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

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FRESH FRUIT QUALITY EVALUATION OF RED RASPBERRY

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This postharvest experiment was carried out in 1986, in order to study the quality properties important for fresh fruit marketing. Five cultivars were evaluated. The postharvest treatment was meant to simulate the handling and storage during marketing, and included cooling, shaking and storage at room temperature. Before postharvest treatment the quality of all cultivars was acceptable. When postharvest treatment included shaking, only 'Chilcotin' was rated acceptable. The quality of 'Glen Moy' and 'Malling Orion' was also satisfactory without shaking.

Key words: cultivars, fruits, postharvest, quality, red raspberry.

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To be suitable for the fresh fruit market, red raspberry cultivars should have an attractive appearance and acceptable taste, and should tolerate storage and handling during transportation and marketing. But shelf life is limited even for the best cultivars, and the fruit has to be handled quickly and with care if it is to be of the high quality required for sale in the fresh fruit market.

Most literature dealing with shelf life of the red raspberry concentrates on fruit rot resistance (Barritt & Torre 1980, Knight 1980, Daubeny & Pepin 1969, Daubeny & Pepin 1981, Jennings & Carmichael 1975) and fruit firmness (Barritt et al. 1980, Keep et al. 1980, Robbins & Sjulin 1986). The literature referred to above documents the cultivar differences for both properties. However, fresh market cultivars have to have some days of shelf life, and this is greatly influenced by postharvest treatment. Cold storage is a prerequisite for satisfactory shelf life (Callesen 1987).

Colour and brightness are important factors of appearance, and according to Daubeny (1980) the fresh fruit market demands a bright, non-darkening red colour.

The purpose of the present investigation was to study quality factors important to fresh fruit marketing, and the effect of postharvest treatment.

MATERIAL AND METHODS

Five clones from different breeding programmes in Europe and Canada were selected for this experiment. The fruits were harvested from a screening test of the red raspberry at the Department of Horticulture, Agricultural University of Norway, where the experiment was carried out.

Tolylfluanid was applied at bloom to prevent fungi infection. No fungicides were used thereafter.

Fruits of the cultivars 'Chilcotin', 'Glen Moy', 'Malling Orion', 'Veten' and the selection 410-08 from the Department of Horticulture, Agricultural University of Norway, were harvested four times during the 1986 season; these will now be referred to as cultivars. The fruits were picked when red ripe, and the ripeness was uniform in all the samples. Three containers of each cultivar were picked from two replicates in the field. The fruits were picked into transparent plastic containers and the weight adjusted to 250 g.

The samples were used for three subsequent quality evaluations. Appearance, brightness and colour intensity were recorded for all the samples immediately after harvest. One sample was evaluated for tast, firmness and soluble solids. The other two were cooled to 2°C by using forced air cooling for two hours. These samples were then stored at 2°C for 24 hours. The postharvest treatment is meant to simulate handling during marketing, and includes cooling, shaking and a period at room temperature.

After the cold storage both samples were evaluated and placed at room temperature (20°C). One was shaken for 4 hours, using Heto Lav equipment, type TB SH 02, speed 150 rpm. Frames, fastened to the plastic containers were attached to the shaker. After 24 hours at room temperature, quality components were evaluated for both the shaken and unshaken samples.

The firmness of 10 fruits from each sample was recorded, using an Instron 1140 instrument with measure-cell 2512/208 and diameter of 2 cm. Measurements were made by recording the force, in Newton, required to close the opening of the fruit. Soluble solids were recorded using a digital hand refractometer on a mixed pulp of 10 fruits from each sample.

Appearance, brightness and taste were recorded by two persons using a subjective rating scale, 0-9, where 9 was best. At 5, the quality was acceptable. Colour intensity was recorded by applying the same scale; 9 was dark purple and 5 was red. The amount of juice in the containers was recorded as a percent of the bottom covered with juice. Fruit rot was recorded as the number of fruits attacked by fruit rot organisms.

RESULTS

Table 1 shows the quality properties of the cultivars after harvest. 'Glen Moy' had the firmest fruits, while the fruits of

Table 1. Quality properties of five red raspberry cultivars after harvest. Mean of four harvesting times in 1986

	Firmness in Newton	Soluble solids %	Taste 0-9	Appearance 0-9	Brightness 0-9	Colour 0-9	Percent juice 0-9
Chilcotin	1.30	8.4	7.3	7.7	7.6	4.8	9
Glen Moy	2.22	8.8	6.5	6.0	4.9	5.1	6
M. Orion	1.34	8.3	6.5	7.0	6.4	5.2	7
Veten	1.38	8.7	5.1	6.0	5.7	6.7	8
410-08	1.14	7.7	5.8	7.0	6.8	4.3	18
Mean	1.48	8.4	6.2	6.7	6.3	5.2	10
L.S.D.5 %	0.26	n.s.	1.1	0.6	0.8	0.6	6

Table 2. Quality properties of five red raspberry cultivars after postharvest treatment; Cooling, shaking and 24 hours at room temperature. Mean of four harvesting times in 1986

	Soluble solids %	Taste 0-9	Appearance 0-9	Brightness 0-9	Colour 0-9	Percent juice	Weight-loss %
Chilcotin	8.4	6.1	6.5	6.8	5.6	24	4.7
GlenMoy	9.0	5.3	4.1	3.6	5.6	22	4.1
M.Orion	8.8	5.3	4.6	4.9	6.6	54	4.8
Veten	8.9	3.3	3.9	4.6	8.1	49	5.6
410-08	8.0	3.9	3.3	4.4	5.3	89	5.5
Mean	8.6	4.8	4.5	4.9	6.2	48	4.9
L.S.D.5%	n.s.	0.8	1.0	0.6	0.7	29	0.7

410-08 were soft. The content of soluble solids was highest in 'Glen Moy', and lowest in 410-08.

The minimum score of acceptance for the subjective rating scale was set at 5, and, as Table 1 shows, all the characters were above this limit, except for brightness in 'Glen Moy'. 'Chilcotin' attained the highest score for taste, appearance and brightness. 'Glen Moy' and Veten had lower scores for appearance than the other cultivars, and 'Veten' had the lowest score for taste. 'Veten' had the darkest colour and 410-08 had the lowest colour intensity. With the exception of 410-08, there was little juice in the boxes after harvesting.

Table 2 shows the quality properties after postharvest treatment, including shaking. Fruit rot is not represented in the table, as only sporadic attacks of fruit rot organisms were visible at the end of treatment, and no difference was found between the cultivars.

The content of soluble solids was approximately the same as at harvest time, but scores for taste, appearance and brightness were lower after postharvest treatment. Colour intensity and amount of juice increased. The postharvest weight loss was about 5%, 'Veten' and 410-08 having the highest, while 'Glen Moy' had the lowest.

'Chilcotin' had the highest score for taste, appearance and also brightness after treatment, and the scores were above the limit of acceptance for all these qualities. 'Chilcotin' also had a low level of juice in the containers.

'Glen Moy' and Malling Orion also had scores above the limit of acceptance with regard to taste, but appearance and brightness were below this limit. 'Glen Moy' had little juice in the containers and had less weight loss than the other cultivars. 'Malling Orion' scored better than 'Glen Moy' with regard to both brightness and appearance, but more than half of the bottom of the container was covered with juice after treatment.

Scores for taste, appearance and brightness were below 5 for 'Veten' and also for 410-08. With regard to juice loss, 410-08 was the poorest of all the cultivars with 89%. 'Veten' had 49% and also had the darkest fruits before and after treatment. After treatment, the fruits of 'Veten' were of a dark purple colour. 'Veten' and 410-08 had the greatest weight loss during postharvest treatment.

The results in Table 2 include shaking during postharvest treatment. Table 3 shows that shaking reduced the fruit quality and increased weight loss during treatment from 3.7% to 4.9%. The amount of juice was more than doubled

Table 3. Quality properties after postharvest treatment. Mean of five cultivars and four harvest times

	Without shaking	With shaking
Weight loss %	3.7	4.9
Juice loss %	23.2	47.6
Appearance	5.2	3.3
Brightness	5.4	4.9

as a mean of all the cultivars, and scores for appearance and brightness decreased when the fruits were shaken. Without shaking, both 'Glen Moy' and 'Malling Orion' had acceptable quality with regard to appearance and brightness. Shaking had no influence on the content of soluble solids, on taste or on colour intensity in any of the cultivars. There was no interaction between treatment and cultivars, or between treatment and time of harvest in any of the quality properties.

The differences between harvest times were significant with regard to the content of soluble solids, taste, brightness, colour intensity and amount of juice (Table 4).

During the season, no tendencies to quality changes were observed except in the case of brightness, which increased with each picking time. When fruits were wet at picking time the amount of juice in the containers increased and the content of soluble solids decreased. Rain during the last days before picking, however, did not seem to have any influence on the quality properties. No interaction between treatment and time of harvest was found.

DISCUSSION

This investigation has revealed that raspberry cultivars can tolerate at least two days of storage if the berries are cooled down quickly and kept at a low temperature for half of the time, as in this experiment. Cooling in 24 hours had little influence on fruit quality, but at room temperature the quality decreased quickly. Shaking also reduced the quality. In this experiment the fruits were shaken continually for 4 hours, and this is regarded as tougher treatment than that administered in commercial marketing. At any rate, it illustrates the importance of care when handling raspberries. Without shaking, the quality of 'Chilcotin', 'Glen Moy' and 'Malling Orion' was acceptable after storage, while only 'Chilcotin' was rated acceptable when shaking was included.

In the present experiment, postharvest fruit rot placed no limitation on quality. This indicates that red rasp-

Table 4. Quality properties after harvest at four different harvest times. Mean of five cultivars

	Harvest time			
	28 July	4 Aug.	7 Aug.	11 Aug
Soluble solids	9.1	7.6	8.1	8.7
Taste	6.4	5.4	6.4	6.7
Brightness	5.9	6.1	6.3	6.8
Colour intensity	5.0	5.6	4.8	5.5
Per cent juice	0	13.4	19.5	5.9
Fruit surface at harvest	Dry	Wet	Wet	Dry
Precipitation,mm,last 3 days	0	13	4	28

berries can tolerate at least two days of storage without being damaged by fruit rot organisms if the fruits are picked at the red ripe stage and cooled down immediately after harvest. Overripe fruits are more susceptible to fruit rot organisms than red ripe (Øydvin 1983), and selection of red ripe fruits at harvest might be necessary for fruit rot susceptible cultivars.

'Glen Moy' had the firmest fruits, and this cultivar also had the least juice leakage, while 410-08 had the softest fruit and also released most juice. Among the other cultivars, however, there were only small differences in firmness, but the amount of juice loss did vary. This indicates that fruit firmness is not the only factor influencing juice loss in the fruits. However, firmness is an important quality property of suitability for the fresh fruit market, as correlation between fruit rot (*Botrytis cinerea*) resistance and firmness has been previously reported (Jennings & Carmichael 1975).

Juice leakage was correlated with weight loss ($r=0.692$). As both juice leakage and weight loss are presumably dependent on skin thickness, this indicates that thick skin might be the most important factor in preventing juice leakage.

CONCLUSIONS

The quality of 410-08 is not good enough for the fresh fruit market. At harvest time the quality was good, but during postharvest treatment quality decreased quickly because of a large proportion of released juice. This was mostly due to soft fruits.

The quality of 'Veten' was poorer than that of 'Malling Orion', 'Glen Moy' and 'Chilcotin'. Neither taste nor appearance was good enough after treatment, and the amount of released juice was high. The dark colour of the fruits gave a negative «overripe» appearance after treatment.

'Glen Moy' is interesting for fresh fruit marketing because of its firm fruits and acceptable taste after treatment. Its appearance is poor, however, mainly because of the dull surface of the fruits.

'Malling Orion' varied between harvest times with regard to taste, and gave a high content of juice in the bottom of the containers. Otherwise, the quality properties of 'Malling Orion' were acceptable. But the large amount of juice loss could cause problems during transportation and handling.

'Chilcotin' had the best quality properties in this investigation, both before and after treatment. 'Chilcotin' is therefore recommended for the fresh fruit market in Canada (Daubeny 1986). This study supports the recommendation of 'Chilcotin' for the fresh fruit market.

SUMMARY

The fruits of the cultivars 'Chilcotin', 'Glen Moy', 'Malling Orion', 'Veten' and the selection 410-08 were harvested four times during the 1986 season in order to study quality properties important to the fresh fruit market. The postharvest treatment included cooling (2°C), shaking and storage at room temperature. The samples were evaluated for firmness, content of soluble solids, weight loss, juice leakage, fruit rot, appearance, brightness, colour and taste.

Before postharvest treatment the quality of all the cultivars was acceptable. After postharvest treatment, only 'Chilcotin' was rated acceptable when shaking was included, but without shaking, 'Glen Moy' and 'Malling Orion' also had an acceptable quality. Shaking increased weight loss and juice leakage, and the scores for appearance and brightness decreased. This illustrates the importance of careful handling of raspberries. Fruit rot occurred only

sporadically, and was no limiting factor in this investigation.

The picking of wet fruits resulted in increased juice leakage and decreased the content of soluble solids.

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AGRONOMIC VALUE OF SOME NORTH NORWEGIAN POPULATIONS OF *AGROSTIS CAPILLARIS* L.

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Karlsen, Å.K., Agronomic value of some North Norwegian populations of *agrostis capillaris* L. Norwegian Journal of Agriccultural Sciences 2:79-95. ISSN 0801-5341

The agronomic value of 13 populations of *Agrostis capillaris* L. has been investigated at three locations in the county of Nordland, North Norway. Spaced plants were harvested at two different regimes in two years.
In a laboratory experiment the populations were tested for tolerance to freezing and for resistance to attacks by *Fusarium nivale* (Fr.) Ces. and *Typhula ishikariensis* Imai.
The most intensive harvesting system increased winter damage and the per cent of IVDMD, while the total harvested herbage as dry matter and protein content remained unaffected by harvesting regimes. Population differentiations were found for winter damage, dry matter yield, IVDMD and protein content, but no interaction with harvesting regimes or experimental sites was detected. However, differences did occur between geographical groups of populations with regard to winter damage and IVDMD. The populations differed in freezing tolerance, but not in resistance to low temperature fungi. Among the populations from the coastal areas there was an increase in tolerance to freezing with increased latitude of origin. This group also had a higher average tolerance against freezing than populations of inland/fjord origin.
The seed multiplying of population No.6 'Hakvåg', No. 10 'Eiteråga' and No.12 'Kløvimoen' is recommended as a basis for larger - scale trials and practical use. Also certain breeding aspects are suggested.

Key words: *Agrostis capillaris*, freezing, *Fusarium nivale*, *Typhula ishikariensis*, yield potential, winter damage.

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The proportion of *Agrostis capillaris* L. amounts to about 22% of dry matter harvested from grasslands of different age in the county of Nordland, situated between 64°75' and 69°N-lat. (Nesheim 1986b). The important role of this species in forage production is also evident from the results of Lundekvam's (1975) investigations in the permanent meadows of West Norway. Moreover, *A. capillaris* is a dominating species in mountain pastures in southeastern parts of the country (Baadshaug 1983).

These more recent Norwegian results confirm earlier findings in northern Europe (Ellingbø 1926, Bradshaw 1959, Hulten 1959, Morrison & Idle 1972). Various investigations of *A. capillaris* populations have revealed that an abundance of adaptive variations are available (Bradshaw 1958, 1960, Helgadóttir 1981, Symeonidis et al. 1985).

The fact that the species is rarely sown but nevertheless widespread in Nordland (Nesheim 1986b) is also an indication of the presence of a large number of populations adapted to diverse climatic and edaphic factors. The different qualities achieved through this process of adaptation might possibly be of agronomic importance and should be exploited in grassland agriculture and grass breeding. 'Leikvin' is the only certified Norwegian cultivar of *A. capillaris* weakly selected among the plants from grazed natural grassland and permanent meadows in the south-eastern highlands of Norway. This cultivar is commonly used in Norwegian field experiments, and considerable variation in yield quantity is found compared with other species (Olsen 1969, Øyen 1985, Larsen 1987, unpubl.).

Agrostis spp. appear to be secondary invaders in newsown swards, next to *Poa* spp., and are the main species after 10-20 years (Lundekvam 1975, Morrison 1978, Nesheim 1986b). It is also evident that populations of *A. capillaris* can be more aggressive than those of *Poa pratensis*, but with variation between populations in this respect due to adaptation to different growth habitats (Helgadóttir 1981).

The aim of the present investigation was to determine the agronomic value of 12 wildgrowing North Norwegian populations of *A. capillaris* for agricultural purposes, and thereby to clarify whether any attention should be paid to the breeding of new cultivars. A separate study was carried out in the laboratory to examine possible differences between the populations in freezing tolerance and resistance to the fungi Fusarium nivale (Fr.) Ces. and *Typhula ishikariensis* Imai.

MATERIAL AND METODS

The plant material

The field experiment

Twelve North Norwegian ecotypes of *Agrostis capillaris* were compared with the Norwegian certified cultivar 'Leikvin', and with 'Tracenta' from the Netherlands. The ecotypes are named after their place of origin. Because 'Leikvin' may be considered as a slightly selected local population, for the sake of brevity both the local ecotypes and this cultivar are termed populations. 'Tra-

Table 1. Populations of *Agrostis capillaris* included in the field trials

Population number	*Name*	*N-lat.*	*Climate*
1	'Skjervøy'	70°00'	Coast
2	'Sørvaranger'	69°54'	Fjord to inland
3	'Lia'	68°52'	Coast
4	'Kvæfjord'	68°45'	Coast
5	'Bjerkvik'	68°35'	Coast to fjord
6	'Hakvåg'	68°00'	Coast
7	'Misten'	67°25'	Coast
8	'Øvre Tollådal'	66°52'	Inland
9	'Dalen'	66°50'	Coast
10	'Eiteråga'	66°10'	Inland
11	'Tjøtta'	65°50'	Coast
12	'Kløvimoen'	65°32'	Inland
13	'Leikvin'	61°08'	Inland
14	'Tracenta'	The Netherlands	

centa' is a synthetic cultivar for moderate maritime and continental climates. Name, latitude and dominating climate of the location of origin of the populations are listed in Table 1.

An extensive collection of the seed of northern populations of *A. capillaris* was carried out in 1972-1977, as described by Schjelderup (1973). The seed of the North Norwegian populations dealt with in the present paper was obtained from that collection and used in the field trials. The populations were selected to represent the broad range of latitudes and climates in Nordland. Nos. 1 and 2 represent even more extreme growth conditions in North Norway. For 'Leikvin', commercial seed was used; the National Seed Council of Norway obtained seed of 'Tracenta' from Mommersteeg International B.V. in the Netherlands.

The laboratory experiments
In addition to the populations listed above, ecotypes 15 'Hammerfall' from 67°20' N-lat. (fjord to inland climate), and 16 'Vågan', from 68°15' N-lat. (coast climate) were tested. For all the populations from North Norway in these tests, the seed was multiplied for experimental use in isolated compartments in a greenhouse or in isolated blocks in the field. For the certified populations seed was obtained as for the field experiment.

Experimental layout and growth conditions

The field experiment
All the plants used in the trials were raised from seed in a greenhouse at Tjøtta Research Station during the spring of 1984. At the two-leaf stage, the plants were transplanted to trays with cells of size 35 x 35 mm and 40 mm deep, for continued growth in the greenhouse until planting in the field in the early summer of 1984 at Tjøtta 65°50', Bodø 67°17' and Sortland 68°40'. These experimental locations were chosen as representative of the common growth conditions and winter climates in the coastal areas of Nordland.

The experiment had a split plot design with two replications. Harvest regimes formed the mainplots and populations formed the subplots. The mainplots were randomly distributed within each replication as were the subplots within the mainplots. The subplots measured 1.45 m x 1.04 m, with a total of 110 plants, at a distance of 14.5 cm x 9.5 cm.

Sand soil was represented at all sites, but soil analyses showed a different loss of ignition (6.1, 3.3 and 12.0 at Tjøtta, Bodø and Sortland, respectively). P-Al and Mg-Al were very high at all sites (> 17 and 15), while K-Al was middling high at Tjøtta (6.1) and Bodø (9.7) and high at Sortland (22.0). pH varied from 5.3 at Bodø to 6.1 at Sortland and 8.0 at Tjøtta.

The prior crop at Tjøtta was fodder rape, with potatoes at Bodø and meadow at Sortland. Manure was applied to the prior crop at Tjøtta and Sortland, and in the planting year at Bodø.

No apparent difference between the populations was found in growth start in the spring, visually estimated when the fields turned green. In 1985 the growth start was set at 02.05 at Tjøtta, 06.05 at Bodø and 14.05 at Sortland. In 1986 the corresponding dates were 30.04, 07.05 and 07.05. In both years the growth start was in accordance with the date when the average daily mean temperature passed 6°C.

A total of 200 kg nitrogen per hectare in an 18-3-15 NPK compound fertilizer was applied each year at all the sites. For H_1 this was split into 100 kg in spring, and 100 kg after the first cut. For H_2 150 kg was applied in spring, and 50 kg after the first cut.

The beginning of heading was visually assessed when half of the populations had 1-2 cm of inflorescences visible in more than 50% of the heading shoots (Simon & Park 1981).

The harvesting regimes were:

H_1 First seasonal cut (1st) one week after beginning of heading.Second seasonal cut (2nd) in the early autumn.

H_2 First seasonal cut 3-4 weeks after beginning of heading.Second seasonal cut in the late autumn.

According to Nesheim (1986a), these harvesting regimes are common among farmers in Nordland: H_1 with two cuts for ensiling grass and H_2 with one cut for hay or silage and subsequent grazing in the autumn.

Dates of harvesting were:

1985

	H_1		H_2	
Cut No	1st	2nd	1st	2nd
Tjøtta	03.07	20.08	19.07	13.09
Bodø	15.07	06.09	05.08	18.09
Sortland	18.07	04.09	25.07	23.09

1986

	H_1		H_2	
Cut No	1st	2nd	1st	2nd
Tjøtta	26.06	25.08	10.07	16.09
Bodø	09.07	03.09	23.07	29.09
Sortland	01.07	04.09	17.07	29.09

In all cases harvesting was earlier at Tjøtta than at the other sites. The 1st cut was late at Bodø except in H_1 the first year, while the 2nd cut was approximately simultaneous with that at Sortland. Thus, the period from growth start to 1st cut was longer and from 1st to 2nd cut shorter at Bodø, with the exception of H_1 1985. Days of growth and the average daily mean temperature from growth start to 1st cut and from 1st to 2nd cut are listed in Table 2.

The daily mean temperature was higher at Tjøtta than at the other sites every year, especially in the period from 1st to 2nd cut when the temperature was from 1.5°C to 2.9°C higher than at Bodø. With few exceptions Bodø had the lowest temperature. At Sortland the temperature equalled that at Bodø in the 1st cut at H_1 1985 and in the 2nd cut at H_1 1986.

All the populations were cut down in late August in the planting year (1984), and in the years of data collection the stubble height at harvest was 5-10 cm.

The end of the seasonal growth period was set at the date when the average daily mean temperature fell below 6°C. In 1985 this occurred on 15.10 at Tjøtta, 07.10 at Bodø and 01.10 at Sortland. The corresponding dates in 1986 were 22.09 at Tjøtta and 15.09 at Bodø and Sortland.

The laboratory experiments

Two experiments were carried out to test the freezing tolerance of the populations and their resistance to attacks by the low temperature fungi mentioned earlier. Standard procedures were used in both experiments (Larsen 1978, Årsvoll 1977). After germination at 18-20°C, the seedlings were transplanted into 10 cm plastic pots filled with a peat-soil/coarse sand mixture in the proportion of 100:80 litres, and pH = 6.0. The plants were than placed in a greenhouse for six weeks with a day/night temperature of 16°C/10°C, and 16 hours' photoperiod, before being transferred to a growth chamber at 10°C and 8 hours' photoperiod for one week. Thereafter the plants were hardened at +1°C and 16 hours' photoperiod for two weeks.

Each experiment was carried out with three replications. The first replication had two pots, each with 9 seedlings in each treatment, while the other two replications had 4 pots, each with 9 seedlings in each treatment.

The plants were frozen in two separate chambers to -9°C and -12°C, respectively, the temperature being decreased by 1°C per hour until the actual temperatures were reached, and held there for 24 hours before thawing. Thereafter the plants were cut to a height of 5 cm and placed in the greenhouse to recover.

The other plants were inoculated separately with isolates of *F. nivale* and *T. ishikariensis* before incubation under

Table 2. Days of growth and average daily mean temperature (xT) from growth start to 1st cut, and from 1st to 2nd cut at two harvesting regimes in 1985 and 1986

Harvesting regime:	H_1				H_2			
Cut No.:	1st		2nd		1st		2nd	
	No. days	xT	No. days	xT	No. days	xT	No. days	xT
1985								
Tjøtta	62	9,9	48	15,2	78	11,2	56	13,8
Bodø	70	9,8	53	13,2	91	10,9	44	11,6
Sortland	65	9,8	48	13,8	72	10,4	60	11,8
1986								
Tjøtta	58	10,5	59	13,5	72	10,7	68	12,9
Bodø	63	9,6	56	12,0	77	10,0	68	10,0
Sortland	55	10,2	65	12,0	71	10,4	74	10,2

a simulated snow cover at +1°C for 8 weeks, as described by Årsvoll (1977). We did not succeed in isolating the actual fungi from the plants of *A. capillaris*, and isolates from *Phleum pratense* L. were used instead. Thereafter the simulated snow cover was removed from the pots and the plants were allowed to recover under greenhouse conditions for one week.

Records and analyses

The field experiment

Winter damage was visually estimated every spring, after the start of growth, as per cent of damage of *A. capillaris* within each subplot. No attempt was made to distinguish between biotic and abiotic damage, but, concurring with Årsvoll (1973) little or no biotic damage was observed.

Before the 1st cut, average straw-length was measured in centimetres from the base to the highest point of five randomly selected plants in each subplot. No significant difference was found between the populations in this respect, and therefore no result is presented.

Dry matter (DM) yields at each cut were determined either by drying the total yield from each plot or by drying a herbage sample of about 1 kg from each plot. The drying temperature was 80°C. The plant material from these samples was used for analyses of chemical components and for determination of per cent in vitro digestibility of the dry matter (IVDMD). Kjeldal-N was determined by means of the near infra-red reflectance spectrometry (NIRS) equipment at Løken Research Station and calculated on the basis of a standard equation (LIGNNY). IVDMD was determined in the laboratory at Vågønes Research Station according to the method of Tilley & Terry (1963). The crude protein content (CP) was calculated as percent N x 6.25.

The laboratory experiments

The freezing damage was assessed after 10 and 20 days, in accordance with a scale for regrowth from 0 to 9 of individual plants within the pots (0 = killed, 9 = no visible damage) (Larsen 1978).

Ten days after the simulated snow cover was removed, the attack within each pot was recorded on a scale from 0 to 9 (0 = killed, 9 = no visible attack).

Statistical analyses

The data from both field and laboratory experiments were subjected to a factorial analysis of variance and a regression analysis, and calculated with the MSTAT program for statistical analysis as described by Nissen & Moslett (1985).

RESULTS

The field experiment

Winter damage

The severity of winter damage was obviously affected by the harvesting regimes, but with a different effect at the experimental sites. The per cent of winter damage in the planted populations was as follows:

	1985/86		1986/87	
	H_1	H_2	H_1	H_2
Tjøtta	13	21	77	48
Bodø	42	11	69	34
Sortland	47	33	63	58
Average	34	22	69	47
P<		0.05		0.05

The first winter after different harvesting management had been conducted (1985/86), the damage was higher at H_2 than H_1 at Tjøtta, but the opposite at Bodø and Sortland.

After the winter of 1986/87 the per cent of winter damage was very high at H_1 but decreased the farther north the location of the experiment. At H_2 the winter damage was considerably lower at Bodø and Tjøtta ($P< 0.09$ and 0.04, respectively).

No significantly different reaction between populations was found at the end of the experimental period as regards experimental years and sites or as regards the effect of postponed harvesting on winter damage. However, in the average of the experimental treatments, highly significant differences in winter damage occurred between the populations ($P<0.001$). The results are shown in table 3.

Table 3. Per cent winter damage in populations of *Agrostis capillaris* after three years. Average of harvesting regimes

Population No.	% winter damage	Population No.	% winter damage
1	61	8	53
2	63	9	55
3	63	10	46
4	54	11	71
5	58	12	55
6	49	13	68
7	62		
$P< 0.001$	$LSD_{5\%} = 10.2$		

Excluding 'Tracenta', which was almost eradicated after one winter, populations 11 and 13 tended to be more winter damaged than the others. The lowest winter damage was recorded in populations 10 and 6.

Grouped according to areas of origin, populations from the middlemost group (between 68°35' and 65°N-lat.)had less winter damage than the others, except at Bodø in the first winter after planting. The results are presented in Figure 1.

The middlemost group (M) recovered better than the others, especially in the first winter after different harvesting management (1985/86), and 'Leikvin' showed less tolerance to winter stress the farther north the location of the experiment.

Dry matter production

In average of populations, years and harvesting regimes, the dry matter production in tons per hectare at the different experimental sites was as shown in Table 4.

Sortland had a significantly higher dry matter yield than the other sites, both in the 1st and 2nd cuts. Also, Tjøtta outyielded Bodø, but significantly so in the 2nd cut only.

The yield difference between H_1 and H_2 was much the same at all the experi-

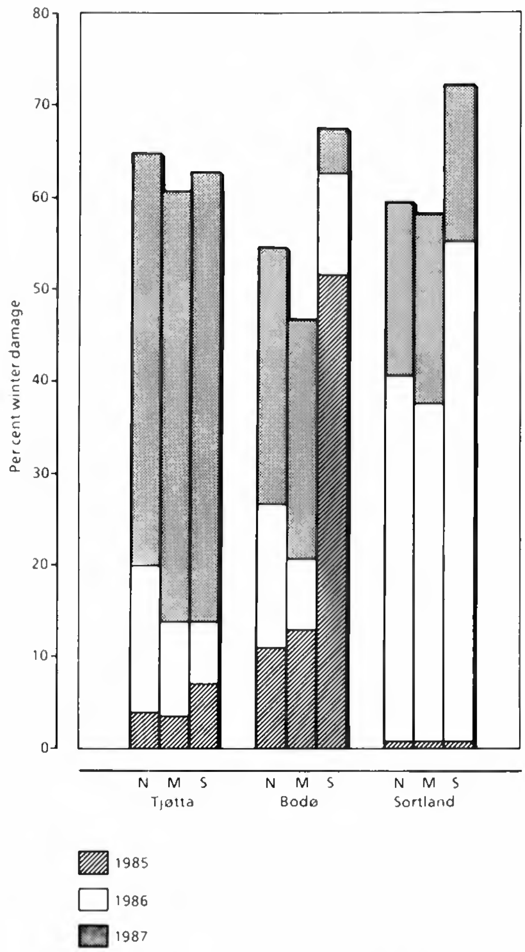

Figure 1. Per cent winter damage in populations of *Agrostis capillaris* grouped according to latitudes higher than 68°35'N (N), between 68°35'N and 65°N (M) and 'Leikvin' from 61°08'N (S).

mental sites in the 1st cut, with an average increase of 34% for delayed harvesting. In the average of the populations and sites the yield figure was as follows (tons per hectare):

1st cut		
H_1	H_2	P<
4.30	+1.46	0.05

The effect of different harvesting regimes on yield varied significantly between experimental sites (P< 0.001) in the 2nd cut. Delayed harvest had a greater negative effect on dry matter production at Bodø than at Sortland and in particular at Tjøtta (Table 5).

The total dry matter yield differed significantly between harvesting regimes only in the experiment at Tjøtta, where postponed harvesting brought about a positive effect. A similar positive effect at Sortland was nonsignificant, as was the negative effect at Bodø.

There were significant differences between the populations in dry matter yield in the 1st and 2nd cuts, and the total as shown in Table 6. No significant interaction could be proved between populations and harvesting regimes, or experimental sites.

In the 1st cut, population No. 6 had the highest dry matter yield, whereas

Table 4. Dry matter production in tons per hectare at each experimental site. Average of populations, years and harvesting regimes

	1st cut	2nd cut	Total
Tjøtta	4,68	3,04	7,72
Bodø	4,48	2,55	7,03
Sortland	5,93	4,35	10,28
P<	0,05	0,001	0,01
LSD 5%	0,95	0,10	0,97

Table 5. Dry matter yield in tons per hectare at harvesting regime H_1 and difference to H_2 at 2nd cut and total

	2nd cut		Total yield	
	H_1	H_2	H_1	H_2
Tjøtta	3,17	−0,25	7,39	+0,67
Bodø	3,48	−1,87	7,21	−0,37
Sortland	4,78	−0,86	9,75	+1,07
Average	3,81	−0,99	8,12	+0,46

No.3 had the lowest yield. 'Leikvin' also had a very low dry matter yield in the 1st cut, but in the 2nd cut this cultivar outyielded all the other populations. Again, No.3 was inferior, although not always significantly so.

Population No. 6 had the highest total dry matter yield, significantly so but for a few exceptions. No. 3 had the lowest total dry matter yield.

There was a significant negative correlation between the winter damage and dry matter yield in the 1st cut ($r=-0.453$, $P<0.001$), but not in the 2nd cut.

Per cent in vitro digestibility (IVDMD)

Quality aspects

The 1st cut herbage had a lower IVDMD than herbage from the 2nd cut at all the experimental sites, but particularly at Bodø and Tjøtta. The 2nd cut herbage at Bodø had a significantly higher IVDMD than the corresponding herbage at the other experimental sites. In the average of the populations, harvesting regimes and years, the results were as follows:

	Tjøtta	Bodø	Sortland	P<	LSD 5%
1st cut	70.6	71.8	71.5	0.10	1.18
2nd cut	72.6	75.3	72.3	0.001	0.86

The IVDMD was significantly influenced by the harvesting regimes (H_1 and H_2) at the 1st cut only. Delayed harvesting reduced the IVDMD by 4.5 %-units, which was a daily average decrease of 0.30 %-units from the 1st cut in H_1 :

	H_1	H_2	P<	LSD 5%
1st cut	73.5	69.0	0.05	2.98
2nd cut	74.4	72.4	0.10	

In the 2nd cut IVDMD was reduced by only 2%-units from H_1 to H_2 , but the daily average decrease was still approximately as in the 1st cut.

Significant differences in IVDMD were found in the 1st cut between the populations ($P<0.01$). This variation could partly be ascribed to a difference in IVDMD between the groups of populations from coastal and inland/fjord

Table 6. Dry matter yield in tons per hectare of populations of *Agrostis capillaris*. Average over years, experimental sites and harvesting regimes in 1st and 2nd cuts, and total

Population No. Name	1st cut	Ranking	2nd cut	Ranking	Total	Ranking
1 'Skjervøy'	4,98	8	3,33	7	8,31	8
2 'Sørvaranger'	4,84	11	3,21	9	8,05	12
3 'Lia'	4,51	13	3,00	13	7,51	13
4 'Kvæfjord'	4,97	9	3,17	11	8,14	11
5 'Bjerkvik'	5,05	7	3,12	12	8,17	10
6 'Hakvåg'	5,59	1	3,48	3	9,08	1
7 'Misten'	5,18	4	3,41	4	8,59	4
8 'ØvreTollådal'	5,14	5	3,20	10	8,34	6
9 'Dalen'	4,92	10	3,49	2	8,41	5
10 'Eiteråga'	5,22	3	3,40	5	8,63	3
11 'Tjøtta'	5,08	6	3,26	8	8,34	6
12 'Kløvimoen'	5,33	2	3,39	6	8,71	2
13 'Leikvin'	4,58	12	3,61	1	8,19	9
P<	0,05		0,05		0,05	
LSD 5%	0,43		0,33		0,64	

areas (P<0.05), and a residual within these groups (P<0.05). The results are presented in Table 7, with populations ranked according to increasing IVDMD within each group.

Table 7. Per cent in vitro dry matter digestibility (IVDMD) in herbage from 1st cut of *Agrostis capillaris* populations. Average of harvesting regimes

Populations from coastal areas Pop. No.	IVDMD	Populations from inland/fjord areas Pop. No.	IVDMD
1,3	72,1 ± 0,1	8,10	71,4 ± 0,2
4,11,6,9	71,7 ± 0,2	12	70,9 ± 0,0
7,5	70,9 ± 0,2	2,13	70,2 ± 0,2
Mean	71,6		70,8
LSD 5%	0,82		0,80

The herbage from populations of coastal origin had a higher IVDMD than the inland/fjord adapted ones. Nos. 5 and 7 deviated negatively from the others in the same group, while the lowest IVDMD was found in herbage from Nos. 2 and 13 in the group of inland/fjord populations.

Crude protein (CP)
The content of CP in the herbage from the three experimental sites differed significantly, in both the 1st and 2nd cuts. The average of the populations, harvesting regimes and years of experiments gave the following results in per cent of dry matter:

	Tjøtta	Bodø	Sortland	P<	LSD 5%
1st cut	13.3	14.5	15.9	0.001	0.73
2nd cut	17.7	20.6	15.5	0.01	2.20

In the 1st cut the content of CP in the herbage increased the farther north the location of the experimental site, and, with the exception of Sortland, the CP content was substantially higher in the 2nd cut.

As shown in Figure 2, absorbed nitrogen in grass from Sortland exceeded the level of N in the applied fertilizer by 56 and 64 kg per hectare in the 1st and 2nd cuts, respectively, in the first experimental year. In the herbages from Tjøtta and Bodø considerably less nitrogen was absorbed and exceeded the level of fertilizer nitrogen in the 2nd cut only.

With the exception of the 1st cut at Bodø, the absorption of nitrogen in the herbage was lower in the second year of harvest than in the first. In the second year the amount of absorbed nitrogen did not reach the level of nitrogen in the fertilizer in the 1st cut, and at Tjøtta in particular the difference was considerable (52 kg per hectare). In the 2nd cut the nitrogen recovered in the herbage did not differ substantially from the average applied level in the fertilizer.

The difference between applied nitrogen in the fertilizer and recovered N

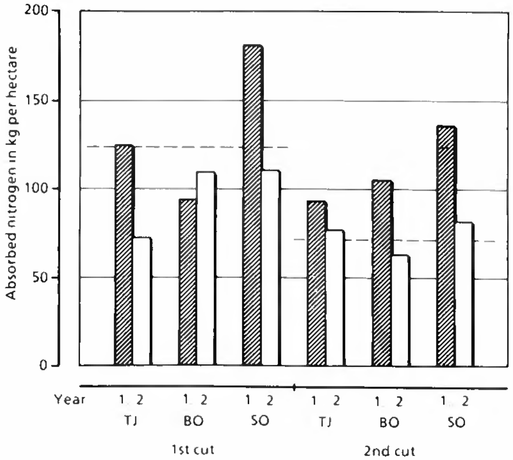

Figure 2. Absorbed nitrogen in kg per hectare. Average of harvesting regimes 1st and 2nd cut at Tjøtta (TJ), Bodø (BO) and Sortland (SO). Stippled lines indicate average amount of applied N-level, which was 125 kg per hectare in the 1st cut and 75 in the 2nd cut.

in the herbage was dependent on the harvesting system and the experimental site in both the 1st and 2nd cuts (Figure 3). At Sortland the level of absorbed nitrogen was higher than that applied in all cases, whereas this was true only in the 2nd cut at harvesting regime H_2 at Tjøtta. At Bodø the applied nitrogen was best utilized in the 2nd cut at harvesting regime H_1.

Table 8 shows the amount of absorbed nitrogen and the content of CP in the 1st and 2nd cuts for the investigated populations.

All the populations had a higher content of crude protein in the 2nd cut than in the 1st cut, with Nos. 3,4 and 5 ranked at the top and No. 13 at the bottom. In the 1st cut no significant difference was found between populations as regards percentage of CP in the herbage. On the other hand there were significant differences between populations in the capacity to absorb nitrogen in this cut. Populations 6 and 8 seemed to be more efficient than the others in this respect, while Nos. 3 and 13 absorbed nitrogen poorly.

There were of course strong correlations between the amount of absorbed nitrogen and dry matter production in both the 1st and 2nd cuts (r = 0.90).

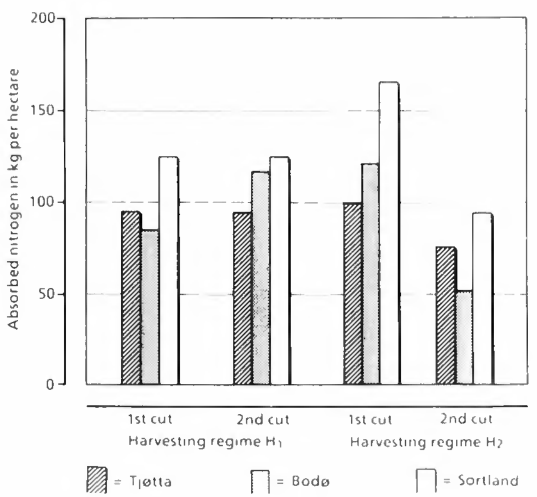

Figure 3. Absorbed nitrogen in kg per hectare in the 1st and 2nd cuts. Average of two years. Stippled lines indicate applied N-level.

Table 8. Absorbed nitrogen in kg per hectare and per cent crude protein of dry matter in various populations of *Agrostis capillaris*. Average of years and treatments. Applied nitrogen = 125 kg per hectare in the spring and 75 kg after 1st cut

Population No.	Absorbed nitrogen 1st cut	Absorbed nitrogen 2nd cut	Crude protein 1st cut	Crude protein 2nd cut
1	117	92	14,7	17,6
2	114	89	15,0	18,0
3	105	88	14,8	18,4
4	118	92	15,1	18,6
5	116	91	14,5	18,5
6	124	97	13,9	17,9
7	119	96	14,5	17,8
8	123	90	15,0	17,8
9	111	96	14,3	17,6
10	118	97	14,2	18,0
11	115	93	14,6	18,2
12	119	94	14,2	17,7
13	103	98	14,5	17,1
Average	116,5	93,5	14,6	17,9
P<	0,05	n.s	n.s	0,01
$LSD_{5\%}$	11,8			0,7

The laboratory experiments

Freezing tolerance

Because of strong and highly significant correlations between scores for freezing damage after 10 and 20 days (r = 0.937), and between scores after different freezing temperatures (-9°C and -12°C, r = 0.591), data have been pooled and the mean scores applied in the evalution of the populations.

Table 9 shows that 'Tracenta' had the lowest freezing tolerance, while populations 1, 3, 4 and 5 had the highest tolerance, although not significantly different from some of the others ($P < 0.001$, $LSD_{5\%} = 1.0$).

The difference between the groups of North Norwegian populations with coastal or inland/fjord adaptations was significant ($P < 0.01$ $LSD_{5\%} = 0.52$). The

Table 9. Freezing tolerance of *Agrostis capillaris* populations. 0 = dead plants, 9 = no damage

Coastal origin			Inland/ fjord origin		
Pop.No	N-lat.	Score	Pop. No	N-lat.	Score
1	70°00'	6,5			
3	68°52'	6,4	2	69°54'	5,2
4	68°45'	6,3	15	67°20'	5,1
5	68°35'	6,4	8	66°52'	5,5
16	68°15'	5,7	10	66°10'	5,7
6	68°00'	5,6	12	65°32'	5,0
7	67°25'	5,7	13	61°08'	5,1
9	66°50'	5,5	14	'Tracenta'	3,8
11	65°50'	5,5			
Average:					
All populations		6,0			5,0
North Norwegian pop.		6,0			5,3

freezing tolerance increased with the increasing latitude of origin in the group from the coastal areas.

Attacks by Fusarium nivale and Typhula ishikariensis

There was no significant difference in the damage caused by these fungi neither between populations or between groups according to the areas of origin. The results are presented in Table 10.

Population No. 2 was less attacked by both fungi than the others.

Grouped in populations from the coastal and inland/fjord areas of origin, the latter, including Nos. 13 and 14, had a negative correlation between attacks by *F. nivale* and *T. ishikariensis*, as shown in Table 11.

Freezing tolerance was positively correlated with resistance to attacks by *T. ishikariensis* within the coastal populations, whereas a negative correlation was found between freezing tolerance and resistance to attacks by *F. nivale* within the inland/fjord populations.

Table 10. Attack by *Fusarium nivale* and *Typhula ishikariensis* in populations of *Agrostis capillaris*. 0 = dead plants 9 = no attack

Population No.	Attacks by *Fusarium nivale*	Population No.	Attacks by *Typhula ishikariensis*
7,14,16	4.9 ± 0.1	5,11,15,16	4.7 ± 0.3
1,4,6,9 11,12,15	5.3 ± 0.1	3,4,6,7,8,9 10,12,13,14	5.6 ± 0.2
2,3,5,8 10,13	5.7 ± 0.2	1,2	6.1 ± 0.1

Table 11. Correlations between attacks by *F. nivale* and *T. ishikariensis*, and between freezing tolerance and attacks by these fungi

Climate of origin	Freezing tolerance	*Fusarium nivale*	*Typhula ishik.*	Corr. coef.	P<
Inland/fjord		X	X	-0,85	0,02
Coast	X		X	0,78	0,03
Inland/fjord	X	X		-0,74	0,06

DISCUSSION

General

The rough topography of northern Norway, with its relatively high mountains, long fjords and more or less isolated islands and peninsulas, provides conditions for the development of genetically distinct populations. The locations thus separated may have very different local climates, which provide a basis for diverse adaptation. The various obstacles against geneflow from one locality to the other act in the same direction (Bradshaw 1959, 1960).

The use of spaced plants in the field trials does not allow for the competitive ability of the genotypes to act, and the herbage yield obtained in such conditions does not necessarily correlate with the yield in a dense sward.

Winter damage

The North Norwegian populations investigated had almost no regrowth after the 2nd cut, and were therefore more or less without green leaves in the periods when conditions for hardening were present, as illustrated in Figure 4.

Unsatisfactory hardening was therefore expected at all the sites in both harvesting regimes in 1985 , and such was also the situation in H_1 at all the sites in 1986. However, hardening conditions existed in H_2 before the 2nd cut at Bodø and Sortland, but not at Tjøtta in the latter year (see date of cuts and end of growth season, pages 82 and 83). In the spring of 1987, considerably greater winter damage was recorded in H_1 than in H_2 (page 84). However, the different reactions to harvesting regimes between the sites in 1985/86 and the high level of winter damage in H_2 at Sortland in 1986/87, indicate that hardening conditions alone cannot explain all the differences in winter damage.

As also shown in earlier investigations (Østgård 1962, Larsen 1972, Olsen 1973), postponement of the 1st cut reduced the winter damage, while increased nitrogen fertilizer applied to the aftermath had a negative influence (Pestalozzi 1960, Årsvoll & Larsen 1977).

It is therefore reasonable to assume that poor hardening conditions, an unsuitable harvesting regime, and a too heavy nitrogen application gave rise to the winter damage at H_1 in the present investigation.

It is remarkable that populations from the southern parts of North Norway overwintered better than those from the northern areas (Figure 1), since freezing tolerance increases with higher latitudes of origin in populations from the coastal areas (Table 9) and hence should have lowered the winter damage of the northernmost group. A similar reaction in overwintering has also been observed in arctic types of *Poa pratensis* (Håbjørg 1979). This is probably due to the adaptation of the northernmost populations to more stable winter conditions than are found in Nordland.

Larsen (1983) tested freezing tolerance and resistance to attack by *T. ishikariensis* and *F. nivale* in populations of

Figure 4. Regrowth in North Norwegian populations of *Agrostis capillaris* at Tjøtta, October 1985. Sown *Phleum pratense ('Bodin') separated the main plots*

A. capillaris. In contrast to the present results (Table 11), no significant correlation was found in his investigation, either between freezing tolerance and resistance to *T. ishikariensis* and *F. nivale*, or in resistance between the two fungi. The occurrence of snow mould fungi is negligible in northern Norway (Årsvoll 1973) and natural selection for resistance to the investigated fungi is therefore unlikely.

The present results should be interpreted with caution because the correlation analysis is based on a very few populations. However, the magnitude of the correlation coefficients at least indicates that freezing tolerance and resistance to snow mould fungi might not be independent of each other.

Dry matter yield

The dry matter yield in the 1st cut was considerably higher (about 24%) in the present investigation than that found in *A. capillaris* dominated grasslands of practical use in Nordland (Nesheim 1986c), although the fertilizer applied was much the same. This might be an effect of spaced plants with less competition for water, light and plant nutrition.

The different dry matter production found between the experimental sites is thought to be due mainly to different nitrogen supply (Figures 2 and 3). This might also have partly influenced the difference between the 1st and 2nd cut's yield, but the shorter growth period from the 1st to 2nd cut works in the same direction.

An increasing dry matter yield from H_1 to H_2 in the 1st cut was expected since the vegetation continues its production until the flowering stage (Baadshaug 1974). The growth period was longer up to the 1st cut at Bodø in H_2 than at the other sites (Table 2). This implied regrowth for the 2nd cut at the later and shorter growth period. Reduced photoperiods and lowered temperature markedly delay the growth of grasses (Andersen & Østgård 1980). Low dry matter yield was therefore expected at H_2 in the 2nd cut at Bodø. Together with the difference in nitrogen supply, this makes the interaction site x harvesting regime in the 2nd cut explainable.

Four of the five highest ranked populations in dry matter yield were among the five populations found to be best in winter survival (Tables 3 and 6). A significant negative correlation between winter damage and dry matter yield was found in the 1st cut, only. This indicates the presence of an ability to repair spaces in the stand after winter damage.

Quality aspects

The IVDMD of the 1st cut herbage in the present investigation was more than 6%-units higher than that found in *A. capillaris* dominated samples in a grassland survey in Nordland (Nesheim 1986c), and likewise when compared with results from field experiments in south-eastern Norway (Olsen 1978). This disparity was probably due to an accelerated development and less withered leaves on spaced plants than on plants in a dense sward.

The daily average decline of IVDMD by postponed harvesting (H_2) in the 1st cut was somewhat lower in the present investigation than that found in the same species in southern Norway (Olsen 1978). This could be a consequence of the better digestibility of the cell walls from the stems, presumably because the rate of lignification cannot keep pace with the rapid rate of stem development at higher latitudes (Deinum et al. 1981).

In phytotron experiments, population 13 ('Leikvin') developed considerably better at 3°C constant temperature than populations from northern areas (Karlsen 1988,in press.). It produced more panicles and matured considerably earlier than the others, especially compared with No. 11 ("Tjøtta'). Similar results were also observed in the field trial at Tjøtta. It is probable that such responses are adaptive traits due to different growth conditions in the early spring in the inland and coastal areas. Populations which are adapted to the coastal climate with its long snowless periods in the early spring, have a later growth start than those adapted to inland conditions with a rapid growth start after the snow thaw. Therefore, although it was not directly recordable in the field trials, development of the inland populations might have been faster than the coastal ones if grown under coastal conditions, hence causing the different IVDMD between these groups.

The very high nitrogen absorption at Sortland in the first experimental year (Figure 2) demonstrates that nitrogen sources other than the applied fertilizer were present. Since legumes were not represented in the stand and the content of nitrogen measured in the rain water at Tustervatn in Nordland in the actual period was less than 10 kg per hectare and year (Statens forurensningstilsyn 1986), the extra nitrogen absorbed must have been produced by mineralization of nitrogen components in dead plants, animals and manure (Salisburry & Ross 1978).

The loss of ignition was much higher at Sortland than at the other sites (page 81). Nesheim (1986c) found that both the percentage of CP in herbage and CP yield decreased with rising loss of ignition, which is in disagreement with the present results. However, Nesheim's (l.c.) investigation was in more or less permanent meadows while the present one was in newly cultivated fields, which allowed a greater mineralization (Sorteberg 1976).

The percentage of CP in herbage increases with increasing nitrogen application (Schjelderup 1970, Simonsen & Skinnes 1979, Nesheim 1986c), and the considerable nitrogen access from the mineralization described above might therefore have raised the percentage of CP to a higher level in the herbage from Sortland compared with that in the other sites (page 87 and Figure 2 and 3).

Absorbed nitrogen in the herbage yield from the 1st cut was equal to the nitrogen in the fertilizer for populations 6 and 8 only (Table 8). However, the high rate of nitrogen absorption was most efficiently used by population 6, which showed a considerably higher dry matter production than No.8 (Table 6). The latter therefore had a higher percentage of protein in the 1st cut. Nitrogen was applied per area unit independent of plant density in the stand. Therefore, the greater absorption in Nos.6 and 8 can be related at least in part to less winter damage and hence a better root capacity than the populations with greater winter damage (Table 3).

In the 2nd cut, population 13 ('Leikvin') had the highest absorption of nitrogen, although not so significantly different from the others. This population also had the lowest percentage of crude protein, which might be expected from the high dry matter production (Table 6).

CONCLUSION

Some of the North Norwegian populations which were included in the trials had considerably higher qualities under the actual growing conditions than the certified cultivars 'Leikvin' and 'Tracenta'. The present results rather imply a warning against the use of these cultivars in the northern part of the country. The high level of winter damage at intensive harvesting, which also hit the best North Norwegian populations, is not acceptable, but an ability to repair spaces in the stand after winter damage was evident, since no negative correlation was found between winter damage and dry matter yield in the 2nd cut. The North Norwegian population had a higher growth rate in the 1st cut compared with 'Leikvin' (62.5% and 56% of total dry matter yield, respectively); also IVDMD was better in this cut. The present investigation did not allow for comparisons between *A. capillaris* and other species, but the high level of winter damage at intensive harvesting, a late growth start in the spring and a poor regrowth after the 2nd cut, exclude the investigated populations from meadow cultivation, where early and relatively frequent cutting is practised. For such conditions it seems probable that a breeding programme based on the most attractive populations and aiming at improved survival after intensive grassland management might be profitable. Also the quality aspects should be considered in this connection. However, in many parts of the country extensive harvesting methods are the only means of meadow cultivation, and in such areas the best population in the present investigation could be introduced.

In any case the seed of populations No.6 'Hakvåg', No.10 'Eiteråga' and No.12 'Kløvimoen' must be multiplied for further experiments.

ACKNOWLEDGEMENTS

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PRIMARY AND SECONDARY INDUCTION REQUIREMENTS FOR FLOWER INITIATION IN FOUR POPULATIONS OF *AGROSTIS CAPILLARIS* L.

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Karslen Å. K.1988. Primary and secondary induction requirements for flower initiation in four populations of *agrostis capillaris* L.Norwegian Journal of Agriccultural Sciences 2:97-108. ISSN 0801-5341

Temperature and photoperiod requirements in the primary and secondary induction for flower initiation have been studied in four populations of *Agrostis capillaris* L. No heading took place after primary induction treatments of less than 10 weeks' duration or at high temperature (21°C), and the presence of an obligate juvenile phase as a condition for panicle production was demonstrated. The populations from northern Norway became more or less neutral to the photoperiod at low temperatures (3°C and 6°C), whereas 'Leikvin' from the southern parts of Norway hardly headed at all in continuous light although the temperature was 3°C.
The critical photoperiod for secondary induction of at least 50% of the plants was about 15 and 17 hours, depending on the place of origin of the populations. The northern ones remained vegetative at photoperiods below 16 hours. The optimum temperature was 15°C for photoperiods below 24 hours, but most panicles were developed at 9°C with continuous light.
Viviparous proliferation was observed instead of inflorescences after incomplete primary induction, and in the flowers after incomplete secondary induction.

Key words: *Agrostis capillaris*, flowering, induction, photoperiod, temperature.

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In the county of Nordland (64°75'-69°18'N-lat.), *Agrostis capillaris* constitutes 22% of the dry matter yield harvested from cultivated meadows, though it is rarely sown by the farmers (Nesheim 1986). This indicates that a large number of *A. capillaris* populations are adapted to various climatic growth conditions. The important role of this species in practical meadow cultivation in Nordland increases the need to investigate the agronomic value of these populations (Karlsen 1988). Also, seed production characteristics should be considered.

Commercial seed production of high latitude grass cultivars in Norway is commonly located in the more southerly parts of the country, with higher summer temperatures, shorter photoperiods and longer growing seasons than in the northern areas, where they have their origin. In *Poa pratensis* L., seed production of the cultivar 'Holt', which is adapted to a climate with a short growing season, low temperatures and long photoperiods, has also been attempted in Denmark and USA., but without success (Rasten 1978, Håbjørg 1978). It was found later that photoperiodic constraints limited flower development and stem elongation of that cultivar in the pring (Håbjørg 1978, 1979b, Heide 1980).

The results from only a few investigations of flowering requirements of *A. capillaris* are available, but they clearly demonstrate an autumn/winter requirement before long days for floral initiation and hence a dual induction. Thus, Cooper & Calder (1964) stated that *A. capillaris* had a «moderate inductive requirement (mainly or solely for short-day)», as heading almost failed after cold induction treatment before continuous light. Furthermore, insufficient vernalization to induce ripeness to flower, or devernalization in subsequent growth at a high temperature (20°C) and a long photoperiod, are discussed as reasons for the low flowering response after 21 weeks of short-day, including a period of 6 weeks of natural cold treatment in December/January for Icelandic and British populations of this species (Helgadóttir 1981).

The only Norwegian commercial cultivar of *Agrostis capillaris* L. is 'Leikvin', which is adapted to highland areas in the southeastern parts of the country (61°N-lat.). This cultivar has been successfully multiplied in Oregon, U.S.A. (Buraas 1986).

Blondon (1972) introduced the terminology primary and secondary induction relating to the dual requirement for flower initiation and flower development in *Dactylis glomerata* L. These terms are also used in the present paper. Primary induction is defined as the impulse needed for flower initiation and flower differentiation. Secondary induction is defined as the impulse needed to complete the flower development and stem elongation.

In the present study the photoperiodic effect on heading and development of panicles in four populations of *A. capillaris* has been studied over a wide range of temperatures in two experiments; one for the primary induction requirement and one for the secondary induction requirement.

MATERIAL AND METHODS

Three North Norwegian ecotypes of *A. capillaris* were compared with the certified cultivar 'Leikvin'. The ecotypes are named after their place of origin. Because 'Leikvin' may be considered as a slightly selected local ecotype, both the local ecotypes and the cultivar are termed populations for the sake of brevity. The name of the population, county and latitude of their locations of origin and their main climatic adaptations are:

Name	*County*	*N-lat.*	*Climate*
'Sørvaranger'	Finnmark	69°54'	Fjord to inland
'Øvre Tollådal'	Nordland	66°52'	Inland
'Tjøtta'	Nordland	65°50'	Coast
'Leikvin'	Oppland	61°08'	Highland

An extensive collection of seed from northern populations of *A. capillaris* was carried out in 1972 - 1977 as described by Schjelderup (1973). Among the numerous populations collected, 'Sørvaranger', 'Øvre Tollådal' and 'Tjøtta' were chosen as representing the variation in climatic and latitudinal adaptation of the collected plant material. The seed of 'Tjøtta' and 'Øvre Tollådal' was multiplied for experimental use in isolated blocks at Tjøtta Research Station, and that of 'Sørvaranger' in a similar block at Holt Research Station. For 'Leikvin', commercial seed was applied.

Plants raised from seed were used in both experiments. After germination at 21°C and in continuous fluorescent light, the plants were potted singly in 10 cm plastic pots in standard soil, and kept for 5 weeks in continuous light and at 21°C before the experiments started.

The experiments were conducted in the daylight phytotron compartments and corresponding adjacent rooms with darkness or low-intensity light from incandescent lamps (irradiance about 2.0 Wm^{-2}, 400-750 nm) at the University of Tromsø. The first replication of the primary induction experiment was conducted between September and July in 1985-86 and the second during the same period in 1986-87. In the secondary induction treatments, the first replication was conducted between March and October 1985 and the second replication between October and July 1985-1986.

From November 26 to January 15 Tromsø has polar nights. In the period from October 1 to March 15 the daylight was therefore complemented with fluorescent light of irradiance about 18.0 Wm^{-2}, 400-750 nm.

Temperatures were controlled at ±0.5°C. A weekly application of a modified Hoagland solution was used throughout the experimental period, except at 3°C, where the fertilizer solution was given every third week.

The experimental treatments were:

Primary induction treatment

Temperatures	Photoperiods	Duration of treatment
3°C	8 hours	(5 weeks)
6°C	16 "	10 "
9°C	24 "	15 "
12°C		
(21°C)		

The parentheses indicate that every combination of these experimental treatments was tested in one replication only, because they then failed completely in flower induction. Six plants per treatment and two replications were involved in the standard procedure.

Each treatment had a constant period of 8 hours with sunlight (or complementary fluorescent light) and was combined with various periods of low intensity light or darkness to give the desired photoperiods. Thus, the daily amount of radiant energy was nearly identical for all the treatments within the experiment.

At the termination of the primary induction treatment, all the plants were moved to a 24 hours' photoperiod and 18°C for recording inductive response.

Secondary induction treatment
To study the secondary induction requirements, the plants were given a primary induction treatment of 10 hours' photoperiod at 6°C for 15 weeks, before the following treatment:

Temperatures	Photoperiods	Duration of treatment
9°C	12 hours	15 weeks
15°C	14 "	
21°C	16 "	
	18 "	
	24 "	

Each treatment had a constant period of 12 hours' daylight. Otherwise the same technique as described for the primary induction treatment was used to give the desired photoperiods.

The experiments were factorial in structure, and the data were subjected to a factorial analysis of variance in accordance with the MSTAT programme for statistical analysis described by Nissen & Moslett (1985).

RECORDINGS

For both the primary and the secondary induction experiment, the inductive response was recorded as:

1. Time in weeks from start of secondary induction treatment to first visible panicle on each plant.
2. Number of plants with visible panicles at termination of the experiment. This is expressed as number of heading plants.

3. Number of visible panicles per plant at termination of the experiments.

In addition to these recordings, some morphological characters were observed in both experiments, but these will be discussed in another paper.

RESULTS

Primary induction

Duration of treatments

No heading took place after 5 weeks of primary induction treatment and a subsequent 15 weeks at 18°C and a 24 hours' photoperiod in the first replication, so this treatment was omitted in the second replication. After 10 and 15 weeks of primary induction treatment, panicles emerged during the subsequent growth at 18°C and 24 hours' photoperiod. However, at termination of the experiment, significant differences occurred between the populations in the number of heading plants for the different durations of treatment, as presented in Figure 1 ($P < 0.05$).

On an average of primary induction treatments, barely 1 out of 6 plants of 'Tjøtta' had visible panicles after 10 weeks of primary induction treatment, compared with 2.1 - 2.7 plants of the other populations. After 15 weeks of treatment, 'Øvre Tollådal' had 4.5 heading plants out of 6 in contrast to 3.6 - 3.8 of the other 3 (Figure 1).

After 10 weeks of primary induction treatment an increase in photoperiod from 8 hours to over 16 to 24 hours caused an almost linear reduction in the number of heading plants, from 2.5 to 1.3 plants out of 6 (Figure 2). A considerably greater number of heading plants was recorded after primary induction treatment of 15 weeks, as is also evident from Figure 1. However, the negative response to increasing the photoperiod from 16 to 24 hours was evidently more pronounced at this duration of treatment (Figure 2).

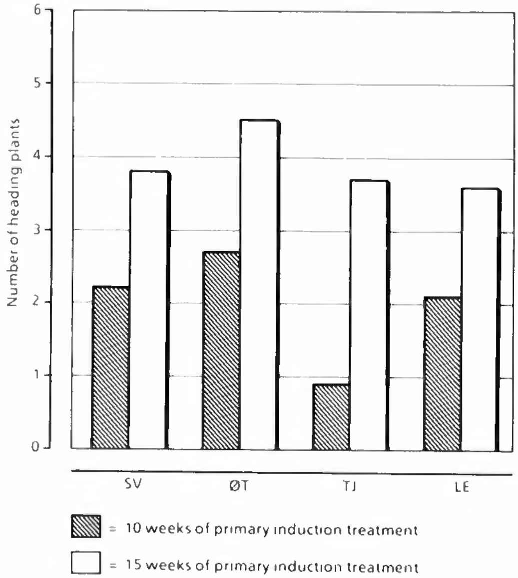

Figure 1. Number of heading plants (out of six) after 10 or 15 weeks of primary induction treatment and subsequent growth during 15 weeks at 18°C and 24 hours' photoperiod. Average of experimental treatments. SV = 'Sørvaranger', ØT = 'Øvre Tollådal', TJ = 'Tjøtta', LE = 'Leikvin'

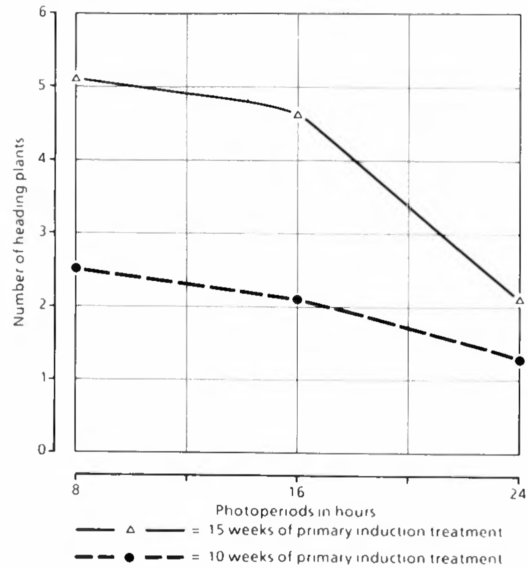

Figure 2. Effect of different durations of primary induction treatment at 8, 16 and 24 hours' photoperiod on number of heading plants (out of six) in subsequent growth at 18°C and 24 hours' photoperiod. Average of temperatures, populations and replications

Photoperiod and temperature
A significant interaction ($P < 0.02$) between photoperiod and temperature was found in the number of heading plants and in the number of panicles per plant (Figure 3).

Increasing the induction temperature to 9°C did not affect the number of heading plants significantly at the 8 and 16 hours' photoperiods. Keeping the plants at 12°C during primary induction caused a considerable reduction in the number of heading plants at both of these photoperiods, and particularly at 16 hours (Figure 3, left). Increasing the photoperiods to 24 hours generally lowered the heading response (as can also be seen from Figure 2), and at 9°C and in particular at 12°C during primary induction the number of heading plants approached zero. A parallel effect was found in the number of panicles per plant, but with a positive effect of increasing the temperature from 3° through 6° to 9°C at both 8 and 16 hours' photoperiods (Figure 3, right). At 24 hours photoperiod, the number of heading plants and the number of visible panicles per plant were reduced at 3°C and 6°C mainly because respectively only one and two plants of 'Leikvin' headed. This might be ascribed to plant elongation (leaf sheath and blade length) during the primary induction period which was negatively correlated with the number of visible panicles at the termination of the experiment ($r = -0.589$, $P < 0.001$). At 24 hours' photoperiod the average elongation of 'Leikvin' was 14 cm and 18 cm at 3°C and 6°C, respectively, whereas the elongation of the others was insignificant.

As shown in Figure 4, increasing temperatures between 3°C and 12°C during the primary induction affected the populations differently.

'Tjøtta' had a linear decrease in the number of heading plants with increasing temperature, while the other populaions showed a more or less pronounced increase up to 6°C before decreasing linearly, although with different slopes. In this respect 'Leikvin' seemed to be less sensitive to increasing temperatures

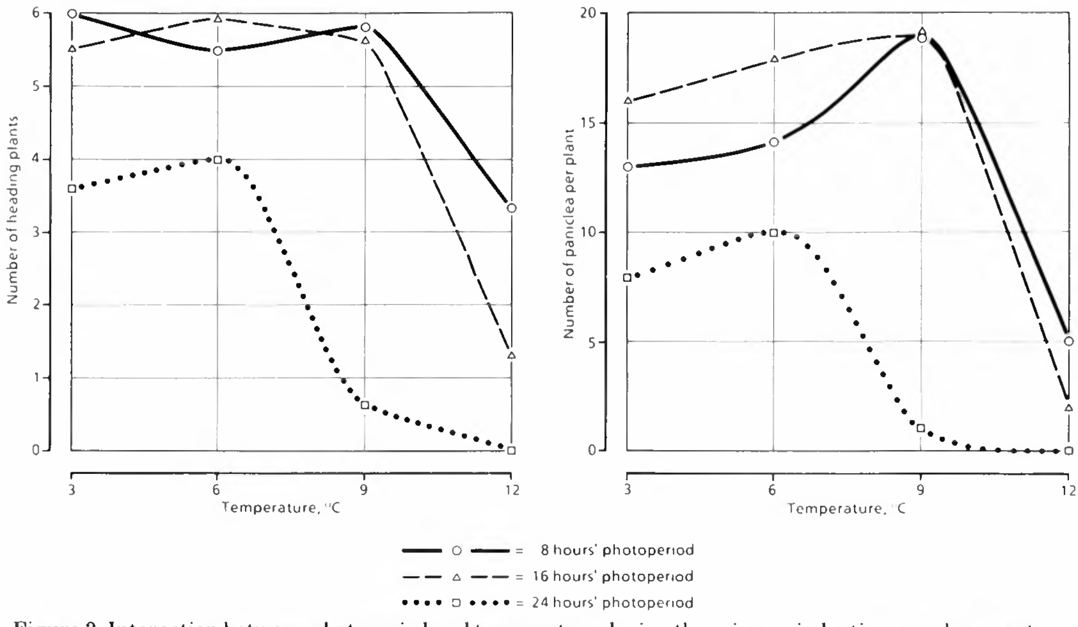

Figure 3. Interaction between photoperiod and temperature during the primary induction on subsequent heading after 15 weeks at 18°C and 24 hours photoperiod. Average of populations. Treatment period = 15 weeks

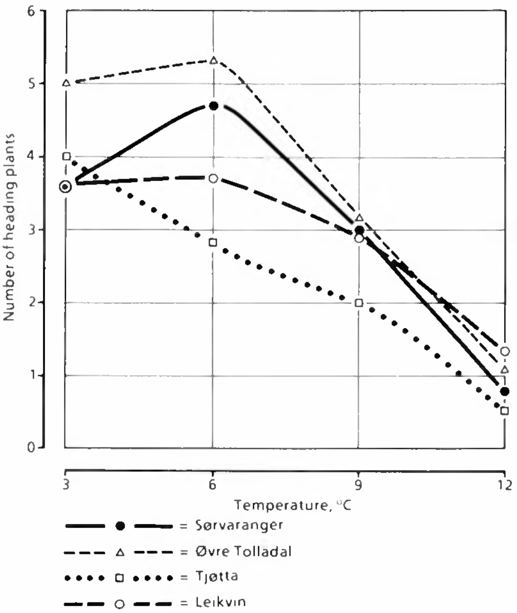

Figure 4. Effect of different temperatures during primary induction on number of heading plants (out of six) in four populations of *Agrostis capillaris*, recorded at termination of the experiment. Average of 8, 16 and 24 hours' photoperiod and of 10 and 15 weeks' duration of primary induction

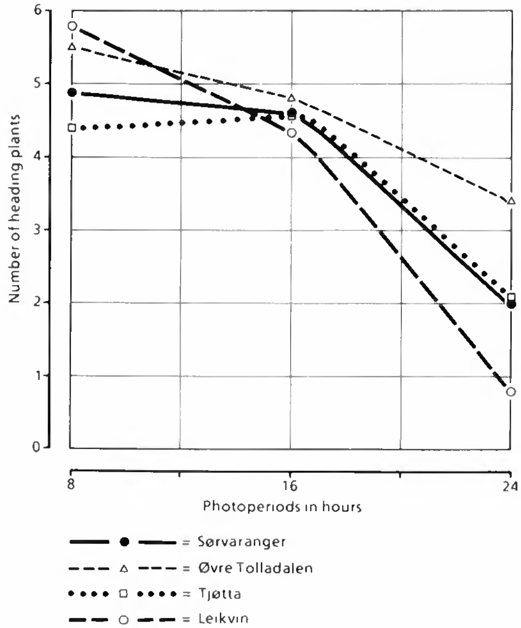

Figure 5. Effect of different photoperiods, during 15 weeks of primary induction, on number of heading plants (out of six) in four populations of *Agrostis capillaris*. 15 weeks' subsequent growth at 18°C and 24 hours' photoperiod. Average of 3°, 6°, 9° and 12°C during primary induction

during primary induction than the North Norwegian populations (Figure 4).

For 'Leikvin' there was a greater reduction in the number of heading plants by increasing photoperiods than there was in the other populations. 'Øvre Tollådal' represented the other extreme with an average of 3.4 heading plants even at 24 hours' photoperiod in the 15 weeks' treatment presented in Figure 5.

No examination of the development of primordia was made when primary induction treatment was terminated. Therefore, in September 1987 five shoots from each of five randomly selected plants of 'Leikvin', 'Sørvaranger' and a new population 'Hakvåg' (Karlsen 1988) were collected from field trials at Bodø and dissected within three days. In all shoots the apices were vegetative at stage 1 according to the scale of Jeater (1956).

Secondary induction

Photoperiod and temperature

The number of heading plants varied both with temperature and with length of photoperiod during the secondary induction (Figure 6.)

Number of heading plants showed a sigmoid development with increasing length of the photoperiod both at 15°C and at 21°C. If a critical photoperiod is set at 50% heading plants, this would be about 16 hours at 15°C and 17 hours at 21°C. At 9°C the heading was restrained at photoperiods lower than 24 hours, and 50% heading required 18 hours' photoperiod at this temperature. The few plants which were induced at 12 and 14 hours photoperiod at 15°C and 21°C,

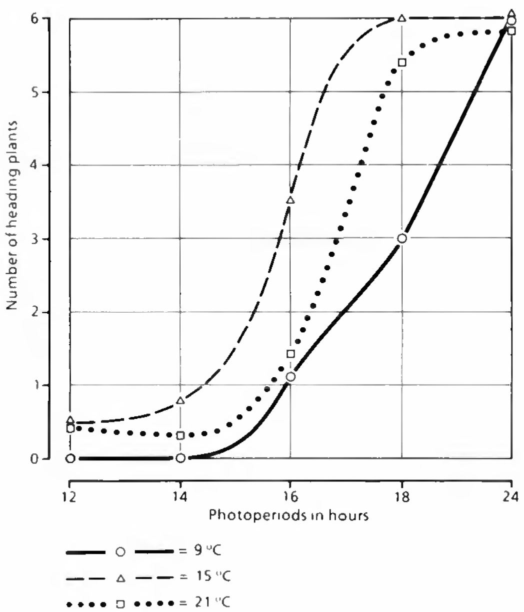

Figure 6. Number of heading plants (out of six) after previous 15 weeks' primary induction at 6°C and 10 hours' photoperiod, succeeded by 15 weeks' secondary induction as indicated in figure. Average of populations

were mainly due to 'Leikvin', as can be seen in Figure 8.

Increasing the photoperiod in the secondary induction, increased the number of visible panicles per plant at termination of the experiment. In Figure 7 this is shown as the percentage of recorded shoots before plants were transferred from primary induction to secondary induction.

At 24 hours' photoperiod the percentage of visible panicles decreased with increasing temperature, from 86% at 9°C to 46% at 21°C. Shorter photoperiods lowered the percentage of visible panicles at all temperatures, but the most pronounced was from 24 to 18 hours at 9°C.

A supplementary experiment with the same populations clearly demonstrated that plant age, from germination to start of primary induction treatment at 6°C and 10 hours' photoperiod for 15 weeks, affected the proportion of shoots producing panicles. The effect was also dependent on population (as shown in Table 1).

Table 1. Number of panicles per plant. 15 weeks of primary induction treatment at 6°C and 10 hours' photoperiod, before 15 weeks at 18°C and 24 hours' photoperiod. Plant age after germination when transferred as indicated

Age in weeks after germination:	<1	2	3	4
'Sørvaranger'	0	11.0	22.3	34.3
'Øvre Tollådal'	0	9.8	24.0	27.0
'Tjøtta'	0	1.3	6.5	23.8
'Leikvin'	3.8	18.0	24.7	27.0

The results reveal the presence of an obligate juvenile phase as a condition for panicle production in the North Norwegian populations. Among these populations, the one with the southernmost location of origin ('Tjøtta') had the strongest age requirement for ability to produce many panicles, whereas the northernmost ('Sørvaranger') showed the most abundant production of panicles of all the populations after a primary induction at an age of 4 weeks from time of germination. 'Leikvin' from South Norway produced very few panicles after a primary induction treatment at an age of less than a week after germination. However, in this respect increasing age after 2 weeks had only a minor effect.

It is therefore obvious that tillers which developed towards the end of the primary induction period had not been induced to flowering and hence had a vegetative development when transferred to higher temperatures and longer photoperiods (Figure 7).

Photoperiod and population

The North Norwegian populations required a two hours longer photoperiod than 'Leikvin' to induce development of

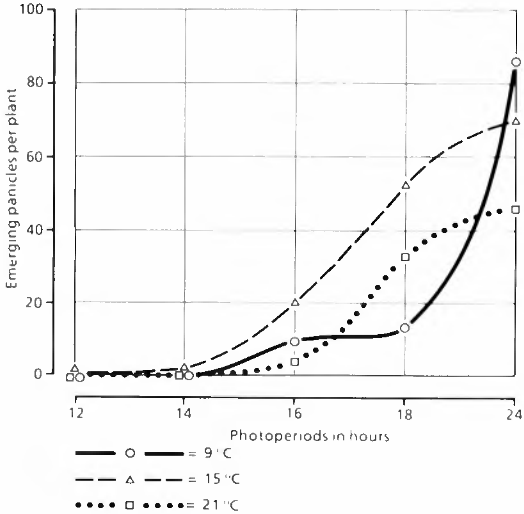

Figure 7. Number of visible panicles per plant at termination of the experiment, expressed as a percentage of the total number of shoots recorded when transferred from primary to secondary induction

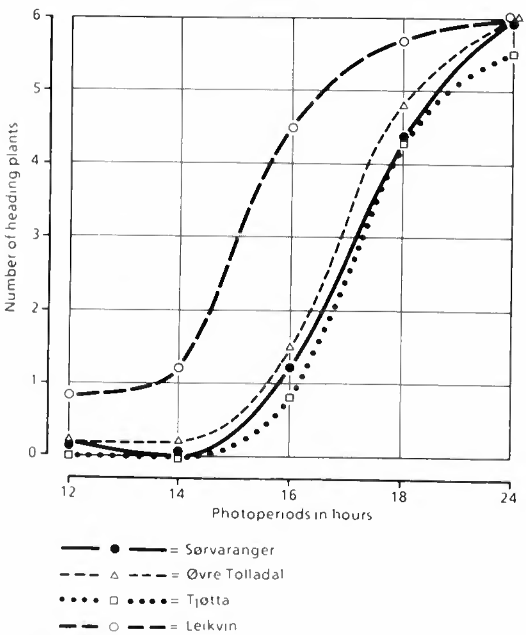

Figure 8. Number of heading plants (out of six) in four populations of *Agrostis capillaris*. 15 weeks of primary induction at 6°C and 10 hours' photoperiod before secondary induction for 15 weeks and photoperiods as indicated in the figure. Average of three temperatures

inflorescences in at least 50% of the plants, 17 and 15 hours, respectively. At photoperiods shorter than 16 hours only sporadic heading was recorded in the North Norwegian populations, whereas scarcely one plant of 'Leikvin' headed at daylengths between 12 and 14 hours (Figure 8).

The different photoperiods affected the populations in the same direction in respect of the number of visible panicles per plant at the termination of the experiment (as given in Table 2).

Table 2. Number of visible panicles per plant in four populations of *Agrostis capillaris*. 15 weeks of primary induction at 6°C and 10 hours' photoperiod before secondary induction for 15 weeks and photo periods as indicated in the table. Average of three temperatures

	Photoperiods in hours				
	12	14	16	18	24
'Sørvaranger'	0	0	1	12	32
'Øvre Tollådal'	0	0	2	11	26
'Tjøtta'	0	0	1	9	23
'Leikvin'	1	2	15	27	41

The optimal length of the photoperiod was 24 hours for all populations, but 'Leikvin' produced a considerably higher number of panicles than the North Norwegian populations. Within the latter there was an increase in the number of panicles per plant with decreasing latitude of origin at 18 and 24 hours photoperiod.

Recordings of weeks from the start of secondary induction treatment to heading were not complete, but available data suggest that in 'Leikvin' heading started 1 - 2 weeks before and in 'Tjøtta' a similar period after the mean week of heading (Table 3).

At shorter photoperiods and lower temperatures the differences between the populations in time to heading seemed to be greater, whereas continuous light and 21°C reduced the difference

Table 3. Number of heading plants (out of six) after 15 weeks of primary induction treatment at 6°C and 10 hours' photoperiod, before secondary induction treatment at 15°C and 18 hours' photoperiod for 15 weeks

	No. of weeks from start of secondary induction treatment to heading:					
	6	7	8	9	10	11
'Sørvaranger'	0	1	4	6	6	6
'Øvre Tollådal'	0	1	5	5	6	6
'Tjøtta'	0	1	2	4	4	6
'Leikvin'	0	5	6	6	6	6

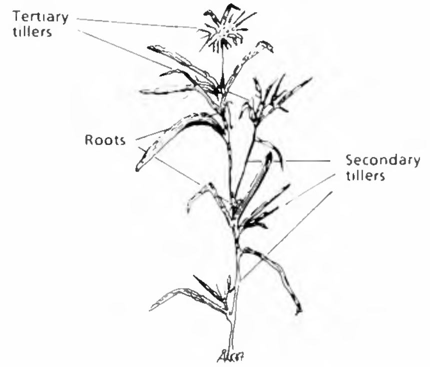

Figure 9. Secondary and tertiary tillers developed from nodes on the upper half of a primary shoot of *Agrostis capillaris*

between 'Leikvin' and the two northernmost populations.

Asexual reproduction

Two forms of above ground asexual reproduction were recorded when the plants were examined at termination of the experiments. After primary induction of short duration (5 weeks) of treatment, high temperature (21°C and partly 12°C) and some photoperiods causing plant elongation, secondary and tertiary tillers emerged from nodes on the upper half of the primary shoots. Roots were also observed to emerge from the new shoots. An example is presented in Figure 9.

With some combinations of temperature and photoperiod during the secondary induction treatment, viviparous proliferations developed in the flowers, but as shown in Table 4 this was most widespread in 'Leikvin' and at the highest temperature used.

The temperature/photoperiod combination 21°C/18 hours gave the highest number of plants with viviparous proliferation in the North Norwegian populations, and the 21°C/16 hours combination in 'Leikvin'. However, in 'Leikvin' this kind of deviation from normal seed development also occurred in all the other photoperiods except 24 hours at this temperature.

At 15°C viviparous proliferation occurred at all the photoperiods, but perhaps more randomly and to a lesser ex-

Table 4. Number of plants (out of six) with viviparous proliferation in the flowers of *Agrostis capillaris* populations. Grown for 15 weeks at indicated conditions after 15 weeks of primary induction at 6°C and 10 hours' photoperiod

Temperature:	15°C					21°C				
Photoperiod in hours:	12	14	16	18	24	12	14	16	18	24
'Sørvaranger'	0	0	0	1.0	0	0	0	0	3.0	0
'Øvre Tollådal'	0.5	0.5	0	0	1.0	0	0	0.5	3.5	0
'Tjøtta'	0	0	0	1.0	0	0	0	0	2.0	0
'Leikvin'	0	0	0.5	0	0	1.5	1.0	3.0	1.5	0

tent than at 21°C. At 9°C only normally developed inflorescences were found, but in some cases at shorter photoperiods inflorescences had barely emerged when the experiment was terminated and viviparous proliferation was not visible.

DISCUSSION

The present work proves a dual requirement for flower initiation and development, since no heading took place either in continuous short or in continuous long photoperiods at moderate temperatures (Figures 3 and 8). This concurs with corresponding experiments in *A. capillaris* (Cooper & Calder 1964, Helgadsttir 1981) and in many other grass species of temperate origin (Evans 1960, Håbjørg 1978, Heide 1980, 1984,1986,1987,1988).

In the investigated populations a duration of more than 10 weeks of primary induction was essential to reach 50% heading (Figure 1), which was longer than recorded in other species of corresponding origin (Håbjørg l.c., Heide l.c.). 'Tjøtta', the only investigated population from the coastal areas, required a markedly longer duration of primary induction than the populations from the inland areas. A similar effect was recorded in the weeks to heading, where 'Tjøtta' was considerably later than the others.

In *Poa pratensis* Håbjørg (1979a) demonstrated a later development of floral primordia in ecotypes from marine and midtemperate areas than those from the northern and high elevational or continental areas. A corresponding connection was recorded in the time to heading (Håbjørg 1979b).

Although *A. capillaris*, like *Dactylis glomerata* (Heide 1987) and *Bromus inermis* (Heide 1984), in all probability does not initiate inflorescence primordia in autumn conditions like *Poa pratensis* (Håbjørg 1979a), the populations of the two species the from similar areas showed parallel responses to change in the durtion of primary induction treatment and in time to heading. This might well be an adaptation to the diverse climatic condtions in inland and coastal areas.

Cooper & Calder (1964) rejected low temperature as interchangeable with a short photoperiod in the primary indution of *A. capillaris*. However, in their experiment low temperature treatment was effected at the one-leaf stage of the seedlings. The present work indicates that *A. capillaris* might have a juvenile stage when the seedlings are insensitive to conditions which later promote floweing (Table 2), as was also found in *D. glomerata* (Cooper & Calder 1964, Heide 1987). In addition, there is evidence for the requirement of a longer duration of low temperature than of short-day treament for primary induction both in *P. pratensis* and *D. glomerata* (Heide 1980, 1987). In the experiment of Cooper & Calder (1964) the period of cold treatment was only 6 or 12 weeks.

While 'Leikvin' was most affected the longer the photoperiod, the North Norwegian populations were more sensitive to increasing temperature (Figures 4 and 5), but became more or less neutral to a photoperiod at low temperatures (page 49). As suggested previously, this difference might be ascribed to a negative correlation between plant elongation and the number of panicles per plant, as also demonstrated in *Alopecurus pratensis* L. and in *D. glomerata* (Heide 1986, 1987). According to Heide et al. (1987) it is not known whether these are causally related phenomena, or whether the two parameters are independently affected by the same conditions.

The differences in critical and optimal photoperiods for secondary induction between 15°C and 21°C (Figure 6) concurred with corresponding investigations in *Bromus inermis* (Heide 1984). The vegetative plants were not dissected when the experiment was terminated. A continuing development and emergence of panicles in photoperiods below 24 hours, cannot therefore be excluded at 9°C if duration of the secondary induction treatment is longer than 15 weeks. At the other temperatures a faster growth within the period makes this very unlikely. In species like *Alopecurus pratensis* (Heide 1986) heading was strongly promoted by long photoperiods and increased temperature during the secondary induction, while *Phleum pratense*, which has a single induction requirement for long-day only, develops a gradual reduction in the ability of the plants to flower at increased temperatures (Langer 1955, Heide 1982).

The number of panicles per plant at the termination of the experiment, as a percentage of the total number of shoots at the end of the primary induction treatment (Figure 7), indicates a depression of the number of panicles at high temperature in the secondary induction treatment. This suggests a composite effect of the secondary induction at lower temperatures : A further development of primordia almost but not completely induced during the primary induction, and induction of additional primordia during the period of secondary induction (Figure 7).

The photoperiod is the only physical factor which is constant from one year to the next, and during the growth season the difference in the length of the photoperiod between southern and northern parts of Norway is 2-3 hours. A similar difference is found in photoperiodic requirement for flower development between populations or cultivars from corresponding areas both in Poa pratensis (Håbjørg 1978) and *Phleum pratense* (Heide 1982) and hence confirms the present results.

The length of the solar day in central parts of southern Norway exceeds 17 hours for about 85 days in the growing season, and hence practical seed production of the North Norwegian populations investigated may work well in such areas.

It is difficult to decide whether development of secondary and tertiary tillers in the upper part of incompletely primary inducted shoots (Figure 9) might be described as viviparous proliferation or as ordinary vegetative reproduction. However, viviparous proliferation may occur in a flower, instead of a flower or instead of an inflorescence (Bragdø-Aas 1971). The secondary and tertiary tillers observed in the present experiments were mostly recorded on shoots which were also visible before the primary induction started. They were found in the upper half of the shoots, and roots could be observed. This indicates vivipary. On the other side, secondary tillers from nodes at the lower part of the shoots were not uncommon after elongation of the main stem.

In many normally seminiferous grasses like *P. pratense* (Junttila & Schjelderup 1984), *D. glomerata* (Heide 1987) and *A. capillaris* (Helgadsttir 1981), vivipary has been found as a result of incomplete floral initiation in the spring/summer conditions. In the present work it was obvious that both temperature and photoperiod were involved in the viviparous proliferation at both inductions. The most effective combination of these factors depends on the place of origin of the plants investigated, and both primary and secondary induction cause viviparous proliferation after growth in incomplete induction conditions independently of each other.

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EFFECTS OF FLUCTUATING IRRIGATION ON NORWAY SPRUCE SEEDLINGS AND NUTRIENT CONCENTRATIONS IN THE GROWTH SUBSTRATE

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Norway spruce seedlings grown in single pots (about 50 ml pot^{-1}) in an unfertilized peat/perlite mixture were subjected to different irrigation frequencies and intensities in a climate chamber: 10, 30, 50 and 70% of the volume of liquid in the growth substrate at container capacity was absorbed before re-irrigation.
Shoot length decreased with decreased irrigation, and the volume and dry weight of the shoots were lower in the two driest, compared with the two least dry irrigation regimes after 83 days in the different regimes. The volume of the roots and the shoot/root-ratio (dry weight, volume) were slightly or not at all affected by different irrigation regimes. The density for shoots and roots was highest in the driest growing conditions, but was otherwise unaffected.
The nutrient concentrations in the growth substrate liquid phase were analysed at container capacity, and a set of equations combining physical and chemical characteristics of the growth substrate were used to calculate nutrient concentrations at maximum dryness.
Nitrogen concentrations close to those suggested as lethal for Norway spruce were obtained. NO_3-N accumulated far more than NH_4-N, and the NH_4-N/NO_3-N-ratio was very low in the growth substrate compared to the nutrient solution.

Key words: Ammonium, Dry weights, Nitrate, Peat, Perlite, Root volume.

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Growers of containerized seedlings are warned about nutrient accumulation in the growth substrate: Quantitative aspects of this accumulation have been reported in substrates mixed with solid fertilizers (Noordwijk & Raats 1980, Holcomb et al. 1982). Forest tree seedlings are primarily fertilized with nutrient solution in nurseries, and an accumulation of nutrient elements was suspected on a general assumption with regard to nutrient supply, nutrient uptake and evapotranspiration (Carlson 1979, Tinus & McDonald 1979). The nutrient supply was determined from nutrient requirements obtained in hydroponic cultures (Morrison 1974, Ingestad 1979), and the element concentrations assumed to be unaffected by the inclusion of a growth medium to the system (Hocking 1972).

The nutrient supply depends on the irrigation regime and the element concentrations in the nutrient solution. The ratio of transpiration to nutrient uptake rate determines the actual accumulation in a given situation: The irrigation regime and element concentrations in the nutrient solution can be controlled by the nursery management. Transpiration also depends on seedling and environmental characteristics (Gross 1976, Jarvis 1985), including the properties of the growth media (Langerud & Sandvik 1988b). Nutrient uptake rates depend, apart from the seedlings, on element concentrations in the liquid phase of the growth substrate (Nye & Tinker 1977).

We were involved with the problem of nutrient accumulation through studies on the production system in Norwegian forest nurseries. Our concern derived initially from straight-forward calculations combining the nutrient element concentration in the seedlings and in the nutrient solution (Ingestad 1979), irrigation regimes used in the forest nurseries (Langerud & Sandvik 1987a), characteristics of the growth media (Langerud & Sandvik 1987b), and transpiration of Norway spruce seedlings (Langerud & Sandvik 1988b): The accumulation of nutrient elements, especially nitrogen, in the growth substrate liquid phase is unavoidable. Combined with low frequency irrigation, the seedlings are subjected to variable nutrient concentrations with time.

The present experiment was directed towards the assertions stated above: To obtain estimates of the element concentrations experienced by Norway spruce seedlings grown under different irrigation regimes. The experiment was performed in a climate chamber under a growing system basically as used in commercial nurseries, and irrigation regimes covered a range within which the nursery practice operates. The growth of Norway spruce seedlings was used to survey the combined effects of fluctuation in nutrient and water conditions.

MATERIALS AND METHODS

Growth media

Growth media were prepared from perlite and horticultural peat with more than 95% (dry weight) particles greater than 1.6 mm in the method of Dinel and Levesque (1976).

Volume, volume fraction of perlite and bulk density of the growth media were obtained before the experiment started and at its termination as described by Langerud (1986). The initial measurements were made on separate samples, while the final values refer to the media in the pots used in the experiment. The volume fraction of gas-filled pores at 'container capacity' (White & Mastalerz 1966) was determined gravimetrically according to Vomocil (1965), always for media in the pots used in the experiment.

The cation exchange capacity and base saturation, obtained by the method of Stuanes et al. (1984), were 92 mmol $(p^+)\ l^{-1}$ and 98.7% for the peat (pH 5.5). The cation exchange capacity decreased to 76 and 56 mmol $(p^+)\ l^{-1}$ by mixing with 0.27 and 0.48 ml ml^{-1} of perlite. Base saturation was 99.0 and 99.2%, and pH 5.9 and 6.2 in the peat/perlite mixtures.

Experimental design

The pots (black PVC, 8.3 cm deep, 47.4 ml, coned bottom with drain) were cut from multipot containers used in commercial nurseries. A total of 80 single pots were mounted on two racks (20 x 30 cm, 40 pots on each with uniform spacing), with the bottom drains in a water saturated atmosphere. The pots subjected to different irrigation regimes (10 pots for each rack and regime) were randomly distributed within each rack, and every pot was treated individually throughout the experiment.

The pots were filled by hand with the media and then soaked in deionized water for three days. The pots were drained, completely surrounded by a water saturated atmosphere, for 24 h before the initial volume fraction of gas-filled pores (fg_{cc}) was determined.

Seeds of Norway spruce (*Picea abies.* (L.) Karst.) from eastern Norway (elevation 150-250 m) were sown on the growth medium surface and germinated in 24 h photoperiods (150 µmol m^{-2} s^{-1}, 22°C, 100% relative humidity). After seed coat disposal (14 days from sowing), one seedling in each pot was grown under a 20 h photoperiod (400 µmol m^{-2} s^{-1}, 22°C, 60% relative humidity). The night temperature was 15°C at 80% relative humidity.

Each seedling was initially given 5 ml nutrient solution every second day (day 14-35 after sowing). The nutrient solution was prepared from laboratory grade chemicals in the element proportions proposed by Ingestad (1979), with a total nitrogen concentration of 10 mmol l^{-1} (NH_4-N/NO_3-N ratio: 4.3/5.7).

Differentiated irrigation regimes started 35 days after sowing (shoot length 2.0 cm, standard deviation 0.3 cm).

The irrigation regimes were defined from the liquid content in the growth substrates at initial container capacity. Nutrient solution was re-added when 10% (IR 0.9), 30% (IR 0.7), 50% (IR 0.5) and 70% (IR 0.3) of that volume of liquid was lost.

MEASUREMENTS AND CALCULATIONS

Evapotranspiration was measured at least once a day, and taken as the difference between the weight of single pots one hour after the last irrigation and the weight at the time of measurement (Langerud & Sandvik 1988b). The correct time for re-irrigation was set by minimum weights calculated for every pot according to the definition of the irrigation regime. A computer program selected the pots to be irrigated and also calculated the volume of nutrient solution required (1.5 times the liquid loss). The nutrient solution was then added in repeated 5 ml doses until the calculated volume was reached.

The weight used to determine the volume fraction of gas-filled pores (fg) was corrected for the fresh weight of the seedling (M_{fs}, g seedling $^{-1}$) by Eq 1.

$$M_{fs} = 0.46 + 0.59V_s \qquad (1)$$

Shoot volume (V_s, ml) and M_{fs} were determined at the termination of the experiment ($1.0 < V_s < 8.0$, R^2: 0.93, df 78).

The definition of the irrigation regimes did not take the increase in seedling weights into account, and the volume fraction of gas-filled pores at maximum dryness increased with time (Table 1).

The shoot length was measured 35 and 55 days after sowing, and then weekly until termination 104 days after sowing. Shoot volume was measured by displacement (Burdett 1979) on individual seedlings at fortnightly intervals. Root volume (displacement) and dry weight of the shoots and roots were measured finally.

Samples of the growth substrate liquid phase were taken at maximum dryness of the growth substrate (fg_{max}), and were obtained by successive additions of 5 ml doses of nutrient solution added at 3 min intervals. The volume of solution needed to start leaching, dependent on the irrigation regime, was recorded. The concentrations of NO_3-N and NH_4-N were determined according to Ogner et al. (1984), in the first 2 ml drained from the pots, and taken as the concentration at container capacity. The element concentration at maximum dryness was calculated using Eqs 2 - 5.

$$V_{cc} = V_p(fg_{max} - fg_{cc}) \qquad (2)$$

V_{cc}: Volume (ml) of liquid in the growth medium at container capacity.

V_p : Total volume (ml) of pores.

fg_{cc}: Volume fraction of gas-filled pores ($ml\ ml^{-1}$) at container capacity.

fg_{max}: Volume fraction of gas-filled pores (ml ml:sup.-1) at maximum dryness, immediately before re-irrigation.

$$V_L = V_A - V_{cc} \quad (3)$$

$$V_T = V_P(1 - fg_{max}) + V_A \quad (4)$$

V_T: Total volume (ml) of liquid in the substrate.

V_L: Volume (ml) of liquid leached.

V_A: Volume (ml) of nutrient solution needed to start leaching.

$$C_f = (C_i V_T - C_a V_A + C_i V_L) / V_P(1 - fg_{max}) \quad (5)$$

C_f: Concentration ($mmol\ l^{-1}$) at maximum dryness.

C_a: Concentration ($mmol\ l^{-1}$) in the nutrient solution.

C_i: Concentration ($mmol\ l^{-1}$) in the 2 ml sample.

Samples were taken twice (Time 1: 84-87 days and Time 2: 99-103 days after sowing) from the substrates in the individual pots as their liquid content reached maximum dryness. More parameters needed for the calculations are given in Tables 1 and 2.

RESULTS

The fraction of perlite was lower finally than initially for media subjected to the high irrigation frequency (IR 0.9, Table 1). Approximately 3.3 ml (360 mg) was lost and the bulk density decreased from 95.2 to 83.5 mg ml^{-1}.

The volume fraction of gas-filled pores at container capacity (fg_{cc}, Table 1) increased from 0.34 to 0.50 ml ml^{-1} during the experiment in IR 0.3. In IR 0.5 and IR 0.7, fg_{cc} increased from 0.34 to 0.41 ml ml^{-1}, while fg_{cc} decreased from 0.30 to 0.26 ml ml^{-1} in IR 0.9.

Shoot length and volume measured 83, 90, 97 and 104 days after sowing, and dry weights of shoots and roots 104 days after sowing are given in Table 2. The shoot length increased with increased application of nutrient solution and there were significant differences between all the irrigation regimes after 104 days. Shoot volume was always significantly lower in IR 0.3 and IR 0.5 than in IR 0.7 and IR 0.9, as was also the case for shoot dry weight after 104 days (Table 2).

Root volume increased with increased irrigation, although the root volumes were the same in IR 0.7 and IR 0.9. The low and the high dry weights of roots were recorded for seedlings in IR 0.3 and IR 0.9, respectively.

The shoot/root-ratio (dry weight) tended towards higher values with increased irrigation, while this ratio was unaffected by irrigation frequency on a volume basis (Table 3). The 'bulk density' of shoots and roots was significantly higher for seedlings in IR 0.3 than for seedlings in the other irrigation regimes (Table 3).

The volume fraction of gas-filled pores at container capacity (fg_{cc}, Table 4) increased with decreased irrigation frequency, from 0.27 ml ml^{-1}. (IR 0.9) to 0.51 ml ml^{-1} (IR 0.3) at Time 2.

The concentration of NO_3-N at container capacity (C_i, Eq. 5) was significantly lower in irrigation regime IR 0.3 than in the other regimes at Time 1 (Table 4). This tendency was also noticeable at Time 2.

The effect of irrigation on NH_4-N concentrations at container capacity was essentially the same at Time 1 as at Time 2. The high value was in IR 0.3 (3.5 mmol l^{-1}), with a gradual decrease towards the low value in IR 0.9 (0.5 mmol l^{-1}).

Table 1. Some physical characteristics of the growth media before the experiment started (Init) and at its termination (Final)

	Fraction perlite[2])		Density		Volume		Gas filled pores[1]) cc		max	
	ml ml^{-1}		mg ml^{-1}		ml pot^{-1}		ml ml^{-1}			
Regime	Init	Final	Init	Final	Init	Final	Init	Final	Init	Final
IR 0.3								.502	.810	.846
								.024	.008	.021
IR 0.5	.477[3])	.477	96.4	95.3			.339		.662	.715
	.016	.023	3.1	2.4			.046		.024	.050
					42.7	41.8		.406		
IR 0.7					1.5	1.3		.054	.531	.647
									.040	.055
IR 0.9	.268	.212	95.2	83.5			.295	.260	.366	.393
	.008	.024	3.4	5.1			.047	.046	.043	.071

1). Volume fraction of gas-filled pores in the growth substrates at container capacity (cc) and at maximum dryness (max).
2). Volume fraction of perlite.
3). Initial values are means of 20 replications with standard deviation.
Final values are means of 20 replications from each irrigation regime, with standard deviation.

The following constants were used in the calculations:

Total porosity:		0.94	ml ml^{-1}
Bulk density:	Peat:	86	mg ml^{-1}
	Perlite:	110	mg ml^{-1}
Ash concentration:	Peat:	5	mg ml^{-1}
	Perlite:	110	mg ml^{-1}
Specific density:	Peat:	1560	mg ml^{-1}
	Perlite:	2300	mg ml^{-1}

Table 2. Shoot length (Ls, cm seedling^{-1}), and shoot volume (Vs, ml seedling^{-1}) of Norway spruce seedlings at different times from sowing. Root volume (Vr, ml seedling^{-1}), and shoot and root dry weight (Ds, Dr, mg seedling^{-1}) were measured after 104 days

	Day 83		Day 90	Day 97		Day 104				
Regime	Ls	Vs	Ls	Ls	Vs	Ls	Vs	Ds	Vr	Dr
IR 0.3	7.3a[1])	1.6a	8.4a	9.4a	2.3a	10.5a	2.7a	524a	1.1a	173a
IR 0.5	8.5b	1.6a	10.0b	11.5b	2.5a	13.0b	3.3a	592a	1.3b	185a
IR 0.7	9.4bc	2.1b	11.1bc	12.8bc	3.1b	14.6c	4.1b	708b	1.6c	214a
IR 0.9	9.9 c	2.2b	12.0 c	14.0 c	3.3b	16.0d	4.4b	766b	1.6c	217a

1) Duncan Range Test. Mean values (20 replications) with the same letter were not significantly different ($P > .05$).

Table 3. Shoot/root-ratio (mg mg^{-1} and ml ml^{-1}) and 'density' (mg ml^{-1}) of shoots and roots for Norway spruce seedlings grown under different irrigation regimes

Regime	Shoot/root-ratio		Density	
	Weight	Volume	Shoots	Roots
IR 0.3	3.04 a[1]	2.61 a	196 a	166 a
IR 0.5	3.33 ab	2.56 a	183 b	144 b
IR 0.7	3.41 ab	2.61 a	174 b	133 b
IR 0.9	3.60 b	2.61 a	180 b	131 b

1) See Table 2, note 1)

The concentration of NO_3-N at maximum dryness (C_f, Eq. 5) was high in all the irrigation regimes, although the concentration decreased with increased irrigation frequency (Table 4). The concentration of NH_4-N in this situation was lower than in the applied nutrient solution (4.2 mmol l^{-1}.), except in IR 0.3. The NH_4-N/NO_3-N-ratio, 0.74 mmol mmol^{-1} in the nutrient solution, was displaced towards much lower values in the substrate liquid phase: This ratio was 0.23, 0.13, 0.11 and 0.05 at container capacity at Time 2 (99-103 days) in IR 0.9, IR 0.7, IR 0.5 and IR 0.3, respectively. The corresponding values at maximum dryness were 0.09, 0.04, 0.06 and 0.01.

The concentration of NH_4-N was related to the volume fraction of gas-filled pores (fg_{max}) as illustrated in Fig. 1. The figure also illustrates the great variation in fg_{max} even in this controlled experiment.

Table 4. Volume fraction of gas filled pores (fg, ml ml^{-1}) and concentrations of NO_3-N and NH_4-N (mmol l^{-1}) at container capacity (cc, ci) and at maximum dryness (max, cf) of the growth substrate

Regime	Time 1[1]						Time 2[2]					
	fg		NO_3-N		NH_4-N		fg		NO_3-N		NH_4-N	
	cc[3]	max[4]	ci[5]	cf[6]	ci	cf	cc	max	ci	cf	ci	cf
IR 0.3	.512a[7]	.843a	13.2a	50.1a	3.4a	4.4a	.509a	.852a	15.7a	62.5a	3.5a	5.4a
IR 0.5	.396b	690b	17.2b	35.5b	2.3b	.6b	.412b	.718b	20.6bc	45.3b	2.7b	1.9b
IR 0.7	.368b	579c	19.1b	29.3c	1.8c	.5b	.383b	.633c	23.0 c	36.0c	2.6b	2.1b
IR 0.9	.275c	389d	20.6b	24.5c	.2d	0c	.267c	.383d	17.8ab	20.8d	.9c	.2c

1) Time 1: Sampled 84-87 days from sowing.

2) Time 2: Sampled 99-103 days from sowing.

3) fg at container capacity.

4) fg at maximum dryness.

5) Concentration at container capacity.

6) Concentration at maximum dryness.

7) See Table 2, note 1.).

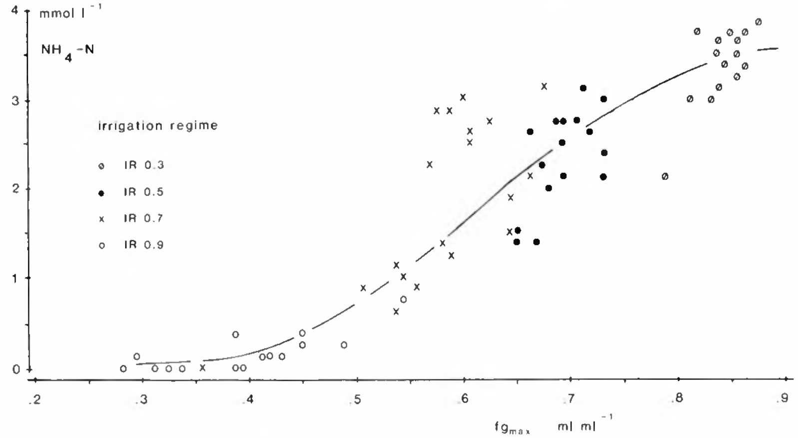

Fig. 1. Concentration of NH_4-N (mmol l^{-1}) in the liquid phase at maximum dryness of the growth substrate plotted against volume fraction of gas-filled pores (fg_{max}, ml ml^{-1})

The function:

$$NH_4\text{-}N = 3.72/(1 + \exp\text{-}(10.5\, fg_{max} - 6.52)$$

($R^2 = 0.81$, df 76)

was fitted to the observations by non-linear regression

DISCUSSION

The lower fraction of perlite in the media subjected to IR0.9 than that in the media subjected to the other irrigation regimes was chosen to obtain a higher liquid-holding capacity (Haynes & Goh 1978, Verdonck 1984, Langerud 1986). The different peat/perlite-ratios had hardly any influence on the element concentrations in the growth substrate liquid phase, and the influence on the physical properties of the growth substrate was discussed by Langerud & Sandvik 1988a). The loss of perlite from the pots subjected to irrigation regime IR 0.9 (Table 1) was quite unexpected, since IR 0.9 substrates were leached the least for the first 86 days: The differences in the volumes leached (V_L, Eqs. 2,3) were caused by the decreased liquid-holding capacity (increased fg_{cc}) of the growth substrate in IR 0.3, IR 0.5 and IR 0.7, and the increased liquid-holding capacity of substrates in IR 0.9.

The influence of irrigation frequency on seedling growth was illustrated by transpiration rates (Langerud & Sandvik 1988b): We observed the combined effects of nutritional and irrigational differences. We noticed that the chemical composition of the growth substrate liquid phase differed from the composition of the prescribed nutrient solution: The chemical environment differed from the environment in which the seedlings' requirements were achieved.

The concentration of NH_4-N at container capacity was at or below the concentration in the nutrient solution, and may be taken as support for the view of a preference for NH_4-N as a nitrogen source for spruce (Brix & Driessche 1974, Nelson & Selby 1974, Ingestad 1979). The reduced NH_4-N concentration may also indicate a participation of the cation exchange complex of the peat, or may suggest nitrification: At the pH of the growth medium used ($5.5 < pH < 6.2$), nitrification have an influence on the NO_3-N/NH_4-N-ratio (Munk 1958). The nitrification rate is not, however, sufficiently high by far to explain the disturbance of the NO_3-N/NH_4-N-ratio.

The very low concentration of NH_4-N in IR 0.9 should expectedly have an influence on the nutritional status. The concentration at maximum dryness (C_f), however, was calculated without taking the cation exchange into consideration, and the prevailing NH_4-N concentration was probably underestimated; NO_3-N is, of course, useful as an N-source for Norway spruce.

The total concentration of nitrogen was high, especially at maximum dryness: Nitrogen concentrations close to those suggested as lethal for Norway spruce seedlings (Ingestad 1979) were recorded in the present study. Even the concentration at container capacity was 2.0-2.5 times the concentration in the nutrient solution. The NO_3-N concentration at container capacity at Time 2 (Table 4) was 2.3 (IR 0.3) to 3.6 (IR 0.9) times higher than in the nutrient solution. At Time 2, this ratio was 2.6 (IR 0.3) to 4.0 (IR 0.7), indicating a gradual accumulation of NO_3-N. The analyses in IR 0.9 showed a lessened accumulation, a result of the increased leaching by the twice a day applications (2 x 5 ml) of nutrient solution from the 86th day.

The present investigation supported the calculations made beforehand with respect to the control of the nutrition of forest tree seedlings: The volumetric growth rates in the period from 97 to 104 days were 0.057 and 0.157 ml day $^{-1}$ in IR 0.3 and IR 0.9, respectively, and may be crudely transformed to (dry) weight growth rates by the 'densities' given in Table 3. With an assumed nitrogen concentration of 2% (Ingestad 1979, Bergmann & Bergmann 1985), 16 (IR 0.3) to 40 μmol N day^{-1} (IR 0.9) was required. In the period from 97 to 104 days, 50-100 μmol N day^{-1} was added, of which 30-60 μmol N day^{-1} as NH_4-N. That is, 30-60 μmol N day^{-1} more than required was added during this period, inevitably leading to elevated nutrient element concentrations.

The problem may be solved by frequent leaching with water or by reducing the strength of the nutrient solution. The growers have to decide on the frequency of leaching and on the volume of water to be used, problems which are being addressed in our laboratory. Leaching with water is used in commercial nurseries (Carlson 1979, Tinus & McDonald 1979), although the effects on the nutrition of the seedlings have been poorly studied. A reduction in the strength of the nutrient solution should be carefully considered, with regard to the effects on nutrient concentrations and ion balance in the growth substrate liquid phase. Reliable decisions are quite difficult, if not impossible, to make at present: Some kind of safety is attained, however, by occasional irrigation with 'pure' water.

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A STUDY OF JUVENILE PEAR SEEDLINGS

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Juvenile pear seedlings of 14 half-sib families were studied during the period 1982 to 1985. A high variability was observed both within and between populations, and the level of heterozygosity was different in the parent varieties for some characters. Morphological and physiological characters such as plant vigour, habitus, leaf size, bud burst, top frost and growth cessation were recorded along with powdery mildew (*Podosphaera leucotricha*) infection. The possible exploitation of these characters in preselection is discussed, and it is postulated that preselection for tall plants with a low number of feathers might be reliable as selection criteria for precocity. Powdery mildew infection decreased with increasing seedling age, and should therefore not be considered in preselection. The choice of parents is essential in pear breeding, but the interaction mother x father was significant for most characters in this study. Hence progeny performance is difficult to predict in pear hybridization.

Key words: Pear, *Pyrus communis* L., seedlings, juvenility, morphology, physiology, variability, preselection.

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The study was carried out on the first seedlings from a pear breeding program started in 1982 at Njøs Research Station. As the work is concentrated on young seedlings, this gives detailed information on the morphology and physiology of such small plants. Records of vegetative traits in young juvenile seedlings can then later be related to fruiting characters in adult trees, and used as preselection criteria. This would be of considerable value in increasing the number of good genotypes in the field; a similar approach has been used in other breeding programs (e.g. Alston, 1975).

Pear seedlings have a long juvenile period (j.p.), and shortening this period would give a shorter generation interval and enhanced breeding progress. The j.p. in pome fruits has been thoroughly studied at Wageningen. Visser (1967) observed a close correlation between precocity of the parents and length of the j.p. in the offspring, and also a positive correlation between length of the j.p. of seedlings and their precocity in the adult phase. In an earlier study, Visser (1964) detected a significant negative correlation between tree size and length of the j.p., and preselection for vigorous seedlings was widely applied in the breeding programs in pome fruits in Wageningen after these findings (e.g. Visser et al., 1976). Length of the j.p. is highly influenced by environmental factors such as weather, soil and cultural practices (Visser, 1964). Better management of the seedlings in combination with preselection for vigour shortened the mean j.p. in pear seedlings from 9.2 years from the crosses in 1950-1954, to 6.2 years from the crosses in 1964 at Wageningen (Visser et al., 1976).

On the basis of diallel crosses in apples and pears, Visser (1976) stated that the j.p. has an additive mode of inheritance.

Like Visser, Zimmerman (1976) found a similar tendency, but the correlation between seedling size and length of the j.p. was not significant for all planting years, progenies or parents, and he therefore does not fully agree with Visser's conclusions. However, Zimmerman (1976) states that a proper choice of parents, and optimal growing conditions will shorten the j.p. So although seedling size is still being used as a preselection criterion in some breeding programs, its preselective reliability is not evident.

Considerable yield losses are caused by spring frost during time of flowering in many countries, and one of the breeding goals in these countries is late flowering. Bud burst is highly correlated with time of flowering, and is suggested to be a reliable preselection criterion (Alston, 1982). In apples, Visser & Schaap (1967) found that early bud burst and low juvenility were positively correlated to precocity; however, this relationship has not been evaluated in pears.

Powdery mildew (*Podosphaera leucotricha*) is seldom observed in pear orchards, but pear seedlings might be seriously infected. Although if correlations to adult trees have not been thoroughly examined, susceptible seedlings have been discarded in some breeding programs (e.g. Alston, 1975). Alston & Bates (1984) reported that varieties like 'Clara Frijs' and 'Williams' give many progenies with high mildew infection, while varieties like 'Bonne Louise' and 'Packham's Triumph' have fairly resistant progenies.

Fireblight (*Erwinia amylovora*) is a serious problem in many pear growing countries, and preselection for resistance is carried out in many pear breeding programs (e.g. Thibault, 1981; Zwet et al., 1979). In countries free of fireblight, it is risky to carry out such a preselection. Even if inoculation was carried out under controlled conditions, there is always a possibility that the pathogen might escape to field plantings.

At Merton, Crane and co-workers carried out genetical studies in pears from the middle of the 1930s (e.g. Crane & Lewis, 1942, 1949). Monogenetical inheritance of five morphological characters on leaves and summer shoots is suggested (Crane & Lewis, 1949). Such discontinuous characters are valuable in pomological classification, as suggested by Zielinski (1977). However, they are not very suitable for the evaluation of genotype merit if they are not linked to horticulturally important traits.

From this brief introduction it is clear that few reliable preselection criteria are available in pears. Hence good records, both on juvenile and adult plants, could contribute to early screening of pear seedlings.

MATERIAL AND METHODS

Seeds from a pollination experiment in pears, carried out at Njøs Research Station in 1981, were retained for the breeding program started in 1982. After stratification at 3°C until March 1982, the seeds were sown in greenhouse. The seedlings were planted in the field in

Table 1. Number of seedlings in the populations studied

Father	Mother BP 1575	Clara Frijs	Sum
Belle lucrative	124	310	434
Bonne Louise	125	271	396
Carola	141	30	448
Colorée de Juillet	112	320	432
Flemish Beauty	102	335	437
Herzogin Elsa	98	345	443
Super Trévoux	92	209	301
Sum	794	2,097	2,891

July 1982, spaced at 60 x 30 cm and with black plastic mulching. The present study was carried out in this field.

BP 1575 (Clapp's Favorite x Conference) is a semi-dwarf selection from Balsgård. Carola (Johantorp x Doyenné du Comice) is a new variety from Balsgård, and Super Trévoux is a large-fruited mutation in Précoce de Trévoux from Holland.

Table 1 shows that seeds from 2 mothers pollinated by the same 7 fathers were retained, so each population had 7 half-sib families. The population sizes ranged from 92 to 345 seedlings, and the number of seedlings with BP 1575 as mother was exclusively smaller than with Clara Frijs as mother.

In spring 1985, when the seedlings were 3 years old, scions from the top of most of the plants were grafted onto older trees. Preselection is often conducted on 2- or 3-year-old seedlings in the field, and due to rather poor initial growth in this field, grafting of 3-year-old seedlings was chosen. In 1986 the seedling field was almost impassable due to the close spacing, and after supplying failed graftings from 1985, the field was wiped out in spring 1986.

Registrations were carried out from 1982 to 1985. The first registrations taken were plant height and stem diameter in autumn 1982. These measurements were taken in successive years, too.

Bud burst was recorded in spring 1983. The number of days from April 20th to the date when a leaf started to split from a bud was evaluated.

Growth cessation, expressed by formation of the terminal bud, was recorded in all seedlings and most parent varieties on September 30th, 1985. This process is more or less continuous, but in this study a 2-graded scale was applied. Plants with the terminal bud appearing as bud scales were given the score 1; the others were given the score 0.

Ten plants of 5 populations were selected in 1983 for a study of growth rhythm. Four of the populations were half-sibs, and plants of approximately the same size were selected. The top shoots were measured on the first of each month from June to October in 1983 and 1984. In 1984, similar records were taken on parent varieties as well.

Powdery mildew (*Podosphaera leucotricha*) infection was recorded on a percentage scale in 1983 and 1985. Due to a severe infection in 1983, the seedlings were sprayed twice with the fungicide Bayleton immediately after the evaluation.

Top frost was recorded on a 1-5 scale in spring 1984. The scores were: 1: >5 cm dead; 2: 2.5-4.9 cm dead; 3: 1.0-2.4 cm dead; 4: <1.0 cm dead; 5: apical bud present.

In each population, 20 plants with acceptable vigour were randomly chosen in early spring 1985 for habitus classification. The three longest sidebranches were measured, and the number of sidebranches, thorns, secondary sidebranches and feathers were recorded. Sidebranches and secondary sidebranches were defined as branches > 10 cm, and feathers were calculated when they exceeded 2 cm.

Leaf breadth, leaf length and petiole length were recorded on 3 well-developed leaves on the terminal shoot of 50 plants of each population. Nine populations were recorded in 1984, the others in 1985. These records were taken on two trees of most parent varieties as well.

In the statistical analysis it was considered that all the populations had a sufficient number of seedlings for expressing the variation, and population means are therefore regarded as true means. The effect of father on the seedling number was regarded as a random effect. Hence the mean value of the mother became a fair estimate without truncation. Clara Frijs as mother had an exclusively higher seedling number than the respective combinations with BP 1575. Therefore, the mean value of fathers was calculated as the mean of the two half-sibs means. In the analysis of variance no consideration was given to unequal cell sizes when estimating the effect of mother, father and the mother x father interaction. As neither mothers nor fathers were chosen randomly, they were looked on as fixed variables, and therefore the main effects were always tested against the residual.

The statistical analysis was carried out mostly using SAS (Statistical Analysis System). The PROC GLM (General Linear Model) was applied for analysis of variance as the material had many missing values and unequal cell sizes. When studying habitus and growth rhythm, the analysis of variance was carried out with MSTAT.

RESULTS

Plant vigour

Stem diameter

There were small differences in stem diameter between mothers in all years. Although the effects of mother, father and the mother x father interaction were significant within each year, it was difficult to find any consistent differences over years. The populations BP 1575 x Carola and BP 1575 x Herzogin Elsa had the largest stem diameters in most years, but no trends for mean merit in stem diameter were observed for the other populations.

Plant height

Vegetative growth of small seedlings is accurately described by plant height, and population means for the years 1982 to 1984 are presented in Table 2.

Table 2 shows that Clara Frijs progenies were about 10 cm taller than the BP 1575 progenies in the year of planting, and the populations with Clara Frijs as mother were exclusively taller than the populations with BP 1575 as mother that year. This difference was highly significant ($P < 0.001$).

The growth increment from 1982 to 1983 is an expression of adaptation to field conditions, as plant height in 1982 reflects size from a greenhouse environ-

Table 2. Mean plant height in cm for pear progenies

	1982	1983	1984
BP 1575 x Belle lucrative	25.6 cd	63.9 bc	107.9 cd
BP 1575 x Bonne Louise	23.4 d	50.3 e	91.2 e
BP 1575 x Carola	27.5 c	67.6 ab	118.1 b
BP 1575 x Colorée de Juillet	23.0 d	56.0 de	97.1 de
BP 1575 x Flemish Beauty	19.8 e	55.9 de	107.2 cd
BP 1575 x Herzogin Elsa	26.4 cd	72.6 a	131.7 a
BP 1575 x Super Trévoux	24.4 cd	57.6 cd	108.4 cd
Clara Frijs x Belle lucrative	31.2 b	55.5 de	101.4 cd
Clara Frijs x Bonne Louise	32.5 b	58.0 cd	102.1 cd
Clara Frijs x Carola	36.6 a	57.8 cd	106.1 cd
Clara Frijs x Colorée de Juillet	37.1 a	58.3 cd	103.1 cd
Clara Frijs x Flemish Beauty	31.9 b	57.9 cd	102.2 cd
Clara Frijs x Herzogin Elsa	39.4 a	71.8 a	121.6 b
Clara Frijs x Super Trévoux	30.4 b	61.1 cd	110.3 c
BP 1575 mean	24.3	60.8	108.4
Clara Frijs mean	34.2	60.2	106.8
Total mean	31.8	60.4	107.2

Ranking was assessed using the Student-Newman-Keul's multiple test for each year. Numbers with the same letters are not significantly different at the 5% level.

ment. The most visible tendency is the high response of the mothers to changing environment. The seedling populations with BP 1575 as mother had a larger growth increment from 1982 to 1983 than the Clara Frijs progenies. This indicates that BP 1575 gives seedlings with better adaptation to field conditions compared to Clara Frijs seedlings.

In the seedlings with Clara Frijs as mother, the only population that had a positive response in plant height from 1982 to 1983 compared with the total mean, was the combination Clara Frijs x Super Trévoux. This population had less than mean height in 1982 but more than mean height in 1983. The population Clara Frijs x Herzogin Elsa had a slight response to changing environment. The highest relative negative response to changing environment was observed in the populations Clara Frijs x Belle lucrative and Clara Frijs x Carola.

The most positive relative response in height increment from 1982 to 1983 was observed in the populations BP 1575 x Carola, BP 1575 x Belle lucrative and BP 1575 x Herzogin Elsa.

From 1983 to 1984 there were smaller differences in the ranking of the populations. However, BP 1575 x Herzogin Elsa, Clara Frijs x Herzogin Elsa and BP 1575 x Carola had the most stable vigorous seedlings, and BP 1575 x Bonne Louise gave the smallest seedlings in both years.

Stability in growth between years was variable in the populations studied, but mean population merit seem to stabilize with increasing seedling age. Plant height in the greenhouse was quite different from height observed after one or two years in the field.

Differences in ranking of plants between years

As plant height discriminates well between genotypes in small seedlings, this character could be applied in the preselection of young seedlings. If seedlings taller than the total mean were selected, 825 seedlings (28.9%) would be taller than the total mean in all years, and 856 (30.0%) would be smaller.

Table 3. Number of seedlings taller than the progeny mean

Taller than mean	Year of recording 1982	1983	1984
In one year exclusively	337	92	164
In 1982 and 1983	165	165	-
In 1982 and 1984	135	-	135
In 1983 and 1984	-	283	283
In all three years	825	825	825
Sum	1,462	1,365	1,407

If selection had been applied in 1982, 1,462 seedlings would have been selected. Of these, 337 (11.8%) would not have been selected in either of the other two years. From the table it can also be seen that 447 genotypes (15.6%) that were taller than the mean in 1984 would have been discarded.

If selection had been applied in 1983, 1,365 seedlings would have been selected. This is 47% of the total number, and few were selected exclusively that year. However, 299 seedlings (7.9%) that were taller than the mean in 1984 would have been discarded.

This table clearly expresses the variability in ranking for individual seedling height between years. Many tall genotypes in 1984 would have been discarded if selection had been carried out in 1982, but the accuracy of the method is much better with increasing seedling age. There was a fairly good correspondence between seedling height in 1983 and 1984.

Physological characters

Bud burst

The populations differed significantly in time of bud burst in 1983, and in Table 4 the population means are presented.

Table 4. Mean number of days from May 1st till bud burst

Father	Mother BP 1575		Clara Frijs		Mean
Belle lucrative	5.9	a	5.6	a	5.8
Bonne Louise	0.9	f	3.1	d	2.0
Carola	2.0	e	4.9	abc	3.5
Colorée de Juillet	1.0	f	4.2	c	2.6
Flemish Beauty	3.2	d	4.9	abc	4.1
Herzogin Elsa	4.1	c	4.4	bc	4.3
Super Trévoux	5.5	ab	4.5	bc	5.0
Mean	3.2		4.7		4.0

Ranking was assessed using the Student-Newman-Keul's multiple test. Numbers with the same letters are not significantly different at the 5% level.

The mother x father interaction was highly significant ($P<0.001$), and the effect of the mother was ambiguous. With regard to the effect of the fathers, Belle lucrative gave the latest sprouting progenies, but there was no significant difference between the two half-sib families. Herzogin Elsa and Super Trévoux performed in the same way as Belle lucrative, except that they gave a slightly earlier mean sprouting date. The other fathers gave significantly earlier sprouting in combination with BP 1575.

The frequency distribution for bud burst differed between populations as illustrated in Fig. 1.

BP 1575 x Belle lucrative had one late peak on about May 8th. BP 1575 x Bonne Louise had peaks on April the 24th, 28th and May 4th. Clara Frijs x Super Trévoux had the greater proportion of the progenies at the mean from May 2nd to 8th. This distribution indicates that bud burst could be controlled by a few genes, along with modifiers and a significant environmental component.

By comparing Table 4 and Fig. 1, it could be stated that the varieties Belle lucrative, Herzogin Elsa, Super Trévoux and Clara Frijs have many genes for late sprouting, and that these genes dominate over early sprouting. An excess of genes for early sprouting is recognized in the varieties BP 1575, Bonne Louise, Colorée de Juillet, Carola and Flemish Beauty.

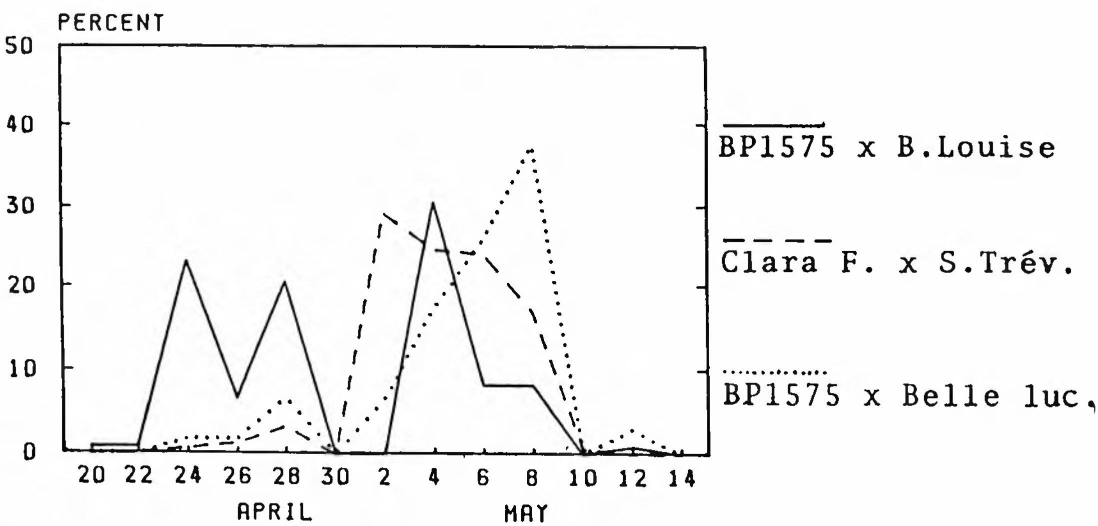

Figure 1. Percent of seedlings sprouting at different dates in 1983 illustrated by three populations

Growth cessation
All the parent varieties had formed terminal buds on September 30th, 1984, but the juvenile populations varied considerably in this character.

The frequencies in Table 5 do not inevitably support a simple gene model. Some of the ratios could be explained by a one- or two-gene model, but the trait is obviously modified by several genes.

Table 5. Percentage of seedlings in each population with terminal bud formed 30/9-1984

	Mother		
Father	BP 1575	Clara Frijs	Mean
Belle lucrative	56	47	52
Bonne Louise	67	39	53
Carola	80	32	56
Colorée de Juillet	64	49	57
Flemish Beauty	79	68	74
Herzogin Elsa	80	67	74
Super Trévoux	51	34	43
Mean	68	49	59

Table 5 shows that BP 1575 exclusively gave a higher proportion of progenies with early growth cessation than Clara Frijs.

A high response for the mother was observed for the fathers Carola and Bonne Louise, which had a much greater number of seedlings with terminal buds in combination with BP 1575.

Many progenies with terminal buds were observed in the combinations with the fathers Flemish Beauty and Herzogin Elsa, while only a few progenies with terminal bud were observed in the combinations with Super Trévoux and Belle lucrative.

The frequencies indicate that early growth cessation dominates over late, and that the varieties BP 1575, Flemish Beauty and Herzogin Elsa have many genes for early growth cessation. Many genes for late growth cessation are found in Clara Frijs and Super Trévoux.

Growth rhythm
The 5 populations which were studied for length of terminal shoot growth throughout the season showed some differences; however, none were significant. The most obvious difference was observed between years as the seedlings had more growth in 1984 than in 1983. This is presented in Fig.2

In 1983, the year after planting, the initial growth was small. The seedlings grew almost linearly throughout July and August, and growth ceased by September 1st. In 1984, top length was greater on June 1st, but growth intensity in July and August and growth cessation were similar to 1983. The slight initial growth in 1983 was probably caused by less potency for growth in young tender seedlings, but it could also have been modified by the cold May that year.

As the seedlings had the greatest variation in top length in 1984, that was the year chosen to illustrate the growth rhythm of the populations.

The top lengths were not significantly different at any date. However, Fig. 3 shows that there was a tendency to different growth for the different populations. The half-sibs with Bonne Louise as father had a somewhat higher growth rate with Clara Frijs as mother after July 1st. The half-sibs with Colorée de Juillet as father showed an opposite trend, as the population with BP 1575 tended to have a higher growth rate. This was due to growth cessation on August 1st for the population Clara Frijs x Colorée de Juillet.
By comparing the growth of the seedlings and their parent varieties, no significant differences were found at any date.

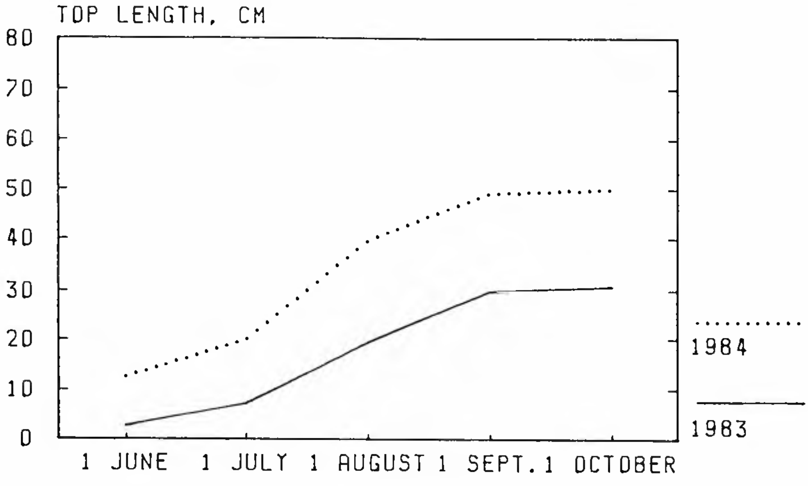

Figure 2. Mean top shoot length in two years. Fifty seedling of five populations

Powdery mildew (*Podosphaera leucotricha*) Infection

Powdery mildew (*Podosphaera leucotricha*) infection was very severe in some populations in 1983, and the mean score of infection is presented in Table 6.

The table illustrates that all combinations with Clara Frijs as mother had a higher degree of infection than the respective combinations with BP 1575. This effect of the mother was highly significant ($P < 0.001$).

The effect of the fathers and the mother x father interaction were also highly significant ($P < 0.001$). Carola and Super Trévoux gave the most susceptible progenies in both combinations, but for the other fathers there were no significant differences in combination with BP 1575.

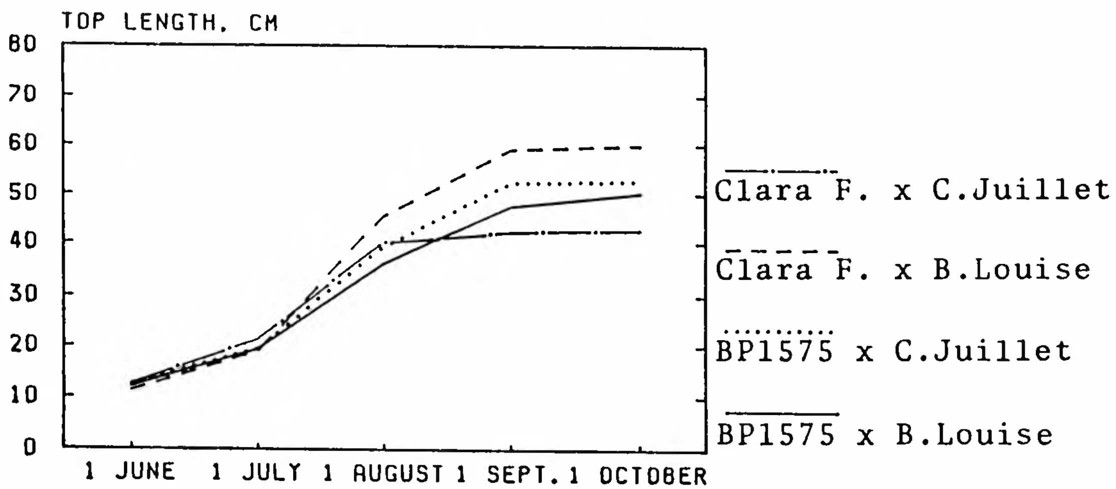

Figure 3. Growth of four half-sib pear populations in 1984. Mean of 10 seedlings in each populations

Table 6. Mean percentage of powdery mildew (*Podosphaera leucotricha*) infection in pear seedlings 1983

Father	Mother BP 1575		Clara Frijs		Mean
Belle lucrative	8	i	57	c	33
Bonne Louise	6	i	35	f	21
Carola	23	h	76	a	50
Colorée de Juillet	9	i	41	e	25
Flemish Beauty	9	i	55	c	32
Herzogin Elsa	14	i	47	d	32
Super Trévoux	30	g	69	b	50
Unweighted mean	15		52		34

Table 7. Mean percentage of powdery mildew (*Podosphaera leucotricha*) infection in pear seedlings 1985

Father	Mother BP 1575		Clara Frijs		Mean
Belle lucrative	5	def	4	efg	5
Bonne Louise	6	cde	8	bc	7
Carola	9	b	20	a	15
Colorée de Juillet	7	bcd	3	g	5
Flemish Beauty	6	cde	2	g	4
Herzogin Elsa	4	efg	4	fg	4
Super Trévoux	4	fg	7	bcd	6
Unweighted mean	6		7		7

Ranking was assessed using the Student-Newman-Keul's multiple test. Numbers with the same letters are not significantly different at the 5% level.

In 1985 the infection was greatly reduced, and the ranking between populations was not as clear as in 1983.

The most obvious tendency in Table 7 compared to Table 6 is the large reduction in infection in the half-sibs with Clara Frijs as mother. The effects of mother and father are ambiguous, and the mother x father interaction was highly significant ($P<0.001$).

The progenies of Carola and Super Trévoux had significantly higher infection in combination with Clara Frijs than with BP 1575 both in 1985 and 1983. Significantly higher infection in combination with BP 1575 was observed in the progenies of Colorée de Juillet and Flemish Beauty in 1985. For the other fathers, no significant effect of the mother was detected.

Differences in susceptibility between 1983 and 1985 might have been due to climatic conditions, but it is more likely that they reflect higher resistance in older plants. The decrease in infection with increasing age is so remarkable that it makes it difficult to predict the response in older seedlings from early scoring for powdery mildew (*Podosphaera leucotricha*).

Top frost

The frequency distribution for this trait shows that many seedlings had more than 5 cm of top damage. This is an expression of the continuous nature of the character, and the scale could favourably have been extended.

With BP 1575 as mother there were more seedlings in classes 4 and 5 than was the case with Clara Frijs, i.e. very slight and no frost damage, and this difference was highly significant ($P<0.001$).

Taking into consideration the percentage of non-damaged seedlings (class 5), significant differences between fathers and populations were also observed as presented in Table 8.

Herzogin Elsa as father gave a high proportion of undamaged seedlings, especially in combination with BP 1575, where more than one half of the progenies showed no damage. The worst damage was in progenies with Carola as father.

The mother x father interaction was also highly significant ($P<0.001$), as expressed by the small effect of the mother for Belle lucrative and Carola, as compared with the other fathers tested.

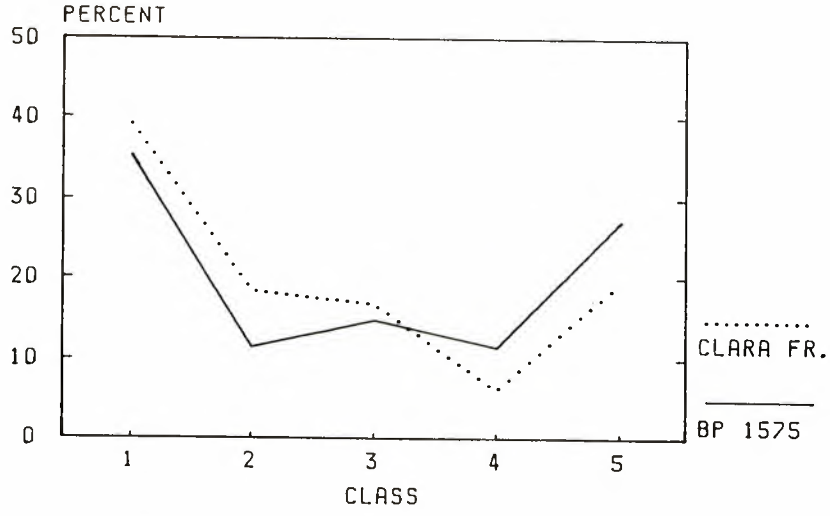

Figure 4. Frequency distribution for top frost. Percent in each class. 1 = >5cm damage. 2 = 2.5-5.0 cm damage. 3 = 1.0-2.4 cm damage. 4 = < 1 cm damage. 5 = No damage

The high frost damage in the progenies with Carola as father indicates that infection with *Podosphaera leucotricha* could be correlated to top frost. The correlation was low, r = -0.208.

Growth cessation also had a low negative correlation (r = -0.298) to top frost damage. This relationship was surprising, as it indicates that late growth cessation is favourable for frost hardiness.

Table 8. Percent seedlings with no frost damage

Father	Mother BP 1575	Mother Clara Frijs	Mean
Belle lucrative	15.4	16.9	16.2
Bonne Louise	24.0	12.0	18.0
Carola	8.8	9.5	9.2
Colorée de Juillet	34.5	27.2	30.9
Flemish Beauty	34.7	19.2	27.0
Herzogin Elsa	56.4	35.1	45.8
Super Trévoux	28.2	10.6	19.4
Unweighted mean	27.2	19.4	23.3

Habitus

Number and length of sidebranches

The number of sidebranches and lengths of the three longest sidebranches were very different between populations. Due to the small number of seedlings studied and the considerable variability, use of the Student-Newman-Keul's multiple test hardly pointed out any differences. This test is therefore not tabulated along with the means in Table 9.

The number of sidebranches was significantly different $P<0.001$) for the fathers, and the varieties Carola and Herzogin Elsa gave a high number of sidebranches as compared with the other fathers. The effects of the mother and the mother x father interaction were not significant.

The mother x father interaction was highly significant ($P<0.001$) for length of the sidebranches. This effect could be seen from the high response of the mother for Colorée de Juillet. This variety had significantly longer sidebranches with Clara Frijs as mother than with BP 1575. There was also a fairly clear tendency for Clara Frijs to produce longer sidebranches than BP 1575.

Table 9. Number and length of sidebranches in three-year old pear seedlings

Father	Mother: BP 1575 Number	Length	Clara Frijs Number	Length	Mean Number	Length
Belle lucrative	6.7	38.4	6.2	42.8	6.5	40.6
Bonne Louise	7.6	34.4	9.2	50.9	8.2	41.2
Carola	11.8	46.6	11.5	43.5	11.6	45.0
Colorée de Juillet	5.3	25.3	8.4	56.0	6.9	40.6
Flemish Beauty	9.4	38.2	7.3	42.5	8.3	40.3
Herzogin Elsa	10.2	49.8	10.7	47.1	10.4	48.4
Super Trévoux	5.1	35.1	7.4	42.4	6.2	38.7
Mean	8.0	38.2	8.6	46.3	8.3	42.1

The correlation coefficient between number and length of sidebranches was 0.422 and highly significant ($P<0.001$). This indicates that plants with fewer branches tend to have short branches and plants with many branches tend to have longer branches. This was mostly an effect of plant size.

By examining the population variances, it was found that the population Clara Frijs x Herzogin Elsa had low variance for length of sidebranches compared with its half-sib with BP 1575 as mother. The varieties Clara Frijs and Herzogin Elsa therefore seem to have fairly corresponding homozygosity in the loci governing this character.

Number of thorns, feathers and secondary sidebranches

The presence of thorns is regarded as a primitive character, so the number of thorns could therefore be an expression of juvenility. Furthermore, secondary sidebranches and feathers give the plant a rather «bushy» habitus, and these are also juvenile characters. All these three characters were positively correlated:

Number of thorns - number of secondary sidebranches $r = 0.587$

Number of thorns - number of feathers $r = 0.582$

Number of feathers - number of secondary sidebranches $r = 0.287$

As none of these three characters had significant interaction mother x father, the mean values of the fathers and mothers are presented in Table 10. The value for the mothers is the mean of 7 fathers, and the value for the fathers is the mean of 2 mothers.

Clara Frijs as mother gave a significantly higher number of thorns, secondary sidebranches and feathers than BP 1575. The level of significance was 0.1% for number of thorns and 1% for number of secondary sidebranches and number of feathers.

Carola as father gave the highest expression of all these 3 characters. When applying the Student-Newman-Keul's multiple test it was observed that the population Clara Frijs x Carola gave a significantly higher number of thorns and feathers than the other populations. Belle lucrative and Super Trévoux gave the fewest thorns and secondary sidebranches, while Flemish Beauty gave few feathers compared with the other fathers.

Clara Frijs gave an exclusively higher variance for number of thorns than BP 1575; Carola also gave a high variance for this character. This indicates that Clara Frijs and Carola are highly heterozygous in the loci governing the number of thorns.

Clara Frijs gave a higher variance for number of feathers than BP 1575, so these genes are obviously quite heterozygous in Clara Frijs, too.

The number of feathers would be a favourable criterion to apply in preselection as this character is manifested early in the seedlings. Regarding the number of thorns as the most juvenile character, a two-way frequency table for number of thorns and number of feathers would give an expression of reliability in indirect selection for juvenility.

The table shows that 165 seedlings had less than 5 feathers and 5 thorns, and this corresponds to 60% of the total number studied. Thirty-four percent had neither thorns nor feathers.

If selection for low juvenility were to be carried out, one could set the culling level at 5 thorns. By selecting genotypes with less than 5 feathers, one would select 27 genotypes that have 5 or more thorns (10%). In this indirect selection for low juvenility, the population would be reduced by 40%, however 8% with less than 5 thorns would be discarded.

Table 10. Number of thorns, secondary sidebranches and feathers in three-year-old pear progenies

	N° thorns	N° sec. sidebranches	N° feathers
Mother			
BP 1575	3.91	2.28	2.53
Clara Frijs	11.85	3.85	4.22
Father			
Belle lucrative	3.43	1.83	2.85
Bonne Louise	7.44	3.38	2.71
Carola	21.18	5.90	7.31
Colorée de Juillet	7.78	2.20	2.43
Flemish Beauty	5.63	2.33	1.65
Herzogin Elsa	5.45	4.70	2.78
Super Trévoux	4.05	1.15	3.80
Total mean	7.81	3.05	3.36

Table 11. Frequency cross table for number of feathers and number of thorns in 273 three-year old pear seedlings

Number of thorns	Number of feathers < 5	5-9	10-14	15-19	>20	Sum
< 5	165	18	4	0	0	187
5-9	13	9	7	0	0	29
10-14	8	8	1	0	0	17
15-19	2	4	2	2	0	10
> 20	4	9	11	3	3	30
Sum	192	48	25	5	3	273

Leaf characters

In Fig. 5 a plot is presented illustrating leaf size for 50 seedlings from each of the 14 populations. Grouping is done in 5 cm classes, and leaf breadth is plotted to leaf length. Two seedlings (0.2%) had leaves that were broader than their length, and in 13 seedlings (1.9%) the length was more than twice the breadth. The seedling mean was 37.5 x 56.4 mm, as compared with a parent mean of 46.8 x 82.9 mm, illustrating that juvenile seedlings have smaller leaves than adult trees.

Leaf breadth
Ranking was assessed using the Student-Newman-Keul's multiple test. Numbers with the same letters are not significantly different at the 5% level.

As can be seen from Table 12, leaf breadth segregation was very good between populations, and significant effects were found in the mother ($P<0.01$), father and mother x father interaction ($P<0.001$).

The table shows that the progenies from combinations with Super Trévoux had broader leaves, and the progenies from Bonne Louise had narrower leaves, especially in combination with BP 1575. The population BP 1575 x Colorée de Juillet also had narrow leaves.

Bonne Louise had the narrowest leaves of the parent varieties recorded, and this character was transferred to its progeny.

Clara Frijs progenies tended to have broader leaves than BP 1575 progenies. This effect was not manifested for all fathers, as demonstrated by Carola, which gave the broadest leaves in combination with BP 1575.

From these findings it seems that narrow leaves have a higher prepotency than broad leaves.

Leaf length
Leaf length showed the same significance levels for mother, father and mother x father interaction as leaf breadth. BP 1575 and Herzogin Elsa had the longest leaves of the parent varieties recorded, and the same tendency was observed in the progenies.

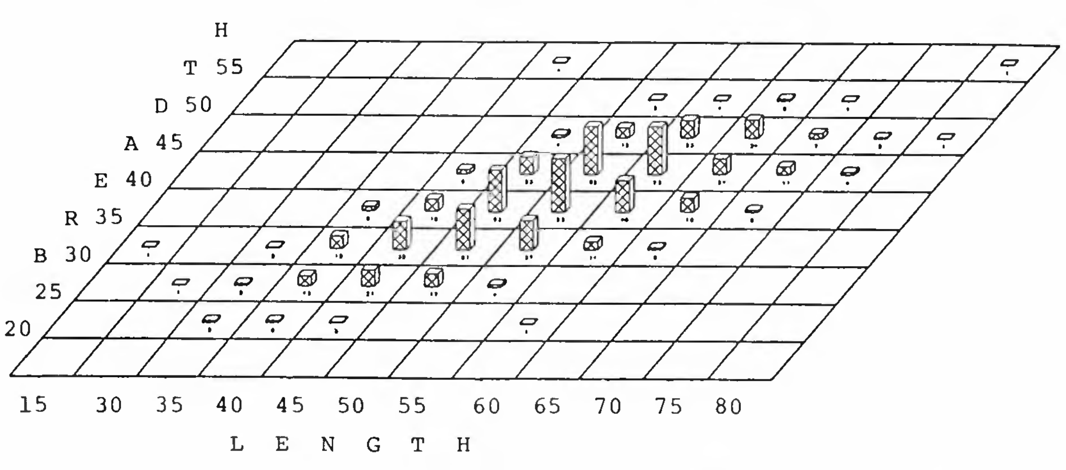

Figure 5. Frequency block chart of leaf breadth to leaf length. Numbers at the axes give lower limits of each 5 mm class. Numbers in cells give number of progenies in each cell

Table 12. Leaf breadth in mm. Fifty seedlings in each population and 2 trees of each parent variety recorded

Father	Mother BP 1575	Clara Frijs	Mean	Parent variety
Belle lucrative	37.1 de	38.7 bcd	37.9	51
Bonne Louise	29.3 g	33.8 f	31.6	38
Carola	38.9 bcd	35.2 ef	37.0	47
Colorée de Juillet	33.8 f	39.4 bcd	36.6	44
Flemish Beauty	37.6 cd	38.3 bcd	38.0	49
Herzogin Elsa	40.4 abc	38.3 bcd	39.4	44
Super Trévoux	41.0 ab	42.4 a	41.7	-
Mean	36.9 38.0	37.5		
Parent variety	53 48			

Ranking was assessed using the Student-Newman-Keul's multiple test. Numbers with the same letters are not significantly different at the 5% level.

Table 13. Leaf length in mm. Fifty seedlings in each population and 2 trees of each parent variety recorded

Father	Mother BP 1575	Clara Frijs	Mean	Parent variety
Belle lucrative	56.7 bc	57.0 bc	56.8	81
Bonne Louise	48.4 d	50.7 d	49.5	80
Carola	56.6 bc	50.8 d	53.7	63
Colorée de Juillet	56.0 bc	57.8 bc	56.9	88
Flemish Beauty	59.8 ab	54.2 c	57.0	73
Herzogin Elsa	61.9 a	60.1 ab	61.0	91
Super Trévoux	60.0 ab	59.0 ab	59.5	-
Mean	57.1	55.6	56.4	
Parent variety	111	75		

Bonne Louise progenies had the shortest leaves, while leaves of Bonne Louise were about the parent mean.

Carola and Flemish Beauty had the shortest leaves of the parent varieties recorded. The progenies of these two varieties had significantly longer leaves in combination with BP 1575 than with Clara Frijs. These findings indicate that long leaves have a high prepotency, and reflect the parents to a great extent.

Petiole length

The effects of mother, father and the mother x father interaction were all signficant ($P < 0.001$), and the character were well segregated between populations.

Table 14 shows that Clara Frijs gave a longer petiole than BP 1575 for all fathers, and the variety Clara Frijs had a much longer petiole than all the other parent varieties recorded.

The longest petioles were observed in the combinations Clara Frijs x Herzogin Elsa and Clara Frijs x Super

Table 14. Petiole length in mm. Fifty seedlings in each population and 2 trees of each parent variety recorded

Father	Mother BP 1575		Clara Frijs		Mean	Parent variety
Belle lucrative	21.3	de	27.4	b	24.3	35
Bonne Louise	16.2	g	20.1	def	18.2	38
Carola	18.1	f	19.2	ef	18.6	26
Colorée de Juillet	18.7	f	27.1	b	22.9	34
Flemish Beauty	23.7	c	28.1	b	25.9	45
Herzogin Elsa	24.3	c	32.1	a	28.2	43
Super Trévoux	21.8	d	31.0	a	26.4	-
Mean	20.6		26.4		23.5	
Parent variety	54		75			

Ranking was assessed using the Student-Newman-Keul's multiple test. Numbers with the same letters are not significantly different at the 5% level.

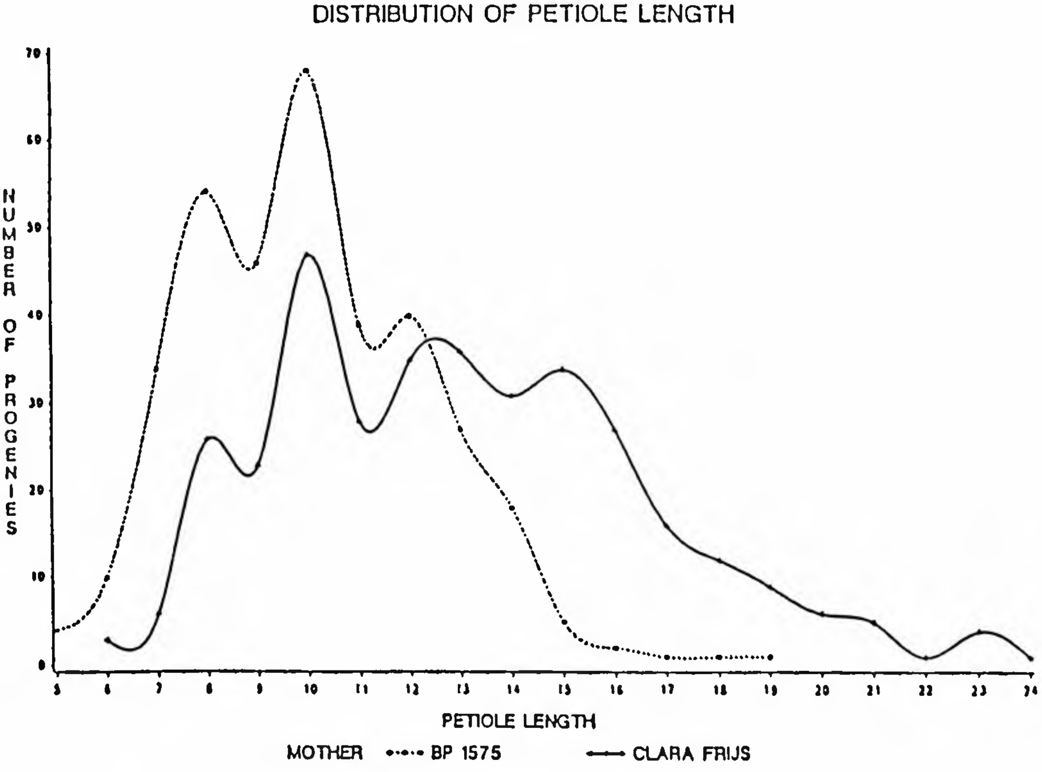

Figure 6. Petiole length in pear progenies. Seven families, each containing 50 progenies for each mother variety. Numbers at the abscissa give 2 mm classes

Trévoux. The shortest petiole was observed in the combination BP 1575 x Bonne Louise. Progeny means did not inevitably correspond to the ranking between father varieties, but the response to a specific cross could to some extent be predicted.

The distribution of petiole length in the half-sibs of the two mothers is presented in Fig. 6.

The distribution shows that there was a bias for petiole length in the Clara Frijs progenies, while petiole length in BP 1575 progenies fitted normality better.

DISCUSSION

In the present study of juvenile pear seedlings significant differences were found between mothers and fathers for most characters. But the study also revealed that most characters showed significant interaction mother x father. Hence it is very difficult to predict the response of a specific combination for these characters, and the main effects of mother and father become quite uncertain.

Regarding vigour, this study supports Zimmerman's (1976) statement that this character is not consistent over years. Ranking differs between years in the first three years, and probably for even longer during the juvenile phase. However, the discrepancy in ranking was highest between the first and the second year of seedling growth. The correlation in plant height between years seems to increase with increasing seedling age, but in this study it has not been possible to estimate the loss of precocious seedlings by preselecting for plant height. In breeding programs where one-year-old seedlings are planted directly in seedling orchards, this kind of preselection would be too uncertain. However, if seedlings are planted in seedling beds first, this correlation could be exploited. In this study it was found that the variety Herzogin Elsa gave the most vigorous progenies, and Bonne Louise the least vigorous progenies.

Bud burst seemed to be controlled by major genes, although modified by polygenes and the environment. Clara Frijs and Belle lucrative gave late sprouting seedlings and early bud burst was observed in the progenies of Bonne Louise and Colorée de Juillet. The variation observed in bud burst proves that breeding for early or late flowering is possible by choosing the right parents.

Growth of the pear seedlings increased with increasing seedling age. The growth curve was sigmoid, and similar for seedling populations and their parent varieties. As for growth cessation, the progenies of Flemish Beauty and Herzogin Elsa had early growth cessation. The two early maturing varieties, Colorée de Juillet and Super Trévoux, had relatively few progenies with terminal buds on September 30th.

Powdery mildew (*Podosphaera leucotricha*) on pear seedlings has been reported previously from the pear breeding program at Njøs Research Station (Hjeltnes, in press). The present study has revealed that the variety Clara Frijs as mother gave many susceptible progenies. This corresponds with the findings of Alston & Bates (1984). However, in the previous study (Hjeltnes, in press), Clara Frijs as father was found to give many resistant seedlings. This indicates that cytoplasmatic factors might be involved. On the other hand the infection greatly decreased with increased seedling age, and young tender pear seedlings should probably not be subjected to high infection pressure of *Podosphaera leucotricha*. Most seedlings will probably not develop the disease once they reach the adult stage, as powdery mildew is seldom a problem in pear varieties.

Top frost had a different reaction on the mothers than on the fathers. Still, it was found that BP 1575 progenies had less damage than Clara Frijs progenies, and this fact could to some extent explain the relatively higher growth increment in the field in the BP 1575 progenies. The most vulnerable seedlings were observed in combinations with Carola and Belle lucrative. The hardiest combination was BP 1575 x Herzogin Elsa, and it was found that the progenies from Herzogin Elsa were the least damaged. Again, this is in accordance with plant height, as these progenies were the most vigorous ones. Top frost had low but significant negative correlations to *Podosphaera leucotricha* infection and growth cessation. Surprisingly, it was found that seedlings with late growth cessation tended to be hardier than seedlings with early growth cessation.

The presence of thorns is common in pear seedlings (Hedrick, 1921), and this primitive character was highly variable between populations. The interaction mother x father was not significant, and BP 1575 as mother gave remarkably fewer thorns than Clara Frijs. The Clara Frijs progenies had higher variances than the BP 1575 progenies, and it is stated that Clara Frijs has a higher heterozygosity than BP 1575 in the loci governing this character. The low number of thorns in the BP 1575 progenies could be inherited from the father, Conference, as this variety is reported to transmit a fairly short juvenile period (Thibault, 1979). From pear orchards it is known that BP 1575 is more precocious than Clara Frijs, and as precocity is closely correlated to length of the juvenile period (Visser, 1967), it is likely that BP 1575 transmits a short juvenile period to its progeny. Carola (Johantorp x Comice) also gave a large number of thorns and high variances, so it is proposed that this variety has a high level of heterozygosity for this character along with the variety Clara Frijs. The high number of thorns in Carola could be inherited from Comice, which is reported to transfer a long juvenile period (Thibault, 1979). Few thorns were observed in combinations with the fathers Belle lucrative and Super Trévoux, and it can be expected that these two varieties will give a short juvenile period.

The habitus classification of some seedlings showed that Carola and Herzogin Elsa gave many sidebranches and secondary sidebranches. Clara Frijs gave a significantly higher number of secondary sidebranches and feathers than BP 1575. This means that Clara Frijs gives more «bushy» seedlings and therefore probably expresses more 'juvenile' genes than BP 1575, as was indicated by the number of thorns. On the basis of population variances it is stated that genes for feathers are more heterozygous in Clara Frijs than in BP 1575. Low variances were observed for length of sidebranches in the population Clara Frijs x Herzogin Elsa and for secondary sidebranches in the populations BP 1575 x Super Trévoux and BP 1575 x Colorée de Juillet. This indicates that these varieties have a somewhat corresponding homozygosity in the loci for these characters.

A selection for feathers is proposed as an indirect selection criterion for juvenility. The proposal is based on the observed correlation between number of feathers and number of thorns, and the assumption that the number of thorns is the better estimate for juvenility. This selection for number of feathers could possibly be carried out on two-year old seedlings in the field, as feathers will be present in the seedlings at this age. However, it must be stressed that recording of habitus was done on only a few seedlings, and in only one year.

By combining this selection for juvenility and selection for plant height, it was found that about 70% of the seedlings would have been discarded by applying the suggested selection intensities. Some populations would have been totally wiped out, so these selection intensities are probably too high. It might have been better to use population means instead of the total mean as the culling level for plant height. When the seedlings become adult the right culling levels for these two characters could possibly be found.

The juvenile seedlings had smaller leaves and shorter petioles than the parent varieties. Populations were well discriminated by leaf breadth and petiole length. These two characters reflected the parents to a certain extent, but the interaction mother x father was highly significant. Narrow leaves seemed to have higher prepotency than broad leaves, as the narrow-leafed variety Bonne Louise transmitted narrow leaves to its progeny. BP 1575 and Belle lucrative had the broadest leaves of the parent varieties recorded, but these were not the most large-fruiting varieties of the parents in this study. Therefore, it is not to be expected that leaf breadth could be used as a preselection criterion for fruit size.

The Clara Frijs variety had long petioles, and this character was transmitted to its progenies. The father varieties studied had short or medium petiole lengths, but the ranking in their progenies was not always in the same order.

Leaf length showed fairly good correspondence between seedlings and parent varieties. On the other hand this character did not segregate as well as breadth and petiole length; even though the variation between parent varieties was greater than it was for leaf breadth and petiole length.

SAMANDRAG

Variasjonar i morfologi, fysiologi og resistens mot mjøldogg vart studerte i 2891 juvenile frøplanter i pære frå 1982 til 1985. Det synte seg at det var stor variasjon både mellom og innan familiar, men det vart observert ulik heterozygoti for somme sortar for enkelte karakterar. Storleiken på plantene vart målt ved stammediameter og trehøgd, og målingane synte til dels svært ulik rangering av genotypar mellom år. Rangeringa vart likare mellom år ved aukande plantealder. Data for knoppsprett og vekstavslutning synte at det vil vera råd å foredla for desse karakterane ved rett valg av foreldre, men vekstavslutning såg ikkje ut til å ha nokon samanheng med haustetid. Det var ingen skilnad mellom populasjonane eller foreldresortane for tilvekst innan år, men det vart observert at veksten var mindre fyrste året i felt enn andre året. Infeksjon av mjøldogg (*Podosphaera leucotricha*) gjekk sterkt ned med alderen på frøplantene, og det er truleg ikkje rett å vraka planter som er infiserte med mjøldogg på eit tidleg stadium. Habitus vart skildra ved tal og lengd på sidegreiner og tal sekundære sidegreiner, torner og forgreiningar på toppskotet. Korrelasjonen mellom tal torner og tal forgreiningar på toppskotet var signifikant, og det er føreslått at preseleksjon for forgreiningar på toppskotet kan gjerast saman med seleksjon for plantehøgd. Variasjonen i bladbreidd, bladlengd og bladstilklengd synte at desse karakterane i stor grad avspeglar foreldra, og bladbreidd skilde best mellom populasjonane. For dei fleste karakterane vart det funne signifikant samspel mor x far, slik at det stort sett vil vera vanskeleg å predikera kva ei bestemt kryssing vil gje.

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SKIN DISCOLOURATION OF FOUR PEAR CULTIVARS IN RELATION TO MATURITY, DEGREE OF RIPENING AND DURATION OF STORAGE

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The cultivars reacted differently depending on the grading practice applied to the fruit. 'Philip' and 'Herzogin Elsa' tolerated handling operations better than 'Moltke' and 'Amanlis'. Susceptibility to friction discolouration decreased with maturity but increased with duration of storage. Tolerance to grading operations differed with years. High discolouration scores were associated with above normal summer temperatures and low yield. Grading at different stages of ripening showed an increase in discolouration as fruit firmness diminished. Grading at harvest or within a limited number of days of storage caused very little skin damage.

Key words: Pear, skin discolouration, maturity, ripening, storage.

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Skin browning of pears is a frequently observed disorder manifested by dark spots caused by damage to the cells of the epidermal and subepidermal region of the fruit.

This damage can occur at all stages in the course of distribution. The injury is caused by the handling practices involved in the different operations from harvest until the fruit reaches the consumer. The liability of the fruit to this disorder has been shown to be related to maturity and duration of storage (Kvåle, 1979, Wang & Mellenthin, 1975).

The objective of the present study was to investigate the tolerance of some major cultivars grown in Norway to grading operations in relation to maturity, degree of ripening and duration of storage of the fruit.

MATERIALS AND METHODS

Fruit samples (approximately 20 kg) of each of the cultivars 'Amanlis', 'Moltke', 'Philip' and 'Herzogin Elsa' were harvested at weekly intervals from the beginning of September throughout the first week of October and stored at 0°C.

Measurements of fruit firmness were carried out on subsamples of 10 pears. Fruit firmness was measured by means of an Effigi pressure tester equipped with an 8 mm plunger.

Friction discolouration tests were carried out in October and November on a Greefa A3 fruit grader. Prior to grading the samples were warmed up for 2 days at 10-12°C. Discolouration of the fruit was evaluated by five judges 1 day after grading. A rating scale ranging from 0 (no discolouration) to 5 (fruit strongly discoloured) was used.

In one experiment grading was also carried out at harvest, in addition to the tests carried out in October and November.

Duncan's multiple range test was applied for mean separation, different letters denoting significant differences at the 5% level.

RESULTS AND DISCUSSION

The four cultivars reacted differently depending on the grading practice applied to the fruit. 'Philip' and 'Herzogin Elsa' appeared to tolerate handling operations better than 'Moltke' and 'Amanlis'. At both dates of grading the discolouration scores were significantly higher with 'Amanlis' and 'Moltke' than with 'Philip' and 'Herzogin Elsa' (Table 1).

It appears from Table 1 that susceptibility to friction discolouration decreased with maturity but increased with duration of storage. All the cultivars showed less skin browning when harvesting was delayed, but a delayed harvest was associated with a loss in fruit firmness at the rate of approximately 0.5 kg a week (Table 2). Prolonged storage led to an increase in discolouration scores. Grading carried out in November caused more visible damage to the pears than grading carried out in October. These results are in accordance with previous findings with 'Moltke' and 'Herrepære' (Kvåle 1979) and the results with 'd'Anjou' pears reported by Mellenthin and Wang (1973).

Tolerance to grading operations differed with years. The pears were more vulnerable to skin browning in 1980 and 1982 than in 1981 (Table 3). Similar results were obtained with 'Moltke' in a previous investigation (Kvåle, 1979).

Climate has been shown to exert an influence on fruit discolouration of pears. Nortje et al. (1974) found the discolouration of canned 'Bon Chretien' pears to be related to climate differences between seasons. In the present investi-

Table 1. Skin discolouration (scores) of four pear cultivars inrelation to date of harvest and duration of storage. Average of 3 years

Harvest No.	Amanlis	Moltke	Philip	Herzogin Elsa*
		Grading in October		
1	2.1 ab	3.1 a	1.2 a	1.2 ab
2	2.3 a	1.8 b	1.0 a	1.5 a
3	1.4 bc	1.4 bc	0.9 a	0.8 b
4	1.7 b	1.1 c	0.9 a	0.7 b
Average	1.9 a	1.9 a	1.0 b	1.1 b
		Grading in November		
1	3.3 ab	3.9 a	2.0 a	2.4 a
2	3.4 a	3.7 a	2.3 a	2.8 a
3	2.8 bc	2.8 b	1.5 b	2.4 a
4	2.5 c	2.1 c	0.6 c	1.1 b
Average	3.0 a	3.1 a	1.6 b	2.1 b

*Average of 2 years

Table 2. Decrease in firmness (kg/week) of the pears over the four-week period of harvest (from August 30th to September 28th)

	Amanlis	Moltke	Philip	Herzogin Elsa
			kg/week	
1980	0.7	0.6	0.6	-
1981	0.7	0.2	0.5	0.7
1982	0.4	0.5	0.5	0.7
Average	0.6	0.4	0.5	0.7

Table 3. Seasonal variation in skin discolouration (scores) of four pear cultivars. Average of four dates of harvest

Year	Amanlis		Moltke		Philip		Herzogin Elsa		Average
	Oct.	Nov.	Oct.	Nov.	Oct.	Nov.	Oct.	Nov.	
1980	2.0ab	3.2a	2.0a	3.0a	1.3a	1.6b	-	-	2.2
1981	1.0b	2.1b	1.6a	2.5b	0.4b	0.8b	0.4b	0.9b	1.2
1982	2.7a	3.8a	2.1a	3.8a	1.4a	2.5a	1.7a	3.5a	2.7

gation skin discolouration of the pears seems to be related to climate and to crop size. The high discolouration scores obtained in 1980 and 1982 are associated with a low yield and above normal summer temperatures, while low discolouration scores were obtained in 1981 when a below normal summer temperature prevailed and the yield was high. These results do not concur with those obtained in a previous investigation with 'Moltke', where the highest discolouration scores were recorded after a relatively cool growing season (Kvåle, 1979).

The seasonal variation in skin browning does not relate to fruit firmness at harvest (Table 4). No significant correlation between fruit firmness at harvest and discolouration scores was found.

Ripening tests with 'Moltke' showed that skin browning is closely related to ripeness of the pears. The grading of pears at different stages of ripening showed increasing discolouration scores

Table 4. Firmness at harvest (kg). Average of four harvest dates

Year	Amanlis	Moltke	Philip	Herzogin Elsa	Average
		Firmness kg			
1980	6.7	7.8	7.2	-	7.2
1981	8.7	8.7	8.2	8.4	8.5
1982	7.7	9.6	9.3	9.9	9.1
Average	7.7	8.7	8.2	9.2	

Table 5. Skin browning of 'Moltke' pears in relation to firmness of the fruit

1982		1983	
Firmness	Discolouration	Firmness	Discolouration
kg	scores	kg	scores
7.8	1.4 a	7.7	0.9a
3.4	2.8 b	5.0	1.7ab
2.2	3.7 b	2.9	2.3bc

Table 6. Skin discolouration of 'Moltke' pears in relation to date of harvest and length of storage, 1982

	Date of harvest				
	Sept. 9		Sept. 27		
Time of grading	Days in storage	Discolour-ation	Days in storag	Discolour-ation	Average
		scores		scores	scores
At harvest	0	0.5	0	0.9	0.7 a
October	39	0.3	21	1.0	0.7 a
November	71	1.8	60	1.5	1.6 b
Average		0.9 a		1.1 a	

with diminishing fruit firmness (Table 5). The results indicate that grading and handling of pears with firmness values of 5 kg or lower may cause visible skin marks on the fruit.

Since skin browning appeared to be closely related to the duration of storage, an experiment was designed to compare grading immediately after harvest with grading in October and November, which is the regular marketing season for Norwegian pears. The results are presented in Table 6. Grading at harvest and in October caused very little damage to the fruit. When the pears were harvested at the preclimacteric stage of development (date of harvest Sept. 10), grading 39 days after harvest did not cause any increase in visible skin marks on the fruit. The corresponding storage period for climacteric pears (date of harvest Sept. 27) was 21 days.

Grading in November caused a significant increase in skin browning both with preclimacteric and climacteric pears.

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THE EFFECT OF FOUR DIETARY LEVELS OF CALCIUM, ADJUSTED BY LIMESTONE MEAL, ON FEED CONSUMPTION, PRODUCTION, EGG QUALITY AND FAT AND MINERAL RETENTION IN LAYING HENS

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The calcium levels in the diet of laying hens were regulated to 2, 3, 4 and 5% by adding limestone meal.

Increasing dietary levels resulted in reduced metabolic energy intake, increased plasma calcium level, improved egg shell quality and albumin height. No significant influence was found either on plasma levels of phosphorus, magnesium and zinc, or on these minerals and calcium and cholesterol in eggs. In absolute terms, the retention of fat was reduced, calcium and magnesium were increased, while the percentage retentions of fat and calcium were increased. No real influence was found on the percentage retention of phosphorus, magnesium and manganese.

Key words: Calcium, egg quality, laying hens, limestone meal, minerals, retention.

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It is a well established fact that the calcium level in the diets of laying hens is a determining factor for egg shell quality. However, unfavourable effects may be caused by excessive levels of calcium, although experimental results are controversial. Decreased feed intake was found by Hurwitz et al. (1969) when calcium in the diet for laying hens was increased from 3 to 4.5%, and decreased egg production was found by Hull & Scott (1969), Scott et al. (1971), and by Damron & Harms (1980) when calcium was increased to 5-6%. On the contrary, however, such effects were not found by Gleaves et al. (1977), Reichmann & Connor (1977) or Atteh & Leeson (1983) when calcium levels in the laying diets were increased to, 5.7 and 4.2%. Keshavarz (1986) suggests that high dietary levels of calcium may produce unfavourable effects on the performance of old hens, but not so with high dietary levels (5.5%) of short duration to young hens.

High dietary calcium levels may also have a decreasing effect on the utilization of trace elements (Maynard & Loosli 1979, Underwood 1977, Hvidsten & Eskeland 1983).

The present experiment is a continuation of earlier studies of dietary calcium to hens (Høie 1978, Lund 1985), and was conducted in order to study the effect of high dietary levels of calcium in the form of calcim carbonate in commercial limestone meal on the performance of laying hens, and also the effect on certain mineral retention and plasma levels.

MATERIAL AND METHODS

The experimental hens comprised 24 White Leghorn hens of commercial strain. They were 36 weeks old and in their 16th week of laying at the start of the experiment, which lasted for 16 weeks (9th March - 28th July). The hens were kept in individual cages (1520 cm^2) equipped for quantitative control of feed intake and produced excrements.

Feeds and water were given ad lib and feed consumption was recorded every week. Basic feed given prior to and during the experimental period consisted of a concentrated mixture with the following composition:

Herring meal 6.0%, soybean meal 6.0%, wheat meal 14.0%, wheat midlings 14.0%, corn meal 21.0%, sorgum meal 12.0%, dried yeast 1.4%, grassmeal 3.1%, NaCl 0.3%, and vitamin mixture 0.1%.

According to the analyses the basic feed contains (in g/100 g) : 88.3% dry matter, 16.6% crude protein, 2.8% fat, 3.6% crude fibre, 59.5% nitrogen free extracts, 5.8% ash, 1.03% calcium and 0.69% phosphorus. The vitamin mixture supply per kg feed: 10000 I.U. vitamin A, 1200 I.U. vitamin D_3 , 5 I.U. vitamin E, and 4 mg riboflavin.

Four experimental feed mixtures, with 2, 3, 4 and 5% calcium, were prepared by mixing 100 kg of the basic mixture with commercial limestone meal in quantities of 4.008, 8.491, 13.378 and 18.726 kg respectively. The limestone meal contained 26.2% calcium. Analyses of the experimental feed mixtures are given in Table 1.

The experiment was performed according to a randomized black design with 6 individual feed hens on each of the 4 treatments. Egg production was recorded every day.In the last two weeks of every 28-day period two eggs from each hen were sampled for evaluating egg quality.

The specific gravity of the eggs was determined on the laying day and calculated on the basis of egg weight and weight in water at 15°C. The weight of the egg shell was determined after the egg content was removed and the shell washed with water and dried at room temperature for 48 hours. Shell thickness (including shell membranes) was measured on the dry shell in the ends and in the equatorial plane.

In the last half of the experiment the hens were taken through two balance periods of 5 days (3rd - 8th May and 14th19th June), when daily feed rations were restricted to 95 g/hen. Correction for feed residue was made at the end of the periods. Excrements, quantitatively collected in the last two days of the 5-day periods, were mixed in a blender and a 50 g sample was taken for drying and analysis.

Blood samples from the wing vein for mineral analysis were drawn two times for all hens, in the middle (May 14th) and at the end (June 25th) of the experimental period.

Mineral analyses of feeds and excrements were performed using conventional methods at the Chemical Research Laboratory, NLH. The atomic absorption technique was used for blood samples. Phosphorus was determined in fresh samples.

RESULTS AND DISCUSSION

Feed intake, weight gain and egg production are given in Table 1. Feed consumption was not significantly affected

Table 1. Minerals in feed, feed consumption, weight and egg production

Treatments		A	B	C	D	Significance of differences
Number of hens			6	6	6	
In feeds:						
Calcium	g/100 g	2,0	3,1	4,4	5,0	
Phosphorus	g/100 g	0,66	0,66	0,63	0,60	
Magnesium	g/100 g	0,20	0,23	0,30	0,31	
Manganese	mg/100 g	10,8	11,4	13,3	13,6	
Feed consumption	g/h/d	105	96	105	100	NS
Metabolic energy in feed	Mj/h/d	1,15a	1,00b	1,04b	0,93b	*
Calcium in feed	g/h/d	2,1	3,0	4,6	5,0	
Live weight at start	kg/h	1,81	1,76	1,72	1,70	
Weight gain	g/h	120	40	50	-130	NS
Number of eggs/h.		83	82	84	75	NS
Egg weight	g	58	57	59	55	NS
Egg mass	g/h/d	43	40	44	37	NS

Means followed by different letters in each column are significantly different ($p<0.05$). NS: Not significant. *: Significance at $p<0.05$

by dietary levels of calcium carbonate, but energy consumption was significantly highest for hens fed diets with the lowest content of calcium carbonate and calcium. Weight gain, number of eggs and egg weight were not significantly affected, but the lower number of eggs in treatment D was nearly significantly different from that in the other treatments.

In the sampling taken on May 14th, plasma calcium had increased significantly for hens fed diets with the highest content of calcium carbonate and calcium. This effect was not found in the June 25th sampling, which on average gave significantly ($p < 0.05$) lower values than the May 14th sampling. (Table 2) An increase in plasma calcium level with increasing dietary calcium was also found by Reichmann & Connor (1977) and Atteh & Leeson (1983), but

Table 2. Content of calcium, phosphorus, magnesium an zinc in blood plasma

Treatsments		A	B	C	D	Significance of mean differences
Calcium	14/5 mg/100 ml	24,9a	28,2ab	30,1ab	33,4b	*
	25/6 "	22,4	26,3	28,7	26,4	NS
Phosphorus	14/5 "	6,40	5,75	6,28	6,20	NS
	25/6 "	5,10	5,24	4,85	4,81	NS
Magnesium	14/5 "	3,20	3,44	3,65	3,13	NS
	25/6 "	3,02	3,35	3,14	2,96	NS
Zinc	14/5 mg/1000 ml	5,02	5,08	5,04	4,76	NS
	25/6 "	3,83	3,85	4,43	3,58	NS

Means followed by different letters in each colomn are significantly different ($p>0.05$). NS: Not significant. *: Significant at $p<0.05$

not by Keshavarz (1986). Plasma contents of phosphorus, magnesium and zinc were not significantly affected by dietary levels of calcium carbonate. For phosphorus and zinc there was a significant ($p < 0.001$) decrease in plasma level from the sampling on May 14th to that of June 25th.

Eggshell quality, (tabel 3) as evaluated by specific weight, shell thickness and shell weight, improved significantly from treatment A to treatment D, and especially from C to D. The number of cracked eggs also decreased in the same direction. These effects of increasing dietary content of calcium carbonate or calcium concur with many other studies. The reduced phosphorus intake may also be an influencing factor.

Albumen height was significantly influenced by the treatments. The highest value was found for eggs from treatment C and indicated the best internal egg quality. The reason may be genetic differences. Haugh number, cholesterol in egg yolk, and content in egg dry matter of calcium, magnesium, phosphoros and zinc showed no significant difference between treatments.

Histological observations on three kidneys from treatments A and D respectively were carried out at the Veterinary College. In one of the kidneys from treatment A a few chalk granula were found in the tubular epithelium, and in two of the kidneys from treatment D necrotic areas with chalk deposition in tubuli were observed, indicating a burden on the kidney resulting from this treatment. The frequency of mortality could not be studied in our experiment. Keshavarz (1986) found the greatest level of mortality in hens on the highest (6.5%) calcium.

Results from the *balance period* are given in Table 4.

The figures for each treatment are the means of 12 observations (6 hens in two balance periods). Dry matter intake and retention were not significantly different in the four treatments.

Fat and crude fat retentions measured in *absolute terms* were decreased significantly from treatment A to treatment D, and especially from C to D. These results are in accordance with the

Table 3. Egg quality and cholesterol and mineral contents in eggs

Treatsments		A	B	C	D	Significance of differences
Specific weight of eggs		1,076a	1,080b	1,082b	1,085c	**
Shell thickness	mm	0,336a	0,344a	0,344a	0,361b	***
Shell weight in percent of egg weight		8,23a	8,66a	8,72a	9,20b	***
Number of cracked eggs		15	3	3	1	-
Haugh number		82	84	88	84	NS
Albumen height	mm	6,7a	7,0b	7,7c	6,8a	***
Cholesterol in egg yolk	mg/100 g	156	155	157	158	NS
In dry matter of egg contents:						
Calcium	mg/g	2,0	2,1	2,1	2,1	NS
Magnesium	mg/g	0,50	0,50	0,51	0,46	NS
Phosphorus	mg/g	8,9	9,7	8,7	8,8	NS
Zinc	mg/100 g	43	45	45	46	NS

Means followed by different letters in each column are sinificantly different. NS: Not significant. ** and ***: Significance at 0.01 and 0.001 levels respectively

Table 4. Balance studies. Means of two balance periods

Treatsments		A	B	C	D	Significance of differences
Number of hens		6	6	6	6	
Feed intake	g/h/d	88,4	85,6	90,4	91,0	
Dry matter intake	"	79	77	82	83	NS
Dry m. retention	"	55	52	54	55	NS
" " "	%	71	67	67	67	NS
Fat intake	g/h/d	2,38a	2,14ab	2,17b	1,89c	***
Fat retention	"	1,89a	1,75a	1,78a	1,63b	***
" "	%	80a	82ab	84ab	86b	***
Crude fat intake	g/h/d	2,82a	2,57ab	2,47b	2,26bc	***
Crude fat retention	"	1,98a	1,80ab	1,71ab	1,52b	***
" " "	%	70	70	69	67	NS
Calcium intake	g/h/d	1,76a	2,57b	3,89c	4,51d	***
Calsium retention	"	1,19a	1,23ab	1,83ab	1,94b	***
" "	%	67a	50ab	47ab	43b	***
Phosphorus intake	g/h/d	0,58	0,57	0,56	0,54	NS
Phosphorus retention	"	0,055	0,103	0,023	0,080	*
" "	%	9,0	17,3	3,6	17,3	NS
Magnesium intake	g/h/d	0,18a	0,20a	0,27b	0,28b	***
Magnesium retention	"	0,032a	0,036a	0,67b	0,074b	***
' "	%	17,7	18,2	25,8	24,9	NS
Manganese intake	mg/h/d	9,5a	9,7b	11,7c	12,3d	***
Manganese retention	"	0,160	-0,212	0,144	0,399	NS
" "	%	1,7	-2,2	1,2	3,2	NS

Means followed by different letters in each column are significantly different ($p<0.05$). NS: Not significant. *, ** and ***:significance at the 0.05, 0.01 and 0.001 levels, respectively

general view that fat digestibility decreaes with the formation of calcium sopes from high calcium content in the diet (Griffith et al. 1961; Håkansson 1975). However, the *percentage* retention increased from treatment A to treatment D for fat, and was not significantly influenced for crude fat. These differences in responses between the absolute and percentage retentions may be explained by the increasing fat intake from treatment A to treatment D. It should also be mentioned that the fat and crude fat contents in the diet (2.7 and 3.2%) were on a more normal level and not as high as used in the referred studies.

Measured in absolute terms, calcium retention increased significantly from treatment A to treatment D. However, the *percentage* retention decreased consistently. These responses were not unexpected and are consistent with the findings of Hurwitz & Griminger (1961), Atteh & Leeson (1983) and Keshavarz (1986).

Phosphorus retention was not significantly influenced by the increased calcium concentration in the diets. The existing differences between treatments followed no trend and may have been accidental. The lack of response to increased levels of calcium is consistent with the findings of Kalango & Ademosun (1973), but not with the reduced effect of phosphorus retention found by Tyler (1946) and Salem & Reda (1955).

The adverse effect on absorption of magnesium as found by Edwards & Nugara (1968) was not confirmed in this experiment. In fact the retention of magnesium in absolute terms was highest in treatments C and D with high dietary calcium concentrations. These results may partly be explained by the higher magnesium intake in these treatments. The percentage retention of magnesium also increased, although not significantly.

The retention of manganese was very variable from treatment to treatment, and no trend could be detected. The concentration of manganese in the diet also increased from treatment A to treatment D as for calcium and magnesium.

SUMMARY

Calcium levels in diets for laying hens were regulated to 2, 3, 4 and 5% (treatments A, B, C and D) by adding limestone meal. The 24 individually fed birds were 36 weeks old at the start of the experiment and were fed the experimental diets for 16 weeks.

The daily feed intake in grams was not significantly influenced by the treatments, but the metabolic energy intake was highest in treatment A, with the lowest dietary content of limestone meal and calcium.

No significant differences were found between treatments in live weight gain, number of eggs, egg weight , or egg mass, but there was a tendency of the highest dietary level of limestone meal (treatment D),to produce an unfavourable effect.

Plasma calcium concentration and egg shell quality increased significantly with increasing dietary levels of calcium. Albumen height was at its maximum at 4% calcium in the diet. There was no significant influence on the egg content of cholesterol, calcium, magnesium, phosphorus, manganese and zinc.

The retention of fat and crude fat in absolute terms decreased significantly with increasing content of limestone in the diet, while the percentage retention increased for fat but not for crude fat. These facts may be explained by the reduced fat intake through increasing the limestone content in the diet.

The increasing intake of calcium and magnesium from treatment A to treatment D resulted in increased retention in absolute terms, while the percentage retention decreased for calcium but was unchanged for magnesium.

The percentage retention of phosphorus and manganese was not influenced by the treatments.

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DIE ROHSTOFFBASE VON WALD-FRÜCHTEN AUF NATÜRLICHEN STANDORTEN UND PLANTAGEN IN POLEN

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In Polen wurde die Rohstoffbase der wichtigeren essbaren Waldfrüchten fur 70 Tsd. Tonnen (darunter Heidelbeeren 30,1 Tsd., Brombeeren 5,0 Tsd., Himbeeren 2,2 Tsd., Preiselbeeren 1,5 Tsd., Moosbeeren 0,5 Tsd.) geschätzt. Das Reichtum und die Rohstoffbase von fruchtbringenden Waldpflanzen wird mittels der Erhebungs-, direkten und statistischen Inventarisation ermittelt. In den Jahren 1962-1963 wurden ca. 900 Versuchsflächen je 25 m2 in den wichtigsten Heidelbeerenbasen gegründet und untersucht. Jede Fläche werde nach einem gleichen Schema bechrieben. Der Ertrag von einer Fläche wird nach der folgenden Skala ermittelt: 1-sehr schwach, 2-schwach, 3-mittelmässig, 4-gut, 5-sehr gut. Zusammen mit den Angaben von vorigen Jahren verfugte man über 2500 Beobachtungen betreffs Ertrag, räumlicher Veränderlichkeit und Ertragsdynamik der Heidelbeere.
Die phänologischen Beobachtungen wurden seit dem Jahr 1972 auf Blühen und Fruchtbringung der Preiselbeere erweitert.

Während der Nachkriegsjahren hat sich in Polen der Plantagenbau der fruchtbringenden Waldpflanzen (runzelige Rose, hohe Heidelbeere, schwarze Aronia, Moosbeere und Preiselbeere) entwickelt.

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Die Waldfrüchte in Polen werden hauptsächlich auf den natürlichen Standorten gewonnen. Mit der Sammlung von Waldfrüchten befassen sich meistens die Einheiten des Wald-Nebenproduktionunternehmens 'Las'. Am Anfang werden im kurzen theoretische und organisatorische Grundlagen der Nebennutzung des Waldes in Polen charakterisiert.

Die Nebennutzung des Waldes umfasst die in den Wäldern gewonnenen Rohstoffe und Produkte mit Ausnahme des Harzes, das den Gegenstand der Hauptnutzung des Waldes darstellt. Die neuzeitliche Forstwirtschaft umfasst sowohl die Produktions- als auch Schutz- und Erholungsfunktionen und wahrscheindlich werden bald der Umfang und die Aufgaben der Nebennutzung des Waldes zum Teil geändert.

In Polen wurde der Begriff der Nebennutzung des Waldes früher und genauer als in vielen anderen Ländern formuliert.

In den Nachriegsjahren ist die polnische Konzeption der Nebenproduktion des Waldes erarbeitet. Ihre Grundlagen sind wie folgt:

- Die Nebenproduktion des Waldes stellt einen integralen Teil der Forstwirtschaft dar und darf sich in einen engen Zusammenhang mit der letzteren entwickeln.

- Sie darf in immer intensiveren, aber nicht destruktiver Weise, unter Berücksichtigung der Gründsatzen des neuzeitlichen Umweltschutzes, geführt werden.

- Die Aufsicht der Rohstoffbasen der Nebenproduktion des Waldes, deren Entwicklung und Nutzung dürfen ausschliesslich der Forstwirtschaft obliegen.

Die Waldnebennutzungen können wie folgt klassifiziert werden:

1. Pflanzliche Nebennutzungen - Waldfrüchte, essbare Pilze, pharmazeutische und technische Pflanzen, Harze, Nadeln, Laubwerk, Rinde, Korbweide, Saft von Waldbäumen.

2. Tierische Waldnutzungen - Schnecken, Waldbienen, Eichen-Seidespimmer.

3. Die aus der Erde gewonnenen Nutzungen, z. B. Torf.

Mit der Harz- und Gerberrindegewinnung befasst sich die Verwaltung der Staatsforste, mit der Gewinnung anderer Rohstoffe und Produkte - fast ausschliesslich die Einheiten des 'Las' - Unternehmens.

Inventarisation der fruchtbringenden Waldpflanzen

Die Hauptgrundlagen der Organisation der Arbeiten über die Erkennung des Reichtums und der Rohstoffbasen der fruchtbringenden Waldpflanzen, d. h. deren Inventarisation, sind in Polen seit ca 30 Jahren gültig. Die Inventarisationsgrundlagen wurden im Forstwirtschafts-Forschingsinstitut in Warschau unter der Leitung von Prof. W. Grochowski, beim Anteil des 'Las' - Unternehmens, erarbeitet.

Die Inventarisation des Reichtums und der Rohstoffbase der fruchtbringenden Waldpflanzen wird nach mehreren Methoden geführt. Zu den wichtigsten gehören die Erhebungs- direkte und statistische Methoden.

Die Inventarisation nach der Erhebungsmethode besteht in Füllung spezieller Formulare durch sämtliche Oberförstereien des Forstwirtschafts- Forschunsinstitutes, in welchen die Charakteristik der fruchtbringenden Waldpflanzen angegeben werden soll. Zu diesen Formularen werden, je nach der Möglichkeit, Kräuterbücher, Aufnahmen, Abbildungen und Beschreibungen der gegebenen Pflanze zugefügt. Die Erhebungsinventarisation kann vom allgemeinen order ein gehenden Charakter sein.

In den unter die Oberförstereien verteilten Fragebogen wird die durch die Beerenpflanzen gedeckte Fläche auf 4 Klassen eingeteilt, und zwar: bis 20%, 21-40%, 41-60% und über 60% Deckung. Bei der Erarbeitung der aus dem Gelande erhaltenen Materialien wurde für einzelne Beerenpflanzenklassen die folgenden reduzierenden Koeffizienzen angenommen: 0,07, 0,25, 0,45 und 0,60. Die mittlere innere Deckung der Beerenpflanzenfläche wurde empirisch für 70% bestimmt.

- Die direkte Inventarissation besteht in den durch Arbeitergruppen durchgeführten Geländeuntersuchungen über Vorkommen und Fruchtbringung der Waldpflanzen. Sie gibt die verhältnismässig zurverlässigsten und genauesten Ergebnisse, aber braucht höhere finanzielle Aufwände.

- Die statistische Inventarisation besteht im Notieren der Menge der gewonnene Waldfrüchte in speziellen Wirtschaftsbüchern in einzelnen Basen und Oberförstereien. Nach vielen Jahren verfügen wir über eine wertvolle information hinsichtlich der Rohstoffbase einzelner Waldfrüchte auf der gegebenen Fläche.

Die Geländematerialien, die fruchtbringende Waldpflanzen betreffen, werden einer kritischen wissenschaftlichen Beurteilung unterworfen und werden durch das Forstwirtschaft-Forschungsinstitut oder durch andere wissenschaftliche Einheiten erarbeitet.

Im Jahre 1956 ist die erste grössere Erhebungsinventarisation in Polen durchgeführt worden, die 12 wichtigsten fruchtbringenden Waldpflanzen umfasste.

In den Jahren 1962-1963 wurden durch die Abteilung Nebenproduktion des Waldes des FFI unter der Leitung von Prof. W. Grochowski in der Zusammenarbeit mit dem Lehrstuhl Forstnutwung der Warschauer Landwirtschaftlichen Universität die komplexen Untersuchungen über das Reichtum der Heidelbeerenfläche begonnen.

Innerhalb zwei Jahre wurden ca 900 Wersuchsflächen je 25 m2 in den wichtigsten Heidelbeerenbasen gegründet und untersucht.

Jede Fläche wurde nach einem gleichen Schema beschrieben. Der Ertrag von einer Fläche wird nach der folgenden Skala ermitelt: 1 - sehr schwach, 2 - schwach, 3 mittelmässig, 4 - gut, 5 - sehr gut.

Zusammen mit den Angaben von vorigen Jahren verfügte man über ca 2500 Beobachtungen betreffs Ertrag, räumlicher Veränderlichkeit und Ertragsfähigkeitsdynamik der Heidelbeere. In diesen Untersuchungen wurde die direkte Inventarisationsmethode vereinigt mit der ausführlichen Erhebunginventarisation, angewendet. Die Erarbeitung der Ergebnisse wurde im Jahre 1968 beendigt.

Durch Dr. S. Glowacki wurde im Jahre 1967 die Klassifikation der Heidelbeerenfläche nach den folgenden Merkmalen erarbeitet: Heidelbeerenflächetyp /I - kleinbüschig, II - büschig, III - schichtförmig, IV - schlagförmig/, Schlussart /a - schwach, b - mässig, c - stark und a/b, a/c und b/c - ungleichmässig/, Höheklasse /1 - niedrig, 2 - mittelhoch, 3 - hoch, 4 - sehr hoch/ und Deckung /0-100%/. Abb. 1.

Es wurde eine deutliche Differenzierung des Reichtums von Niederungs- und Gebirgsheidelbeeren festgestellt. Es

ABB 1

KLASSIFIKATION DER HEIDELBEERENFLÄCHE

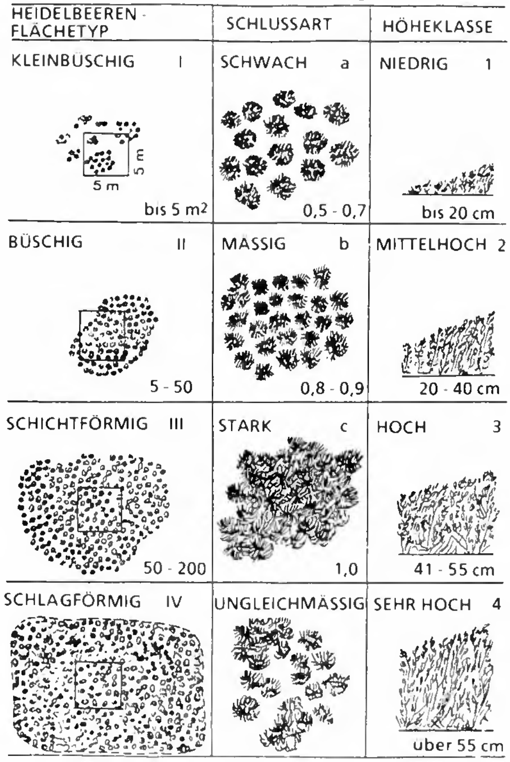

Abb.1. Klassifikation der Heidelbeerefläche nach S. Glowacki

wurde kein eindutiger Einfluss der natürlichen Waldteile und der Beerenflächekategorie auf den Reichtum von Beerenflächen festgestellt. Andererseits aber wurde ein signifikanter Zusammenhang zwischen dem Reichtum von Beerenflächen und dem Fruchtbringungsgrad derselben bewiessen.

Auch wurden die Regressionsgleichungen für die Beerenflächen berechnet, und zwar:

- für Niederungsflächen:

$$y = 27,17\, x^2 - 0,14\, x + 0,02$$

- für Gebirgsflächen:

$y = 34{,}40\,x^2 + 22{,}50\,x + 3{,}58$
wo: y - Beerenflächereichtum in kg/ha,
x - der in 5-Gradskala bestimmte Beerenertrag. Abb. 2.

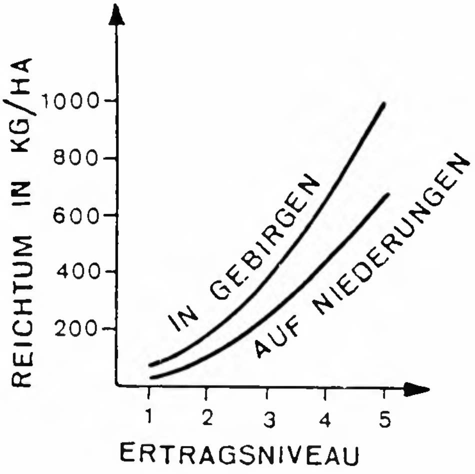

Abb. 2. Theoretischees Reichtum der Heidelbeere-Produktionsfläche in Polen(nach W. Grochowski und A. Zdanowski)

Durch S. Glowacki wurde für die Heidelbeerenflächen in den Bieszczadü - Gebirgen eine allgemeine Formel für die Regressionsgerade die die Abhängigkeit des Ertrages von der Produktivität der gegebenen Beerenfläche dargestellt, und zwar:

$y = 308x - 329$

A. Zdanowski aus dem Forstwirtschafts - Forschungsinstitut hat auf Grund von über 70 Tsd. Beobachtungen für die Jahre 1949-1969 die Charakteristik der Heidelbeere in Polen hinsichtlich ihrer Phänologie und der Ertragsbildung erarbeitet.

Nach den Untersuchungen dieses Authors soll die Prognose des wirklichen Ertrages /u/ auf Grund des Blühens /r_1/ mit Hilfe der Gleiching.

$u = 0{,}54\,r_1 + 1{,}04$

und auf Grund der ersten reifen Früchte /r_2/ mit Hilfe der Gleichung

$u = 1{,}49\,r_2 - 1{,}44$

korrigert werden.

Die auf Grund der ersten reifen Früchte gestellte Prognose /r_2/ ist im allgemeinen richtig und braucht keine Korrektur.

Die phänologischen Beobachtungen wurden seit dem Jahr 1972 auf Blühen und Fruchtbringung der Preiselbeere erweitert.

Die Heidelbeere gehört in Polen zu den wichtigsten Waldfrüchten und tritt auf 11% Gesamtfläche unsrer Wälder auf. Ihre Früchte stellen 60 - 70% Gesamtgewinnung und über 90% aller exportierten Waldfrüchten dar.

Die Höhe der Heidelbeerbüsche reicht bei uns 50 cm und nach S. Glowacki kann in günstigen Bedingungen sogar 70 cm und mehr hoch sein.

Die Heidelbeere blüht in Polen in April und Mai. Die ersten Beeren sind reif nach 5 - 8 Wochen. Die Früchtbildung dauert seit Anfang Juni bis Ende September.

Die durch S. Glowacki in den Jahren 1964 - 1966 auf den Heidelbeereflächen durchgeführten Untersuchungen erlaubten die folgenden Zusammenhänge zu bestimmen:

- massenhaftes Blühen der Heidelbeere fängt dann an, wenn die mittlere Dekadetemperatur höher als + 10°C ist.
- die Exposition der Heidelbeerenfläche nach gegebener Himmelsrichtung beeinflusst den Beerenertrag,
- der Typ der Beerenfläche und die Geländeneigung üben keinen signifikanten Einfluss auf den Beerenertrag.

Die Vieljährigen Untersuchungen von T. Cübulko und L. Antkowiak haben den Einfluss der mineralischen Düngung auf die Mehrerträge der Heidelbeere bewiesen.

Die Früchte der Heidelbeerbüsche sind in Polen gleichmässig in Bezug auf ihre chemische Zusammensetzung. Dies wurde durch die Untersuchungen von K. Rogalinski und S. Glowacki bestätigt.

Die Manipulationsfläche der Heidelbeere in Polen beträgt 679 Tsd. ha (darunter 654 Tsd. auf Niederungen und 25 Tsd. ha auf den Gebirgsflächen), während die reduzierte Fläche 245 Tsd. ha beträgt (darunter auf Niederungen 239 Tsd. ha und auf den Gebrigsflächen 6 Tsd. ha) . Abb. 3.

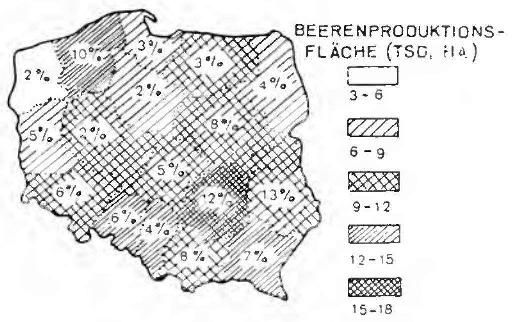

Abb. 3. Reduzierte Heidelbeere-Produktionsfläche in plinischen Wäldern und prozentischer Anteil der gewonnen Heidelbeeren in einzelnen Woiwodschaften (1963 - 1972)

Die Preiselbeerenfläche umfasst in Polen 1,6% Gesamtfläche unserer Wälder. Die reduzierte Fläche betragt - 104 Tsd. ha.

Seit ca 15 Jahren wurde durch den Lehrstuhl Forstnutzung Warschauer Landwirtschaftlicher Universität die Untersuchungen über Bestimmung der Rohstoffbase von Waldfrüchten /Heidel- und Preiselbeeren/ unter der Leitung des Authors in erwählten Waldobjekten /Oberförstereien/ geführt. Die Rohstofbase wird mittels der direkten Inventarisation ermittelt.

Die Rohstoffbase von Waldfrüchten in Polen

Auf Grund der durch das Forstwirtschaft-Forschungsinstitut angesammelten und durch das 'Las' - Unternehmen gelieferten Materialien wurden gemeinsam durch die Wissenshaftler und Praktiker die Rohstoffbase der wichtigeren essbaren Waldfrüchten im Lande erarbeitet. Sie besteht aus folgenden Pflanzenarten:

Heidelbeere (*Vaccinium myrtillus L*)	-	30,1 Tsd. Tonnen
Brombeere(*Rubus sp.*)	-	5,0 Tsd. Tonnen
Eberesche (*Sorbus aucuparia L.*)	-	4,7 Tsd. Tonnen
Schwarzer Holunder (*Sambucus nigra L.*)	-	3,7 Tsd. Tonnen
Schwarzdorn (*Prunus spinosa L*)	-	3,3 Tsd. Tonnen
Rosa(*Rosa sp*)	-	3,1 Tsd. Tonnen
Himbeere (*Rubus idaeus L.*)	-	2,2 Tsd. Tonnen
Weissdorn (*Crataegus sp. L*)	-	1,5 Tsd. Tonnen
Preiselbeere (*Vaccinium vitis-idaea L*)	-	1,3 Tsd. Tonnen
Moorbeere (*Vaccinium ulginosum L.*)	-	0,5 Tsd. Tonnen
Moosbeere (*Oxyoceus Quardripetalus Gilib.*)	-	0,5 Tsd. Tonnen
Erdbeere (*Fragaria vesca L*)	-	0,3 Tsd. Tonnen
andere	-	14,3 Tsd. Tonnen

Die Rohstoffbase sämtlicher Waldfrüchte in Polen wurde/beim mitteleren Ertrag/ für 70 Tsd. Tonnen geschätzt.

Waldfrüchtegewinnung in Polen

Die Waldfrüchtegewinnung durch das 'Las' - Unternehmen stieg systematisch in den Nachkriegsjahren. In Zeitraum von 1951-1985 betrug die mittlers jährliche Waldfrüchtegewinnung durch das 'Las' - Unternehmen 14,8 Tsd. Tonnen/darunter die Heidelbeere 9,7 Tsd. Tonnen. Im Jahre 1966 ist die höchste, Rekordgewinnung von Waldfrüchten erreicht, und zwar 39,4 Tsd.

Tonnen, darunter der Heidelbeere 26,0 Tsd. Tonnen. Allerdings in den 70-er Jahren begann eine deutliche Abnahme der Waldfrüchtegewinnung und jedes der 80-er Jahren betrug sie nicht einmal 10 Tsd. Tonnen jährlich. Abb. 4. Dies wurde durch ökonomische Verhältnisse (Arbeitskraftmangel im Dorfe) und ungünstige meteorologische Bedingungen (in den letzten Jahren häufige späte Fröste während des Blühens der fruchtbringenden Waldpflanzen) verursacht.

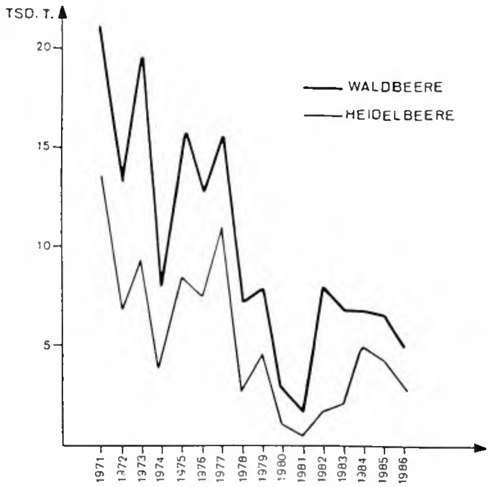

Abb. 4. Gewinnung der Waldbeeren/einschliesslich der Heidelbbere/durch die Einheiten des AS-Unternehmen in den Jahren 1971 - 1986

Der Anteil anderer Unternehmen in der Waldfrüchtegewinnung ist weiterhin verhältnismässig klein, da sie nur 1-2 Tsd. Tonnen jährlich, fast ausschliesslich Heidelbeere, einkaufen.

In den obigen Berechnungen wird die Gewinnung durch individuelle Sammler nicht berücksichtigt. Diesbezügliche Mengen werden durch den Autor für ca 20 - 25 % industrieller Sammlung geschätzt.

Export der Waldfrüchte in Polen

Der Export von Heidelbeeren hat in Polen eine lange Tradition, da schon vor dem Krieg nach England exportiert wurde. Nach dem Krieg erfolgte eine rasche Steigerung des Exports von Heidelbeeren und erreichte am Ende der 60-er Jahren 10 Tsd. Tonnen jährlich. Zur Zeit ist der Export der Waldfrüchte im Zusammenhang mit der niedrigeren Gewinnung kleiner.

Ausser der Heidelbeere werden aus Polen im frischen Zustand auch andere Waldfrüchte, aber in viel kleineren Mengen exportiert, und zwar: Preiselbeere, Rosefrüchte, Eberesche, Schwarzdorn, schwarzer Holunder, Weissdorn. Die Hauptabnehmer sind: BRD, DDR, Westberlin, England, Schwaden, Finland, Halland und Belgien.

Am Ende der 60-er Jahre begann der Export höher Mengen gefrorenen Heidelbeeren, meistens nach Vereinigtigen Staaten Amerikas. Es werden auch gewisse Mengen der getrockneten oder verarbeiteten Waldfrüchten (wie z. B. Pulpe, Säfte, Mosten) exportiert.

Die Waldfrüchte werden durch Vermittlung der Aussenhandelsunter nehmen, wie 'Agros', 'Rolimpex' und 'Hortex' esportiert.

II. Plantagemässiger Anbau der Fruchtbringenden Waldpflanzen in Polen

Die Entwicklung der grossen städtischen Agglomerationen zur systematischen und unabwendbaren Einschränkung der Fläche der fruchtbringenden Waldpflanzen, besonders der Heidelbeere. Sogar in fruchtbaren Jahren gibt es auf dem Markt ein Mangel an Waldfrüchte, wie Erdbeere oder Moosbeere.

In diesem Zusammenhang begann die Entwicklung der künstlichen Vermehrung und des Anbaus der Waldpflanzen auf den Plantagen. Dabei wird eine teilweise Mechanisierung der Arbeiten sowie der Düngung und Melioration der Plantagen möglich. Bisher sind in Polen die Versuche mit dem Anbau der hohen (amerikanischen) Heidelbeere, Zuchtrose und schwarzer Aronie besonders weit fortgeschritten. Verhältnismässig kleiner sind die Plantagen der Moosbeere, Preiselbeere und Hasel.

Der Anbau der hohen (amerikanischen) Heidelbeere

Der Anbau der hohen Heidelbeere wurde in den Vereinigten Staaten Amerikas am Anfange des XX. Jahrhunderts begonnen. Zur Zeit gibt es in den Vereinigten Staaten über 8000 ha hohen Heidelbeereplantagen. In Europa begann der Anbau der hohen Heidelbeere in Holland und dann seit dem Jahr 1924 in Polen (von der Initiative von Prof. Hoser). Allerdings war diese wertvolle pflanze nur im kleinen Masstab angebaut. Erst nach dem Krieg wurden einige Sorten der hohen Heidelbeere vom Prof. S. A. Pieniazek aus USA bezogen. Die Frucht der hohen Heidelbeere enthält zweimal höhere Zuckermengen, aber kleine Mengen der Mineralsalze und Vitamin C im Vergleich mit der gewöhnlichen Heidelbeere. Die Büsche der ersteren lassen sich nur mit grossen Schwierigkeiten vermehren. Sie vermehren sich am besten auf leichten, humusreichen Böden und sind empfänglich auf längere Dürre. Die Plantagen der hohen Heidelbeere werden durch die Landwirtschaftliche Universität in Warshau (Dr. K. Pliszka), durch das 'Las' - Unternehmen und durch den Author experimentelt geführt. Die Untersuchungen bestätigten einen hohen Nährwert der hohen Heidelbeere. Zur Zeit befassen sich mit dem Anbaü dieser Pflanze meistens Gartenbaubetriebe. Die gesamte Anbaufläche der hohen Heidelbeere beträgt gegenwärtig in Polen ca 200 ha.

Schwarze Aronia (Aronia melanocarpa Elliot.)

Schwarze Aronia stammt aus den östlichen Regionen der Vereinigten Staaten Amerikas. Nach ihrer Einführung in Europa wurde sie anfänglich als dekorative Pflanze angebeut. Erst I. W. Mitschurin hat ihren gartenbaulichen Wert bemerkt. Die sowjetischen Forschungen haben festgestellt, dass die Aronia-Früchte 1,5 - 2,0 mal mehr mineralische Verbindungen als andere Früchte enthalten. Sie enthalten auch hohe Mengen von Vitamin P /2500 - 3000 mg%/ und zeichnen sich mit den Bakterien- und Fungizideigenschaften. Sie sind auch in der Behandlung der Strahlungskrankheit effektiv. Die Aronia-Plantagen können auf weniger fruchtbaren Böden angelegt werden.

Die Untersuchungen über Aronia-Anbau in Polen werden durch das Forstwirtschafts-Forschungsinstitut (R. Ostalski und M. Cichowicz) feführt. Zur Zeit gibt es in Polen ca 600 ha Aronia-Plantagen.

Zuchtrose (Rosa sp.)

Am Beginn der 50-er Jahre wurde entschieden, die Plantagen der fruchtbringenden Rose anzulegen. Die Plantagen waren anfänglich durch das 'Las' - Unternehmen geführt. Die Untersuchungen über die Rosenfrüchten-qualität wurden gemeinsam durch das Forstwirtschafts-Forschungsinstitut und die Warshauer Landwirtschaftliche Universität durchgeführt. Die Untersuchungen bestätigten einen hohen Nährwert der Zuchtrosefrüchte und einen hohen Vitamin C - Gehalt in denselben. Für den Plantageanbaü wurde runzelige Rose wegen Grösse und hoher Erträge der Früchte und der kleinen Bodenforderungen gewählt. Die Anbauweise der runzeligen Rose wurde ziemlich gut beherrscht. Die stratifizierten Samen werden in März auf den im Herbst vorbereiten Beeten in der Menge von ca 0,5 kg per 1 Ar gesät. Sämlinge werden im Herbst in einer Baumschule im Abstand von 10 x 15 cm x 10 x 15 cm gepflanzt. Die Rosen werden auf der Plantage im Abstand von 2,5 z 1,5 m oder 2,5 x 1,0 m gepflanzt.

Am Anfang der 70-er Jahre hatte das 'Las' - Unternehmen ca 600 ha Plantagen der runzeligen Rose (*Rosa rugosa Thunb.*). Leider wurde letztens die Plantagenfläche eingeschränkt und zur

Zeit gibt es nur ca 200 ha Roseplantagen.

Moosbeere (Oxycoceus macrocarpus Pers.)
Die ersten Moosbeereplantagen wurden in dem Vereinigten Staaten Amerikas im Jahre 1833 (in Boston) angelegt. In Europa wurden die ersten Plantagen in Deutschland angelegt (1871). Die Moosbeere ist eine lichtliebende Pflanze und ist für sehr feuchte und sauere Böden tolerant. Die Früchte vertragen die Temperatur bis - 18°C. Die erste Plantagen in Polen wurden im Jahre 1963 durch das Institut für Meliorationswesen und Grünlandforschung gemeinsam mit dem Institut für Gartenbauwirtschaft angelegt. Die Setzlinge wurden aus den USA importiert und auf den ausgebeutenen Torfflächen gepflanzt. In den Jahren 1979 - 1980 betrug der mittlere Mossberenertrag ca 8 Tonnen/ha.

Preiselbeere (Vaccinium vitis-idaea L.)
Die ersten Zuchtarbeiten mit der Preiselbeere wurden in Schweden begonnen (1966). Im Jahre 1969 wurden die ersten Preiselbeerenplantagen in Finland angelegt. Weitere Preiselbeerenplantagen enstanden im Jahre 1978 in der BRD (Hannover). Es gibt drei Vermehrungsweisen der Zucht-Preiselbeere:

- Übertragung aus natürlichen Standorten,
- Vermehrüng durch Samen,
- Vermehrung durch Spress- und Rhizomstecklinge.

Das beste Substrat ist Torf. Im Jahre 1977 wurden die Preiselbeeresetzlinge aus der BRD importiert (Koralle-Sorte). Im Jahre 1981 wurden von einem Busch im Mittel 109,3 g Früchte gesammelt /9,12 T/ha/.

Andere fruchtbringende Waldpflanzen
Im nördlichen Teil Polens werden seit vielen Jahren der Plantageanbau des Sanddornes (*Hippophäe rhamnoides L.*) und in den südöstlichen Regionen des Landes wird die grossfrüchtige Hasel angebaut, die letztere in einer Privatbaumschule.

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ZUSAMMENFASSUNG

Die Hedelbeere gehört in Polen zu den beliebtsten Waldfrüchten. Sie tritt in 11 % Gesamtfläche unserer Wälder auf. Mit der Gewinnung von Waldfrüchten auf den Natürlichen Standorten befasst sich in erster Linie das Nebenwaldproduktionsunternehmen 'Las'.

Das Reichtum und Rohstoffbase von früchtbringenden Waldpflanzen wird mittels der Erhebungs-, direkten und statistischen Inventarisation ermittelt. In den Jahren 1962 - 1963 wurde die Inventarisation der Heidelbeerenflächen in den Staatsforsten durch das Forstwirtschafts-Forschungeinstitut bei der finanziellen Unterstützung des 'Las' - Unternehmens durchgefürt. Die Erträge auf den Versuchflächen wurden auf Grund der 5-Gradskala: (1 - sehr schwach, 2 - schwach, 3 - mittelmässig, 4 - gut, 5 - sehr gut) ermittelt.

Es wurde ein signifikanter Zusammenhang zwischen dem Reichtum (y) der Beerenflächen und dem Ertragsfähigkeitsgrad (x) nachgewiesen. Es wurden die Regressionsgleichungen für:

- die Niederungs-Beerenflächen $y = 27{,}7\,x^2 - 0{,}14\,x + 0{,}02$
- die Gebirgs-Beerenflächen $y = 35{,}40\,x^2 + 22{,}50 + 3{,}58$ berechnet.

S. Glowacki (1967) hat die Klassifikation von Heidelbeerenflächen nach den folgenden Merkmalen erarbeitet: Beerenflächetüp, Schlussweise, Höhe- und Deckungsklassen.

In Polen wurde die Rohstoffbase der wichtigeren essbaren Waldfrüchte für 70 Tsd. Tonnen (darunter Heidelbeeren 30,1 Tsd., Brombeeren 5,0 Tsd., Himbeeren 2,2 Tsd., Preiselbeeren 1,5 Tsd., Moosbeeren 0,5 Tsd.) geschätzt.

Im Zeitraum von 1951 - 1985 betrug die mittlere jährliche Waldfrüchtegewinnung dürch das 'Las' - Unternehmen 14,8 Tsd. Tonnen (darunter 9,7 Tsd. Tonnen Heidelbeeren).

Der Export der Waldfrüchte erfolgt meistens im frischen Zustand. Die Hauptabnehmer sind BRD, Westberlin, USA, Schweden u. a. Zur Zeit beträgt der Export ca 3 - 5 Tsd. Tonnen jährlich.

In den Nachkriegsjahren hat sich in Polen der Plantagenbau der fruchtbringenden Waldpflanzen entwickelt. Die ersten Plantagen wurden mit der runzeligen Rose angelegt (zur Zeit ca 200 ha). Dünamisch entwickeln sich die Plantagen der hohen (amerikanischen) Heidelbeere (150 - 200 ha) und schwarzer Aronia (ca 600 ha). Die wirtschaftlichen Versuchsplantagen wurden auch der Moosbeere und Preiselbeere geführt.

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HEAVY METAL POLLUTION OF OMBROTROPHIC BOGS IN THE KRISTIANSAND AREA, VEST-AGDER, NORWAY

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The heavy metal contents of peat and plant material in twelve ombrotrophic bogs in the Kristiansand area are analysed (i.e. Ni, Pb, Cu, Co, Cd and Zn). The sampling sites are located at increasing distances from the smelting factories in the area and in accordance with the prevailing wind directions. The nickel concentration in the surface layer of the peat ranges from 40 ppm dry weight at a distance of 12 km from the nickel smelting factory in the city of Kristiansand, to 532 ppm at a distance of 3 km from the smelter. The lead concentration increases from 120 to 550 ppm. Similar patterns are found for cobalt and copper. The cadmium concentration is generally high in the Kristiansand area, and this is reflected in our material. However, the amount of cadmium is higher in the inland areas. In general, the concentration of the different heavy metals decreases downward in the peat.

Key words: heavy metal pollution, ombrotrophic bogs, nickel, cobalt, copper, lead, zinc, cadmium.

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Most of the heavy metals are rare and are found only in small concentrations in nature. The impact of industrial pollution on the environment is a serious problem, however, and heavy metal contamination of the soil, peat, water and plant material is rapidly increasing. Different methods of monitoring heavy metal pollution can be used, and in this paper an indirect control of airborne heavy metal pollution through the application of chemical analyses of ombrotrophic bogs is discussed.

Ombrotrophic bogs are well suited as study objects because they receive all their nutrition from the atmosphere. Furthermore, the bogs act like chemical filters, since most of the heavy metals are strongly sorbed to organic matter by so-called complex binding (Kononova 1966, Rühling & Tyler 1970, Bergseth & Stuanes 1976, Bergseth & Krogstad 1979, Livett et al. 1979, Tummavuori & Aho 1980).

Several investigations of the heavy metal content of ombrotrophic bogs have been carried out in Northern Europe: in Scandinavia by Hvatum (1965, 1971, 1974, 1984), Sillanpää (1972), Pakarinen & Tolonen (1977a, 1977b), Pakarinen et al. (1981, 1983), Damman (1978), Aaby & Jacobsen (1979), Aaby et al. (1979); in Great Britain by Livett et al. (1979); in West Germany by Wandtner (1981). From North America the study of Pakarinen & Gorham (1983) can be mentioned. The results of these investigations show that urban areas have higher concentrations of heavy metals than more remote areas, and the upper peat layers a higher content than the lower ones. In Scandinavia there is a gradient for many heavy metals from north to south, where the highest concentrations are found in peat in the southern parts, which have more direct contact with air pollution from the big industrial areas of the European Continent and Great Britain.

The present paper is based on a study carried out at the Agricultural University of Norway (Fjeldstad 1986), with the co-authors as scientific advisers. The Kristiansand area was chosen because of the heavy metal pollution from the smelting industry there, and because for a long time this part of Norway has been receiving longe-range transported air pollutants. In addition, local small industry, traffic and heating plants contribute to the total amount of air pollution.

The main questions in the investigation were the following:

- How much of the heavy metal content in the bogs is due to local sources, and how much to longe-range transport?

-How important are the wind relationships for the local distribution of the heavy metals?

-How strongly are the heavy metals bound in the bogs, and do they have historical implications?

-Is the species composition of the vegetation affected by the heavy metal content in the bogs?

THE INVESTIGATED AREA

Kristiansand and surroundings are shown in Fig. 1. All localities are situated in the muncipalities of Kristiansand and Vennesla, Vest-Agder. The topography is rugged, with pronounced crevice valley systems. The hills often have poorly developed soil with oligotrophic *Pinus sylvestris* and *Quercus robur* forests with an understorey vegetation of *Calluna vulgaris*, *Vaccinium myrtillus* and other ericaceous plants. Depressions and valley bottoms have deeper soils developed on marine clay, moraine deposits, glaciofluvial deposits, etc. These areas are usually dominated by *Picea abies* forests, but thermophilous deciduous forests and agricultural areas are also found. Furthermore, there are some depositions of organic soils such as peat (Låg 1957, Andersen 1960).

The bed rocks of the Kristiansand area belong to the southern Norwegian Precambrian district. The dominant ones comprise of different types of gneisses, but amphibolite and some minor areas of marble etc. can also be found (Falkum 1977, 1982). Most of the bed rocks are hard, and weather slowly.

The outermost parts of the Kristiansand Fjord (at Oksøya) have an annual precipitation of about 1100 mm, but 14 km inland (at Kjevik) the precipitation increases to about 1300 mm (Trægde 1977). The maximum precipitation is in the autumn, but there are considerable local variations. Wind from the northeast dominates in winter, and from the southeast in summer (Det norske meteorologiske institutt 1986). The prevailing wind directions are visualized in Fig. 2.

The bog frequency increases with the higher amount of precipitation as a function of altitude. Highest frequencies of

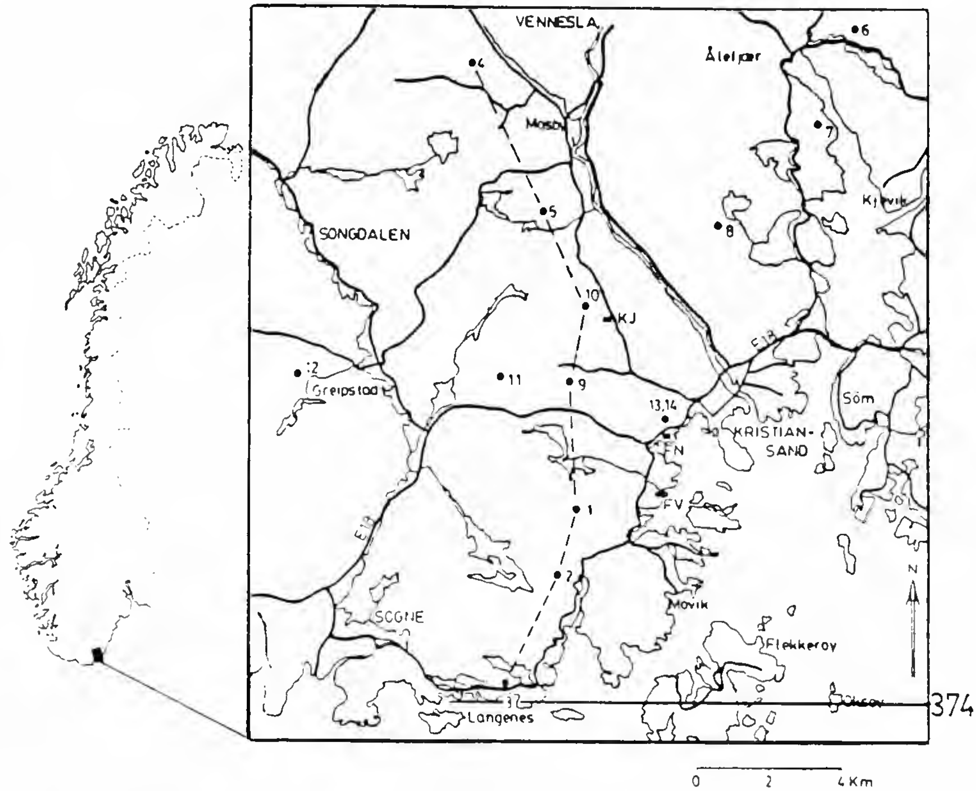
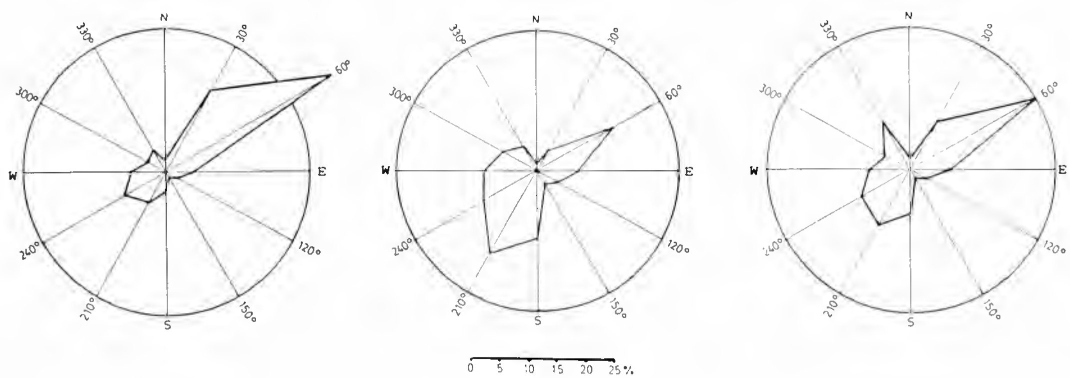


Fig 1. Map showing location of Kristiansand and surrounding area. The dashed line indicates the gradient presented in the diagrams. Distances from the coast are measured from the horizontal line 374 (UTM grid 32 V MK). Abbreviations (see text): FN = Falconbrigde Nikkelverk A/S, FV = Fiskaa Verk A/S, KJ = Kristiansand Jernstøperi. The numbers indicate the position of the investigated localities



Winter (Desember - February)
8.5% quiet weather

Summer (June - August)
5.6% quiet weather

Year (average)
7.3% quiet weather

Fig. 2. Frequencies of different wind directions measured at Kjevik Meteorological Station

bog areas are found around 400 m above sea level. Bogs cover about 2-3% of the land area in the lower part of Vest-Agder county, but bog areas increase to about 15% at 300-400 m above sea level (Moen & Pedersen 1981). The bogs comprise a total of about 360 km2 of Vest-Agder county (about 8.5% of the land area).

The bog vegetation is characterized by oligotrophic species with affinity to ombrotrophic and poor minerotrophic bogs (cf. Table 1). Dominant species in the field layer are *Erica tetralix*, *Myrica gale*, *Oxycoccus quadripetalus*, *Narthecium ossifragum*, *Molinia caerulea*, *Scirpus cespitosus*, *Eriophorum angustifolium*, *E. vaginatum and Carex pauciflora*. The bottom layer is dominated by *Sphagnum* spp., namely *S. rubellum*, *S. magellanicum*, *S. tenellum*, *S. imbricatum*, *S. papillosum*, *S. cuspidatum* and *S. fallax*. The investigated bogs were all at least 130 cm deep.

SOURCES OF HEAVY METAL POLLUTION

Smelting factories seem to be responsible for most of the heavy metal pollution in the Kristiansand area. The positions of the most important metallurgic factories are indicated in Fig. 1. These factories are:

Falconbridge Nikkelverk A/S. A nickel refinery and source of local pollution for several decennia. This refinery has caused damage to the pine forests and the epiphytic lichen vegetation (cf. Egerhei 1978). Emissions of SO_2, Ni, Cu and Co.

Fiskaa Verk. Produces ferrosilica and electrode material. Emissions of SO_2, SiO_2 particles, Fe, Zn and Cr.

Kristiansand Jernstøperi A/S. Iron smelting. High emissions of Fe, Zn and Cr.

Other sources of aerial transport of heavy metal pollutants are long-range transported pollution from England and the European Continent and fuel emissions from traffic (the latter of minor importance compared with industrial pollution).

METHODS

Two sites were examined at each of the twelve investigated bogs. Relevées (1 m^2) were analysed using the Hult-Sernander-Du Rietz scale. Peat was sampled in two vertical profiles, 10 to 60 m apart, but never nearer the edge of the bogs than 10 m. The samples were taken at 5, 10, 20 and 50 cm below the surface.

The selection of ombrotrophic bogs was difficult because the typical convex shape was missing. The main criteria for the selection of sites were based on the knowledge of the typical ombrotrophic bog communities.

The Ni concentration of the peat was determined in all samples, while Pb, Co, Cd, Zn, Cu, Fe and Cr were analysed in only some samples. Mosses and vascular plants were analysed for Ni, Pb, Cu, Zn and Cd at only one site in each bog. Two humus samples from the top soil about 400 m north of Falconbridge Nikkelverk A/S (sites 13 and 14) were also analysed. All the elements were analysed using flame atomic absorption spectrophotometry. The concentrations are given in ppm air dry matter. The chemical analyses were carried out at the Agricultural University (Ås). The heavy metal accumulation in the bogs is concentrated in the uppermost 20 cm (cf. Fig. 4). In this part of the profile the heavy metal content in the samples is more dependent on precise measurement of depths than it is at deeper depths. Because the sample depth varies somewhat within 5 cm, there is a chance that the two profiles in each bog do not show the same values.

The heavy metal contents of each sample layer of the bogs were tested using Multiple Regression Analysis (see standard textbooks, e.g. Orlóci 1978), and an attempt was made to correlate

Table 1. Relevées from the bog vegetation of the different sites. Coverage in accordance with the Hult-Sernander-Du Rietz scale

Locality	1		2		3		4		5		6		7		8		9		10		11		12	
Sample site	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
Total cover C layer	8	6	7	8	7	7	8	9	9	9	8	8	8	7	8	6	9	9	6	7	8	8	10	10
Total cover D layer	10	10	10	10	10	10	10	10	10	10	7	10	6	9	9	10	3	2	10	10	10	8	7	7
FIELD LAYER C																								
Erica tetralix	5	5	5	5	5	4	5	5	5	5	5	5	5	5	5	5	5	5	5	5	4	5	3	3
Myrica gale	1	3	2	2	4	4	2	2	2	4	3	3	3	2	4	4	1	2	2	4	1	2	1	1
Calluna vulgaris	.	.	1	1	2	3	3	1	2	3	3	1	3	4	2	2	3	4	.	.	4	1	.	.
Oxycoccus quadripetalus	3	2	4	4	3	2	.	.	4	4	2	4	2	2	3	2	1	1	2	3	.	.	.	.
Andromeda polifolia	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	1	.	.	.	.	.	.
Betula pubescens	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Narthecium ossifragum	3	3	.	.	.	.	4	5	3	3	3	4	.	3	3	.	5	4	5	.	2	5	5	5
Scirpus caespitosus	5	3	.	.	.	.	1	2	.	.	.	.	2	2	5	4	1	2	4	.	3	2	5	2
Molinia caerulea	.	.	1	2	1	1	1	1	5	3	5	4	.	.	.	.	2	2	.	.	.	2	.	.
Eriophorum augustifolium	1	1	2	3	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Eriophorum vaginatum	.	.	1	.	2	1	5	3	.	.	.	.	.	.	.	.	.	.	2	5	2	1	.	.
Drosera rotundifolia	.	.	3	2	.	.	.	.	.	.	.	1	.	.	.	.	.	.	1	1	1	.	2	1
Carex spp.	.	.	.	.	.	.	.	.	.	.	.	.	2	2	1	1	.	.	1	.	.	.	.	.
BOTTOM LAYER D																								
Sphagnum rubellum	.	1	5	5	2	2	3	3	2	4	1	2	1	1	3	3	2	.	.	.	1	1	1	2
Sphagnum magellanicum	.	4	2	2	.	5	5	5	.	.	5	5	5	5	5	5	2	.	5	5	5	5	5	5
Sphagnum recurvum	.	2	.	.	5	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.
Sphagnum tenellum	5	5	.	.	.	.	.	.	.	.	.	.	2	1	.	.	.	.	4	4	.	.	.	.
Sphagnum imbricatum	.	.	3	4	.	.	.	.	2	2	.	.	4	3	.	.	.	.	4	4	.	.	.	.
Sphagnum papillosum	.	.	3	2	2	4	.	.	5	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sphagnum cf. fallax	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	4	1	3	.	.	4	3	3	2
Aulacomnium palustre	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Polytrichum strictum	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

them with distance from pollution sources, frequencies of wind in relation to these sources, distance to coast and elevation. Correlations between heavy metals were calculated to estimate the co-variation. The calculations were run on a computer, using the program package SAS (Statistical Analyses System) and the procedures STEPWISE and GLM.

The nomenclature follows Lid (1985) for vascular plants, Nyholm (1956-69) for musci.

RESULTS

Nickel. The Ni contents of analysed samples from peat 5 cm and 10 cm deep, vegetation (ericaceous plants, graminids, herbs) and *Sphagnum* material are presented in Fig. 3. The concentrations are highest around the main source of nickel pollution, i.e. Falconbridge Nikkelverk A/S. The values for locality 1 are 533 ppm and 330 for peat samples from 5 and 10 cm depths, respectively. The moss material, too, has a high Ni content (62 ppm). All values diminish towards the interior, and are also low at the coast. The Ni con-

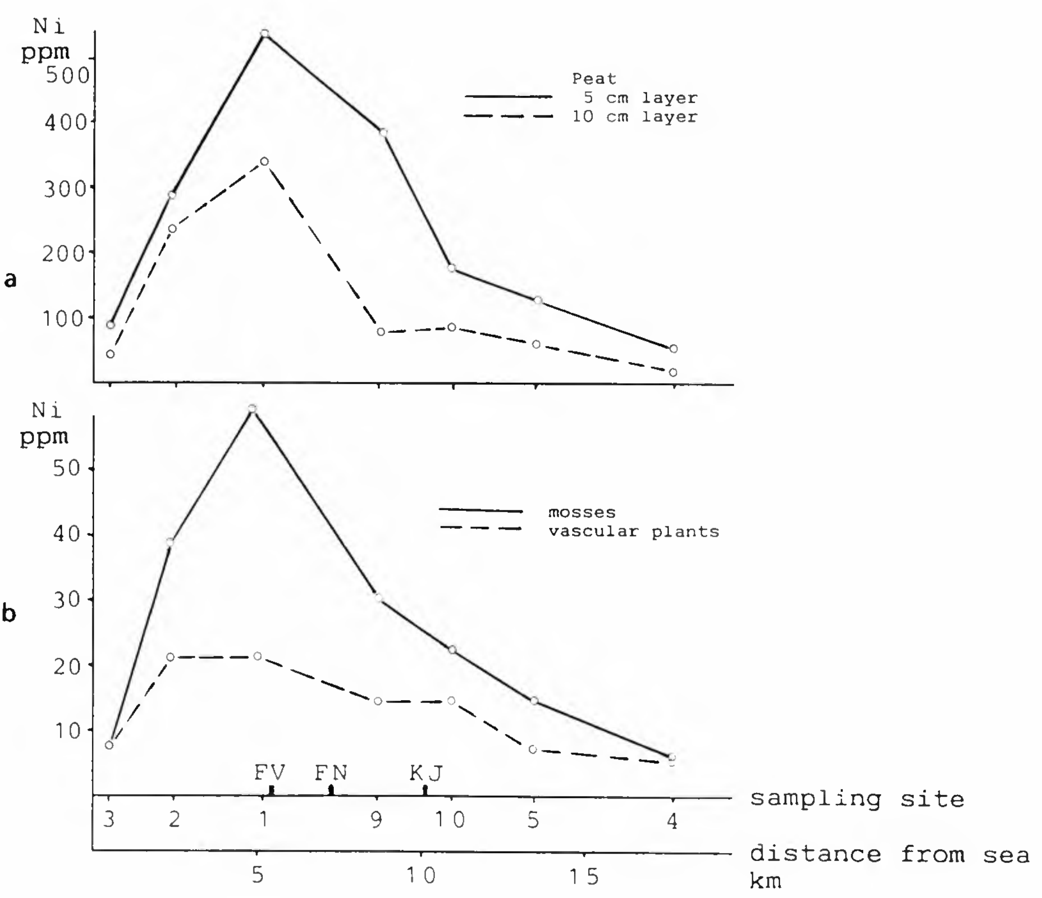


Fig. 3. Ni content at different localities for (a) peat samples and (b) plant material. For location of the sites, see Fig. 1

centration in peat drops abruptly below 20 cm in all localities (Fig. 4).

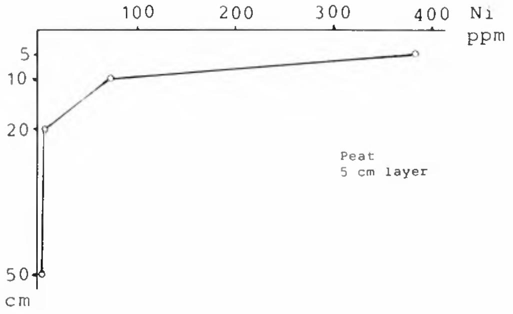


Fig. 4. Distribution of Ni downwards in the peat profile, exemplified from locality 9. All other profiles show the same pattern

Zinc. The Zi content of peat and plant material is presented in Fig. 5. There is a general increase in the values from coast to inland (in peat at 5 cm, the content varies from 70 ppm to ca. 140 ppm). The high value at locality 9 (162 ppm) is probably the result of local pollution from Kristiansand Jernstøperi A/S. The Zn content downwards in the peat profile shows a similar pattern to the Ni content.

Lead. The Pb content of peat and plant material shows a similar trend to Zn (Fig. 6), with lowest values near the coast (135 ppm at 5 cm) and higher values in the inland areas (265 ppm at 5 cm). Here, too, there is a very high local value around Kristiansand Jernstøperi A/S (565 ppm). The Pb content drops abruptly beyond 20 cm downwards in the peat profile.

Copper. The Cu content is very high around Falconbridge Nikkelverk A/S (320 ppm at locality 9, peat at 5 cm), but is relatively low in the interior parts (Fig. 7). There is low Cu content beyond 10 cm in the peat profiles.

Cobalt. The Co content is high around Falconbridge Nikkelverk A/S (between 10 and 15 ppm), but decreases in the interior parts (Fig. 8).

Cadmium. The Cd content is relatively high in the whole area, but shows some fluctuation (Fig. 9). The highest value is found near Kristiansand Jernstøperi A/S (about 12 ppm).

Reference sites. Two humus samples were analysed adjacent to Falconbridge Nikkelverk A/S (localities 13 and 14, in Fig. 1). The heavy metal content here has extremely high values of Ni and Cu (cf. Table 2). The Ni and Cu contents of locality 13 are as high as 13 750 ppm and 5 600 ppm, respectively.

DISCUSSION

Parameters such as distance from the pollution sources, frequency of wind direction, precipitation pattern and distance from the coast are important in reading the heavy metal content of the bogs. The deposition of long-range transported air pollutants (e.g. Pb) increases as the annual precipitation increases from coast to inland (Steinnes 1983). Distance from the coast is therefore used as an independent relative variable for increasing precipitation and deposition of longe-range air pollutants, because data on precipitation for each bog are not available. Table 3 shows the variables which can best explain the variation of the heavy metal content of the bogs.

Nickel. In addition to the long-range transported air pollutants brought to the southern part of Norway, the Kristiansand area also has local pollution sources. Falconbridge Nikkelverk A/S is the main Ni polluter of the area. Ni production here has existed for about 70 years, and the annual production is now about 40 000 tons. Besides Ni (40%) the imported ore also contains Cu (35% Co (1,2%) and Pb (130 ppm).

In the southern parts of Norway the background values of Ni in the top layer of peat are measured at about 4 ppm at the coast (Lista), and 3 ppm inland at Åmli (Hvatum 1984). In the investigated area the lowest value found in the top

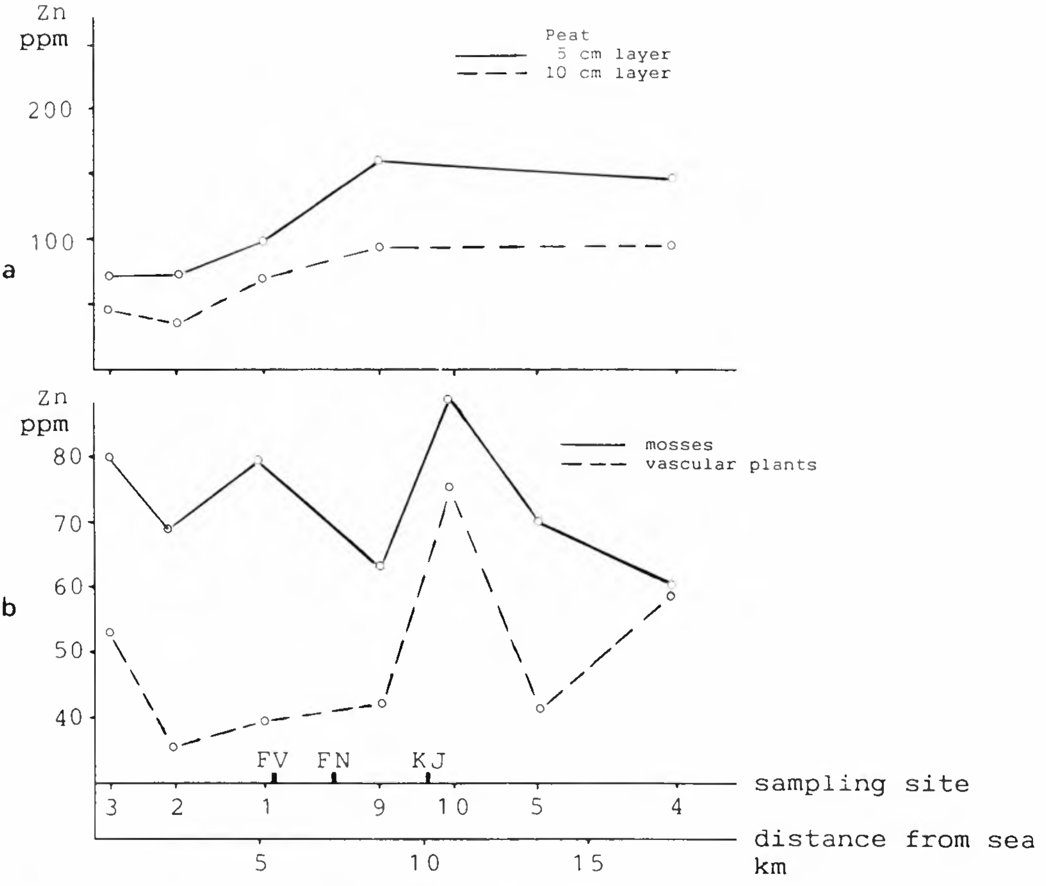


Fig. 5. Zn content at different localities for (a) peat samples and (b) plant material. For location of the sites, see fig. 1

layer was about 50 ppm, i.e. more than 10 times above the background level.

The Ni content of the top layer of the bogs increases significantly towards the pollution source, i.e. Falconbridge Nikkelverk A/S (cf. Table 3). The two soil samples from the humus layer (localities 13 and 14) about 400 m north of Falconbridge Nikkelverk A/S have a Ni content of 7 000 and 13 750 ppm, respectively (cf. Table 2).

The frequencies of wind direction with regard to Falconbridge Nikkelverk A/S also show significant values. Average frequencies based on the year, the summer and the winter are treated statistically by Multiple Regression Analysis. The winter values (December-February) seem to explain the Ni distribution best, in addition to the distance from the source. This is probably due to temperature inversions in the wintertime. NILU (Statens forurensningstilsyn 1985) has registered this tendency in many cities where the Pb and SO_2 concentrations in the air are about twice those of the summer values.

In all except one of the bogs the highest Ni concentrations are in the top layer (5 cm) of the peat; the Ni concentrations decrease downwards in the profile to a minimum (3-5 ppm) at 20 to 50 cm

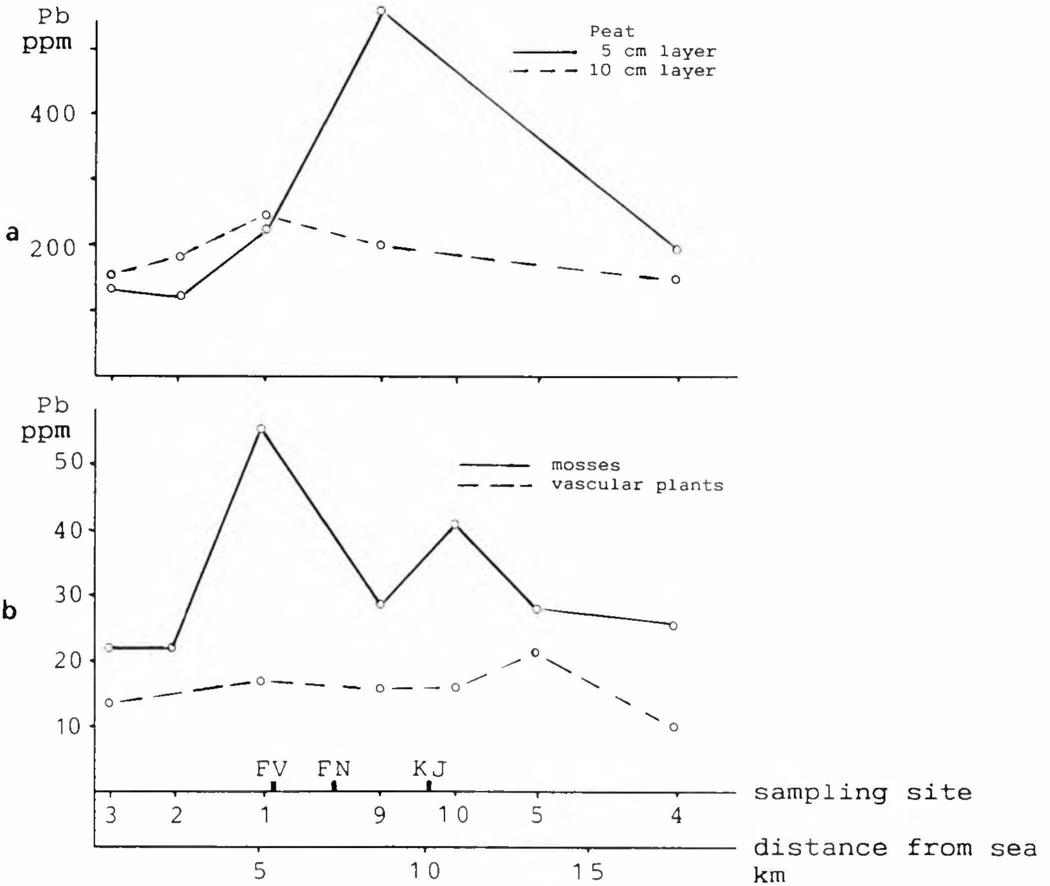


Fig. 6. Pb content at different localities for (a) peat samples and (b) plant material. For location of the sites, see fig. 1

depths (cf. Fig. 3). Ni is almost totally absorbed in peat in low concentrations (Tummavuori & Aho 1980). The same results (Rühling & Tyler 1970) are found in experiments on the moss *Hylocomium splendens*. The strong gradients found in the studied bogs are in good agreement with this.

The distribution pattern of Ni in vegetation reflects the Ni content in the bogs (Table 4, Fig. 3). Statistically, the same variables are significant, but the Ni level is about 1/10 of the concentration found in the upper peat layer (5 cm). The Ni content in mosses is above the same level found in vascular plants. The less polluted the bogs, the smaller the difference, similarly, the more polluted the bogs the greater the difference. In almost unpolluted bogs, Hvatum (1984) found higher Ni concentrations in vascular plants (about 2 ppm) than in the moss *Sphagnum fuscum* (about 1 ppm). The lowest values registered in the area are 5 ppm in mosses and 3.5 ppm in vascular plants (locality 4).

The reason for these differences between mosses and vascular plants probably lies in their anatomical structure. The tissue in the moss leaves consists of only one cell layer. All the cells therefore come in good contact with the polluted

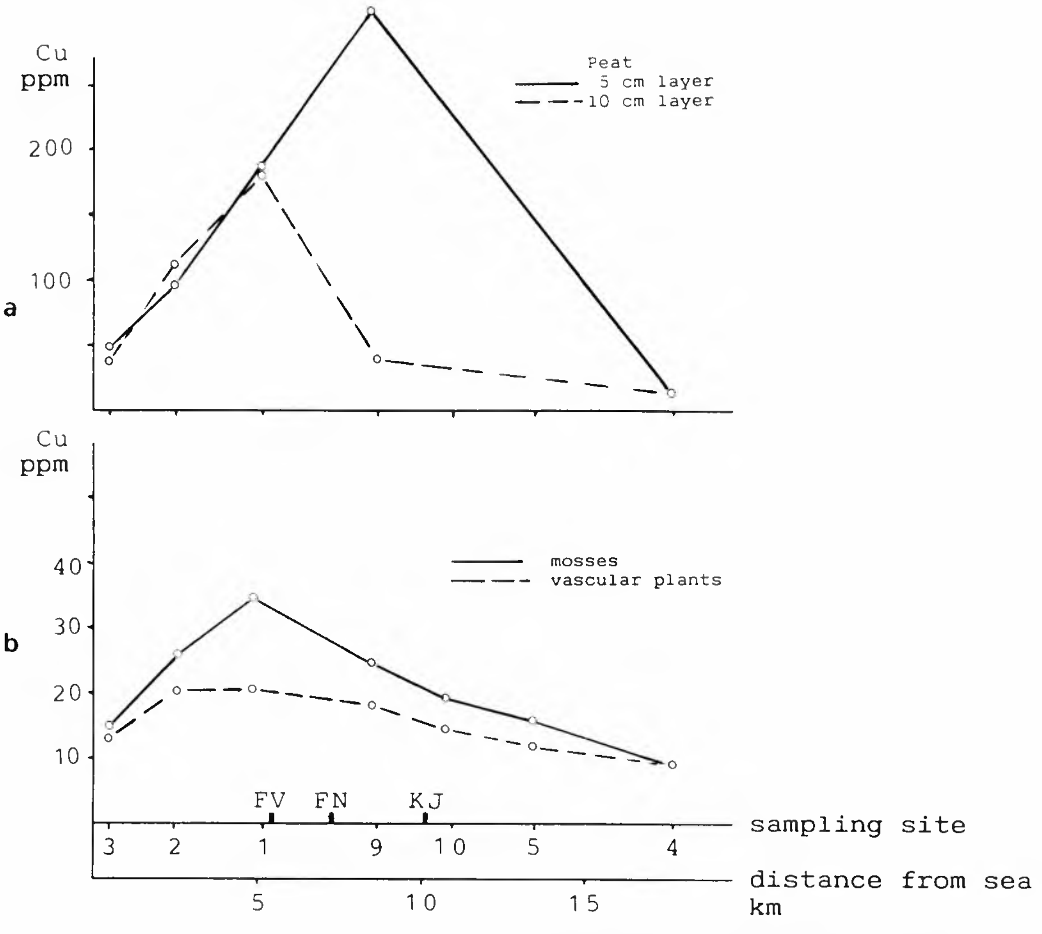


Fig. 7. Cu content at different localities for (a) peat samples and (b) plant material. For location of the sites, see fig. 1

air and precipitation and the metals are directly absorbed. Furthermore, the vertical water transport is rather limited (Rühling 1985). Vascular plants, however, have roots and tissue for vertical transport of water and nutrients. The leaf tissue is relatively thick and is protected by cuticula. Nutrients can then be selectively absorbed and the cells are less exposed to the polluted air and precipitation.

The heavy metal pollution in the Kristiansand area probably has not lasted long enough to have caused the evolution of more heavy metal-tolerant plant varieties. Ernst (1982) believes this process has changed the plant communities in areas with strong heavy metal pollution over several years. In natural heavy metal-polluted soils such a process has been recognized in experiments with *Calluna* cuttings (Kusel-Fetzmann 1982).

Zinc. Zn concentrations in the bogs are positively correlated with the distance from the coast (Table 3). This distribution is probably due to the increasing precipitation the more inland one goes. The Zn content is about 70 ppm at the coast and between 130 and 140 ppm in the northern part of the area. The high concentrations at locality 9 (up to

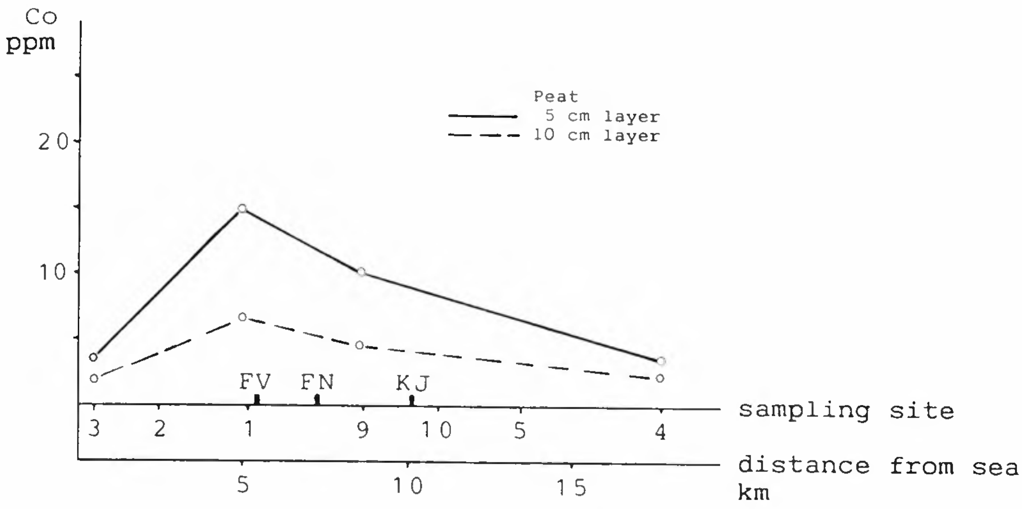


Fig. 8. Co content at different localities (peat samples only). For location of the sites, see fig. 1

180 ppm) are probably a result of pollution from Kristiansand Jernstøperi A/S.

Zn is more poorly absorbed in peat than Pb, Cu, Ni, Cd and Co (Tummavuori & Aho 1980). In their experiments, Livett et al. (1979) found that neither Pb nor Cu leached out of peat when washed with sulphuric acid (0.05 M), while 25% of the Zn content was leached out.

The concentration of Pb in peat is higher than the concentration of Zn in spite of Zn being twice as high in the precipitation (Statens forurensningstilsyn 1985). Along with a high content of sulphate, Zn might easily be exposed to leaching and transfer in the peat. Steinnes (1985a, b) suggests that in areas near the sea, cations of Mg and Na from the sea will exchange Zn^{2+} in mosses, particularly in extremely exposed coastal areas.

Zn concentrations in bogs have the highest values in the top layer. As Zn is a nutrient for plants, active uptake by the vascular plants may diminish the Zn leaching.

Lead. The Pb content in peat is a result of both longe-range transported air pullutants and local sources. The most important local source is exhaust from cars and the Ni-smelter, Falconbridge Nikkelverk A/S. The bogs near Falconbridge Nikkelverk A/S were used in the statistical analysis as an independent variable on local Pb pollution, and those away from coast as an independent variable on increasing precipitation. Both of the variables resulted in significant values (Table 3), and this is illustrated in Fig. 10. The 'N' line indicates the expected Pb content in the top layer of peat for a similar area with only long-range transported air pollutants (Hvatum 1984, Steinnes 1985 a,b); the scratched area indicates the local Pb contribution.

The background values of Pb in peat (1963 and 1979) in this part of Norway were registered by Hvatum (1984) as 73-76 ppm at Lista (on the coast), where the annual precipitation is about the same as that found at locality 3. In humus samples, Solberg & Steinnes (1983) found that a Pb content of more than 200 ppm at 20-30 km from the coast was the result of high annual precipitation. A similar tendency was found at localities

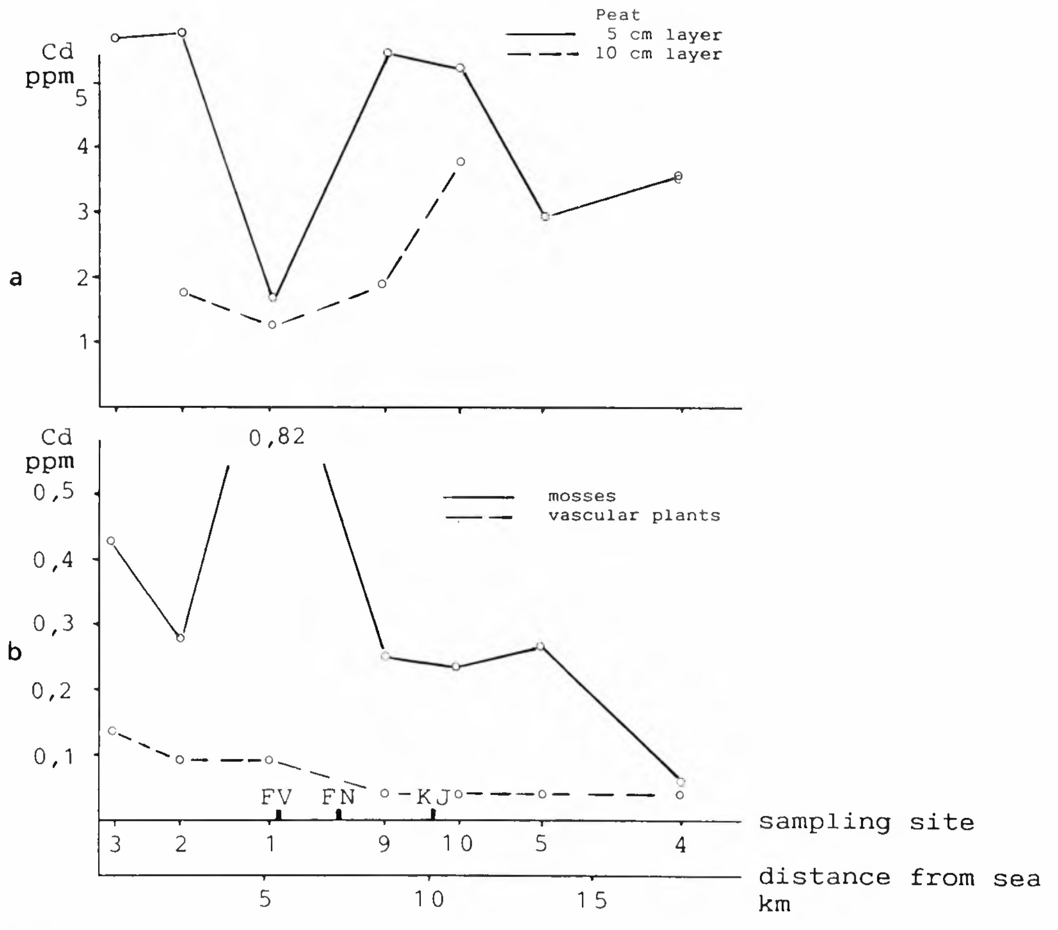


Fig. 9. Cd content at different localities for (a) peat samples and (b) plant material. For location of the sites, see fig. 1

4 and 6, with a Pb content of 190 and 265 ppm.

Lead in the peat profile almost follows the Ni distribution in the most polluted bogs, with the highest concentrations in the top layer (5 cm deep). In the less polluted bogs, the maximum concentration is found deeper in the profile, at 10 to 20 cm depths. Tyler (1972), Pakarinen & Tolonen (1977), Damman (1978), Pakarinen et al. (1983), and Pakarinen & Gorham (1983) have found maximal concentrations at 20 to 30 cm depth in the bogs. The water table is believed to be the main factor for this distribution. However, Hvatum (1984) found maximal concentrations in the upper 5 cm layers of the bogs, but this difference may have been caused by different ways of sampling (on or beside hummocks). The special situation in this area, which is strongly polluted by Ni and Cu, could also contribute to the change from the more normal Pb distribution in the profile.

In bog vegetation, only mosses show significant Pb concentrations in relation to distance from Falconbridge Nikkelverk A/S (Fig. 6, Table 4). The Pb content has a peak at localities 1 and 10,

Table 2, The table gives the heavy metal contents (ppm) in two samples from the top soil layer about 400 m north of Falconbridge Nikkelverk A/S

	pH	Ni	CO	Zn	Cu	Pb	Cd
Locality 13	3,8	13750	312	84	5600	510	0,2
Locality 14	4,0	7000	175	70	1760	235	0,01

probably as a result of local sources. As was also found for Ni, the Pb concentrations in the mosses are at a higher level than those found in vascular plants. The background values (Hvatum 1984) found in vegetation samples at Lista and Åmli (40 - 50 ppm) are about twice those found in the Kristiansand area (10 - 20 ppm). However, the content in mosses decreases to about 30 ppm at the localities farthest away from Kristiansand, and shows the same values as found further inland at Åmli.

Steinnes (1977) found values at 100 ppm in *Hylocomium splendens* at about 20 km east (in Ulvøysund) and 20 km northeast (at Birkeland) off Kristiansand. As moss analyses are suited to reflecting the previous year's heavy metal pollution in an area, it would seem that Pb pollution has been steadily decreasing from the late 1970s up until the present day.

Cobalt and Copper. The Co and Cu concentrations in peat show the same distribution pattern as Ni in the Kristiansand area, with maximal concentration in the top layer of the peat in the localities close to Falconbridge Nikkelverk A/S. Humus samples from the upper layer of mineral soils about 400 m north of Falconbridge (localities 13 and 14) contain up to 312 ppm Co and 5600 ppm Cu (Table 2). The lowest and high-

Table 3, The table gives the results from statistical analyses (Multiples Regression), The models are an attemt to explain the heavy metal content in peat (5 cm) by means of the distance from Falconbridge Nikkelverk A/S, frequency of wind from Falconbridge Nikkelverk A/S in winter, and the distance from the coast, 'Corr' indicates whether the variable is negatively or positively correlated, R^2 indicates how much of the variation is explained by the model, PROB > F shows the significance level, $P<0,001$ = ***, $P<0,01$ = **, $P<0,05$ = *, $P>0,05$ = not significant (ns)

		DEPENDENT VARIABLES			PROB > F	
VARIABLES	CORR	Ni	Co	Pb	Zn	Cu
Distance from FN A/S	-	0,0001 ***	0,0006 ***	0,0035 **		0,0039 **
Frequency of wind from FN A/S in winter	+	0,0010 ***				
Distance from coast	+			0,0111 *	0,0183 *	
R^2		0,73	0,70	0,60	0,41	0,54
F		28,69	23,85	7,55	7,65	13,28
PROB > F		0,0001 ***	0,0006 ***	0,0101 *	0,0183 *	0,0039 **

Table 4, Correlations between heavy metal content in (a) vascular plants and (b) mosses and different variables, using Multiple Regression Analyses, For explanation, see Table 3

A, VASCULAR PLANTS		DEPENDENT VARIABLES		PROB>F	
VARIABLES	CORR	Ni	Cu	Pb	Cd
Distance from FN A/S	-	0,0006 ***	0,0035 **	0,3312 ns	
Frequency of wind from FN A/S in winter	+	0,0103 *	0,0136		
Distance from coast	-				0,0010 ***
R^2		0,85	0,79	0,09	0,068
F		25,46	17,44	1,04	21,08
PROB>F		0,0002 ***	0,0008 ***	0,3312 ns	0,0010 ***
B, MOSSES					
VARIABLES	CORR	Ni	Cu	Pb	
Distance from FN A/S	-	0,0015 ***	0,0004 ***	0,0316 *	
Frequency of wind from FN A/S in winter	+	0,0028 **	0,0024 **		
R^2		0,85	0,88	0,38	
F		26,17	33,05	6,24	
PROB>F		0,0002 ***	0,0001 ***	0,0316 *	

est concentrations in the peat are 3 and 15 ppm Co and 10 and 500 ppm Cu, respectively. The background level in this part of Norway is below 2 ppm Co and up to 7 ppm Cu (Hvatum 1984).

The Co and Cu concentrations decrease abruptly the deeper one goes in the profile. These gradients indicate a strong absorption of the elements in peat. This tendency is also supported by other authors with regard to Cu (cf. Bergseth & Stuanes 1976, Livett et al. 1979, Tummavuori & Aho 1980). Tummovuori & Aho (1980) found strong absorption of Co in peat, while Krogstad (1983) observed the opposite result.

Cadmium. The Cd content in peat is generally found to be at a high level in the Kristiansand area, with concentrations up to 11.6 ppm at locality 12. This is ten times the average concentration found by Hvatum (1984) in the southern part of Norway. The values, however, vary greatly from bog to bogs. Rühling & Tyler (1970) found in experiments that Cd is strongly absorbed by the moss *Hylocomium splendens* in pure ion dilutions, but weakly so in mixed dilutions. The high pollution of Ni, Cu and Pb in the area may provide leaching of Cd by

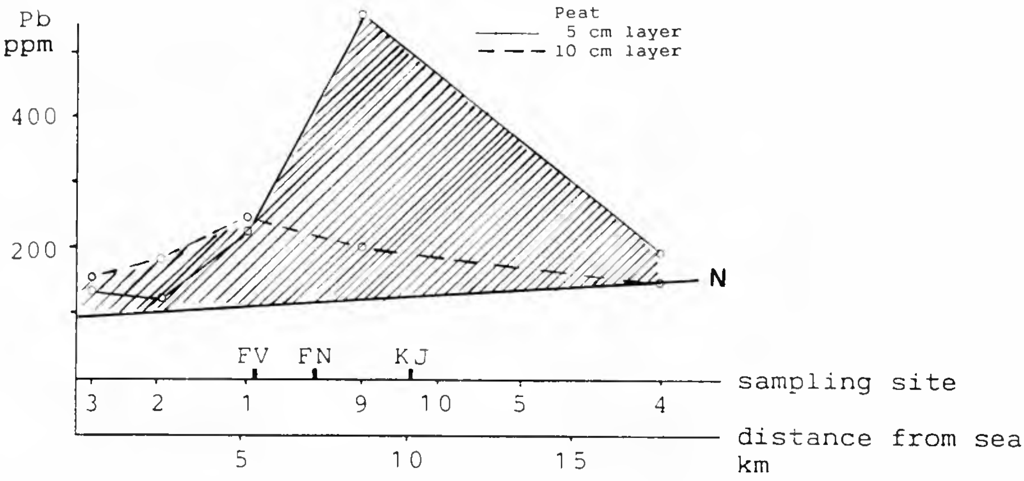


Fig. 10. Diagram depicting the distribution of Pb in peat (5 and 10 cm depths, respectively) in accordance with increased distance from the coast. The shadowed area above the solid line indicates the approximate contribution from local pollution, while the area below the solid line indicates the natural background level of Pb

ion exchange. The Cd content in the vegetation decreases significantly towards the coast (Table 4). In the bogs the Cd content is probably due to longe-range transported air pollutants.

Correlations. The correlations (R^2) between the elements in the top layer of the bogs (5 cm deep) are presented in Table 5. Ni, Cu and Co are significantly correlated. This is a result of one common pollution source (Falconbridge Nikkelverk A/S). The table also presents significant correlations between Pb and Zn. This is expected, because the precipitation seems to be the most important factor in explaining the Zn and Pb deposition in the Kristiansand area.

Vegetation analyses. The analyses of the vegetation (Table 1) do not give any indication that the plant communities have shown any changes due to the high heavy metal concentrations now found in the bogs. After all, the plant cover shows a low heavy metal content, even although the content in the peat varies quite considerably. This may reflect a certain tolerance to high heavy metal content throughout recent decades.

Table 5. The table gives the correlations between the heavy metals in peat (5 cm depth). $P<0.001$ = ***, $P<0.01$ = **, $P<0.05$ = *, $P>0,05$ = not significant (ns). For explantion, see Table 3

CORRELATIONS (R^2)
PEAT (5 cm)

	Cu	Co	Pb	Zn	Cd
Ni	0,47 **	0,91 ***	ns	ns	ns
Cu		0,34 *	ns	ns	ns
Co			ns	ns	ns
Pb				0,61 **	ns
Zn					ns

CONCLUSIONS

(1) Falconbridge Nikkelverk A/S is the main local source of heavy metal pollution in the area. This is the case

for Ni, Cu and Co, which are in considerably higher concentrations in the bogs than is normal for this part of Norway.

(2) Combustion of gasoline in motor vehicles and Pb from Falconbridge Nikkelverk A/S are the main local Pb pollution sources in the area.

(3) Zn and Cd deposition in the Kristiansand area are mainly a result of long-range transported air pollutants. This can also explain much of the Pb deposition in the area.

(4) The distance from the pollution source seems to best explain the distribution of the local pollution, and the wind (blowing from the source) influences this distribution to a lesser degree.

(5) The normal (natural) level of heavy metal accumulation in the bogs appears to be found at depths of 20 to 50 cm.

(6) There are no indications in the plant communities that the vegetation is influenced by heavy metal pollution.

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CROSSBREEDING FOR INCREASED MILK PRODUCTION IN THE TROPICS

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The data used for this study were extracted from reports on the crossbreeding of *Bos indicus* and *Bos taurus* cattle for milk production. Traits studied were age at first calving, milk yield and calving interval. The results were summarized by least squares and multiple regression procedures.
All traits improved with increasing proportions of *Bos taurus* inheritance in the crosses up to the 50% level. A further increase in the proportion of *taurus* genes had only a slight effect on age at first calving and milk yield, while calving interval was significantly prolonged. Estimates of heterosis were favourable for all traits:

Age at first calving:	- 5.3	months
Milk yield:	432	kg
Calving interval:	- 28	days

Epistatic loss (due to recombination of genes) was suggested for milk yield, but not for the other traits studied.

Key words: *Bos indicus*, *Bos taurus*, crossbreeding, epistasis, heterosis, milk, tropics.

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One of the many constraints on milk production in the tropics is the poor genetic potential of the indigenous animals. Tropical cattle are mostly of *Bos indicus* (zebu) type. These cattle are well adapted to the conditions prevailing in the tropics. Natural selection over hundreds of generations has provided them with a high level of heat tolerance, some resistance to many tropical diseases, and the ability to survive long periods of feed and water shortage. However, their dairy potential is poor, they have low milk yield, are late maturing, and often do not let down milk unless stimulated by the suckling of the calf.

The fastest way to improve the dairy potential of tropical cattle is to introduce inheritance from *Bos taurus* (European type) dairy breeds. This introduction has been facilitated by the recent development in reproduction techniques (use of frozen semen and embryo transfer). Many large-scale crossbreeding schemes using *Bos taurus* inheritance are already in operation. However, the best breeding policy to adopt is still a matter for discussion. The purpose of the present paper is to offer a contribution to this discussion on the basis of the available evidence.

DATA AND METHODS

The data used for this study were results extracted from reports on the crossbreeding of *Bos indicus* cattle with *Bos taurus* breeds for milk production. The traits considered were age at first calving, milk yield and calving interval. Milk yield records were mostly for first lactation (total lactation or 300-305 days), but in some cases subsequent lactations had also been included. The various genetic groups within a project were, for obvious reasons, not strictly contemporaneous, but in most cases the results used were means obtained from a least squares analysis accounting for possible time trends.

The means were arranged in data sets, each comprising records on crosses between a given *Bos taurus* and a given *Bos indicus* breed in a particular location; records on one or both pure breeds were also included whenever available. Altogether, 54 sets were found. All the sets contained information on milk yield, but records on age at first calving or calving interval were missing in some sets. The number of genetic groups represented in a set ranged from two to nine, except for one set which had no less than forty different groups. F_1 was included in all the sets, and each of the parental breeds occurred in about one half of the sets. First backcrosses to *Bos taurus* were also represented in many sets, while backcrosses to *Bos indicus* were rare. F_2 (from F_1 x F_1) appeared in seventeen sets.

The distribution of sets by breeds was as follows:

Bos indicus stock	*Bos taurus* breed		
	Friesian	Jersey	Others
Improved	14	6	8
Non-improved	9	11	6

The *Bos indicus* breeds considered to be 'improved' were Sahiwal, Red Sindhi, Tharparkar, Gir, Guzerat and Jenubi. Friesian and Jersey were the most widely used *Bos taurus* breeds, among the 'others' were Brown Swiss, Ayrshire, Dairy Shorthorn and Red Dane.

Altogether, the data included 19,145 individual records of age at first calving, 34,594 records of milk yield and 25,939 records of calving interval.

The means were subjected to a least squares analysis according to this model:

$$\bar{Y}_{ij} = \mu + a_i + c_j + \bar{e}_{ij} \qquad (1)$$

where

$\bar{Y}_{ij}$ = the mean of the j-th genetic group in the i-th data set,
μ = the overall mean,
a_i = the effect of the i-th set,
c_j = the effect of the j-th genetic group, and
$\bar{e}_{ij}$ = the residual

The genetic groups considered in this analysis were both parental breeds, F_1, grades with 1/8, 1/4, 3/8, 5/8, 3/4 and 7/8 *Bos taurus* inheritance (purebred sire) and F_2. Least squares means were estimated for each genetic group.

In another analysis the various genetic groups were coded for proportion of *Bos taurus* inheritance and for *taurus vs. indicus* heterozygosity. The model used was:

$$\bar{Y}_{ij} = \mu + a_i + b_1 \cdot (t_j - \bar{t}_j) + b_2 \cdot (h_j - \bar{h}_j) + \bar{e}_{ij} \qquad (2)$$

where

t_j = proportion of *Bos taurus* inheritance and
h_j = proportion of heterozygosity in the genetic group considered
$\bar{t}_j$ and $\bar{h}_j$ are the corresponding overall means
b_1 and b_2 are partial regression coefficients, and
$\bar{Y}_{ij}$, μ, a_i and $\bar{e}_{ij}$ are as in the model (1).

The model was expanded also to include the expected proportion of recombination loss (epistatic loss) as an additional independent variable. Coefficients of recombination loss were according to the model presented by Dickerson (1973).

In all analyses the various means were weighted by the number of records included in the mean.

RESULTS

Age at first calving
Age at first calving decreased almost linearly as the proportion of *Bos taurus* inheritance increased up to the 50% level (Fig. 1, top). From this point onwards there was rather a slight increase. However, purebred *Bos taurus* calved at a younger age than any other genetic group.

Grouping of the sets according to *taurus* breed (Table 1) revealed that Jersey and Jersey crosses calved earlier than Friesian and Friesian crosses. Age at first calving was lower in improved than in non-improved *indicus* stock, but this difference was not apparent in their crosses.

For all sets combined *Bos taurus* were 12 months younger than *Bos indicus* at first calving (Table 2). The estimate obtained by multiple regression was slightly lower (10 months). Heterosis was estimated at about - 5 months by both methods.

There was no indication of epistatic loss in age at first calving.

Milk yield
Milk yield per lactation increased with an increasing proportion of *Bos taurus* inheritance, but the increase was only slight beyond the 50% level (F_1) (Fig. 1, middle). *Bos taurus* and high grades produced on average about twice as much milk as the *Bos indicus* stock. In F_2 (from F_1 x F_1) a sharp decline in milk yield was noticed.

When the data were grouped according to *Bos taurus* breed (Table 3), the difference in milk yield between *Bos indicus* and *Bos taurus* was nearly the same for all breeds. The lower milk yield in the Jersey rather than in the Friesian sets was partly due to the fact that most of the Jersey sets were with non-improved *Bos indicus* stock, while the Friesian sets in most cases were with improved *indicus* breeds.

Grouping of the sets into improved

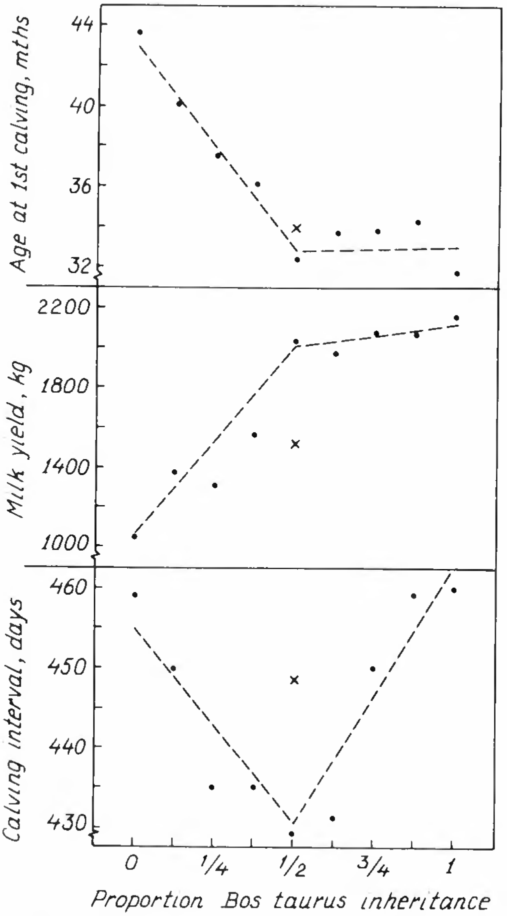

Fig. 1. Effect of proportion of *Bos taurus* inheritance on age at first calving (top), milk yield (middle) and calving interval (bottom)

Symbols:
· Least squares means of genetic groups with a purebred sire
---- Values calculated according to equation (2)
x Least squares mean of F_2

vs. non-improved *Bos indicus* stock revealed a clear difference between the two groups. When the foundation stock consisted of improved *indicus* there was no improvement beyond the 50% *taurus* level, while the milk yield continued to increase in the 'non-improved' group. Improved and non-improved *Bos indicus* produced 60% and 34%, respectively, of

Table 1. Age at first calving of *Bos indicus* and *Bos taurus*, their first crosses (F_1), and backcrosses to the *taurus* breed

	Age at first calving (least squares means), months			
	Indicus	*Taurus*	F_1	Backcrosses
Bos taurus breed:				
Friesian	43.5 ± 0.9	30.7 ± 1.8	33.5 ± 0.7	35.8 ± 1.0
Jersey	47.1 ± 1.5	28.4 ± 1.8	31.6 ± 1.1	31.1 ± 3.8
Others	40.9 ± 0.8	33.4 ± 0.9	31.6 ± 0.5	31.9 ± 0.8
Bos indicus breed:				
Improved	41.5 ± 0.8	30.1 ± 1.0	32.3 ± 0.6	34.3 ± 0.8
Non-improved	45.3 ± 1.0	32.7 ± 1.6	32.6 ± 0.7	33.1 ± 1.4
All sets	43.6 ± 0.6	31.6 ± 0.9	32.4 ± 0.5	33.9 + 0.7

Table 2. Difference in age at first calving (in months) between *Bos taurus* (P_2) and *Bos indicus* (P_1), and heterosis in their crosses

	Difference between *taurus* and *indicus*		Heterosis	
	P_2-P_1	Regression[1)]	$F_1 - \frac{P_1+P_2}{2}$	Regression[1)]
Bos taurus breed:				
Friesian	-12.8	- 8.3 ± 1.1	-3.6	-4.6 ± 0.8
Jersey	-18.7	-18.1 ± 2.2	-6.1	-6.3 ± 1.3
Others	-7.6	- 7.8 ± 1.0	-5.5	-5.4 ± 0.7
Bos indicus breed:				
Improved	-11.4	- 7.8 ± 0.9	-3.5	-5.4 ± 0.7
Non-improved	-12.6	-12.5 ± 1.6	-6.4	-6.3 ± 1.0
All sets	-12.0	-10.0 ± 0.8	-5.2	-5.3 ± 0.6

1) Estimated from the partial regressions of age at first calving on proportion of *Bos taurus* inheritance and proportion of F_1 heterozygosity in the genetic group in question

Table 3. Milk yields of *Bos indicus* and *Bos taurus*, their first crosses (F_1), and backcrosses to the taurus breed

	Milk yield (least squares means), kg			
	Indicus	*Taurus*	F_1	Backcrosses
Bos taurus breed:				
Friesian	1245 ± 53	2499 ± 85	2296 ± 36	2275 ± 54
Jersey	780 ± 75	1830 ± 124	1658 ± 60	1681 ± 145
Others	1019 ± 93	2136 ± 83	2082 ± 65	2215 ± 87
Bos indicus breed:				
Improved	1414 ± 65	2358 ± 54	2362 ± 38	2326 ± 55
Non-improved	714 ± 47	2076 ± 95	1695 ± 38	1856 ± 71
All sets	1052 ± 39	2162 ± 50	2039 ± 28	2091 ± 45

the yield of purebred *Bos taurus* cattle in the same projects.

Estimates of differences in milk yield between *Bos taurus* and *Bos indicus*, and estimates of heterosis in their F_1 crosses are presented in Table 4. The two types of estimates (from least squares means and multiple regression, respectively) are in good agreement, and the same applies to the estimates from the various groups of data. For all the sets combined, heterosis is estimated at 432 kg by both methods. This is 27% of the mean of the parental breeds.

The large decline in milk yield from F_1 to F_2 (516 kg, or 300 kg more than was expected due to reduced heterozygosity) might be ascribed to loss of epistatic combinations of genes (recombination loss). However, the inclusion of coefficients of recombination loss as an additional independent variable in the multiple regression analysis did not reveal any significant effect of this variable ($P \approx 0.09$). The analysis estimated epistatic loss at 103 ± 61 kg.

Calving interval

The calving interval was shortest at intermediate levels of *Bos taurus* inheritance and increased towards both extremes (Fig. 1, bottom).

The largest reduction in calving interval by crossbreeding was observed when the *taurus* breed was Jersey (Table 5). Non-improved *indicus* stock had longer calving intervals than improved breeds.

The estimates of the difference in calving interval between *taurus* and *indicus* were inconsistent. The estimates of heterosis, on the other hand, were very consistent across various groups of data. The results obtained by the two methods were also very similar (-31 and -28 days, respectively).

There was no sign of epistatic loss in this trait.

DISCUSSION

This study is an updated and expanded version of another study by the same author undertaken a few years ago and based partly on the same data (Syrstad 1985a, b). The amount of data included in this new study is nearly twice as extensive as in the previous one, so the estimates are considerably more precise. However, crosses with less than 50% *Bos taurus* inheritance were poorly repre-

Table 4. Difference in milk yield (in kg per lactation) between *Bos taurus* (P_2) and *Bos indicus* (P_1), and heterosis in their F_1 crosses

	Difference between *taurus* and *indicus*		Heterosis	
	P_2-P_1	Regression[1)]	$F_1 - \frac{P_1 + P_2}{2}$	Regression[1)]
Bos taurus breed:				
Friesian	1254	1066 ± 71	424	452 ± 51
Jersey	1050	1035 ± 145	353	366 ± 84
Others	1117	1170 ± 108	505	507 ± 74
Bos indicus breed:				
Improved	944	882 ± 67	476	443 ± 46
Non-improved	1362	1318 ± 93	300	334 ± 60
All sets	1109	1075 ± 54	432	432 ± 32

1) Estimated from the partial regressions of milk yield on proportion of *Bos taurus* inheritance and proportion of F_1 heterozygosity in the genetic group in question.

Table 5. Calving interval of *Bos indicus*, *Bos taurus*, their first crosses (F_1) and backcrosses to the *taurus* breed

	Calving interval (least squares means), days			
	Indicus	*Taurus*	F_1	Backcrosses
Bos taurus breed:				
Friesian	451 ± 7	465 ± 13	434 ± 5	459 ± 7
Jersey	492 ± 11	424 ± 17	429 ± 7	435 ± 23
Others	444 ± 9	464 ± 10	423 ± 7	442 ± 9
Bos indicus breed:				
Improved	439 ± 6	442 ± 6	421 ± 3	437 ± 5
Non-improved	471 ± 7	484 ± 16	436 ± 6	460 ± 11
All sets	459 ± 5	460 ± 7	429 ± 4	450 ± 6

Table 6. Difference in calving interval (in days) between *Bos taurus* (P_2) and *Bos indicus* (P_1), and heterosis in their F_1 crosses

	Difference between *taurus* and *indicus*		Heterosis	
	P_2-P_1	Regression[1)]	$F_1 - \frac{P_1 + P_2}{2}$	Regression[1)]
Bos taurus breed:				
Friesian	14	17 ± 8	-24	-27 ± 6
Jersey	-69	-66 ± 19	-29	-30 ± 11
Others	20	18 ± 12	-31	-37 ± 8
Bos indicus breed:				
Improved	3	3 ± 6	-20	-21 ± 4
Non-improved	13	14 ± 13	-42	-44 ± 8
All sets	1	9 ± 7	-31	-28 ± 4

sented in the data, and the least squares means of these groups still have large sampling errors.

A possible bias in some of the data might have been caused by preferential treatment of purebred *Bos taurus* animals. These animals were often imported at considerable cost, and it is reasonable to assume that they were in some cases given a better environment than animals born locally. However, this is not borne out by the results, as the pure exotics were similar to high grades (3/4 and 7/8 *Bos taurus*) in both milk yield and calving interval. The unexpectedly low age at first calving for pure *Bos taurus* might be explained by the fact that some of these heifers were already pregnant at the time of importation.

When lactation records are summarized, lactations below a given length are often omitted. Short lactations occur frequently in *Bos indicus* cattle, partly because of poor milking ability and partly as a result of failure to let down milk properly. This might have led to an inflated estimate of milk yield in pure *Bos indicus*.

Maternal effects were not considered in this study. In most cases the effect of the genetic group of the dam could not be separated from the effect of the genetic group of the animal itself, because the two were completely confounded. It is believed that the maternal environment would have only a small effect on traits expressed as late in life as milk yield and calving interval, although there is some indication to the contrary (Robison et al. 1981).

The results presented in this paper confirm most of those obtained in the previous study. The advantage of *Bos taurus* over *Bos indicus* in age at first calving and milk yield (but not in calving interval) is well established, and favourable heterosis is demonstrated beyond doubt in all three traits studied. The estimates of heterosis with respect to age at first calving and milk yield were larger in this study than in the previous one.

The study is inconclusive with regard to the presence of epistatic loss. The two estimates of epistatic loss with respect to milk yield differed widely in magnitude, although both were in the same direction. It might look as if epistatic loss occurred only in F_2 and later generations, i.e. when both parents were crossbred. Poor performance in F_2 has also been observed in maize (Wright 1977, cited by Hill 1981) and in poultry (Sheridan 1981).

Many crossbreeding projects in the tropics have been initiated with the aim of deriving a new breed of mixed *indicus/taurus* origin. The outstanding performance of F_1 has sometimes led to the conclusion that the optimum combination is obtained with around 50% of the genes from each of the two types. The large reduction in heterosis from F_1 to F_2 and later generations has often been overlooked. This reduction in heterozygosity from the foundation generation to later generations (from *inter se* matings) is much less at extreme levels of the two breeds. In the backcrosses 50% of the F_1 heterozygosity has already been lost, and the additional loss in generations produced by *inter se* mating is only 12.5%. Under most conditions the backcross to the *taurus* breed (3/4 *Bos taurus*) is probably better than F_1 as a starting point for the composite breed.

The alternative to a composite breed is rotational crossbreeding. This strategy exploits a little more of the heterosis, and also retains more of the parental gene combinations (epistasis). On the other hand it is much more complex to manage. From the previous study it was concluded that the slightly larger heterosis did not justify the increased complexity of rotational crossbreeding. It seems that this conclusion is still valid. However, should the largest estimate of epistatic loss obtained in the present study be verified, then rotational crossbreeding might again require some serious consideration.

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