory and winter survival and DM yield in the first cut were higher, although none of them exceeded 0.5 (Table 11).

As with several other researchers (e.g. Julen & Mårtensson 1974, Frandsen & Fritsen 1982, Shenk & Westerhaus 1982), highly significant genetic variation was observed for the quality characters IVDDM% and crude protein content. Like DM yield these characters showed strong genotype-environment inter-

actions. There was, however, no clear clinal variation along the latitude gradient as reported by Deinum et al. (1981). There was a tendency towards negative genotypic correlations between DM yield in the first cut and IVDDM% as well as crude protein content. Comparisons between mixed Pc progenies with different yield potential showed that these relationships cannot be very close, however (cf. Tables 6 and 7).

The mixed progenies from two of the polycrosses (18/80 and 19/80) were included in the series in order to test for cytoplasmic effects in population crosses. There were no indications of such cytoplasmatic effects, however.

The results from this series of experiments have been used in the construction of new synthetic populations which are under multiplication.

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Variation in seed dormancy in genetically homogeneous material of small grain species

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This study investigates why some kernels of a genetically homogeneous sample with a certain degree of seed dormancy germinate readily, while others display delayed germination or remain dormant. Considerable variation in the intensity of seed dormancy was found between fields of cereal cultivars, between individual plants, stems of the same plant, spikelets within spikes or panicles, and between kernels at different positions of the spikelets. Frequently there was close correlation between stage of development of the plant and the intensity of seed dormancy. The variation in the seed dormancy recorded may be the reason for single kernels initiating germination at different points in time during the germination test, whilst there is no satisfactory explanation for some kernels in a sample of deep dormancy germinating readily while most of the kernels resist prolonged exposure to optimal germination conditions.

Key words: Barley, dormancy, oats, wheat.

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Seed dormancy is a stage of incomplete physiological ripeness of the seed; it blocks or postpones the initiation of the germination process. It is genetically controlled and its mode of inheritance is fairly well known. However, the intensity of seed dormancy is strongly influenced by environmental factors during both the ripening period and, later, the storage of threshed seed. Environmental factors also have a strong influence on the manifestation of seed dormancy (Strand 1989a,1989b).

For each seed the dormancy character is of a qualitative nature - the seed either does or does not germinate. In a sample of seed, however, the character appears to be quantitative, because some seeds germinate readily while others remain dormant, or onset of the germination process is delayed. This happens even in seed samples grown in the same field from cultivars homozygous for the dormancy character. This study investigates why it is that some seeds in a sample respond favourably to optimal germination conditions while others do not.

It is known from earlier investigations that dormancy develops gradually during the ripening period. It attains its maximum at yellow ripeness or a few weeks later and thereafter it disappears slowly as a function of time and temperature. This means that plants and seeds at different developmental stages might also be at different stages of rise or decline in dormancy. Based on these assumptions the possible effects of stage of development on seed dormancy were investigated. This included differences between single plants, between main stem and lateral stems, seed positions in spi-

kes or panicles, seed positions in spikelets, and between seed in central and lateral rows of the spikes of six-row barley.

MATERIAL AND METHODS

Kernels on different plants or on different stems of plants having at least two heads of normal size were harvested for determination of seed dormancy. One kernel from each of the specified positions in the spikes, panicles or spikelets was collected from each of 100 plants. The samples were germinated at 10, 20 or 30°C for 7 or 10 days depending on the dormancy level of the material in order to obtain dormancy readings at the best level of differentiation on the percentage scale, (Strand 1991). The dormancy tests were carried out by germinating 100 kernels on wet filter paper. The filter paper, specified as 100 g per sq m, was moistened with 200 ml water per 100 g paper. The percentage of dormant seeds in such tests was used as a measure of the intensity of seed dormancy. The seeds were considered as having germinated at the first sign of morphological development.

RESULTS AND DISCUSSION

In a grain field there are always minor differences between plants in the stages of development. There are also differences between main stem and lateral stems on the same plant, between spikelets at different positions in the spikes or panicles and between kernels at different floret positions in the spikelets. Differences in developmental stages interacting with increasing or decreasing seed dormancy have the potential for creating variation in the intensity of seed dormancy in samples of grain.

Differences in seed dormancy between plants and between main stem and lateral stems

There were significant or highly significant differences in seed dormancy between plants in five of the eight fields investigated (Table 1). The low number of kernels on each plant (wheat and two-row barley) and main-lateral stem interaction made the test of differences between plants less effective. The non-significant differences for field Nos 7 and 8 are probably due to a too low and a too high germination temperature, respectively, in relation to the dormancy level of the plants, which resulted in weak differentiation.

Table 1. Percentages of dormant seed. Lowest and highest means of ten single plants in eight different fields of wheat and two-row barley

Field No	Means for single plants		Difference
	Lowest	Highest	
1	15.0	50.5	35.5 ns
2	4.0	81.5	77.3 **
3	4.0	51.5	47.5 *
4	14.0	75.0	61.0 **
5	.0	41.5	41.5 *
6	12.0	48.0	36.0 **
7	1.0	11.0	10.0 ns
8	95.0	100.0	5.0 ns

The differences in seed dormancy between kernels on main stem and on lateral stems are given in Table 2.

Table 2. Percentages of dormant seed on main stems and on lateral stems. Means of ten plants in each of eight different fields of wheat and two-row barley

Field No	Main stems	Lateral stems	Difference
1	36.3	30.4	5.9 ns
2	47.9	58.4	-10.5 *
3	25.4	41.2	-15.8 *
4	50.9	31.3	19.6 **
5	18.1	18.4	- .3 ns
6	22.2	33.0	-10.8 **
7	3.6	8.6	- 5.0 ns
8	98.0	98.8	- .8 ns

Significant differences in seed dormancy between kernels on main stems and on lateral stems were observed in

four of the eight fields (Table 2). The kernels on lateral stems were often the most dormant, but the opposite result was also obtained. These results were attributable to the highly significant field x main-lateral stem interaction.

Variation within panicles of oats

In oats the dormancy of kernels from different parts of the panicles was investigated. The effects of three different positions in the panicle were determined by separate dormancy tests of kernels on lower whorl branches, on central whorl branches and on the branches of the upper whorls of the panicles. The dormancy of the first and second kernels of the spikelets was determined by separate dormancy tests. Test results of samples from six oat fields are presented in Table 3.

Table 3. Percentages of dormant seed in different whorl branches of oat panicles. Means of 20 plants from each of six fields

Field No	Whorl of branches		
	Lower	Central	Upper
1	76	80	77
2	89	79	82
3	72	62	74
4	75	73	71
5	42	30	39
6	67	69	76
Means	70	65	70

The analyses of variance showed significant differences in dormancy levels between fields (Table 3). There was no significant difference between the mean dormancy of kernels from the three parts of the panicles when tested against the field x position interaction. However, the field x position interaction was highly significant, showing that kernels of highest dormancy may be found in any part of the panicle. Based on this material no explanation can be offered to account for the pattern of variation in seed dormancy within the oat panicles.

Table 4. Percentages of dormant seed from the first and the second floret of oat spikelets

Field No	Kernels		Second - first kernel
	First	Second	
1	71	83	12**
2	69	87	8**
3	63	76	13**
4	69	76	7**
5	26	48	22**
6	61	80	19**
Means	62	75	13**

The oat seed from the second position in a spikelet had a consistently higher dormancy than those from the first position (Table 4). There was significant interaction between field and spikelet position in the material, showing that the difference in dormancy between the first and second kernels may vary from field to field.

Variation in seed dormancy in barley

The possible effects of differences in kernel development on the variation in seed dormancy in the spike were investigated in six fields of six-row barley. The collected spikes were divided into five parts from base to top. Kernels from central rows and from lateral rows were kept separate. Seed dormancy percentages of kernels in the five positions from base (position 1) to top (position 5) are presented in Table 5.

The differences in dormancy of ker-

Table 5. Percentages of dormant seed from different positions of barley spikes. Means for six fields and 50 plants per field

Position No	Percent dormant kernels
1 (Base)	89
2	84
3	82
4	77
5 (Top)	79

nels from the five different positions on the barley spike were significant (Table 5). Dormancy was strongest in the most recently developed kernels. Such results were to be expected for fields sampled on the downward slope of the dormancy curve. Spikelets in the central or upper third part of the spike were earliest, closely followed by the spikelets at the top. The spikelets at the base of the spike were slowest in development. In two-row barley the difference between the earliest and the latest developing kernels may be 2-3 days. In six-row barley the difference is 1-2 days more because kernels in the lateral rows are later in development than the central ones.

The interaction between field and spikelet position was significant, indicating that seed with the strongest dormancy may be found in different parts of the spike. Thus, sampling fields on an increasing or a decreasing part of the dormancy curve can be expected to give opposite results.

The mean dormancy of kernels in the central rows was 84.0% and in the lateral rows 80.3%. The difference is significant, $p < 0.05$. Sampling of fields at other maturity stages may give different results, however.

Variation within spikes of wheat

Possible differences in seed dormancy between kernels within spikes of wheat were investigated in eight fields. Like the barley, the wheat spikes were divided into five parts from base to top. Kernels from the first and second positions in the spikelets were kept separately. The percentages of dormant seed in the five different positions of the spikes are presented in Table 6.

Kernels from the lowest spikelets were significantly more dormant than those in the rest of the spike (Table 6).

The mean dormancy percentage of the lowest kernel in a spikelet was 69% and that of the second kernel was 67%. The difference is not significant. However, the field x kernel position interaction was highly significant. In different fields the dormancy of the first and second kernels in the spikelets varied from 65% and 54% to 78% and 90%. There was also a significant spikelet position x kernel position interaction. In the spikelets at the base of the spike the mean dormancy percentages of the first and second kernels were 79% and 70% respectively. In the upper part of the spike the corresponding figures were 65% and 71%.

Table 6. Percentages of dormant seed in different parts of wheat spikes. Means for eight fields and 50 plants per field

Position No	Percent dormant kernels
1 (Base)	74
2	67
3	65
4	67
5 (Top)	66

CONCLUSIONS

There was considerable variation in the intensity of seed dormancy between fields, between plants in a field, stems on the same plant, in different parts of spikes or panicles and between kernels at different positions in the spikelets. There was a close connection between stage of development and the intensity of seed dormancy. The mechanism seems to be that kernels at the most advanced stages of development have the strongest dormancy when the dormancy is on the increase and the lowest dormancy when the dormancy is in decline. However, this relationship between stage of development and dormancy was not clear in all cases. Whatever the differences in dormancy between kernels in a field of fairly homozygous plants may mean for the dormancy character, it has been shown that variation occure and that the dormancy should therefore be treated as a quantitative character.

The recorded variations between ker-

nels may explain why single kernels initiate germination at different times during the germination test. It is, however, simply not enough to explain why some kernels in a sample of deep dormancy germinate readily as if no dormancy was involved, while most of the seeds do not respond to prolonged exposure to optimal germination conditions. This occurs regularly even for hand-threshed seeds where there could be no mechanical damage involved in broken dormancy. As far as this investigation is concerned,the reasons for most of the variations in seed dormancy between kernels in a sample will have to be left undisclosed.

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The intensity of seed dormancy in small grain cultivars

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Seeds of two barley, two oat and three wheat cultivars harvested one week past yellow ripeness were stored at 20°C and samples were taken for dormancy tests each week until most of the dormancy had disappeared. Dormancy was determined by germinating the samples on moist filter paper at 5, 10, 15, 20, 25 and 30°C. During a germination period of 14 days germinated kernels were recorded and removed every second or third day.
Dormancy was reduced by approximately 1.0 percentage units per day of storage at 20°C. The percentage of dormant seeds was increased by 3.6 units per 1.0°C higher germination temperature. On average germination started in 4.2% dormant kernels per day in the period from the 5th to the 14th day of germination.
The best differentiation of the cultivars was obtained at a sample mean of about 30% dormant seeds, but good differentiation was obtained in the whole range of 15 to 75% dormant seeds. With low germination temperature there was no differentiation between samples of low dormancy, and with a high germination temperature differentiation between high dormancy samples was poor. Therefore, it is recommended that germination temperature of 10°C be used for high dormancy material, 20°C for medium, and 30°C for low dormancy material. The differences between two successive temperatures were approximately 36% dormant seeds.

Key words: Barley, oats, wheat.

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Seed dormancy is an important character in small grain cultivars because of its potential to prevent pre-harvest ear-sprouting and subsequent loss of quality.

Testing of seed dormancy has been carried out in many countries and local cultivars are classified for their seed dormancy character - no doubt on very different scales - but there is no standard method available for comparing the results. A Nordic barley cultivar classified as resistant to ear-sprouting usually represents a much higher level of seed dormancy than white wheat of the same classification. In order to range species or cultivars of very different dormancy levels on the same scale a standard method is needed.

MATERIAL AND METHODS

In order to study methods for measuring the intensity of seed dormancy freshly harvested seeds of the barley cultivars Lise and Herta, the oat cultivars Titus and Mustang and the spring wheat cultivars Runar, Reno and Tjalve were used. On a scale commonly used to classify commercial cultivars in Norway cv. Lise

and cv. Titus are rated as high dormancy cultivars. Cv. Herta is rated as intermediate and the cv. Mustang and the spring wheats are rated as intermediate to low in dormancy. Most of the cultivars chosen have formerly been included in long term studies of seed dormancy, (Strand 1989a, 1989b).

The seeds were harvested one week past yellow ripeness, and dried and stored at 20°C. Each week samples were taken for dormancy tests until there was no longer any dormancy manifested at that particular germination temperature.

The dormancy tests were carried out by germination of samples of 100 kernels on filter paper moistened with 200 g water per 100 g of filter paper. The germination tests were conducted at temperatures of 5, 10, 15, 20, 25, and at 30°C. During the 14-day test period germinated seeds were recorded and removed every second or third day. The seeds were considered as having germinated at the first sign of morphological development.

RESULTS

Seed storage and the intensity of seed dormancy

It may be recalled that seeds of the seven cultivars were stored at 20°C and sampled each week or every second week for determination of seed dormancy at the six germination temperatures. The results are presented in Figure 1.

At the start of the experiment the mean effect of germination temperature on the manifestation of seed dormancy was 3.6% more dormant seeds per a 1.0°C increase in temperature. During the first eight weeks of storage dormancy was reduced by 1.03, 1.04 and 0.91% dormant seed per day at germination temperatures of 20, 25 and 30°C, respectively. From eight weeks on the curves leveled off because the cultivars of lowest dormancy approached the zero dormancy level. At 10 and 15°C the manifestation of dormancy was relatively weak because

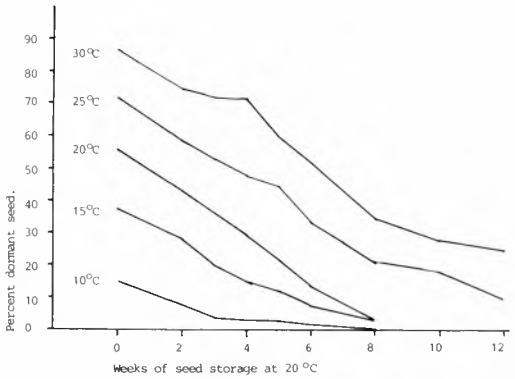

Figure 1. The effects of germination temperature and time of storage on seed dormancy

the low dormancy cultivars showed no dormancy at these temperatures. At a germination temperature of 5°C dormancy was noticeable only for a few weeks in the high dormancy cultivars, Lise and Titus.

Germination temperature, length of germination periods and the manifestation of seed dormancy

Under optimal conditions most non-dormant kernels began to germinate after 30 - 50 day-degree centigrade (DDC) and all had started after 70 DDC, i.e. 7 days at 10°C or 3-4 days at 20°C.

Differences between non-dormant kernels in time of onset of germination are mostly due to water inhibition rate, which mainly depends on the contact surface between kernels and the filter paper. Samples which do not germinate close to 100% or take a longer time to complete germination are regarded as more or less dormant. For dormant seeds increasing the germination temperature enhances the manifestation of dormancy. For a sample of kernels this is recorded as slow germination with only a few percent of the kernels beginning to germinate every day, or as a certain percentage of kernels remaining ungerminated at the termination of the test, or both.

In Figure 2 the manifestation of seed dormancy at different germination tem-

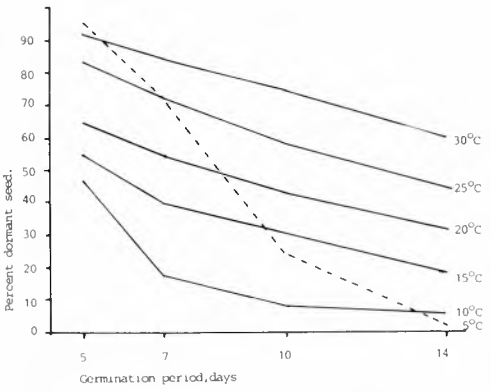

Figure 2. Manifestation of seed dormancy at different germination temperatures and germination periods of different length

peratures and germination periods is illustrated.

The strong deviation in the shape of the curve for 5°C and in the first part of the curve for 10°C is attributable to incomplete germination because of an insufficient heat sum. At the 5°C the dormancy is not manifested after 14 days (70 DDC) of germination.

Figure 2 shows that the manifestation of seed dormancy expressed as percent dormant seed in the germination tests can be regulated by choice of germination temperature and the length of the germination period. With tests of at least 70 DDC the effect of germination temperature on the recorded dormancy was 2.7% dormant seed per degree centigrade after 5 days, 3.3% after 7 days, 3.4% after 10 days and 2.7% after 14 days of germination. The mean increase in dormant kernels was 3.0% per 1.0°C higher germination temperature. These values are somewhat lower than those in Figure 1 because the percentage of dormant seed in low dormancy cultivars soon approached the zero level.

The curves in Figure 2 also show that prolongation of the germination period reduced the recorded dormancy. The mean reduction was 4.2% per day from the 5th to the 14th day of the germination period, approximately the same at all temperatures.

When cultivars of widely different dormancy levels are tested, low germination temperatures may not differentiate satisfactorily between cultivars because the manifestation of dormancy is too weak at these temperatures. On the other hand, the dormancy may be so strong that the higher germination temperatures do not give any differentiation. The two situations are illustrated in Figure 3.

Figure 3 shows that freshly harvested samples of the cv Lise germinated at 20, 25 and 30°C had more than 80% dormant seeds, which means weak differentiation. For seeds of cv. Herta stored for some time there was no differentiation between samples at germination temperatures of 5, 10 and 15°C because the comparatively low level of dormancy was not manifested at these temperatures. Thus, wide variation in seed dormancy may not always be assessed satisfactorily by application of just one germination temperature.

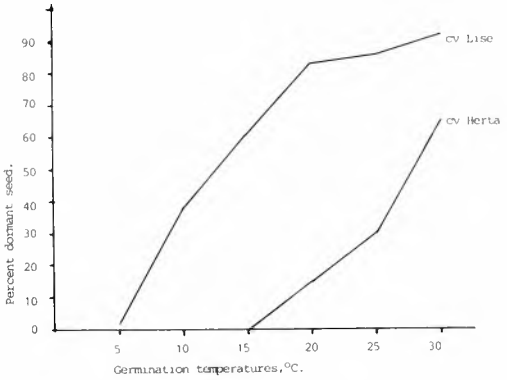

Figure 3. The effects of germination temperature on the manifestation of seed dormancy

The efficiency of cultivar differentiation

Since the manifestation of seed dormancy depends on germination temperature and time of exposure to favourable germination conditions it is possible to adjust

the degree of dormancy manifestation to the level of maximum differentiation between samples.

Figure 4 shows that the curve is skewed and that the best differences between cultivars were obtained when the sample mean was 30-40% dormant seed, but the differentiation was fairly good in the whole range from 15 to 75% dormant seed. Thus, test conditions which result in very weak (<15% dormant seed) or very strong (>75% dormant seed) manifestation of seed dormancy should be avoided.

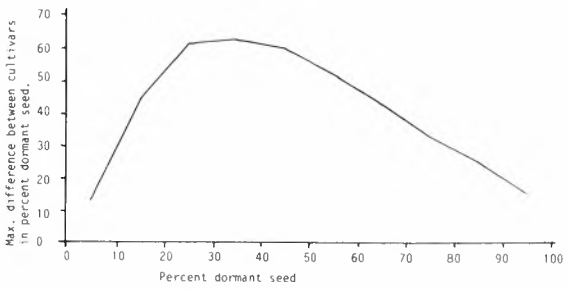

Figure 4. Maximum difference in percent dormant seed between high and low dormancy cultivars at different levels of dormancy manifestation. Means of seven cultivars

Methods for measuring intensity of seed dormancy

Earlier investigations have shown that seed dormancy starts to develop 3-4 weeks prior to yellow ripeness. It reaches maximum level at yellow ripeness or a few weeks later and thereafter it disappears slowly. In field, dormancy, besides genetical factors, is strongly influenced by weather conditions, especially temperature, radiation and moisture factors. After harvest the rate of dormancy declines as a function of time and temperature only. The general shape of the dormancy curve and the factors affecting it should be kept in mind when a method for measuring intensity of seed dormancy is worked out and when the method is applied for comparing cultivars with different times of maturity.

A certain level of seed dormancy may be manifested to different degrees depending on manifestation conditions. Duration of the germination test has to be at least 70 DDC, which is approximately the sum of day-degrees required for a complete germination of non-dormant cereal seed. Longer test periods will mean a stronger test of dormancy because a few kernels germinate every day, in this study 4.2% per day on average.

The germination temperature had a strong effect on the manifestation of seed dormancy. In the part of the percentage scale where good differentiation was obtained (15-75% dormant seed) the mean effect was 3.6% per 1.0°C. i.e. the dormancy increased by 36 percentage units when the germination temperature was increased by 10°C.

If the test results are to be kept in the 15-75% range of the scale and a wide variation in dormancy is to be covered, than it will be necessary to use more than one germination temperature. In Figure 3 it is shown that for the strong dormancy (cv. Lise) germination temperature of 10°C must be used because 20°C, 25°C, and 30°C gave poor differentiation. For intermediate dormancy (cv. Herta) 20°C must be used because 5°C, 10°C, and 15°C did not give any differentiation. For low dormancy material it may be necessary to use a germination temperarure of 30°C.

CONCLUSIONS

There are three main factors affecting seed dormancy and its manifestation which should be considered when a test method is beeing planned.

1. The cultivars should be sampled when the increasing dormancy curve has flattened out in order to minimize possible effects of cultivar differences in maturity. For cultivars adapted to Nordic conditions this means 1-2 weeks past yellow ripeness.

2. Duration of the germination test must be at least 70 DDC i.e. 7 days at 10°C or other combinations of time and temperature giving the same sum of day-degrees. Because it is advantageous to have a standard length for the test period it is recommended that the test is carried out within 7 days also when higher temperatures are applied.

3. The germination temperature should be chosen to secure maximum differentiation between cultivars. Based on the results presented in this paper it is recommended that 10°C is used for strong dormancy material, 20°C for medium dormancy material and a germination temperature of 30°C for low dormancy material. The methods could be denoted as D_{10}, D_{20} and D_{30} respectively. The mean difference in results obtained by the different methods is approximately 35 percentage units for a 10°C difference in germination temperature.

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Studies on seed dormancy in small grain species. III. Oats

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Seed dormancy was studied in three oat cultivars grown under field conditions for periods of 10 to 16 years. The percentage of dormant seed in germination tests carried out at 10°C and at 20°C on samples harvested 10 days and 30 days after yellow ripeness was used as a measure of the intensity of seed dormancy. A Dormancy Index was also used.
For cv. Mustang very few significant correlation coefficients were found between dormancy parameters and the climatic factors temperature, global radiation, rainfall, relative air humidity and a rainfall/temperature ratio. For cv. Titus and cv. Svea the intensity of seed dormancy was positively correlated with temperature and global radiation and negatively correlated with the moisture factors. These correlations with climatic factors are the opposite of those found earlier in barley and wheat cultivars.
The most efficient method for testing oat cultivars for differences in seed dormancy was by germination tests at 20°C of samples harvested 10 days or 30 days after yellow ripeness.

Key words: Air humidity, global radiation, rainfall, temperature.

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This paper, which deals with seed dormancy in oats, forms the third part of a more comprehensive study on seed dormancy in small grain species and cultivars. The first paper (Strand 1989a), dealing with barley, contains some general information and discussions on the subject and may therefore be read as an introduction to or in connection with this paper. The results for the wheat cultivars were reported in the second paper (Strand 1989b).

MATERIAL AND METHODS

The spring oat cultivars used in the main part of the study were the cvs. Mustang and Titus grown for 16 years, and the cv. Svea grown for 10 years in field. In the part of the study designed for testing cultivar differences in seed dormancy, another eight cultivars grown in field for seven years were included. The developmental stages of the plants were defined as follows: Heading (H), when 50% of the panicles were completely out of the boots; Yellow ripeness (YR), when moisture content of the kernels was 38% of fresh weight. Seed samples were harvested approximately 150 day-degrees or 10 days (HT 1) and 450 day-degrees or 30 days (HT 2) past yellow ripeness. The germination tests were carried out at the State Seed Testing Station in accordance with the official method for testing germination of cereals, which entails germination in moist sand for 10 days at 10°C and at 20°C using 200 kernels in each test. The percentage of dormant seed in such

tests was used as a measure of the intensity of seed dormancy, directly or indirectly, in parameters calculated from such data.

The following dormancy parameters (dependent variables) were applied in the study:

1. Percent dormant seed at 10°C germination temperature.
2. Percent dormant seed at 20°C germination temperature.
3. The Dormancy Index (DI) (Strand 1965) calculated in the following way:
   DI = (% dormant seed at 10°C * 2 + % dormant seed at 20°C) /3
4. The ratio (% dormant seed at 10°C)/(% dormant seed at 20°C)
5. The means of the Dormancy Index of the first and the second harvest.
6. The ratio (DI HT 1)/(DI HT 2).

The climatic parameters (independent variables) were:

1. Temperature, daily mean in degrees centigrade.
2. Global radiation in MJm^{-2} day^{-1} measured as the sum of direct and diffuse short wave radiation on horizontal surface (GR).
3. Rainfall in mm per day.
4. Relative air humidity in percent (RH).
5. The rainfall/temperature ratio (R/T).

The climatic data were recorded at the Meteorological Station of the University, which is situated 1 km from the experimental field. The data were calculated as means of the following sub-periods of the total developmental and after-ripening periods of the cultivars.

1. Sowing to heading.
2. Heading to yellow ripeness.
3. Sowing to yellow ripeness.
4. The first 10-day period past sowing.
5. The first 10-day period past heading.
6. The period -20-10 days prior to yellow ripeness.
7. The period -10-0 prior to yellow ripeness.
8. The period 0+10 days past yellow ripeness.
9. The period +10+20 days past yellow ripeness.
10. The period +20+30 days past yellow ripeness.

The notation of the time periods should be interpreted in the following way: The yellow ripeness is zero time; the -20-10 period therefore includes the 10 days between the 20th and the 10th day prior to yellow ripeness. In the same way the 0+30 period designates the 30 days between yellow ripeness and the second harvest. Two or more 10-day periods were later pooled in order to obtain periods of different length.

The statistical methods applied for analysing the data were the analysis of variance and the correlation and regression analysis technique.

RESULTS AND DISCUSSION

Data on the cultivars and on the climatic factors

Table 1 gives the 16-year means of climatic parameters for the three sub-periods of the growth season, namely sowing-heading (S-H), heading-yellow ripeness (H-YR) and yellow ripeness-2nd harvest (YR-H2). The climatic conditions of the period were fairly close to the long-term averages and therefore give a good indication of the climatic conditions under which the investigations were carried out.

Information on the oat cultivars Mustang, Titus and Svea used in the study is given in Table 2. The means of growth periods and dormancy parameters are supplemented by their Standard Deviation, which indicates the annual variation of the characters.

Table 1. Means of climatic parameters for a period of 16 years. (The observation period for cv. Mustang)

Climatic factors	Developmental periods		
	Sowing-heading	Heading-Y.Ripeness	Y.Ripeness 2nd harvest
Temperature,C, daily means	13.3	16.4	14.5
Global rad. $MJ^{-2}day^{-1}$	19.0	18.4	14.8
Rainfall, mm per day	2.14	2.38	1.73
Rel.air humidity,percent	60.1	65.4	65.5

Table 2. Developmental characteristics and dormancy parameters for three oat cultivars. Means and standard deviations for the experimental periods of 16 years for cvs. Mustang and Titus and 10 years for cv. Svea

Cultivar characteristics and dormancy parameters	Mustang		Titus		Svea	
	Mean	SD	Mean	SD	Mean	SD
Growth period						
No. of days	99.7	4.8	96.1	7.5	99.4	5.7
Heat sum, day-degrees, basis 0 C	1416	73.1	1349	98.4	1399	96.9
Dormancy parameters						
HT 1. Dormant seed, % at 10 C	4.7	3.7	19.5	18.0	15.3	15.7
" 20 C	50.4	21.1	77.4	21.0	69.4	20.9
Dormancy Index	20.1	8.0	38.9	17.2	33.3	16.1
HT 2. Dormant seed, % at 10 C	0.5	1.1	6.9	8.6	4.6	4.4
" 20 C	7.9	8.2	36.9	23.0	25.3	22.6
Dormancy Index	3.1	2.8	16.7	12.8	11.5	10.3

The effects of climatic factors on the intensity of seed dormancy

The correlation coefficients between dormancy parameters and climatic parameters are given in Tables 3, 4 and 5 for the cultivars Mustang, Titus and Svea, respectively.

For cv. Mustang almost no effect of climatic factors could be proved (Table 3). There were, however, a few significant correlation coefficients for the sowing to heading period. If real, they are hard to explain.

For cv. Titus there seemed to be some effects of temperature, global radiation and rainfall on dormancy of the first harvest samples germinated at 20°C (Table 4). It should be noted that the reactions are contrary to those observed for the barley cultivars, in most cases also to those of the wheat cultivars. For the oat cultivars both high temperature and high global radiation induced stronger dormancy while higher rainfall reduced it. Other correlation coefficients were low and non-significant.

For the most part cv. Svea (Table 5) reacted in the same way as cv. Titus but the reactions to climatic factors were stronger in the 2nd harvest samples.The reactions of the three oat cultivars were not significantly different. The reactions of cv. Svea, however, were significantly different from those of the barley and wheat cultivars.

The reactions of the cultivars to climatic factors in relation to the manifestation of seed dormancy, seemed to be influenced by the germination temperature. This was most clearly illustrated

Table 3. Correlation coefficients between dormancy parameters and climatic parameters in different developmental periods for cv. Mustang

Climatic factors and developmental periods		HT1			HT2		
		10°C	20°C	DI	10°C	20°C	DI
Temp.	S-H	-.01	-.31	-.29	-.16	-.69+	-.74++
	H-YR	-.13	.29	.25	-.14	.27	.27
	-20-0	-.31	.15	.06	-.45	.09	-.02
	-20+10	-.32	.27	.15	-.41	.25	.14
	0+30				-.30	.15	.08
	-20+30				-.37	.14	.06
Global radiation	S-H	-.40	-.27	-.34	.11	-.56+	-.56+
	H-YR	-.37	.35	.20	-.22	.13	.09
	-20-0	-.56+	.25	.06	-.48	.11	0
	-20+10	-.41	.24	-.11	-.29	.21	.14
	0+30				-.19	.11	.07
	-20+30				.02	.09	.10
Rainfall	S-H	.55+	-.06	.10	.09	.23	.30
	H-YR	.27	-.27	-.14	.24	-.23	-.21
	-20-0	.32	-.18	-.06	.48	-.25	-.13
	-20+10	.13	-.35	-.25	.28	-.44	-.36
	0+30				-.10	-.35	-.41
	-20+30				-.22	-.35	-.31
RH	S-H	.27	.21	.27	.01	.36	.37
	H-YR	.37	.05	.17	.01	0	0
	-20-0	.30	-.12	-.01	.29	-.12	-.05
	-20+10	.13	-.19	-.12	.20	-.22	-.15
	0+30				-.05	-.08	-.08
	-20+30				.09	-.09	-.06
R/T	S-H	.52+	-.01	.14	.14	.40	.48
	H-YR	.24	-.28	-.17	.23	-.25	-.23
	-20-0	.30	-.18	-.07	.48	-.22	-.11
	-20+10	.15	-.34	-.24	.35	-.32	-.29
	0+30				.06	-.34	-.39
	-20+30				.25	-.33	-.29

by the opposite reactions of cv.Runar to the temperature and to the moisture factors when germination temperatures of 10°C and 20°C were applied (Strand 1989b). This may also explain the opposite reactions of cv. Svea to climatic factors as compared with the barley and wheat cultivars.

Non-significant correlation coefficients between seed dormancy and climatic factors for some cultivars in this study may be due to the germination temperatures applied (10°C and 20°C) being between or outside the range of germination temperatures at which the cultivars in question react to climatic factors or react in opposite ways. This explanation is supported by two facts. First, the wheat cultivar Runar had an opposite reaction to temperature and moisture factors at 10°C as compared with a 20°C germination temperature. Therefore, at some temperatures between 10°C and 20°C the correlation coefficients are expected to be at zero. Secondly, wide annual variation in the intensity of seed dormancy occurs even when no significant correlation between seed dormancy

Table 4. Correlation coefficients between dormancy parameters and climatic parameters in different developmental periods for cv. Titus

Climatic factors and developmental periods		HT1			HT2		
		10°C	20°C	DI	10°C	20°C	DI
Temp.	S-H	-.40	-.27	-.39	-.24	-.28	-.28
	H-YR	.13	.38	.24	.02	-.07	-.04
	-20-0	.26	.43	.35	.10	.01	.05
	-20+10	.39	.47 +	.47 +	.28	.25	.28
	0+30				-.04	.17	.09
	-20+30				.01	.13	.08
Global radiation	S-H	-.28	.06	-.17	-.38	-.28	-.36
	H-YR	.01	.48 +	.20	-.31	.13	-.23
	-20-0	.12	.64 + +	.29	-.13	.04	-.04
	-20+10	.05	.54 +	.21	-.14	.03	-.05
	0+30				-.20	-.09	-.15
	-20+30				-.17	-.07	-.12
Rainfall	S-H	.10	-.19	-.01	.35	.27	.33
	H-YR	.21	-.40	-.02	.28	.14	.22
	-20-0	-.12	-.61 + +	-.33	.01	-.09	-.05
	-20+10	-.16	-.69 + +	-.39	.05	-.15	-.07
	0+30				.20	.02	.11
	-20+30				.13	-.04	.03
RH	S-H	.09	-.32	-.07	.31	.30	.33
	H-YR	.01	-.41	-.15	.12	.15	.15
	-20-0	.01	-.44	-.13	-.05	-.08	-.08
	-20+10	0	-.38	-.12	-.15	-.17	-.17
	0+30				-.01	.03	.02
	-20+30				-.09	.02	-.03
R/T	S-H	.18	-.12	.07	.41	.32	.38
	H-YR	.16	-.41	-.05	.26	.15	.21
	-20-0	-.15	-.62 + +	-.36	-.01	-.10	-.07
	-20+10	-.20	-.70 + +	-.42	.04	-.14	-.07
	0+30				.20	-.03	.08
	-20+30				.15	-.05	.04

and climatic factors can be proved by using germination temperatures of 10°C and 20°C.

Calculated from first harvest samples in Table 2, dormant seed as a mean of the three cultivars was 13.2% at 10°C and 65.6% at a germination temperature of 20°C. This means an increase of 5.2% dormant seed per 1.0°C higher germination temperature. The comparable results for the two barley cultivars were 4.9% (Strand 1989a), and for the three wheat cultivars 3.9% (Strand 1989b). The annual variation in seed dormancy of the oat cultivars was of the same magnitude as that for the barley and the wheat cultivars. Thus, both the intensity of seed dormancy and its manifestation in oats are as equally strong in barley and wheat cultivars. In oats, however, using germination temperatures of 10°C and 20°C revealed fewer effects of environmental factors than in barley and wheat.

Table 5. Correlation coefficients between dormancy parameters and climatic parameters in different developmental periods for cv. Svea

Climatic factors and developmental periods		HT1			HT2		
		10°C	20°C	DI	10°C	20°C	DI
Temp.	S-H	-.53	-.59	-.61	-.52	-.75 ++	-.69 +
	H-YR	.57	.62 +	.64 +	.53	.70 +	.65 +
	-20-0	.57	.56	.61	.56	.54	.55
	-20+10	.51	.58	.58	.55	.61	.59
	0+30				.48	.71 +	.64 +
	-20+30				.54	.71 +	.66 +
Global radiation	S-H	-.41	-.10	-.31	-.46	-.46	-.48
	H-YR	.43	.59	.53	-.01	.16	.09
	-20-0	.42	.50	.48	.05	.17	.14
	-20+10	.58	.66 +	.64 +	.20	.34	.29
	0+30				.48	.72 ++	.65 +
	-20+30				.32	.53	.47
Rainfall	S-H	.30	.17	.26	.01	.02	.01
	H-YR	-.56	-.58	-.60	.08	-.06	0
	-20-0	-.74 ++	-.58	-.72 +	-.14	-.15	-.14
	-20+10	-.79 ++	-.66 +	-.79 ++	-.27	-.35	-.32
	0+30				-.21	-.32	-.28
	-20+30				-.19	-.26	-.24
RH	S-H	-.13	-.08	-.12	.10	.23	.22
	H-YR	-.31	-.35	-.35	-.14	-.19	-.16
	-20-0	-.52	-.63 +	-.60	-.25	-.30	-.26
	-20+10	-.55	-.65 +	-.62	-.25	-.32	-.28
	0+30				-.25	-.34	-.29
	-20+30				-.27	-.35	-.31
R/T	S-H	.44	.34	.43	.18	.26	.23
	H-YR	-.60	-.62	-.65 +	-.01	-.16	-.11
	-20-0	-.76 ++	-.61	-.75 ++	-.21	-.21	-.20
	-20+10	-.80 ++	-.68 +	-.81 ++	-.32	-.38	-.35
	0+30				-.23	-.35	-.31
	-20+30				-.23	-.30	-.28

The influence of climatic factors in different developmental periods on the intensity of seed dormancy

The investigations in barley and wheat (Strand 1989a,1989b) showed that the influence of climatic factors on seed dormancy commenced approximately three weeks prior to the stage of yellow ripeness and continued for at least four weeks after yellow ripeness. Climatic factors also had a significant effect on seed dormancy for at least 40-50 days beyond the termination of climatic observations. For the oat cultivars in this study such effects of climatic factors on seed dormancy were hard to prove, probably because of the generally low correlation coefficients between dormancy and climatic factors. For the same reason, most probably, no significant effects of climatic factors on the ratio between the dormancy observed at the two germination temperatures or on the ratio of dormant seed of the first and the second harvests, could be proved.

In Table 6 correlation coefficients between dormancy parameters and climatic data for a 30-day period prior to harvest are calculated for the three oat cultivars.

Table 6. Correlation coefficients in three oat cultivars between dormancy parameters and climatic parameters of the 30-day period prior to the two harvest times (-20 + 10 for HT 1 and 0 + 30 for HT 2)

Cultivars and climatic factors		HT 1		HT 2	
		10°C	20°C	10°C	20°C
Mustang	Temperature	-.32	.27	-.30	.15
	Global rad.	-.41	.24	-.19	.11
	Rainfall	.13	-.35	.10	-.35
	Air humidity	.13	-.19	.05	-.08
	R/T ratio	.15	-.34	.06	-.34
Titus	Temperature	.39	.47	-.04	.17
	Global rad.	.05	.54^{+}	-.14	.03
	Rainfall	-.16	-.69^{++}	.20	.02
	Air humidity	0	-.38	-.01	.03
	R/T ratio	-.20	-.70^{++}	.20	-.03
Svea	Temperature	.51	.58	.48	.71^{+}
	Global rad.	.58	.66^{+}	.48	.72^{++}
	Rainfall	-.79^{++}	-.66^{+}	-.21	-.32
	Air humidity	-.55	-.65^{+}	-.25	-.34
	R/T ratio	-.80^{++}	-.68^{+}	-.23	-.35

The figures in Table 6 illustrate very clearly the different dormancy responses of these cultivars to climatic factors during the 30-day period prior to harvest. For cv. Mustang no significant correlation coefficient was obtained. It should be noted, however, that the correlation coefficients between both temperature and radiation and percentage of dormant seed at a germination temperature of 10°C were all negative, while all of those obtained at 20°C were positive. For the moisture factors the reactions were the opposite.

The dormancy of cv. Titus was strongly related to all climatic factors in the first harvest samples germinated at 20°C. Cv. Svea reacted in the same way, and in addition the first harvest 10°C correlation coefficients and the second harvest temperature and radiation correlation coefficients were significant.The reactions of the cvs. Titus and Svea show very clearly that high temperature and radiation values increased seed dormancy, and that high moisture factor values reduced seed dormancy in oats. These reactions are the opposite of those found for barley cultivars and also for most wheat cultivars,(Strand 1989a,1989b). In this connection it should also be borne in mind that for the cv. Mustang there are strong indications that the dormancy reactions to climatic factors are the opposite at germination temperatures of 10°C and 20°C.

Efficiency of different methods for testing cultivar differences in seed dormancy

When testing cultivars and breeding material it is important to have methods by which the genetically controlled seed dormancy can be determined precisely and cheaply. The seven methods for testing seed dormancy described in Section II were compared and the results are given in Table 7. The F-value from the analysis of variance, i.e. the ratio between the cultivar variance and the cultivar x year interaction variance, is assumed to be the best criterion for determining the efficiency of the different methods.

Table 7 indicates that a germination temperature of 20°C gave better differentiation than 10°C. The best combination of time of harvest and germination tem-

Table 7. The efficiency of methods for testing cultivar differences in seed dormancy. F-values in tests of differences between eight cultivars grown for seven years

Methods	Percent dormant seed. Means	F-values
HT 1 10°C	18.8	2.81
" 20°C	71.6	9.33
DI	36.4	3.73
HT 2 10°C	7.4	4.31
" 20°C	35.9	11.59
DI	16.9	9.02
Mean DI	26.8	8.38
Mean for HT1	45.2	6.07
Mean for HT 2	21.7	7.95
Mean for 10°C	13.1	3.56
Mean for 20°C	53.8	10.46

For P = .05 F = 2.24
For P = .01 F = 3.10

perature was at the second harvest with a germination temperature of 20°C. The comparatively low F-value for the Dormancy Index (DI) at the first harvest is most probably due to cultivar x germination temperature interactions.

The mean percent dormant seed varied from 7.4 to 71.6 with the different methods. In an investigation of the intensity of seed dormancy for best differentiation between cultivars (Strand 1991) it was shown that the best differentiation between cultivars was obtained when the mean percentage of dormant seed of the material was 30-40 but good differentiation was secured in the whole range of 15 - 75% dormant seed. According to this, the low F-values for the 10°C germination test may be due to the low manifestation of dormancy at this temperature or, more correctly, that the dormancy test was too strong in relation to the dormancy level of the material.

MAIN CONCLUSIONS

One interesting and surprising result of the investigation is that the effects of climatic factors on seed dormancy in oat cultivars may be the opposite of the reactions found in barley and wheat cultivars. For two barley cultivars investigated earlier (Strand 1989a) high temperature and high global radiation during the ripening period very consistently reduced seed dormancy, while high rainfall and high air humidity increased it. Also, three wheat cultivars reacted in the same way (Strand 1989b). However,for some of the wheat cultivars there were strong indications that dormancy reactions to climatic factors could be the opposite at germination temperatures of 20°C compared with 10°C.

Of the three oat cultivars in this study cv. Mustang had the most similar reaction to those of the barley and wheat cultivars when germinated at a temperature of 10°C, but displayed an opposite reaction at 20°C. However, none of the correlation coefficients reached a significant level.

For cv. Titus no significant correlation coefficients between dormancy parameters and climatic factors were obtained for samples germinated at 10°C, while the dormancy parameters from the 20°C germination tests showed strong correlations. In all cases the effects of climatic factors on seed dormancy were the opposite of those observed for barley and wheat.

For cv. Svea the dormancy reactions to climatic factors were similar to those of cv. Titus and, in addition, the results of the 10°C germination tests were also significant.

These and earlier investigations (Strand 1989a, 1989b) show very clearly that seed dormancy is a very complex character. Besides genetical control, seed dormancy is strongly affected by environmental factors during the ripening period. Furthermore, it is strongly influenced by temperature and moisture conditions during manifestation of the dormancy, i.e. during germination tests or when the grain is exposed to ear-sprouting conditions in field.

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

III. Effects of sample preparation, maturity stage and species

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Crude protein (CP), crude fibre (CF), digestible crude protein (DCP), *in vitro* DMD (IVDMD) and fattening feed units (FU) in samples of fresh herbage, silage and hay were determined by traditional methods or by near infrared reflectance (NIR) analysis. The samples for NIR analysis were prepared in different ways, and the NIR predictions for each of these were compared with the traditionally determined values by regression. Chemical values (CP and CF) and DCP were predicted with higher accuracy (R^2 = 0.92 - 0.94) than values for IVDMD (R^2 = 0.77) and FU (R^2 = 0.71). Undried hay samples were predicted with a lower degree of accuracy than oven-dried hay samples. Different types of mills influenced the accuracy of the predictions. The results indicated that samples with values outside the range represented in the NIR equations were predicted with a lower degree of accuracy. The results underline the importance of having calibration sets and sets for practical NIR analysis which cover the same range, and with both containing the same type of samples.

Key words: Chemical composition, feeding value, fresh herbage, hay, near infrared reflectance analysis, sample preparation procedure, silage.

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Near infrared reflectance analysis (NIR) is a rapid and non-labourious analytical method, and one of its applications is to predict the feeding value of forages. The predictions are made from calibration equations which are based on samples where the feeding value is determined in a traditional way (reference method). A good calibration equation must consist of the total range of the samples which are later going to be predicted by the equation. If the purpose is to predict samples of different maturity stages and different kinds of meadow crops, then a so-called broad-based calibration equation which covers the actual diversity of samples should be developed.

Such is the case when NIR is used to predict the feeding value of forage samples from farms throughout Norway. For this purpose the National Association of Milk Producers in Norway (NML) has developed calibration equations for fresh forage (pasture), silage and hay. These

equations are made as broad-based as possible. However, relatively few early- or late-cut samples were available, and so the calibration sets consist mainly of samples covering the «medium» range of quality.

This study was carried out to find out how well samples of different species, harvested at different maturity stages, were predicted by these equations. The effects of mill type were also considered.

MATERIALS AND METHODS

Forage samples

The forage samples in this study comprised a variety of the most common meadow crops, preserved as fresh frozen herbage, silage and barn-dried hay. The samples were the same as those described by Kjos (1990a). The different forage samples are given in Table 1.

Chemical analyses

Crude protein (CP) and crude fibre (CF) were determined according to the Weende method (A.O.A.C. 1980). Digestible crude protein (DCP) and fattening feed unit (FU) were calculated from digestibility experiments with sheep. 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. For silage, the value number 0.80 was used. *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 given as mean values.

Preparation of the NIR samples

Each of the forage samples was divided into two subsamples for different drying procedures. In addition, there was a subset of hay samples without further drying (undried). After drying, each of these subsets (with the exception of the hay samples) was ground on three different mills. All of the mills were equipped with a 1.0 mm aperture screen. The different preparation procedures are given in Table 2.

Table 1. The different samples of meadow crops preserved by different methods

Species of meadow crop		Number of samples of the different qualities: Fresh herbage Total	Silage Total	Hay Total
Meadow grass	*(Poa pratensis)*	5	5	4
Meadow fescue	*(Festuca pratensis)*	8	6	4
Cocksfoot	*(Dactylis glomerata)*	2	2	2
Smooth broomegrass	*(Bromus inermis)*	4	4	4
Timothy	*(Phleum pratense)*	6	7	5
Rye grass	*(Lolium perenne)*	4	4	4
Red clover	*(Trifolium pratense)*	4	4	3
Meadow fescue/Timothy		3		
Cut:				
Early cut (one week prior to heading)		15	15	12
Normal cut (at heading)		5	2	1
Late cut (at flowering)		13	15	13
Second cut		3		
Total		36	32	26

Table 2. Preparation of the NIR samples

	Drying procedure	Grinding procedure		Number of samples in the test sets
Fresh herbage	60°C, 24 hours	Retsch cutting mill	(R OD60)	27
		Christy & Norris hammer mill	(HM OD60)	36[1]
		Tecator cyclone mill	(CM OD60)	27
	70°C, 24 hours	Retsch cutting mill	(R OD70)	27
		Christy & Norris hammer mill	(HM OD70)	26
		Tecator cyclone mill	(CM OD70)	27
Silage	60°C, 24 hours	Retsch cutting mill	(R OD60)	21
		Christy & Norris hammer mill	(HM OD60)	32[1]
		Tecator cyclone mill	(CM OD60)	21
	70°C, 24 hours	Retsch cutting mill	(R OD70)	21
		Christy & Norris hammer mill	(HM OD70)	21
		Tecator cyclone mill	(CM OD70)	21
Hay	60°C, 24 hours	Retsch cutting mill	(R OD60)	19
		Christy & Norris hammer mill	(HM OD60)	21[1]
	70°C, 24 hours	Christy & Norris hammer mill	(HM OD70)	19
	No further drying	Christy & Norris hammer mill	(HM BD)	26[1]

[1] Only these preparation procedures include all the samples in this study.

Table 3. The calibration equations used in this study (NML 87, personal communications)

Equation	Forage samples	Constituents to be predicted	Wavelengths (nm)				
GRA7	Fresh herbage	Crude protein (% of dry matter)	1632	1824	1856	2136	2192
		Digestible crude protein (g/kg dry matter)	1632	1824	1856	2136	2192
		In vitro DM digestibility (%)	1104	2204	2228	2248	2256
SUR4	Silage	Crude protein (% of dry matter)	1720	1832	2152	2188	
		Digestible crude protein (g/kg dry matter)	1712	1824	2156	2188	
SUR7	Silage	Fattening feed unit (per 100 kg dry matter)	1208	1264	1676	1684	2124
HO10	Hay	Crude protein (% of dry matter)	1372	1748	2144	2200	
		Crude fibre (% of dry matter)	2296	2332	2356	2472	
		Digestible crude protein (g/kg dry matter)	2124	2188	2268	2436	
		Fattening feed unit (per 100 kg dry matter)	1676	1740	1884	1908	2040

NIR analyses

The NIR analyses of the samples were carried out at a forage laboratory («Grovfôrlaboratoriet») run by the 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 wavelength range of 1100 - 2500 nm, and the NIR spectrum for each sample was stored on a floppydisk. Each of the samples was run in duplicate. From the NIR spectra the nutritive value of each sample was predicted by means of calibration equations developed and used by the forage laboratory. These equations are described in Table 3. The calibration samples were oven-dried at 60°C, and

ground with a Retsch mill or a hammer mill.

Statistical analyses

The chemically determined (LAB) values were compared with the NIR-predicted (NIR) values. This was carried out using SAS (1982). The results are given as mean values for each sample set, 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 (R^2) between LAB and NIR values.

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. The correlations are also shown in figures where NIR values are plotted against LAB values.

The NIR predictions obtained for the different grinding procedures were also compared. The results are given as the mean corrected standard error of difference (SED(C)). No significant effect of the NIR duplicates was found, and therefore the mean value for each of the NIR samples was used in the statistical tests. The effects of preparation procedures were tested according to a n x 6 factorial design, where n = number of forage samples. The tests were performed using the model

$$y_{ij} = \mu + a_i + b_j \qquad \begin{matrix} i = 1 - n \\ j = 1 - 6 \end{matrix}$$

where Y_{ij} = the mean of the NIR-estimated value, μ = the overall mean effect, a_i = the effect of forage sample and b_j = the effect of preparation procedure. The analyses of variance were carried out by PROC GLM in SAS (1982).

RESULTS

Chemical analyses.

Some mean values from the chemical analyses are given in Table 4. A full survey of the chemical composition of the samples is given by Kjos (1990a).

Effect of preparation procedure on the NIR predictions

In Table 5 the mean values of the NIR predictions for the different preparation procedures are given. The significance levels for the effect of preparation procedure on the NIR predictions are also given.

The effect of preparation procedure was significant for all of the predictions, with the exception of CP in the hay samples.

The different oven-drying temperatures (60°C or 70°C did not affect the mean of the predicted values, except for IVDMD in the fresh herbage samples, and FU in the hammer-milled silage samples. However, a tendency toward more accurate predictions for the samples dried at 60°C was observed. Undried and oven- dried hay samples gave predictions with different mean values. The oven-dried hay samples were predicted with a greater degree of accuracy than the undried samples (cf. Table 6).

The effect of mill type was different for the different predictions. The means of the predicted values for CP and DCP in the hammer-milled and cyclone-milled samples of dried fresh herbage were not significantly different. For silage and hay, this was the case for CP and DCP predictions of Retsch-milled and hammer-milled samples. In general, sample preparation using different mills seemed to have an influence on the prediction levels of the samples. The accuracy of the predictions for samples prepared in the different mills, irrespective of drying procedure, is given in Table 7, and the relationship between pairs of corresponding samples prepared on different mills in Table 8.

Table 4. Nutritive value, given as average values for the different maturity stages, for the material in this study

	Maturity stage	Fresh herbage		Silage		Hay	
		Mean	Range	Mean	Range	Mean	Range
Crude protein (% of DM)	Early cut	26.1	17.8 - 36.9	23.0	17.1 - 31.0	24.1	17.9 - 33.0
	Normal cut	15.9	12.0 - 18.7	13.8	10.8 - 16.8	14.2	
	Late cut	12.6	8.9 - 19.6	10.6	6.9 - 16.6	10.5	6.4 - 17.6
	Second cut	17.8	14.8 - 22.6				
	Total	19.0	8.9 - 36.9	16.8	6.9 - 31.0	16.9	6.4 - 33.0
Digestible crude protein (g per kg DM)	Early cut	211	127 - 317	186	133 - 253	193	136 - 260
	Normal cut	118	81 - 141	99	61 - 131	103	
	Late cut	80	49 - 137	65	34 - 113	64	31 - 132
	Second cut	125	95 - 183				
	Total	144	49 - 317	125	34 - 253	125	31 - 260
In vitro DM digestibility (%)	Early cut	74.4	64.3 - 81.2				
	Normal cut	67.4	62.3 - 73.2				
	Late cut	62.2	58.3 - 66.4				
	Second cut	68.1	63.5 - 72.6				
	Total	68.5	58.3 - 81.2				
Crude fibre (% of DM)	Early cut					24.7	19.3 - 30.8
	Normal cut					30.8	
	Late cut					34.7	26.3 - 38.0
	Total					29.9	19.3 - 38.0
Fattening feed unit (per 100 kg DM)	Early cut			79.6	58.1 - 86.8	78.4	67.9 - 91.4
	Normal cut			75.5	73.9 - 77.1	70.5	
	Late cut			62.9	52.8 - 71.3	51.7	41.9 - 65.0
	Total			71.5	52.8 - 86.8	64.8	41.9 - 91.4

Table 5. The mean values of the NIR predictions of test sets prepared by different procedures

	Preparation procedure[2)]	Crude protein % of DM	Digestible crude protein g per kg DM	Crude fibre % of DM	*In vitro* DM digestibility %	Fattening feed unit per 100 kg DM
Fresh herbage (n = 27)[1)]	R OD60	17.6[a]	119[a]		69.8	
	R OD70	17.9[a]	121[a]		69.1[b]	
	HM OD60	16.9[b]	112[b]		68.8[b]	
	HM OD70	16.7[b]	110[b]		68.0[a]	
	CM OD60	17.0[b]	113[b]		67.9[a]	
	CM OD70	17.0[b]	113[b]		66.9	
		p<0.001	p<0.001		p<0.001	
Silage (n = 21)[1)]	R OD60	17.0[a]	126[a]			76.3[ab]
	R OD70	17.0[a]	126[a]			75.9[b]
	HM OD60	16.7[a]	124[a]			77.7[c]
	HM OD70	16.7[a]	124[a]			77.0[ad]
	CM OD60	15.9[b]	119[b]			77.2[cd]
	CM OD70	16.1[b]	121[b]			76.9[ad]
		p<0.001	p<0.01			p<0.001
Hay (n = 19)[1)]	R OD60	16.8[a]	131[a]	30.3		66.9
	HM OD60	16.2[a]	127[a]	31.9[a]		68.6[a]
	HM OD70	16.3[a]	128[a]	31.8[a]		68.5[a]
	HM BD	16.2[a]	113	28.8		63.7
		NS	p<0.001	p<0.001		p<0.001

[1)] Only forage samples with all of the preparation procedures are compared.
[2)] Abbrevations for preparation procedure, see Table 2.
a, b, c, d - Same letters indicate non-significant difference (p < 0.05) between pairs of prediction sets.

Table 6. Accuracy of the NIR predictions of the hammer-milled forage samples[1)]

		n	BIAS	Standard error of prediction SEP	Mean corrected standard error of prediction SEP(C)	R^2	Relative percentage[2)]
Crude protein (% of DM)	Fresh herbage	36	2.5	3.18	2.02	0.94	47
	Silage	32	0.4	2.06	2.07	0.93	75
	Hay, oven-dried	26	1.0	2.40	2.23	0.92	65
	Hay, undried	26	1.0	2.73	2.61	0.92	62
Digestible crude protein (g/kg DM)	Fresh herbage	36	34	41.76	24.23	0.92	31
	Silage	32	3	20.62	20.77	0.93	75
	Hay, oven-dried	26	-1	16.86	17.13	0.94	77
	Hay, undried	26	12	25.35	22.75	0.93	62
Crude fibre (% of DM)	Hay, oven-dried	26	-0.9	2.92	2.83	0.92	54
	Hay, undried	26	2.1	3.92	3.38	0.87	46
In vitro DM digestibility (%)	Fresh herbage	36	-0.1	3.65	3.57	0.77	72
Fattening feed unit (per 100 kg DM)	Silage	32	-5.9	8.31	5.97	0.71	47
	Hay, oven-dried	26	-4.5	9.33	8.34	0.71	31
	Hay, undried	26	0.0	9.20	9.38	0.69	35

1) Samples of fresh herbage and silage were oven-dried at 60°C. Hay samples were oven-dried at 60°C or undried.

2) For crude protein and crude fibre: Relative percentage of samples with NIR values within 2 units from reference.
For digestible crude protein: Relative percentage of samples with NIR values within 20 units from reference.
For *in vitro* DM digestibility and fattening feed unit: Relative percentage of samples with NIR values within 4 units from reference.

Table 7. Accuracy of the NIR predictions of forage samples, oven-dried at 60°C or 70°C and ground with a Retsch mill (R), hammer mill (HM) or cyclone mill (CM). The oven-dried samples are put together in one group

		Mill	n	BIAS	Standard error of prediction SEP	Mean corrected standard error of prediction SEP(C)	R^2
Fresh herbage	Crude protein (% of DM)	R	54	1.3	2.21	1.82	0.93
		HM	53	2.1	2.75	1.82	0.92
		CM	54	2.1	2.72	1.78	0.94
	Digestible crude protein (g/kg DM)	R	54	25	32.95	21.99	0.73
		HM	53	31	37.29	20.72	0.90
		CM	54	32	38.31	21.94	0.92
	In vitro DM digestibility (%)	R	54	-0.9	3.42	3.34	0.73
		HM	53	0.1	3.70	3.73	0.72
		CM	54	1.2	3.61	3.45	0.73
Silage	Crude protein (% of DM)	R	42	0.0	2.49	2.52	0.90
		HM	42	0.3	2.07	2.08	0.92
		CM	42	0.9	2.54	2.40	0.93
	Digestible crude protein (g/kg DM)	R	42	0	25.72	26.03	0.90
		HM	42	2	21.73	21.86	0.91
		CM	42	6	25.82	25.30	0.92
	Fattening feed unit (per 100 kg DM)	R	42	-5.0	8.27	6.71	0.57
		HM	42	-5.9	8.42	6.07	0.67
		CM	42	-5.6	8.99	7.10	0.54
Hay	Crude protein (% of DM)	R	19	-0.4	2.65	2.69	0.89
		HM	38	0.2	1.89	1.90	0.94
	Digestible crude protein (g/kg DM)	R	19	-10	22.93	21.25	0.93
		HM	38	-6	15.24	14.08	0.96
	Crude fibre (% of DM)	R	19	0.6	2.15	2.13	0.89
		HM	38	-0.9	2.84	2.72	0.94
	Fattening feed unit (per 100 kg DM)	R	19	-4.8	8.38	7.04	0.82
		HM	38	-6.5	8.90	6.17	0.80

Only the forage samples which are prepared by all mill types are used in this comparison.

Table 8. The relationship between predictions of samples prepared in the different mills used in this experiment, compared with differences between NIR duplicates

	Samples to be compared[1] x	y	Fresh herbage	Silage	Hay
			(mean corrected standard error of difference (SED(C))		
Crude protein	R	HM	0.79	0.84	1.63
	R	CM	0.63	0.86	-
	HM	CM	0.94	0.97	-
	Duplicates[2]		0.56	0.51	0.47
Digestible crude protein	R	HM	6.87	7.65	14.00
	R	CM	5.45	7.06	-
	HM	CM	8.10	8.47	-
	Duplicates[2]		4.79	4.46	4.68
Crude fibre	R	HM	-	-	2.46
	Duplicates[2]		-	-	1.12
In vitro DM digestibility	R	HM	1.26	-	-
	R	CM	1.02	-	-
	HM	CM	1.01	-	-
	Duplicates[2]		1.11	-	-
Fattening feed unit	R	HM	-	3.81	2.64
	R	CM	-	3.13	-
	HM	CM	-	2.30	-
	Duplicates[2]		-	0.97	1.28

[1] Abbrevations are described in Table 2.
[2] Indicates the difference between the NIR duplicates.

Table 7 shows that the accuracy of the predictions was different for the different mills. For fresh herbage, the Retsch-milled samples produced the best predictions. However, R^2 was highest for the cyclone-milled samples. The best predictions of the silage samples were observed in the hammer-milled samples, but the Retsch-milled samples had the lowest BIAS. Also for silage, the cyclone-milled samples gave the highest R^2 values, except for FU. For hay, the best CP and DCP predictions were obtained for the hammer-milled samples, which also had the highest R^2 values.

From Table 8 it can be seen that for the NIR-predicted values, SED(C) between pairs of mills was higher than SED(C) between duplicates, except for some of the differences for the fresh herbage samples (Retsch mill against cyclone mill, and hammer mill against cyclone mill for IVDMD).

Accuracy of the NIR predictions (effects of maturity stage and species).

The accuracy of the predictions made on hammer-milled samples dried at 60°C is also given in Table 6. The NIR values are plotted against the LAB values in Figures 1-5.

CP, DCP and CF were predicted with a relatively high level of accuracy. However, CP and DCP in the fresh herbage samples were strongly underestimated. IVDMD was predicted with a lower level of accuracy, and for FU the accuracy was lower still. For FU in the hay samples, and especially in the silage samples, there was a strong tendency towards over-

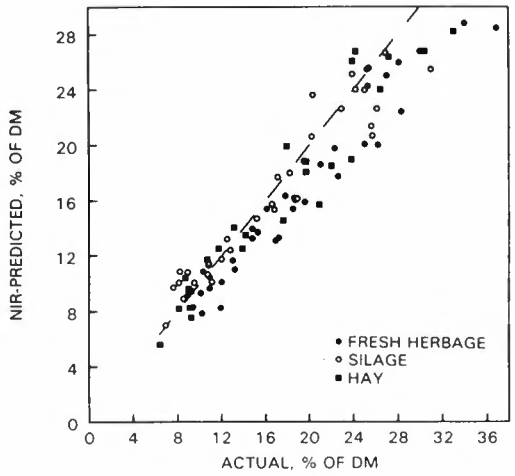

Figure 1. Plot of actual and NIR predicted crude protein content in the dried samples of fresh herbage, silage and hay.
--- NIR = ACTUAL

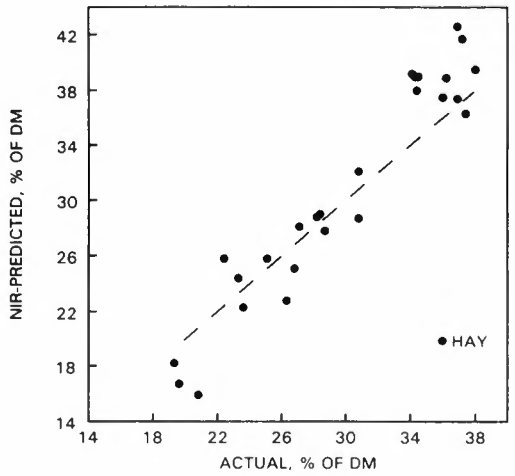

Figure 3. Plot of actual and NIR predicted content of crude fiber in the dried samples of hay.
--- NIR = ACTUAL

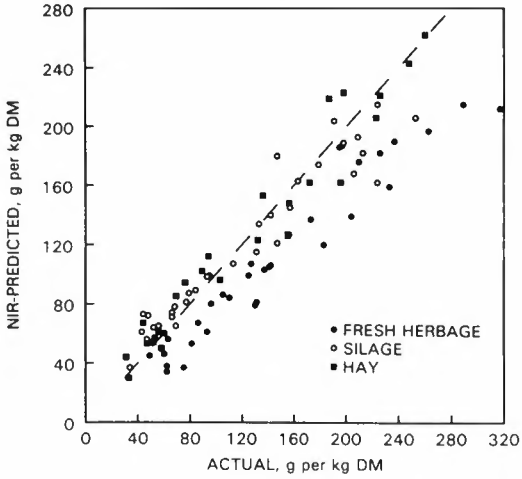

Figure 2. Plot of actual and NIR predicted content of digestible crude protein in the dried samples of fresh herbage, silage and hay.
--- NIR = ACTUAL

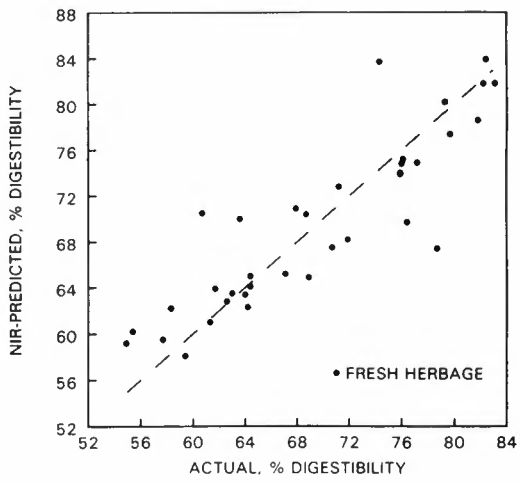

Figure 4. Plot of actual and NIR predicted IVDMD in the dried samples of fresh herbage.
--- NIR = ACTUAL

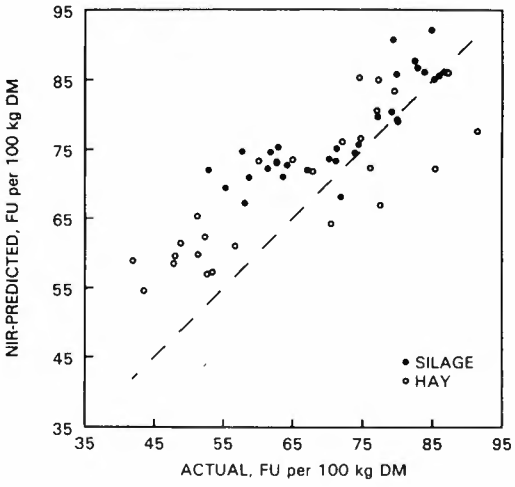

Figure 5. Plot of actual and NIR predicted fattening feed unit (FU) in the dried samples of silage and hay.
--- NIR = ACTUAL

estimation by the NIR prediction equations.

In Table 9 the accuracy of the early- or late-cut samples is given. For CP and DCP there was a tendency towards underestimation for early-cut samples (high values). For CF there was a tendency towards overestimation for the late-cut samples, which all had a high CF content. For CP and DCP, late-cut samples were predicted with a higher level of accuracy than the early-cut samples. The accuracy of the CF predictions was somewhat similar for both of the maturity stages, while IVDMD was predicted with a relatively low accuracy level for both the early- and the late-cut samples. For FU, the best predictions were obtained for the early-cut silage samples, and the late-cut hay samples. However, the late-cut samples of both silage and hay were strongly overestimated.

Because of a small number of observations for each of the species, it was difficult to find any effect of species on the accuracy of the predictions. However, R^2 between LAB and NIR values seemed to be lowest for the red clover and smooth bromegrass samples.

In Table 10, the effects of species on the accuracy of the predictions of CP and DCP for all preservation methods taken together are given. Meadow grass, meadow fescue and timothy were taken as a whole since they gave predictions of approximately the same accuracy. This table shows that when samples of red clover, and also smooth bromegrass or rye grass were added, the accuracy of the predictions became altered.

In Table 11 it is indicated how difficult it is to find any distinct tendency attributable to species. For the early cut herbage, rye grass seemed to have the highest bias values. The late-cut red clover samples of fresh herbage also had high bias values.

Table 9. Accuracy of the NIR predictions of forage samples harvested at early or late stage of maturity[1)]

		Maturity stage	n	BIAS	Standard error of prediction SEP	Mean corrected standard error of prediction SEP(C)	R^2
Fresh herbage	Crude protein (% of DM)	Early	15	3.2	3.98	2.47	0.77
		Late	13	1.6	2.06	1.36	0.86
	Digestible crude protein (g/kg DM)	Early	15	48	54.21	26.66	0.77
		Late	13	20	23.10	12.17	0.82
	In vitro DM digestibility (%)	Early	15	-2.0	4.46	4.15	0.41
		Late	13	-1.2	2.96	2.83	0.40
Silage	Crude protein (% of DM)	Early	15	1.2	2.69	2.49	0.59
		Late	15	-0.5	1.22	1.14	0.86
	Digestible crude protein (g/kg DM)	Early	15	14	27.06	24.04	0.56
		Late	15	-9	12.47	9.26	0.83
	Fattening feed unit (per 100 kg DM)	Early	15	-2.7	4.96	4.29	0.69
		Late	15	-9.9	11.05	5.00	0.19
Hay	Crude protein (% of DM)	Early	12	1.8	3.22	2.82	0.64
		Late	13	0.3	1.30	1.33	0.80
	Digestible crude protein	Early	12	5	21.02	21.33	0.79
		Late	13	-8	12.64	10.49	0.80
	Crude fibre (% of DM)	Early	12	0.7	2.21	2.19	0.79
		Late	13	-2.3	3.50	2.73	0.80
	Fattening feed unit (per 100 kg DM)	Early	12	0.6	7.84	8.16	0.04
		Late	13	-10.0	10.69	4.01	0.62

[1)] Hammer-milled samples dried at 60°C.

Table 10. Accuracy of the predictions of samples[1] of the different species of fresh herbage, silage and hay together

	Maturity stage	Species	n	BIAS	Standard error of prediction SEP	Mean corrected standard error of prediction SEP(C)	R^2
Crude protein (% of DM)	Early	Basic group[2]	21	2.4	3.19	2.03	0.67
		" and Cocksfoot	24	2.3	3.03	1.98	0.71
		" and Smooth bromegrass	27	2.2	3.23	2.44	0.55
		" and Red clover	26	1.8	3.00	2.37	0.56
		" and Rye grass	27	3.0	3.76	2.32	0.81
	Late	Basic group[2]	20	0.1	1.30	1.33	0.61
		" and Cocksfoot	23	-0.1	1.32	1.35	0.59
		" and Smooth bromegrass	26	-0.2	1.21	1.22	0.69
		" and Red clover	26	0.4	1.64	1.62	0.82
		" and Rye grass	26	0.1	1.47	1.48	0.46
Digestible crude protein (g/kg DM)	Early	Basic group[2]	21	29	36.49	23.31	0.57
		" and Cocksfoot	24	28	35.52	22.97	0.59
		" and Smooth bromegrass	27	25	36.02	26.81	0.42
		" and Red clover	26	23	34.97	26.80	0.43
		" and Rye grass	27	31	41.62	28.30	0.66
	Late	Basic group[2]	20	3	15.18	15.36	0.34
		" and Cocksfoot	23	2	16.02	16.29	0.29
		" and Smooth bromegrass	26	3	14.20	14.19	0.46
		" and Red clover	26	0	16.18	16.50	0.65
		" and Rye grass	26	0	16.58	16.91	0.25

[1] Hammer milled samples dried at 60°C.
[2] Meadow grass, meadow fescue and timothy are put together in one group, called basic group.

Table 11. BIAS values for the predictions of samples of early cut or late cut of the different species[1]

		Fresh herbage			Silage		Hay		
Cut	Species	Crude protein	Digestible crude protein	*In vitro* DM digestibility	Crude protein	Digestible crude protein	Crude protein	Digestible crude protein	Crude fibre
Early	Meadow grass	4.6	70	-2.2	1.6	15	4.2	22	2.1
	Meadow fescue	2.8	45	0.2	2.3	30	3.8	23	0.3
	Cocksfoot	2.2	47	0.6	0.2	10	0.9	4	1.3
	Smooth bromegrass	3.0	37	5.9	2.2	20	2.3	-25	1.6
	Timothy	2.6	34	-4.1	0.3	4	1.3	18	0.8
	Red clover	0.9	27	-4.2	-1.5	-14	-2.2	-26	4.9
	Rye grass	6.8	89	7.0	2.9	28	4.2	1	2.0
Late	Meadow grass	1.0	16	-2.3	-1.7	-20	-0.1	9	1.7
	Meadow fescue	1.3	13	-0.6	-0.5	-12	-0.5	11	3.6
	Cocksfoot	2.2	32	-3.4	-0.7	5	-1.0	16	-1.5
	Smooth bromegrass	-0.4	2	1.6	0.1	3	-0.5	10	-4.1
	Timothy	1.0	19	1.2	-1.5	13	0.8	3	3.3
	Red clover	3.4	29	-5.5	0.7	0	2.2	-4	-1.4
	Rye grass	3.0	33	0.2	0.2	-2	0.2	-10	3.1

[1] Hammer-milled samples dried at 60°C.

DISCUSSION

Effects of preparation procedure

The results from this experiment confirm those described by Kjos (1990b) obtained on some of the samples from this experiment. Samples dried at 60°C or 70°C have approximately the same predicted values, while the predicted values for samples prepared in different mills were somewhat different. There were no appreciable differences in the accuracy of the predictions of sets prepared in different mills, with the exception of the hay samples. The results indicate that the effect of mill type influences the accuracy of the predictions in different ways for the different calibration equations. The SED(C) values are highest between predictions of samples ground with a hammer mill or a cyclone mill.

Although the samples prepared in a mill type other than the one used for the calibration samples can give acceptable predicted values, the best results can be expected when calibration samples and prediction samples are prepared in the same way. A fine and homogeneous particle size, as in the samples prepared in the cyclone mill, is favourable. This has been discussed previously by Kjos (1990b).

Undried compared with oven-dried hay samples

For hay, the undried samples are predicted with a lower level of accuracy than the oven-dried samples. The undried samples had a lower moisture content than the oven-dried samples (87% DM vs 95% DM), and many of them are therefore outside the DM range represented in the calibration equation. The higher degree of accuracy of the predictions for low moisture samples is confirmed by Winch & Major (1981) and Fales & Cummins (1982). According to Winch & Major (1981), who had two moisture levels (5-8% and 9-13%), the moisture content had no great effect on the predictions of nitrogen in the samples, but the predictions of *in vitro* and *in vivo* digestibility were affected. Fales & Cummins (1982) predicted ADF in sets of samples with different moisture levels by a prediction equation based on oven-dried samples, and they found that the accuracy of the predictions was lower for samples with a moisture content of 8.9% and 11.7% than for samples with less than 5% moisture. It is possible to make calibration equations for samples covering a wide range of moisture content (fx. undried hay samples), but there are problems associated with among other things swelling of the fibre fraction in the high moisture samples, and also the moisture content itself. These factors cause an altered spectra compared with dried samples. According to Coleman et al. (1985), some of these effects can be eliminated by using moisture in the sample as covariate to the NIR spectra, but the best calibrations will possibly be obtained by using dried samples.

Accuracy of the NIR predictions

The accuracy of the NIR predictions in this study is rather low compared with what is commonly found in the literature, among others: Hellamaki (1983), Hellamaki & Moisio (1983), Bengtsson & Larsson (1984), Köwitsch et al. (1985), Marten et al. (1985), Valdes et al. (1985), Murray (1986), Redshaw et al. (1986), Brown & Moore (1987), Wetherill & Murray (1987), Lindgren (1988) and Surprenant & Michaud (1988). The SEP and R^2 values reported for CP, DCP, CF and *in vitro* digestibility are mostly in the given ranges: CP: 0.4-1.6; 0.88-0.99 (0.80- 0.97 for silage); DCP: 11; 0.89 (one reference); CF: 1.30- 3.80; 0.72-0.91; and *in vitro* digestibility: 2.0-5.0; 0.64- 0.92. No predictions for FU are reported, but for metabolizable energy (ME) determination coefficients in the range 0.40-0.90 are obtained. Higher SEP values, and lower R^2 values are often reported for silage samples, compared with fresh herbage and hay. The SEP values for CF and *in vitro* digestibility in this study are

within the range of the reported values, while prediction of CP has a somewhat higher SEP value. The predictions of chemical composition (CP and CF) have higher determination coefficients than the predictions of animal responses (*in vitro* digestibility, FU), because of a higher variability in the animal responses. The determination coefficient for the prediction of DCP, however, is in the same range as CP. Similar results are reported by Redshaw et al. (1986). With the exception of the hay equations, the wavelengths used to predict CP and DCP were nearly the same. The predictions of CP and DCP are probably closely related, and therefore DCP can be predicted with a higher level of accuracy than other animal responses.

Hellämäki & Moisio (1983) reported that 95% of their CP predictions and 84% of their CF predictions on silage samples differed from the chemical values by less than 2 units. The percentages reported for the predictions in this study are lower, especially for the fresh herbage samples. For the prediction of *in vitro* organic matter digestibility, Brown & Moore (1987) reported that 58% of the predictions were found within a 4 unit difference of the wet chemistry values, while the corresponding percentage in this study was 72%.

The underestimation observed for CP and DCP in fresh herbage was partly due to a correction being made for the CP and DCP values in the calibration samples. If the same correction was used on the fresh herbage samples in this study, the following values for BIAS and SEP(C) would be obtained.

CP : BIAS = 0.6 and SEP(C) = 1.71
DCP: BIAS = 20 and SEP (C) = 19.44
R^2 was not affected by this correction.

The high level of error in the predictions, compared with the literature, is partly caused by relative heterogeneous prediction sets (different maturity stages and different species), and partly by the fact that the calibration equations are made on sets with relatively few samples of early or late maturity stages. The relationship between the different calibration sets and prediction sets is given in Table 12. CP and DCP in the early-cut samples are predicted with a relatively high level of error, while the SEP values for the late-cut samples are within the reported range. The early-cut samples (especially the samples of fresh herbage) had a very high content of CP and DCP, and therefore the values of CP and DCP in these samples were more extreme than, for example, the values for CF content. To make better estimates of the early-cut samples, more of these samples should be included in the calibration equations. The low determination coefficient observed for the predictions of IVDMD in early-cut fresh herbage samples is caused by two outlier samples. If these are omitted, the following SEP and R^2 values for early-cut samples are obtained: 3.07 and 0.62. A low determination coefficient was also observed for the FU in early-cut hay samples, and if the three samples with the poorest predictions are omitted , SEP and R^2 values of 4.17 and 0.63 respectively, are obtained.

The high BIAS values observed for the prediction of FU in the late-cut samples of silage and hay can be explained by the fact that samples with such FU values are poorly represented in the calibration sets. This underlines the importance of having samples for prediction which are within the range of the calibration samples.

No clear conclusion can be drawn from this study concerning the effect of species on the accuracy of the predictions. The high BIAS values observed for the early-cut rye grass samples can be explained by the extreme laboratory values obtained for these samples compared with the other samples. However, the difference in the predictions of legumes and grasses which are indicated is also reported in the literature. Grass samples

are best predicted by calibration equations made on grass samples only, and when mixed calibration sets (containing both grass and legume samples) are used, the grass samples are predicted with a lower R^2 value and a higher SEP value, according to Winch & Major (1981) and Bengtsson & Larsson (1984). However, the «mixed» calibration equation give a smaller number of samples with large errors of prediction when used on a mixed calibration set, compared with «grass» equations. Also, Brown & Moore (1987) report that specific calibrations, made on samples of the same species, gave more accurate predictions than a general equation, when used on the specific samples. The difference in the accuracy of the predictions made by the two kinds of equations was higher for *in vitro* digestibility than for CP. The difference in accuracy when CP was predicted was almost neg-

Table 12. A comparison between the different calibration sets and test sets in this study

		Mean	Standard deviation	Range	R^2	Test set relative to[1] calibration set		
		Calibration set				%		
Crude protein (% of DM)	Fresh herbage	15.4	4.1	6.7 - 25.7	0.98			
	Silage	13.0	3.2	5.2 - 19.9	0.94			
	Hay	13.1	4.0	7.5 - 23.1	0.97			
		Test set				Lower	Adequate	Higher
	Fresh herbage	19.0	7.1	8.9 - 36.9	0.94	-	80	20
	Silage	16.8	6.8	6.9 - 31.0	0.93	-	66	34
	Hay	16.9	7.7	6.4 - 33.0	0.92	-	80	20
		Calibration set						
Digestible crude protein (g per kg DM)	Fresh herbage	99	35	24 - 188	0.98			
	Silage	91	29	22 - 163	0.93			
	Hay	88	38	40 - 184	0.97			
		Test set				Lower	Adequate	Higher
	Fresh herbage	144	69	47 - 317	0.92	-	75	25
	Silage	125	66	32 - 254	0.93	-	69	31
	Hay	125	72	21 - 262	0.94	8	67	25
Crude fibre (% of DM)		Calibration set						
	Hay	32.8	4.3	21.7 - 40.0	0.94			
		Test set				Lower	Adequate	Higher
	Hay	29.9	6.0	19.3 - 38.0	0.92	20	80	-
		Calibration set						
Fattening feed unit (per 100 kg DM)	Fresh herbage[2]	75.0	8.2	56.0 - 90.0	0.87			
	Silage	75.1	4.7	62.6 - 85.4	0.76			
	Hay	60.0	8.1	44.3 - 83.0	0.89			
		Test set				Lower	Adequate	Higher
	Fresh herbage[2]	76.5	13.1	53.3 -110.6	-	6	80	14
	Silage	71.5	10.3	50.5 - 87.2	0.71	37	54	9
	Hay	64.8	14.8	37.8 - 93.4	0.71	8	52	40

[1] Percentage of samples in the test sets which are lower, adequate or higher than the range of the calibration sets.

[2] The range of the *in vitro* digestibility for the fresh herbage calibration samples was not available, therefore fattening feed unit is used for the comparison.

ligible. Minson et al. (1983) included information on the forage species in the calibration equation, since BIAS is often associated with the species to be predicted. In doing so, they observed a reduced level of error in the predictions. However, the effect of this kind of bias must be examined more closely before any recommendation can be made on its practical use. The BIAS connected to species can be reduced, but not eliminated, by increasing the number of samples in the calibration equation (Minson & Butler 1983). Köwitsch et al. (1985) developed a calibration equation for CF based on nine species and mixtures of species, and found that cocksfoot and white clover were not predicted with sufficient accuracy.

The conclusion here is that when mixed sample sets consisting of different species of grass and legumes are to be predicted, a calibration equation based on a mixed set consisting of the same kind of samples should be used. The predictions of samples containing species which are expected to give a high level of error should be examined carefully.

SUMMARY

1. Crude protein (CP), crude fibre (CF), digestible crude protein (DCP), *in vitro* DMD (IVDMD) and feed units (FU) were predicted by NIR in samples of fresh herbage, silage and hay, using NIR equations obtained from samples dried at 60°C and ground by means of a cutting mill or a hammer mill. There were samples of different species of meadow crops harvested at different stages of maturity.

2. The samples for NIR analysis were either undried (hay samples) or ovendried at 60°C or 70°C. They were ground by Retsch cutting mill, Christy & Norris hammer mill or Tecator cyclone mill. The accuracy of the NIR predictions was assessed by comparison with traditionally determined values. The effect of preparation procedure was also studied.

3. CP, DCP and CF were predicted with the highest level of accuracy by the NIR equations, with R^2 = 0.92-0.94. For CP and DCP, late-cut samples were predicted with a higher degree of accuracy than early-cut samples, the latter being underestimated. For CF, the late-cut samples were overestimated.

4. In general, NIR predicts animal responses with a lower degree of accuracy than it predicts chemical constituents. IVDMD (fresh herbage samples) in this study was predicted with R^2 = 0.77, while FU (silage and hay) was predicted with R^2 = 0.71. The NIR equations for FU used here gave poor predictions for many of the samples.

5. There was hardly any effect on the accuracy level of drying at 60°C versus 70°C. The undried hay samples, however, were predicted with a lower level of accuracy than the ovendried hay samples. NIR equations can be made from undried samples, but such equations are expected to result in less accurate predictions than ovendried samples. The type of mill used had an effect on the accuracy of the NIR predictions.

6. It was difficult to find any distinct tendencies attributable to effect of species in this study. However, some indications of differences between predictions of grass and legumes were observed.

7. Compared with equations in the literature, the NIR equations used here resulted in predictions with a slightly lower level of accuracy. An explanation for this may be that heterogeneous sets of samples, and a relatively high number of samples

with values outside the range represented in the NIR equations were used. This underlines the importance of having calibration sets and test sets covering the same range, and having the same type of samples in both sets.

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The temporal and spatial distribution of arthropod predators of the aphids *Rhopalosiphum padi* W. and *Sitobion avenae* (F.) in cereals next to field-margin habitats

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The value of field-margins for enhancing natural enemy populations in arable land was tested using six transects of gutter-traps set up at 1, 5, 10, 25, 35 and 50 m from the field-margins in two oatfields. Three trapping lines caught predators moving into the fields and three caught those moving out. The traps were emptied each week and predators were identified in each catch. More predator species occurred out to 10 m from the field-margins; 68-85 % of the species were aphid-feeders. Also, a greater early season abundance of several predator groups occurred in that 10 m zone. The distributions evened out through the season and traps detected a net movement of individuals into the field up until that stage. Predation of freeze-killed aphids placed next to each trap related to the patterns of predator abundance. Overall, field-margins enhanced the numbers of predator species and their abundance in adjacent cereals at the time of aphid population establishment.

Key words: Abundance, aphid populations, arthropods, field-margins, predators, spatial dynamics, species-richness.

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The arthropod predators which occur in arable land in Norway (Andersen 1982) closely resemble the range of species found in cereals in Sweden (Ekbom & Wiktelius 1985). In Sweden, a combination of field-manipulation of field-densities of predators (Chiverton 1986), analysis of diet using the enzyme-linked immunosorbent assay (ELISA) and gut dissection (Chiverton 1987) and behavioural studies (Chiverton 1988) was used to identify those predators which fed on the bird-cherry oat aphid *Rhopalosiphum padi* W. when its populations were establishing in cereals in spring. Furthermore, the grain aphid *Sitobion avenae* (F.) affected cereals in Norway (Dennis unpubl. data) and therefore ELISA and gut dissection studies carried out in Britain (Sunderland et al. 1987) were used to select those aphid antagonist species which occurred in Norway.

In the present study, gutter traps were used to detect the spatial and temporal activity of the predators, selected on the basis of their aphid-feeding behaviour. This activity was monitored across cereal fields from the grassy field-margins to the centre of the crop. The layout of the traps was such that the following questions could be raised. In Norway, what proportion of predatory arthropods

active in cereals are aphid antagonists? How do numbers of these species change away from field-margins? Does their season of activity correspond to the time of early aphid population development in cereals before yield loss occurs? Does predator abundance correlate with the occurrence of the natural vegetation of the field-margin? Is there a link between the predatory pressure exerted on baits placed in the field and their vicinity to field-margins?

MATERIALS AND METHODS

Two oatfields were chosen for size and the presence of a uniform grass-strip on at least one of the field-margins. A 100 m section of field-margin with uniform structure and vegetation was chosen. Six transects, 15 m apart, were used out from the field-margin. Gutter-traps comprised a 1.2 m length of 10.2 cm wide plastic guttering fitted with an end piece with a down junction. A plastic pitfall cup was attached on the outside of this downward drainage tube. When dug into position, a large hole around the pitfall cup allowed easy sample collection and resetting without disturbance to the trapping edges of the guttering. A 20% ethanol solution was used as a preservative in the pitfall cup. The traps were dug in so that only one face of the gutter-trap, providing a 130 cm surface catchment-area, would catch ground-active beetles. A partial barrier was created on the other side by placing soil from the trap ditch over a c.60 cm wide strip parallel to the guttering. This made the traps sensitive to the direction of movement of ground-active arthropods. Catches of three transects discriminated for movement out from the field-margins and three for movement towards them. Traps were placed at 1, 5, 10, 25, 35 and 50 m from the field-margin on all transects. Trapping took place from 27 May to 20 July and samples were collected once a week. The arthropods were identified at x50 and counted with x6 magnification using a binocular microscope.

Once identified, species were compared with the lists of aphid-feeding predators from previous studies (Sunderland *et al.* 1987; Chiverton 1987). The spatial and temporal distribution of aphid-feeding predators (abundant in catches in the present study) was presented and the differences in catch of individuals out from the field-margins were tested for each direction.

At the time of aphid activity in the crop (13 July) the predation pressure exerted by the predatory species observed was measured by placing baits adjacent to the 36 traps on each site. Ten freeze-killed aphids were set out on a 9 cm diameter filter paper protected by a waxed-paper cover held above the ground on two 10 cm long nails. After 24 h the remaining aphids were counted.

RESULTS

Distribution of predatory species

The number of species known to be aphid predators was greater at the edge of fields adjacent to grassy field-margins (Fig. 1a; $\underline{F}_{5,266} = 7.88$; $\underline{P} < 0.001$). The pattern of distribution was similar for total arthropod predators (Fig. 1b; $\underline{F}_{5,266} = 5.99$; $\underline{P} < +0.001$) and comprised 68-85% (95% confidence range) aphid feeders (Fig. 1a). The overall abundance of aphid-feeding species was greater at the field edge until mid-June, after which the appearance of high numbers of ladybirds within the field reversed this pattern.

Distribution of individuals

Trapping showed that several species are more abundant at the edge of the field (1-10 m), especially in June when their populations were highest (Figs. 2-5). Some species (e.g. *Clivina fossor*, Fig. 3d) do not use field-margin habitats and spend their life-story in the cultivated (disturbed) parts of the agricultural landscape, showing early and even distribution across

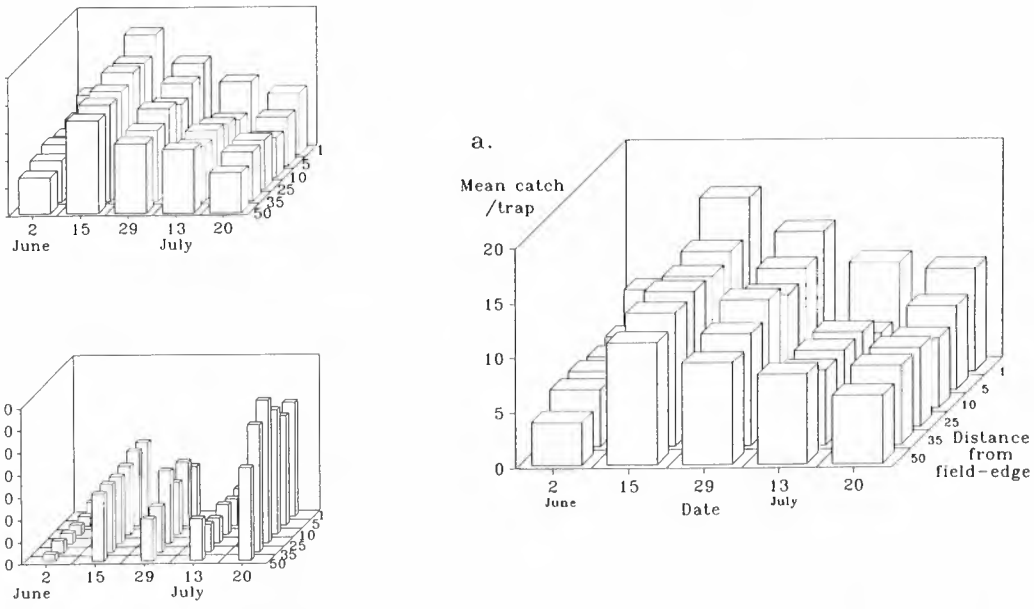

Fig. 1. Number of a. aphid-feeding and b. predatory species of arthropod in cereal crops from field-margin to field-centre (50 m) during 1989. c. Distribution and abundance of predatory individuals in cereal fields out to 50 m from grassy field-margins

fields ($F_{5,266}$ = 0.63; NS). *Pterostichus* spp. (Fig. 3c) were active in the field later in the season and move in from a larger area; their size and speed of movement allows them to cover greater distances than the other ground-walking species (Wallin & Ekbom 1988).

The distribution patterns of aphid-feeding groups could be divided into nine categories based on time of activity related to aphid population growth (Fig. 6) and spatial pattern across the field from the field-margin (Figs. 2-5). The aphid-feeding groups were divided up into these categories to distinguish those with the potential to regulate aphid populations (Table 1).

Table 1. Categories of aphid-feeding predators defined by period of activity and pattern of distribution into cereal fields inwards from the field-margin. 1. *Bembidion* spp.; 2. *Trechus* spp.; 3. *Pterostichus* spp.; 4. *Clivina fossor*; 5. Other Carabidae; 6. *Stenus biguttatus*; 7. Other Staphylinidae; 8. *Adalia septempunctata*; 9. Linyphiidae; 10. Lycosidae; 11. Opiliones; 12. Chilopoda; 13. Syrphidae larvae; 14. *Formica* sp.; and 15. Cantharidae

	Period of activity Aphid population growth stage		
	Resident	Establishment	Exponential
Gragarious	4	4, 5, 7	6, 3, 9, 13, 15
Field-edge	2, 10	1, 6, 9, 14	5, 11, 12
In-field			8, 15

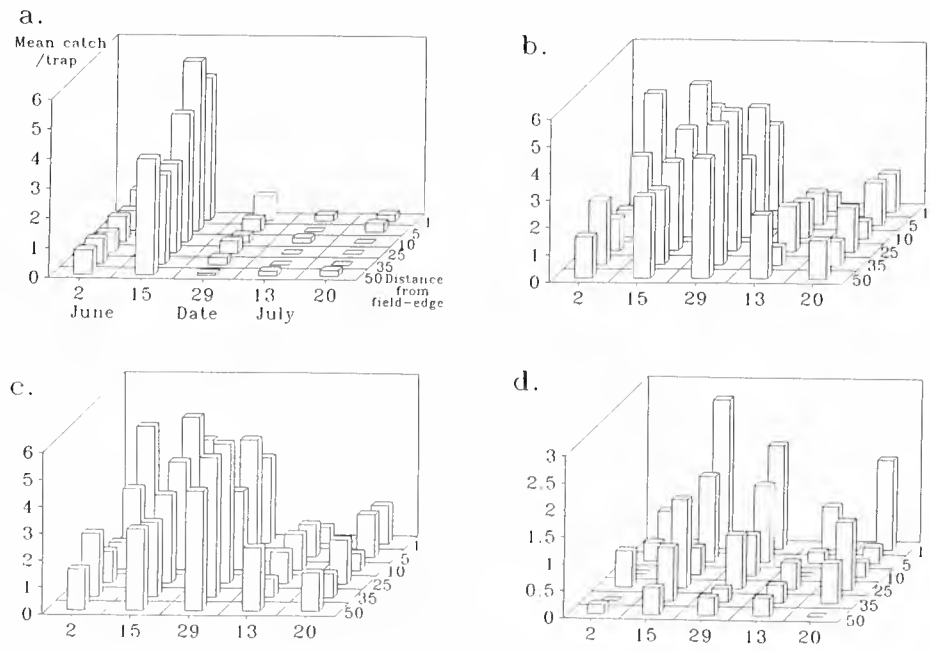

Fig. 2. Distribution and abundance of a. *Bembidion* spp.; b. *Stenus biguttatus*; c. Linyphiidae; and d. *Trechus* spp. in cereal fields out to 50 m from grassy field-margins

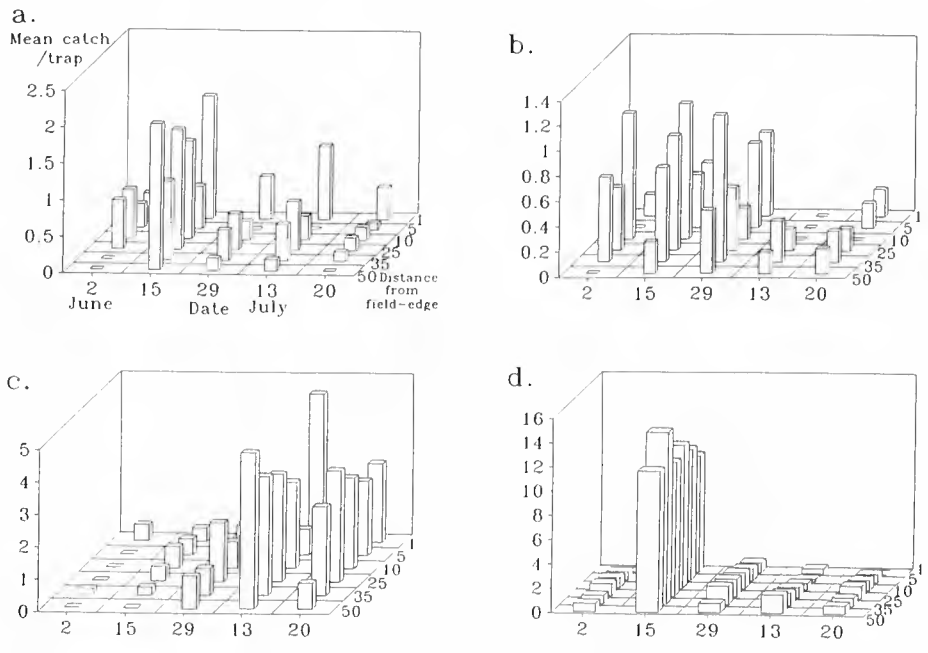

Fig. 3. Distribution and abundance of a. Other Carabidae; b. Other Staphylinidae; c. *Pterostichus* spp.; and d. *Clivina fossor* in cereal fields out to 50 m from grassy field-margins

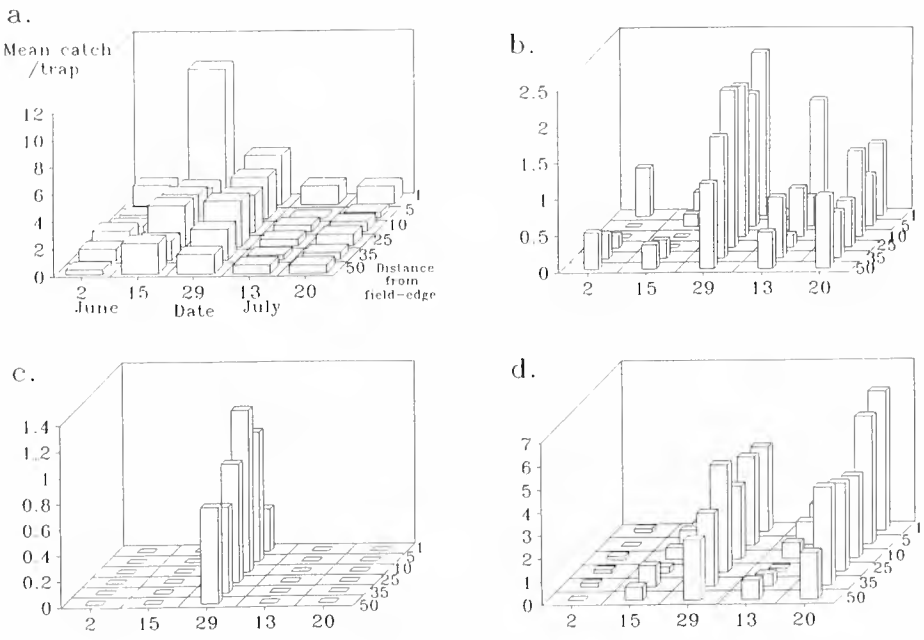

Fig. 4. Distribution and abundance of a. Lycosidae; b. Opiliones; c. Cantharidae; and d. Chilopoda in cereal fields out to 50 m from grassy field-margins

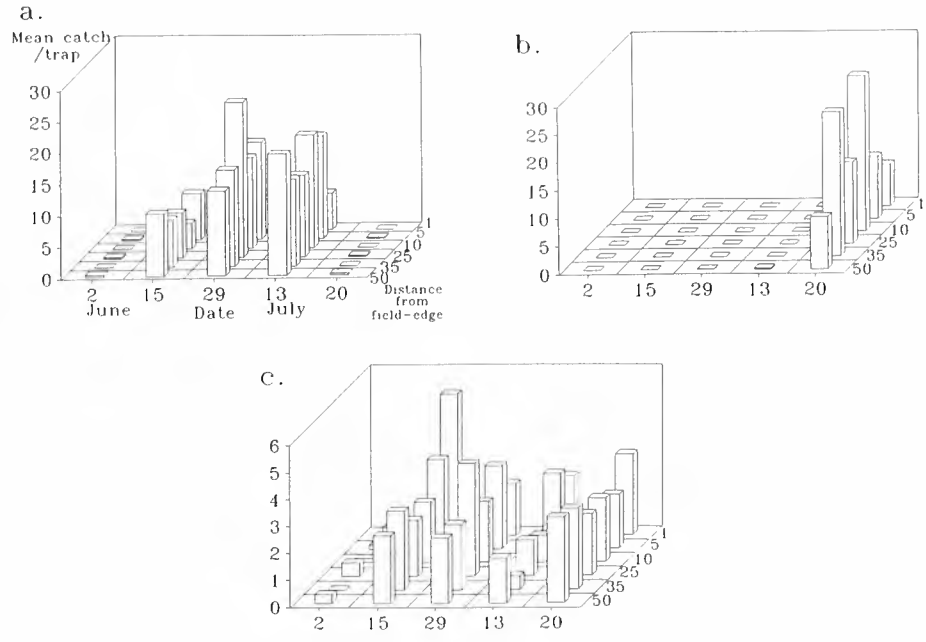

Fig. 5. Distribution and abundance of a. *Adalia septempuctata*; b. Syrphidae larvae; and c. *Formica* sp. in cereal fields out to 50 m from grassy field-margins

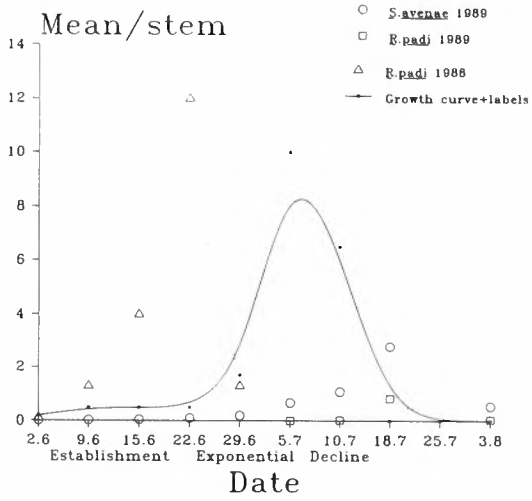

Fig. 6. Aphid population growth on oats in 1988 (Rygg 1989) and 1989 defining growth phases used to evaluate the temporal activity of predatory groups (after Chiverton 1987).

Directionality

Catches up until 29 June were different for some of the known aphid predator groups in the traps which descriminated between two directions (Fig. 7a-c). Traps which caught arthropods moving into the field at 1 and 5 m contained more of the four aphid-feeding groups which included *Trechus secalis, Bembidion lampros, B. quadrimaculatum* (Carabidae), Lycosidae (Araneae) and *Formica* spp. (Formicidae) (Fig. 7a). The differences in catch were less marked at 10 and 25 m (Fig. 7b) and 35 and 50 m (Fig. 7c). However, for total individual predators a significant difference in out or back catch ($F_{1,78}$ = 9.68; $P < 0.01$) was shown at 1 and 5 m and 10 and 25 m (Fig. 7d).

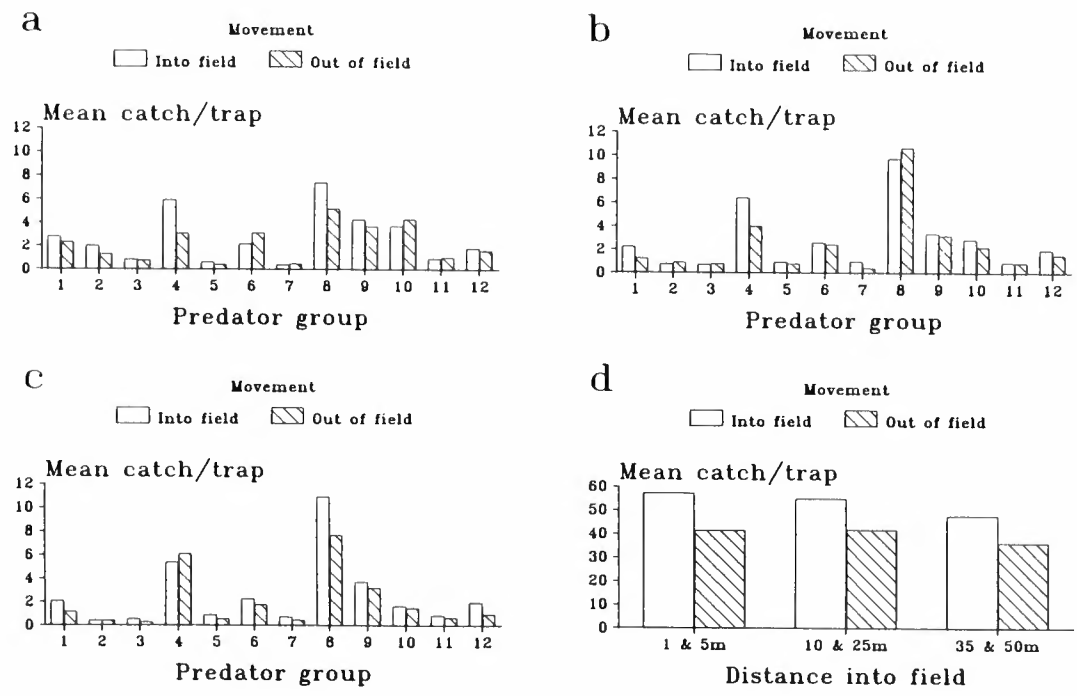

Fig. 7. Numbers of predators caught in traps discriminating direction of movement at a. 1 and 5 m; b. 10 and 25 m and c. 35 and 50 m in cereal fields with grassy field-margins. 1. *Bembidion* spp.; 2. *Trechus* spp.; 3. *Pterostichus* spp.; 4. *Clivina fossor;* 5. Other Carabidae; 6. *Stenus biguttatus*; 7. Other Staphylinidae; 8. *Adalia septempunctata*; 9. Linyphiidae; 10. Lycosidae; 11. Opiliones; and 12. Chilopoda. d. Total predator catch at three distance categories

Predation pressure

Predation rates of aphid baits (placed at the same distances from the field-margins as the traps on 13 July) related to the patterns of abundance of the aphid-feeding species (Fig. 8).

DISCUSSION

Regarding sampling, the use of gutter-traps forfeited the measure of density (Greenslade 1964) but gave a continuous and comparative measure of activity between distances into cereals from field-margins. Catch should have been unaffected by the habitat surrounding each trap because all traps were in oatfields at the same growth stage. Catches of predators are greater in autumn-sown compared with spring-sown crops (Pauer 1975; Jensen *et al.* 1989. Capture efficiency of different groups could have hidden their relative abundances. Some predators can detect trap edges, so avoiding capture, or they fly or climb out of the trap after capture (Halsall & Wratten 1988). In general, processes which cause the observed trapping patterns cannot be identified by trapping. However, the use of directional traps did disprove some hypotheses and further inferred others.

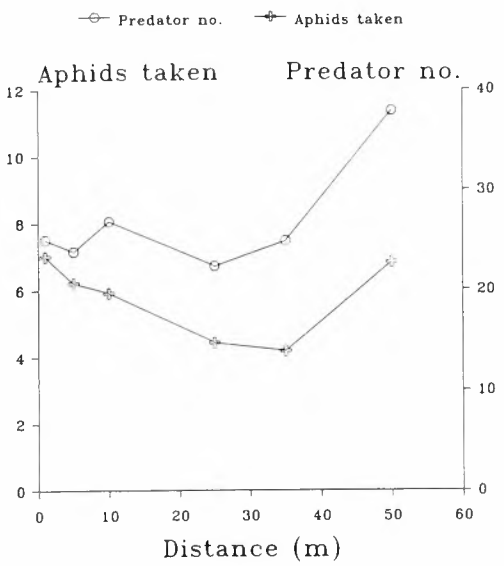

Fig. 8. Predation of aphid baits and numbers of aphid-feeding individuals in cereal fields out to 50 m from grassy field-margins on 13 July (r_{12} = 0.622; $P<0.05$)

Field-margins influenced the number of species active in cereal crops (Fig. 1 a & b). The significantly ($P<0.001$) higher numbers of both total predators (Fig. 1b) and aphid-feeding species (Fig. 1a) indicated that field-margins provide conditions in the field-edge that are not found from 10 m outwards. The present work cannot identify the process. Predator species may aggregate around field-margins because the vegetation makes the microclimate in the adjacent crop more favourable (Pollard *et al.* 1974); the extra species may also use flight dispersal and aggregate around field-margins as windbreaks (Lewis 1969). It could be due to the edge effect between the crop and field-margin habitats, where predators restricted to field-margins wander into the crop for short distances; illustrated in beetle communities of limestone islands surrounded by peat moorland (Bauer 1989).

Greater (aphid-feeding) species richness at the field-edge could prevent pest populations from reaching damaging levels bacause greater links are forged between the pest and the predators' trophic level (van Emden & Williams 1974). Indeed, Chambers *et al.* (1982) found that aphid populations across a field were non-random and that numbers were greater away from the field-edges, correlating inversely to numbers of predators in pitfall catches. The trend could be driven by the number of species as opposed to abundance of individual species, providing greater potential for consistent predation rates between generations compared with fewer species away from the field-margin.

The patterns of abundance of some predator groups were aggregated at the field-edge in the early season but levelled

out through the season (Table 1 and Wallin 1985), although the numbers of predatory species remained highest adjacent to field-margins (Fig. 1a & b). Two forms of dispersal were inferred from pitfall and vacuum-net catches on transects into cereal fields (Coombes & Sotherton 1986): a wave of dispersal outwards from overwintering habitats in the field-margins by species which walk and a rapid dispersal across the whole field by flight dispersing species from the same overwintering sites. Neither process can be proved from the sampling data of Coombes & Sotherton (1986) or Jensen *et al.* (1989), which fit several alternative hypotheses. From both these studies it is assumed that adjacent field-margins supported source (overwintering) populations of the predator groups. However, the observed patterns could result from other factors which could have an influence on species number (see above). In particular, the microclimate effect (Lewis 1969; Pollard *et al.* 1974) could produce the spatial dynamics observed by trapping without the field-margin being the overwintering habitat. Predators could disperse from overwintering habitats other than field-margins into fields and distribute around field-margins due to microclimatic constraints of the crop at early growth stages. This has been disproved by the net outward movement of predatory individuals in directional traps early in the season (Fig. 7d). On a larger than field scale, field-margins could act as corridors from overwintering to crop habitats adjacent to the field-margins. In this way, dispersal would be greatest into the most favourable crops (Jensen *et al.* 1989). For this hypothesis, densities of overwintering predators in the field-margin would not account for the numbers in the observed distribution. The crop would be a sink for populations of predators from sites outside the field/field-margin system and continual flux of immigration would occur through the field-margin until equilibrium was reached with adjacent fields.

Predatory species number and abundance peak in late June when aphid populations increase to damaging levels. In July, predation was shown to relate well to the abundance of the predators (Fig. 6). Predation would delay or remove the need to spray an insecticide if enough aphid-feeding occurred early in the aphid population development (Chambers *et al.* 1982; Dennis & Wratten 1990). The rate of feeding would have to match the rate of reproduction of the aphids at that stage of their development (mid-June). Both the number of aphid-feeding species and their abundance peak at 0-10 m at that time. Not spraying that zone could be a sensible practice to maximise natural control of aphids and reduce pesticide inputs. Greater numbers of predator species at 0-10 m will prevent the prey (pest) population increasing to levels likely to cause crop-yield loss at the field-edge (Fig. 1a; Chambers *et al.* 1982). The practice could protect adjacent natural biotopes from insecticide drift and encourage the proliferation of general arthropod diversity both of direct nature conservation value and as food to other wildlife. It would also provide a pool of natural enemies available to reinvade the insecticide sprayed crop and feed on aphids, reducing the risk of population resurgence after spraying.

SUMMARY

The data do not show that field-margins act as refugia for predators although this has been shown in other work for several species (Coombes & Sotherton 1986; Jensen *et al.* 1989; Dennis 1989). However, the presence of field-margins does influence the distribution and abundance of predators across cereal fields. A high proportion of these predators were known to feed on aphids. In effect, crop areas next to these natural habitats may have much less potential for pest outbreaks because of the greater richness of predators. When considering the economic value of

predators along with the value of the same habitats to nature conservation (see above) and the role of field-margins in preventing pollutants reaching watercourses (Schlosser & Karr 1981) and preventing soil erosion (Forman & Baudry 1984), the arguments for maximal field-size in efficient crop production give way to evidence that optimal field-size would be a better policy for sustainable agriculture.

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A study of extraction methods for assessing soil zinc availability: I. Soil zinc extractability and soil zinc buffering capacity in relation to soil properties

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Wu, X., I. Aasen & A.F. Selmer-Olsen 1991. A study of extraction methods for assessing soil zinc availability: I. Soil zinc extractability and soil zinc buffering capacity in relation to soil properties. Norwegian Journal of Agricultural Sciences 5: 89-107. ISSN 0801-5341.

Five soil zinc extractants – DTPA, ammonium acetate – EDTA (AA- EDTA), 0.2 N HCl, 0.5 M $Mg(NO_3)_2$ and H_2O – were compared using non-calcareous soil samples collected from 109 barley fields in southeastern Norway.
The extraction power of the five extractants followed the order: HCl > AA-EDTA = DTPA > $Mg(NO_3)_2$ > H_2O. DTPA-extractable zinc content was found to be highly correlated with AA-EDTA (r = 0.9895) and HCl-extractable zinc content, (r = 0.9014), while $Mg(NO_3)_2$-extractable zinc content was found to be more closely related to H_2O-extractable zinc content (r = 0.7023).
The soil zinc extractability estimated by DTPA, AA-EDTA and HCl was not significantly influenced by the soil properties studied, while that estimated by $Mg(NO_3)_2$ and H_2O decreased and the soil zinc buffering capacity estimators increased with increasing soil alkalinity (SA), exchangeable base cation concentration (BC), cation exchange capacity (CEC) and soil organic carbon content (C%). The magnitude of the influence followed the sequence: BC > SA > CEC > C% > clay%.

Key words: Non-calcareous soils, soil properties, zinc buffering capacity, zinc extractability, zinc extractants.

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Zinc deficiency has been recognized as one of the most wide-spread problems limiting plant growth in many countries of the world (Jahiruddin & Hoque 1983, Ponnamperuma et al. 1981, Liu et al. 1983), and various extraction methods have been used under different soil conditions for predicting soil zinc availability (Cox & Kamprath 1972, Lindsay & Cox 1985, Viets & Lindsay 1973). Lindsay & Cox (1985) have given a list of the extractants used in soil micronutrient testing, which includes various concentrations and combinations of HCl, H_2SO_4, DTPA, EDTA, NH_4OAC, $NaHCO_3$, NH_4F, dithizone, KCl and $CaCl_2$. In general, the extractants used can be grouped, according to their chemical properties, into neutral salts, acids, bases and chelating agents.

Neutral salts having cations with an electronic structure similar to that of zinc have been chosen mainly for determining the intensity level of zinc in the soil solution (John & Evans 1968, Levesque &

Mathur 1986, Mathur & Levesque 1988, Stewart & Berger 1965). More powerful extractants, such as dilute acids and chelating agents, have been used for estimating both the potentially available quantities and the mobile reserves of soil zinc.

Among acid extractants, 0.1 N HCl (Nelson et al. 1959, Tucker & Kurtz 1955, Wear & Sommer 1947) and 0.2 N HCl (Ellis et al. 1964) have been used mostly on acid soils. For soils with a pH above 7, the inclusion of other soil properties becomes important or even essential in addition to the acid-extractable zinc for predicting soil zinc availability.

One of the generally adopted chelation methods for zinc is the DTPA-TEA-$CaCl_2$ extraction method, which was originally developed for calcareous soils by Lindsay et al. (1967) and Lindsay & Norvell (1969); it was further modified by Lindsay & Norvell (1978), Soltanpour & Schwab (1977) and Baker & Amucher (1981) for simultaneous determination of zinc, manganese, iron and copper, and for several other purposes. Other studies have shown that the DTPA extractable zinc level is closely correlated with the soil zinc labile pool or soil zinc quantity (Graham 1973, Lindsay & Cox 1985, Page et al. 1982).

Another chelating agent, EDTA, and its combination with other reagents, has also been tested for determining the availability of micronutrients including zinc in many studies (Alley et al. 1972, Haynes 1983, Lakanen & Ervio 1971, Leclaire et al. 1984, Gupta & Mittal 1981, Ponnamperuma et al. 1981). Generally, ammonium acetate-EDTA was found to be comparable with the DTPA method.

Khasawneh (1971) emphasized the importance of three factors - intensity, replenishment and relative intensity - in determining the functional relationship between the ion uptake by plants and the status of ions in the growth media. The interaction of soil zinc intensity (I), quantity (Q) and buffering capacity (B) in relation to soil properties, soil zinc adsorption and soil zinc availability has been studied by Maskina et al. (1980), Nair (1984), Nair et al. (1984), Pasricha et al. (1987), and Mengel (1982) with different extraction methods.

Based on a relatively large number of samples, the present investigation was carried out to compare five different extractants for assessing zinc availability in non-calcareous soils and to study the influence of soil properties on soil zinc extractability and buffering capacity.

MATERIALS AND METHODS

Plant and soil samples

Barley plants and corresponding soil samples were collected from 109 farm fields in different districts of southeastern Norway during the plant growing season between stages 10.0 and 10.1 (Feekes scale, Large 1954). The sampling sites were carefully selected to ensure that the samples would be sufficiently representative of the major cereal production area of southeastern Norway, containing broad variations in soil pH, soil texture and in the level of the concerned micronutrients in both plants and soils.

Depending on the plant growth status, the sampling area of each barley sample varied from 0.094 to 0.25 m^2. The plants were cut to a height of about 4 cm above the ground with precautions being taken to avoid contamination. The soil samples, about 1 kg of soil each, were taken from the 20-cm surface horizon in the same area where the barley plants were collected. The plant samples were dried at 70° C for 48 hours and milled to pass through a 0.8 mm sieve. After careful removal of the plant roots, the soil samples were air-dried and passed through a 2-mm sieve. In order to analyse the total zinc content and the soil organic carbon content, 10 g of each soil sample was further ground into fine particles to obtain homogeneity.

Total zinc content

The total zinc content in both plant and soil samples was determined as follows: Two grams of a ground plant sample, or a 1 g sample of ground soil was heated in an oven at 550° C for 6 hours. After ashing, 5 ml of a concentrated HNO_3-HCL (1:3) mixture was added and the solution was gently heated on a thermoplate until completely dry. The residual was dissolved in 5 ml of 6 N HCl and transferred through an S&S blue ribbon filter paper into a 50 ml volumetric flask using deionized water. The zinc concentration of the solution was determined by atomic absorption spectrophotometry (AAS). The analysis of total zinc content in plant materials was repeated twice.

Extractable zinc content

Five extractants – DTPA, ammonium acetate-EDTA (AA-EDTA), HCl, $Mg(NO_3)_2$ and H_2O – were selected for determining extractable zinc levels in the soil samples:

DTPA:	0.005 M DTPA + 0.1 M TEA + 0.01 M $CaCl_2$ (Lindsay & Norvell 1978).
AA-EDTA:	1 M ammonium acetate-0.02 M EDTA (Levesque & Mathur 1988.
HCl:	0.2 N HCl (Ellis et al. 1964).
$Mg(NO_3)_2$:	0.5 M $Mg(NO_3)_2$ (Solbraa & Selmer-Olsen 1981).
H_2O:	Deionized water.

The soil samples were shaken with the above extractants for a certain period (Table 1), centrifuged and then filtered with an S&S blue ribbon filter paper and the zinc content measured by AAS. Parallel analyses were carried out for all five extractants.

Relevant soil properties

Soil pH was determined using a 1:2 soil:water volume ratio. Soil titratable alkalinity (TA), defined as the milliequivalents of an acid required to acidify a soil to a specific pH (pH 5), was determined using the procedure given by Nelson et al. (1959). The ammonium acetate (pH 7) method was used for determining the soil potential cation exchange capacity (CEC). Soil organic carbon content was determined by a carbon determinator, and soil mechanical analysis was carried out using the hydrometer method.

To obtain the soil volume:weight ratio, 10 ml of each air-dried soil sample was measured and weighed five times and the average value was used. The soil zinc content and relevant soil factors are all expressed on an oven-dry soil volume basis by conversion using the volume: weight ratio.

Soil zinc extractability and buffering capacity

The soil zinc extractability with respect to different extractants is defined, as

$$E\text{-}D = 100(ZnD/ZnT) \quad (1),$$
$$E\text{-}A = 100(ZnA/ZnT) \quad (2),$$
$$E\text{-}H = 100(ZnH/ZnT) \quad (3),$$
$$E\text{-}M = 100(ZnM/ZnT) \quad (4),$$

Table 1. Soil weight, solution volume and shaking time used for different extraction methods

	DTPA	AA-EDTA	HCl	$Mg(NO_3)_2$	H_2O
Soil weight (g)	4	4	4	8	10
Solution volume (ml)	40	40	40	40	20
Shaking time (h)	1	1	1	2	24

and E-W = 100(ZnW/ZnT) (5)

where ZnD = DTPA-extractable zinc content,
ZnA = AA-EDTA-extractable zinc content,
ZnH = HCl-extractable zinc content,
ZnM = $Mg(NO_3)_2$-extractable zinc content,
ZnW = water-extractable zinc content and
ZnT = total soil zinc content (more properly,. the HNO_3-HCl-soluble zinc content).

The soil zinc content was given as mg l^{-1}.

Based on the extraction functions of the extractants, the soil extractable zinc contents obtained by DTPA, AA-EDTA and HCl were regarded as estimators of soil zinc quantity (Q, the reversibly exchangeable fraction), and those obtained by $Mg(NO_3)_2$ and water as estimators of soil zinc intensity (I, the soluble plus readily exchangeable fraction). The soil zinc buffering capacity (B), which is generally defined as the derivative of Q with respect to I, was estimated as

B-D = d(Q-D)/I = ZnD/ZnM (6),
B-A = d(Q-A)/I = ZnA/ZnM (7),
and B-H = d(Q-H)/I = ZnH/ZnM (8).

Here B is assumed to be a constant for a given soil but to vary with soil types.

Statistical analysis

Analyses of variance, correlation, regression and scatter plotting were carried out using SAS (Statistical Analysis System) programs on an IBM computer. The descriptive statistics and the correlation matrix for the soil properties are given in Tables 2 and 3, respectively.

RESULTS AND DISCUSSIONS

Extraction power and correlations

The extraction power of the five extractants was found to follow the order (Table 4):

HCl > AA-EDTA > DTPA > $Mg(NO_3)_2$ > H_2O.

On average, AA-EDTA extracted a slightly higher amount of zinc from the soils than DTPA. The difference between

Table 2. Descriptive statistics of the soil properties (number of samples = 109)

Variable[a]	Mean	SD	Minimum	Maximum
pH	6.35	0.587	4.55	7.89
TA (meq. 100 ml^{-1})	2.00	1.47	0.02	9.15
BS (%)	66.8	16.69	17.83	99.74
EA (meq. 100 ml^{-1})	8.77	6.19	0.10	53.39
E-Ca (meq. 100 ml^{-1})	15.89	8.31	2.15	52.94
BC (meq. 100 ml^{-1})	18.32	8.62	2.97	54.88
CEC (meq. 100 ml^{-1})	27.09	9.25	10.25	75.88
C (%)	3.03	2.14	1.10	22.8
Clay (%)	10.30	5.51	4.00	36.4
Silt (%)	46.02	17.49	7.40	85.8
Sand (%)	43.67	19.43	6.00	87.2

a: TA = titratable alkalinity, BS = base saturation
EA = exchangeable acidity, E-Ca = exchangeable calcium
BC = exchangeable base cation concentration
CEC = cation exchange capacity, C = soil organic carbon

Table 3. Correlation matrix of soil properties (n = 109)

	pH	TA	BS	EA	E-Ca	BC	CEC	C%
pH	1.00							
TA[a]	0.83	1.00						
BS	0.83	0.91	1.00					
EA	-0.81	-0.70	-0.85	1.00				
E-Ca	0.54	0.68	0.73	-0.42	1.00			
BC	0.53	0.67	0.72	-0.39	0.99	1.00		
CEC	0.12	0.33	0.31	0.12	0.84	0.86	1.00	
C%	0.05	0.23	0.16	0.13	0.57	0.58	0.72	1.00
Clay%	-0.17	-0.16	-0.13	0.28	-0.08	-0.01	0.15	1.00
Silt%	0.03	-0.00	0.02	-0.01	0.03	0.05	0.06	-0.08
Sand%	0.02	0.05	-0.00	-0.09	-0.01	-0.04	-0.09	0.10

	Clay%	Silt%	Sand%
Clay%	1.00		
Silt%	0.22	1.00	
Sand%	-0.48	-0.96	1.00

a: See notes below Table 2.

Table 4. Means and variation ranges of soil zinc contents (mg l^{-1}) determined by different methods (n = 109)

Variable	Mean	SD	Minimum	Maximum
ZnT[a]	149.69	79.54	15.89	432.98
ZnD	2.89	3.66	0.29	27.93
ZnA	3.44	4.20	0.35	32.63
ZnH	9.07	8.21	0.94	44.52
ZnM	0.53	0.48	0.00	2.65
ZnW	0.17	0.14	0.00	0.67

a: ZnT = total zinc content, ZnD = DTPA-extractable zinc content,
ZnA = ammonium acetate-EDTA-extractable zinc content,
ZnH = HCl-extractable zinc content,
ZnM = $Mg(NO_3)_2$-extractable zinc content,
ZnW = water-extractable zinc content.

Table 5. Coefficient (r) of the correlations between soil zinc contents determined by different methods (n = 109)

	ZnT[a]	ZnD	ZnA	ZnH	ZnM	ZnW
ZnT	1.0000					
ZnD	0.6458	1.000				
ZnA	0.6458	0.9895	1.000			
ZnH	0.7709	0.9014	0.9137	1.000		
ZnM	0.5213	0.6369	0.5722	0.6438	1.0000	
ZnW	0.4673	0.4269	0.3924	0.4690	0.7023	1.0000

a: See notes below Table 4.

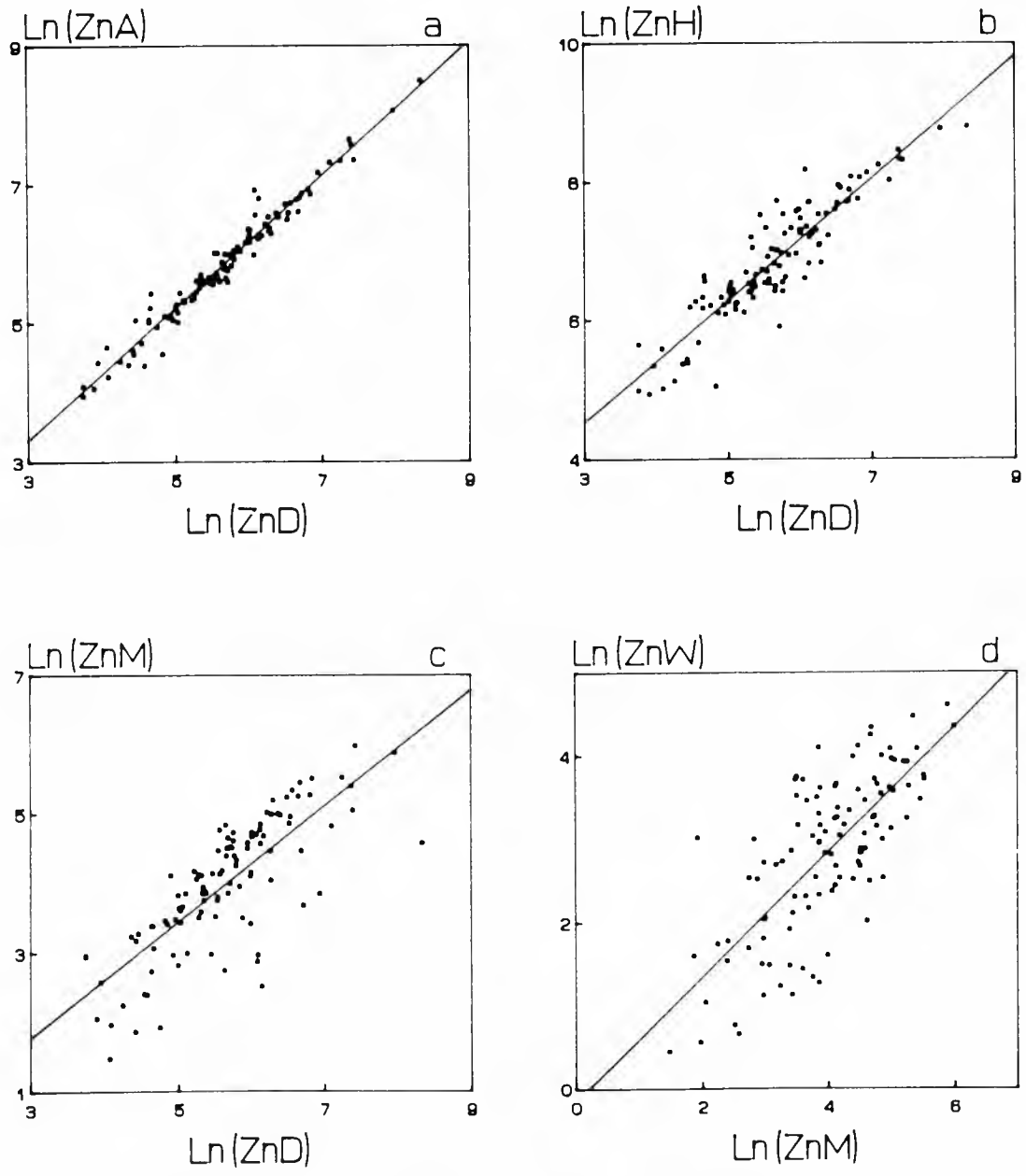

Fig. 1. Relationship between soil zinc contents (mg l^{-1}) determined by different extraction methods. Ln denotes the natural logarithm. ZnD, ZnA, ZnH, ZnM and ZnW represent DTPA-, AA-EDTA, HCl-, $Mg(NO_3)_2$- and water-extractable zinc contents

the two extractants, however, is not significant ($P > 0.1$).

The levels of correlation between the extractable zinc and the total zinc (more properly, the HNO_3-HCl-soluble zinc) were found to be in the sequence (Table 5):

$$ZnH > ZnD = ZnA > ZnM > ZnW$$

Again the difference between the coefficient values for ZnD and ZnA is very small. The highest r values obtained for the correlation between ZnH and ZnT suggest that the HCl-extractable zinc is less influenced by other soil properties.

The five extractants can be divided into two groups according to their mutual correlation levels: (1) HCl, DTPA and AA-EDTA and (2) $Mg(NO_3)_2$ and H_2O. The three extractants in the first group are correlated with each other at extremely high levels of significance with r values higher than 0.9 (Table 5). As shown in Figure 1a and 1b, the behaviours of DTPA, AA-EDTA and HCl are quite similar, indicating that these three extractants extracted zinc from approximately the same soil zinc pool. Relatively larger variation is noticeable in the HCl-DTPA plot (Fig. 1b), which suggests the occurrence of significant variation in carbonate levels among the present samples, namely, HCl may have extracted more zinc than DTPA from the soils richer in carbonates.

The two extractants in the second group are also closely correlated with each other (Table 5) but with much greater variations as evidenced by the scatter plotting (Fig. 1d). The r values of the correlations between extractants in different groups are much lower than those within each group (Table 5 and Fig. 1c) The variation in behaviour of the five extractants should be explainable by variations in soil properties or by variations in soil zinc extractability and buffering capacity. The mean values and the variation range of the estimated soil zinc extractability (E) and buffering capacity (B) are shown in Table 6. The r values of the correlations between soil zinc extractability, buffering capacity and relevant soil properties are given in Table 7.

Total soil zinc content (ZnT)

Because of the extremely low r values, the influence of the total soil zinc content (ZnT) on soil zinc extractabilities estimated by DTPA, AA-EDTA and HCl (E-D, E-A and E-H) is almost eliminated (Table 7). The slightly negative correlations between the extractability by $Mg(NO_3)_2$ and H_2O (E-M and E-W) and the total soil zinc content (ZnT) imply that the re-

Table 6. Means and variation ranges of estimated soil zinc extractability (E) and buffering capacity (B) (n = 109)

Variable[a]	Mean	SD	Minimum	Maximum
E-D = ZnD/ZnT (%)	1.96	1.78	0.36	12.74
E-A = ZnA/ZnT (%)	2.32	1.88	0.41	11.31
E-H = ZnH/ZnT (%)	5.90	3.43	1.41	17.23
E-M = ZnM/ZnT (%)	0.40	0.38	0.03	2.29
E_W = ZnW/ZnT (%)	0.12	0.10	0.00	0.49
B-D = ZnD/ZnM	6.83	6.72	2.21	42.41
B-A = ZnA/ZnM	8.66	10.40	2.60	72.52
B-H = ZnH/ZnM	24.92	29.30	4.91	202.01

a: See notes below Table 4.

Table 7. Coefficient (r) of correlations between soil zinc extractability (E), buffering capacity (B) and soil properties (n = 109)

	Extractability					Buffering capacity		
	DTPA	AA-EDTA	HCl	$Mg(NO_3)_2$	H_2O	DTPA	AA-EDTA	HCl
	E-D[a]	E-A	E-H	E-M	E-W	B-D	B-A	B-H
ZnT	0	0	0	-	-	0.50	0.50	0.52
pH	-[b]	-	0	-0.49	-0.38	0.45	0.42	0.49
TA[c]	-	-	0	-0.44	-0.44	0.66	0.58	0.69
BS	-	-	0	-0.51	-0.42	0.54	0.53	0.56
EA	+	+	0	0.24	+	-0.42	-0.40	-0.43
E-Ca	+	+	+	-0.47	-0.46	0.75	0.76	0.72
BC	+	+	+	-0.48	-0.46	0.75	0.77	0.72
CEC	0	0	0	-0.39	-0.31	0.48	0.52	0.44
C%	+	+	0	-	-0.32	0.40	0.46	+
Clay%	-	-	0	-	-	-	-	0

a: See Table 4 for the definitions of E-D, E-A, E-H, E-M, E-W, B-D, B-A and B-H.
b: -: $-0.30 < r < -0.20$, +: $0.20 < r < 0.30$, 0: $|r| < 0.19$.
c: See notes below Table 2.

lative (not the absolute) level of water-soluble plus readily exchangeable zinc tends to decrease with increasing soil total zinc content, suggesting that in soils with a higher total zinc content, relatively larger amounts of zinc may be present in reserve forms than in soluble and readily exchangeable forms. The positive correlations between ZnT and the buffering capacity factors (B-D, B-A and B-H) indicate, as expected, that soils richer in native zinc will have a higher zinc buffering capacity.

Soil alkalinity (SA)

The next four factors in Table 7, soil pH, soil titratable alkalinity (TA), base saturation (BS) and soil exchangeable acidity (EA), are mutually dependent variables. They represent, or closely relate to, soil alkalinity conditions (Table 3). As a general trend, the soil alkalinity was found to have a negative influence on soil zinc extractability and a positive influence on soil zinc buffering capacity (Table 7). In comparison, however, the effect of soil alkalinity factors on the extractability estimated by DTPA (E-D), AA-EDTA (E-A) and HCl (E-H) is much less pronounced. Among the soil alkalinity factors, soil titratable alkalinity (TA) tends to be more closely related to soil zinc buffering capacity than BS, EA and pH.

A decrease in soil zinc availability with increasing soil alkalinity is a generally recognized phenomenon. Low soil zinc solubility, low soil zinc diffusity and high zinc distribution coefficients associated with alkaline conditions are attributed to high levels of zinc adsorption and fixation (Bar-Yosef 1979, Bruemmer et al. 1988, Cavallaro & McBride 1984, Clarke & Graham 1968, Harter 1983, Kinniburg & Jackson 1982, McBride & Blasiak 1979). The following reaction can be used to describe the reversible cation exchange processes,

$$Soil\text{-}H_2 + Zn^{2+} \rightleftharpoons Soil\text{-}Zn + 2H^+ \quad (R\text{-}1).$$

Assuming equilibrium condition, the reaction constant, K, will be given as

$$K = (Soil\text{-}Zn)(H^+)^2/(Soil\text{-}H_2)(Zn^{2+}) \quad (9).$$

If using Q (zinc quantity) to denote the exchangeable quantity of zinc associated with the soil solid phase, (Soil-Zn), I to

denote the soluble zinc concentration in solution, (Zn^{2+}), and X to denote the available adsorption sites at equilibrium, (Soil-H_2), then Equation 9 becomes

$$Q = KI(10)^{2pH}X \quad (10),$$

where $10^{2pH} = 1/(H^+)^2$. Then, the zinc buffering capacity will be

$$B = dQ/dI = K(10)^{2pH}X \quad (11),$$

which indicates that B is positively related to two factors, the soil pH and the available adsorption sites, X. Based on Equation 3, it can be concluded that the coefficient of the correlation between soil zinc buffering capacity and pH for a given X will be positive,

$$r(B, pH|X) > 0 \quad (12),$$

and likewise that between soil zinc buffering capacity and X (the adsorption capacity) for a given pH,

$$r(B, X|pH) > 0 \quad (13).$$

Notice that the correlation between B and X may not be positive (> 0) if soil pH or soil alkalinity varies.

The dependence of soil zinc buffering capacity on soil alkalinity does not necessarily indicate that the soil zinc buffering capacity is negatively related to soil zinc availability. Like soil alkalinity factors, soil zinc buffering capacity (B) alone cannot be considered as an index to reflect the soil available zinc level. In general, for soils with the same level of intensity (I), the uptake of zinc by plants will be higher in soils with higher B values because of their higher zinc quantity (Q), while for soils with the same level of zinc quantity, the uptake of zinc by plants will be lower in soils with higher B values because of their lower intensity. Thus, for a given I, the plant uptake will be positively related to soil zinc buffering capacity, while for a given Q, the plant uptake will be negatively related to soil zinc buffering capacity. Presumably, this should also hold for the relationship between zinc uptake and soil alkalinity. For instance, if soil pH had no other influence on plant growth, zinc uptake might also be positively correlated with pH in soils having the same zinc intensity level, since higher pH levels are associated with higher levels of soil zinc quantity.

The low degree of dependence of the DTPA-, AA-EDTA- and HCl- extractable zinc contents on soil alkalinity conditions may infer certain degrees of inadequacy in applying these extractants for predicting soil zinc availability on non-calcareous soils with significant variation in alkalinity. In fact, even for calcareous soils with nearly constant soil pH levels, Nelson et al. (1959) showed that the inclusion of soil titratable alkalinity (TA) is of importance in differentiating between zinc deficient and non-deficient soils.

Exchangeable base cation concentration (BC)

In the present soil samples, exchangeable calcium (E-Ca) contributes a major portion of the exchangeable base cation concentration (BC). Thus the two variables, E-Ca and BC, were found to be highly correlated with each other ($r = 0.9921$, Table 3), and their influence on soil zinc extractability and buffering capacity was found to be consistent (Table 7). The exchangeable base cation concentration, BC, was also found to be positively correlated with soil alkalinity factors (Table 3), indicating that among the present soil samples, soils with high levels of exchangeable base cations are mostly alkaline in reaction. However, the influence of BC did not always appear to be consistent with that of soil alkalinity. As seen in Table 7, like the soil alkalinity variables, BC is negatively related to the two zinc extractability factors estimated by the $Mg(NO_3)_2$ and water methods, E-M and E-W, and positively related to the three soil zinc buffering capacity factors, B-A,

B-D and B-H, but unlike the soil alkalinity variables, BC has a slightly positive effect on the extractability factors estimated by the DTPA, AA- EDTA and HCl methods, E-A, E-D and E-H.

Despite the close relationship between exchangeable base cation concentration, BC, and base cation saturation, BS, BC is not necessarily correlated with soil alkalinity because soils with high amounts of exchangeable base cations may also contain large amounts of exchangeable hydrogen and aluminium ions. Thus, soils (e.g. a sandy soil and a loamy soil) with the same pH level may differ considerably in their exchangeable base concentrations while soils (e.g. a loamy soil and a clay soil) with the same levels of BC may also vary considerably in their alkalinity conditions.

In soils with nearly the same total zinc level, the positive effect of BC on the three soil zinc extractability factors, E-A, E-D and E-H, may suggest that soils retaining more exchangeable bases also have an ability to retain more zinc in exchangeable or reserve forms. If so, the increase in BC may not be a cause of but rather an event associated with the increase in soil zinc quantity or the soil zinc labile pool. In fact, BC itself is also a quantity factor and represents the base cation exchange capacity. Thus, it should be expected that for a given total zinc level, soils retaining a higher amount of exchangeable bases will also retain a higher amount of exchangeable zinc in the labile pool.

Cation exchange capacity (CEC)

The effect of soil cation exchange capacity (CEC) on the extractability and buffering capacity of soil zinc can be approximately described by either

$$\text{Effect of CEC} = \text{Effect of BC} + \text{Effect of EA} \quad (14),$$

or

$$\text{Effect of CEC} = \text{Effect of BS} + \text{Effect of EA} \quad (15)$$

(Table 7). This agrees fairly well with the quantitative definition of CEC

$$\text{CEC} = \text{EA} + \text{BC} = \text{EA} + (\text{CEC})\,(\text{BS}) = (\text{EA})/(1\text{-BS}) \quad (16).$$

As both the base saturation, BS, and the exchangeable acidity, EA, have little influence on E-D, E-A and E-H, the three soil zinc extractability variables are nearly independent of CEC. The negative effect of CEC on E-M and E-W caused by the residual effect of BS indicates that $Mg(NO_3)_2$ and H_2O extracted relatively lower amounts of exchangeable zinc from soils with higher cation exchange capacities.

Due to the counteraction between the exchangeable base concentration, BC, and the exchangeable acidity, EA, the r values for correlations of buffering capacity variables with CEC are much lower than those with BC. Although the soil zinc buffering capacity (B) and the soil cation exchange capacity (CEC) both represent the ability of a soil to retain cation or cations in exchangeable forms, these two parameters are not necessarily correlated with each other. The main reason for this is that the soil zinc adsorption is highly pH-dependent and one fraction of CEC, EA, determines the soil acidity condition. Apparently, in soils with high CEC values, the ratios of the adsorbed zinc to the soluble zinc will be low if EA levels are high. Thereby the soil zinc buffering capacity (B) will only increase with increasing soil CEC at a given EA level, which is actually equivalent to an increase in B with increasing BC.

The fact that the soil zinc buffering capacity, B, will be more closely related to the exchangeable base cation concentration, BC, than to CEC can be demonstrated as follows:

Since $\text{CEC} = \text{BC} + \text{EA}$,

for a given EA, the correlation between the buffering capacity, B, and CEC, $r(B, \text{CEC}|\text{EA})$, is equal to the correlation between B and BC,

$$r(B, CEC|EA) = r(B, BC + EA|EA) = r(B, BC|EA \quad (17).$$

However, for a given BC, the correlation between B and CEC can be negative because the increase in CEC is equivalent to the increase in EA, namely,
$r(B, CEC|BC) = r(B, BC + EA|BC) = r(B, EA|BC)$

At a given BC level, zinc adsorption will decrease with increasing EA (namely, decreasing pH), Thus,
$r(B, EA|BC) < 0$,
and then $r(B, CEC|BC) < 0$ (18).

Furthermore, for a given CEC, the variation in soil zinc buffering capacity, B, cannot be explained by the variation in CEC, while the correlation between B and BC will still be positive as it is proportional to the correlation between B and minus EA,

$$r(B, BC|CEC) = r(B, CEC\text{-}EA|CEC) = r(B, -EA|CEC) > 0.$$

Thus, in general,
$r(B, CEC) < r(B, BC)$ (19).

Equation 17 is comparable with Equation 13, considering that a given pH level is equivalent to a given soil exchangeable acidity (EA) level. Based on Equation 11 as well as on Equations 17, 18 and 19, it can be argued that the exchangeable base concentration, BC, is a better estimator of the X factor (the adsorption site factor) than CEC simply because the effects of pH (or EA) and X are not additive.

Soil organic carbon content (C%) and clay content (Clay%)

The soil organic carbon content (C%) was found to be highly correlated with CEC in the present soil samples ($r = 0.72$, Table 3). Thus, the effect of C% on soil zinc extractability (E) and buffering capacity (B) variables resembles that of CEC. As C% has almost no influence on the extractability estimated by HCl (E-H) and a slightly negative influence on that estimated by $Mg(NO_3)_2$ (E-M), the r value of the correlation between the buffering capacity determined by HCl (B-H) and C% approaches zero (Table 7). This may cast some doubt on the use of the HCl method for soils with high levels of organic matter since it is known that organic matter plays an important role in complexing and thus buffering the soil zinc intensity level.

The extractability and the buffering capacity of soil zinc was found to be little affected by the soil clay content (Clay%). Lins & Cox (1988) reported that the critical level of zinc deficiency was not influenced by the soil clay content while in some other studies, clay soils were found to have higher adsorptive capacities, higher binding energies and higher zinc buffering capacities than sandy soils (Mengel 1982, Shuman 1975).

C% and clay% are two major factors positively related to CEC. As soils with high C%, clay% and CEC levels are generally rich in adsorptive sites, these three soil properties may be regarded as soil adsorption capacity factors. For this reason, the influences of these three factors on soil zinc buffering capacity are expected to be similar. Since the correlation between zinc buffering capacity, B, and CEC is lower than that between B and the exchangeable base cation concentration, BC, it should follow that,

$$r(B, C\%) < r(B, BC) \quad (20),$$
and $$r(B, Clay\%) < r(B, BC) \quad (21).$$

This may explain why the effects of CEC, C% and Clay% on soil zinc adsorption and availability were found to be inconsistent in other investigations (Harter 1983, Kurdi & Doner 1983, Lins & Cox 1988).

In the present soil samples, BC is highly correlated with CEC ($r = 0.86$) and C% ($r = 0.58$) (Table 3). Thus, the positive effect of CEC and C% on B may mainly represent the effect of BC. On the other hand, the correlation between BC and the soil texture factors, clay, silt and

sand contents, is very low with r values below 0.1 (Table 3). The clay effect on the soil zinc status is apparently masked by the soil alkalinity condition.

The influence of soil alkalinity (SA), exchangeable base cation concentration (BC), cation exchange capacity (CEC) and soil organic carbon content (C%) on soil zinc extractability (E-M and E-W) and buffering capacity (B-D, B-A and B-H) are further illustrated in Figures 2, 3, 4, 5 and 6. In general, the two extractability (E) variables decrease and the three buffering capacity (B) variables increase with increasing SA, BC, CEC and C%. Compared to the close relationship between B, BC and SA, the trends of increasing soil zinc buffering capacity towards increasing CEC and C% are not so distinctive.

One noticeable outlier, marked as A in Figures 2, 3, 4, 5 and 6, represents a loamy soil sample collected from an area free of liming. Because of its extremely low level of BC (the lowest) and relatively high level of EA (next to the highest), pH, TA and BS (base saturation) of this sample are the lowest in the present soil samples. The presence of this outlier shows the interactions between soil zinc buffering capacity (B), pH, titratable alkalinity (TA) and exchangeable base cation concentration (BC). The influence of pH, BC and TA on the quantitative relationship between soil zinc quantity and intensity will be discussed further in the next paper.

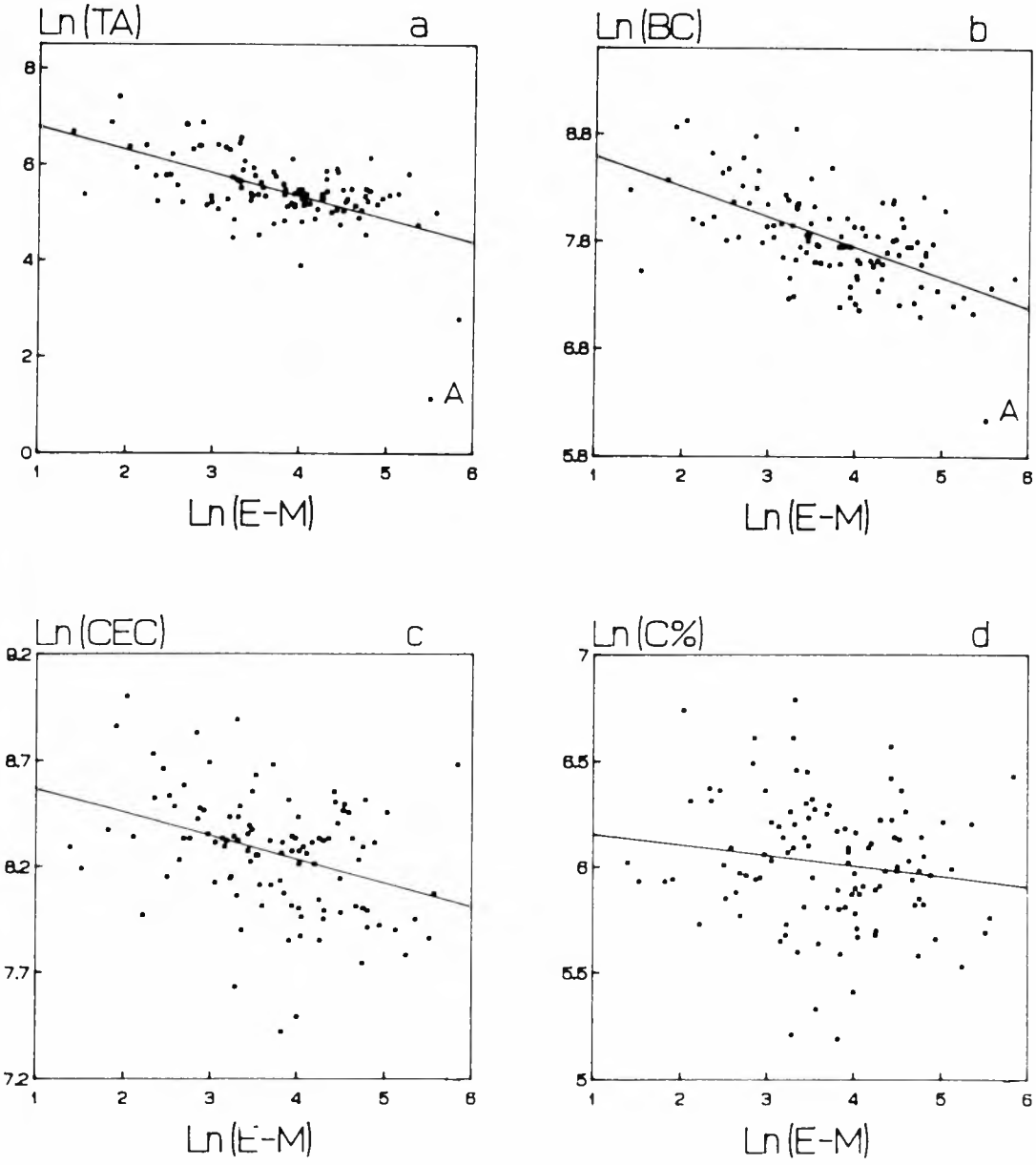

Fig. 2. Soil zinc extractability estimated by the $Mg(NO_3)_2$ method (E-M) in relation to soil titratable alkalinity (TA, meq. 100 ml^{-1}), exchangeable base cation concentration (BC, meq. 100 ml^{-1}), cation exchange capacity (CEC, meq. 100 ml^{-1}) and soil organic carbon content (C%). Ln denotes the natural logarithm and A represents an outlier

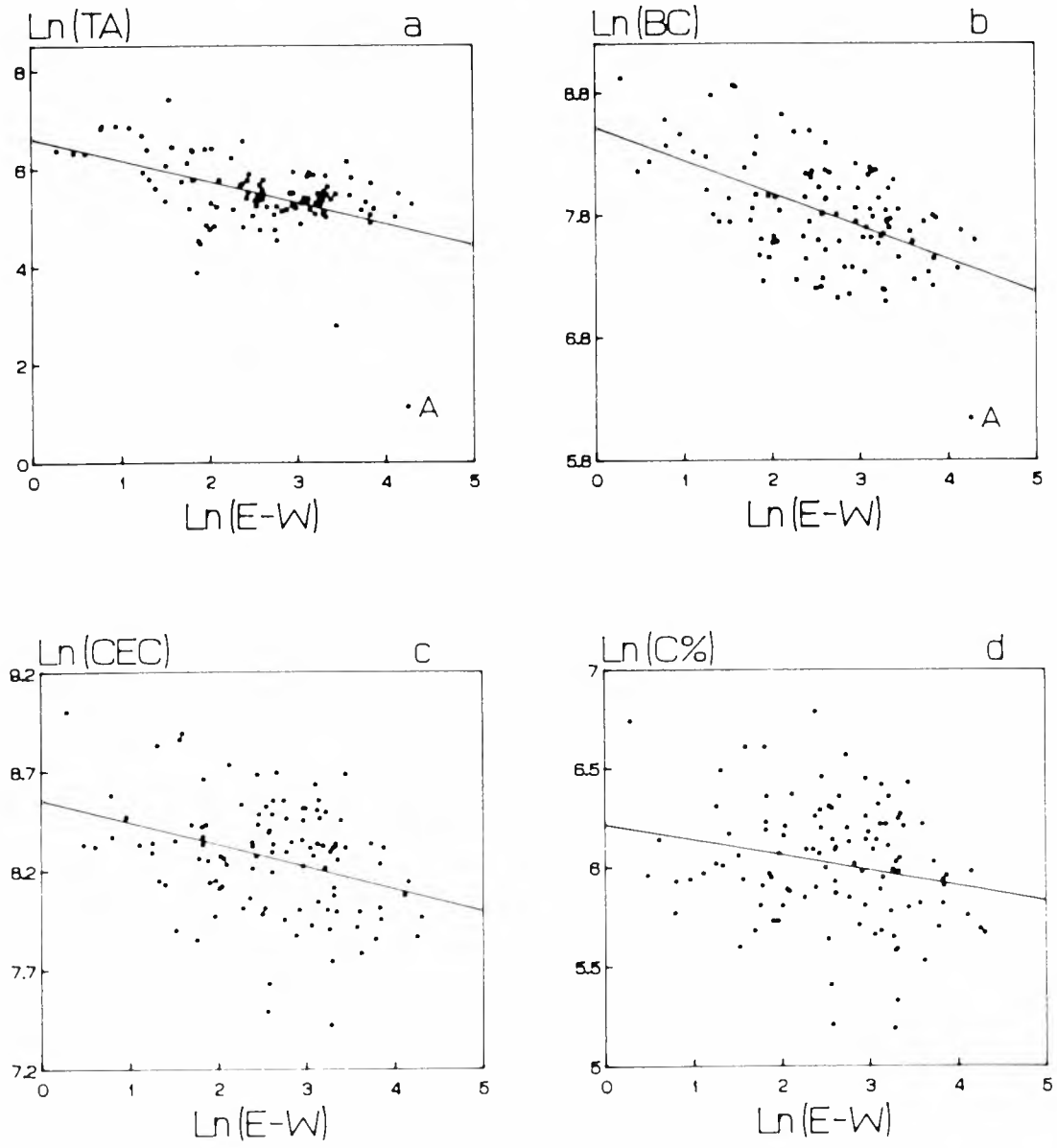

Fig. 3. Soil zinc extractability estimated by the water extraction method (E-W) in relation to soil titratable alkalinity (TA, meq. 100 ml^{-1}), exchangeable base cation concentration (BC, meq. 100 ml^{-1}), cation exchange capacity (CEC, meq. 100 ml^{-1}) and soil organic carbon content (C%). Ln denotes the natural logarithm and A represents an outlier

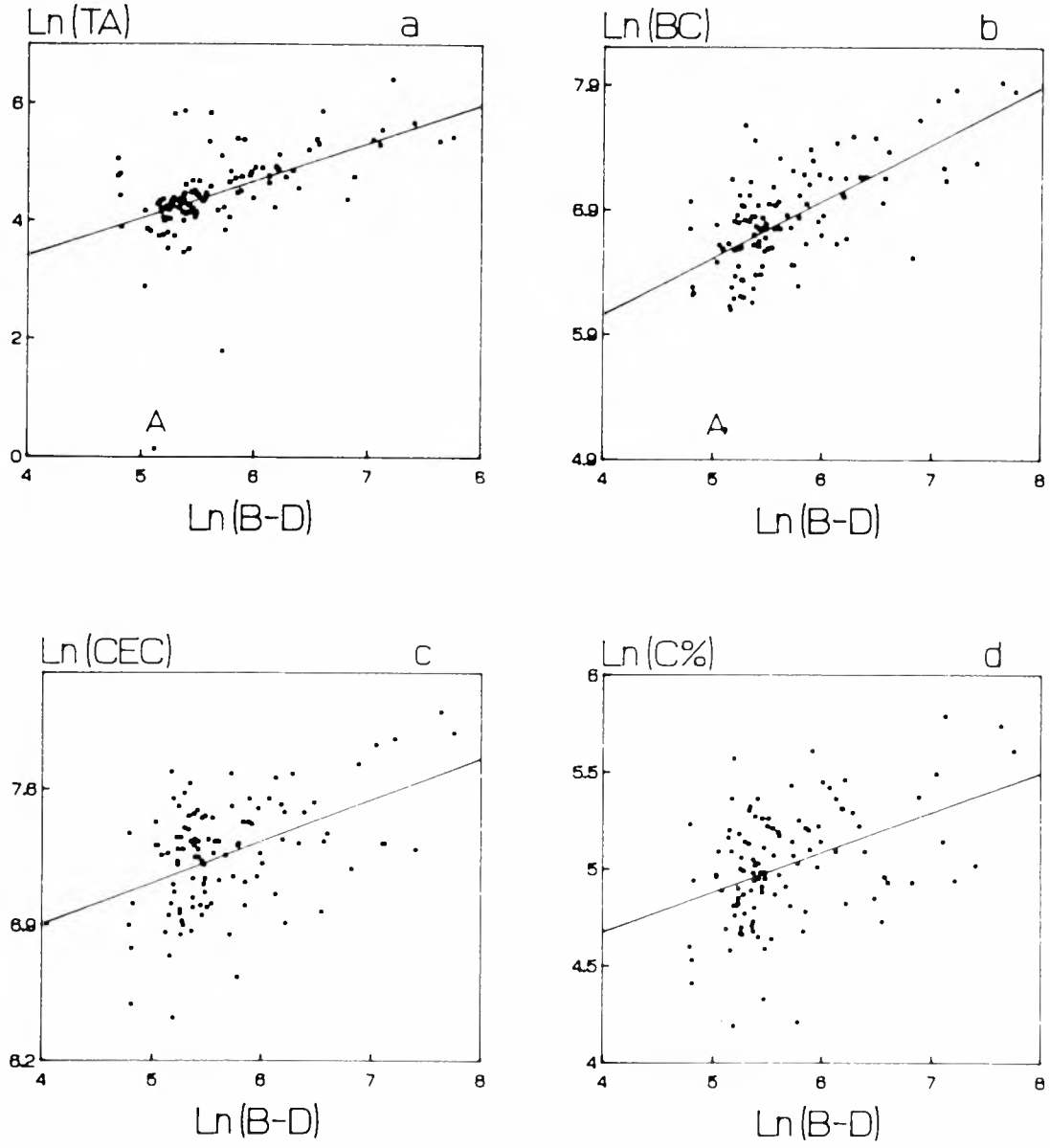

Fig. 4. Soil zinc buffering capacity estimated by the DTPA method (B-D) in relation to soil titratable alkalinity (TA, meq. 100 ml^{-1}), exchangeable base cation concentration (BC, meq. 100 ml^{-1}), cation exchange capacity (CEC, meq. 100 ml^{-1}) and soil organic carbon content (C%). Ln denotes the natural logarithm and A represents an outlier

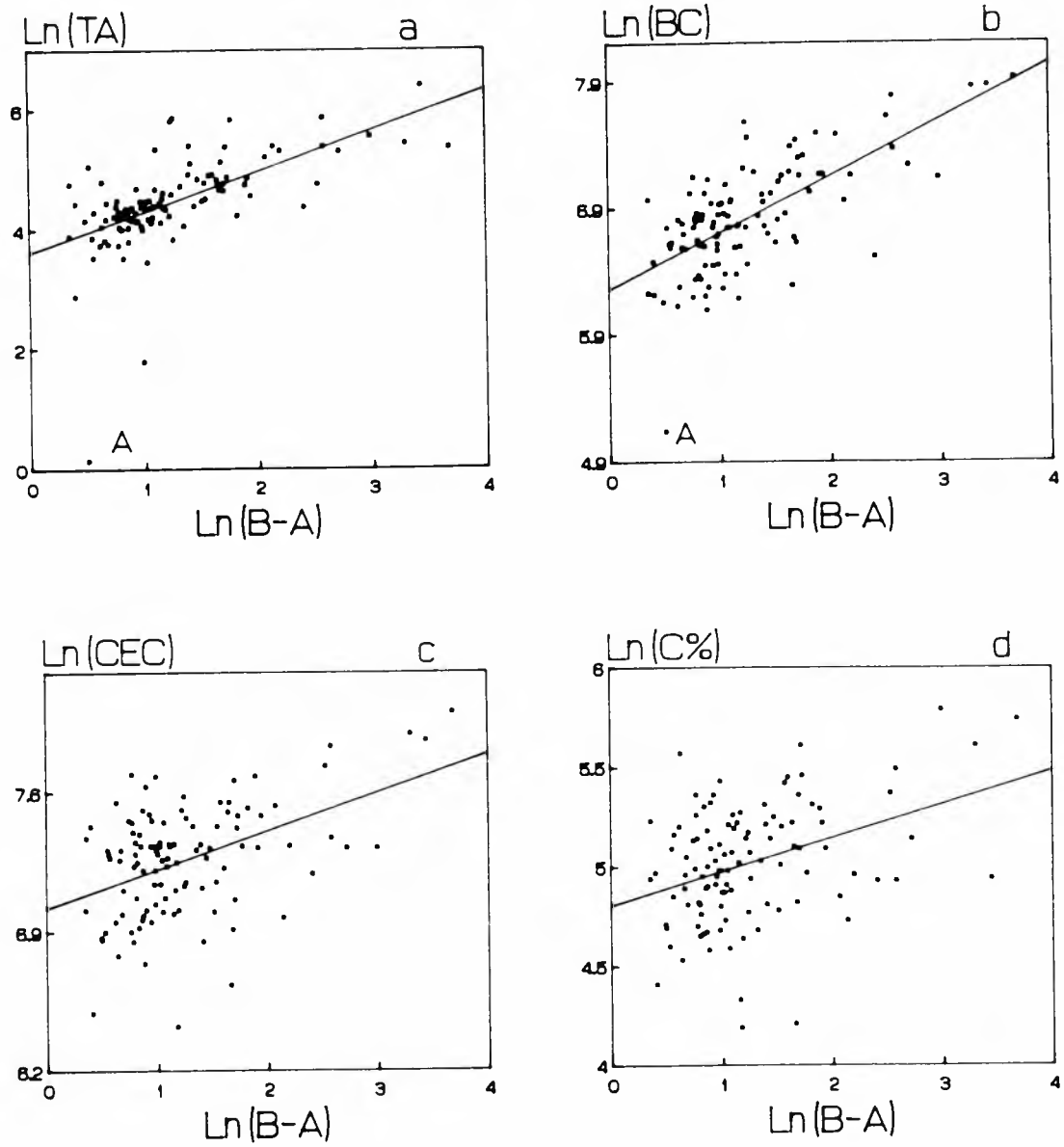

Fig. 5. Soil zinc buffering capacity estimated by the AA-EDTA method (B-A) in relation to soil titratable alkalinity (TA, meq. 100 ml^{-1}), exchangeable base cation concentration (BC, meq. 100 ml^{-1}), cation exchange capacity (CEC, meq. 100 ml^{-1}) and soil organic carbon content (C%). Ln denotes the natural logarithm and A represents an outlier

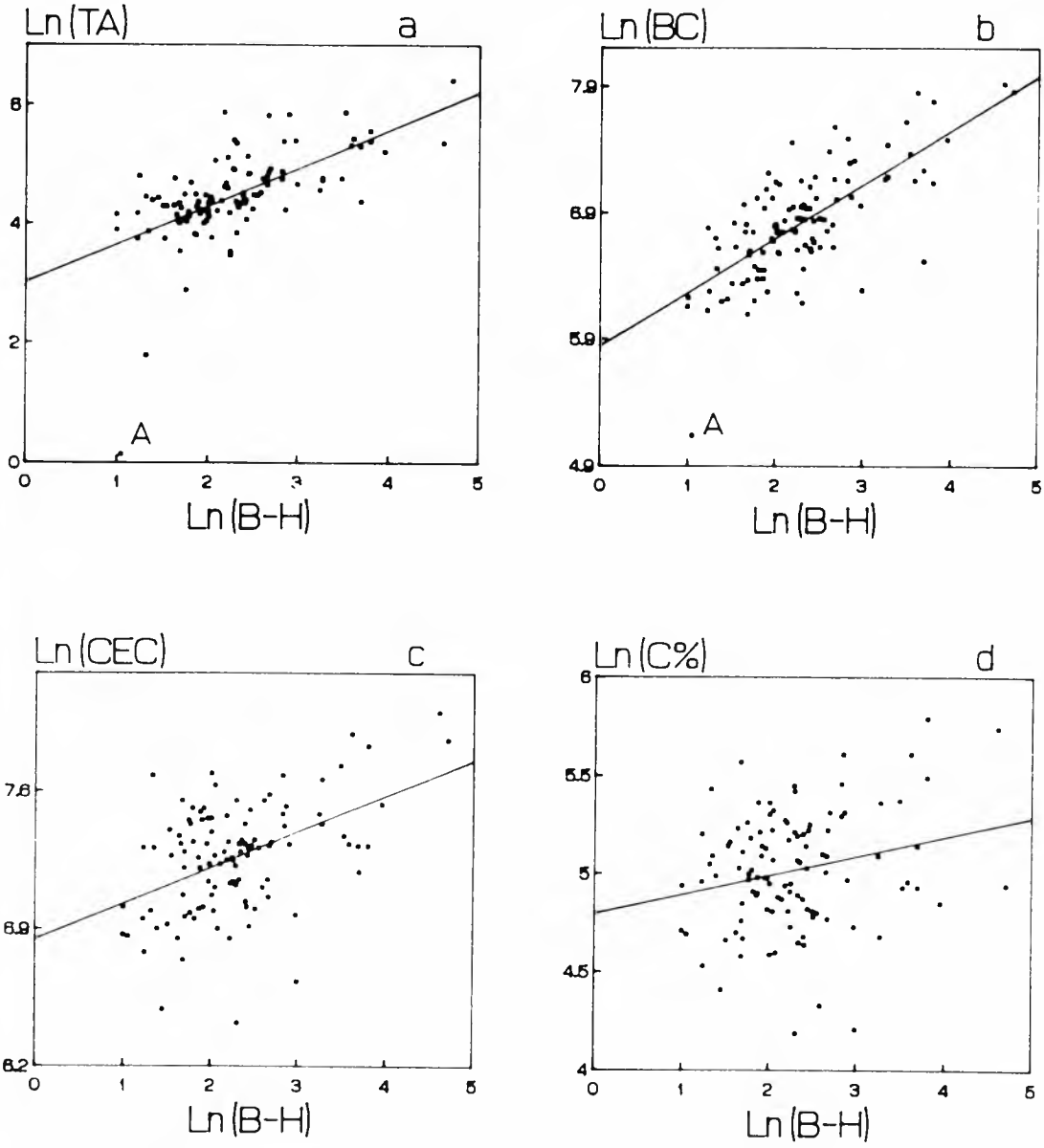

Fig. 6. Soil zinc buffering capacity estimated by the HCl method (B-H) in relation to soil titratable alkalinity (TA, meq. 100 ml^{-1}), exchangeable base cation concentration (BC, meq. 100 ml^{-1}), cation exchange capacity (CEC, meq. 100 ml^{-1}) and soil organic carbon content (C%). Ln denotes the natural logarithm and A represents an outlier

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