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

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NUTRIENT CONCENTRATIONS IN THE LIQUID PHASE OF GROWTH SUBSTRATES

BJØRN R. LANGERUD & MARTIN SANDVIK
Norwegian Forest Research Institute, Division of silviculture, Aas Norway.

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Samples of the liquid phase of growth substrates at container capacity were obtained using a dilution technique, and a chemical analysis was carried out. The measured concentrations were combined with the physical characteristics of the growth substrates to calculate nutrient concentrations immediately before the nutrient solution was re-added.
The results of two laboratory studies indicated high and fluctuating nutrient concentrations close to the levels regarded as lethal for Norway spruce. Differences in element concentrations between the growth substrate liquid phase and the nutrient solution were discussed in terms of a disparity between the water and nutrient uptakes of the seedlings.
Periodic heavy leaching with water did not bring the concentrations in the liquid phase to the same level as concentrations in the added nutrient solution.
The high concentration of nutrients in the substrates were supported by foliar analysis. Even seedlings grown with deionized water for 56 days after the last addition of nutrient solution grew just as well as the fertilized ones. However, malnutrition was obvious from foliar analysis.

Key words : Ammonium, Calcium, Magnesium, Nitrate, Peat, Perlite, Phase distribution, *Picea abies*, Potassium, Transpiration.

Bjørn R. Langerud, Division of silviculture, Norwegian Forest Research Institute, Box 61, N-1432 Aas-NLH, Norway.

Considerable efforts have been directed towards the composition of an 'optimal' nutrient solution for a variety of conifers in hydroponic cultures (Morrison 1974). Commercial growing systems differ from hydroponics by their inclusion of growth media and small volumes of liquid: Disparities in water and nutrient uptakes should affect the nutrient concentrations more with decreasing volumes of liquid.

The inclusion of a solid phase complicates control of nutrient concentration in the liquid phase of growth substrates. Some inorganic growth media have been regarded as 'inert' (Joiner & Conover 1965, Verwer & Welleman 1980, Langerud & Sandvik 1987a), although peat or peat based media are predominantly used in commercial forest nurseries (Carlson 1979, Tinus & McDonald 1979).

The high nutrient-holding capacity of peat is desirable when mixed with solid fertilizers, but is undoubtedly a complicating factor in routines based on nutrient solution applications. Suggestions for an 'ideal' growth medium have not taken into account the implications

of different forms of fertilization (Puustjaervi 1973, Bunt 1976).

Most recommendations for nutrition in the commercial production of seedlings have been based on experiments with prescribed nutrient solution input and measurement of the resultant growth (Hocking 1972). The scant information that exists on nutrient concentrations in the liquid phase of growth substrates has derived from solid fertilizers being mixed with the medium (Holcomb et al. 1982), while the literature abounds in indirect estimates based on the chemical composition of plant tissue (ISOSC 1984).

A few methods have been suggested on how to obtain samples of the liquid phase of soils: Saturated paste (Bower & Wilcox 1965) and displacement (Mubarak & Olsen 1976) are destructive and useless in studies of changes with time. Vacuum extraction (Holcomb et al. 1982, Langerud 1986) is time-consuming, and the suction filter method (Nielsen 1972) is hardly applicable with small volumes of growth media. We have suggested combining analyses of diluted liquid from the substrates with physical characteristcs of the substrates as a means of calculating the actual concentration of nutrient elements in the growth substrate liquid phase (Langerud & Sandvik 1988a). A considerable accumulation of nutrient elements in the growth substrates has been indicated, and this was pursued in the present experiments: High concentrations of nutrient elements in the substrate would involve high concentrations in the foliage of Norway spruce seedlings. The accumulation would depend on the strength and quantity of the applied nutrient solution, and could be prevented by frequent leaching with water.

MATERIALS AND METHODS

Multipot containers were filled with peat/perlite mixtures at a random commercial nursery. The ratio of peat to perlite was 1:1 (0.505 ml ml^{-1} standard deviation 0.061), the bulk density 114.8 (5.3) mg ml^{-1} and the volume 37.9 (1.3) ml pot^{-1}. The media characteristics were analysed (sample size 66) in accordance with Langerud (1986) and Langerud & Sandvik (1987b, c).

Four multipot containers, with 95 pots each, were soaked in deionized water for three days; seeds of Norway spruce (*Picea abies* (L.) Karst.) were sown and germinated in continuous light (photon flux density (PAR) 120 µmol m^{-2} s^{-1}) at 22°C in a water saturated atmosphere. The seedlings were grown in a climate chamber under a 20 h photoperiod (22°C, 70% relative humidity, 400 µmol m^{-2} s^{-1} PAR) from the time of seed coat disposal (14 days). The night temperature was 15°C at 70% relative humidity.

For the first three weeks, the multipot containers were submerged in nutrient solution to 1.5 cm below the substrate surfaces for 30 min every second day, and thereafter once a day for 30 min. The nutrient solution was prepared from laboratory grade chemicals to 10 mmol nitrogen l^{-1} (HN_4/NO_3 ratio : 4.3/5.7) in element proportions suggested by Ingestad (1979). The nutrient solution was changed once a week and stirred daily in the atmosphere for aeration.

Seedlings of uniform stem length (14.4 (0.3) cm) were removed from the multipot containers 147 weeks from sowing, and used in two experiments: (1) *Transpiration experiment.* Nutrient concentrations and changes in the volume of liquid present in the growth substrate were observed along with evapotranspiration from individual pots with one seedling. This experiment was similar to the one described by Langerud & Sandvik (1988a), but the seedlings were transplanted to the single pot system and were older than the seedlings in the previous experiment. (2) *Leaching experiment.* A multipot con-

tainer was reduced in size to hold 30 seedlings, 2 cm being cut off the bottom of each pot. In this experiment different strengths of nutrient solution, including pure water, were added in different quantities.

The transpiration experiment

Five seedlings were transferred with their root plugs intact to tared single pots cut from a multipot container. Five additional tared single pots were filled with growth media only. All the pots were initially soaked in nutrient solution for 30 min before being fitted into opaque plastic bottles, thus keeping a water-saturated atmosphere around the bottom drains. The temperature under a 20 h photoperiod was 27°C with 60% relative humidity and photon flux density of 400 µmol m^{-2} s^{-1}. The night temperature was 15°C with 80% relative humidity.

For the first week, 10 (2x5) ml pot^{-1} of nutrient solution was applied every day. Thereafter 20 (4x5) ml pot^{-1} was applied when 60% of the liquid held by the growth substrate at container capacity was lost.

The volume fraction of gas-filled pores was estimated gravimetrically according to Vomocil (1965). Wet weight of the growth substrate was corrected for the fresh weight of the seedling as described earlier (Langerud & Sandvik 1987c).

The pots were drained for one hour after the addition of nutrient solution before the initial weight was recorded. Evapo(transpi)ration was estimated gravimetrically by recording weight loss of single pots at irregular intervals (1-24 h) throughout the experimental period.

Samples of the growth substrate liquid phase were taken from all the pots 12, 14 and 26 days after the experiment had started. An additional sampling was performed on pots with a seedling after 22 days.

Samples of the substrate liquid phase for chemical analyses were obtained as described by Langerud & Sandvik (1988a); these were analysed for NO_3-N and NH_4-N (all samples), Ca and Mg (all but the samples after 12 days) and K (samples after 26 days only) according to routine procedures (Ogner et al. 1984).

The experiment was terminated after 26 days, and shoot length and shoot dry weight were recorded for individual seedlings.

The leaching experiment

Seedlings were transferred to the modified multipot container fitted into an opaque container to keep a watersaturated atmosphere surrounding the protruding plugs.

Six groups of five seedlings each were subjected to different irrigation regimes and strengths of nutrient solution (Table 1): For the first 30 days, 10 (2x5) or 20 (4x5) ml pot^{-1}, and for the last 26 days, 15 (3x5) or 30 (6x5) ml pot^{-1}, were added every day or every second day, respectively, to different groups of seedlings.

The experiment was terminated after 56 days with a sampling of the growth substrate liquid phase: Samples were taken from the total volume of solution drained in response to a sequence of 5 x 5 ml pot^{-1} of deionized water added at 3 min intervals. The liquids were analysed for NO_3-N, NH_4-N, K, P, Ca, Mg, Fe and Mn using routine procedures (Ogner et al. 1984). The foliage was analysed for total N and elements determined in the solution.

Shoot length and shoot dry weight were recorded at the end of the experiment.

RESULTS

The transpiration experiment

The mean shoot length was 14.4 (0.3) cm when the experiment started, and 17.4 (0.5) cm at its termination. The

Table 1. 'Leaching experiment': Concentration of some elements in the nutrient solutions

Solution[1]	Concentration (mmol l^{-1})							
	NO_3-N	NH_4-N	K	P	Ca	Mg	Fe	Mn
Deion.water[2]								
Nutr. soln., double conc.[3]	11.4	8.6	4.0	1.52	0.80	0.80	0.035	0.020
Nutr. soln., four times conc.[4]	22.8	16.8	8.0	3.04	1.60	1.60	0.070	0.040

[1] All solutions were added every (../1) or every second (../2) day. Double and four times concentration refers to the nutrient solution used in the «transpiration experiment».
[2] Notation 0x/1 and 0x/2.
[3] Notation 2x/1 and 2x/2.
[4] Notation 4x/1 and 4x/2.

final shoot dry weight was 1690 (250) mg seedling^{-1}.

The mean hourly evaporation and evapotranspiration in a random 9 day period is given in Fig. 1: Evaporation in pots without a seedling decreased from 0.09 to 0.07 ml pot^{-1} h^{-1} during this period without irrigation. The volume fraction of gas-filled pores increased from 0.11 (0.017) to 0.51 (0.069) ml ml^{-1} during these 9 days (Table 2).

For pots with a seedling, evapotranspiration ranged from 0.25 to 0.41 ml pot^{-1} h^{-1} (Fig. 1). The low values were recorded for the first few hours following application of the nutrient solution. The mean evapotranspiration for the entire experimental period of 27 days was 0.35 ml pot^{-1} h^{-1} and evaporation 0.08 ml pot^{-1} h^{-1}.

The volume fraction of gas-filled pores at the times for sampling of the liquid phase is given in Table 2. The nutrient element concentrations in the 12 and 14 day sampling were not significantly different; averages are shown in

Table 2. 'Transpiration experiment': The volume fraction[1] of gas-filled pores (ml ml^{-1}) at maximum (fgmax) and minimum dryness (fgmin 1 h after re-irrigation) at times for chemical analysis of the growth substrate liquid phase

Seedling	After 12/14 days		After 22 days		After 26 days	
	fgmax	fgmin	fgmax	fgmin	fgmax	fgmin
Without	0.213 (0.012)[2]	0.112 (0.017)	0.509 (0.069)	0.165 (0.024)	0.707 (0.009)	0.216 (0.016)
With	0.645 (0.016)	0.173 (0.034)	0.657 (0.015)	0.160 (0.044)	0.700 (0.014)	0.166 (0.016)

[1] Total porosity: 0.94 ml ml^{-1}
[2] Mean and standard deviation calculated on five replications.

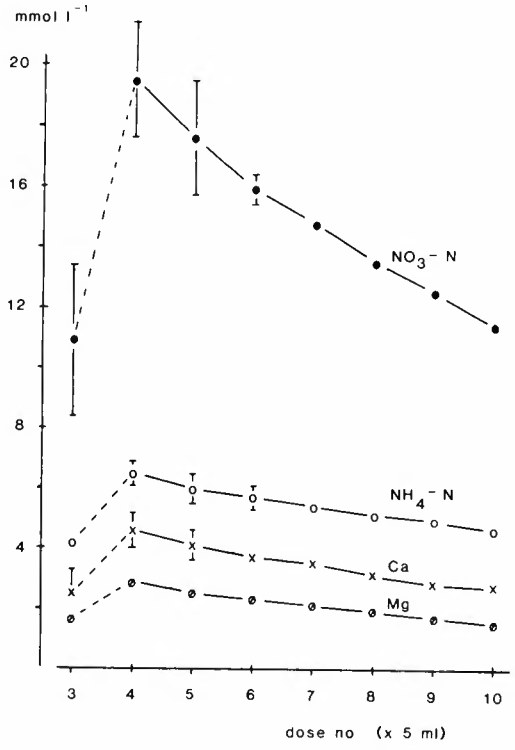

Figure 1. "Transpiration experiment": Water loss (evapo(transpi)ration) from pots with and without a seedling. Arrows indicate times for nutrient solution applications. Mean values (n=5, s < 0.001 ml pot-1h-1) represent either the period from last measurement or last nutrient solution application. Duration of dark periods indicated on the abscissa.

Fig. 2. Samples were obtained in response to the third and fourth doses of nutrient solution from pots with a seedling, while samples were obtained in response to all four doses from the pots without a seedling.

The NO_3-N and NH_4-N concentrations were at the same level as in the nutrient solution in samples from pots without a seedling (Fig. 2). In pots with a seedling, NO_3-N and NH_4-N concentrations were four times (22 mmol l^{-1}) and 1.5 times (6.4 mmol $l.^{-1}$) higher in the substrate than in the nutrient solution added. The concentrations were unaffected by the number of doses, but the variation was reduced from the third to the forth dose. A similar reduction in variation was noted for Ca and Mg concentrations (Fig. 2). The concentration of these elements in the nutrient solution was 0.40 mmol l^{-1}. The Ca concentration, on the other hand, was 1.4 mmol l^{-1} in pots without a seedling and 4.0 mmol l^{-1} in pots with a seedling. The Mg concentration was high only in pots with a seedling.

The nutrient concentrations in pots with a seedling after 22 days are given in Fig. 3. A total of 10 doses of nutrient solution were added and samples obtained in response to the third through the tenth dose.

The variation decreased significantly from the third to the fifth dose and became negligible by the tenth dose. Generally, the element concentrations increased from the third to the forth dose, and then decreased towards the tenth.

The NO_3-N concentration peaked at 19.5 mmol l^{-1} for the forth dose and reached 11.4 mmol l^{-1} for the tenth dose, still twice the concentration in the nutrient solution.

The NH_4-N concentration peaked at 6.5 mmol l^{-1} and reached a level close to that in the nutrient solution after the tenth dose. The Ca concentration stayed at a level 7 to 11 times that in the nutrient solution, while the Mg concentration increased four to eight times.

After 26 days, seven doses of nutrient solution were added to all the pots, and the element concentrations were still higher in the pots with a seedling than in those without (Fig. 4). Samples were obtained in response to the third through the seventh dose. All element

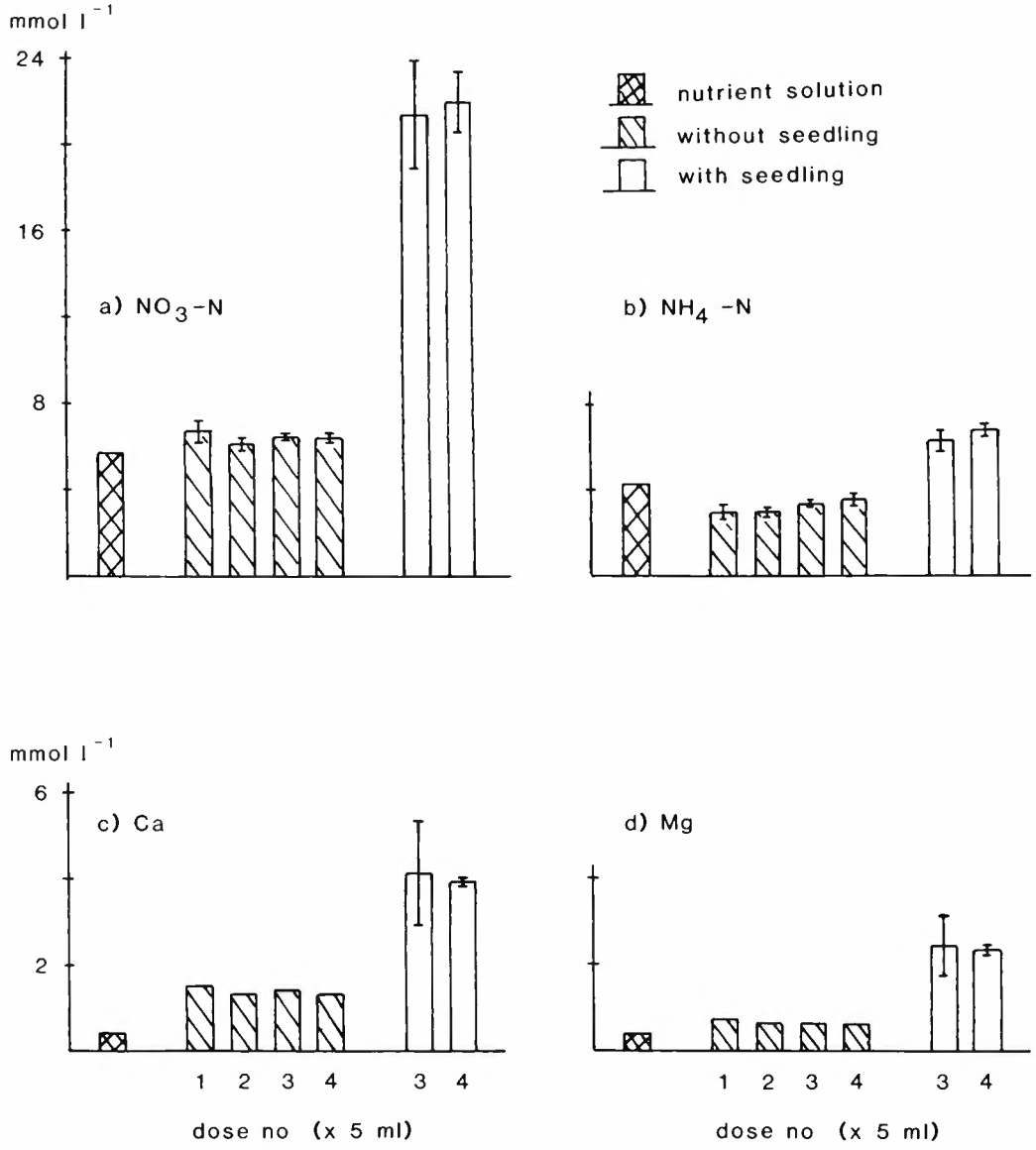

Figure 2. "Transpiration experiment": Concentrations (mmol l^{-1}) of elements in the growth substrate liquid phase at container capacity after 12/14 days. Means of five (Ca, Mg) or 10 (NO_3-N, NH_4-N,) replicates and standard deviations.

concentrations in the growth substrate were independent of the number of doses: Mean NO_3-N concentration was 13.4 mmol l^{-1} and 12.1 mmol l^{-1} for pots with a seedling and those without a seedling, respectively (Fig. 4). In pots with a seedling, the mean NH_4-N concentration was 5.7 mmol l^{-1} but 3.8 mmol l^{-1} in pots without a seedling.

Mean concentration of 3.0 mmol Ca l^{-1} and 1.6 mmol Mg l^{-1} was recorded in samples after 26 days (Fig. 4). The concentration of K in the nutrient solution was 2.0 mmol l^{-1}, and 4.4 mmol l^{-1} and

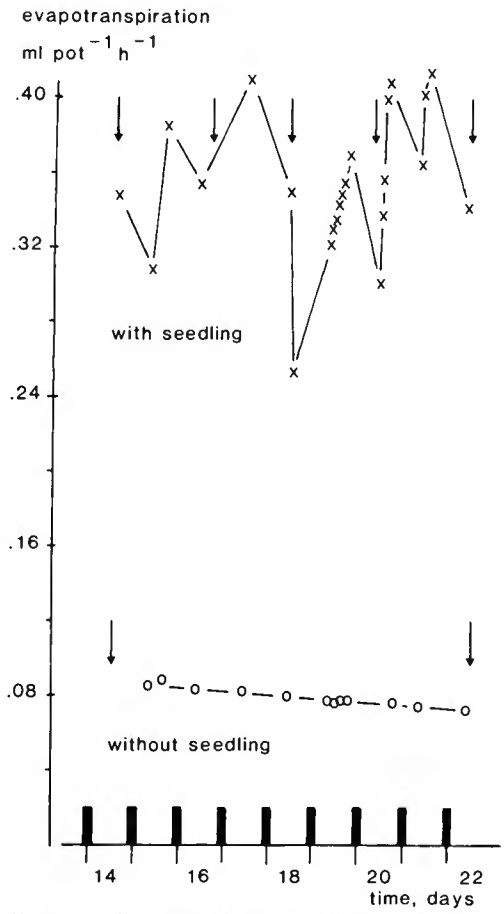

Figure 3. "Transpiration experiment": Concentrations (mmol l^{-1}) of elements in the growth substrate liquid phase at container capacity after 22 days. Only pots with a seedling are included. Means of five replicates and standard deviations.

3.2 mmol l^{-1} in the output solution from pots with a seedling and those without a seedling, respectively.

The leaching experiment

Final shoot length and dry weight were unaffected by the irrigation regime. With all 30 replicates, mean shoot length was 20.7 (0.5) cm and shoot dry weight 2010 (288) mg seedling^{-1}.

Regardless of irrigation frequency, the concentration of NO_3-N, NH_4-N, K and P increased with the concentration in the nutrient solution (Table 3). The concentration of these elements was negligible in pots given only deionized water. Ca concentration ranged from 1.2 to 1.7 mmol l^{-1}, while Mg and Fe concentration increased with increased concentration in the nutrient solution. Mn concentration in the substrate was higher with 4x solution than with H_2O and 2x solutions. The concentration of Ca, Mg, Fe and Mn was high throughout the experiment in pots given deionized water.

The concentration of elements in the foliage of Norway spruce seedlings was unaffected by irrigation frequency (Table 3). N, K and, to some extent Mn, concentrations increased with increasing strength of the nutrient solution, while P and Fe were low when deionized water was added and were otherwise independent of the strength of the nutrient solution. Foliar Ca and Mg concentrations were unaffected by the strength of the solution.

DISCUSSION

The mean, absolute water loss was 8.4 ml day^{-1} in the 'transpiration experiment', quite a low value for seedlings of this size (Gross 1976, Langerud & Sandvik 1988b, c). This was partly due to the drying of the substrates before re-irrigation (Table 2). Still, the evapotranspiration was high compared with the nutrient uptake: The total nitrogen content in 8.4 ml of the 2x normal nutrient solution in the 'leaching experiment' was 0.17 mmol (Table 1). The total amount of N in a seedling given nutrients every second day was 4.4 mmol (Table 3), an amount supplied by the solution in about 26 days, although accumulated over 203 days. The remaining supply was leached or accumulated. The results suggested accumulation, despite frequent leaching: Even 50 ml pot^{-1} (about 40 l m^{-2}) did not bring the concentrations back to that of the nutrient solution (Fig. 3). The curve relating liquid phase concentration to the added volume of nutrient solution was asymptotic, and leaching to the concentration in the nutrient solution was practically impossible. Leaching with

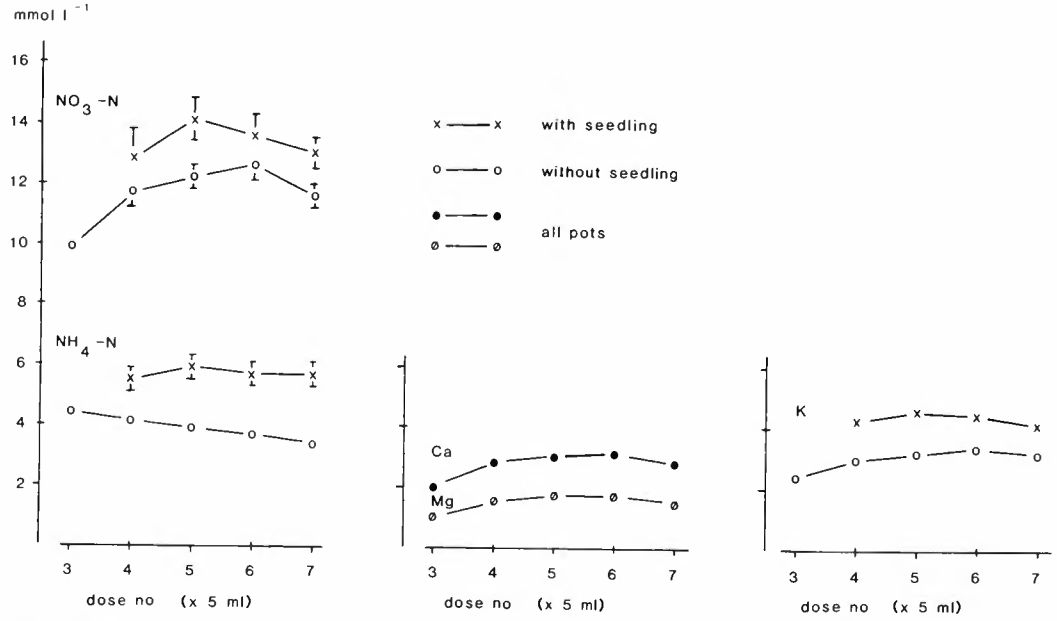

Figure 4. "Transpiration experiment": Concentrations (mmol l^{-1}) of elements in the growth substrate liquid phase at container capacity after 26 days. Means of five replicates and standard deviations.

water ('leaching experiment') brought the concentrations down, but 25 ml pot^{-1} (about 20 l m^{-2}) was necessary when high concentration inputs had been used (Table 3).

The nutrients accumulated quickly in the liquid phase of substrate without a seedling: The NO_3-N concentration approached the same level as in pots with a seedling after 26 days (Fig. 4). The NH_4-N accumulation was significantly slower, probably due to the cation exchange in the peat.

The technique used for sampling of the growth substrate liquid phase allowed for calculations of short-term element budgets, and calculation of the nutrient concentrations in the growth substrate liquid phase as the substrate became drier (Langerud & Sandvik 1988a). Precipitation of salts, cation exchange and nitrification were assumed to be negligible, and equilibrium was presumed between the solid and liquid phase for the ions concerned. The content of liquid was calculated from the volume fraction of gas-filled pores at container capacity (fgmin, Table 2), and at maximum dryness (fgmax). Concentrations at container capacity were calculated from the total amount of nutrients brought into the solution by additions of nutrient solution ('transpiration experiment') and deionized water ('leaching experiment'). The loss of nutrients by leaching was calculated from fgmax, fgcc and the volume of nutrient solution added. All calculations assume an even distribution of all ions throughout the liquid phase at any time.

An example of a calculation is shown in Table 4. The physical description of the substrate was from the 'transpiration experiment' (Table 1, after 26 days with a seedling) and the chemical parameters were derived from the 'leaching experiment'. The concentrations at container capacity and at maximum

Table 3. 'Leaching experiment': Element concentrations in the growth substrate liquid phase at container capacity (liq., mmol l^{-1}) and in the foliage of Norway spruce seedlings (fol., mmol kg^{-1} dry weight)

	NO_3 N		NH_4 N	N	K		P		Ca		Mg		Mn		Fe	
Solution	liq.	liq.	fol.	liq.	fol.	liq.	fol.	liq.	fol.	liq.	fol.	liq.	fol.	liq.	fol.	liq.	fol.
0x/1	0.4a[1]	0.02a	906a	0.4a	190a	0.04a	59.2a	1.4a	171a	0.3a	68.2a	0.020a	2.4a	0.018a	0.61a
0x/2	0.4a	0.02a	949a	0.3a	213a	0.04a	60.0a	1.4a	156a	0.3a	66.6a	0.020a	3.0a	0.011a	0.68a
2x/1[2]			2040b		369b		93.3b		162a		72.6a		7.0b		0.98b
2x/2	12.9b	8.0b	2204b	4.6b	356b	1.9b	80.7b	1.2a	186a	0.8b	84.1a	0.018a	6.0b	0.048b	0.94b
4x/1	32.5c	23.9c	2540c	11.1c	418c	4.6c	85.4b	1.5a	161a	1.7c	77.4a	0.030b	9.4c	0.105c	1.06b
4x/2	29.6c	21.7c	2540c	10.2c	448c	4.7c	76.8b	1.7a	165a	1.7c	80.1a	0.035b	6.1b	0.123c	0.99b
Bergmann & Bergmann (1985)[3]			1700		256		65		170		80		5.5		
Ingestad (1979)			2430[4]		15		132		25		49				

[1] Means with different letters were significantly different in a Duncan's range test (5% level).
[2] The liquid samples were erroneously diluted.
[3] Bergmann, E. & H. W. Bergmann. Potash Review, Subj. 5, No. 2, 52th suite: 1-10. 1985.
[4] Hydroponic culture with 57 mmol nitrogen l^{-1}.

dryness were hardly separated in time and the nutrient uptake by the seedlings could be safely ignored.

The pots given deionized water for 56 days had very low concentrations of most elements. Both Fe and Mn concentrations were still higher than in the nutrient solution usually used. This was in accordance with earlier observations on an initial decrease in the concentration of these ions when nutrient solution percolated through growth media (unpublished).

The high concentration of nutrients in the growth substrate liquid phase was reflected by foliar analysis. The high concentration nutrient solution (86 mmol N l^{-1}) used by Ingestad (1979) was lethal to Norway spruce seedlings. The concentration at container capacity in

Table 4. 'Leaching experiment': Calculated[1] element concentrations (mmol l^{-1}) in the growth substrate liquid phase at minimum (min) and maximum dryness (max)

Solution	NO_3-N min	max	NH-N min	max	K min	max	P min	max
0x/1	0.40	0.6	0.02	0.03	0.4	0.6	0.04	0.1
0x/2	0.36	0.9	0.02	0.04	0.3	0.8	0.04	0.1
2x/1[2]	-	-	-	-	-	-	-	-
2x/2	11.2	28.3	7.4	18.5	4.2	10.7	1.7	4.3
4x/1	28.9	56.5	21.3	41.6	9.9	19.3	4.1	8.0
4x/2	27.2	68.9	20.0	50.7	9.4	23.7	4.3	10.9

[1] Calculations based on concentrations at minimum dryness of the growth substrate (Table 2). Evapotranspiration as in the "transpiration experiment" (Fig. 1) and liquid content of each pot at max and min calculated with fg = 0.40 and 0.70 (Table 1) for every second day applications, respectively. The total volume of growth substrate in each pot was 41.7 ml, with a total porosity of 0,94 ml ml^{-1}.
[2] See Table 3, note 2.

the 'leaching experiment' was 47 mmol N l^{-1} at the most. Although a final concentration of 119.6 mmol N l^{-1} was reached, no visual damage to the seedlings was observed.

In Ingestad's (1979) experiment, with constant proportions between major elements, the concentration of N in the foliage was 2430 mmol kg^{-1} with 57 mmol N l^{-1} in nutrient solution. This illustrates the magnitude of the concentrations prevailing in the liquid phase of the 'leaching experiment': Foliar N as high as 3000 mmol kg^{-1} was reached. The nutrient uptake kinetics of Norway spruce was similar to that of other plants (Jensen & Pettersson 1978), although concentration - uptake curves (Sabater 1982, Nissen & Nissen 1983) are unknown. However, the high foliar concentration of nutrients in the seedlings from the 'leaching experiment' indicated a very high substrate liquid phase concentration of nutrients.

In conclusion, salt accumulation seems unavoidable: Reduction of the nutrient concentrations in the nutrient solution, or frequent leaching with water will certainly reduce the 'salt accumulation'. Still, the suspected imbalance in the ionic composition of the liquid phase of the growth substrate compared with the nutrient solution, has to be studied in order to obtain information with regard to the interaction between nutrient solution and growth media.

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EVALUATION OF LIMING MATERIALS AS AMELIORANTS OF ACID SOILS IN HIGH RAINFALL AREAS OF ZAMBIA

BAL RAM SINGH[2]
Soil Productivity Research Programme (SPRP), Misamfu Regional Research Station, Kasama, Zambia

Singh, Bal Ram. 1989. Evaluation of liming materials as ameliorants of acid soils in high rainfall areas of Zambia. Norwegian Journal of Agricultural Sciences 3:13-21. ISSN 0801-4341

Three indigenous liming materials, Chilanga, Isoka, and Ndola were evaluated in a field study with and without phosphorus (P), for their suitability and agronomic effectiveness for amelioration of soil acidity and crop production. In all, 14 treatments were laid out in a randomized block design with a commonly practiced maize-groundnut cropping sequence.

The result showed that both groundnut and maize responded highly significantly to P application in all of the five study years. Unexpectedly, however, no significant direct response was observed with regard to lime applied through different sources and at different rates. Under the soil-crop conditions used, the three sources of lime in general have similar agronomic effectiveness and are found to have a beneficial effect on yields even at the lower dosage.

The result of the soil analysis show that both lime and P application generally increase the pH and Ca levels and decrease Al 3 + saturation to desired levels in the first year and keep them under tolerable limits in the subsequent years up to the 5th year after lime application.

Key words: Acid soils, ameliorants, groundnut, high rainfall areas, liming materials, maize, phosphorus, soil properties, Zambia.

Bal Ram Singh, Department of Soil Sciences, Agricultural University of Norway, P.O. Box 28, 1432 Ås-NLH Norway

Acid soils, belonging mainly to Oxisols and Ultisols, occupy about 35 % of the total arable land in Zambia and 38 % in the tropical areas as a whole. Their management is of great importance for improving crop production and unless these soils are managed properly, sustained production of food crops will not be feasible.

These soils are characterized by low pH (often < 5,0), high Al and Mn, low nutrient retention and organic matter content, medium to high P fixation, and low moisture retention capacity. Among the subsistence farmers, these constraints have dictated the traditional shifting cultivation system, mainly based on natural vegetation and long bush fallow (> 10 - 15 years) for regenerating soil fertility.

The shifting cultivation system in many areas including Northern Zambia is reaching its limit due to the rapid increase in population and land use. Recent advances in soil management research have helped dispel many earlier misconceptions regarding the agricultural potential of acid tropical soils, and have proved that with appropriate use of amendments and fertilizers sustained

and stable food crop production is possible in these soils.(Vicente-Chandler et al.,1974; Sanchez et al.,1982). There is a general mandate that liming along with P fertilization is the keystone to soil management of acid tropical soils (Laroche, 1966; Pearson, 1975; Kamprath, 1984).

To meet the increasing demand for lime in the agricultural sector, especially for amelioration of acid soils of the northern high rainfall areas, a concerted effort has been directed of late towards development of indigenous deposits of limestone. In this study, preference has been given to testing liming materials, viz. Isoka and Ndola lime, available within the high rainfall areas in comparison with limestone from Chilanga, Lusaka. Not only has the latter become scarce, it is also becoming a costlier proposition due to increasing freight charges at the expense of the small marginal farmers. The preliminary chemical analysis of the Isoka and Ndola limes has shown them to be good materials, so the field testing for their agronomic effectiveness under local soil-crop conditions was started.

A common benefit ascribed to liming is that it renders P more available. But there has been controversy over its benefit and published results show that the interaction between liming and P can be positive or negative (Evans and Kamprath, 1971; Kamprath, 1972; Amersiri and Olsen, 1973).

The objectives of this study were: (1) to assess the suitability and agronomic effectiveness of different liming materials with and without P fertilization for amelioration of soil acidity and crop production, and (2) to study the effect of lime and P on soil chemical properties.

MATERIALS AND METHODS

A field study was initiated in the 1982/83 cropping season to assess the agronomic effectiveness of Isoka and Ndola liming materials in comparison with Chilanga material, with a crop sequence of groundnut-maize on Misamfu sandy loam series (Oxic Paleustult). The chemical characteristics of the liming materials used are presented in Table 1.

Table 1. Results of chemical analyses of liming materials

Liming material	$CaCO_3$ (%)	$MgCO_3$ (%)	Neutralising Value (NV*)
Chilanga (Lusaka)	75	14	90
Ndola	98	Traces	98
Isoka	45	25	90

*NV is the acid neutralising ability expressed on a mass basis relative to $CaCO_3$. $MgCO_3$ (relative molecular mass 84) has an NV of 119

Analytical results of the soil showed that it was sandy loam in texture and had acidic pH of 4,4 with a high Al3+ saturation of 70 %. Although the absolute level of exchangeable Al3+ was not very high, its relative value of saturation was high due to the low effective C.E.C. of the soil. The initial level of available P was moderately high but exchangeable K+ content was low. Two assumptions were made while setting the objective of this trial: first that the groundnut and maize crops, being the important crops in the area, would respond to liming of the acid soil, and, second, that if the chemical characteristics of the three liming materials were similar, then their agronomic effectiveness could only differ as a result of differences in their Mg content, especially under conditions of Mg deficiency in the soil.

Based on the soil characteristics and requirements of groundnut-maize cropping sequence, two levels of lime dose, i.e. 2 and 4 t ha-1, were selected for each of the three types of liming material.

Since the soil under the study has indicated P responses in earlier tests and a positive lime x P interaction has been

widely indicated in the literature, it was considered appropriate to include two levels of P with different lime levels, e.g. 0 and 33 kg ha-l. Thus, 14 treatments in all (7 X 2 factorial) were laid out in the randomized block design. In November 1982, at the beginning of the experiments, lime was applied to the top soil (15 cm). Basal doses of N and K at the rate of 50 kg and 40 kg ha-l,respectively, were applied as NH4NO3 and KCl to each crop in the rotation, except in the case of maize crop in 1985/86, where 100 kg N and 40 kg ha-l were topdressed.

Soil samples from each treatment (composite samples of four replicates) from 0-20 and 20-40 cm depths were collected after each harvest. The samples were air dried, ground, sieved through a 2 mm sieve, and stored for chemical analysis.

Soil pH was measured in a 0,0 1M CaC12 solution. Available P was determined by the method described by Bray and Kurtz (1945). Exchangeable cations were determined by NH4OAC extraction procedure (Schollenberger and Simon, 1945) where Ca and Mg were determined by atomic absorption spectrophotometer and K and Na by flamephotometer. Exchangeable Al was extracted with normal KCl and determined by atomic absorption spectrophotometer. Although soil samples from both 0-20 and 20- 40 cm depths were analyzed for selected soil chemical properties and are reported accordingly in the SPRP Research Report (1983/86), for the sake of brevity in this paper only analytical data from the 0-20 cm depth will be reported. Analysis of variance was performed on yield data to evaluate variations due to lime and P application and their interaction.

RESULTS AND DISCUSSION

The results on crop yields of five cropping seasons are presented in Figs. 1 - 5. Groundnut and maize crops were grown in rotations, therefore groundnut yield is presented in Figs. 1, 3, and 5 and that of maize in Figs. 2 and 4 in accordance with

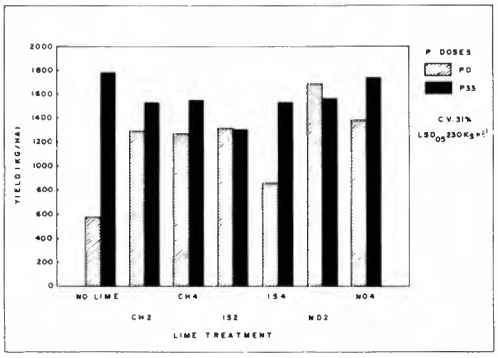

Fig. 1. Groundnut response to lime and P. CH, IS, and ND represent Chilanga, Isoka, and Ndola lime, respectively and subscripts 2 and 4 are lime rates 2 and 4 t ha-l. P0 and P33 are phosphorous rate at 0 and 33 kg P ha-l (1982/83)

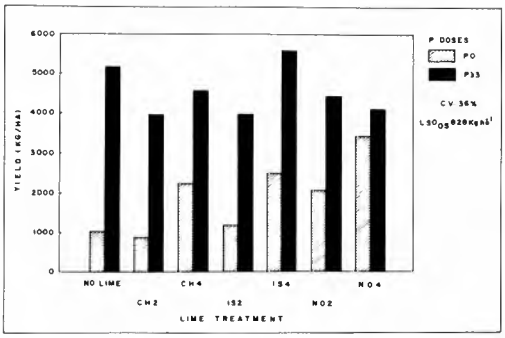

Fig. 2. Maize response to lime and P. The legend is the same as in Fig. 1 (1983/84)

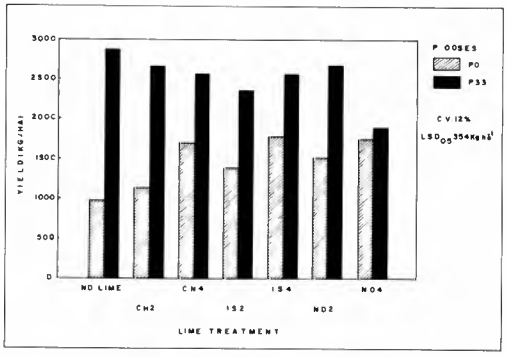

Fig. 3. Groundnut response to lime and P. The legend is the same as in Fig. 1 (1984/85)

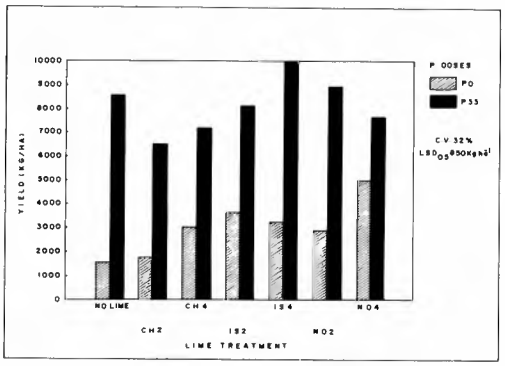

Fig. 4. Maize response to lime and P. The legend is the same as in Fig. 1 (1985/86)

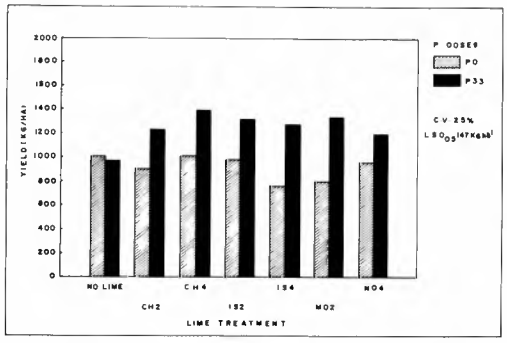

Fig. 5. Groundnut response to lime and P. The legend is the same as in Fig. 1 (1986/87)

their cropping sequence. Both maize and groundnut responded significantly ($P < 0,05$) to P fertilization in all years under study. However, the response to P fertilization was greater in maize (Figs. 2 and 4) than in groundnut (Figs. 1, 3 and 5). Quite unexpectedly there was no significant direct response to lime applied through different sources and at different rates. Absence of response to lime in both the crops was perhaps due to low level of exchangeable Al3+ in the soil initially. It has been reported that neutralization of Al by liming increases relative growth at low rates of applied P. However, with larger amounts of applied P there was no benefit from liming when the Al saturation was <60%. It has also been shown that if the Al saturation is <60%, the amount of Al in the soil solution is relatively low as compared with Al saturation >60% (Evans and Kamprath, 1970). At these lower concentrations of Al, the larger P addition either precipitated Al internally and still provided sufficient P for metabolic purposes (Wright, 1937), or removed the detrimental effects of Al by precipitating it in the soil (Munns, 1965). This would seem to be the case in this study, as is evident from the yields over the five-year period (Figs.1 - 5). Liming increased groundnut and maize yields several-fold without P fertilization in all these years except the last year, when yield differences between limed and non-limed treatments were not very marked. But when P was applied along with lime, the effect of lime was not evident and invariably the yield of both maize and groundnut were lower in limed than in non-limed plots.

Although leaf analysis for Zn was not available, sporadic zinc deficiency symptoms in limed plots were observed during growth, especially in the maize crop. This may have caused yield reduction in limed plots. Lime-induced zinc deficiency is commonly reported (Kamprath, 1971; Singh and Steenberg, 1974; Mengel and Kirkby, 1982). Similar to the finding of this study, Abruna et al.(1975) reported that maize yield was depressed to a lesser degree by a given level of soil acidity in the Oxisols than in Ultisols. Although there was a response to lime in two of three Oxisols, it did not reach the level of significance. In two of three soils good yields were obtained at pH levels below 5.0 and there was no significant relationship between percent Al saturation and yields on the Oxisols as a group. These results indicate that low pH is not as deleterious to plants grown in highly weathered soils as in those with less severe weathering. Liming effectively eliminated Mn toxicity and Ca deficiency as important yield factors in either group of soils. The infe-

rence, then, is that the soil solution Al level was probably lower at a given pH value in more highly weathered soils, a conclusion also supported by this study and the studies of Brenes and Pearson (1973), who found consistently low soil solution Al in Oxisols of the U.S.A. and Puerto Rico as compared with Ultisols of South East U.S.A.

The significance ($P < 05$) of lime x P interaction in the 1984/85 groundnut crop, though, made it possible to indirectly compare the agronomic effectiveness of the different lime sources, but only at the no P level. The results indicated that there was significant ($P < 05$) response of lime applied through different sources at two levels with the exception of Chilanga lime applied at the rate of 2 t ha-l (Fig.3). The responses to lime disappeared when P was applied, although the yield levels with lime and P application were significantly ($P < 05$) higher than those recorded with lime but without P application. It may thus be concluded, though not finally, that under soil-crop conditions studied the three sources of lime generally have similar agronomic effectiveness and could have beneficial effects of liming on yields at the lower dose. However, in soils with Mg deficiency, Chilanga and Isoka lime may be more effective than Ndola lime.

In the last cropping season of 1986/87 (Fig.5), as in previous years the groundnut crop responded significantly to P application but, contrary to previous groundnut crops. (Fig. 3), the effect of lime x P interaction was not found to be significant. Similarly, yield differences between limed and non-limed plots without P application were not very marked. This probably was due to low yield levels obtained in the last season. During 1985/86, the rate of N to maize crop was doubled and it is surmised that the residual N was utilized by the subsequent groundnut crop resulting in excessive vegetative growth. It has been experienced that when the above-ground growth is profuse, pod formation and consequently groundnut yield are generally reduced (SPRP Research Report, 1983-1986).

The preliminary conclusion that the three liming materials used in this study have in general similar agronomic effectiveness is further supported by their effect on some selected soil properties. The result of the soil analysis summarized in Tables 2 and 3 indicate that any lime material at 2 t ha-l will increase the

Table 2. Effect of sources and rates of lime application with and without phosphorus on some selected soil properties in 0 - 20 cm soil depth (1982/83)

Lime Source	Lime Rate (t ha^{-1})	P Rate (Kg ha^{-1}) 0				33			
		pH ($CaCl_2$)	Avail. P (ppm)	Exch. Ca^{2+} (m.e./100 g)	Al^{3+} Sat. (%)	pH ($CaCl_2$)	Avail. P (ppm)	Exch. Ca^{2+} (m.e./100 g)	Al^{3+} Sat. (%)
-	0	4,3	26	0,93	69	4,8	56	1,97	14
Chilanga	2	5,3	38	2,56	0	6,3	49	5,71	0
Chilanga	4	5,6	32	3,45	0	5,7	60	4,38	4
Isoka	2	4,4	33	0,78	65	4,8	46	1,74	14
Isoka	4	5,9	42	2,75	0	5,0	37	1,58	8
Ndola	2	4,4	11	0,69	77	5,3	42	3,50	0
Ndola	4	6,2	43	4,21	0	6,5	76	6,49	0

Table 3. Effect of sources and rates of lime application with and without phosphorus on some selected soil properties in 0 - 20 cm soil depth (1983/84)

Lime Source	Lime Rate (t ha^{-1})	P Rate (Kg ha^{-1}) 0 pH ($CaCl_2$)	Avail. P (ppm)	Exch. Ca^{2+} (m.e./100 g)	Al^{3+} Sat. (%)	33 pH ($CaCl_2$)	Avail. P (ppm)	Exch. Ca^{2+} (m.e./100 g)	Al^{3+} Sat. (%)
-	0	4,4	17	1,3	29	4,9	3	1,4	14
Chilanga	2	4,6	8	0,8	27	4,8	3	1,4	14
Chilanga	4	5,4	17	4,0	0	5,1	7	1,9	4
Isoka	2	4,9	9	1,1	10	4,7	2	0,8	28
Isoka	4	5,2	10	1,3	5	5,4	7	1,5	11
Ndola	2	5,3	9	1,6	0	5,1	13	1,7	23
Ndola	4	5,3	4	2,3	0	5,1	13	2,3	16

pH level and generally decrease Al3+ saturation to the desired level in the first year after lime application, maintaining it through the second year.

Analysis of the soil after harvesting of the fourth crop (Table 4) showed that the residual effect of 2 t ha-l still kept the Al3+ saturation within tolerable limits. This was perhaps the reason for the improved yields of groundnut and maize in the third and fourth cropping seasons, respectively. Shown in table 5 is the analysis of soil taken after the fifth groundnut crop. The analysis showed that the residual effect of lime still persisted and that lime kept both pH and Al saturation within tolerable limits.

The other important finding of the trial was the significant response to P in both crops over the whole five year period. The response to P in the first crop of groundnut was observed even when the initial soil P level was moderately high. Perhaps this was the reason for the

Table 4. Effect of sources and rates of lime application with and without phosphorus on some selected soil properties in 0 - 20 cm depth (1985/86))

Lime Source	Lime Rate (t ha^{-1})	P Rate (Kg ha^{-1}) 0 pH $CaCl_2$	Avail. p (ppm)	Exch. Ca^{2+} (m.e./100g)	Al^{3+} Sat. (%)	33 pH $CaCl_2$	Avail. P (ppm)	Exch. Ca^{2+} (m.e./100g)	Al^{3+} Sat. (%)
-	0	4,3	13	0,5	53	4,7	21	1,4	18
Chilanga	2	4,4	7	0,6	30	4,6	18	1,1	26
Chilanga	4	4,6	9	0,9	20	5,2	18	2,2	-
Isoka	2	4,5	12	0,9	27	4,5	15	0,8	31
Isoka	4	5,3	14	2,0	-	4,8	18	1,5	9
Ndola	2	4,9	10	1,5	10	4,8	25	2,0	8
Ndola	4	5,4	16	2,3	-	5,2	23	2,3	-

Table 5. Effect of sources and rates of lime applicaton with and without phosphorus on some selected soil properties in 0 - 20 cm soil depth (1986/87)

Lime Source	Lime Rate (t ha^{-1})	P Rate (Kg ha^{-1}) 0 pH ($CaCl_2$)	Avail. P (ppm)	Exch. Ca^{2+} (m.e./100 g)	Al^{3+} Sat. (%)	33 pH ($CaCl_2$)	Avail. P (ppm)	Exch. Ca^{3+} (m.e./100 g)	$Al3+$ Sat. (%)
-	0	4,3	15	0,4	56	5,1	64	1,9	4
Chilanga	2	4,9	17	1,4	5	4,6	23	1,2	18
Chilanga	4	5,3	16	2,1	4	5,4	36	2,7	3
Isoka	2	4,6	15	0,8	14	4,6	32	2,9	20
Isoka	4	5,4	20	2,2	3	5,1	37	1,9	4
Ndola	2	5,2	19	2,2	4	4,9	55	2,1	4
Ndola	4	4,4	20	2,5	3	4,7	7	2,4	7

lower response to applied P, i.e.of 16 kg grain/kg P in 1982/83 compared with 31,8 kg grain/kg P in 1984/85. However, this response to P in 1986/87 dropped to 9,5 kg grain/kg P, perhaps due to the reason given above. In the case of the maize crop, there was also an increase in response from 79,9 kg grain/kg P in 1983/84 to 155,2 kg grain/kg P in 1985/86. But this tremendous increase in P response was mainly due to the double dose of N applied to the 1985/86 crop. Perhaps in 1983/84, too, the response of maize to P could have been higher had nitrogen been applied at a higher rate.

The results of the experiment showed that with the exception of the last groundnut crops, the test crops generally had a better yield from one season to the next under the improving soil conditions, due to liming and optimum P application (Fig. 6).

Moreover, the high yields of maize in the 1985/86 season due to higher N application underlines the basic principle of soil fertility that not only is it necessary to apply those nutrients initially diagnosed as deficient in the soil but also those found deficient later, due to intensive cropping or other reasons. The results also suggest that under the soil-crop conditions used, P application alone was sufficient to sustain maize-groundnut yield at a high level and that the soil acidity amelioration required for these crops can be met only by P application.

It is interesting to note further that in the absence of P application, lime alone is able to maintain a yield level of 1 to 1,5 t ha-l of groundnut and 2 to 3,3 t ha-l of maize. This suggests that lime application is able to render P available from organically bound P sources, e.g.

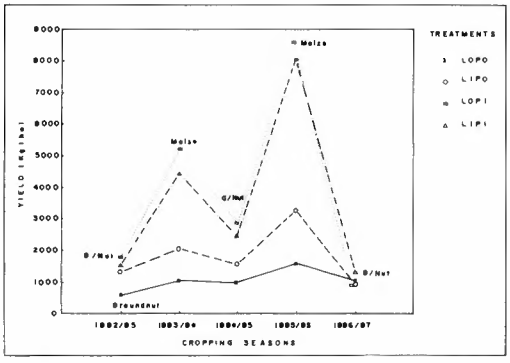

Fig. 6. Crop yield at different levels of lime and P. L0 P0 = No Lime and No P, L1 P0 = LIME ONLY, L0 P1 = P ONLY, and L1 P1 = LIME AND P

initial organic matter and crop residue recycled in the system.

In order to test the relative agronomic effectiveness of three liming sources, further studies are needed under conditions where liming is known to give a highly significant response and where liming doses are based on their neutralizing values and amount of exchangeable Al3+ present in the soil.

SUMMARY AND CONCLUSIONS

A field study was conducted on Misamfu sandy loam soil series (Oxic Paleustult) to assess the suitability and agronomic effectiveness of different liming materials, with and without P fertilization, for amelioration of soil acidity and crop production as well as to examine the effect of these liming materials and P on soil chemical properties. Three indigenous liming materials, Chilanga, Isoka and Ndola, were applied at 2 and 4 t ha-1; phosphorus was applied at 0 and 33 kg ha-1. In all 14, treatments (7 x 2 factorial) were laid out in a randomized block design. A commonly practiced maize-groundnut cropping sequence with appropriate fertilizers was used.

The results showed that both groundnut and maize responded highly significantly to P application in all five of the study years. Unexpectedly, however, no significant direct response to lime applied through different sources and at different rates was observed. Absence of response to lime was associated with low initial level of exchangeable Al3+ in the soil. Under the soil-crop condition used, the three sources of lime generally have similar agronomic effectiveness and were found to have beneficial effect on yields even at the lower dose. However, in soils with Mg deficiency, Chilanga and Isoka lime may be more effective than Ndola lime. The result of soil analysis showed that both lime and P application generally increased the pH and Ca levels and decreased Al3+ saturation to acceptable levels in the first year and kept them under tolerable limits in the subsequent years up to the 5th year after lime application. The results also suggest that under the soil-crop conditions studied, application of P alone is sufficient to ameliorate soil acidity to the required levels and to sustain yield at high levels over the five year period. The results further suggest that lime in the absence of P application is able to maintain a yield level of 1 to 1,5 tha-1 of groundnut and 2 to 3,3 t ha-1 of maize, possibly by making P more available from organically bound P sources, e.g. initial organic matter content and crop residue recycled in the system.

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A SIMPLE TWO-PHASE SYSTEM FOR EFFICIENT IN VITRO TUBERIZATION IN POTATO

CATHRINE LILLO
Dept. of Botany, The Agricultural University of Norway, Ås-NLH,

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In vitro tuberization was induced by simply overlayering the solid propagation medium with a liquid induction medium. Nodal cuttings were grown for three weeks in hormone-free Murashige-Skoog (MS) medium, then a liquid modified MS-medium with 10% sucrose, 10 mg/l benzyladenine (BA) and 1.2 ml/l commercial cycocel was added. During tuber induction, the incubation vessels were placed at 20°C, 8 h day 40 $\mu Em^{-2}s-1$. Almost full tuberization was achieved within four weeks for all cultivars tested, and after ten weeks, a tuber size of 200-400 mg was obtained.

Key words: *Solanum tuberosum* L., tissue culture, tuberization.

Cathrine Lillo, Dept. of Botany, The Agricultural University of Norway, Box 14, N-1432-Ås-NLH, Norway.

In vitro propagation of potato is an efficient way of rapidly multiplying new or existing cultivars in disease-free conditions. Propagation may be achieved by serial culture of nodal cuttings (Hussey and Stacey 1981, Rosell et al. 1987). The in vitro grown shoots can be induced to produce tubers (Hussey and Stacey 1984, Wang and Hu 1982, Tovar et al. 1985), which are very convenient for storing, transporting and handling. In vitro tubers are suggested to be the ideal end product of in vitro propagation (Rosell et al. 1987). The process of in vitro tuberization has been studied by several investigators, and there is general agreement on several factors which favor tuberization. High sucrose concentrations, cytokinins, and the gibberellin biosynthesis inhibitor chlorocholine chloride generally promote tuberization. These substances are usually added together (Hussey and Stacey 1984, Tovar et al. 1985, Rosell et al. 1987), although this is not strictly necessary for all cultivars. Temperatures at 25° to 30°C are clearly inhibitory and a temperature of 18° or 20°C is commonly used (Koda and Okazawa 1983, Wang and Hu 1982). There is evidence that short days also promote in vitro tuberization (Hussey and Stacey 1984, Wang and Hu 1982). Both a solid induction medium and a liquid medium which generally give larger minitubers have been used (Rosell et al. 1987). Based on these generally accepted effects of media components and environmental factors we have developed a very simple, quick and reliable method for producing in vitro tubers in a solid/liquid two-phase system.

MATERIALS AND METHODS

Plant material

The materials used were: The commercial cv. Beate propagated by taking nodal cuttings after initial meristem culture. The breeding line F x Aq (good resistance to late blight), N73-20-262 (highly resistant to gangrene) and the two pollen sterile lines N-80-37-34 (nematode resistant, highly resistant to gangrene) and CT-81-22-25 (complex hybrid, highly resistant to late blight) were propagated from tuber sprouts after surface sterilization. N-80-21-135 x 'Rosamunda' (later referred to as xRosamunda) was propagated from one true seedling. *Solanum acaule* (primitive, non-tuber producing) propagated from one true seedling was also used in some of the experiments.

Media and incubation conditions

The plants were grown either in Magenta boxes (350 ml) or, as in one experiment, in glass jars (350 ml). The medium routinely used was the TM5-medium of Shahin (1985), which is a modified half-strength MS medium with 1% sucrose and no hormones. Shoot tips or nodal cuttings were transferred to fresh medium about once a month. The vessels were incubated at 20°C, 12 h day 120 $\mu Em^{-2}s^{-1}$. Regular hormone-free MS medium with 3% sucrose was also used for propagation, and was always the medium chosen prior to induction of tubers.

Two different media for tuberization were investigated. 1) A solid modified MS medium after Tovar et al. (1985) with 8% sucrose, 5.0 mg/l benzyladenine (BA) and 0.6 ml/l cycocel (American Cyanamid 320 g/l cholinechloride, 460 g/l chloromequatchloride) (CCC). 2) Liquid MS medium with 10% sucrose, 10 mg/l BA and 1.2 ml/l CCC. Vessels with plantlets for induction of tubers were exposed to 8 h daylengths at 40 $\mu Em^{-2}s^{-1}$ and 20°C.

RESULTS

Each top shoot with 2-3 leaves was cut from 4-week-old plants and transferred to the solid induction medium (Table 1). Although tuberization was efficiently induced, the tubers were smaller than reported by others (Tovar et al. 1985,

Table 1. Number of tubers per shoot and weight of tubers after three different tuber induction treatments. Apical shoots with 2-3 or 6 leaves were transferred to Magenta boxes with solid induction medium, or liquid induction medium was added to the solid propagation medium. The number and the fresh weight of tubers were scored 10 weeks after transfer to or addition of induction medium. On average, there were 14 shoots per treatment

	Shoots with 2-3 leaves solid medium		Shoots with 6 leaves solid medium		Shoots with 6 leaves solid/liquid medium	
Plant material	Tuber/shoot	weight/tuber mg	Tuber/shoot	weight/tuber mg	Tuber/shoot	weight/tuber mg
Beate	0.7	56	1.1	96	1.0	209
xRosamunda	0.7	45	1.5	50	1.7	337
FxAq	1.4	67	1.1	72	1.6	306
CT-81-22	1.1	28	1.0	52	1.3	142
N-80-37-34	1.0	46	NA	NA	1.1	336
S. acaule	1.1	10	NA	NA	1.2	33
Mean	1.0	42	1.2	68	1.3	227

(NA = not available)

Table 2.The effect of various amounts of solid and liquid medium on tuberization. One shoot was cut into one top shoot with 2-3 leaves and six nodal segments each with one leaf and axillary bud. The cuttings were placed in Magenta boxes with 10 or 20 ml hormone-free MS-medium. After 3 weeks, 10, 20 or 40 ml induction medium was added. There were 14 cuttings per treatment. The number of tubers was scored after 4 weeks and 10 weeks, and fresh weight was measured after 10 weeks

Plant material	Solid propagation medium ml	Liquid induction medium ml	Tubers/shoot after 4 weeks	Tubers/shoot after 10 weeks	Weight/tubers ml
Beate	10	10	0.9	1.0	162
	10	20	1.0	1.0	245
	20	20	0.9	1.0	312
	20	40	0.9	0.9	374
xRosamunda	10	10	0.8	1.0	88
	10	20	0.9	1.3	159
	20	20	0.9	1.3	288
	20	40	0	1.8	230

Hussey and Stacey 1984). When shoots with 6 leaves were transferred to the induction medium, the result was an increase in tuber weight (Table 1). However, in both cases, growth was inhibited on the induction media; this was probably due to the lack of a root system to absorb minerals and sugar. Therefore, in the next experiments the top shoots with 2-3 leaves were transferred to MS medium with 3% sucrose and no growth regulators. After three weeks the shoots had grown to about the 6th leaf stage and had a well-developed root system. At this stage 20 ml liquid MS medium with 10% sucrose, 10 mg/l BA and 1.2 ml/l CCC was poured into the vessels, and the vessels transferred to 8 h day, low light intensity. This treatment efficiently induced tuberization and the average weight of *S. tuberosum* tubers was high (Table 1, Fig. 1). Also *S. acaule*, which usually does not produce tubers in the field, produced tubers in vitro, demonstrating that the conditions chosen were highly inductive.

In the experiment presented in Table 2, shoots with 7-8 leaves were cut into nodal segments and placed in vessels with 10 or 20 ml MS-medium. After 3 weeks, 10, 20 or 40 ml liquid induction medium was added. This experiment showed that 20 ml of solid and 20 or 40 ml of liquid medium was suitable, and both nodal segments and top segments could be used.

The type of vessel or sealing used was important to good growth and tuberization. Figure 2 shows tuberized plants about 7 weeks after the liquid induction medium was added to plants of the cultivar Beate grown in glass jars sealed with parafilm and for plants grown in Magenta boxes. The plants in the glass had thick stems and poorly-developed leaves, typical effects of ethylene, whereas the plants in the Magenta boxes had well-developed leaves and also produced larger tubers.

DISCUSSION

The experiments showed that the in vitro tubers obtained when shoots were transferred to solid induction medium were rather small. The reason for this poor development was probably the lack of a root system for efficient absorption of nutrients. Roots did not develop due to the high concentration of BA in the medium. Such tubers are probably too small for good production of tubers in the next step, and dormancy breakage may

Fig 1. In vitro tubers of 'Beate' produced on a solid (left) a solid/liquid (right) medium. The scale bar is 10 mm

Fig 2. Tuberized plants grown in glass jars and sealed with parafilm (left) and Magenta boxes (right)

also be a problem (Tovar et al. 1985). However, full tuberization was obtained by simply overlayering the solid propagation medium with a liquid induction medium when the plants already had a welldeveloped root system. The high sucrose concentration (10%) of the induction medium caused dehydration of the solid medium and the roots were progressively exposed to higher sucrose concentrations, a situation which is probably beneficial to the tuberization process. Concentrations of BA and CCC were doubled compared with the protocol of Tovar et al. (1975), since these substances have to diffuse into the solid

medium before they can be taken up by the roots. The tubers produced by this method were about 5 times larger than those produced when solid medium was used only. These tubers were also larger than the tuber sizes reported in other investigations (Hussey and Stacey 1984, Tovar et al. 1985). This method could easily be combined with mass propagation by serial nodal cuttings or layering of detopped shoots on the solid medium. Tuberization could then be induced at any time by adding the liquid induction medium and transferring the plants to short days and low light intensity. Studies of dormancy breakage and further applications of the in vitro tubers are in progress.

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NUMBER OF PISTILS, AN ALTERNATIVE CRITERION WHEN SELECTING FOR HIGH PRODUCTIVITY IN *RUBUS*

KÅRE RAPP
Holt research station, Tromsø, Norway

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To avoid the strongly environmental caused errors when selecting for increased berry production using the characteristics fruit size and berry yield per plant, an alternative selection, the number of pistils per flower, is examined in the dioecious, insect pollinated species cloudberry (*Rubus chamaemorus* L.).
The broad sense heritabilities estimated for number of pistils and berry weight are (h^2b =) 0.91 and 0.31, respectively. A correlation coefficient calculated between number of pistils and berry weight among corresponding genotypes is only (r =) 0.14 $^{(ns)}$. The present results show that number of pistils per flower is a better criterion than berry weight when selecting for increased productivity in cloudberry.

Key words: Rubus, Productivity, Selection criteria.

Kåre Rapp, Holt research station, P.o.box 100, N-9001 Tromsø, Norway

Common characteristics to use when selecting for high productivity in small fruit are berry yield and fruit size (Caldwell & Moore 1982, Daubeny et al. 1986). These characteristics, however, are composed of several basic components (characters), e.g. the number of flowers per plant, flower fertility, the number of droplets per berry, and the crop development potential (Ourecky 1975). Berry yield is also very much influenced by environmental factors, such as air temperature, air humidity, ground water, wind, and number of pollinating insects.

The cloudberry (*Rubus chamaemorus* L.) is a dioecious small fruit which grows mainly on peat land in countries around the Arctic Ocean (Fægri 1970, Hultén 1950, Polunin 1940, Taylor 1971). This species has only a few relatively large flowers per plant, so yield is very much based on climatic factors and on the number of pollinating insects during time of flowering and pollination (Sandved 1958, Østgård 1964). Accordingly, when selecting for high productivity using berry weight per flower in cloudberry, many genotypes which carry a genetic potential for still higher productivity may be exc luded. In order to avoid this error, an alternative selection using the more basic character 'number of pistils per flower' is carried out in cloudberry.

MATERIAL AND METHODS

Plant material

Ripe cloudberry fruits were collected from about 100 different plants in a native community at Andøya (69° La., 15° Lo., 20 m.a.s.l.). The seeds were washed

out of the berries and sown in wet *Sphagnum* peat in trays. The trays were thereafter placed outdoors for natural stratification under snow cover during the winter. In April, the material was brought into a greenhouse (20°C) for germination. Five weeks old seedlings were planted in Jiffy pots, transplanted to 12 cm plastic pots some weeks later, and grown on in a plastic greenhouse until maturity for flowering (3 to 5 years). The plants were cloned into at least two ramet-plants in order to get replications of the genotypes. To achieve better fertili zation and fruit set, the flowers were handpollinated using a soft brush in addition to the natural insect pollination.

Selection procedure and statistical analysis

After two years of flowering, pollination, and fruit set, a selection for high berry weight was done among the cloned genotypes. Plants with a berry weight of 1.0 g or more per flower were chosen and propagated. One year later, a selec tion for 'number of pistils per flower' was carried out among the same genotypes. Plants with 11 pistils or more per flower were chosen and propagated. The following year, the number of pistils per flower as well as the berry weight per flower were observed on corresponding, selected, cloned genotypes.

The statistical analysis of the data, and a genetic explanation of the mean squares for 'berry weight' and 'number of pistils' among the cloned material are in accordance with Burton & DeVane (1953) and Rapp & Stushnoff (1979), as fol lows:

Item	*Df.*	*Exp.Msq.*	*Sign*
Total	(N-1)		
Replication	(R-1)		
Clones	(C-1)	RVg + Ve	M1
Error	(R-1)(C-1)	Ve	M2

The phenotypic variance (Vp) = RVg + Ve, where Vg = variance due to genetic factors, and Ve = variance due to environmental factors. Broad sense heritability (h^2b) was estimated using the formula Vg/Vg+Ve = ((M1-M2)/R)/((M1-M2)/R+M2). Finally, a phenotypic correlation coefficient (r) between berry weight and number of pistils per flower among corresponding genotypes was calculated.

An MSTAT program package of an Reinbow 100 computer was used for the statistical analysis and for drawing the figures.

RESULTS AND DISCUSSION

A phenotypic frequency distribution for berry weight (grams per berry) and the number of pistils per flower among the selected genotypes are given in figures 1 and 2. Mean values are given at the top of the figures. The phenotypic distributions observed may be characterized as normal. However, the distribution is somewhat wider and more variable for berry weight (fig. 1) than for number of pistils (fig. 2). For berry weight there are for example no genotypes in the 0.7 g -

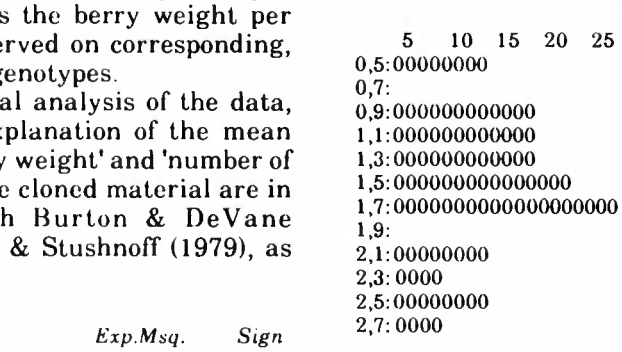

Fig. 1. Frequency (%) distribution for berry weight (gram/ berry) among genotypes of the Andøya population of *Rubus chamaemorus* L.

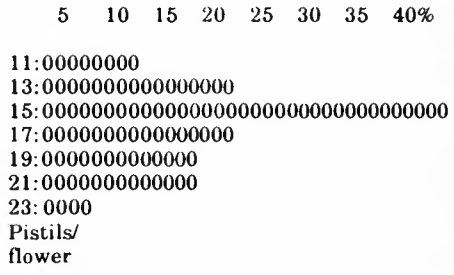

Figure 2. Frequency (%) distribution for number of pistils per flower among genotypes of the Andøya population of *Rubus chamaemorus* L.

and 1.9 g classes. For number of pistils, the 15 pistils class is fairly high.

Estimated components of phenotypic variance (Vp), genotypic variance (Vg), and environmental variance (Ve), and the broad sense heritability estimated (h^2b) for berry weight and number of pistils per flower are given in Table 1. The phenotypic variabilities among genotypes (clones) within populations are statistically significant ($P < 0.001$) for berry weight and number of pistils per flower. The broad sense heritability is estimated as higher ($h^2b = 0.91$) for number of pistils than for berry weight ($h^2b = 0.31$) per flower (Table 1).

The present data, especially the heritability estimates, indicate that the characteristic berry weight is much more influenced by environmental conditions than the character number of pistils per flower. In addition, in parent-offspring research on *Rubus*, the heritability is found relatively low for berry weight (Caldwell & Moore 1982). Environmental factors such as air temperature, rain, and wind in some years may disturb the pollination by insects and accordingly destroy the berry crop, whereas the number of pistils per flower usually remains unaffected. In red raspberry too, it is found that environmental factors have a great influence on fruit size (Moore et al. 1970).

A correlation coefficient calculated between berry weight and number of pistils per flower for corresponding genotypes gave ($r = 0.14^{(ns)}$). This coefficient is good proof that a selection for berry weight in the present material mostly have chosen quite other genotypes than a selection for number of pistils per flower. Accordingly, these two selection criteria will give different expectations for an increased productivity.

Table 1. Phenotypic-(Vp), genotypic-(Vg), and environmental- (Ve) variance components, and the broad sense heritability (h^2b) estimated from the ANOVA for berry weight and number of pistils per flower among clones of *Rubus chamaemorus*

Item	Number of genotypes	Vp	Vg	Ve	h^2b
Berry weight	36	38,95***	6,05	26,85	0,31
Pistils	36	24,64***	11,22	2,2	0,91

*** Significant at the 0.001% level

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NUTRIENT LEACHING AND SURFACE RUNOFF IN FIELD LYSIMETERS ON A CULTIVATED SOIL. NUTRIENT BALANCES 1974-81

GOTFRED UHLEN
Department of Soil Sciences, Agricultural University of Norway, Aas, Norway

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12 field lysimeter plots, each 75 m^2, with 4.5% slope, are given varying fertilizer treatments and planted with different crops.
Surface runoff coming mainly from snowmelt has a high content of total-P, PO_4-P, NH_4-N and K, whereas considerable losses of NO_3-N, Cl, SO_4-S together with Ca, Mg and Na occur in late autumn drainage.
Total balances are given, and also differences in relation to the figures for unfertilized spring grain. Of the added inorganic N, 40-45% is immobilized in soil organic matter according to the total-N (and-C) analysis. Another 37-48% is removed with the grain and row crop harvests. Leaching of N increases after surplus applications. However, the greatest impact is caused by cropping systems and varying weather conditions.
Large negative balances are registered for K, owing to plant uptake, and for Ca, Mg and Na, owing to heavy leaching losses.
Cl in crops and runoffs equals additions, whereas only half of the S added is accounted for.

Key words: Water use, chemical composition of surface runoff and drainage water, N-immobilization. P-, Cl-, S- and cation balances.

Gotfred Uhlen, Department of Soil Sciences, Agricultural University of Norway, P.O. Box 28, N-1432 Aas-NLH, Norway

The results for the first 3-5 years from two field lysimeter experiments on sloping land at Ås, Norway, have been reported earlier (Uhlen 1978a, b, c). Measurements of surface runoff drainage water continued to be taken for 8 years on 12 subplots with 4.5% slope in experiment II. In this report nutrient balances are also dealt with in relation to topsoil chemical analysis.

MATERIALS AND METHODS

The field lysimeters were constructed in 1973 on sloping cultivated land at Ås, Norway. The soil of the area is loam of glacial deposits high in organic matter (3% C). The clay content of the topsoil was found to be 20-25%, and that of the subsoil 30-40%.

From the 12 subplots, each 20 m x 3.75 m, surface and drainage runoffs were collected and measured in individual containers (1.2 m^3), from which representative samples could be drawn. The surface runoffs were caught in 3.75 m long gutters made from 160 mm polyvinyl chloride tubes. The gutters were

connected to the plot surfaces by 35 mm plastic strips.

In order to catch the percolating water, double 0.06 mm polyethylene sheets were placed at 90 cm depths and on the side walls of each plot. Two 50 mm drain tubes, length 20 m respectively, were placed on the polyethylene sheets. For this operation the subsoil and the topsoil were pushed aside, which of course disturbed the natural soil profile. To reduce variability between plots, the topsoil from the whole area was thoroughly mixed before it was replaced. The treatments comprised different cropping systems as follows:

A Clean fallow, 1 plot
B Continuous spring cereals, 5 plots
C Perennial grassland, 3 plots
D Row crops, interrupted by 2-year clovergrass hay, 3 plots.

The crop sequence in D was two years of potatoes, one year of fodder rape, two years of clovergrass, one year each of potatoes, marrow stem and potatoes. Furthermore, one of the three plots in D was left without crops in 1980 and 1981.

The plots within the cropping systems were given different fertilizer or manure treatments (Table 1). One of the spring cereal plots received large doses of domestic sludge during the first 2 years of the experimental period. Farm manure was applied off-season on 2 plots (row crop and grassland) during the first 3-4 years in order that the effect of winter-spread manure on water pollution might be investigated (Uhlen 1978b). The exact quantities of added nutrients can be seen from the input-output figures in the tables. The treatment combinations for the 12 individual plots are listed in Table 1. The fertilizer in most cases was a complex NPK type (20-5-9), or on some plots , ammonium nitrate limestone, superphosphate, potassium chloride or potassium sulphate. After the first cut, calcium nitrate was used on grassland plots.

Field operations on the plots were carried out using tractor and ordinary farm implements.

The chemical analyses of water and plant samples were carried out according to standard methods at the Chemical Analytical Laboratory, Agricultural University of Norway, and the soil analyses were carried out at the State Soil Investigation Laboratory.

It should be noted that no real replications of treatments were carried out. However, moderate and high fertilizer rates were used in the three cropping systems, and, furthermore, regression analyses between nutrient balances and soil analytical figures helped in assessing the reliability of the results.

Precipitation and air temperature were recorded daily at a station 100 m from the experimental site. The average annual precipitation Jan. 1 to Dec. 31 amounted to 771 mm for the 8-year period, a figure very close to the 30-year normal of 785 mm for the period 1930-60 at Ås. At the main meteorological station at Ås the average precipitation for 1974-81 was only 721 mm. The difference of 50 mm could seem to be due to the incidence of more snow and rain during winter at the experimental site.

RESULTS AND DISCUSSION

Crop yield and water runoff

The average crop yields for the 8-year period (Table 1) were somewhat below the normal yields for small grain, owing to poor yields in 1975 and 1976. The hay yields, on the other hand, were somewhat above average for the district. The highest level of inorganic fertilizer (2) did not increase the grain yields, and the effect on the yields of grasses and row crops was also relatively small. It should be noted, however, that these high levels of fertilizers (2) were chosen to represent excessive applications of plant nutrients.

Table 1..Treatments, crop yields and runoffs for individual plots. Average pr year 1974-81. Yield in dry matter, tons pr hectare

Crop system	Fallow	Spring grain					Row crops + ley			Perennial grass		
Plot No	10	6	4	3	5	2	8	9	7	13	11	12
Fertilizer[1]	0	0	1	1	2	2	1	1	2	1	1	2
Organic Manure				+				+			+	
Yields 1[2]		2.3	3.6	3.9	3.4	3.7	6.2	7.0	7.0	6.0	5.9	6.3
2		1.9	3.5	3.9	4.1	4.1				2.1	2.2	3.0
Runoffs, mm												
Surface	172	164	165	130	146	157	175	152	169	184	153	137
Drainage	262	254	228	247	251	275	201	224	193	199	198	196

1) Fertilizer 1 in kilograms pr hectare and year:

For	small grain (75)	100 kg N,	25 kg P	and 50	kg K
"	row crop	100 kg ",	25 kg "	100	kg "
"	grassland	150 kg ",	25 kg "	100	kg "

Fertilizer 2 contains in most cases the amount double of those of the elements in 1. Organic manure for small grain (plot 3) was sewage sludge, applied in 1974-76, totalling 200 tons per ha and for row crops (plot 9) and grassland (plot 11) 200 and 100 tons respectively farm manure pr ha, applied 1974-77.

2) Yields 1 and 2 represent grain and straw yields respectively for spring grain and the first and second cuts respectively for perennial grassland, during the season.

Table 1 gives the average annual runoff in millimetres of surface and drainage water for each plot, and in Fig. 1 the runoffs for each month of the year are shown. This figure includes data for Nov. 1971-Dec. 1973 from another field lysimeter experiment. The figure represents, therefore, 10 years of arable cropping, fallow and grassland.

The freezing conditions during winter together with the depth of the snow layer have a great impact upon the amount of surface runoff during snowmelt. As can be seen from the figure, the main part of the annual surface runoff occurred in March-April. The freezing of the soil may start in Nov.-Dec. interrupted by mild and rainy days which cause some surface runoff during this period also. Heavy rainstorms occasionally give surface runoff from arable land, in summer too.

The main part of the runoff through the tile drains took place in Oct.-Nov. before freezing. In some years the snow may have fallen in large amounts on unfrozen soil, causing an increase in drain water instead of surface water upon melting in March-April the following season.

The total water use per year may be calculated as the difference between precipitation and total runoff for the 8-year period, assuming that no other losses of water from the system occur. Furthermore, because of varying water storage, for instance in the form of snow, the period Nov. 1-Oct. 31 is preferred instead of the calendar year. The results of these calculations are given in Table 2.

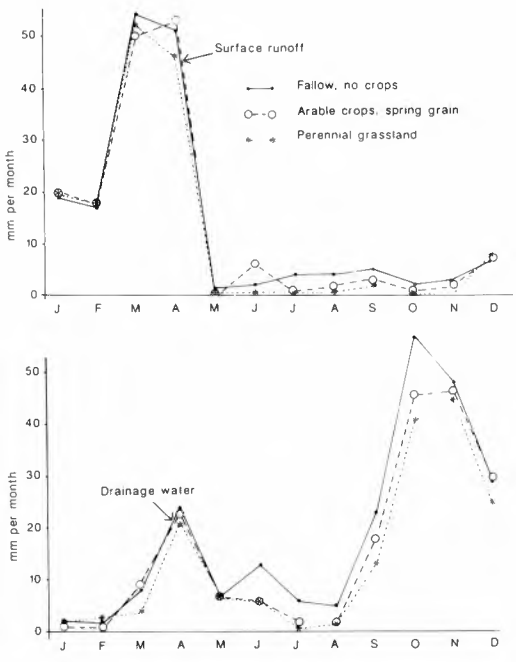

Figure 1. Surface and drainage water runoff in field lysimeters. Average per month 1972-81

The calculation in Table 2 demonstrates the fact that high rainfall in the summer months causes high water use. In the dry summers, especially the summer of 1976, there was a shortage of water for evaporation as well as for plant use, resulting in much less of a difference between precipitation and water runoff for the whole year. The high figures for water use in the later years could partly have been explained by high yields. However, some leakages and error in collecting the runoff water should not be ruled out. As expected, grassland used somewhat more water than spring grain, whereas less water was used on the one plot without vegetation. As can be seen from Table 1 the runoff figures vary a good deal from plot to plot. In addition to the effect of differences in crop yields and reduced surface runoff due to organic amendments (Uhlen 1978a) differences in the snow layers might also be responsible for such variations.

Chemical composition of surface and drainage water

The average contents of the different elements in the collected surface runoff and drainage water are given in Table 3. For most of the elements the drainage water contained the greater part of the total runoff losses. This was the case for NO_3-N Cl, SO_4-S and for the cations Ca, Mg and Na also.

The runoff losses of phosphorus took place mainly as surface runoff. The difference between tot-P and PO_4-P is due to P in soil particles. As reported earlier (Uhlen 1978a), considerable erosion losses occurred in 1974, owing to abnormal

Table 2. Precipitation and water uses in mm for for the individual years

	1974	1975	1976	1977	1978	1979	1980	1981	Average
Precipitation									
Nov 1 - Oct 31	895	700	595	755	828	713	897	695	760
May 1 - Aug 31	265	149	102	228	256	277	308	281	233
Water uses = Precipitation ÷ runoffs Nov 1 - Oct 31									
Spring grain, 3 plots	342	331	276	294	410	437	422	443	369
Grassland, 3 plots	393	345	285	312	416	438	474	448	389
Fallow, 1 plot	333	302	239	225	397	377	412	348	329

Table 3. Concentrations of elements in surface (S) and drainage water (D). Milligrams per litre. Averages for 1975-81

Crop		Fallow	Spring grain					Row crops 2 yrs ley			Perennial grass		
Plot No		10	6	4	3	5	2	8	9	7	13	11	12
NO_3-N	S	1.25	.88	.97	1.01	1.01	1.08	.95	.75	1.25	.59	.67	.73
	D	31.2	8.2	14.5	19.6	21.9	22.0	15.1	27.0	23.5	6.5	6.6	16.2
NH_4-N	S	1.10	.79	.81	.90	.98	.93	1.14	8.77	1.11	1.17	1.56	2.27
	D	.12	.10	.09	.11	.09	.10	.11	.10	.11	.11	.10	.11
PO_4-P	S	.10	.07	.07	.07	.08	.07	.14	1.73	.15	.26	.60	.56
	D	.02	.03	.03	.03	.02	.02	.02	.03	.03	.02	.03	.02
Tot-P	S	.25	.24	.17	.14	.21	.16	.21	2.51	.22	.32	.76	.67
	D	.07	.07	.06	.07	.06	.07	.08	.08	.07	.07	.08	.05
Cl	S	2.2	1.9	1.9	1.7	2.0	2.2	2.4	10.8	2.8	3.7	3.7	4.4
	D	3.7	3.3	15.0	12.0	19.5	22.2	14.4	13.6	22.0	12.3	15.2	27.8
SO_4-S	S	2.1	2.0	1.8	1.5	1.8	1.5	2.3	3.5	3.0	2.0	2.9	3.3
	D	8.3	7.5	9.3	11.9	8.2	10.1	14.9	13.0	20.0	6.0	8.9	13.9
K	S	2.1	1.5	1.5	1.3	2.0	2.0	3.7	16.8	3.7	5.3	6.7	6.2
	D	1.8	1.2	1.2	1.2	1.4	1.0	1.4	1.4	1.6	1.3	1.1	1.4
Na	S	1.0	.9	.9	.8	.8	.8	.8	5.7	1.0	.9	1.1	.9
	D	5.8	5.2	8.4	7.8	7.8	8.9	6.4	8.6	8.4	4.9	6.2	6.4
Ca	S	2.6	2.7	2.1	2.3	2.0	1.9	3.4	6.2	4.5	2.4	3.2	4.0
	D	42.0	19.9	31.1	25.9	38.5	37.3	36.5	45.8	51.0	19.5	24.0	41.9
Mg	S	1.0	.9	.6	.5	.7	.5	.7	1.7	1.0	.6	.7	.6
	D	10.2	5.3	10.0	12.5	11.0	15.3	9.1	12.9	13.4	4.7	5.8	10.1

weather conditions as well as to the to relatively loose soil in the first year of the experiment. That year is therefore not included in Table 3, also the grass crop was first established in 1975.

The NH_4-N concentration was higher in surface than in drainage waters. This can be explained by the fact that ammonium is nitrified in the soil profile. The K content was also lower in drainage than in surface water. The potassium ions appeared to be firmly held in this illitic clay soil, and it was demonstrated that the exchangeable K, measured by the neutral ammonium acetate method, was less mobile in the soil solution than exchangeable Mg, while in the

subsoil it was even less soluble than the exchangeable Ca (Uhlen 1978a).

The relatively high content of P, NH_4-N, K and Cl in surface runoff from plot 9 was as a consequence of application of farmyard manure on frozen snow-covered ground. It should also be noted, that surface runoff from grassland had an increased content of P, K and NH_4-N owing to leaching from crop residues.

Nutrient balances

Nitrogen

Table 4 showes the 8-year additions and withdrawals of nitrogen in kilograms N pr hectare for the 12 individual plots. The total balance for each plot also includes 5 kg N/ha/year in precipitation. The nitrogen in harvested clover was subtracted, based on the assumption that nitrogen fixation equalled the nitrogen amounts in the above-ground crop of clover. This is only a rough estimate, since the amount of nitrogen fixed by clover has not been investigated.

The total nitrogen in the plough layer, 0-20 cm, was determined in about 10-15 subsamples per plot. In this way rather reliable estimates of the nitrogen quantities per hectare were obtained for the 12 plots. The mixing of the plough-layer soil on the site before the start of the experiment no doubt reduced the variation in the soil parameters. As is seen in Fig. 2 the differences in soil nitrogen correlate well with the calculated nitrogen balances, and the standard deviations from the regression line were ± 160 kg N per hectare.

An attempt was made to calculate the differences in input and output of nitrogen relative to the figures obtained for the spring grain plot without nitro-

Table 4 Nitrogen balances 1974-81. Kilogram nitrogen pr ha. Sum 8 years

Crop	Fallow	Spring grain					Row crops + 2 yrs ley			Perennial grass		
Plot No	10	6	4	3	5	2	8	9	7	13	11	12
N added	0	0	825	775	1450	1500	800	500	1600	1100	1100	2150
+ Org. N				+1433		+60		+933			+444	
		+ 40 kg N in precipitation. Sum 8 years										
N in crop	0	337	699	821	880	918	722	648	979	1056	1163	1571
N clover							126	150	126	60	30	40
N leached	783	243	293	453	471	509	347	688	470	157	160	313
N-balance (Clover excluded)	÷743	÷540	÷127	+974	+139	+173	÷229	+137	+191	÷73	+261	+306
		In topsoil 0-20 cm. Tons per hectare (2250 tons dry soil)										
Tot-N	5.40	5.58	5.92	6.78	6.19	6.28	5.92	6.23	6.30	6.13	6.18	6.33
Tot-C	68	70	73	79	74	75	76	81	80	76	78	78
		Per cent recovery of added N relative to plot No 6										
In crops		-	44	22	37	37	48	22	40	65	54	57
Leached N		-	6	10	16	17	13	31	14	(÷8)	(÷5)	3
N 0-20 cm		-	41	54	42	45	42	45	45	50	39	35
Total recovery		-	91	86	95	99	103	98	99	107	88	95

gen fertilizer. The calculated total balance for 8 years on this plot was 540 kg. nitrogen per hectare, versus 743 kg for the fallow plot with no nitrogen. The total nitrogen in the topsoil layer in 1981 was, however, 180 kg less in the latter case.

By the differential calculations the utilization of added N in fertilizer was 37-48% for spring grain and row crops and somewhat higher for grass crops. The crop uptake of the nitrogen added in organic amendments was very low in this experiment.

Leaching losses of nitrate varied considerably from year to year and were especially high during the first 3 years, as demonstrated by the following figures for two spring grain plots (in kg/ha). *See table at the bottom on the page.*

The high losses in 1974 resulted from the cultivation without plants in 1973. Dry weather and very small yields of grain in 1975 and 1976 explain the high leaching losses in these two years.

The additional leaching losses of nitrogen, mainly as nitrates in drainage water, amounted to 6% for the moderate rate, and 16-17% for the excess nitrogen application to spring grain. The losses from the row crop plots were somewhat greater, whereas leaching from the moderately fertilized grass plots was even less than from the unfertilized grain. The high figure for nitrogen leached from the row crop plot with manure (Plot 9) needs additional explanation. On this plot large amounts of farm manure were applied off-season in 1974-77. Heavy surface runoff losses of ammonium nitrogen occurred during snowmelt, especially in 1977 (Uhlen 1978b). In 1980 and 1981 the same plot (No.9) was left without vegetation, causing a total leaching loss of nitrogen of 200 kg per hectare for the two years.

The results reported in Table 4 and

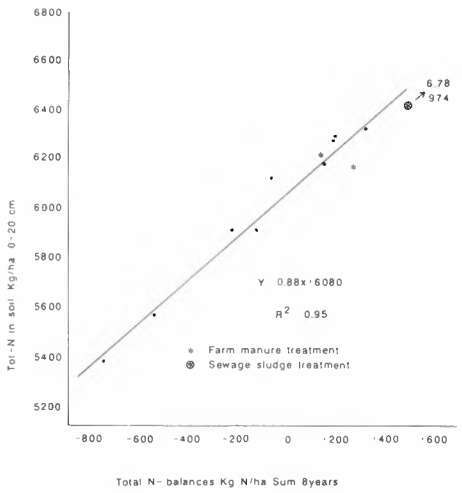

Figure 2. Tot-N in top soil 0-20 cm in relation to calculated N-balances. 1974-81

Fig. 2 indicate that 40-45% of the nitrogen applied as inorganic fertilizer during the 8 years remained in the topsoil. Some of this nitrogen could have been interlattically fixed ammonium; however, the greater part was in organic compounds as shown by the corresponding changes in organic carbon (Table 4). There was a tendency toward a decreased carbon-nitrogen ratio following increased N application and an increased ratio after farm manure (plots 9 and 13).

The amounts of nitrogen in the 0-20 cm layer were calculated on the basis of 1.125 kg dry soil per litre. If 1 kg/l had been chosen, the percentages of added N recovered in the topsoil would have been correspondingly reduced. Other sources of error in the differential calculation may have been differences in mineral nitrogen content, mainly nitrate, in the 20-90 cm layers at the end of the experimen-

	1974	1975	1976	1977	1978	1979	1980	1981
No fertilizer	48	40	42	18	14	18	15	10
100 kg N + PK	37	56	94	28	13	17	13	10

tal period. The analyses of the last set of samples of drainage water in 1981, revealed that the nitrate content in the deep layers was higher in the fallow plots (9 and 10) than in cropped soil. However, such differences can account for only a few percent of the added nitrogen.

The sum of the nitrogen recovered in crops, in runoff and in the topsoil layers came rather close to 100%, indicating small gaseous losses of fertilizer nitrogen. The lower nitrogen recovery on the plot with sludge and one of those with farm manure, could have been due to experimental error, although other explanations might apply. Finally, it should be borne in mind that relatively small differences in added nitrogen attributable to denitrification do not rule out some denitrification independent of the amount of added nitrogen. A comparison of total nitrogen in the top soil in 1981 and in 1974 was not possible as only a few soil samples were taken in 1974.

The main finding in this experiment was that nearly half of the nitrogen annually added as inorganic fertilizers was immobilized in plant residues or microorganisms and existed in organic form in the topsoil layer at the end of the 8 years.

A rapid and substantial microbial immobilization of added inorganic nitrogen has been demonstrated in great many investigations (Bobritskaya et al. 1975, Bakken 1982, Nielsen & Jensen 1986). Bakken (1982), working with soil from the field lysimeter experiment dealt with in this publication, found 35-50 % of nitrogen added as organic nitrogen after a 2-year period, however, only 6-12% of the nitrogen added was found in the microbiomass owing to rapid turnover rates.

The mineralization rate of the immobilized nitrogen is important. Based on long-term Norwegian fertilizer experiments of 8, 12, 30 and 50 years duration, a half life of 15-20 years was estimated for the organic nitrogen in soil derived from inorganic fertilizer (Uhlen 1986).

Phosphorus

The total balance of phosphorus in the soil is of little direct importance to the phosphorus availability to plants. Most of the phosphorus applied will be fixed in the soil. Leaching through the soil will generally be of very little consequence; however, some phosphorus may be lost through surface runoff and erosion.

From Table 5 it can be calculated that the additional uptake of phosphorus on P-fertilized plots compared with the non-fertilized plots (6 and 13) amounted to about 10% of the added P. The total P-balances were positive on all plots with added phosphorus. Fertilization did not increase the amount of P in drainage. Increased phosphorus losses in runoff following winter spreading of manure on snow and frozen soil have been demonstrated (Uhlen 1978b). Furthermore it was found in this investigation that grass residues and P-fertilizer led to a slight increase in the P concentration in the surface runoff water during snowmelt on grassland plots (Uhlen 1989).

The phosphorus status of the soils was assessed by means of an ammonium lactate-acetate extraction of easily soluble phosphorus, according to Egner et. al (1960). Fig.3 shows the relationship between the phosphorus balances and the easily soluble P in 1981 expressed in kilograms per hectare of the topsoil layer. The plot with the large P application of domestic sludge is not included in the calculated regression. The amount of easily/soluble phosphorus is strongly buffered against the changes in output as well as input of phosphorus. A 100 kg P excess in P-balance increased the P-Al by only 25-30 kg in the plough layer. The same relationship holds true in phosphorus shortage situations. These results agree with many other investigations of easily/soluble and available phosphorus in Norwegian soils, for instance Uhlen & Steenberg (1982).

Table 5. Phosphorus, sulphur and chlorine balances. Kilograms pr ha. Sum 8 years

Crop	Fallow	Spring grain					Row crops + 2 yrs ley			Perennial grass		
Plot No	10	6	4	3	5	2	8	9	7	13	11	12
P added	0	0	219	1238	359	390	194	395	415	0	257	388
P in crops	0	90	116	145	118	132	120	102	142	150	171	197
P runoffs	12.3	7.0	5.0	3.6	4.7	4.6	6.8	30.7	5.5	7.6	12.5	9.0
P-balance	÷12.3	÷97	+98	+1090	+236	+253	+67	+262	+267	÷158	+73	+182
S added	0	0	117	371	165	204	394	302	757	4	248	524
S in crops	0	43	66	83	79	82	111	65	149	92	101	120
S runoffs	213	189	204	310	210	267	276	289	335	147	193	261
S-balance*	÷133	÷152	÷73	+58	÷44	÷65	+87	+28	+353	÷155	+34	+223
Tot-S 0-20 cm in soil	715	704	737	836	770	715	803	858	825	726	836	836
Cl added	0	0	388	352	628	778	401	513	722	935	1029	1521
Cl in crops	0	46	240	238	345	368	284	269	438	764	794	967
Cl runoffs	121	107	294	249	425	536	240	358	341	272	335	513
Cl-balance[1)]	÷61	÷93	÷86	÷75	÷82	÷66	÷63	÷54	+3	÷41	÷40	+99
	Per cent recovery of added Cl, relative to plot 6											
In crops		-	50	55	48	44	59	43	54	77	73	61
Leached		-	48	40	50	55	33	49	32	18	22	27

* The balance includes 10 kg S and 7.5 kg Cl per annem in precipitation. The amount of phosphorus in precipitation is assumed to be neglictible for balance calculations. P in runoffs based on tot-P determinations. The large amount of P in runoff from plot No 9 was caused by farm manure surface applied in winter.

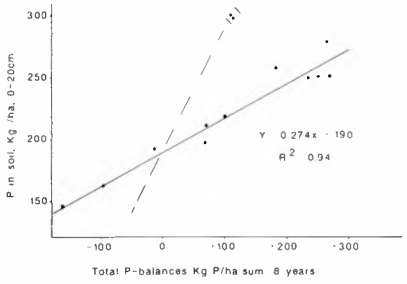

Figure 3. Easily soluble phosphorus (P-AL) in soil in relation to calculated P-balances 1974-81

Sulphur and chlorine

S and Cl in precipitation were also included in the balance calculations. Positive balances of sulphur were found on plots which received large applications of S in organic or inorganic fertilizers. Superphosphate with 12% S was used on the grassland plots; potassium sulphate was applied to potatoes instead of potassium chloride. Two to four times more S was removed in the runoff than taken up by the crops.

An attempt was made to measure the added sulphur left in the topsoil layer. The fate of the added sulphur, measured as the difference between the fertilized and the non-fertilized plots (6, 10 and 13), was as follows in percentage of added sulphur: increased uptake 15%, increased leaching 15%, and increase in total S in the topsoil layer 23%. About

one half of the amount added could not be accounted for. The explanation for this residual sulphur might be fixation of sulphate ions in the deeper layer of the soil (20-90 cm).

In an earlier work of Ødelien (1965) an acid ammonium acetate extraction was employed to assess the sulphur status of soils. Relatively good recovery of applied sulphate was found by extraction shortly after incorporation; however, after some time part of the sulphate became unextractable. In the field lysimeters it was further shown, that the leaching of sulphate was somewhat delayed compared with the leaching of nitrate and chloride (Uhlen 1978c).

In contrast to sulphate and nitrate the recovery of added chloride in crops plus runoffs was nearly 100%, based on comparison between the with and without treatments. In grain plots about 50% of the total amount of chloride added in 8 years appeared in the crops, and the other half was leached out. Large amounts of Cl were taken up by hay crops, leaving less Cl ions for leaching. The total loss of Cl was somewhat higher for the non-fertilized spring grain than for the fallow plot. By using the fallow plot as the control, recoveries slightly above 100% were obtained for the grain plots. The small positive balance figures for the grass plot after a high rate of Cl-addition (plot 12), and likewise after high rates of potassium chloride added to fodder rape (plot 7), can partly be explained by the fact that some of the chloride was left in the soil. The last sample of drainage water taken in 1981 from plot 12 contained 15-20 mg more Cl per litre than drainage from the unfertilized plots. The total water content at field capacity in 0-90 cm was about 350 mm (Uhlen 1978c). If all the soil water had had the same Cl content the extra Cl in plot 12 soil would have been 60 kg per hectare, or 4% of the Cl added to this plot.

The conclusion drawn with regard to the leaching losses and balances of the other elements is supported by the Cl-balance calculation. Fixation of Cl did not take place. Since leaching and crop recovery account for all added Cl, it is reasoned that the leaching figures for nitrogen and sulphur are reliable also.

Potassium, sodium, calcium and magnesium

In spite of relatively high application rates of potassium, the K-balances were negative for all the plots (Table 6). The grass crops in particular took up large quantities of potassium. The total losses of K in surface and drainage waters were rather small, and were not increased by K-applications in inorganic fertilizers. Winter spreading of farm manure gave high surface runoff of potassium during snowmelt (plot 9).

In soil samples from the 0-20 cm topsoil layer exchangeable K, K- AL according to Egner et. al (1960) and acid-soluble K according to Reitemeier (1951) ($K\text{-}HNO_3$) were determined. The AL-extraction gave practically the same values as exchangeable K in neutral ammonium acetate.

Both exchangeable K and acid-soluble K were correlated with the calculated negative K-balances as shown in Fig.4. However, these correlations were not as close as those found for the easily soluble P in soil relative to the P-balances. The regression coefficients demonstrate the fact that 10 and 50% of the actual K-balances were recovered as exchangeable and acid—soluble K, respectively. The results can be explained by the steady release and absorption of potassium in the soil.

The sodium balances were, with one exception, negative, mainly owing to the relatively high leaching losses. The sodium in the fertilizers was not more than the estimated amount in precipitation, 5 kg Na year/ha. The total removal in the crops was, however, only 25-50% of the Na added in fertilizer and precipitation.

As was expected, the calcium and

Table 6. Potassium, sodium, calcium and magnesium balances. Kilogram pr. ha. Sum 8 years

Crop	Fallow	Spring grain					Row crops + 2 yrs ley			Perennial grass		
Plot No	10	6	4	3	5	2	8	9	7	13	11	12
K added	0	0	423	503	696	925	796	872	1442	991	1245	1591
K in crops	0	300	627	710	828	882	1262	862	1440	1700	1777	2080
K in runoffs	74	52	48	42	57	52	77	205	76	99	99	87
K balance*	÷66	÷344	÷244	÷241	÷181	÷1	÷535	÷187	÷66	÷800	÷623	÷568
	K in 0-20 cm, mg K/100 g dry soil											
K-exch.	14.2	13.1	14.0	13.3	17.3	19.0	12.0	14.9	17.3	13.0	14.7	15.3
K-HNO_3	95	91	92	90	102	108	90	98	101	85	90	90
Na added	0	0	24	48	30	36	24	129	60	24	127	60
Na in crops	0	9	27	39	29	33	16	12	22	17	16	20
Na in runoff	146	127	168	171	168	218	121	217	144	99	116	114
Na-balance*	÷106	÷96	÷131	÷122	÷127	÷175	÷73	÷60	÷66	÷52	+35	÷34
Ca added	0	0	262	1790	337	423	562	745	1165	501	1011	1760
Ca in crops	0	52	109	136	139	132	259	213	315	276	264	315
Ca in runoff	963	487	611	756	792	821	668	887	847	419	481	754
Ca-balance*	÷915	÷491	÷410	+946	÷546	÷482	÷317	÷307	+51	÷146	+314	+739
	Ca in 0-20 cm, mg Ca/100 g dry soil:											
Ca-exch.	106	119	115	157	101	114	122	130	121	132	140	132
pH (H_2O)	5.28	5.30	5.27	5.70	5.09	5.22	5.15	5.35	5.20	5.26	5.35	5.35
Mg added	0	0	40	407	76	89	21	132	60	10	82	26
Mg in crops	0	35	56	69	66	68	88	76	102	76	79	97
Mg in runoff	244	132	188	261	222	336	167	257	223	99	117	177
Mg-balance*	÷236	÷159	÷196	+85	÷207	÷307	÷226	÷193	÷257	÷157	÷106	÷240
	Mg in 0-20 cm, mg Mg/100 g dry soil:											
Mg-exch.	8.4	9.4	8.7	10.5	8.5	8.8	7.7	11.9	7.4	9.4	10.3	6.8

* In the balances are included 1 kg K, 5 kg Na, 6 kg Ca and 1 kg Mg pr ha and year in precipitation.

magnesium inputs and outputs revealed, the similarities between these two elements. Large negative balances followed the great leaching losses.The soil was not limed during the 8-year period and soil pH-values in 1981 showed that lime was needed in most of the plots. Positive balances were obtained after addition of sludge. With regard to Ca, positive balances also occured after high rates of fertilizer application to the grass crops and row crops + grass (plots 7 and 12, Table 6). On the grain plot a complex NPK fertilizer, low in Ca, was used in all years. The grassland and row crop plots were fertilized annually with ammonium nitrate limestone, containing 8-9% Ca, and superphosphate with 22% Ca. The complex fertilizer (D-20-5-9) contained 1.2% Mg and the ammonium nitrate, superphosphate and potassium salt contained less than .5%. For Ca and Mg no close correlations existed between calculated balances and the amount of

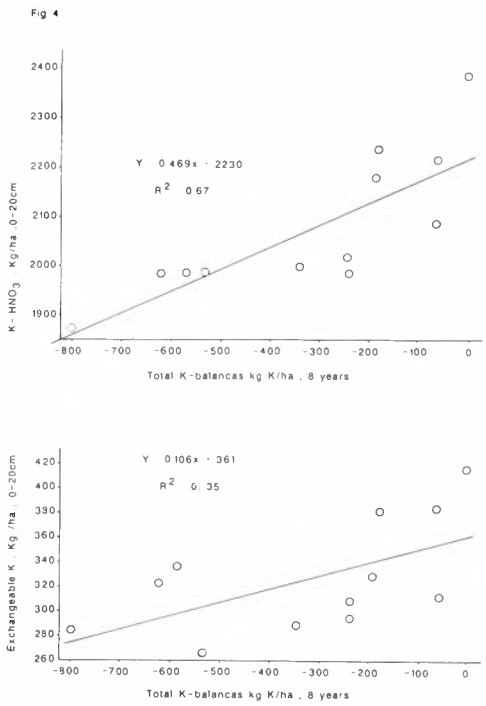

Figure 4. Acid soluble and exchangeable potassium in soil in relation to calculated K-balances 1974-81

exchangeable cations in the topsoil after 8 years. As is the case for K, the removed exchangeable Ca and Mg can be replaced by weathering processes in soil. Furthermore, we have to take into account the changes in the cationic composition in the leachate as it passes through the subsoil layers. Comparisons were made between leachate collected at a depth of 25 cm with that at 90 cm for 2 + 2 plots in 1974 and 1975 (Uhlen 1978a). These results displayed the fact that some K and Ca in the soil solution at 25 cm depths were replaced by Mg and Na as the leachates passed through the subsoil layer. The amount of exchangeable Mg and Na relative to K and Ca was higher in the subsoil than the topsoil. From this it can be deduced that the losses by leaching from the 0-25 cm layer were somewhat greater for Ca and K, and somewhat less for Mg and Na, than the composition of the final drainage at 90 cm seemed to indicate. It has also been demonstrated (Uhlen 1978c) that the cationic composition of the leachate varied with the ionic strength in accordance with the reduced activity ratio

$$\frac{(K + Na)}{\sqrt{(Ca + Mg)}}$$

It can be taken from this that the relative leaching losses of Ca and Mg increase more than the losses of K and Na following fertilizer salt application.

The total losses by leaching were determined by the excess of soluble anions, NO_3^-, Cl^-, SO_4^{2-} and HCO_3^- in the soil. The NH_4^+ from the ammonium nitrate is rapidly converted to nitrate, giving 2 H^+ per NH_4^+ added, and the H^+ replaces a basic cation on the exchangeable complex. The NO_3^- produced, if not utilized by the plants, causes additional leaching of equivalent quantities of cations. In this soil, heavy application of fertilizer resulted in large leaching losses of Ca and Mg, as these ions were the dominant exchangeable cations.

Owing to the complexity of the system, and the interchange between the cation species, no close correlation was expected between calculated cation balances and soil analysis of the top-soil layer.

SUMMARY

Nutrient balances were investigated over an 8-year period in field lysimeters on a loam soil rich in organic matter (20-25% clay, 3% organic C) at Ås, Norway. The experiment comprised 12 plots of 3.75 m x 20 m respectively on a 4.5% slope, all with different crops or fertilizer applications. Surface runoffs and drainage, collected by means of a polyethylene sheet placed at a depth of 90 cm, were measured continuously.

Average annual precipitation for the 8 years was 771 mm of which 159 and 227 mm were collected as surface runoff

and drainage respectively. The calculated water use was somewhat higher for grass than for spring grain and was lowest on a plot without vegetation. The water use decreased as a consequence of water shortage during the summer months in some years.

The surface runoff water, which originated mainly from snowmelt on frozen soil, showed a higher content of total-P, PO_4-P, NH_4-N and K than the drainage water. The greatest losses by leaching through the soil of NO_3-N, Cl, SO_4-S, Ca, Mg and Na took place in late autumn. The soil loss by erosion was rather small except in the first year of the experiment. Phosphorous and potassium fertilizer applications did not increase the leaching of these elements, whereas surplus application of ammonium nitrate led to a substantial increase in nitrate leaching from grass and especially from grain and row crops.

Total inputs and outputs were tabulated for all plots and differences in relation to such figures obtained on the unfertilized grain plot or the without-vegetation plot were calculated.

For nitrogen the additional uptake in crops + additional leaching + increased content of total nitrogen in the topsoil layer (0-20 cm), came to nearly 100% of the N added during the 8 years, indicating small gaseous losses of nitrogen. The nitrogen immobilized in organic form amounted to 40-45% of the fertilizer nitrogen; this percentage seemed to be rather independent of crop and fertilizer rates. The figures for total-N in the soil were highly correlated with the calculated N-balances ($R^2 = .95$).

Also for Cl about 100% of the amount added was accounted for in increased uptake in crops + increased leaching, whereas only 50% of the added SO_4-S was recovered in crops + leached SO_4-S + increased content of total-S in the topsoil. The rest of the S added was assumed to be retained in the 20-90 cm soil layers.

Only 10% of the added P was removed in the crops, and 25-30% of the residual phosphorus could be extracted from the soil by an ammonium lactate solution (P-AL-method).

Nutrient balances for the cations, K, Na, Ca and Mg, were predominantly negative. For K this was caused by the large uptake in the plants; the others were due to heavy leaching losses.

The contents of exchangeable K, Ca, Mg and acid-soluble K were correlated with the calculated nutrient balances for the same elements. However, owing to release processes in the soil, no exact relationship was expected between the input-output figures and exchangeable cation quantities in the topsoil layer after 8 years.

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SURFACE RUNOFF LOSSES OF PHOSPHORUS AND OTHER NUTRIENT ELEMENTS FROM FERTILIZED GRASSLAND

GOTFRED UHLEN
Department of Soil Sciences. Agricultural University of Norway, Aas, Norway

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Losses of phosphorus and other nutrients in surface snowmelt runoff are investigated in field lysimeters on sloping land over a period of 3-10 years. The P losses, mainly as PO_4-P, vary from less than .1 to 1.3 (1.9) kg per hectare per year, as determined by the following three factors:a) millimetre runoff during snowmelt, b) amount of grass residues left on the ground in the autumn, and c) fertilizer P in the previous years. R^2 = .86. Soil test P does not contribute significantly to the regression.

Phosphorus concentrations in the surface water showed a characteristic very high-low-high pattern during the snow- and ice melting period. Snowmelt runoff losses of NH_4-N, K and Cl, but not of NO_3-N, increase after fertilizer application of these elements the year before. The effect is, as in phosphorus, mainly indirect through increased levels in residual grass yields. Vegetable leaf mulch may cause heavy nutrient runoff in snow melt water.

Key words: Snowmelt, grass residues, nutrient losses

Gotfred Uhlen, Department of Soil Sciences. Agricultural University of Norway, P.O. Box 28, N-1432 Aas-NLH, Norway

Phosphorus additions are thought to play a key role in the eutrophication processes of many inland lakes in Norway. As has been demonstrated in a former publication (Uhlen 1989), the concentrations of soluble and particle-bound phosphorus tend to be much higher in the surface waters than in the drainage water from agricultural land, whereas the situation is quite the opposite with regard to the nitrogen runoff.

Rotational and perennial grasslands account for more than 50% of the agricultural areas in Norway. The runoff of phosphorus and other nutrients from grassland is therefore quite important. Furthermore, the extensive grass growing in many districts involves surface application of farm manure, a practice which implies an increased risk of nutrient runoff, especially if the manure is spread off-season (Uhlen 1978b). In field lysimeter experiments, relatively high phosphorus content was found in the surface water from grassland plots, with no farm manure top dressing. The aim of this investigation, therefore, was to measure the impact of fertilizers and grass residues on the losses of phosphorus and other nutrient elements in surface runoff, especially during the snowmelt period.

MATERIALS AND METHODS

Two field lysimeters were built on sloping land; No. I in 1971 with 9% slope, and No. II in 1973 with 4.5% slope. More information is given in earlier reports

Table 1. Phosphorus (PO_4-P) in surface runoff from grassland and spring grain. Kg/ha/year

	P in fertilizer	1975	1976	1977	1978	1979	1980	1981
Perennial grass	0	.31	.23	.34	.21	.30	1.17	.60
" "	48	.51	.42	.54	.14	.70	1.86	.68
" "	24 [1]	1.77	.31	.63	.02	.77	1.58	.70
Spring grain	0	.08	.06	.09	.06	.18	.16	.06
" "	24	.04	.08	.09	.04	.17	.17	.17
" "	48	.02	.08	.11	.05	.12	.24	.17
Drainage water	0	.06	.06	.03	.06	.07	.04	.03
(average for grass	24	.06	.07	.03	.04	.09	.05	.03
and grain plots)	48	.07	.06	.03	.04	.05	.04	.02

1) Additional P in farm manure in autumn 1974 and in spring 1979 on this plot.

(Uhlen 1978a and 1989). In the period 1974-81 only three of 13 plots in experiment II were used for perennial grassland. In 1982-83 grass crops were established on six of the plots formerly used for arable cropping in experiment No II. Likewise ley crops were established on five plots of the experiment I in 1981-82. A clover-timothy mixture was seeded in late spring, giving only a small crop the first year.

Yield figures will not be reported here; however, the hay crops, harvested twice each year, were large. Clover made up about one-third of the harvested crops on plots which received no nitrogen in spring. On plots with nitrogen fertilization, however, the proportion of clover in the hay crops was 10% or less.

The amount of grass residue, regrowth after the second cut, was measured in one microplot on each of the main plots in order to relate the phosphorus surface runoff to the phosphorus in the grass residue.

The fertilizer treatments are given in Table 2.

In experiments I and IIb phosphorus was spring-applied as superphosphate, 9% P. N additions as ammonium nitrate limestone, 26% N, or calcium nitrate, 15.5% N, and K as potassium chloride were applied twice per season. In experiment II a complex NPK fertilizer containing 20% N, 4,8% P and 9% K was used in spring, and all plots received additional N and K after the first cut.

Measurements of surface runoff from plots with spring grain ploughed in autumn were carried out on a few plots. Mulching with plant residues from vegetable crops and grasses was also tried out on single plots in 1983-84.

Soil erosion losses were rather small, also from arable land during snowmelt in all years. However, losses were measured during summer rainstorms in three years out of ten.

The chemical analysis of the runoff water was carried out according to standard methods. Water-soluble P, named PO_4-P, was determined by an ascorbic acid molybdenum blue procedure, and likewise total-P analyses were also made after drying and ashing.

RESULTS AND DISCUSSIONS

Phosphorus in surface runoffs

The surface runoff figures for soluble phosphorus (PO_4-P) from three grassland plots in the period 1975 to 1981 are given in Table 1. For comparison, corres-

Table 2. Phosphorus in surface runoff from grassland

	Exp. I 1982			Exp. II a 1983			Exp. II b 1975		
Fertilizer treatments in kg/year:									
P-added	0	24	48	0	24 *	48 *	0	24	48
N	175	175	175	50	150	250	150	150	300
K	150	150	150	50	100	150	150	150	300
Surface runoff mm:									
1983/84	212	175	176	164	204	209	175	150	162
1984/85	75	56	56	41	38	42	86	103	106
1985/86	240	223	240	237	248	241	217	201	208
Dry matter yields of grass residues in fall, tons/ha:									
Nov 1983	1.07	1.14	1.33	.57	.63	.52	1.31	1.83	3.74
" 1984	.54	.38	.49	.66	.75	.85	.86	1.02	1.68
" 1985	.69	.49	.59	1.09	1.31	2.73	1.92	2.08	3.03
P in grass residues - Kg/ha:									
Nov 1983	3.0	2.3	3.7	1.2	1.3	1.3	3.4	4.9	13.6
" 1984	1.1	.7	1.1	1.8	1.9	2.1	2.3	2.8	4.7
" 1985	1.4	1.2	1.5	2.8	3.5	8.5	4.1	4.0	10.1
PO_4P-runoff - Kg/ha:									
1983/84	.21	.23	.37	.16	.23	.33	.30	.51	1.26
1984/85	.09	.10	.19	.08	(.05)	.10	.10	.25	.49
1985/86	.22	.43	.71	.42	.54	1.06	.41	.45	.82
Average	.17	.25	.42	.22	.27	.50	.27	.40	.86
Tot-P-runoff - Kg/ha:									
1983/84	.27	.27	.42	.22	.30	.40	.34	.54	1.28
1984/85	.13	.14	.24	.11	(.08)	.13	.12	.30	.56
1985/86	.29	.52	.82	.52	.67	1.23	.55	.56	1.02
Average	.23	.31	.49	.28	.35	.59	.34	.47	.95

* In addition 5 and 10 kg P in NPK fertilizer applied after the second cut in 1985.

ponding figures were reported for the surface runoff from spring grain plots, and also some averages for the drainage water PO_4-P in the same years.

The amount of surface water runoff varied from year to year. This fact may partly explain the yearly variations in P-runoffs. As will be demonstrated later, the amount of grass residue left on the grassland in the autumn also had a great impact on the amount of phosphorus in surface runoff. Under the prevailing climatic conditions surface runoff was confined mainly to the snowmelt period. See Fig. 1 in the former paper (Uhlen 1989).

The losses of soluble P were much greater from grassland plots than from grain crop plots. Phosphorus addition in fertilizer increased runoff losses from grassland. In the surface runoff from arable plots, as well as in the drainage runoff from all plots, no effects of fertilizer applications on losses of PO_4-P were found. Heavy losses of soluble P after off-season farm manure application without incorporation, have been demonstrated in an earlier report (Uhlen 1978b).

The result from the three-year period 1983-86 are reported in Table 2. Relatively large surface runoff losses of phosphorus during winter and spring snowmelt were found in 1983-84 and in 1985-86. In 1984-85, however, the total amount of water as surface runoff was much less, resulting in lower P losses as well.

It is apparent from the figures in Table 2 that the phosphorus losses are determined by the following three factors:

1) Surface runoff water in mm during snowmelt

2) Grass residue, or the P-content of such residue, left on the ground in late autumn

3) Fertilizer application of phosphorus in the preceding years.

There was no surface runoff during summer and autumn before freezing of the soil.

Observations of 14 plots over 3 years resulted in the following calculated regression

$y = 1.62\,a + 2.05\,b + 4.51\,c + 6.4\,d - 266$. $R^2 = .86$

y = Total P-runoffs in g per ha per year
a = runoff during snowmelt, mm
b = g dry matter in grass residue per m^2 in autumn
c = kg P in fertilizer per ha in the preceding years
d = P-Al values in topsoil (mg P/100 g)

The impact of each of the first three factors was highly significant ($P < .001$), whereas the additional effect of factor d, easily soluble P, according to Egner et al. (1960), was insignificant.

The relationship between the calculated and observed values is shown in Fig. 1. The above equation may be used to calculate the effect of phosphorus fertilizer application upon the phosphorus runoff from grassland if the winter runoff, amount of grass residues, and P-fertilizer rates in the preceding year are known.

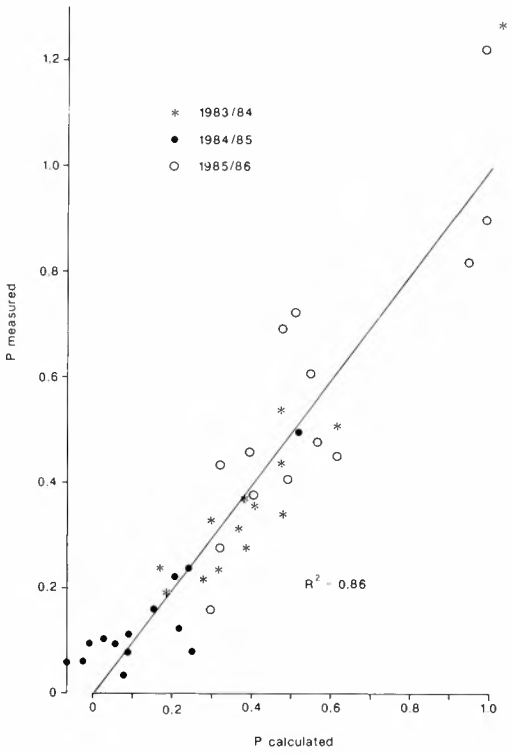

Figure 1. Phosphorus runoff from grassland plots. Kg tot-P per ha and year

From Table 2 it can be seen that the overall effect on the phosphorus runoff of the higher dose of P-fertilizer, 48 kg minus 24, is greater than that of the 24 kg

P rate of application. It is obvious, however, that this result may be explained by the higher yield of dry matter and phosphorus in grass residue after the 48 kg P treatment, especially in experiment IIb. In experiments IIa and b phosphorus treatments were combined with additional nitrogen rates and the higher residual grass yields were probably caused by the additional nitrogen. A phosphorus rate of 24 kg/ha/year is sufficient for maximum yields. Therefore, it is likely that on grassland higher rates of nitrogen as well as phosphorus fertilizer can lead to additional runoff of phosphorus during snowmelt.

The effects of fertilizer, and those of the amounts of grass residue left on the ground before winter, are further demonstrated in Figs. 2 and 3, which show the variations in P concentrations during the runoff periods in 1984 and 1985-86, respectively, for some of the treatments.

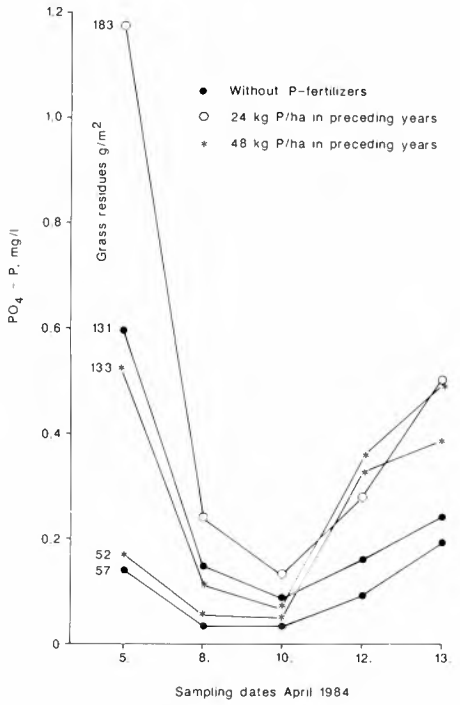

Figure 2. PO_4-P in snowmelt surface runoff from grassland 1984

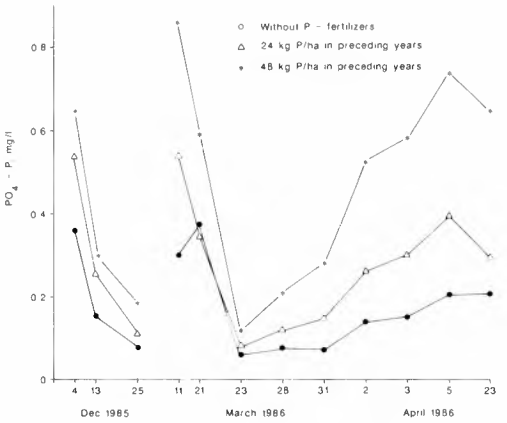

Figure 3. PO_4-P in snowmelt surface runoff from grassland 1985/86

The picture of the runoff of phosphorus and of other nutrients during snowmelt varied from year to year, as was also seen in earlier investigations (Uhlen 1978b). A high P-content at the outset of the snowmelt period was found in most cases.

It is shown, most clearly in 1984, that the phosphorus in the first runoffs was related strongly to the amount of grass residue, whereas the P-fertilizer rate had a greater impact in the later part of the runoff period.

The mechanism behind the liberation of phosphorus from plant residues upon freezing is, according to Heber (1967), the altering of permeability of biological membranes after frost, death and dehydration. Drying has been shown to greatly increase the leaching of phosphorus and nitrogen from plant materials (Timmons et al. 1970). Increased release of nutrients in runoff occurs especially if the plants are green at freezing (White 1973). An early study (Harley et al. 1951) showed that a large pro-

portion (78%) of the phosphorus in an orchard grass mulch was released by leaching with natural rain. The corresponding loss of nitrogen was much less (31-34%). Relatively greater losses of P than of N from plant residues have been demonstrated in many investigations (Uhlen 1979, Ulen 1984). The fate of the released P depends upon the amount of surface water leaving the field. In the present investigation, large quantities of surface water runoff occurred from snowmelt on frozen ground. In addition to the total amount of runoff water in mm per season, the number of runoffs per year were found to have a great impact on the total yearly losses from pastures (McLeod & Hegg 1984). Fig. 3 also indicates that new high peaks in phosphorus content in the runoff can likewise occur under shifting, freezing and thawing conditions during winter. Similar results were found in 1984-1985.

The results demonstrate the effect of P-fertilization on the phosphorus runoff from grassland in snowmelt water the following spring. According to the calculated regression, 4.5 g P was lost in runoff for each kg P added in fertilizer the preceding year. Sharpley & Syers (1976) found under field conditions in New Zealand a loss of 3.2% of added P as dissolved P in surface runoff from pasture in four months on a 13% undrained slope. The corresponding figure on a 6% drained slope was .7%. Soluble phosphorus surface runoff losses due to plant residues have been reported from U.S. studies (Rømkens et al. 1973, Barisas et al 1978, Wendt & Corey 1980). In Europe, surface runoff as well as soil erosion studies have so far gained little interest. Only a few grams of phosphorus per hectare in surface runoffs were found in a German experiment on grassland (Müller 1983).

Nitrogen, potassium and other elements in the surface runoff

In Table 3 average yearly runoffs of some elements other than phosphorus are given. It should be noted that in experiment I the applications of N, K and Cl were the same for all three treatments, as shown in Table 2. In experiment II the fertilization rates of N, K and Cl were varied. The Ca and S additions in the NPK-complex fertilizer were rather small, compared with the situation when superphosphate was used.

Increased rates of nitrogen fertilization increased NH_4-N in the surface runoff during snowmelt, whereas no effect upon NO_3-N was found. The explanation must be that the NH_4-N originates from breakdown of the plant residue. Nitrogen can be leached from dead plant tissue, although to a lesser degree than phosphorus, as already discussed. The sums of NH_4-N + NO_3-N come to 75-

Table 3. Nutrient elements in surface runoff from grassland

Fertilizer treatment	Kg/ha/year Average 3 years Exp I			Exp II a			Exp II b		
	$P_0N_2K_2$	$P_1N_2K_2$	$P_2N_2K_2$	$P_0N_1K_1$	$P_1N_2K_2$	$P_2N_3K_3$	$P_0N_2K_2$	$P_1N_2K_2$	$P_2N_3K_3$
NH_4-N	1.3	.9	1.0	1.4	1.8	2.5	1.7	1.6	3.3
NO_3-N	1.1	.8	.9	1.0	1.2	1.1	1.1	1.1	1.1
Tot-N	3.0	2.2	2.4	3.1	4.0	4.7	3.4	3.4	5.0
K	5.2	4.2	4.7	5.0	5.9	8.3	7.1	7.0	11.7
Cl	7.2	5.9	6.1	4.8	6.3	8.0	6.7	6.4	10.4
SO_4-S	2.7	2.5	3.4	2.2	2.8	2.8	2.5	3.3	3.7
Ca	4.1	4.5	5.1	7.1	5.9	4.9	3.6	4.1	5.2

80% of the total-N as determined by persulphate digestion.

The potassium and chloride contents of snowmelt surface water are also affected by K and Cl application. The explanation is most likely the same as for NH_4-N. Fertilizer additions have caused higher K and Cl contents of the herbage, and both elements are easily leached out of dead plant and other organic residues left on the ground (Uhlen, 1978b). Calculated as a percentage of the amount added in fertilizers, about 3% of K and Cl, 1% of N and less than 1% of P, were recovered in the winter runoffs.

Calcium and sulphur were added in normal superphosphate (9% P, 12% S, 22% Ca) in experiments I and IIb. The increases in SO_4-S and Ca in runoff during snowmelt may be explained by a delayed solvableness of gypsum particles left in the ground. Fig. 4 represents a

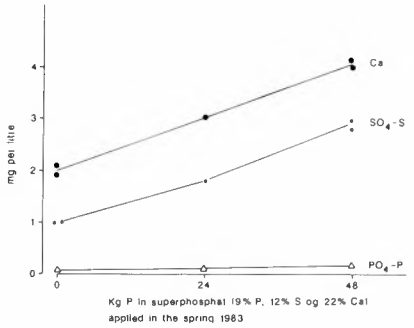

Figure 4. Ca, SO_4-S and PO_4-P in surface water runoff from grassland. January 1984

runoff episode in January 1984. The Ca and SO_4-S contents of snowmelt water were increased after applications of superphosphate in the preceding year, whereas the PO_4-P content was much less affected. The summer and autumn rains may have brought the water-soluble phosphorus into the soil, thus protecting it from the surface water. Somewhat more of the gypsum could have been left on the surface owing to the relatively low water- solubility of this salt.

The effects of mulching

The results reported here indicate that uncut grass residue left on the ground will give elevated runoff losses of phosphorus and other elements during winter and spring as long as the soil is frozen and no downward movement of water occurs.

On the other hand, grassland can give full protection against soil erosion. Under conditions of serious soil erosion hazard, the total losses of phosphorus in soil particles from arable land can be much greater than the losses of the more soluble P from grassland. Mulching, which covers the surface with plant residue, gives some protection aginst soil losses in surface water.

A simple trial on runoff plots in experiment II (4.5% slope) was carried out in 1983-84. Plant residues in the form of vegetable leaves (cauliflower, broccoli and carrots) were spread on one plot and hay (timothy + clover) on two other plots, Nov. 3rd 1983. The amount of dry matter in vegetable mulch was 1.9 tons per hectare, and of P, 9 kg per hectare. The grass mulch, 1.5 tons of dry matter per hectare, contained only 2.6 kg of P. The results are given in Table 4. The surface water from the vegetable leaf mulch plot had a much higher content of NH_4-N, P and K than the water from the control plot. Hay mulch did not increase NH_4-N and P in the surface runoff water in this trial, and the K -content was increased only a little. It should be borne in mind that replicates were not used in the trial, and the results may also have been influenced by earlier use of the plots. The high nitrate content of the surface runoff from the control plot could have resulted from the fact that this plot was without crops in the 1983 season. Nevertheless, since as much as one-tenth of the total-P in the vegetable leaf mulch was recovered in surface runoff, this trial points to the fact that different

Table 4. Nutrient surface runoff from mulched plots. Dec. 3 1983 - April 9 1984

	Surface runoff, mm	Runoff losses in kg/hectare					
		NH_4-N	NO_3-N	Tot-N	PO_4-P	Tot-P	K
a. Control	268	1.7	3.7	6.5	.15	.36	2.7
b. Vegetable leaf mulch	265	8.5	2.4	12.7	.63	1.26	16.9
c. Hay mulch	242	2.2	1.3	4.5	.16	.29	4.9

kinds of plant residues, left on the ground without incorporation, may cause pollution in the off season surface runoff.

SUMMARY

Losses of phosphorus and other nutrients in surface runoff during snowmelt were investigated in field lysimeters at Ås, Norway. On five grassland plots with 9% slope and on nine plots with 4.5% slope and given different rates of phosphorus and other nutrient additions, runoffs were measured for a three-year period. For three of the plots on permanent grassland, results from a 10-year period were available. Different types of mulch on arable land were also included on single plots in one season. Plot size was 20 m x 3.75 m. The runoffs were from frozen topsoil, and no drainage occurred during the snow melt in the years 1983-84 to 1985-86.

The phosphorus losses during 1983-86, mainly as PO_4-P, varied from less than .1 kg to 1.3 kg P per hectare and year, determined by the following three factors:

a) millimetre runoff during snowmelt (40-240 mm per season)

b) amount of grass residues, or P-content of such residues, left on the ground in late autumn, and

c) P-fertilizer regime in the preceding seasons (spring applied superphosphate and complex fertilizers).

Phosphorus soil test figures did not contribute significantly to improving the regression model for P-runoff (R^2 = .86).

The concentrations of PO_4-P in surface runoff were examined by frequent analysis during the runoff seasons. A very high P-concent in water at the outset of the snowmelt period was followed by low content after a few days. In the latter part of the melting of the snow and ice layers, the P-content rose again to a relatively high level. In the first snowmelt runoff water the P-content was primarily caused by grass residue P, whereas in the latter part, the P-content correlated more strongly with the P-fertilizer rates in the preceding years.

The runoff losses for NH_4-N, K and Cl, but not those for NO_3-N, were increased by fertilizer applications in the preceding years. The increases amounted to about 3% of the K and Cl added, versus 1% or less for N and P. However, since such effects are indirectly caused by the nutrients in plant residues, nitrogen fertilizers may lead to elevated runoff losses also of P and other elements. During the prevailing snowmelt runoff, conditions in south eastern Norway, plant residues left on the ground as mulch may increase the danger of water pollution.

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BARLEY-PEA MIXTURES FOR WHOLE CROP FORAGE. EFFECTS OF DIFFERENT CULTURAL PRACTICES ON YIELD AND QUALITY

TOR LUNNAN
Agricultural University of Norway, Department of Crop Science, Norway

Lunnan, T. 1989. Barley-pea mixtures for whole crop forage. Effects of different cultural practices on yield and quality. Norwegian Journal of Agricultural Sciences 3: 57-71. ISSN 0801-5241.

In this study it was found that barley germinates and developes leaf area faster than peas. The forage pea 'Timo' competes better with the barley than the white-flowered cultivars 'Bodil' and 'Tammi', but lodges heavily late in the growth period. Sowing in separate rows increases the 'Bodil' and 'Tammi' content of composite yields. A high proportion of peas in the seed mixture and late harvest improve the intercropping efficiency, expressed as Land Equivalent Ratio values. Barley separated from mixture plots has a higher protein content than barley grown in pure stand at the same N rates. Pea-rich mixtures increase the protein content of DM by about 5 %-units compared with pure barley. The amount of biologically fixed nitrogen is highest in monoculture peas, but appreciable quantities are fixed in the mixtures even at N rates of 80 kg ha-1.

Key words: Forage crops, intercropping, *Hordeum vulgare*, *Pisum sativum*, yields, quality, nitrogen fixation.

Tor Lunnan, Department of Crop Science, Agricultural University of Norway, P. O. Box 41, N-1432 Ås-NLH Norway

Green fodder mixtures such as oats (*Avena sativa* L.) with peas (*Pisum sativum* L.) have been grown in Scandinavia for a great many years (Hagerup 1927, Bengtsson 1966), while mixtures of barley (*Hordeum vulgare* L.) and fodder rape (*Brassica napus* L. ssp. *oleifera* Sinsk. f. *biennis*) have become popular in parts of Norway during recent years (Østgård 1983). Barley/fodder rape mixtures provide an alternative ensilage crop after successive severe winter damages to leys; they give stable yields with suitable dry matter content for ensiling, and utilize farmyard manure well. Mixtures with fodder rape or legumes such as peas, vetches (*Vicia sativa* L.) or field beans (*Vicia faba* L. var. *minor*) improve the quality of the barley forage. The object of the present experiments was to study the effects of plant densities of component crops, nitrogen fertilization, harvest times and spatial arrangement on yields and quality of mixtures of barley and different pea cultivars. The yield relationships between mixtures and monocultures were also examined.

MATERIALS AND METHODS

Two field experiments with barley and peas were carried out at the Vollebekk Experimental Farm at the Agricultural

University of Norway. The experiments in 1985 and 1987 were conducted on a silt loam, pH 6.2-6.5 and in 1986 on a silty clay loam, pH 5.8-5.9. The content of organic matter in both cases was 6-7%. The fields received a basal dressing of 48 kg P and 93 kg K per hectare. Some information about the plant materials used in the experiments is given in Table 1.

Light measurements were made five times in 1986 and seven times in 1987 using a LI-COR LI-1858 photometer with a photosynthetic active radiation (PAR) sensor. Light energy at ground level was measured as a percentage of incident energy above canopy. In addition, leaf area was measured six times in both 1986 and 1987 using a LI-COR LI-3000 leaf area meter.

The 1985 and 1987 seasons were favourable for forage plant growth with cool and moist weather (Table 2). In 1986 a wet May was followed by a very dry period in June-July. The drought stress led to low yields and early maturing, the peas suffering more than the barley.

Experiment 1

A factorial design (split-split-plot) with two replications was used with harvest times on the largest plots, nitrogen rates on the medium-sized plots and mixtures and pure stands of barley cv. 'Bamse' and

Table 1. Plant materials used in the experiments

Plant material	Cultivar	Characteristics	Owner
Barley, *Hordeum vulgare* L.	'Bamse'	six-rowed early maturing	Svalöf AB Sweden
Pea, *Pisum sativum* L. ssp. *arvense* Asch. et Graebner.	'Timo'	purple flowers green/brown seeds tall stems in moist weather	Svalöf AB Sweden
Pea, *P.sativum* L. convar. *sativum* Alef.	'Bodil'	white flowers yellow seeds short stems	R.J.Mansholt The Netherlands
Pea, *P.sativum* L. convar. *sativum* Alef.	'Tammi'	white flowers green seeds short stems semi-leafless late flowering and maturing	Hankkija, Finland

Table 2. Air temperature and rainfall at Ås 1985-87 and mean values 1931-60

Month	Mean air temperature (°C)				Rainfall (mm)			
	1985	1986	1987	1931-60	1985	1986	1987	1931-60
April	2.0	2.1	4.0	4.3	50	19	27	48
May	11.0	10.0	8.6	10.2	23	76	57	49
June	13.6	15.4	11.3	14.4	98	16	119	70
July	15.7	15.2	15.4	16.8	98	63	66	79

the two pea cultivars 'Timo' and 'Bodil' on the smallest plots.

Sowing and harvest dates in the three years were:

	Sowing date	Early harvest	Late harvest
1985	9 May	5 July	24 July
1986	7 May	7 July	23 July
1987	29 April	8 July	29 July

Harvest times were set to one week after heading and to medium dough stage of barley corresponding to early flowering and pod filling in peas.

Nitrogen fertilizer, 0, 40 and 80 kg N ha^{-1} as calcium nitrate, was dressed on the plots between sowing and emergence. Barley plots adjacent to the experimental field received 120 kg N ha^{-1} for an extended comparison of yields between mixtures and monocultures.

Seed rates in monocultures were 100 and 440 viable seeds m^{-2} of peas and barley, respectively. Two mixtures of 50% peas + 50% barley or 25% peas + 75% barley, according to seed rates in monoculture, were used (Table 3).

Table 3. Seed rates (kg ha^{-1}) in the experiments

	Pure stand	25% pea mixture	50% pea mixture
Barley, 'Bamse'	196	147	98
Pea, 'Timo'	222	56	111
Pea, 'Bodil'	356	89	178
Pea, 'Tammi'	294	74	147

The seed was mixed and sown in rows at 13.3 cm intervals with an Øyjord plot driller. Pea seeds were not inoculated with *Rhizobium* bacteria. Small plot size was 7.5 m x 1.5 m of which 6 m x 1.5 m was harvested with a Hege plot harvester. One sample from each plot was dried at 70°C for 48 hours, and, in addition, one sample from each plot with mixtures was sorted by hand into barley and peas before drying. In 1985 and 1987 the fields were sprayed against weeds with bentazon + cyanazin. The weed content in the yields was negligible.

Experiment 2

This experiment was carried out in 1986 and 1987 according to a factorial design (split-split-plot) with two replications. Spatial plant arrangements were on the largest plots, nitrogen rates on the medium-sized plots and mixtures and monocultures of barley cv. 'Bamse' and the three pea cultivars 'Timo', 'Bodil' and 'Tammi' on the smallest plots. Seed rates and mixtures are given in Table 3. The nitrogen rates were 50 and 100 kg N ha^{-1} applied as calcium nitrate after sowing. Spatial arrangements of 10 rows, 13.3 cm apart, per plot are shown in Fig. 1. With mixed sowing, barley and peas were mixed in the seed bags and sown out together. With alternate rows sowing was carried out in two steps, with sowing in 5 drill coulters one way and sowing on the same plots and through the same coulters in the opposite direction. The same procedure was used with double rows by placing the coulters in the proper positions.

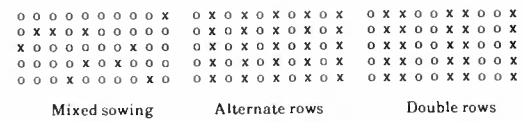

Figure 1. Spatial arrangements in Exp. 2. o Barley, x Peas

Sowing time was the same as for the corresponding years in Exp. 1, and harvest time was at medium dough stage of barley kernels, 23-24 July 1986 and 30 July-3 August 1987. The field was harvested with a Hege plot harvester in 1986, but due to lodging a forage harvester was used in 1987.

Analyses

In both experiments monocultures and mixture components were analysed for

Kjeldahl-N, which when multiplied by 6.25 gives the crude protein content. Monocultures were also analysed for in vitro digestibility.

Yield relationships were studied by the Land Equivalent Ratio (LER) concept as defined by Willey (1979). LER was calculated according to:

$$LER = La + Lb = YaSa^{-1} + YbSb^{-1}$$

La and Lb are the Land Equivalent Ratios for the mixture components a and b. Y_a and Y_b are the individual crop yields in intercropping. S_a and S_b are their sole crop yields. Mixture yields were compared with monoculture yields of heavily N-fertilized barley and with peas given no nitrogen, which are the alternative monocultures to intercropping for practical farming in Norway. When comparing mixtures with monocultures grown at the same total plant density, and at the same N rates, LER equals the Relative Yield Total, RYT (de Wit & van den Bergh 1965).

The data from the experiments were subjected to a complete factorial analysis of variance. Interactions with years were used as errors. With only 2 or 3 years to go on there were very few degrees of freedom for error, which consequently made it difficult to point out statistically significant effects.

RESULTS AND DISCUSSION

Light and leaf area measurements

The barley germinated and developed leaf area faster than the peas (Fig. 2). The barley leaf area index culminated 1-2 weeks before heading, while that of peas culminated later and was the higher at the end of the growth period. The light measurements (Figs. 3 and 4) show that the barley intercepted more light than peas or mixtures during early growth. The mixtures were intermediate in light interception with the heaviest N-fertilized mixtures closest to the bar-

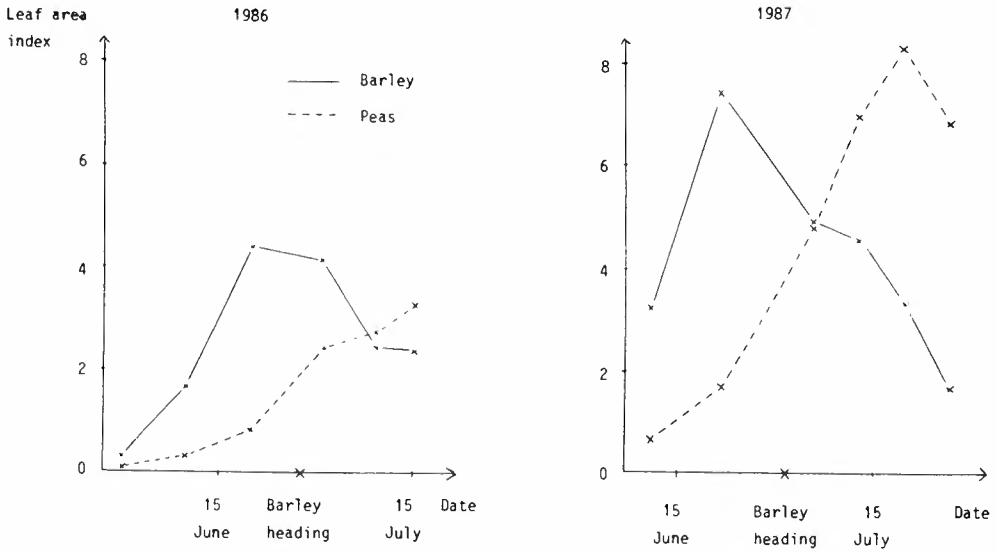

Figure 2. Leaf area index of barley (120 kg N ha^{-1}) and peas (0 kg N, average of 3 cultivars) in 1986 (left) and 1987 (right)

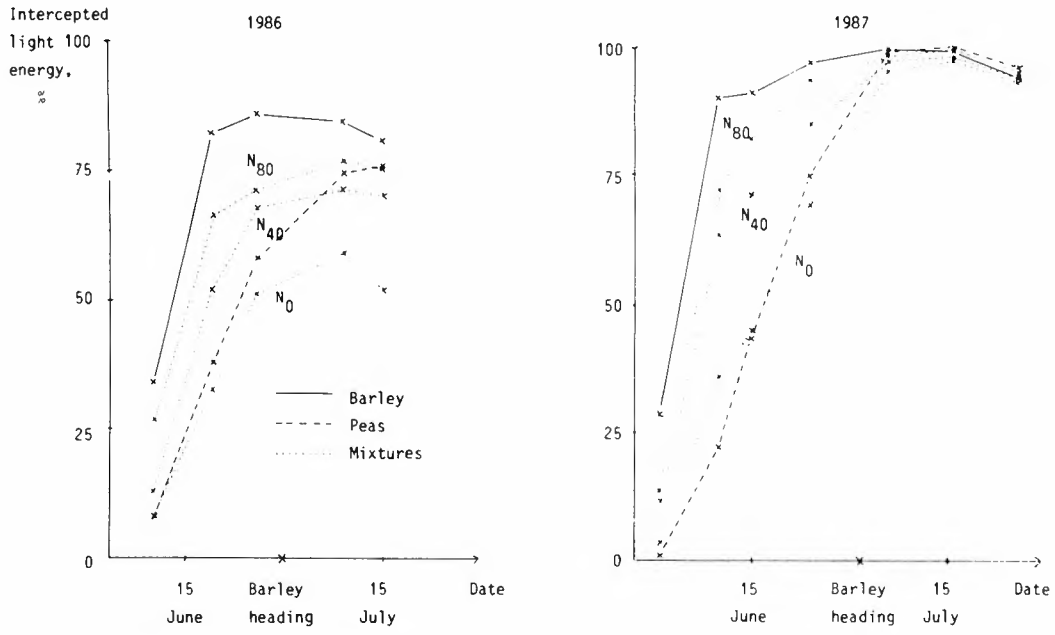

Figure 3. Intercepted light energy at ground level expressed as percentage of PAR above stand, Exp. 1. Average of 2 pea cultivars. Mixtures at 0, 40 and 80 kg N, and barley at 120 kg N ha^{-1} in 1986 (left) and 1987 (right)

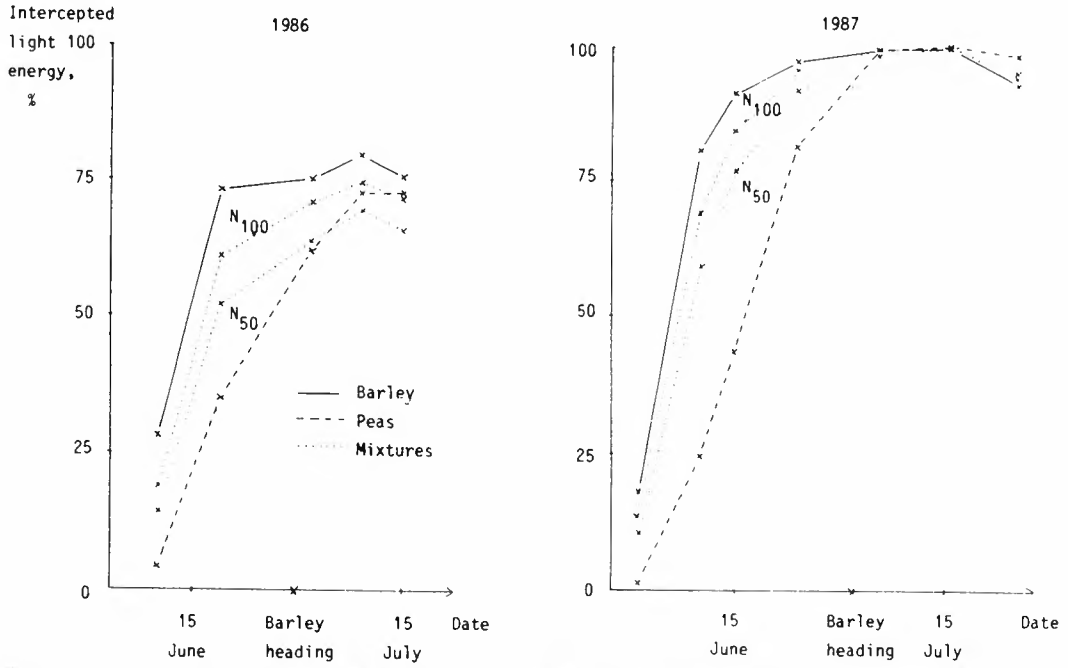

Figure 4. Intercepted light energy at ground level expressed as percentage of PAR above stand, Exp. 2. Average of 3 pea cultivars. Mixtures at 50 and 100 kg N and barley at 100 kg N ha^{-1} in 1986 (left) and 1987 (right)

ley. In 1986 leaf area and light interception were low due to the dry growth conditions, but barley managed better than peas or mixtures. In 1987 peas grew well and developed a very high leaf area during the last part of the growth period. That year almost all light energy was intercepted after the first week of July.

Pea content of the mixture yields

In Exp. 1 the average pea content of DM yield was 49.6, 32.7 and 39.1% in 1985, 1986 and 1987, respectively. In 1986, drought caused more harm to the peas than to the barley, and 'Bodil' peas suffered especially. In 1987 the cold and moist spring and summer weather favoured barley growth more than pea growth. As shown by the light and leaf area measurements (Figs. 2-4), barley grew faster after germination while the peas retained the leaf area longer and intercepted more light late in the growth period. Consequently the relative content of peas increased with delayed harvest time. Similar results were obtained in mixtures of oats with peas or vetches (Hagerup 1927, Lein 1983) and in mixtures of barley with peas or field beans (Øyen 1987). On the other hand, Bengtsson (1966) found that the pea content decreased with delayed harvest time in mixtures of oats with peas/-vetches. The decrease was most pronounced when a late maturing oat cultivar was used. In other experiments with cereal/pea mixtures the pea content was fairly constant at different harvest times (Henderson & Davies 1955, Klebesadel 1969, Lein 1987). The relationship is probably such that early cultivars of peas or cereals compete best at early stages of growth, while late maturing cultivars compete better at a later stage. From light measurements Skuterud (1977) found that barley shaded more than oats during early growth, while oats shaded more after heading. This means that barley is probably a stronger competitor than oats early in the growth period, while the opposite is true after heading.

The pea cultivar 'Timo' competed better than 'Bodil', especially at the late harvest time ($p < 0.01$) and with nitrogen application ($p < 0.01$) (Table 4).

The high pea content of 'Timo' mixtures at the late harvest time was partly due to heavy lodging which depressed the barley. The decline in pea content was strong from 0 to 40 kg N ha^{-1} and less from 40 to 80 kg N. Similar results were obtained by Bengtsson (1966), Hostrup (1987) and Lein (1987).

The 25% pea mixtures with 'Bodil' and 'Tammi' contained only about 12% peas of DM yield at 100 kg N ha^{-1} in Exp. 2. For weak competitors like 'Bodil' or 'Tammi' the seed rates of peas should be high, and the seed rates of barley should be low to ensure a high pea content of the yields. There was a tendency to interaction ($p = 0.21$) between pea cultivars and spatial arrangements (Table 5). Sowing in separate rows gave better pea establishment and a higher pea content of the yields for 'Bodil' and 'Tammi'.

Table 4. Effect of pea cultivar on pea content of mixtures expressed as percentage of DM yield at different harvest times and nitrogen rates (Exp. 1). Average of 3 years and 2 mixtures

Pea cultivar	Harvest time		Nitrogen, kg ha^{-1}		
	Early	Late	0	40	80
'Timo'	40.4	55.2	62.0	46.4	35.0
'Bodil'	29.9	36.4	51.9	28.2	19.4
Average	35.1	45.8	56.9	37.3	27.2

Table 5. Effects of spatial arrangements and pea cultivars on the pea content. Exp. 2. Percentage of DM yields. Average of 2 years, 2 N rates and 2 mixtures

	Mixed sowing	Alternate rows	Double rows
'Timo'	35.7	39.1	37.7
'Bodil'	16.8	23.1	26.0
'Tammi'	19.2	24.0	28.1

Yields

The yield levels of mixtures after harvest at medium dough stage of barley were 6.2, 3.7 and 7.5 tons DM ha^{-1} in 1985, 1986 and 1987 respectively in Exp. 1, and 4.1 and 8.7 tons in 1986 and 1987 respectively in Exp. 2. In Exp. 1 a 16-21 days delay of harvest gave a substantial increase in DM yield. The average daily DM yield increase during this period was 131, 81 and 160 kg DM ha^{-1} in 1985, 1986 and 1987 respectively, which is within the same range as found in Sweden with oats and peas (Bengtsson 1966), and in England with peas (Anslow et al. 1983).

There was a strong interaction ($p<0.01$) between mixtures and monocultures on the one hand, and nitrogen fertilization on the other, in both experiments (Table 6). Peas in pure stand gave no yield response to increased N rates in contrast to barley, which when given 120 kg N ha^{-1} yielded 5.90 tons DM ha^{-1}. The nitrogen effect on yields of the mixtures decreased with increasing pea content in both experiments. This is a common attribute of mixtures of legumes and grasses or cereals.

Mixtures with the pea cultivars showed different yield responses ($p<0.05$) to increased N rates (Table 7). 'Timo' mixtures showed a negative yield response, most probably due to heavy lodging. A similar interaction was found in another experiment (Lunnan 1988).

There was a weak interaction ($p=0.12$) between mixtures and spatial arrangements (Table 8), which indicates that the pea content in mixtures should be high when sown in separate rows. The difference in DM yield between the two mixtures was negligible in mixed sowing. In contrast, the pea-rich mixture (50% peas) outyielded the mixture with 25% peas when sown in alternate rows, and in particular when sown in double rows. When sown in separate rows the 25% pea mixture probably gave too few pea plants for any use to be made of the good growing conditions during early growth.

Yield relationships between mixtures and monocultures

In Fig. 5 it is shown that without nitrogen fertilizer both components of the mixtures yielded more than expected from monoculture yields; a mutual co-

Table 6. Effects of nitrogen rates on yields (tons DM ha^{-1}) of barley, peas and mixtures. Average of 3 years, 2 harvest times and 2 pea cultivars (Exp. 1), and 2 years, 3 spatial arrangements and 3 pea cultivars (Exp. 2)

	Exp. 1. kg N ha^{-1}			Exp. 2. kg N ha^{-1}	
	0	40	80	50	100
Barley alone	1.73	3.79	5.22	5.08	6.96
25% pea mixture	3.15	4.63	5.21	5.79	6.50
50% pea mixture	4.12	5.12	5.42	6.41	6.73
Peas alone	4.29	4.32	4.21	5.73	5.40

Table 7. DM yield (tons ha $^{-1}$) for mixtures of barley and different pea cultivars at 50 and 100 kg N ha $^{-1}$. Exp. 2. Average of 2 years, 3 spatial arrangements and 2 mixtures

Pea cultivar	N rates, kg ha $^{-1}$ 50	100	Increase
'Timo'	6.46	6.18	-0.28
'Bodil'	5.84	6.87	+1.03
'Tammi'	6.01	6.80	+0.79

Table 8. DM yields (tons ha $^{-1}$) for spatial arrangements and different mixtures, Exp. 2. Average of 2 years, 2 N rates and 3 pea cultivars

Mixture	Mixed sowing	Alternate rows	Double rows
25% peas + 75% barley	6.37	6.19	5.88
50% peas + 50% barley	6.31	6.60	6.81

operation situation (Willey 1979). This led to very high Relative Yield Total (RYT) values (Table 9). However, in practice the comparable monocultures are heavily N-fertilized barley, and peas without N-fertilizer. When compared with these crops the Land Equivalent Ratio (LER) values for mixtures without N-fertilizer became small because of low barley yields.

Nitrogen fertilization increased the LER values because the increase in barley yields was higher than the decrease in pea yields. A high pea content of the seed mixtures also improved the values. This is in agreement with Ofori & Stern (1987), who state that the LER values follow the density of the legume component rather than the cereal.

The LER values were not significantly affected by the pea cultivar. At 40 kg N ha^{-1} 'Bodil' was depressed by the barley in Exp. 1 (Fig. 5), and both white-flowered cultivars were depressed at 50 kg N in Exp. 2 (Fig. 6). The forage pea 'Timo' competed much better and yielded as expected from monoculture yields up to 100 kg N ha^{-1}.

The average LER value of all treatments was 0.82 at early harvest and 0.96 at late harvest in Exp. 1. The LER values were always greater at the late harvest time. This was probably an effect of

Table 9. Yields of mixtures compared with monocultures at different N rates. Average of 3 years, 2 harvest times and 2 pea cultivars (Exp. 1), and of 2 years, 3 spatial arrangements and 3 pea cultivars (Exp. 2). The RYT values show mixtures compared with monocultures grown at the same N rates; the LER values are based on barley grown at 120 kg N (Exp. 1) or at 100 kg N ha $^{-1}$ (Exp. 2), and on peas grown without N

Mixture		N rates, kg ha $^{-1}$ 0	40	80
Exp. 1				
25% pea mixture	RYT	1.25	1.17	1.05
50%	RYT	1.39	1.27	1.13
25% pea mixture	LER	0.64	0.88	0.95
50%	LER	0.88	1.03	1.05
Exp. 2			50	100
25% pea mixture	RYT		1.11	0.97
50%	RYT		1.22	1.04
25% pea mixture	LER		0.89	0.97
50%	LER		1.01	1.04

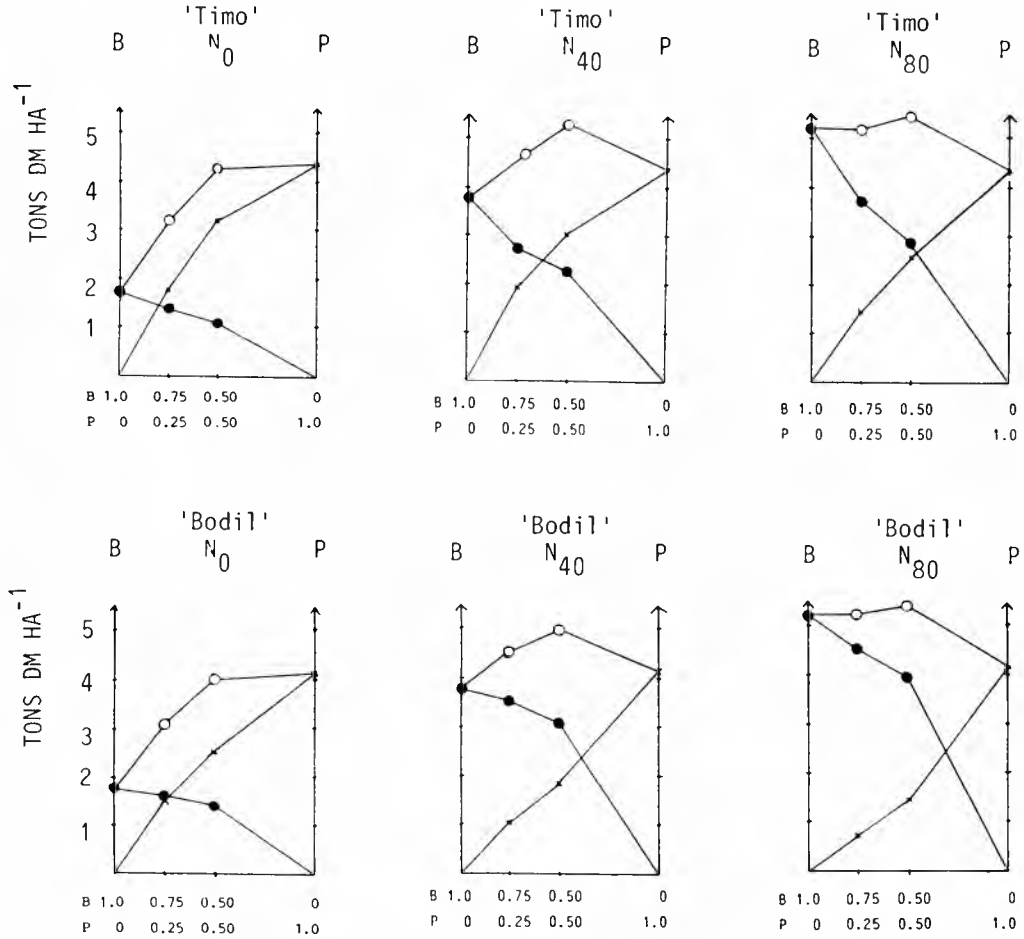

Figure 5. Inter-species competition at different nitrogen rates. Exp. 1. Average of 3 years and 2 harvest times. • Barley yields (B), x Pea yields (P), o Total mixture yields

reduced competition from barley on peas after heading followed by vigorous pea growth.

There were some advantages of intercropping (Table 10). At late harvest the 50% pea mixture gave LER values of 1.08 and 1.10 at 40 and 80 kg N ha^{-1}, respectively. In the wet years of 1985 and 1987 LER values reached 1.14 and 1.15 for the same N rates. However, in 1986 all LER values fell below 1.00. That year the peas ceased growth early because of drought stress, and the results were probably mainly an effect of reduced seed rates and low nitrogen rates in barley.

Very few experiments have been carried out in temperate annual forage crops where yield relationships between mixtures and monocultures have been examined. In most mixture experiments monocultures have not been included. Bengtsson (1966) calculated positive 'joint cultivation effects' for mixtures of oats, peas and vetches. Yield and crude protein advantages for mixtures increased with delayed harvest and a proportion of 40-60% peas in the seed mixture

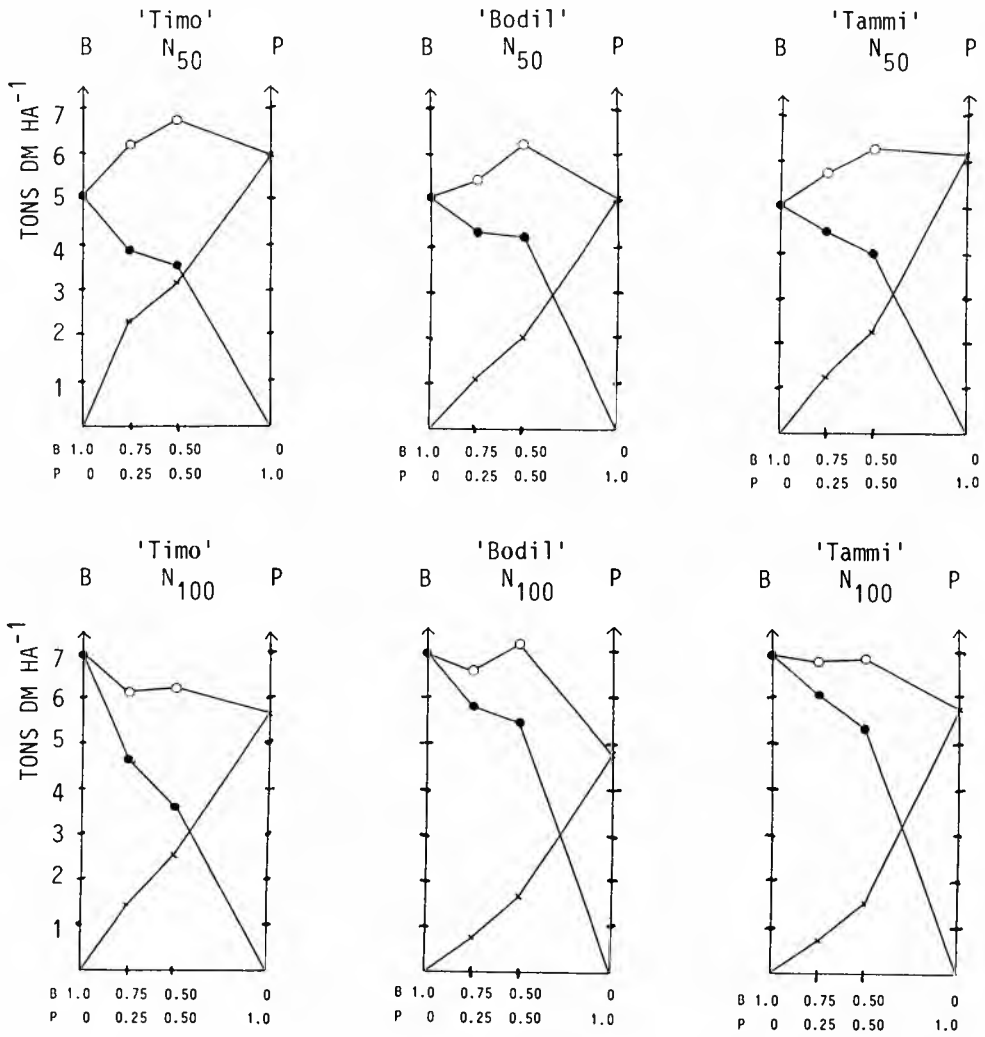

Figure 6. Inter-species competition at different nitrogen rates. Exp. 2. Average of 2 years and 3 spatial arrangements. o Barley (B) yields, x Pea (P) yields, o Total mixture yields

gave highest intercropping advantages. Mixtures also had a higher dry matter content than expected from monocultures. In Danish experiments with barley and peas for ensiling there was no yield advantage for intercropping when compared with barley grown at 120 kg and peas grown at 0 kg N ha^{-1}. At low nitrogen levels a high proportion of peas in the seed mixture gave the highest LER values (Hostrup 1987). In Canada, Berkenkamp & Meeres (1987) found mostly negative yield effects when intercropping with different mixtures of annual forage crops. In their experiment the seed rate of cereals in mixtures was only 20 kg per hectare, giving a lower total plant population in mixtures than in monocultures.

Table 10. LER values at the later harvest time, Exp. 1. Average of 2 pea cultivars. The mixtures are compared with pure barley grown at 120 kg N ha^{-1} and peas without N

	N rates, kg ha^{-1}		
	0	40	80
Average 3 years			
25% pea mixture	0.69	0.93	1.00
50%	0.93	1.08	1.10
1985 + 1987			
25% pea mixture	0.76	0.98	1.05
50%	1.01	1.14	1.15
1986			
25% pea mixture	0.49	0.75	0.86
50%	0.73	0.90	0.94

Dry matter percentage and lodging

The average dry matter percentage of mixtures was 17.7, 32.8 and 20.2% in 1985 ,1986 and 1987 respectively in Exp. 1, and 37.2 and 22.7% in 1986 and 1987 respectively in Exp. 2. The dry matter percentage decreased with increasing pea content. In both experiments 'Timo' mixtures had the lowest dry matter percentage due to a higher proportion of peas and more lodging. Delayed harvest caused a greater increase in the dry matter content of barley than in that of peas ($p < 0.01$) (Table 11).

In the dry summer of 1986 and at the earlier harvest time lodging was no problem. At the later harvest time 'Timo' mixtures lodged heavily in 1985 and 1987, leading to leaf loss and decay at the bottom of the stand. In these years the stem length of 'Timo' was measured to more than 2 metres. Lodging also hinders harvesting and implies danger from soil contamination. There was no lodging in 'Tammi' mixtures, and the somewhat late, easy lodging in 'Bodil' mixtures was of little importance.

Table 11. Dry matter percentage of barley, peas and mixtures at two harvest times, Exp. 1. Average of 3 years, 3 N rates and 2 pea cultivars

	Harvest time		
	Early	Late	Increase
Pure barley	25.2	36.1	+10.9
25% pea mixture	22.0	27.2	+ 5.2
50% pea mixture	20.4	24.6	+ 4.2
Pure peas	16.9	18.7	+ 1.8

Protein content

Barley

The protein content of intercropped barley was 10.0, 7.1 and 8.0% of DM in 1985, 1986 and 1987 respectively in Exp. 1, and 7.6 and 7.5% in 1986 and 1987 respectively in Exp. 2. The average content at early harvest was 8.9% of DM, and 7.8% at late harvest. Nitrogen fertilization increased the protein content of intercropped barley by about 0.2 %-units per 10 kg N ha^{-1} in both experiments ($p < 0.05$):

	Exp. 1			Exp. 2	
	kg N ha^{-1}			kg N ha^{-1}	
	0	40	80	50	100
Protein content, % of DM	7.6	8.2	9.3	7.1	8.1

There was a significant increase in barley protein content with increasing proportion of peas in both experiments (Table 12).

The forage pea 'Timo' gave about 1 %-unit higher barley protein content in mixtures than 'Bodil' and 'Tammi', prob-

Table 12. Protein content, (% of DM) of barley in pure stand or mixtures. Average of 3 years, 2 harvest times, 3 N rates and 2 pea cultivars (Exp. 1), and 2 years, 3 spatial arrangements, 2 N rates and 3 pea cultivars (Exp. 2)

	Exp. 1	Exp. 2
Pure barley	7.0	7.1
25% pea mixture	7.9	7.2
50% pea mixture	8.8	8.0

ably because of a higher pea content of the yields. A similar increase in cereal protein content was found in oat/pea mixtures (Bengtsson 1966) and in barley/pea mixtures (Hostrup 1987, Lunnan 1988). This increase in cereal protein content may have been caused by transfer of nitrogen from pea nodules, although neither leaching of nitrogen from pea leaves during rainfall nor decomposition of pea roots can be excluded. However, there is no evidence yet for a direct transfer of nitrogen from the legume to the cereal in association with it (Davis et al. 1986). Also the fact that the barley nitrogen yield was higher in monoculture than in the mixtures in both experiments indicates that no transfer occurred. Danso et al. (1987) found that a higher proportion of nitrogen was taken from the atmosphere by field beans in mixtures with barley than in pure stand. The barley was the stronger competitor to nitrogen derived from soil and fertilizer. This means that barley in mixtures had almost the same access to nitrogen as barley in pure stands at equivalent nitrogen fertilization rates. The barley yield was lower in mixtures, and hence the nitrogen concentration and the protein content of barley became higher in mixtures than in pure stands. This explanation is consistent with the results of the present experiments; the higher the pea content of the crop, the higher the protein content of the barley.

Peas

The average protein content of peas was 16.6, 13.9 and 17.4% of DM in 1985, 1986 and 1987 respectively in Exp. 1, and 13.4 and 16.4% in 1986 and 1987 respectively in Exp. 2. The drop in 1986 was probably an effect of drought stress on nitrogen fixation. It is common to find reduced protein content in legumes which have been subjected to drought stress (Sprent et al. 1983).

There was no significant effect of nitrogen rates or pea proportion of the mixtures on protein content of the peas. 'Timo' had a higher protein percentage of DM than the other cultivars; see below ($p < 0.05$):

	Exp. 1	Exp. 2
'Timo'	16.8	15.6
'Bodil'	15.1	13.8
'Tammi'		14.8

3. Mixtures

The protein content of both barley and peas decreased with delayed harvest, but in the mixtures this decrease was somewhat compensated by increased pea content of the total yield. The average protein content of mixtures was 11.8% of DM at early harvest and 11.0% at late harvest in Exp. 1. Due to a high proportion of peas in the yield of mixtures not fertilized with N, this treatment had the highest average protein content, 12.2% of DM. The corresponding protein contents at 40 and 80 kg N ha^{-1} were 11.0 and 11.1% respectively. In Exp. 2 no difference in protein content of herbage between 50 and 100 kg N ha^{-1} could be detected. The increase in barley protein content at higher nitrogen rates was offset by a lower pea content of the yields.

Inclusion of peas to the barley forage led to a considerable increase in protein content (% of DM):

	Exp. 1	Exp. 2
Pure barley	7.0	7.1
25% pea mixture	10.4	8.8
50% pea mixture	12.4	10.3

'Timo' mixtures gave higher protein content than mixtures with 'Bodil' or 'Tammi'. This was due to a higher proportion of peas in the yields and to a higher protein content of both components in the 'Timo' mixtures:

	Protein content, % of DM	
	Exp. 1	Exp. 2
'Timo' mixtures	12.6	11.0
'Bodil' mixtures	10.2	8.7
'Tammi' mixtures	-	8.9

Nitrogen yield and biological nitrogen fixation

Nitrogen yield of mixtures was positively affected by increasing pea content and by delayed harvest (Table 13). The barley absorbed most of the nitrogen during the early growth, while delayed harvest of peas and mixtures augmented the nitrogen production considerably. Biological nitrogen fixation is calculated by the difference method (Williams et al. 1977). It is assumed that pure stands of peas and barley take up the same amounts of nitrogen as the mixtures from fertilizer and from the soil pool. Although this might not be correct, the figures in Table 13 should give a good indication of the amounts of nitrogen fixed biologically by the peas. Peas also contain more nitrogen in the roots and stubble than barley, and this difference comes in addition to the figures when estimating total biological nitrogen fixation.

Small amounts of nitrogen fertilizer, e.g. 40 kg N ha^{-1}, reduced the fixation very little. Even at amounts of 80 kg N ha^{-1} the fixation reached appreciable quantities. The most efficient examples were measured in monoculture peas in 1985 and 1987, when amounts of 130-140 kg N ha^{-1} were fixed at the latest harvest time without N-fertilizer.

In vitro digestibility

There was no consistent difference in the in vitro digestibility between herbage from different harvest times (Table 14), probably because of the development of the highly digestible seeds and grains which outweighed the decline in digestibility of the stems. There was a tendency to reduced digestibility with increasing N rates in barley, probably due to taller and more lignified stems.

The dry growing conditions in 1986 evidently favoured development of highly digestible grains and seeds (Table 15). In Tables 14 and 15 clear-cut differences in digestibility between the pea cultivars are evident. Thus, in both cases 'Bodil' had the highest digestibility and 'Timo' the lowest. The same ranking was found in another experiment (Lunnan 1988). 'Timo' probably had lower digestibility because of a higher proportion of stem materials than the white-flowered cultivars.

Table 13. Nitrogen yield and estimated biological nitrogen fixation (kg N ha^{-1}) in above-ground plant parts at early and late harvest and at different N rates. Exp. 1. Average of 3 years and 2 pea cultivars

	Nitrogen yield					Nitrogen fixation				
	Harvest		kg N ha^{-1}			Harvest		kg N ha^{-1}		
	early	late	0	40	80	early	late	0	40	80
Pure barley	36	45	18	40	63	-	-	-	-	-
25% pea mixture	57	89	59	75	84	21	44	41	35	21
50% pea mixture	77	120	91	100	105	41	75	73	60	42
Pure peas	101	134	117	120	115	65	89	91	80	52
Average	68	97	71	84	92	42	69	68	58	38

Table 14. In vitro digestibility (% of DM) of barley and peas from monoculture plots. Average of 3 years. Exp. 1

	kg N ha^{-1}	Harvest time Early	Late
Barley, 'Bamse'	0	78.6	77.1
»	40	76.7	75.6
»	80	75.3	75.7
»	120	74.8	75.5
Pea, 'Timo'	0	76.6	77.4
Pea, 'Bodil'	0	79.6	80.1

Table 15. In vitro digestibility (% of DM) of barley and peas from monoculture plots. Exp. 2

	Mean value	1986	1987
Barley, 'Bamse'	76.3	79.4	73.2
Pea, 'Timo'	78.3	81.9	74.8
Pea, 'Bodil'	84.0	86.9	81.1
Pea, 'Tammi'	81.9	85.1	78.7

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IMMUNOAFFINITY CHROMATOGRAPHY FOR PURIFICATION OF CYTOKININS IN PLANT EXTRACTS

CARL ERIK HANSEN, COR. KOPPERUD & OLA M. HEIDE
Department of Botany, Agricultural University of Norway, Ås-NLH, Norway

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Immunoaffinity chromatography columns were developed for purification of the cytokinins *trans*-zeatin riboside (ZR) and isopentenyladenosine (IPA). The columns were used in combination with ion-exchange cellulose DE52 pre-columns for one-step purification of cytokinins from crude plant extracts. A large amount of UV-absorbing impurities present in crude plant extracts were entirely removed in this purification step. The purified cytokinins were finally analysed using HPLC and enzyme immunoassay (EIA), showing large differences in type and level of cytokinins in various plant species.

Key words: Cytokinins, immunoaffinity chromatography, plant hormones, enzyme immunoassay.

Present address: Carl Erik Hansen, Nestlé Research Centre, P.O. Box 353, CH-1800 Vevey, Switzerland.

Several different analytical techniques, including bioassays, mass spectrometry and immunoassays, have been used for the detection, isolation and identification of cytokinins (Horgan 1984). Many problems concerning specificity and sensitivity have been overcome by using immunoassays which have been developed for all classes of plant hormones (Weiler 1984). Immunoassays are now widely used and seem particularly well suited as quantitative methods in physiological studies that generate large numbers of samples. However, several authors have shown that an extensive purification of the plant extracts is necessary prior to determination with enzyme immunoassay (EIA) or radio immunoassay (RIA) (Hansen *et al.* 1985, MacDonald *et al.* 1981). Here we describe a purification method for cytokinins using immunoaffinity chromatography. The method is used to overcome problems caused by interfering substances in extracts containing low levels of the endogenous cytokinins, *trans*-zeatin (Z), *trans*-zeatin riboside (ZR), isopentenyladenine (IP) and isopenetyladenosine (IPA).

MATERIALS AND METHODS

Preparation of immunoaffinity columns
Antibodies were coupled to CNBr-activated Sepharose 4B (Pharmacia, Uppsala, Sweden) in accordance with the methods recommended by the manufacturer and Cuatrecasas (1970). A mixture of anti-ZR and anti-IPA antibodies was used to develop a column for isolating the prevalent cytokinins Z, ZR, IP and IPA. One gram of CNBr-activated Sepharose 4B was re-swelled for 15 min,

and then washed with 200 ml 1 mM HCl in a sintered glass filter (G3) using a vacuum pump. The gel was washed with 5 ml coupling buffer containing 0.2 M $NaHCO_3$, 0.5 M NaCl, pH 8.6 adjusted with 1 N NaOH, and then immediately transferred to an antibody solution (10 mg in 2 ml coupling buffer) in a tube. The gel:buffer ratio was 1:2, and the tube was inverted gently every 5 min for 2 h at room temperature. To prevent gel damage, the use of magnetic stirrers should be avoided. After coupling, the buffer was exchanged with 1 M ethanolamin-HCl pH 8 for 2 h to block any remaining active groups, and the gel was transferred back to the glass filter. Excess absorbed protein was washed off with 4 cycles of alternating pH. Each cycle consisted of 0.1 M acetate buffer, 0.5 M NaCl, pH 4 and of coupling buffer pH 8.6. Finally, the gel was packed into a polypropylene syringe plugged with cellulose paper. The column was stored in the coupling buffer in the presence of 0.02% thimerosal at 4°C. One gram of Sepharose 4B gives approximately 3.5 ml of swollen gel.

Preparation of DE52 pre-columns

Pre-swollen ion-exchange cellulose DE52 (Whatman, Maidstone, Kent, UK) was stirred gently for 15 min in 2 M ammoniumacetate pH 6.5, using 25 ml per gram cellulose. The pH was adjusted to 6.5 after 5 min. After incubation when the slurry had settled, the solution was sucked off, and the cellulose re-dispersed in 40 mM ammoniumacetate pH 6.5. The cellulose was packed into polypropylene syringes plugged with cellulose paper and stored in 40 mM ammoniumacetate pH 6.5 in the presence of 0.02% thimerosal.

Sample preparation and purification

Fresh plant tissues were homogenized using three volumes of icecold ethanol containing 20 mg l^{-1} of the antioxidant butylated hydroxy toluene (BHT) in a corex tube with a Polytron PTA LOS homogenizer (Kinematica, Luzern, Switzerland). The extract was cleared by centrifugation, taken to dryness at 40°C in a rotatory evaporator, and the residue dissolved in 20 ml 40 mM ammonium acetate pH 6.5. The extract was cleared by centrifugation, heated to 37°C, and applied onto the DE52 pre-column. The column was eluted directly into the immunoaffinity column at room temperature, and the two columns washed with 60 ml of 40 mM ammonium acetate pH 6.5. The DE52 column was then discharged, and the immunoaffinity column washed with 10 ml of 40 mM ammonium acetate pH 6.5, followed by 5 ml 40 mM ammonium acetate, 0.5 M NaCl pH 6.5, then with 10 ml H_2O, and finally eluted with 10 ml methanol (MacDonald and Morris 1985). The methanol extract was evaporated to dryness at 40°C, dissolved in 0.5 ml H_2O and analysed by HPLC and EIA as described in detail elsewhere (Hansen *et al.* 1984, Hansen *et al.* 1985).

The DE52 columns were used only once, whereas the immunoaffinity columns were re-used at least 20 times after washing with 10 ml H_2O and several washings with 40 mM ammonium acetate pH 6.5. The columns were stored at 4°C in 0.02% thimerosal.

RESULTS

An extract prepared from 20 g of freshly harvested clubroots from *Brassica oleracea* was divided into three equal aliquots. Internal standard, 500 pmol ZR and 500 pmol IPA, was added to one aliquot, and the extract was purified by immunoaffinity chromatography followed by HPLC and EIA. The other two aliquots of the plant extract were purified in the absence of internal standard, including or excluding the immunoaffinity column, respectively. As a comparison, the same amount of internal standard dissolved in H_2O but without the plant extract was purified in parallel. Fig. 1 shows the pattern of UV-

absorption in the fractions eluted from HPLC after purification of the extracts. The standards of ZR and IPA going through the extraction procedure and immunoaffinity chromatography were eluted with expected retention times using HPLC (Fig. 1A). Other unidentified minor peaks were also present in the UV-pattern. When a plant extract containing the same amount of standards, ZR and IPA, was purified, the two major peaks of ZR and IPA were detected (Fig. 1B). The almost clean pattern of UV-absorbing compounds shows that the immunoaffinity column is a very powerful one-step purifier of ZR and IPA from the original crude ethanol extract. By comparison, the same amount of plant extract, without undergoing the immunoaffinity chromatography step, showed a vast number of UV-absorbing compounds in the HPLC-fractions (Fig. 1C). An extract without internal standards was also analysed after passing over the immunoaffinity column. The amount of endogenous ZR and IPA was not sufficient for detection by UV-absorption using HPLC in this particular type of plant extract (Fig. 1D). It is therefore necessary to include the EIA after separation on HPLC for analyses of endogenous ZR and IPA in the plant extract.

The immunoaffinity column was also tested for its ability to retain cytokinins other than ZR and IPA, since a considerable excess of antibodies are used in the column. A standard mixture of ZR, Z, IP, IPA, 7-glucoside of Z, 9-glucoside of Z, O-glucoside of Z and O-glucoside of ZR was analysed after purification on the immunoaffinity column. This experiment showed that the cytokinins Z, IP and the 9-glucoside of Z can also be purified by the immunoaffinity column developed for ZR and IPA (data not shown).

It was found that the DE52 pre-column was necessary for the removal of interfering substances which otherwise would bind with the Sepharose and be eluted along with the cytokinins by the methanol from the immunoaffinity column. A presentation of the purification and quantification procedure is shown in Fig. 2.

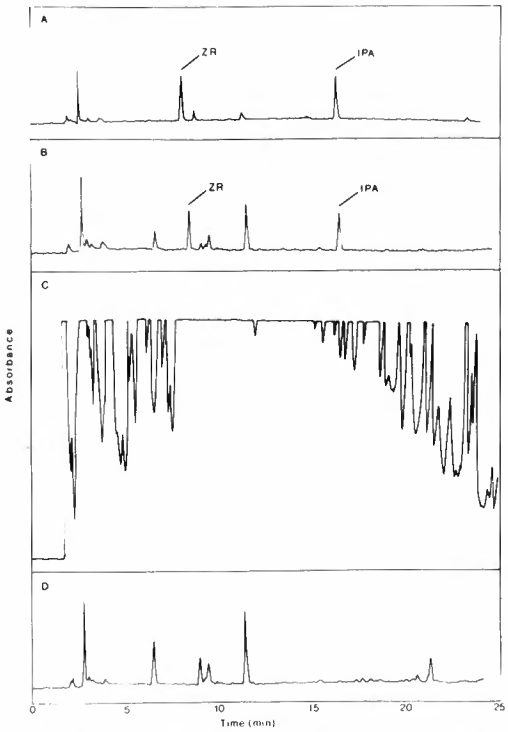

Figure 1. The UV-absorbance (270 nm) in extracts purified by immunoaffinity chromatography and separated by HPLC. Cytokinins were separated from (A) a solution of standards, (B) a solution of standards added to a purified plant extract, (C) a plant extract without the immunoaffinity purification, and (D) a plant extract without internal standard added. Extracts A, B and D were subjected first to immunoaffinity chromatography, whereas extract C was applied directly onto HPLC. Retention times are measured at a flow rate of 1.5 ml min^{-1}

Cytokinins were analysed in extracts from several different plant species using immunoaffinity purification. The Norwegian cabbage cultivar Garo of *B. oleracea* var. *capitata* and the cultivar Nagayoka of *B. campestris* var. *pekinensis* contained predominantly IPA and IP, whereas Z and ZR were not detectable. No evident correlation was found between healthy roots and club-

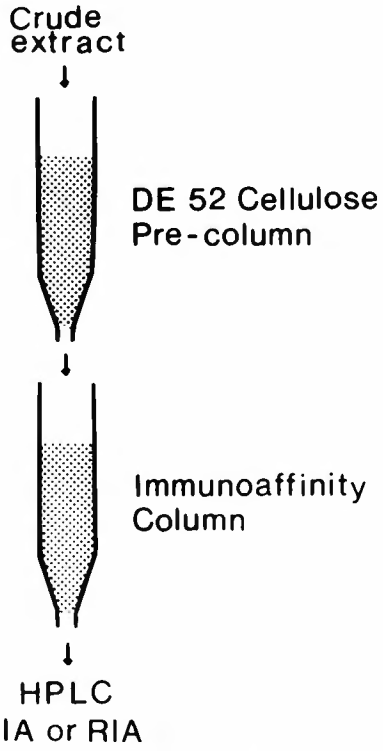

Figure 2. Schematic presentation of the procedure used for purification of cytokinins from crude ethanol extracts using immunoaffinity chromatography. The cytokinins were analysed and quantitatively determined by HPLC and EIA

roots induced by the fungus *Plasmodiophora brassicae*, and the levels of IP and IPA ranged between 1.0 and 70.0 pmol/g fr.w. In leaves of *Begonia*, all four cytokinins Z, ZR, IP and IPA have been analysed in more detail (Hansen *et el.* 1988). The most predominant cytokinin, Z, was present in leaves of up to approximately 100 pmol/g fr.w. More recently, we analysed leaves and root exudates of *Bryophyllum*, and the preliminary results show the presence of Z and ZR.

DISCUSSION

Most reports dealing with measurements of cytokinin levels in plants are based on the quantitative use of bioassays (Horgan 1984). However, one major problem with such analyses has been the presence of interfering substances in the plant extracts assayed. Gas chromatography in combination with mass spectrometry provides another, highly specific method (Scott & Horgan 1980) but it is expensive, time consuming, and not suitable for measuring a large number of samples. These difficulties can be largely overcome by using sensitive and specific immunoassays (Weiler 1984). By this method cytokinins can be detected at low pmol levels, but the extraction procedure is still labour-intensive, and in some cases results in overestimated levels due to the presence of interfering substances. To overcome these problems, we have developed immunoaffinity columns for use in purification of cytokinins from plant extracts by adopting the method of MacDonald & Morris (1985). A crude plant extract contains large amounts of UV-absorbing substances. The method developed removes almost all UV-absorbing impurities in this single step immunoaffinity purification.

The considerable excess of antibodies in the column results in high capacity, and by using internal standards it was shown that at least 1 nmol cytokinins can be purified with 50-100% recovery from the crude ethanol extract.

Unlike a competitive immunoassay (Hansen *et al.* 1984), the column will also bind cytokinins with a medium or high level of crossreactivity in an EIA. The cytokinins Z and IP having approximately 30% crossreactivity in the EIA (Hansen *et al.* 1984) and the 9-glucoside of Z having only 6.4% crossreactivity, can also be purified using an immunoaffinity column developed for ZR and IPA. This is very likely due to the considerable excess of antibodies which exclude binding competition between various cytokinins.

The immunoaffinity columns can be re-used several times, and although the

cytokinins are eluted with 100% methanol, no decrease in binding capacity was found after purification of 20 samples. The life-time of the columns can be prolonged dramatically by the one-time use of DE52 pre-columns. This column removes the large amounts of pigments and anionic substances present in a crude plant extract, and concurs with the findings of MacDonald & Morris (1985).

The method described seems well suited for the simple and sensitive determination of cytokinins in physiological studies which generate a large number of samples. The method can be developed for other groups of plant hormones, and we have tested it for extracts of various different plant species. The types and levels of endogenous cytokinins vary greatly between different plant materials, and this must always be taken into consideration during hormone analyses. Our method makes it possible to combine rapid and specific purification with sensitive quantification of several cytokinins using HPLC-EIA.

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POTENTIAL EFFECTS OF ULTRAVIOLET B-RADIATION ON PLANTS AND PLANT PRODUCTION IN THE NORTH

ANNE KJERSTI BAKKEN
Kvithamar Research Station, Stjørdal, Norway

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A reduction in the stratospheric ozone layer will mean that the solar radiation reaching the earth's surface will probably be enriched with UV-B radiation (280-315nm). UV-B is known to affect and damage important growth and developmental processes in plants - their photosynthesis, guard cell activity, biomass allocation and flower development. Genetic alterations have also been found after UV-B radiation. So far, little is known of the sensitivity of the most important crop species at northern latitudes, still leaving much work to be done in evaluating the potential UV-B effects on plant life and productivity in the north.

Key words: Damaging effects, plant production, protective mechanisms, sensitivity, UV-B radiation.

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

The ozone layer in the earth's atmosphere strongly absorbs ultraviolet radiation with wavelengths shorter than 315 nm (UV-B and UV-C), whereas absorption of wavelengths in the region of 315-400 nm (UV-A) is almost insignificant (Caldwell 1977). A reduction of the stratospheric ozone layer would therefore enrich solar radiation at the earth's surface with the shorter ultraviolet wavelengths. However, below 280 nm, in the UV-C region, the ozone absorption coefficient is so large that even with a 90 % ozone reduction, the atmosphere would be effectively opaque to UV-C radiation.

Thus, any consideration of the biological effects of increased solar UV-flux resulting from reduced atmospheric ozone should be confined to the waveband between 280 and 315 nm (UV-B). In the case of a moderate ozone reduction, only the 290 to 315 nm wavebands would be of concern (Caldwell 1977).

The increase in biologically damaging solar irradiation resulting from a given level of ozone reduction for a specific set of conditions is known as the Radiation Amplification Factor, RAF (Caldwell et al. 1986). The increase in total UV-B flux resulting from ozone reduction is inconclusive unless the RAF is calculated taking the biological effectiveness of each wavelength into account. To give an approximation, there would be a predictable increase of about 2% in solar UV-B radiation weighted for biological effectiveness for each 1% reduction in the atmospheric ozone columns (Caldwell 1977). Today, there are natural latitudinal and altitudinal gradients of UV-B irradiance reaching the earth's surface. Along a gradient from the Arctic (70° N) at sea level to equatorial latitudes at high elevations, the maximum UV-B irradiance can vary by a full order of magnitude, and the total daily effec-

tive radiation can vary by a factor of seven (Caldwell & Robberecht 1980). Today plants, at high elevations in the tropics receive doses of UV-B of more than three times the dosage which would occur with a 16% ozone reduction at temperate latitudes (Caldwell & Robberecht 1980). This is an important point to remember when evaluating potential UV damage on plants and their adaptive and protective mechanisms against UV radiation.

With crop productivity in mind, the most important findings concerning UV-B effects on the higher plants referred to in the literature will be summarized in this article. The ability of plants to protect themselves from damaging ultraviolet radiation and to repair UV lesions will also be discussed.

DAMAGING EFFECTS OF UV-B ON HIGHER PLANTS

Nucleic acids

When DNA absorbs UV-radiation a number of photochemical lesions results. The most common of these involve dimers of pyrimidine bases. UV radiation is also efficiently absorbed by RNA, but it has to be exposed to much higher doses than those absorbed by DNA before inactivation occurs. UV-C effects on nucleic acids are studied most, but many of the same photochemical lesions can be elicited by UV-B radiation, although radiation in this waveband is less effective (Harm 1979).

As well as the lethal UV damage caused by unrepaired nucleic acid lesions, the non lethal genetic effects of UV may also be of ecological significance (Caldwell 1981). These include mutations that are not immediately lethal, in addition to reduced growth due to impaired cell division or cell enlargement.

According to Caldwell (1981), there are no indications that higher plants growing in nature would suffer mortality as a direct result of solar UV-B radiation, at least not in the sporophyte phase of their life cycle. The DNA of higher plants appears to be much better protected against UV damage than that of bacteria or algae.

Photosynthesis

UV radiation at flux rates now being received at temperate latitudes has been shown to reduce photosynthesis in sensitive species (Bogenrieder & Klein 1977, Sisson & Caldwell 1977). Unfortunately, many studies addressing the effects of UV-B radiation on carbon assimilation rates or the component reactions of the photosynthetic apparatus, utilized either very high UV-B radiation levels or used other parameters that deviated considerably from those present under ambient field conditions (Sisson 1986). Especially important is the flux rate of photosynthetic active radiation given during the experiments (Teramura et al. 1980, Teramura 1986). UV-B radiation was found to affect net photosynthesis at low photosynthetically active radiation levels, but had little effect on the levels that normally saturate photosynthesis in the field.

The damaging effects on photosynthesis are found to be on the photosystems, on the carboxylating enzymes, and via guard cell activity. The primary site of UV damage has been shown to be in the reaction centre of photosystem II (PS II) (Noorudeen & Kulandaivelu 1982, Iwanzik et al. 1983, Renger et al. 1986).

Renger et al. (1986) suggest that UV radiation disrupts the plastoquinones of PS II by modifying the binding protein of the primary and secondary plastoquinones of the PS II acceptor site. As a consequence there will be a loss of activity in the primary acceptor.

Chlorophyll reductions are reported only in plant leaves which have been exposed to particularly large doses of UV-B flux (Sisson and Caldwell 1976, Brandle et al. 1977, Teramura et al. 1980) and in plants exposed to UV-B while in an environment of very low vi-

sible irradiance (Vu et al. 1982). With regard to carboxylating enzymes, phosphoenolpyruvate-carboxylase activity in the C4 plant sweet corn was found to be lowered by UV-B irradiation (Vu et al. 1982). Ribulosebisphosphatecarboxylase activity in soybeans and peas was significantly reduced after irradiation with UV-B (Vu et al.1982).

Guard cell activity is very sensitive to ultraviolet radiation (Negash 1988). In short-term experiments the stomata respond to UV-B by closing, and the guard cells continuously lose ions. This indicates that both the plasmalemma and the tonoplast are affected. UV-B radiation could also indirectly affect the ATP supply needed for ion transport into guard cells.

Growth and developmental alterations

UV-B radiation significantly depresses growth and biomass accumulation of many sensitive higher plant species (Sisson & Caldwell 1976, Van et al.1976, Biggs & Kossuth 1978, Vu et al. 1981). Whether growth delay and inhibition is a direct or indirect effect is difficult to deduce. Inhibition of photosynthesis will certainly reduce the dry matter production and consequently the growth. It has been argued that UV-induced growth delay represents an active protective reaction by which cell division does not occur or is reduced when the DNA is exposed to potentially damaging radiation (Beggs et al. 1986).

Lydon et al. (1980) found that enhanced UV-B radiation affected biomass allocation in soybean, total plant dry weight, its average seed dry weight and seed protein and lipid concentration. Relative growth rate, leaf area and height growth rate were also significantly different from those of controls.

Caldwell (1981) emphasizes that the disproportionate growth of plant organs, the depressed flower development, the loss of apical dominance, the abscission of leaves and the altered mineral nutrient concentrations, which were observed after UV-B treatments, still remain to be demonstrated as occurring in nature outside laboratories and growth chamber conditions.

The plant growth regulators Indoleacetic acid (IAA) and Abscissic Acid (ABA) are found to absorb UV-B and could be involved directly as chromophores for alterations of plant growth and development (Caldwell 1981).

UV-B SENSIVITY

Sullivan and Teramura (1988) point out that about two-thirds of the 200 plant species so far tested appear to be sensitive to UV-B. The sensitivity of more than 45 different crop species has been screened under a diverse range of environmental conditions (Van et al. 1976, Teramura 1983). Monocotyledons seem to be less affected by UV-B radiation than dicotyledons, and crops with the C3 photosynthetic pathway are more affected than those with the C4 pathway. Among important crop species which appear to be sensitive are pea (*Pisum sativum* L.), collard (*Brassica oleracea* L. var acephala) cabbage (*Brassica oleracea* L var capitata), soybean (*Glycine max* L) and oat (*Avena sativa* L.) (Van et al. 1976).

In many plant species there are also intraspecific differences in UV-B response. Different sensitivities have been reported in cultivars of soybean (Biggs et al. 1981), cotton (Ambler et al. 1975), collard and cabbage (Van et al. 1976), wheat, barley, corn and rice (Biggs & Kossuth 1978). These phenotypic differences show genetic variations of potential importance in the future breeding of UV-B-resistant cultivars of crop species.

DEFENSIVE MECHANISMS AGAINST UV RADIATION

Strategies of defence against solar ultraviolet radiation can be categorized in-

to radiation repair and radiation avoidance.

The pyrimidine dimers of damaged DNA can be repaired by three processes (Beggs et al. 1986). Photoreactivation or photoenzymatic repair involves an enzymatic process using light energy. The photoreactivating enzyme binds to dimer sites and, using light energy (usually UV-A and blue radiation), splits the dimer. Excision repair of DNA involves the removal of the UV photoproduct and its replacement by a new resynthesized correct sequence. The third form of repair, post replication repair, has yet to be found in plants. The undamaged portions of the DNA strand undergo normal replication leaving a gap in place of the lesion. After this replication has occurred, a DNA strand is synthesized using the redundant information in the cell as a template, and the functional DNA strand is restored (Caldwell 1981).

The second category of protective mechanisms consists of those that reduce the amount of UV radiation reaching the target. Plants will avoid the damaging radiation. These mechanisms may be structural aspects of the plant or screening molecules which absorb the UV radiation. They may be static, which means that they are always present; they may appear as the plant develops, without any special outside stimulus; or they may be inducible and appear after a special stimulus such as radiation treatment (Beggs et al. 1986).

Structural attenuation of UV radiation appears to play a minor role in most plants (Caldwell et al.1983). The cuticle and cell walls as such do not absorb UV radiation, although in some cases external secretions or powders may contain large quantities of flavonoids which efficiently absorb this kind of radiation. The main location for flavonoids is in the cell vacuoles; it has been suggested that one of their major functions is to absorb the UV radiation that might cause damage to the plant (Caldwell 1981, Wellmann 1983). These theories are supported by the fact that these pigments have the strongest absorption in the UV waveband and that they are usually accumulated in the outer cell layers of the plant. Flavonoid production is also frequently stimulated by radiation, although often there is also a separate and widespread UV-B induction by visible radiation.

As mentioned before, UV-induced growth delay or inhibition represents an active protective reaction. When the DNA is exposed to potentially damaging radiation, cell division does not occur or is reduced. In this way, repair mechanisms can act before cell division starts again (Beggs et al.1986).

CONCLUSION

Several studies have shown that ultraviolet radiation in the UV-B part of the spectrum can affect plants and plant productivity, but the minimum radiation doses found to cause the damage are far from constant. Species and ecotypes differ in sensitivity, and the damaging effect depends on other environmental factors. Most important, perhaps is, the level of photosynthetic active radiation (PAR) given together with the UV-B radiation. In many of the experiments performed so far, there have been great differences between the light regimes in the experiments and natural field conditions. There is still very little information available about the UV-B sensitivity of crops and herbages of northern latitudes. In the evaluation of the potential UV-B effects on plant life and productivity under changing solar UV regimes in the north, there is a great deal of work still to be done. It will be important to simulate the northern temperature and light climate in experiments with the most important species such as potato, barley, different grasses and clovers, carrot and Brassicae. Their sensitivity to UV-B and their adaptive and protective mechanisms against damaging radiation will have to be evaluated. Differences be-

tween ecotypes along latitudinal and altitudinal gradients will also have to be taken into consideration.

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STUDIES ON SEED DORMANCY IN SMALL GRAIN SPECIES. I. BARLEY

ERLING STRAND
Agricultural University of Norway, Department of Crop Science, Aas, Norway

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Seed dormancy has been studied in barley cultivars grown under field conditions for periods of up to 20 years. The percentages of dormant seed in germination tests carried out at 10°C and at 20°C on samples harvested 10 and 30 days after yellow ripeness were used as measures of the intensity of seed dormancy.A Dormancy Index (DI) was calculated.

The climatic factors - temperature, global radiation, rainfall, air relative humidity, and the rainfall/temperature ratio - all had significant effects on the intensity of seed dormancy.While seed dormancy was reduced with high temperature and high global radiation,it was increased with high rainfall,high air humidity,and a high rainfall/temperature ratio.

The climatic factors had their greatest effect on dormancy in a period extending from approximately three weeks prior to and 30 days after yellow ripeness. The effects of climatic factors in every 10-day period were accumulated and were significant for at least until 40 days beyond termination of the climatic period observed.The climatic factors also influenced the date of maximum dormancy, the rate of dormancy disappearance, and the manifestation of seed dormancy at different germination temperatures. Combinations of climatic factors favouring high dormancy could temporarily increase dormancy on the downward slope of the dormancy curve.

Seed dormancy was influenced most strongly by climatic factors and the determination of genetically controlled seed dormancy was most efficient on samples from the second harvest.The most accurate parameter of seed dormancy was the mean of the Dormancy Index from the first and the second harvest.The most accurate single test for seed dormancy was 20°C germination temperature of samples from the second harvest.

Key words: Temperature, rainfall, air humidity, global radiation.

Erling Strand, Department of Crop Science,Agricultural University of Norway, P.O.41, N-1432 Aas-NLH, Norway.

Understanding seed dormancy in small grain and other plant species is still a great challenge to research workers. In spite of numerous investigations on the subject,the factors and their mode of action in controlling the development, intensity,longivity and disappearence of seed dormancy are only partly understood. For a summary of our present knowledge of seed dormancy, the reader is referred to the comprehensive review articles by BELDEROK (1968), MAQUIRE (1980), KAHN (1982), and others.

This paper deals mainly with two aspects of seed dormancy in barley. The first is the manifestation of seed dormancy as influenced by germination temperatures and time pattern i. e. the dormancy curve,and the evaluation of dormancy testing procedures towards obtaining the most precise determination of the genetically controlled seed dormancy of barley cultivars.

The second aspect is the effect of different climatic factors on the rate of development,maximum intensity, date of maximum intensity,and the variation in the intensity of seed dormancy during the pre-harvest post-ripening period. Finally, the interactions between cultivars,dates of harvest, germination temperatures,and climatic factors are dealt with.

In an earlier investigation on the disappearance of seed dormancy in stored barley (STRAND 1965), it was found that under storage conditions seed dormancy was reduced very regularly as a function of time and temperature. Under experimental conditions were temperature is the only variable environmental factor, valid results could be obtained in a few seasons. The build-up of seed dormancy,however,takes place under field conditions where the developing seeds are exposed to a number of climatic factors. All these factors may affect the development of seed dormancy,and possible effects can be determined over a long period of time. This investigation is based on data from periods of up to 17 and 20 years.

MATERIAL AND METHODS

The plant material used in the main part of the study was the six-rowed barley cv Lise, and the two-rowed barley cv Møyjar grown under field conditions for periods of 20 years and 17 years respectively. In parts of the study other cultivars and other time periods were also included. All cultivars were well adapted and have been widely grown in the area.

The developmental stages of the plants were defined as follows: *Heading*, when 50 % of the spikes were completely out of the boots. *Yellow ripeness*(YR), when moisture content of the kernels was 38 % of fresh weight.

The germination tests were carried out by the State Seed Testing Station according to official methods, i. e. germination in moist sand for 10 days at 10°C,and at 20°C using 200 kernels in each test. Percent dormant seed in these tests was used as a measure of the intensity of seed dormancy.

The dormancy parameters (dependent variables) recorded for the material were:

1. Percent dormant seed at 10°C germinating temperature.
2. Percent dormant seed at 20°C germinating temperature.
3. The Dormancy Index (DI) (STRAND 1965), which is calculated from results of germination tests at 10°C and at 20°C.

$$DI = \frac{\%\ \text{dorm.seed at } 10°C * 2 + \%\ \text{dorm.seed at } 20°C}{3}$$

4. The ratio percent dormant seed at 10°C/percent dormant seed at 20°C.
5. The ratio DI HT 2/DI HT 1.
6. Mean of the Dormancy Index of the first and second harvests.

These six dormancy parameters were determined on seed samples harvested approximately 150 day degrees or 10 days (HT 1) and 450 day degrees or 30 days (HT 2)after the date of yellow ripeness. In a few years the cultivars were also sampled three or five times at 10-day intervals from yellow ripeness.

The independent variables were

1. Temperature,daily mean in 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

Initially the daily maximum and mean temperatures of the six warmest hours of the day were also included in the study.

The correlation coefficients between seed dormancy and these two temperature parameters, however, were no higher than those obtained when the daily mean temperature was used. They were therefore omitted from further study. The climatic data were recorded at the meteorological station of the university,which is approximately two km away from the experimental site.

The data for the five independent variables were calculated as means of the following sub-periods of the total developmental and post-ripening periods of the cultivars.

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

Notation of the time periods should be interpreted in the following way:The yellow ripeness stage is zero time;the -20-10day period comprises the 10 days between the 20th and the 10th day prior to yellow ripeness. In the same way the -20+30-day period (Tables 3 and 4) designates the 50- day period beginning 20 days prior to yellow ripeness and terminating 30 days post yellow ripeness.

Correlation coefficients between seed dormancy parameters and climatic data for the first 10-day period after sowing, and the first 10 days after heading were all low and not significant. Data for these two periods were therefore omitted from further study. In some cases the other 10-day periods were combined in order to obtain periods of different lengths.

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

RESULTS

Dormancy and climatic parameters

Because of dormancy a seed may or may not germinate under optimum germination conditions. Therefore, for each seed, the character is qualitative. However, even in a genetic homogeneous breeding line some of the seed may germinate while others do not or, the germination may be delayed in speed or in time. The reason for this is most probably the different morphological or physiological stages of development of the seed at the date of harvest, i. e. differences between plants, between main shots and tillers and the different seed positions in the spike. In a sample of grain, threfore, seed dormancy behaves as a quantitative character and is treated as such in this study.

The dormancy parameter used is percent dormant seed in ordinary germination tests, or parameters calculated from such data, i. e. the Dormancy Index. The main advantage of the «percent dormant seed method» is that any intensity of seed dormancy may be measured on a 0-100 scale. The best differentiation of the character and the most accurate results are obtained when the dormancy readings are in the middle of the percentage scale. Low mean values for a period of years compared with the Standard Deviation indicate low or zero readings in a number of years. In such cases the possible effects of climatic factors on seed dormancy are recorded only in part. Table 1 shows that this has been the case for both cultivars germinated at 10°C, especially from the second harvest.

Germination at 10°C and at 20°C in moist sand for 10 days is a very strong test for seed dormancy. However, it has been used in order to obtain results in conformity with official seed testing. Purely for experimental purposes a different choice of germination temperature could have been made to obtain readings in a more favourable range of the percentage scale. As seed dormancy manifests itself more strongly at high germination temperatures such temperatures should be applied to low dormancy material and vice versa.

In Table 1 the mean and Standard Deviation of dormancy parameters are given for the two barley cultivars at two dates of harvest and for two germinating temperatures. In the bottom line of the table the Dormancy Index characterizing the cultivars is presented.The two lines above illustrate the manifestation of dormancy at 10°C and at 20°C germination temperatures. The changes in the intensity in dormancy of grain left unthreshed in the field for 20 days of the post-ripening period can be seen by comparing the results obtained at the first and second harvests.

Parameters characterizing the climatic conditions of the experimental period are given in Table 2. The climatic factors included are temperature, rainfall, air humidity, and global radiation. The growth period is divided into the sub-periods sowing to heading,heading to yellow ripeness, and yellow ripeness to second harvest.

The effects of climatic factors on the intensity of seed dormancy

In order to survey the material, all the logical correlation coefficients between dormancy parameters and climatic factors for growth periods of different length were calculated. The large number of correlation coefficients implies that some would reach significant levels by chance. Therefore, significant correlation coefficients without logical explanation were ignored or handled with care. However, the results indicated that the

Table 1. Means and Standard Deviation of dormancy parameters for the cv Lise and cv Mlyjar at two dates of harvest and at two germination temperatures

Dormancy parameters		cv Lise	cv Møyjar
First harvest			
Precent dormant seed, 10°C	Mean	31.6	37.3
	SD	27.4	24.9
Percent dormant seed, 20°C	Mean	83.5	82.9
	SD	11.4	15.1
Dormancy Index	Mean	49.0	52.6
	SD	19.6	19.7
Second harvest			
Precent dormant seed, 10°C	Mean	18.3	11.3
	SD	24.3	14.9
Percent dormant seed, 20°C	Mean	52.3	45.9
	SD	24.9	30.1
Dormancy Index	Mean	29.6	22.6
	SD	22.8	18.8
Mean of 1st and 2nd harvests:			
Percent dormant seed, 10°C	Mean	25.0	24.3
Percent dormant seed, 20°C	Mean	67.9	64.4
Dormancy Index	Mean	39.5	37.6

Table 2. Climatic parameters. Means for the 20.year period

Climatic factors	Development periods		
	Sowing-heading	Heading-y.ripeness	Y.ripeness-2nd harvest
Temperature, C	13.0	16.3	15.1
Rainfall, mm day ^{1}	2.15	2.55	1.77
Air rel, humidity %	59.8	64.2	63.4
Global rad, MJ m ^{2}day ^{1}	19.2	19.2	16.

majority of the significant correlation coefficients were concentrated within certain developmental stages. These were subjected to more detailed analyses.

Most of the dormancy-climate relationships studied are based on the correlation coefficients between percent dormant seed at 10°C and 20°C germination temperatures and the Dormancy Index at two dates of harvest as dependent variables, and climatic data in different developmental periods as independent variables. The results are presented in Table 3 for cv Lise and in Table 4 for cv Møyjar.

The tables show good agreement between the results obtained for the two cultivars. A main feature of the results is that the correlation coefficients between dormancy and climate parameters of the second harvest samples are much higher than the comparable coefficients of the first harvest samples. Another feature is that in spite of the fact that dormancy is considerably reduced from the first to the second harvest, the reactions to variations in climatic factors are much more precise in the second harvest.

It may also be noticed that the correlation analysis of the relationship between the first harvest samples germinated at 20°C and climatic parameters yielded no significant coefficients. Germinating the same samples at 10°C resulted in 18 significant coefficients out of a possible 40. There are no indications of such differences between the results of the 10°C and the 20°C germination tests in the second harvest samples.

All climatic factors included in the study showed significant effects on the intensity of dormancy. Higher temperatures and more intense global radiation reduced seed dormancy, while higher rainfall, higher air moisture and higher rainfall/temperature ratios increased seed dormancy. There are, however, indications of a few exceptions to this general pattern of reactions. For both cultivars, the correlation coefficients between temperature and all dormancy parameters for the sowing to heading period were positive. This reaction, if it holds, is the opposite of the reactions observed in the post-heading periods. Except for the reaction of Møyjar to air humidity the correlation coefficients for the sowing to heading period are low and non-significant.

It has already been mentioned that dormancy parameters of the first harvest samples showed low correlations with climatic parameters. The lower correlation coefficients are at least in part due to highly significant cultivar x year and cultivar x germination temperature interactions as shown by an analysis of variance test. The interactions consist mainly in correlation coefficients of r = -.68** and r = -.52* respectively for the cv Lise and the cv Møyjar between the sums of and differences in percent dormant seed germinated at 10°C and at 20°C, i. e. the stronger the dormancy the smaller the differences in the results

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

Climatic factors and development periods		HT 1			HT2		
		10 C	20 C	DI	10 C	20 C	DI
Temp.	S-H	.56**	-.13	.50*	.52*	.55*	.57*
	H-YR	-.35	.20	-.29	-.48*	-.46*	-.51*
	-20-0	-.36	-.14	-.35	-.52*	-.60**	-.59*
	-20+10	-.41	-.02	-.39	-.53*	-.60**	-.60*
	0+30				-.47*	-.57**	-.54*
	-20+30				-.53*	-.63**	-.61*
GR	S-H	.09	.10	.11	.13	.18	.16
	H-YR	-.48*	-.32	-.39	-.59**	-.55*	-.62*
	-20-0	-.60**	.02	-.55*	-.56**	-.70**	-.65*
	-20+10	-.51*	.05	-.46*	-.45*	-.60**	-.54*
	0+30				-.58*	-.53*	-.60*
	-20+30				-.60**	-.63**	-.66*
Rainfall	S-H	.24	-.02	.20	.09	.04	.09
	H-YR	.60**	-.13	.54*	.69**	.64**	.72*
	-20-0	.49*	.13	.49*	.63**	.65**	.68*
	-20+10	.60**	.07	.57**	.66**	.75**	.74*
	0+30				.58**	.36	.54*
	-20+30				.76**	.61**	.76*
RH	S-H	.14	-.03	.12	.32	.19	.29
	H-YR	.39	-.08	.34	.55*	.37	.52*
	-20-0	.44*	.09	.43	.51*	.53*	.55*
	-20+10	.46*	.08	.49*	.52*	.50*	.55*
	0+30				.61**	.43	.59**
	-20+30				.60**	.49*	.60**
R/T	S-H	.07	-.02	.04	-.04	-.06	-.06
	H-YR	.59**	-.15	.53*	.70**	.62**	.73**
	-20-0	.49*	.13	.49*	.67**	.66**	.71**
	-20+10	.60**	.05	.36	.71**	.76**	.79**
	0+30				.61**	.40	.58**
	-20+30				.78**	.64**	.79**

from the 10°C and the 20°C germination tests.

It should be noted that some of these reactions might have been due to an effect of the scale used, i. e. that the higher portion of dormant seed at the first harvest and the 20°C germination temperature resulted in smaller differences at the top of the percentage scale. For the lower dormancy level of the second harvest this effect would have been negligble. Due to the interactions between the cultivars and the climatic factors, the correlation coefficients between the mean of the two cultivars and the climatic factors are reduced. However, both cultivars, individually, also showed weaker correlation with climatic factors at the first harvest than at the second harvest.

For the second harvest the same correlation coefficients were r = -.12 and r = .75**. The difference between these two coefficients is highly significant, P<.001 and the reason is a different cultivar reaction to the 10°C germination test. The correlation coefficient between the mean and the difference in DI

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

Climatic factors and development periods		HT 1			HT2		
		10 C	20 C	DI	10 C	20 C	DI
Temp.	S-H	.41	.15	.38	.17	.34	.39
	H-YR	-.19	.14	-.13	-.44	-.60**	-.56*
	-20-0	.02	.12	.05	-.48*	-.63**	-.59*
	-20+10	-.08	.13	-.03	-.46	-.73**	-.65**
	0+30				-.43	-.80**	-.66**
	-20+30				-.49*	-.83**	-.71**
GR	S-H	-.51*	-.22	-.48*	-.45	-.61**	-.55*
	H-YR	-.60**	-.26	-.58*	-.45*	-.60**	-.62**
	-20-0	-.46	-.18	-.43	-.62**	-.74**	-.73**
	-20+10	-.50*	-.15	-.51*	-.71**	-.82**	-.77**
	0+30				-.67**	-.76**	-.77**
	-20+30				-.71**	-.82**	-.82**
Rainfall	S-H	.28	-.20	.18	.20	.30	.26
	H-YR	.56*	-.20	.46	.69**	.73**	.75**
	-20-0	.21	-.17	.14	.63**	.42	.56*
	-20+10	.34	-.21	.24	.68**	.60**	.58*
	0+30				.43	.36	.42
	-20+30				.64**	.47	.59*
RH	S-H	.42	-.06	.36	.64**	.52*	.61**
	H-YR	.53*	.09	.48*	.67**	.65**	.70**
	-20-0	.43	.09	.39	.61**	.58*	.63**
	-20+10	.44	.07	.39	.68**	.63**	.70**
	0+30				.69**	.65**	.71**
	-20+30				.71**	.67**	.73**
R/T	S-H	.18	-.22	.09	.16	.21	.19
	H-YR	.53*	-.03	.44	.69**	.75**	.77**
	-20-0	.20	-.18	.13	.66**	.47	.61**
	-20+10	.36	.20	.21	.70**	.67**	.65**
	0+30				.48*	.45	.49*
	-20+30				.67**	.55*	.65**

between the cultivars was r = .67**, i. e. at higher dormancy levels the cv Lise showed a greater increase in percent dormant seed than the cv Møyjar. For the remaining combinations, first harvest and 10°C germination temperature, and for both harvests and 20°C germination temperature the correlation coefficients were low.

The interactions between cultivars, climatic factors and germinating temperatures indicate that the manifestation of seed dormancy is controlled by a number of factors in a rather complicated way. The low correlation coefficients between climatic factors and first harvest dormancy parameters indicate that the experimental technique employed has been little effective in uncovering the pattern of dormancy reactions at early dates of harvest.

In order to facilitate the interpretation of the large number of correlation coefficients in Tables 3, and 4, the results are grouped and summarized in Tables 5 and 6. The correlation coefficients between the different climatic factors and the dormancy parameters at the

Table 5. Correlation coefficients between dormancy parameters and climatic factors. Mean for the two cultivars and for all development periods

Dormancy parameters	Climatic factors: Temperature	Global rad	Rainfall	Rel. humidity	Temp./ rainfall	Means ignoring signs
HT 1						
Percent dorm.seed 10°C	-.27	-.43	.39	.40	.37	.37
- » - 20°C	-.14	-.15	.09	.06	.12	.11
Dormancy Index	-.26	-.39	.34	.37	.33	.34
HT 2						
Percent dorm.seed 10°C	-.42	-.52	.49	.55	.51	.50
- » - 20°C	-.56	-.56	.43	.49	.45	.50
Dormancy Index	-.51	-.57	.49	.57	.51	.53
Mean of HT 1 and HT 2						
Percent dorm.seed 10°C	-.35	-.47	.44	.48	.45	.44
- » - 20°C	-.41	-.41	.31	.35	.33	.38
Dormancy Index	-.40	-.49	.42	.48	.43	.45
Mean for HT 1	-.23	-.35	.30	.32	.29	.30
Mean for HT 2	-.50	-.55	.47	.54	.49	.51
Mean for each climatic factor	-.39	-.46	.39	.44	.41	

two harvest dates are summarized in Table 5. The table shows that global radiation and air humidity present the highest correlation coefficients and temperature and rainfall the lowest. The differences, however, are minimal. In relation to the considerable attention paid to temperature as a dormancy controlling factor these results are surprising. The table also shows, as already mentioned, that the second harvest dormancy parameters are much stronger correlated with climatic factors than the first harvest dormancy data.

Table 6. Correlation coefficients (signs ignored) between dormancy parameters and climatic factors for different periods prior to harvest. Means for all correlation coefficients involving climatic factors, germination temperatures and cultivars

Time periods	HT 1	HT 2	Means
Sowing-heading	.25	.31	.28
Heading-ripeness	.42	.65	.55
Sowing-ripeness	.39	.47	.43
Periods prior to -20-10	.25	.39	.32
or post yellow -10-0	.39	.59	.49
ripeness. days 0+10	.29	.46	.38
+10+20		.49	
+20+30		.47	
10 days prior to harvest	.21	.43	.32
20 «	.26	.48	.37
30 «	.26	.56	.41
40 «		.61	
50 «		.66	

In principle, the highest correlation coefficients are obtained at germination temperatures where the resulting dormant seed has values in the middle of the percentage scale. Reduced differentiation because of compaction of the data at either end of the percentage scale therefore results in lower correlation coefficients. Percent dormant seed at 10°C germinating temperature gave slightly higher correlation coefficients with climatic factors than percent dormant seed at 20°C. The results obtained indicate that the reduction in the 20°C based correlation coefficients in high dormancy years occurred more frequently than the reduction in the 10°C based

correlation coefficients in low dormancy years.

The correlation coefficients between dormancy parameters and climatic data from 10-day periods at different developmental stages or periods of different length prior to harvest are calculated in Table 6. The table shows that the effects of climatic factors on dormancy are almost equally strong in each of the 10-day periods from 20 days prior to yellow ripeness to 30 days after yellow ripeness (HT 2). The lower values for the H-20-10-day period are due mainly to the weak effect of rainfall in that period (see also Tables 3, 4 and 5). It was mentioned earlier that the climatic data for the first 10-day period after heading showed low correlation coefficients with dormancy parameters. It can be concluded from this that the effects of climatic factors on seed dormancy in barley increase greatly from a point approximately 3 weeks prior to yellow ripeness.

Increasing the length of the climatic observation periods improved the correlations between dormancy and climatic factors. The heading to ripeness period, which on the average was 37 days, yielded most information on the development of dormancy for the combined first and the second harvest. The high correlation coefficients between second harvest dormancy and climatic factors during the ripening period are of particular interest. They show that the climatic conditions of that period largely determine dormancy development regardless of weather conditions during the last 30 days prior to harvest. This fact, and the increase in information obtained by extending the length of the observation periods prior to the second harvest, shows very clearly that the effects of climatic factors on dormancy development take place over a long period of time and that they are accumulative.

The different climatic factors are intercorrelated, negatively or positively showing r-values ranging from r = .67 to r = -.70 as listed in Table 7. The simple correlation coefficients between dormancy parameters and each of the climatic factors, are therefore more or less influenced by other factors. The partial regression analysis technique was applied in order to obtain a better estimate of the real effect of each climatic factor.

Table 7. Correlation between climatic factors calculated for the period from heading to second harvest

Climatic factors	Correlation coefficient
Temperature - rainfall	-.60**
Temperature - air humidity	-.57**
Temperature - global radiation	.67**
Rainfall - air humidity	.67**
Rainfall - global radiation	-.61**
Air humidity - global radiation	-.70**

In Table 8 the contribution by each climatic factor in each growth period is calculated as the mean result of all possible successions of the independent variables in the multiple regression analysis. The results in the table show that with regard to dormancy the two barley cultivars reacted differently to climatic factors. The ranking of the factors by this technique of analysis is fairly close to the results obtained by using the simple correlation analyses in Tables 3 and 4. The multiple correlation coefficients show that 83 % and 94 % of the variation in seed dormancy for the two cultivars respectively can be ascribed to the effects of the climatic factors.

A third approach to the problem of separating the effects of the different climatic factors on seed dormancy was to apply the partial correlation analysis technique. The temperature and the global radiation factors, which are closely related in nature and in effect on seed dormancy, are both negatively correlated with dormancy. These were combined as one variable in the analyses. The three moisture factors - rainfall, air

Table 8. Percent contribution by each climatic factor and each growth period to the variation in the second harvest Dormancy Index for the barley cultivars Lise and Møyjar

Climatic factors or growth periods	cv Lise	cv Møyjar	Mean
Climatic factors			
Temperature	16.0	19.2	17.6
Global radiation	19.8	30.8	25.3
Rainfall	35.3	24.0	29.7
Air relative humidity	12.2	20.1	16.2
Sums in terms of 100 R^2	83.3	94.1	
Growth periods			
Sowing-heading	16.9	22.0	19.5
Heading-ripeness	34.0	34.3	34.2
30 days post yellow ripeness	32.4	37.8	35.1
Sums in terms of 100 R^2	83.3	94.1	
R	.91**	.97**	

humidity and the rainfall/temperature ratio - are also closely related and are all positively correlated with dormancy. These were combined as one moisture factor in the analysis. The developmental period used extended from 20 days prior to yellow ripeness and to second harvest, i. e. 50 days in all.

Table 9. Simple and partial correlation coefficients between the Dormancy Index and temperature-radiation and moisture factors

Variables	cv Lise	cv Møyjar
Simple corr. coefficients		
DI and temp.-radiation	-.67**	-.81**
DI and moisture factors	.78**	.66**
Partial corr. coefficients		
DI and temp.-radiation	-.22	-.65**
DI and moisture factors	.57**	.25

The simple and partial correlation coefficients between the Dormancy Index and these two factors are presented in Table 9. The results show that the simple correlation coefficients are all significant and of the same magnitude. The partial correlation coefficients, however, show that the moisture factor had the greatest effect on seed dormancy of cv Lise and that the temperature/radiation factor had the greatest effect on the seed dormancy of Møyjar.

Effects of climatic factors on the dormancy curve and on the manifestation of seed dormancy at different germination temperatures

Besides the effects of climatic factors on the intensity of seed dormancy there are also other dormancy/climate relationships which are of interest. The correlation coefficients between the climatic factors and the DI HT 2/DI HT 1 ratio and the ratio of dormant seed at 10°C and at 20°C germination temperatures for three developmental stages are calculated in Table 10. The DI HT 2 / DI HT 1 ratio describes the rate of increase or rate of decrease in dormancy from the first to the second harvest. The negative correlation coefficients between this ratio and temperature and global radiation show that high values of these climatic parameters induce a sharper decline in seed dormancy from the first to the second harvest, and vice versa. Rainfall, air humidity and the rainfall/temperature ratio had the opposite effect, making the dormancy more long

Table 10. Correlation coefficients between climatic factors on one side and the HT2/HT1 Dormancy Index ratioes and the ratioes of dormant seed at 10°C and 20°C germination temperatures on the other. Mean results for cv Lise and cv Møyjar

Climatic factors and development periods	Dormancy Index HT 2/HT 1	Percent dormant seed 10°C/20°C HT 1	HT 2
Temperature			
Heading-yellow ripeness	-.60**	-.33	-.51*
30 days prior to HT 1	-.72**	-.33	-.54*
30 days prior to HT 2	-.64**	-.50*	-.47*
Global radiation			
Heading-yellow ripeness	-.54*	-.59**	-.52*
30 days prior to HT 1	-.63**	-.56*	-.55*
30 days prior to HT 2	-.67**	-.56*	-.63**
Rainfall			
Heading-yellow ripeness	.69**	.63**	.68**
30 days prior to HT 1	.70**	.54*	.67**
30 days prior to HT 2	.46*	.40	.56*
Air relative humidity			
Heading-yellow ripeness	.48*	.45	.45
30 days prior to HT 1	.54*	.48*	.60**
30 days prior to HT 2	.63**	.46*	.69**
Rainfall/temperature ratio			
Heading-Yellow ripeness	.71**	.61**	.69**
30 days prior to HT 1	.76**	.54*	.71**
30 days prior to HT 2	.51*	.45	.59**
Means for climatic factors			
Heading-yellow ripeness	.60	.52	.57
30 days prior to HT 1	.67	.49	.61
30 days prior to HT 2	.58	.47	.59

lasting. It may be noted that the correlation coefficients between the DI HT 2/ DI HT 1 ratio and the climatic factors in most cases are higher than those between parameters describing the intensity of seed dormancy and the same climatic factors in Tables 3, and 4.

There was also a highly significant correlation, r = .61**, between the DI HT 2/DI HT 1 ratio and the mean dormancy of the season (mean DI of the first and second harvests.) Mathematically, this means that strong dormancy is reduced more slowly or peaks at a later date, and vice versa. In a few high dormancy years, the dormancy was even stronger at the second harvest than at the first. (see also Fig. 2) This makes it clear that those factors that induce strong dormancy also retard its rate of disappearance.

The ratios between percent dormant seed in samples germinated at 10°C and at 20°C were also strongly influenced by the climatic factors. High temperature and high global radiation reduced the ratios, which gave rise to greater differences in dormancy manifestation measured at 10°C and at 20°C germination temperatures. Rainfall, air humidity, and the rainfall/temperature ratioes had the opposite effects, reducing the differences in dormancy observed at 10°C and at 20°C. Regarding the main effects of the climatic factors on dormancy in Tables 3 and 4, the results presented in

Table 10 show that the effects of climatic factors on these other dormancy/climate relationships also extended beyond the periods of climatic observation. The effects of the climatic factors in a period terminating 30 days prior to the second harvest (the heading to yellow ripeness period) had an equally strong effect on dormancy as the effect of the same factor in the 30-day period preceding the second harvest.

Seasonal and short term fluctuations in seed dormancy

In two years six barley cultivars were harvested at five developmental stages, namely at yellow ripeness, and later at 10 - day intervals. The mean results for the six cultivars are presented in Fig. 1. In 1961 the climatic conditions were close to the means of the period and showed low variation. The resulting dormancy curve was close to the long term average. In 1960 the mean temperatures for the 10-day periods varied from 9.7°C to 14.7°C, and the mean rainfall from .72 mm to 7.84 mm per day. The resulting dormancy curve varied greatly, as shown in the figure. The least significant difference (Lsd, p=. 05)between Dormancy Index figures at the different dates of harvest is approximately 6.0 percentage points. The increase in seed dormancy from 10 to 20 days and from 30 to 40 days, and the decrease in dormancy from 20 to 30 days by 10 percentage points in each case, are therefore all highly significant.

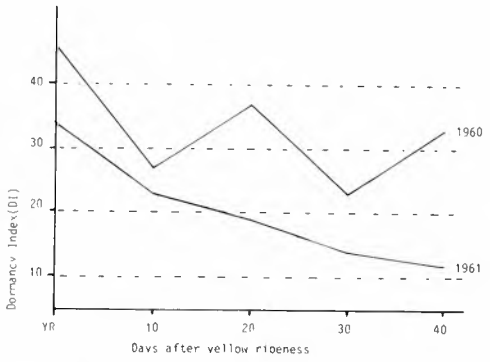

Figure 1. Dormancy Index at 10 days intervalls. Mean of six cultivars

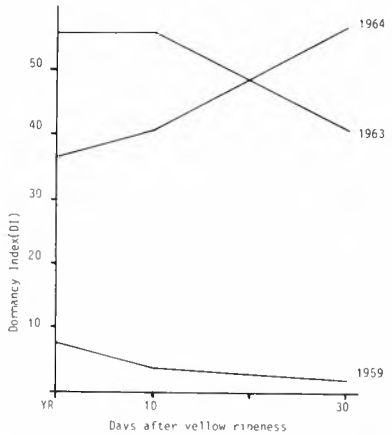

Figure 2. Dormancy Index in selected years of extreme climatic conditions. Means of six cultivars

The reactions of seed dormancy in the years selected for extreme climatic conditions are illustrated in Fig. 2 where the curves are drawn from the mean results of six barley cultivars harvested at yellow ripeness and at 10 days and 30 days later. In 1959, a season of very high temperature and low rainfall, dormancy was extremely low, and it decreased steadly during the postripening period. A cool and moist ripening period in both 1963 and 1964 resulted in high dormancy at yellow ripeness. In 1963 the weather then became warmer and drier and dormancy decreased. In 1964 the cool and moist weather continued during the postripening period, and the dormancy increased at least to 30 days after yellow ripeness.

The conclusions drawn from the results presented in Figs. 1 and 2 are that seed dormancy in the field may vary greatly from season to season due to variation in temperature and moisture factors, that combinations of low temperature and high rainfall can temporarly increase seed dormancy and that maxi-

mum dormancy may occure very late in the post-ripening period.

The efficiency of different methods for testing cultivar differences in seed dormancy

Seed dormancy is a genetic character, but it is strongly influenced by environmental factors. In cultivar testing and breeding it is important to have methods by which the cultivar controlled seed dormancy can be determined precisely and cheaply. The seven methods for testing seed dormancy described in section II are compared in Table 11. The material used for the comparisons consist of three different sets of six barley cultivars grown in the field for periods of 6, 9, and 10 years. The efficiency of the different methods are compared using the F values for testing cultivar differenses in the analysis of variance. The F-value, i. e. the ratio between the cultivar and the cultivar x year interaction variance, is assumed to be the best criterion for determining the efficiency of the different methods.

Table 11 shows that the manifestation of dormancy at 20°C germination temperature gave a better basis for differentiation between cultivars than 10°C germination temperature. Dormancy measured at the second harvest gave higher F-values than those of the first harvest. The highest F-value for a single test was obtained at 20°C at the second harvest.

In Table 5 it is shown that the highest correlation coefficients between dormancy and climatic parameters were obtained from second harvest samples. In Table 11 the second harvest samples also gave the best differentiation between cultivars with regard to seed dormancy. In Table 5 it is shown that the 10°C germination temperature gave slightly higher correlation coefficients with climatic factors than the 20°C germination temperature.. In Table 11, however, a much better cultivar differentiation was obtained for the 20°C germination temperature. This means that the temperature which gives the most sensitive dormancy reactions to climatic factors is not necessarily the most favourable for testing differences between cultivars.

It is also important that the testing methods can be used over a wide range of dormancy intensities. The mean percent of dormant seed for the four combinations of germination temperatures and dates of harvest for the material were

HT 2, 10°C	13.8
HT 1, 10°C	22.9

Table 11. The efficiency of methods for testing cultivar differences in seed dormancy. F-values for testing differences between cultivars

Methods	1960-65 6 cultivars	1971-79 6 cultivars	1976-85 6 cultivars	Means
HT 1 10°C germ. temp.	7.86	9.22	5.24	7.44
» 20°C «	15.26	12.71	1.76	9.91
» DI	13.64	15.18	6.16	11.66
HT 2 10°C germ. temp.	9.17	6.57	5.46	7.07
» 20°C «	18.83	17.43	13.41	16.56
» DI	13.61	16.65	17.04	15.77
Mean DI	26.33	22.42	15.84	21.53
Mean for 10°C	8.52	7.90	5.35	7.26
20°C	17.05	15.07	7.59	13.26
HT 1	11.56	10.97	3.50	8.68
HT 2	13.75	12.00	9.44	11.73

HT 2, 20°C	36.1
HT 1, 20°C	68.2

The results show that by these methods the figures for the same dormancy intensity are located in different parts of the percentage scale. For higher efficiency of the dormancy test, the germination temperatures and the dates of harvesting should be chosen in such a way that figures at either end of the percentage scale are avoided. However, the mean Dormancy Index, which is based on all methods, can be used for most cereal cultivars and breeding material. Finally, because of cultivar dissimilarities in the manifestation of seed dormancy at different temperatures, the temperature chosen for the dormancy test should in principle be close to the temperature prevailing at the time when the crops are most exposed to pre-harvest sprouting damage.

DISCUSSION AND CONCLUSIONS

In a number of research reports reviewed by BELDEROK (1968) and others, and also in reports which have appeared more recently, most attention has been paid to temperature as a seed dormancy controlling environmental factor. The results presented in this paper confirm that temperature has a significant effect on rate of development, intensity, longevity, and rate of disappearance of seed dormancy. However, the investigations also showed that other climatic factors such as global radiation, rainfall, and air humidity, have an equal or stronger effect on seed dormancy than the temperature.

It is difficult to determine the effects of each climatic factor on the seed dormancy parameters because they are more or less strongly intercorrelated (see Table 7).

Using the partial regression and partial correlation analysis, attempts were made to separate the effects of each climatic factor on the seed dormancy parameters and to allocate these effects to the proper climatic factor. The results are presented in Tables 3, 4, 5,6,9,10 and 11.

Since seed dormancy is influenced by many climatic factors during the ripening and post-ripening periods, the correlation coefficients between seed dormancy and each climatic factor are comparatively low. For the same reason the contribution by each climatic factor for a shorter time, i. e. 10 days, to the variation in seed dormancy is also low. The sum of the effects,however, adds up to 80-90 % of the total variation in seed dormancy. Because reactions are recorded over a long period of years, most of the correlation coefficients are highly significant.

The most important conclusions which can be drawn from the results obtained are as follows.

1. The climatic factors temperature, global radiation, rainfall, air humidity and the rainfall/temperature ratio all had significant effects on the rate of development, intensity, variation, longevity, rate of disappearance and also on the manifestation of seed dormancy at different germination temperatures.

2. The influence of climatic factors on seed dormancy commences at approximately 20-25 days prior to yellow ripeness, and continues for at least 30 days beyond the stage of yellow ripeness. There are also indications of temperature effects in the preheading period.

3. The effects of climatic factors on seed dormancy seem to be equally strong throughout the period of influence and the effects are accumulative. This means that the longer the periods of climatic observation the more precisely can the dormancy reactions be predicted.

4. From the first to the second harvest (20 days) the intensity of dormancy was

reduced from 49.0 to 29.6 = 19.4 DI-points for cv Lise and from 52.6 to 22.6 = 30.0 DI-points for cv Møyjar. For cv Lise the reduction, 1.0 per day, is approximately the same as that found in the storage study (STRAND 1965) using a closely related cultivar. The cv Møyjar showed a much faster reduction in dormancy, indicating that cultivar differences may also exist for this aspect of the dormancy character.

5. In addition to inducing high dormancy, steady climatic conditions favourable for high dormancy may delay the date of maximum dormancy to at least 30 days after yellow ripeness. With the same climatic conditions occurring when the dormancy is on the downward slope of the curve, there may be a temporary increase in dormancy.

6. The cultivars reacted differently to the temperature/radiation and the moisture factor group of climatic factors with regard to seed dormancy parameters. The manifestation of seed dormancy at the two germination temperatures was different for the cultivars. It may be concluded from this that other cultivar x climate factor interactions or other interactions involving cultivars may also occure.

7. Cultivar differences in seed dormancy were determined more precisely at the 20°C rather than at the 10°C germination temperature and more precisely at the second harvest than at the first. The best factor combination for a single test was the 20°C germination temperature and the second harvest. The Dormancy Index was the most efficient method for determining the genetically controlled seed dormancy of barley cultivars and breeding material.

8. For some unknown reason the effects of climatic factors on dormancy were weakly manifested at the first harvest. The efficiency of the methods for testing cultivar differences in seed dormancy was also low at the first harvest. This indicates that the experimental methods or experimental techniques employed were less effective in uncovering cultivar differences in seed dormancy and seed dormancy/climate relationships at early harvest stages.

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STUDIES ON SEED DORMANCY IN SMALL GRAIN SPECIES. II. WHEAT

ERLING STRAND
Agricultural University of Norway, Department of Crop Science, Aas, Norway

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The occurrence of seed dormancy in spring wheat was investigated in cultivars grown in the field for 11 to 20 years. The intensity of seed dormancy was measured as percent dormant seed in germination tests carried out in moist sand for 10 days at 10°C and at 20°C. The seed samples in most cases were harvested 10 days and 30 days post yellow ripeness.The effects on the dormancy character of temperature, global radiation, rainfall and air humidity in periods of 10 days or longer were studied.

Seed dormancy was stronger in samples harvested 10 days post yellow ripeness than in samples harvested 30 days post yellow ripeness, and was more strongly manifested at 20°C than at 10°C germination temperature. Higher temperatures and more intense global radiation in pre-harvest periods generally reduced seed dormancy, while higher rainfall and higher air humidity had the opposite effects. In some cases climatic factors had the opposite effects on seed dormancy at 20°C and 10°C germination temperatures. Some of the wheat cultivars reacted most strongly to the temperature-radiation factors, while others had strongest reaction to the moisture factors.

Climatic effects on seed dormancy were more strongly manifested in samples harvested 30 days post yellow ripeness than in those harvested 10 days post yellow ripeness.The seed dormancy builds up during a period beginning approximately 20 days prior to yellow ripeness.

The climatic factors affected the ratio of dormant seed obtained at 10°C and at 20°C germination temperatures and also the slope of the dormancy curve between the first and second harvests. It is shown that 9.9% to 64.5% of the non-genetic variation in seed dormancy could be ascribed to variation in climatic factors.

The genetically controlled seed dormancy can be determined by either of the methods applied, as there were no important differences in the efficiency of the tests based on samples from the two stages of harvest, or on the two germination temperatures. Finally, the possibilities of working out a warning system for pre-harvest ear sprouting damage based on climate-seed dormancy relationships are discussed.

Additional key words: Temperature, rainfall, air humidity, global radiation.

Erling Strand,Department of Crop Science,Agricultural University of Norway, P.O.41, N-1432 Aas-NLH

This paper, which deals with wheat, is the second part of a more comprehensive study on seed dormancy in small grain species and cultivars. The first paper (STRAND 1989), dealing with barley, contains some general information and discussion on the subject and may therefore be read as an introduction to or in connection with this present paper.

MATERIAL AND METHODS

The spring wheat cultivars used in the

main part of the study were cv Runar grown for 20 years, cv Reno grown for 17 years, and cv Drabant grown for 11 years under field conditions. In part of the study other spring wheat cultivars and other time periods were also included. Most of the cultivars are well adapted and have been widely grown in the area.

The developmental stages of the plants were defined as follows: *Heading* when 50% of the spikes were completely out of the boots; *yellow ripeness*(YR) when the moisture content of the kernels was 38% of fresh weight.

The germination tests were carried out by the State Seed Testing Station in accordance with the official methods, namely, germination in moist sand for 10 days at 10°C and at 20°C using 200 kernels in each test. Percent dormant seed in these tests was used as a measure of the intensity of seed dormancy directly or indirectly in parameters calculated from such data.

The dormancy parameters (dependent variables) recorded for the material were

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) which is calculated in the following way:

$$DI = \frac{\%\ \text{dorm.seed at } 10°C * 2 + \%\ \text{dorm.seed at } 20°C}{3}$$

4. Mean of the Dormancy Index of the first and second harvests.
5. The ratio percent dorm.seed at 10°C/percent dorm.seed at 20°C.
6. The ratio DI HT 2/DI HT 1.

The six dormancy parameters were determined on seed samples harvested approximately 150 day-degrees, or 10 days post yellow ripeness, (Ht 1), and 450 day-degrees, or 30 days (Ht 2) post yellow ripeness.

The 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 (R).
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.

The data for the five independent variables were calculated as means of the following sub-periods of the total developmental and post-ripening periods of the cultivars:

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

Notation of the time periods should be interpreted in the following way. The -20-10 period comprises the 10 days between the 20th and the 10th day prior to yellow ripeness. In the same way the -20+30 period (see Tables 3,4 and 5) designates the 50- day period beginning 20 days prior to and terminating 30 days post yellow ripeness.Two or more of these 10-day periods were later combined in order to obtain periods of different length. The statistical methods used

for analysing the data were the analysis of variance, and the correlation and regression analysis.

RESULTS

Data on the cultivars and the climate factors

The means of climatic parameters for a period of 20 years are given in Table 1. The data in the table describe the climatic conditions under which the plants were grown. Information on the plant material used in the study is presented in Table 2. For each of the three spring wheat cultivars the mean length of the growth period (sowing to yellow ripeness) and the heat sum of the period are calculated. The dormancy parameters characterizing the cultivars are given for the two dates of harvest and for the two germination temperatures. As well as characterizing the cultivars, the data also illustrate the intensity of the dormancy at the two dates of harvest and the effects of germination temperatures on the manifestation of seed dormancy.

Effects of climatic factors on the intensity of seed dormancy

The main results of relationships between seed dormancy and climatic factors for the Runar, Reno and Drabant cultivars are given in Tables 3, 4 and 5, respectively. Correlation coefficients between all dormancy parameters and climatic data for each 10-day period were calculated. Based on the results obtained the 10-day periods were then pooled to 20, 30, or 50-day periods. The correlation coefficients between the dormancy parameters and the climatic data for these new periods are presented in Tables 3, 4 and 5 respectively. Other results of the

Table 1. Climatic parameters. Means for period of 20 years (Runar)

Climatic factors	Development periods		
	Sowing-heading	Heading-yellow ripeness	Yellow ripeness-HT 2
Temperature (C)	12.9	16.0	13.5
Rainfall (mm per day)	2.04	2.45	2.17
Air rel. humidity (%)	59.7	63.4	66.4
Global rad. (MJm^{-2} day^{-1})	19.1	18.5	13.8

Table 2. Growth periods and dormancy parameters of the three spring wheat cultivars

		Runar		Reno		Drabant	
		Mean	SD	Mean	SD	Mean	SD
Growth periods							
	Days	105		107		112	
	Heat sum (day degrees)	1498		1523		1590	
Dormancy parameters							
HT 1	Dorm.seed (% at 10°C)	3.5	4.3	5.8	5.2	3.2	4.4
	Dorm.seed (% at 20°C)	40.6	20.1	48.3	20.5	41.4	15.7
	Dormancy Index	15.5	9.0	20.0	8.5	16.0	6.6
HT 2	Dorm.seed (% at 10°C)	1.6	2.9	3.5	3.5	4.8	7.3
	Dorm.seed (% at 20°C)	13.2	12.5	28.1	13.0	30.2	17.0
	Dormancy Index	5.5	4.9	11.8	5.3	13.4	8.7
Mean	Dormancy Index	10.8	4.9	15.9	5.5	15.1	5.6

study of the 10-day periods are given in Figures 1 and 2.

It is apparent from the tables that the effects of climatic factors on the intensity of seed dormancy in the three wheat cultivars, especially for the first harvest samples, are low and very varied compared with the results obtained for barley (STRAND 1989). The results showed that for cv Runar (Table 3), the variation in temperature during the 20-year period of observation had no significant effect on the intensity of seed dormancy. Global radiation had significant effect on seed dormancy of the second harvest samples germinated at 10°C. More intense global radiation reduced seed dormancy and vice versa. The effects of rainfall, air humidity, and the rainfall/temperature ratio on seed dormancy were more consistent, as shown by the higher correlation coefficients. For these factors, larger amounts of rainfall,higher air humidity,and higher R/T ratios increased seed dormancy. Regarding the three climatic factors, some effects were also noted in samples from the first harvest. Second harvest samples

Table 3. Correlation coefficients between dormancy and climatic parameters in different developmental periods of cv Runar

Climate factors and developmental periods		HT 1			HT 2		
		10°C	20°C	DI	10°C	20°C	DI
Temp.	S-H	.37	-.11	.03	.02	-.37	-.25
	H-YR	-.25	.28	.11	-.01	-.40	-.34
	-20-0	-.28	.22	.05	-.19	.44	.21
	-20+10	-.33	.17	-.01	-.21	.29	.14
	0+30				-.37	.06	-.18
	-20+30				-.35	.19	-.08
GR	S-H	.23	-.06	.05	-.27	-.07	-.15
	H-YR	.21	.09	.18	-.44	-.09	-.26
	-20-0	-.08	.21	.18	-.51*	.33	.02
	-20+10	-.18	.26	.17	-.50*	.19	-.05
	0+30				-.39	.08	-.18
	-20+30				-.50*	.21	-.10
Rainfall	S-H	0	-.10	-.11	.11	-.15	-.12
	H-YR	-.13	-.27	-.25	.47*	-.11	.17
	-20-0	-.48*	-.29	-.45*	.62**	-.19	.08
	-20+10	-.38	-.41	-.49*	.72**	-.20	.01
	0+30				.32	-.01	.11
	-20+30				.64**	-.13	.14
RH	S-H	-.18	-.15	-.20	.49*	-.18	.04
	H-YR	-.17	-.26	-.28	.56**	-.19	.07
	-20-0	-.30	-.45*	-.50*	-.50*	-.34	-.02
	-20+10	-.21	-.42	-.42	.52*	-.31	-.06
	0+30				.37	-.26	-.01
	-20+30				.46*	-.34	-.04
N/T	S-H	-.10	-.05	-.10	.11	-.10	-.04
	H-YR	-.46*	-.38	-.46*	.48*	-.02	.19
	-20-0	-.47*	-.13	-.45*	.53*	-.20	.03
	-20+10	-.37	-.24	-.49*	.75**	-.18	.15
	0+30				-.10	-.01	.23
	-20+30				.32	-.11	.20

Table 4. Correlation coefficients between dormancy and climatic parameters in different developmental periods of cv Reno

Climate factors and developmental periods		HT 1			HT 2		
		10°C	20°C	DI	10°C	20°C	DI
Temp.	S-H	.24	-.14	-.02	.46	-.02	.20
	H-YR	-.40	.32	.09	-.50	-.39	-.53*
	-20-0	-.53*	.06	-.17	-.43	-.16	-.30
	-20+10	-.57*	.04	-.21	-.60*	-.18	-.40
	0+30				-.72**	-.27	-.54*
	-20+30				-.71**	-.27	-.53*
GR	S-H	.30	.15	.24	-.18	.31	.21
	H-YR	-.15	.24	.12	-.31	-.02	-.12
	-20-0	-.31	.32	.13	-.56*	.05	-.18
	-20+10	-.31	.39	.18	-.62*	.04	-.23
	0+30				-.58*	-.11	-.34
	-20+30				-.64**	-.04	-.30
Rainfall	S-H	-.04	.16	.15	.50*	-.26	.01
	H-YR	.06	-.36	-.26	.47	.08	.23
	-20-0	-.09	-.25	-.23	.33	-.10	0
	-20+10	-.02	-.27	-.23	.44	-.18	.01
	0+30				.29	.29	.13
	-20+30				.45	-.07	.11
RH	S-H	-.12	-.21	-.21	.22	-.51*	-.35
	H-YR	-.21	-.40	-.40	.34	-.37	-.20
	-20-0	-.05	-.53*	-.44	.30	-.08	.02
	-20+10	-.04	-.54*	-.44	.34	-.20	-.05
	0+30				.34	-.15	0
	-20+30				.34	-.15	-.01
N/T	S-H	-.04	.18	.14	.40	-.27	-.05
	H-YR	.11	-.38	-.25	.49	.13	.28
	-20-0	-.04	-.27	-.23	.38	-.09	.03
	-20+10	.04	-.31	-.23	.51*	-.15	.06
	0+30				.47	.02	.23
	-20+30				.58*	-.02	.20

germinated at 20°C yielded no significant correlation coefficients with climatic factors. Of the first harvest samples germinated at 20°C, only one correlation coefficient reached a significant level.

In a number of cases the correlation coefficients between climatic factors and dormancy based on 10°C and 20°C germination temperatures revealed opposite signs; for the second harvest 26 out of 30 pairs, and for the first harvest 18 out of 30 pairs of correlation coefficients had opposite signs. For a number of pairs the differences between the correlation coefficients were significant.

Interactions between germination temperatures and developmental stages had been observed earlier. Dormancy in very young seed is more strongly manifested at low germination temperatures. From a developmental stage of 14-17 days prior to yellow ripeness the manifestation of dormancy became strongest at higher temperatures (STRAND 1965). The opposite reactions of the samples germinated at 10°C and at 20°C implyes that the correlation coefficients between

Table 5. Correlation coefficients between dormancy and climatic parameters in different developmental periods of cv Drabant

Climate factors and developmental periods		HT 1			HT 2		
		10°C	20°C	DI	10°C	20°C	DI
Temp.	S-H	.24	-.06	.06	.28	.42	.43
	H-YR	-.31	.25	.06	-.68*	-.73**	-.85**
	-20-0	-.16	-.02	-.09	-.66*	-.67*	-.81**
	-20 + 10	-.32	.14	-.03	-.68*	-.70**	-.84**
	0 + 30				-.71**	-.62*	-.79**
	-20 + 30				-.73**	-.66*	-.83**
GR	S-H	.03	-.11	-.08	-.08	.38	.20
	H-YR	-.21	.27	-.12	-.71**	-.34	-.62*
	-20-0	-.20	.06	-.05	-.67*	-.49	-.70*
	-20 + 10	-.33	.16	-.02	-.65*	-.58	-.74**
	0 + 30				-.55	-.58	-.68*
	-20 + 30				-.64*	-.57	-.72**
Rainfall	S-H	.70*	-.02	.28	.24	.29	.31
	H-YR	.01	-.44	-.34	.45	.23	.40
	-20-0	-.06	-.06	-.06	.25	.23	.30
	-20 + 10	.21	-.12	.01	.40	.46	.52
	0 + 30				-.15	.12	-.02
	-20 + 30				.05	.28	.20
RH	S-H	.06	.19	.18	.32	-.08	.14
	H-YR	.15	.12	.17	.55	.22	.46
	-20-0	.10	.22	.23	.48	.32	.48
	-20 + 10	.24	.17	.25	.47	.44	.55
	0 + 30				.35	.25	.36
	-20 + 30				.43	.31	.45
N/T	S-H	.58	-.03	.23	.16	.19	.20
	H-YR	.03	-.44	-.32	.53	.32	.50
	-20-0	-.06	-.13	-.11	.36	.30	.40
	-20 + 10	.18	-.19	-.06	.49	.50	.60*
	0 + 30				.23	.45	.40
	-20 + 30				.36	.51	.52

climate factors and the Dormancy Index become less significant than the coefficients for either of the germination temperatures.

The results for cv Reno (Table 4) are very similar to those obtained for cv Runar. One difference may be that cv Reno reacted more strongly to the temperature-radiation factors and less strongly to the moisture factors. Opposite signs of the correlation coefficients obtained at 10°C and at 20°C germination temperatures also occurred for cv Reno, but the differences between the correlation coefficients are less significant.

The results for cv Drabant (Table 5) showed most similarity with those of cv Reno. The effects of the temperature-radiation factors on seed dormancy, however, were much stronger than for the other two cultivars. On the other hand the effects of the moisture factors were weaker, as shown by the fact that only one of the correlation coefficients between dormancy and the moisture factors in the post-heading periods was significant. For cv Drabant, it may be noted

that the second harvest samples germinated at 20°C showed correlation coefficients almost as high as the samples germinated at 10°C. There were no strong indications of differences between the correlation coefficients based on 10°C and on 20°C germination temperatures.

In spite of the fact that on average the annual variation in seed dormancy of the first harvest samples was equally as high as the seed dormancy recorded for the second harvest (Table 2), the variation in the first harvest dormancy was not or only weakly correlated with the climate factors. Attention should be drawn to some possible reasons for the low correlation coefficients between climate factors and dormancy of first harvest samples.

It is a well-known fact that mechanical damage to the kernels tends to break seed dormancy. Kernels of oat and barley are protected by the adhering lemmas during the threshing operation. The naked kernels of wheat are more exposed to mechanical damage during threshing. To give a precise and unbiased determination of seed dormancy in wheat, is therefore, more difficult.

Despite careful threshing using a machine equipped with a rubber bar drum, mechanical damage to the kernels may have occurred in some high moisture years, especially at the first harvest. An indication of such damage is the recording of lower germination capacity of first harvest high moisture samples than of the drier samples from the second harvest. It is also possible that minor damage, not resulting in lower germination capacity, may have reduced seed dormancy. However, the omitting from the material of three years showing reduced germination of first harvest samples did not improve the correlation coefficients. As far as the results of this

Table 6. Percent contribution by each climatic factor to the variation in dormancy parameters

Cultivars and climate factors	Dormancy parameters						Means
	HT 1			HT 2			
	10°C	20°C	DI	10°C	20°C	DI	
Runar							
Temperature	16.1	.9	3.2	6.0	1.8	4.5	5.4
Global rad.	4.4	3.0	2.9	4.7	2.0	2.6	3.3
Rainfall	20.1*	10.7	18.3*	4.4	.2	.6	9.1
Air humidity	5.8	7.8	8.4	5.0	5.9	3.0	6.0
R	.68**	.47	.57*	.45	.31	.33	
100 R^2	46.4	22.4	32.8	20.1	9.9	10.7	
Reno							
Temperature	37.0**	7.4	20.0*	37.6**	11.8	31.7**	24.3
Global rad.	3.3	13.4	8.5	8.7	1.2	3.8	6.5
Rainfall	1.9	3.4	3.0	2.8	2.3	1.4	2.5
Air humidity	5.5	20.8*	18.2	4.8	7.4	7.2	10.6
R	.69**	.67**	.70**	.73**	.48	.66**	
100 R^2	47.7	45.0	49.7	53.9	22.7	44.1	
Drabant							
Temperature	5.1	7.0	1.1	35.8*	26.7*	41.4*	19.5
Global rad.	3.5	3.1	3.3	14.4	12.0	11.7	8.0
Rainfall	1.2	2.0	1.1	3.3	.8	1.3	1.6
Air humidity	1.8	17.3	13.0	11.0	7.5	8.7	9.9
R	.34	.54	.43	.80*	.69*	.79*	
100 R^2	11.6	29.4	18.5	64.5	47.0	63.1	
Means 100 R^2	35.2	32.3	33.7	46.2	26.5	39.3	

investigation are concerned, the question of the reasons for the annual variation in seed dormancy at the first harvest must to a large extent remain unanswered.

In Tables 3, 4 and 5 simple correlation coefficients between seed dormancy parameters and climatic factors are presented. In Table 6 the effect of each climatic factor on seed dormancy parameters is estimated. The results in the table are the mean for each factor obtained from the multiple regression analysis in which the independent variables (climatic factors) in turn were arranged in all possible successions.

The results in Table 6 are very varied and there are indications of interactions involving cultivars, climate factors, stage of harvest and germination temperatures. Attention is drawn to the strong effects of rainfall on the seed dormancy of cv Runar. Cv Reno reacted most strongly to temperature variations. This was also the case for cv Drabant, but only at the second harvest. The reactions of the second harvest samples of Drabant to global radiation,and the reaction of the first harvest samples of cv Runar and cv Reno to air humidity should be noted. The differences in the effects of climate factors on the manifestation of seed dormancy at 10°C and at 20°C are striking in a number of cases.

In spite of the relatively few significant correlation coefficients in Tables 3, 4 and 5 some conclusions can be drawn. Effects of climatic factors on seed dormancy are more weakly manifested at the first harvest than at the second harvest. This is in accordance with the findings in the study of barley cultivars (STRAND (1989). The cultivars responded differently to variations in climatic factors, to dates of harvest and to germination temperatures as shown by the correlation coefficients. It is also evident that cv Drabant reacted more strongly to variations in the environmental factors than the other two cultivars.

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

In the report on seed dormancy in barley (STRAND 1989) it was shown that climatic factors had significant effects on the intensity of seed dormancy at least 40-50 days beyond the termination of the period of climate observation. In this material the longevity of climatic effects on seed dormancy in wheat is illustrated in Figures 1 and 2.

Figure 1 shows that the effects of temperature and global radiation on the intensity of seed dormancy are strong

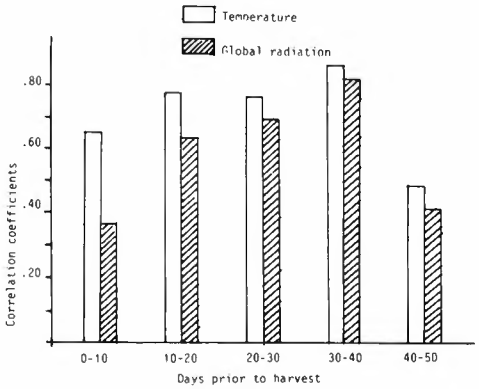

Figure 1. Correlation coefficients between temperature and global radiation in periods of 10 days prior to harvest and 2nd harvest Dormancy Index

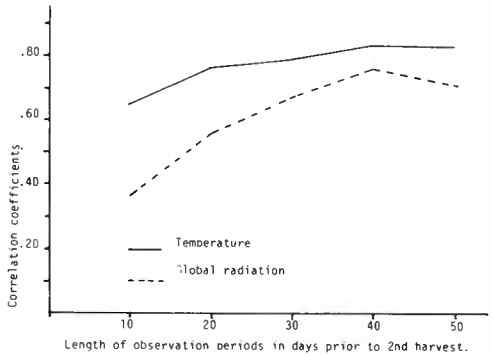

Figure 2. Correlation coefficients between temperature and global radiation in periods of different lenght prior to harvest and 2nd harvest Dormancy Index

during a period of 10-40 days prior to the second harvest.(the -10+20 period).The particular 10-day period with the strongest effects occurs 30-40 days prior to the second harvest, which in this case is the last 10 days prior to yellow ripeness.

The 10-day period 40-50 days prior to the second harvest (the -20-10 period) seems to be too early in the seed development to have any strong influence on dormancy. This is supported by the fact that the correlation coefficients obtained for the first 10-day period after heading (79-69 days prior to the second harvest) were low and non-significant.

The curves in Figure 2 illustrate the accumulated effects of temperature and global radiation on seed dormancy. The mean climatic data for a period of approximately 40 days preceding the second harvest showed highest correlation coefficients with second harvest dormancy parameters. The shorter and longer periods both resulted in lower correlation coefficients.

Table 7. Correlation coefficients between the 10°C/20°C ratio of dormant seed and climatic factors in different developmental stages

Climate factors and developmental periods		cv Runar		cv Reno		cv Drabant	
		HT 1	HT 2	HT 1	HT 2	HT 1	HT 2
Temp.	S-H	.59**	-.23	.20	.31	.34	.26
	H-YR	-.44	.34	-.48	-.38	-.47	-.62*
	-20-0	-.52*	.17	-.52*	-.34	-.29	-.62*
	-20+10	-.54*	.07	-.52*	-.42	-.45	-.63*
	0+30	-.52*	-.03	-.54*	-.53*	-.38	-.64*
	-20+30	-.57*	.02	-.60*	-.53*	-.36	-.67*
GR	S-H	.24	-.03	.06	-.31	.19	-.11
	H-YR	-.27	-.11	-.37	-.32	-.26	-.67*
	-20-0	-.36	-.12	-.59*	-.61*	-.28	-.62*
	-20+10	-.50*	.01	-.60*	-.65*	-.43	-.60*
	0+30	-.37	.24	-.42	-.57*	-.31	-.48
	-20+30	-.42	.10	-.55*	-.65*	-.31	-.57
Rainfall	S-H	.12	.07	-.05	.40	.67*	.26
	H-YR	.01	.10	.50	.55*	.08	.37
	-20-0	-.41	.30	.37	.49	-.03	.18
	-20+10	-.30	.47*	.47	.62**	.30	.31
	0+30	.10	-.15	.25	.42	.12	-.22
	-20+30	-.20	.08	.44	.65**	.09	-.06
RH	S-H	.01	.25	.23	.45	-.03	.32
	H-YR	.09	.32	.23	.53*	.12	.51
	-20-0	.02	.29	.38	.42	.10	.43
	-20+10	.05	.26	.42	.50*	.26	.42
	0+30	.09	-.02	.25	.48	.26	.34
	-20+30	.07	.15	.33	.49	.21	.40
R/T	S-H	-.06	.09	-.12	.33	.54	.18
	H-YR	.06	.01	.52*	.56*	.11	.45
	-20-0	-.34	.26	.44	.54*	-.01	.29
	-20+10	.22	.41	.54*	.67**	.29	.40
	0+30	.23	-.16	.41	.58*	.28	.12
	-20+30	-.04	.04	.55*	.75**	.23	.24

Effects of climatic factors on the manifestation of seed dormancy, and on the dormancy curve

The main effects of cultivars and of environmental factors on seed dormancy are dealt with in the preceding sections. In Tables 7 and 8 the results of investigations into certain interactions between cultivars, dormancy and environmental factors are presented. In Table 7 the correlation coefficients between the ratio of percent dormant seed at 10°C and at 20°C germination temperatures and climate data for the different developmental periods are calculated. A negative correlation coefficient means that high values of the climate parameter induce wider differences in the manifestation of seed dormancy at 10°C and at 20°C germination temperatures,and vice versa. It is surprising that the temperature has a significant effect on the relation between the manifestation of seed dormancy at 10°C and at 20°C in first harvest samples of cv Runar and cv Reno, whilst no significant main effects of temperature on the dormancy level could be proved (Tables 3 and 4). For cv

Table 8. Correlation coefficients between the DI HT 2/DI HT 1 ratios and climatic factors in different developmental periods

Climate factors and developmental periods		Cultivars		
		Runar	Reno	Drabant
Temperature	S-H	-.27	.20	.47
	H-YR	.06	-.36	-.82**
	-20-0	.22	-.14	-.79**
	-20+10	.12	-.14	-.82**
	0+30	.10	-.27	-.85**
	-20+30	.15	-.26	-.87**
Global radiation	S-H	.07	-.03	.22
	H-YR	.08	-.21	-.61*
	-20-0	.34	-.35	-.66*
	-20+10	.23	-.41	-.69*
	0+30	-.04	-.50*	-.67*
	-20+30	-.15	-.49	-.70*
Rainfall	S-H	-.13	-.08	.12
	H-YR	.02	.48	.48
	-20-0	-.20	.42	.39
	-20+10	-.14	.50*	.49
	0+30	-.19	.40	-.20
	-20+30	-.31	.60*	.10
Air humidity	S-H	-.15	.06	.04
	H-YR	-.04	.33	.39
	-20-0	-.05	.48	.44
	-20+10	-.09	.45	.47
	0+30	..01	.43	.23
	-20+30	-.05	.47	.35
Rainfall/ temperature ratios	S-H	-.07	-.12	.02
	H-YR	-.17	.48	.57
	-20-0	-.21	.45	.51
	-20+10	-.12	.54*	.59*
	0+30	-.21	.53+	.25
	-20+30	-.31	.65**	.45

Drabant the correlation coefficients are highest for the second harvest samples. The other climatic factors also seem to have different effects on the manifestation of seed dormancy in the different cultivars, at different germination temperatures,and at different developmental stages.

The correlation coefficients between the DI HT 2/DI HT 1 ratio and climate factors in different developmental stages are calculated in Table 8. Negative correlation coefficients mean that higher values of climate parameters cause stronger reductions in seed dormancy from the first to the second harvest.

The high correlation coefficients for cv Drabant for temperature and global radiation strongly indicate that this cultivar reacts differently from the other two. There are also indications that cv Runar and cv Reno have opposite reactions to the moisture factors.

Methods for testing cultivar differences in seed dormancy

Seed dormancy is a cultivar character which is important in order to avoid preharvest sprouting damage in the ears. In testing cultivars and breeding material it is therefore necessary to use methods by which the cultivar- controlled seed dormancy can be determined precisely and cheaply. The seven methods for testing or recording seed dormancy were compared and the results are presented in Table 9. The material used in the comparisons consisted of three sets of spring wheat cultivars, namely 7 cultivars grown for 5 years, 9 cultivars grown for 4 years and 6 cultivars grown for 7 years. The efficiency of the methods for determining cultivar-controlled seed dormancy is evaluated using the F-value for testing cultivar differences, i.e. the ratio between the cultivar variance and the cultivar x year interaction variance. The results in the table show that there are only small differences in the efficiency of the methods for determination of seed dormancy. The cultivar x method interactions, however, are significant in most of the material studied. This means that the different methods do not rank the cultivars in the same order with regard to seed dormancy. The mean Dormancy Index, which is calculated from the results for both dates of harvest and for both germination temperatures, covers up most of the interactions and is therefore the best all-round parameter for seed dormancy. If one or only a few of the methods are applied it is important that the crops are sampled at the developmental stage at which the pre-harvest ear-sprouting most commonly occurs and that the germination temperatures used are fairly close to the daily mean in that part of the season. It is interesting to note that the determination of cultivar seed dormancy on first harvest samples shows high efficiency as compared with

Table 9. The efficiency of methods for testing cultivar differences in seed dormancy. F-values in analysis of various tests

		Seven cultivars 1960-64	Nine cultivars 1982-85	Six cultivars 1982-87	Means
HT 1	10°C	12.0	5.5	2.8	6.7
	20°C	14.0	1.7	.7	5.5
	DI	21.2	2.3	1.4	8.3
HT 2	10°C	10.9	1.1	.9	4.3
	20°C	15.2	1.4	1.9	6.2
	DI	11.2	1.9	2.1	5.1
Mean	DI	24.6	2.8	2.7	10.0

the very low correlation coefficients in the climate reaction study. The use of the dormancy test in a warning system for pre-harvest ear-sprouting is further discussed in the next section.

The possibilities of a warning system for pre-harvest sprouting damage

In areas of moist harvest weather pre-harvest sprouting in the ears may cause serious quality damage particularly to bread grain crops. In principle, seed dormancy can protect the crop against such quality damage, as the dormant seed by definition does not start sprouting under environmental conditions that are otherwise favourable for germination.

The application of our knowledge on seed dormancy in an attempt to work out a warning system for pre-harvest sprouting damage in wheat was first made by BELDEROK (1965), who found a close connection between the heat sum above 12.5°C during the dough-ripe stage and the length of the dormancy period. Based on these findings he proposed a scheme for warning wheat growers when the wheat fields might become sucseptible to ear-sprouting. OLSSON & MATTISSON (1976),LALLUKKA (1976),GRAHL & SCHRODTER (1975),MITCHELL et al. (1980), and others who have tested the Belderok system, did not find a satisfactory close connection between weather conditions and duration of the seed dormancy period as a warning of ear-sprouting in farmers' fields. There may be other reasons for the discrepancies between the results of the different investigations. Attention is drawn here to some of them.

Based on visual estimates the length of the dough-stage period of ripeness is imprecisely defined.The dough stage is said to occur between the milky ripeness and the harvest ripeness stages of development. The matrix of the grain should be soft and doughy. The duration of the dough stage could be from 10 to 23 days (BELDEROK 1965). Johansson (1976) assumes that the dough stage is the part of the ripening period in which the moisture content of the kernels decreases from 42% to 22%.

The ripening process is strongly controlled by temperature; the higher the temperature, the faster the ripening process, and vice versa. Under otherwise constant environmental conditions the heat sum of the ripening period is fairly constant. The heat sums of the dough-ripe period, therefore, make up a certain part of the heat sum of the total ripening period. In this study it was assumed that the dough ripe period makes up approximately 40% of the ripening period, depending on the definition of the dough-ripe period. In terms of moisture content of the kernels, this would mean the period when the moisture content decreases from approximately 55% to 38%. The lowest figure corresponds to morphological ripeness when the consistency of the kernel matrix changes from doughy to vaxen. According to this definition the dough stage of ripeness of this material lasted from 13 to 26 days for cv Runar and cv Reno and from 14 to 27 days for cv Drabant. The mean lengths of the period were 19-20 days, which is very close to the -20-0 period of this investigation.

In Table 10 the correlation coefficients between dormancy parameters and the Belderok heat sum are compared with the correlation coefficients between the same dormancy parameters and the mean temperatures of the -20-0 period. The results show that the correlation coefficients in the two groups are of the same magnitude. Only for the first harvest samples of Reno, germinated at 10°C, and the second harvest samples of Drabant, germinated at both temperatures, were the correlation coefficients significant. The low correlation coefficients and the late response (second harvest) of the dormancy to the variations in temperature rendered both methods unsuitable as a warning of preharvest ear-sprouting damage in wheat fields.

Table 10. Correlation coefficients between the heat sum during the dough-ripe stage and dormancy parameters and between the mean temperature of the -20-0 period and the same dormancy parameters

Dormancy parameters		Runar		Reno		Drabant	
		Heat sums	Mean temp.	Heat sums	Mean temp.	Heat sums	Mean temp.
HT 1	10°C	-.18	-.28	-.53*	-.53*	-.13	-.16
«	20°C	.07	-.22	-.13	-.06	-.04	-.02
«	DI	-.05	.05	-.32	-.17	-.09	-.09
HT 2	10°C	-.20	-.19	-.36	-.43	-.59*	-.66*
«	20°C	.23	.44	-.13	-.16	-.67*	-.67*
«	DI	.10	.21	-.24	-.30	-.76*	-.81*
Means. signs ignored		.14	.23	.29	.28	.38	.40

In Tables 3, 4, and 5 it is shown that the correlation coefficients between the first harvest Dormancy Index and the climate parameters of the -20-0 period for cv Runar are significant for rainfall, air humidity, and the rainfall/temperature ratio, but not for temperature and global radiation. For cv Reno and cv Drabant there are no significant correlation coefficients. Correlation coefficients between the first harvest Dormancy Index and the sum of the daily mean temperature above 12.5°C during the dough-ripe stage were low and non-significant for all cultivars. Based on the results of this investigation the Belderok (1965) system could work only if other climatic factors showed very low variation compared to temperature. Because of the strong cultivar-climate-dormancy interactions the prediction of resistance against ear-sprouting of unknowm material based on observations of climate factors will be impresice.

The risk of quality damage due to visible or hidden preharvest ear-sprouting is not just a question of seed dormancy. High temperature and dry weather in a period prior to harvest generally reduce seed dormancy. Under such weather conditions, however, no ear-sprouting takes place because of the lack of moisture. Low temperature and high moisture in the same period increase seed dormancy, but also create favourable conditions for ear-sprouting. The most unfavourable weather conditions are hot and dry weather during the ripening period followed by high moisture; these conditions postpone harvest and promote earsprouting.

If a warning system were to be based on seed dormancy, probably the best procedure would be to determine the seed dormancy level at yellow ripeness or one week later and thereafter to estimate the possible changes in seed dormancy from weather conditions based on the relatively high correlation coefficients between climate factors (mainly temperature and rainfall) and second harvest seed dormancy. A still better warning system might be based on frequent determinations of both seed dormancy and Falling number, the latter stating the actual conditions of the starch and the seed dormancy indicating the potential resistance of the crop to pre-harvest ear-sprouting damage.

DISCUSSION AND CONCLUSIONS

The investigations have shown wide variation in seed dormancy levels due to differences between cultivars, developmental stages, manifestation at different germination temperatures and the effects of climatic factors. In a number of cases there were also significant interactions between dormancy parameters and the factors influencing them. Atten-

tion is drawn to some of the more important and interesting results.

1. Based on the significant correlation coefficients, higher temperatures and more intense global radiation in the pre-harvest periods reduced seed dormancy. In a number of cases the correlation coefficients obtained at 20°C germination temperature were non-significantly positive and in a few cases the differences between the correlation coefficients obtained at 10°C and at 20°C germination temperatures were significant.

2. Higher values of the moisture factors, i.e. rainfall, relative air humidity and the rainfall/temperature ratio in the pre-harvest periods generally increased seed dormancy. Also, opposite results were obtained for these climatic factors for the 10°C and 20°C germination temperatures, especially for cv Runar and cv Reno.

3. The three wheat cultivars each reacted differently to variations in the climate factors. For cv Runar no significant effects of temperature on seed dormancy could be proved. Global radiation had some effect on second harvest samples germinated at 10°C. The highest numbers of significant correlation coefficients were found between seed dormancy and the moisture factors; they were positive and were obtained from second harvest samples germinated at 10°C.

For first harvest samples germinated at both temperatures and for second harvest samples germinated at 20°C the correlation coefficients were negative, but less significant. In some cases, however, the differences between the correlation coefficients of the first and second harvests and between the 10°C and the 20°C germination temperatures were highly significant.

For cv Reno the significant correlation coefficients indicated very clearly that higher temperatures and more intense global radiation in pre-harvest periods reduced seed dormancy. For the moisture factors the reaction pattern of seed dormancy was very similar to that found for cv Runar, but the correlation coefficients were less significant.

For cv Drabant the first harvest samples showed low correlation coefficients between seed dormancy and the temperature-radiation factors. The second harvest samples, however, showed highly significant correlation coefficients between the same variables. The correlation coefficients between seed dormancy and the moisture factors were mostly positive, but of little significance.

4. It has been shown that the effects of climatic factors on seed dormancy build up over a period of 40-50 days prior to the second harvest. The single 10-day period which had the strongest effects on seed dormancy was that between the 30th and the 40th day prior to the second harvest.

5. The climatic factors affected the ratio of dormant seed obtained at the 10°C and 20°C germination temperatures. High temperature-radiation factor values increased the difference in dormant seed between the 10°C and 20°C germination tests. The moisture factors had the opposite but lesser effect on the ratios of the dormant seed. It is interesting to note that the temperature had a significant effect on the ratio of dormant seed at the 10°C and 20°C germination temperatures, whilst no such effect on the mean intensity of the dormancy could be proved.

6. The climate factors also affected the slope of the dormancy curve between the first and second harvests. For cv Drabant, higher values of the temperature-radiation factors caused a very significant stronger decline in seed dormancy from the first to the second harvest. For the other two cultivars the effects were weaker and not significant. The moisture factors had the opposite effect.

Very few of these correlation coefficients, however, were significant. The different responses of the cultivars were, at least in part, due to the date of appearance of maximum dormancy. Maximum dormancy at an early date (first harvest or earlier) resulted in negative correlation coefficients, while maximum dormancy at later stages reduced the correlation coefficients or made them positive in such cases when maximum dormancy occurred close to the second harvest or later.

7. It is shown (Table 6) that 9.9 to 64.5% of the variation in dormancy, depending on cultivars and dormancy parameters, can be ascribed to variation in climate factors. Cv Runar reacted most strongly to variation in rainfall, while cv Reno and cv Drabant reacted most strongly to variation in temperature.

8. The genetically controlled seed dormancy of the cultivars may be determined by either of the methods applied, as there were no great differences in the efficiency of the tests between the two stages of harvest or between the two germination temperatures. It is interesting to note, however, that the second harvest samples germinated at 10°C, which in this test showed the lowest efficiency, came out with the highest number of significant correlation coefficients in the dormancy-climate study (Tables 3, 4, and 5).

9. From the results of this investigation it is hard to imagine how a warning system for pre-harvest sprouting damage in wheat based on dormancy readings could work satisfactorily. The Belderok system (BELDEROK 1965) which is based on the heat sum above 12.5°C during the dough-ripe stage, did not result in any higher correlation coefficients with seed dormancy than with the mean temperature of the same period.

The most efficient warning system for pre-harvest ear-sprouting damage most probably should be based on frequent determination of both seed dormancy and Falling Number. The Falling Number stating the actual condition of the starch and the intensity of the dormancy indicating the potential resistance of the crop to sprouting damage.

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