Norwegian Journal of Agricultural Sciences

Vol. 6 1992 No. 3

Norwegian Agricultural Advisory Service, Ås, Norway

NORWEGIAN JOURNAL OF AGRICULTURAL SCIENCES

Norwegian Journal of Agricultural Sciences fills a need created by the folding of Scientific Reports of the Agricultural University of Norway and Research in Norwegian Agriculture for a forum for publishing Norwegian research with international interest within the following areas: Aquaculture, Animal Science, Soil Science, Agricultural Engineering and Technology, Natural Resources and Environment, Food Technology, Crop Science, Forestry, Economics and Society Planning.

PUBLISHER

The journal is published by Norwegian Agricultural Advisory Service, Moerveien 12, N-1432 Ås, Norway. Norwegian Journal of Agricultural Sciences (ISSN 0801-5341) is published four times a year, each issue containing approximately 100 pages. Four issues comprise one volume. Annual subscription NOK 500,–. Subscribers receive supplement issues free of charge, but these can also be ordered separately through the publisher.

CORRESPONDENCE

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

ISSN 0801-5341

Effects of ozone and temperature on growth of several wild plant species

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Mortensen, L.M. & J. Nilsen 1992. Effects of ozone and temperature on growth of several wild plant species. Norwegian Journal of Agricultural Sciences 6: 195-204. ISSN 0801-5341.

The effects of ozone (O_3) concentrations ranging from 15 to 80 nmol mol^{-1} given 8 h day^{-1} were studied on 24 wild plant species which originated from South Sweden in the south (56°N) up to Spitsbergen in the north (79°N). Raising the O_3 concentration from 20 to 50 nmol mol^{-1} decreased the dry weight and also caused leaf chlorosis in *Plantago lanceolata*, but leaf chlorosis only in *Centaurea jacea*, *Chrysanthemum leucanthemum*, *Hypericum perforatum* and *Solidago virgaurea*. Increasing the O_3 concentration from 20-40 to 80 nmol mol^{-1} resulted in a decrease in the dry weight of *Polygonum viviparum* and *Silene acaulis*. Leaf chlorosis occurred in *Betula nana* and *Potentilla crecta*, and the leaves of *Betula pubescens* were severely injured by 80 nmol mol^{-1} O_3. No effect on dry weight and no visible leaf injury were found on *Poa alpina vivipara*, *Saxifraga cernua* and *Saxifraga cespitosa* at O_3 levels up to 80 nmol mol^{-1} and on *Campanula rotundifolia*, *Lotus corniculatus*, *Prunella vulgaris* and *Solidago virgaurea* at O_3 levels up to 50 nmol mol^{-1}. Neither were there any visible effects of O_3 observed on *Andromeda polifolia*, *Calluna vulgaris*, *Oxyria digyna*, *Rubus chamaemorus* and *Vaccinium vitis-idaea* at concentrations up to 80 nmol mol^{-1}. When the O_3 sensitivity of the different species was compared, *Phleum pratense*, which was grown as a reference species, was by far the most sensitive, followed by *Betula pubescens* and *Potentilla crecta*. The growth effect of increasing the temperature from 15/11°C to 20/16°C (12 h/12 h) indicated that plants of *Saxifraga cernua* and *Saxifraga cespitosa* which originated from 79°N had a lower temperature optimum for growth than plants from 70°N. The effect of O_3 was higher at low compared with at high temperatures in *Phleum pratense*. This interaction could not be stated with other species because of a low sensitivity to O_3 in these species.

Key words: Alpine plants, ozone, temperature.

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Recently, much attention has been paid to ozone pollution and its effects on plants (Heck et al. 1983; Guderian et al. 1985; Heagle 1989; Blank et al. 1990; Mortensen 1991). Most experiments have included species of economic interest in relation to agriculture, horticulture and forestry, and these experiments show large variations in O_3 sensitivity between species. Ashmore (1984) exposed several native British plant species to a short-term, very high O_3 concentration and found large variations in O_3-sensitivity between these species. However, few studies have included wild plant species exposed to

moderate O_3 concentrations (about 50 nmol mol^{-1}) which are typical for parts of the growth season in Scandinavia (Pedersen & Semb 1990).

This paper presents results on the effect of moderate O_3 concentrations on species from latitudes ranged between 56 and 79°N. Two temperature regimes were included for some of the species in order to investigate whether a particular O_3 dose would have different effects on plant growth. If so, this would be important to know in order to understand where in nature O_3 effects are likely to be found.

MATERIALS AND METHODS

Experiment 1: The first experiment included different species propagated from seeds harvested in 1990 at different locations (Table 1). The seeds were sown on 12 April and the seedlings were planted on 16 May in standard fertilized peat (Floralux). The peat contained 230 g N, 100 g P, 290 g K, 360 g Mg, 2.4 kg Ca, 150 g S, 18 g Fe, 4 g Mn, 4 g Cu, 4 g Zn, 1 g B and 1 g Mo per m^3 peat, and the pH was 5.5. Each pot (0.5 l) included from 1 to 5 seedlings (Table 1). *Betula nana* was sown on 26 February and planted on 15 April. Small vegetative plants were taken directly from two mother plants of *Poa alpina vivipara* and rooted. In addition to the species from seed, *Alchemilla alpina* (Table 1) and some other species (Table 8) were transplanted from the field into pots in June-July 1990.

Table 1. Experimental period, start dry weight, number of pots per chamber and number of plants per pot in the different species in Experiment 1. All species except *Alchemilla alpina* were grown from seed

Species	Origin		Experimental period (days)	Start dry weight (g pot^{-1})	No. of pots per chamber	No. of plants per pot
Alchemilla alpina L.	Hunnedalen	(58°N)	66	0.29	4	1
Betula nana L.	Strynefjellet	(62°N)	43	1.05	7	1
Poa alpina vivipara L.	Tromsø	(70°N)	44	0.04	5	3
Polygonium viviparum L.	Tromsø	(70°N)	66	0.06	8	5
Saxifraga cernua L.	Spitsbergen	(79°N)	44	0.69	5	3
Saxifraga cernua L.	Tromsø	(70°N)	44	0.34	4	3
Saxifraga cespitosa L.	Spitsbergen	(79°N)	66	0.01	2	3
Saxifraga cespitosa L.	Tromsø	(70°N)	66	0.01	8	3
Silene acaulis (L). Jacq.	Tromsø	(70°N)	66	0.29	3	5
Phleum pratense L.	cv. Forus	(59°N)	40	-	5	3

Two temperature regimes were established in eight growth chambers with a volume of 1080 l (Mortensen 1982), which were placed in a plastic greenhouse, four chambers to each regime. The low temperature treatment was 15/11°C in 12h/12h (08.00-20.00h/20.00-08.00 h) and the high temperature treatment was 20/16°C (Table 2). Three O_3 levels were established: 15, 40 and 80 nmol mol^{-1} given in 8 h day^{-1} (10.00-18.00 h). The highest O_3 level included two replicates (chambers), while the other two included only one. The daily maximum O_3 concentration was 15% higher than the mean at all three treatments. The O_3 concentration for the rest of the diurnal period was < 15 nmol

mol^{-1}. Ozone was generated from dry air using a high voltage O_3 generator (Nomizon, Nordmiljø ab, Sweden). The O_3 concentration was measured twice an hour by a scanner switching air flows from the chambers sequentially to an O_3 analyser (Model 1008 AH, Dasibi Environmental Corp.). Recordings of the mean and maximum O_3 concentrations throughout the daily 8-h application period and the rest of the diurnal period were recorded separately by datalogger. The concentrations of nitrogen oxides (NO_x) as measured by a Monitor Labs. Inc. (Model 8840) analyzer were <5 nmol mol^{-1}. The CO_2 concentration was 350 ± 30 µmol mol^{-1} as measured by an infrared gas analyser (ADC, Model 225 MK3) as frequently as the O_3 concentration measurements.

Table 2. Mean O_3 concentrations, mean temperatures during 12h/12h (08.00-20.00/20.00-08.00h) and mean relative humidities (RH) at the different treatments and replicates (chambers) in Experiment 1. Standard deviations are given except for temperature where the deviation was about ± 1.0°C

	Low temperature O_3 level				High temperature O_3 level			
	Low	Moderate	High		Low	Moderate	High	
			Rep.1	Rep.2			Rep.1	Rep.2
O_3 conc. (nmol mol^{-1})	18 ± 3	44 ± 9	81 ± 9	81 ± 9	15 ± 3	37 ± 6	80 ± 7	79 ± 8
Temperature (°C)	14.8/10.9	14.7/11.0	14.3/10.6	14.8/10.9	19.8/15.5	20.1/15.6	19.9/15.8	20.7/16.8
% RH	74 ± 14	70 ± 15	72 ± 14	74 ± 14	64 ± 12	65 ± 13	68 ± 11	68 ± 13

Supplementary light was provided by means of a high pressure sodium lamps (Thorn SON XL-T) at a level of 120 µmolm^{-2}s^{-1} photon flux density in 24 h day^{-1}. This corresponded to a daily photon flux of 10.4 mol m^{-2}. Continuous light was given since the photoperiod is 24 h at high latitudes during summer. The light was measured by a Lambda LI-185B instrument with a quantum sensor. The photosynthetic photon flux from the daylight inside the chambers was 20 mol m^{-2} day^{-1} (data from The Meteorological Station at Særheim Research Station, 59°N), which means that the total photon flux density at plant level was about 30 mol m^{-2} day^{-1}.

The plants were watered regularly. The electrical conductivity in the pots was kept at 1.5-2.0 mS cm^{-1}. A complete nutrient solution was supplied when needed, and this consisted of (mg l^{-1}): N, 188; P, 37; K, 242; Ca, 130; Mg, 41; S, 53; Fe, 2.0; Mn, 0.6; Zn, 0.14; Cu, 0.29; B, 0.34; Mo, 0.027; Co, 0.009 - giving an electrical conductivity of 1.7 mS cm^{-1}. After 43-66 days the experiment was terminated, and fresh and dry weights per pot, leaf chlorosis and wilting as well as any visible O_3 injury were recorded. In addition, root weight, shoot length, stem diameter and number of branches of *Betula nana* were recorded.

Growth chamber construction for Experiment 2: Six growth chambers constructed of 4 mm plexiglass on an alumina frame and measuring 150 cm in width, 200 cm in length and 150 cm in height made up a volume of 4.5 m^{-3}. The air was circulated by a 390-watt fan through a channel and a perforated polyethylene sheet on which the plants were placed (2.4 m^2). The sheet was perforated with 13 mm holes which made up 10% of the total plant floor. The air speed above the plant floor could be controlled between

0.05 to 0.5 m s^{-1} by varying the velocity of the fan. A computerized system (Kieback & Peter, DDC-150, Energi management system, Germany) controlled the temperature by controlling the flow of cold water from a central cold water storage through a shunt and a cooler placed in the chamber channel. An electrical heater (150-1000 watts) was switched on when heating was needed. The temperature in the chambers could be controlled between 10 and 30°C at a greenhouse temperature of 20°C and in full sunshine. The number of air exchanges could be controlled between 0 and 50 per hour. The CO_2 concentration was controlled within ± 30 µmol mol^{-1} and recorded by equipment made by the Agricultural Instrument Service at Ås, Norway. A scanner switched the air flows from the different chambers sequentially to an infrared CO_2 analyser (ADC, Model 225 MK3) four times an hour. When the CO_2 concentration was lower than the preset value, CO_2 from bottles was supplied to the chambers at a preset flow rate.

Experiment 2: The effects of two O_3 concentrations (5 and 50 nmol mol^{-1}) were studied on some plant species propagated from seeds from Sweden (Svenskt Ängsfrø 1990, Väståkra gård, Lund) (Table 3). Four of the decribed growth chambers were used, two chambers at each O_3 level (Table 4). The seeds were sown in the middle of February and the seedlings were potted in peat (Floralux) in 0.5 l pots after 3-4 weeks. Supplementary light at a level of 140 µmol$m^{-2}s^{-1}$ in 16 h day^{-1} was provided by the same lamp type as the one used in Experiment 1, which corresponded to a photon flux of 8.1 mol m^{-2} day^{-1}. The mean contribution from the daylight at plant level was about 15 mol m^{-2} day^{-1}, and the total photon flux was then about 23 mol m^{-2} day^{-1} as a mean. At the end of the experiment shoot fresh and dry weights, leaf chlorosis and any visible O_3 injury were recorded. All data were subjected to an analysis of variance based on pots as replicates, and standard errors are given.

Table 3. Experimental period, start dry weight, number of pots per chamber and number of plants per pot for the different species in Experiment 2

Species	Experimental period (days)	Start dry weight (g pot^{-1})	No. of pots per chamber	No. of plants per pot
Campanula rotundifolia L.	42	0.19	5	5
Centaurea jacea L.	42	0.35	6	5
Chrysanthemum leuchanthemum L.	46	-	6	5
Hypericum perforatum L.	42	0.05	6	5
Lotus corniculatus L.	33	-	4	3
Plantago lanceolata L.	42	0.36	6	5
Prunella vulgaris L.	33	-	3	5
Rumex acetosa L.	37	-	6	5
Solidago virgaurea L.	35	-	2	3

RESULTS

The dry weight of *Polygonum viviparum, Silene acaulis* and *Phleum pratense* decreased when the O_3 concentration increased from 15 to 80 nmol mol^{-1} in Experiment 1 (Tables 5-6). A high O_3 level (80 nmol mol^{-1}) caused severe leaf wilting in *Phleum pratense* (Table 6), leaf chlorosis in *Betula nana* (Table 7) and yellow mottling in *Betula*

Table 4. Mean O_3 concentrations, mean temperatures and mean relative humidities at the different treatments and replicates (chambers) in Experiment 2

	O_3 level			
	Low		High	
	Rep.1	Rep.2	Rep.1	Rep.2
O_3 concentrations (nmol mol^{-1})	5 ± 5	5 ± 5	50 ± 15	53 ± 17
Temperature (°C)	17.2 ± 0.3	16.6 ± 0.5	16.9 ± 0.4	17.1 ± 1.1
% RH	68 ± 12	62 ± 14	67 ± 12	66 ± 14

pubescens (Table 8). This means that 5 of the 14 species in Experiment 1 were affected by 80 nmol mol^{-1}. The dry weight of *Phleum pratense* decreased by 78% at 15/11°C and by 46% at 20/16°C when the O_3 level increased from 15 to 80 nmol mol^{-1} and the interaction between O_3 and temperature was significant (Table 6). The dry weight of *Saxifraga cernua* from Spitsbergen decreased while the same species from Tromsø was unaffected when the temperature increased from 15/11 to 20/16°C (Table 5). In *Saxifraga cespitosa* from Spitsbergen and Tromsø it was found that an increase in temperature resulted in no effect and a positive effect respectively. This indicates that *Saxifraga* plants from Spitsbergen have a lower temperature optimum for growth than the plants from Tromsø. The dry weight of *Poa alpina* (Table 5), *Phleum pratense* (Table 6) and *Betula nana* (Table 7) was enhanced by the higher temperature. The shoot:root dry weight ratio and the shoot length of *Betula nana* increased as the temperature increased.

Table 5. The effects of O_3 concentration and temperature on dry weights and percentage dry weight of different species. Significance levels: ns, not significant; *, $P<0.05$; **, $P<0.01$; ***, $P<0.001$. Standard errors are given

		O_3 concentrations (nmol mol^{-1})			Temperature (°C)		Significance level		
		15	40	80	15/11	20/16	O_3	Temp.	O_3 x Temp
Alchemilla alpina	D.W.(g)	5.5 ± 0.4	5.1 ± 0.4	5.9 ± 0.3	5.7 ± 0.3	5.5 ± 0.3	ns	ns	ns
	%D.W.	28.7 ± 0.4	31.6 ± 0.8	30.5 ± 0.5	29.3 ± 0.5	31.4 ± 0.5	**	***	ns
Poa alpina vivipara	D.W.(g)	9.5 ± 0.7	10.7 ± 0.7	10.1 ± 0.4	8.8 ± 0.3	11.4 ± 0.4	ns	***	ns
	%D.W.	17.6 ± 0.8	17.5 ± 0.9	16.3 ± 0.4	17.0 ± 0.6	16.8 ± 0.5	ns	ns	ns
Polygonum viviparum	D.W.(g)	0.45 ± 0.06	0.57 ± 0.06	0.35 ± 0.04	0.45 ± 0.04	0.41 ± 0.04	**	ns	ns
	%D.W.	-	-	-	-	-	-	-	-
Saxifraga cernua (Spitsbergen)	D.W.(g)	3.7 ± 0.4	4.2 ± 0.3	4.0 ± 0.2	4.3 ± 0.2	3.6 ± 0.2	ns	*	ns
	%D.W.	11.3 ± 0.3	11.1 ± 0.3	11.2 ± 0.2	11.7 ± 0.2	10.7 ± 0.2	ns	**	ns
Saxifraga cernua (Tromsø)	D.W.(g)	2.6 ± 0.5	2.7 ± 0.4	2.3 ± 0.3	2.8 ± 0.3	2.1 ± 0.3	ns	ns	ns
	%D.W.	11.3 ± 0.3	11.0 ± 0.3	11.1 ± 0.4	10.7 ± 0.3	11.5 ± 0.3	ns	ns	ns
Saxifraga cespitosa (Spitsbergen)	D.W.(g)	0.62 ± 0.15	0.63 ± 0.14	0.81 ± 0.14	0.74 ± 0.01	0.70 ± 0.08	ns	ns	ns
	%D.W.	-	-	-	-	-	-	-	-
Saxifraga cespitosa (Tromsø)	D.W.(g)	0.58 ± 0.10	0.39 ± 0.08	0.46 ± 0.08	0.33 ± 0.04	0.63 ± 0.08	ns	**	ns
	%D.W.	-	-	-	-	-	-	-	-
Silene acaulis	D.W.(g)	15.2 ± 1.8	13.3 ± 0.8	11.3 ± 0.3	12.9 ± 0.7	-	*	-	-
	%D.W.	16.0 ± 0.2	16.9 ± 1.1	17.1 ± 0.6	16.7 ± 0.4	-	ns	-	-

Table 6. The effects of O_3 concentration and temperature on growth of *Phleum pratense*. Leaf wilting was scaled from 0 (no) to 5 (>50% wilted leaves). Standard errors are given

Temperature (°C)	O_3 concentrations (nmol mol^{-1})	n	Shoot dry weight (g)	% dry weight	Leaf wilting
15/11	15	5	1.59 ± 0.17	15.1 ± 0.4	0.0 ± 0.0
	40	5	1.22 ± 0.11	15.2 ± 0.4	0.8 ± 0.2
	80	10	0.36 ± 0.06	17.7 ± 0.6	3.4 ± 0.2
20/16	15	5	2.39 ± 0.05	16.7 ± 0.7	0.0 ± 0.0
	40	5	3.09 ± 0.17	19.9 ± 1.3	0.6 ± 0.3
	80	10	1.28 ± 0.19	17.2 ± 0.5	3.0 ± 0.0
Significance levels					
O_3			***	ns	***
Temp.			***	*	*
O_3 x Temp.			**	**	ns

Table 7. The effects of O_3 concentration and temperature on growth of *Betula nana*. Leaf chlorosis was scaled from 0 (no) to 4 (severe chlorosis of older leaves). Standard errors are given

	n	Shoot dry wht. (g)	Shoot: root d.w. ratio	% shoot dry wht.	Shoot length (cm)	Stem diameter (mm)	No. of branches	Leaf chlorosis
O_3 conc. (nmol mol^{-1})								
15	14	8.12 ± 0.51	4.3 ± 0.3	35.8 ± 0.8	40.6 ± 2.2	7.6 ± 0.3	15.2 ± 1.6	0.3 ± 0.1
40	13	7.62 ± 0.65	3.7 ± 0.3	35.9 ± 0.9	39.7 ± 3.2	7.3 ± 0.3	12.8 ± 0.6	0.6 ± 0.2
80	28	7.03 ± 0.32	4.3 ± 0.2	35.8 ± 0.5	39.1 ± 1.7	7.3 ± 0.1	14.6 ± 1.0	2.4 ± 0.2
Temperature (°C)								
15/11	28	6.55 ± 0.30	3.5 ± 0.2	36.8 ± 0.6	33.2 ± 1.3	7.2 ± 0.2	15.1 ± 0.9	1.7 ± 0.3
20/16	27	8.38 ± 0.36	4.8 ± 0.2	34.8 ± 0.4	46.3 ± 1.3	7.5 ± 0.1	13.6 ± 0.9	1.2 ± 0.3
Significance level								
O_3		ns	ns	ns	ns	ns	ns	***
Temp.		***	***	**	***	ns	ns	ns
O_3 x Temp.		ns	ns	ns	ns	ns	ns	ns

No effect of O_3 level on flowering was found on the species included in Experiment 1 (data not presented). A rise in the temperature, however, caused a decrease in the number of flowers in *Saxifraga cespitosa* from both locations, *Saxifraga cernua* from Spitsbergen and *Poa alpina vivipara* (data not presented).

In Experiment 2 the dry weight of *Plantago lanceolata* decreased when the O_3 concentration increased from 5 to 50 nmol mol^{-1} while no effect was found on the other eight species (Table 9). Leaf chlorosis, however, was enhanced by an increase in O_3 level in five of the species. A few plants of *Phleum pratense* were included in the

Table 8. Visual observations of different species exposed to different O_3 concentrations during June-August, 1991 in Experiment 1. The plants were transplanted from the field

Species	Origin	Experimental period (days)	O_3 concentrations (nmol mol^{-1})	Visual O_3 injury
Andromeda polifolia L.	Sirdalen (59°N)	60	15,80	None
Betula pubescens Ehrh.	Liljell (60°N)	60	15,80	Yellow stipples, necrosis and wilting of older leaves at 80 nmol mol^{-1}
Calluna vulgaris L. (Hill)	Forsand (59°N)	30	15,40,80	None
	Klepp (59°N)	90	15,40,80	None
	Liljell (60°N)	60	15,80	None
Oxyria digyna (L.) (Hill)	Forsand (59°N)	30	15,40,80	None
Potentilla erecta (L.) Räusch.	Klepp (59°N)	60	15,40,80	Leaf chlorosis at 80 nmol mol^{-1}
Rubus chamaemorus L.	Liljell (60°N)	40	15,40,80	None
Vaccinium vitis idaea L.	Hunnedalen (59°N)	60	15,40,80	None

experiment and high O_3 levels caused leaf wilting (data not presented). No effect of O_3 was found on flowering in the species which flowered during the experiment (*Campanula rotundifolia, Centaurea jacea, Lotus corniculatus, Plantago lanceolata* and *Rumex acetosa*).

Table 9. The effect of O_3 consentration (20 and 50 nmol mol^{-1}) on dry weight and leaf chlorosis of different plant species in Experiment 2. The leaf chlorosis was scaled from 0 (no) to 4 (severe chlorosis). Standard errors are given

	Dry weight (g) O_3 concentrations (nmol mol^{-1})		Significance level	Leaf chlorosis O_3 concentrations (nmol mol^{-1})		Significance level
	5	50		5	50	
Campanula rotundifolia	7.6 ± 0.4	8.4 ± 0.5	ns	0.0 ± 0.0	0.0 ± 0.0	ns
Centaura jacea	14.6 ± 0.4	13.3 ± 0.8	ns	0.0 ± 0.0	2.4 ± 0.2	***
Chrysanthemum leucanthemum	13.3 ± 0.7	12.1 ± 0.1	ns	0.0 ± 0.0	1.4 ± 0.2	***
Hypericum perforatum	8.0 ± 0.4	8.2 ± 0.6	ns	0.0 ± 0.0	1.2 ± 0.1	***
Lotus cornilatus	5.2 ± 0.6	5.0 ± 0.6	ns	0.0 ± 0.0	0.0 ± 0.0	ns
Plantago lanceolata	22.3 ± 0.9	19.3 ± 0.1	**	0.0 ± 0.0	1.2 ± 0.2	***
Prunella vulgaris	6.7 ± 0.2	6.2 ± 0.1	ns	0.0 ± 0.0	0.0 ± 0.0	ns
Rumex acetoza	[1]69.3 ± 6.5	57.5 ± 4.0	ns	0.0 ± 0.0	0.0 ± 0.0	ns
Solidago virgaurea	13.7 ± 1.0	13.8 ± 1.1	ns	0.0 ± 0.0	2.8 ± 0.5	**

[1] Fresh weights are given

DISCUSSION

Ozone exposure at the 50-80 nmol mol^{-1} level enhanced leaf chlorosis in seven and caused dry weight decreases in four out of a total of 23 species included in the present experiments. Altogether 13 different families were represented. Most species included in

the experiments had a relatively low sensitivity to O_3 compared to the reference species, *Phleum pratense*, which is known to be very sensitive to O_3 (Ashmore 1984; Mortensen 1992a). An exception was *Betula pubescens*, which previously also was found to be very sensitive to O_3 (Mortensen & Skre 1990). Another species, *Betula nana*, which belongs to the family *Betulaceae*, was found to be only slightly affected by 80 nmol mol^{-1} O_3 and may therefore be ranked as relatively tolerant to O_3.

The mean 7-h O_3 concentration in Norway during parts of the growth season is 40-50 nmol mol^{-1} (Pedersen & Semb 1990). Among the species included in the present experiments, only the growth rate of *Betula pubescens* and *Phleum pratense* is likely to be negatively affected by such concentrations. However, leaf chlorosis may also be enhanced by realistic O_3 levels in species such as *Centaurea jacea, Chrysanthemum leucanthemum, Hypericum perforatum, Plantago lanceolata* and *Solidago virgaurea*. Leaf senescence without any O_3 specific injury has recently been observed in *Betula pubescens* at O_3 concentrations as low as 35 nmol mol^{-1} (Mortensen & Skre 1990). As shown by the present results, growth reductions do not necessarily accompany visible leaf injury or vice versa, as also emphasized by Tingey (1985).

Wide variations in O_3 sensitivity between species are likely to be found, as shown by Ashmore (1984) who tested about 200 native British species. This is explained by different absorption rates of O_3 in leaves (Reich 1987) and/or by differences in tolerances to the absorbed O_3 (Chameides 1989). Most of the present species grow at altitudes up to 1500-2000 m in South Norway, and some of them also at very high latitudes. However, on the basis of the relatively few species tested here it is not possible to conclude whether alpine plant species are more or less sensitive than other plants. Reich (1987) classified agricultural crops as the most sensitive to O_3, hardwoods as moderately so and conifers as the least sensitive to O_3. In order to obtain a better understanding of the ecological influence of O_3 in the mountain regions, it is necessary to investigate additional alpine species in long-term O_3 exposure experiments at realistic concentrations.

The tropospheric O_3 concentration in Europe has been estimated to increase by about 1% per year (Hartmannsgruber et al. 1985). It would be very useful if some very sensitive alpine species could be identified and used as indicator plants with respect to O_3 effects on the ecosystems. In this connection it would be interesting to test *Phleum commutatum* which grows at altitudes of up to 1800 m in South Norway and latitudes of up to 70°N. This is because the genus *Phleum* seems to be very sensitive to O_3.

It is interesting to note that *Phleum pratense* was more affected by O_3 at low than at high temperatures. This is in accordance with previous results on *Betula pubescens* (Mortensen 1992b) and can be explained by a lower leaf diffusion resistance and higher O_3 uptake at the low-temperature regime as a result of a lower water vapour deficit and more open stomata at low temperatures than at high temperatures. Unfortunately, the species in Experiment 1 generally had a low sensitivity to O_3, and therefore any interaction between O_3 and temperature could not be stated for species other than *Phleum pratense*. However, in order to analyse the O_3 sensitivity of plants it seems important that experiments are conducted at realistic temperature and air humidity levels. In future, O_3 exposure experiments should include higher CO_2 concentrations than today's concentration of 350 µmol mol^{-1}, since the global CO_2 level is increasing rapidly (Idso 1989). The stomata of many plant species will partly close when the CO_2 concentration increases and this will decrease the O_3 absorption (Pearcy & Bjørkman 1983). The effect of O_3 will then be decreased as previously shown with wheat (Mortensen 1990).

ACKNOWLEDGEMENTS

This work was carried out as a part of the national work on «Critical loads» supported by the Ministry of Environment, and by the National Agricultural Research Council of Norway.

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Plasma level of growth hormone in two genetic lines of dairy cattle selected for high and low milk yield

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Klemetsdal, G., B. Tveit, M. Vingelen, J. Starova & K. Sejrsen 1992. Plasma level of growth hormone in two genetic lines of dairy cattle selected for high and low milk yield. Norwegian Journal of Agricultural Sciences 6: 205-210. ISSN 0801-5341.

The plasma level of growth hormone (GH) was studied in two genetic lines of dairy cattle differing by approximately 1200 kg of milk. Data on a total of 45 first and 42 second and third lactation cows fed grass silage *ad libitum* and kept on two fixed concentrate levels during the lactation periods were collected over two years in weeks 2-12 of lactation. The data were ln-transformed and analyzed with a repeatability animal model REML procedure which included main effects of the following interaction terms: stage of lactation (5) x genetic line (2) x feeding level (2) and year (2) x calving period (2). Results from the first lactation showed an overall significantly ($P<0.01$) higher level of GH in the high genetic line than in the low genetic line. Corresponding results were observed in the second and third lactation periods, but these were not significant ($P>0.05$). Additional analyses were carried out using weekly calculated energy balance, based on the Dutch feed evaluation system, as a covariate. Generally, this approach reduced the overall differences between all genetic lines x feeding level combinations, and none of them were significant ($P<0.05$).

Keywords: Animal model, energy balance, lactation physiology, REML, selection.

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In 1979 the Department of Animal Genetics and Breeding initiated a selection experiment in cooperation with NRF - the Norwegian Cattle Association. Two selection lines of dairy cattle representing different levels of milk production capacity were established at eight agricultural colleges. In these herds the following mating strategy was carried out every year:

High line: The cows were mated with the best bulls progeny- tested for milk production.

Low line: The cows were mated with the lowest ranking bulls, from the progeny-testing for milk production in 1978 and 1979.

In 1986, third generation progeny, with a difference of approximately 1000 kg between lines (Steine, 1986), were brought to the university farm for further studies. The main focus of interest was on the consequences of selecting for higher milk production capacity. Plasma level of growth hormone (GH) was among the parameters studied. The objective of this study is to present results obtained for the two lines in the first as well as in the second and third lactation periods.

MATERIAL

In the registration period grass silage was fed *ad libitum*. Roughage intake (RI) was measured weekly as average intake of a four-day period, while ordinary feedstuff analysis (Weende Method, e.g. Bondi, 1987) was carried out on samples collected during four-week periods. The same routine was carried out for concentrate, which was given completely according to stage of lactation. Animals from both selection lines were given two levels of concentrate feeding both in the first (Fig. 1) and in the second and third lactation periods (Fig. 2). The same animals were allocated concentrates at the same level over lactations. The project was carried out over a period of two years (1987/1988 and 1988/1989) and for both concentrates and grass silage, separate digestibility analyses were carried out on sheep. Milk yield was recorded twice a week and the protein, fat and lactose percentages were determined in one sample each week. Live weight was recorded twice first week after calving, and then once in the succeeding weeks. The level of growth hormone was determined by the methodology described by Purchas et al. (1970) from blood samples taken every Tuesday morning before feeding and every Tuesday evening two hours after feeding. Data were available on a total of 45 first lactation and 42 second and third lactation cows in weeks 2-12 *post partum*.

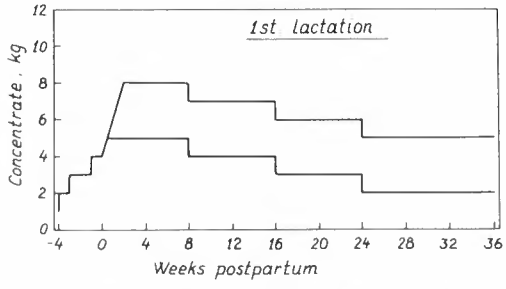


Fig. 1 Kg concentrates fed per day during the first lactation period

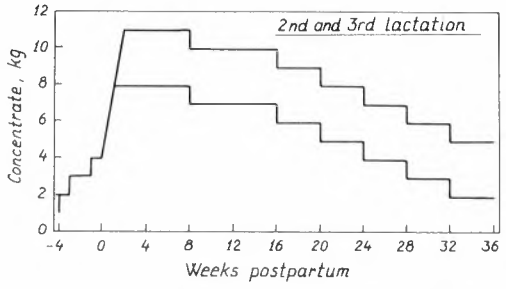


Fig. 2. Kg concentrates fed per day during the second and third lactations

METHODS

Individual energy balance

The weekly energy balance (EB) in VEM·d^{-1} was calculated as the difference between corresponding nutritive value of consumed grass silage (VEMgs) and concentrates (VEMc) and requirements for milk production (VEMmp) and maintenance (VEMma) as:

$$EB = VEMgs + VEMc - VEMmp - VEMma$$

Calculation of VEMgs and VEMc:
For both grass silage and concentrate, metabolizable energy (ME) and gross energy (GE) were calculated in $kJ \cdot kg^{-1}$ according to Van der Honing & Alderman (1988). The nutritive values, here shown for grass silage, were calculated with a slightly modified formula relative to Van Es (1975):

$$VEMgs = RI\ [0.6\ [1-0.004\ (100 \cdot \frac{ME}{GE} - 57)] \cdot 0.9752 \cdot ME/6.900]$$

Calculation of VEMmp:
The requirement for milk production was calculated by the multiple regression equation given by Van der Honing & Alderman (1988):

$$VEMmp = 440 \cdot ECM + 0.0007293 \cdot ECM^2$$

where ECM is $kg \cdot d^{-1}$ of energy-corrected milk yield calculated according to Saunja et al. (1990).

Calculation of VEMma:
Finally, the energy requirement for maintenance was found as:

$$VEMma = 42.4 \cdot V^{0.75}$$

where V is the weight of the cow.

Statistical methods
The level of GH and EB in the two selection lines allocated at two concentrate levels in five lactation periods (lactation week(s) 2, 3, 4-6, 7-9 and 10-12) making up a total of 20 subgroups were calculated and tested as fixed effects in a repeatability animal model. The estimates were corrected for four fixed interaction classes originating from the two years considered and two chosen calving periods (calving week < 45, calving week ≥ 45) in addition to random animal and permanent environmental effects. Additionally, energy balance was included as a covariate in the statistical analysis of GH.

A derivative-free REML algorithm and a computing program by Meyer (1989) were used to estimate variance components for growth hormone and back solutions for fixed effects. Data were ln-transformed to reduce impact of the periodic segregation of growth hormone on statistical inferences.

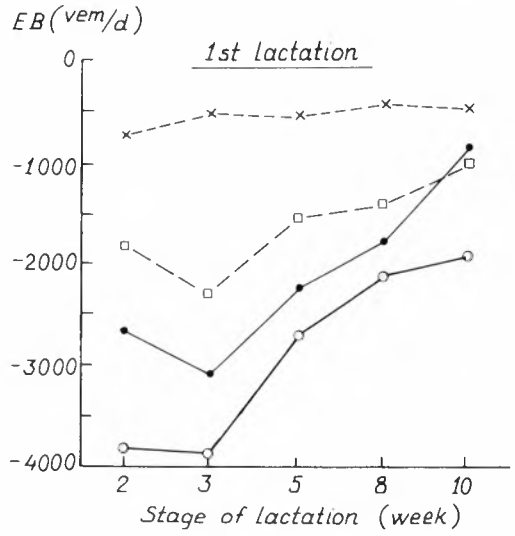
RESULTS AND DISCUSSION

Summary statistics for EB and ln-transformed GH (ln(GH)) are presented in Table 1, while Fig. 3 shows the energy balance in first lactation. The energy balance in the high line was more negative than that in the low line ($P < 0.01$) in first lactation period. Within lines the lowest values were observed at low concentrate levels. However, significant differences were only observed in the low line ($P < 0.01$).

Table 1. Total number of observations, and summary statistics for energy balance (EB) and ln-transformed GH (ln(GH)) in first, second and third lactation periods

Lactation	Variable	N	$\bar{x}$	Sd	Min	Max
1	EB	390	-992	1839	-185	-6997
1	ln(GH)	390	0.97	0.50	-1.20	2.95
2+3	EB	414	-1523	2424	-159	-10097
2+3	ln(GH)	414	1.08	0.51	-0.48	3.03

Fig. 3. Energy balance (EB) among first lactation cows in weeks 2-12 *post partum*

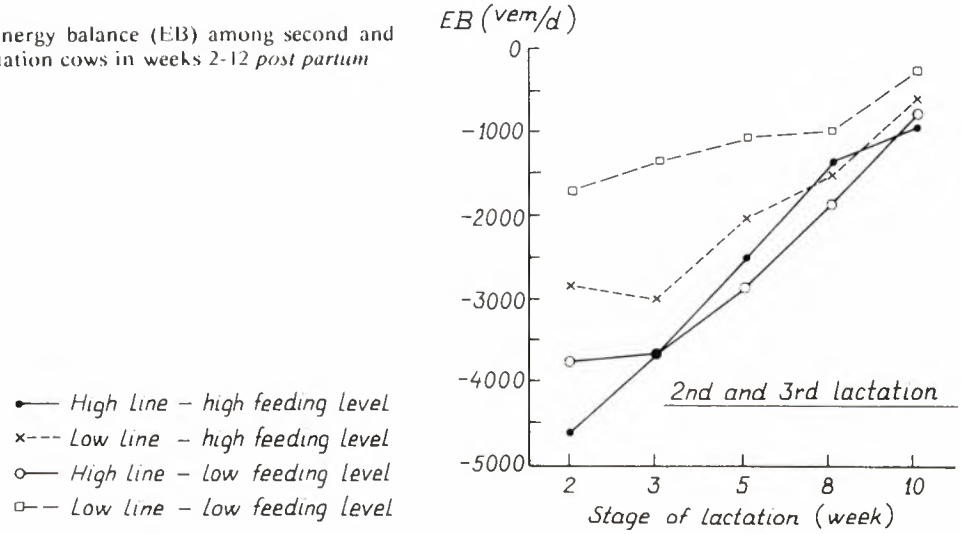


Corresponding results in the second and third lactation periods (Fig. 4) indicate a re-ranking of the four groups. In the low line the high concentrate group had a more negative energy balance than the low concentrate group ($P > 0.05$), while the energy balances in the high line were equal at the two concentrate levels. As in the first lactation, the energy balance was significantly lower ($P < 0.01$) in the high line than in the low line.

These results indicate effect of the concentrate level in the first lactation period on the energy balance in the later lactation periods. Potential utilization of this effect should be clarified in future research.

The level of ln(GH) in the first, second and third lactations is shown in Figs. 5 and 6, respectively. In both figures, the level of ln(GH) is somewhat higher in the high line at low concentrate levels than in the other groups. Further on, the low line on high concentrate level had lower values than the other groups in the first lactation. Although one should be aware of these tendencies, none of the selection lines x feeding level combinations were significant. In fact, correction for energy balance affected the results obtained, as exclusion of energy balance from the statistical model resulted in an overall significantly ($P < 0.01$) higher level of GH in the high than in the low genetic line in the

Fig. 4. Energy balance (EB) among second and third lactation cows in weeks 2-12 *post partum*



first lactation. Corresponding results obtained in the second and third lactation periods, however, were not significant. Thus, correction for energy balance reduced the differences between lines. The remaining variations between lines may be due to either unsatisfactory correction for energy balance or true genetic differences. The findings of Løvendahl et al. (1991) support the first theory as they did not find any difference in ln(GH) in heifers from the same selection lines after injection of growth-releasing factor (GRF). The correction for energy balance may be improved by correcting growth hormone for energy balance within lines. Furthermore, requirements for milk production and maintenance may also be different in the two lines. In an ongoing project the problem of different energy balance is reduced by pursuing the same underfeeding in both selection lines.

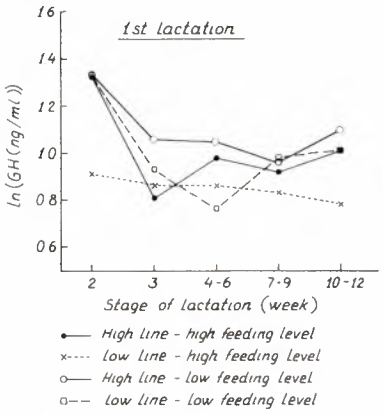


Fig. 5. Ln-transformed growth hormone (ln(GH)) level among first lactation cows in weeks 2-12 *post partum*

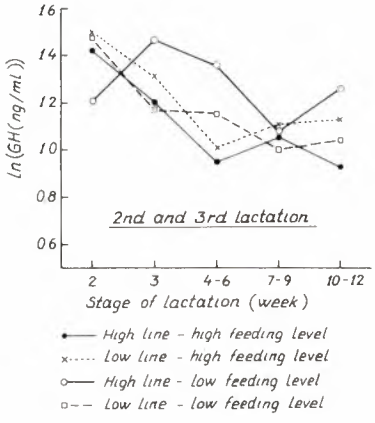


Fig. 6. Ln-transformed growth hormone (ln(GH)) level among second and third lactation cows in weeks 2-12 *post partum*

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Deepfrozen salmon: Differences in quality after storage at different temperatures following different storage periods

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Some effects of various sub-zero storage temperatures on quality of Atlantic salmon (*Salmo Salar*), were sensorically assessed. The fish were fed three different diets, containing 12, 17 and 22 % fat. After two months of storage at -30°C, the fish were kept at -13°C, -18°C and -35°C and sensorically assessed after one, three and five months. The two lowest temperatures were chosen as representing relevant domestic freezer temperatures while storage at -35°C was used as the control. Fish fed the medium fat diet (17%) were significantly less red and had less of a salmon taste. Fish stored at -35°C were significantly redder, had a better consistency, and were softer and juicier than fish stored at -13°C. The taste of fish oil increased during the six months of storage.

Key words: Deepfrozen salmon, fat content, sensoric assessment, ANOVA, PCA

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It is commonly believed that frozen salmon and other fatty fish become rancid after a few months' frozen storage because of the high content of unsaturated fatty acids which easily become oxidized, giving the fish a rancid smell and taste.

Experiments performed at SINTEF (The Foundation for Scientific and Industrial Research at the Norwegian Institute of Technology) indicated that the storage temperature in the freezer was important for the keeping quality of different kinds of fat fishes (salmon, trout, herring and mackerel). The results of these unpublished experiments are mentioned in NFFR (Norwegian Fisheries Research Council) yearbook 1988. According to this yearbook there was an improvement in the quality when storage temperatures were reduced to -60°C.

The aim of this experiment was to assess the possible effects of various sub-zero storage temperatures on the quality of salmon, following two months' storage at -30°C. Temperatures at -13°C and -18°C were chosen as representing relevant domestic freezer temperatures, and storage at -35°C was used as the control.

MATERIALS AND METHODS

Atlantic salmon *(Salmo Salar)* were fed three different diets containing 22, 17 and 12% fat. In November 1989 the fish were slaughtered, gutted and stored in ice for three days at 4°C before freezing. The gutted fish each weighed between 3 and 4 kg, and the length varied between 65 and 70 cm.

The fish were frozen in a nitrogen freezer where the temperature was regulated to about -60°C. The temperature was measured at two different places on the surface and inside the fish as illustated in Figure 1. After one hour the temperature inside the fish was -30°C (point 3 in the figure), while on the surface the temperature was respectively -44 and -38°C. The deepfrozen fish were cut with a meat saw. A portion of each fish, taken posterior to the dorsal fin and anterior to the adipose fin, was packed in plastic bags and kept at -30°C for two months. Parts of six fish from each of the diet fat categories were sorted and kept at -13, -18 and -35°C, two at each temperature, until they were sensorically evaluated after one, three and five months.

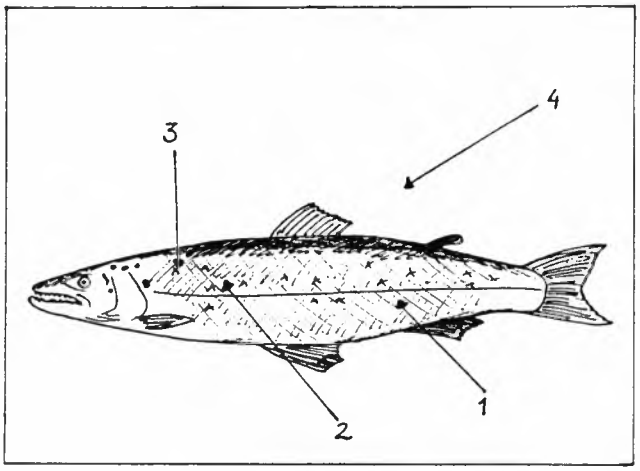

Figure 1. Temperature measurements during freezing in nitrogen. Points one and two measured on the surface of the fish. Point three inside the fish and point four in the freezer

Four to six assessors were chosen from the employees at the Department of Dairy and Food Industries and the Institute of Aquaculture Research. The fish samples were assessed at two sittings per day, nine samples at each sitting. The assessment included a 1-5 score for colour (redness), two consistency parameters (soft/hard, dry/juicy) and four parameters relating to taste (salmon taste, fish oil taste and rancidity). In addition, the assessors scored the consistency and the taste hedonically using a 1-5 scale.

The fish were removed from the freezer and thawed at room temperature. The following day the fish were still slightly frozen and so could easily be divided into cutlets 2-3 cm thick. The fish were cooked at 100°C for 15 minutes prior to sensoric assessment.

The results were treated statistically with an ANOVA-test, and a Principal Component Analysis (PCA) was performed to relate the parameters.

The following model was used for the ANOVA-test:

$$x_{ijkl} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + \gamma_k + (\alpha\gamma)_{ik} + (\beta\gamma)_{jk} + (\alpha\beta\gamma)_{ijk} + \varepsilon_{(ijk)l}$$

The value of each observation is given by the mean value plus the effects of fat content in the feed (α_i), the storage temperature (β_j), the storage time (γ_k) the interaction effects, and the error ($\varepsilon_{(ijk)l}$). The replicates (l) are treated as a random variable nested under the experiment factors which are considered to be fixed. The null-hypothesis was rejected at a level of five%. When significant effects were found, the Tukey's HSD-test was performed to test the differences between mean values (Tukey 1953).

RESULTS AND DISCUSSION

The fat content in fish diet significantly affected the colour (redness) and the taste of salmon as indicated in Table 1. The colour was significantly less red and the taste of salmon was less strong in fish fed 17% fat in their diet.

Storage temperature, as illustated in Table 1, affected colour, hedonic consistency, hardness and juiciness. The redness was significantly lower in the fish stored at -13°C than in fish stored at -18 or -35°C. The assessors preferred the consistency of the fish stored at -35°C as compared with that of fish stored at -13°C. The fish were harder and less juicy following storage at -13°C.

	fat content in fish diet (in percent)		
	12	17	22
redness	2.895a	2.542 b	2.708
taste of salmon	2.632	2.501b	2.797c
	storage temperature (°C)		
	-13	-18	-35
redness	2.411a	2.807b	2.927c
hedonic consistency	2.979a	3.098	3.252c
hardness	3.384a	3.227	2.969c
juicyness	2.539a	2.702	2.950c
	storage time (months)		
	2	4	6
taste of fish oil	1.202a	1.233	1.431c

Table 1. Significant differences ($p<0.05$) between fish fed different fat diets, stored at different freezing temperatures for different periods; mean values

a,b,c indicate significant differences within a row using Tukey's HSD-test

Storage time

After six months of storage the taste of fish oil significantly increased independent of the storage temperature and diet.

The PCA-plot
(Figure 3) illustrates the relationship between the different variables (colour, consistency, taste etc.) on two principal components (Factor 1 and Factor 2). The proportion of original variance explained by the two factors was 0.59. Factor 1 may be considered as a taste axis whereas Factor 2 describes variation in consistency. Taste of salmon, redness and juiciness are located in the positive part of the plot, whereas hardness, taste of fish oil and rancid taste are located in the negative part of the plot.

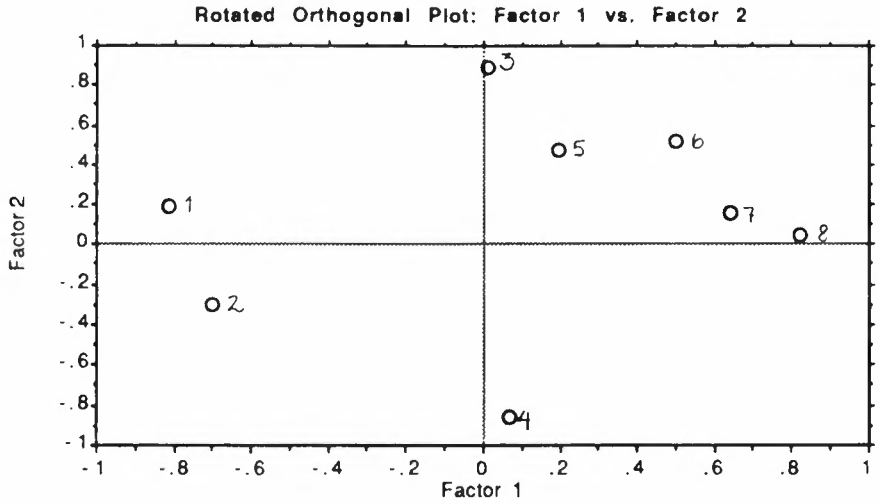

Figure 2. PCA-plot. Rotated Orthogonal Plot showing Factor 1 vs. Factor 2

(1) Taste of fish oil	(5) Redness
(2) Rancidity	(6) Hedonic consistency
(3) Juicyness	(7) Taste of salmon
(4) Hardness	(8) Hedonic taste

CONCLUSIONS

Fish fed a low fat diet and stored at -35°C kept their colour better than fish fed a high fat diet and stored at high temperatures. The consistency score was dependent upon storage temperature. The flavour was dependent on fat in diet and length of storage. Fish fed a high fat diet had a more salmon taste than fish fed low fat diets. The flavour of fish oil developed after six months, independent of diet fat content and storage temperature. The PCA-plot indicates that salmon taste, redness and juiciness were assessed as positive qualities, whereas hardness, taste of fish oil, and rancid taste were assessed as negative characteristics.

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Dormancy and germination of temperate grass seed as affected by environmental conditions - A literature review

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Aamlid, T.S. 1992. Dormancy and germination of temperate grass seed as affected by environmental conditions - A literature review. Norwegian Journal of Agricultural Sciences 6: 217-240. ISSN 0801-5341.

Knowledge about seed dormancy and germination in the grass family (*Graminae*) is important from both an ecological and economical point of view, and particularly with regard to seed testing. Seed dormancy can be grouped according to physiological mechanism (embryo dormancy vs. cover-imposed dormancy) or whether dormancy is imposed before (primary dormancy) or after (secondary dormancy) separation from the mother plant. Primary dormancy often dissipates within a few months after harvest, but it can be manifest for years. Low temperature during seed maturation aggravates primary dormancy and narrows the temperature interval conducive to germination. Secondary dormancy is most commonly imposed when moist seed is subjected to high temperatures or anaerobic conditions. Endogenous germination rhythms can sometimes be observed irrespective of storage condition and seed maturity. Remedies helpful in overcoming dormancy include dry afterripening at high temperatures, moist pre chilling, alternating temperature, light, KNO_3 and gibberellins. The use of these treatments in seed testing is outlined, and their physiological mechanisms are briefly discussed.

Key words: Afterripening, gibberellins, KNO_3, light, pre chilling, seed maturation, temperature.

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Besides the legumes, no family within the plant kingdom has greater economical importance than the grasses. Not only are all the cereals and most of the forages classified in this group, but the family *Gramineae* also encompasses some of the worst agricultural weeds. Because seed formation is the most widespread way of maintenance and multiplication within the family, factors controlling germination and establishment become crucial from both an ecological and an economical point of view. For the many seed-testing laboratories around the world, it is also essential to develop methods which give the correct germination capacity of a given seed lot within a minimum amount of time.

In this literature review, the emphasis will mostly be on seed dormancy and germination of the cultivated forages, but some references to cereals and weeds will be included for comparison. No attempt is made to cover seed vigor or other aspects of seed quality beyond those measured by ordinary germination tests.

THE OCCURRENCE AND CAUSES OF SEED DORMANCY

Seed dormancy is so common in grasses that it can be regarded as the rule rather than the exception (Simpson 1990). One of the most well-known examples is wild oats - *Avena fatua* L.; its ability to lie dormant in the soil for a number of years has made this weed notorious in grain-producing areas throughout the world. In the cereals, dormancy is also very significant, especially in connection with pre-harvest sprouting problems in wheat and barley (Strand 1965, King 1983, Ringlund 1987) and with utilization of barley in the brewing industry. Among the temperate turf and forage grasses, Simpson (1990) presents evidence of seed dormancy in smooth bromegrass (*Bromus inermis* L.), red fescue (*Festuca rubra* L.), tall fescue (*Festuca arundinacea* Schreb.), meadow fescue (*Festuca pratensis* Huds.), sheep fescue (*Festuca ovina* L.), perennial ryegrass (*Lolium perenne* L.), Italian ryegrass (*Lolium multiflorum* L.), Kentucky bluegrass (*Poa pratensis* L.), annual bluegrass (*Poa annua* L.), rough bluegrass (*Poa trivialis* L.), orchardgrass (*Dactylis glomerata* L.), reed canarygrass (*Phalaris arundinacea* L.), meadow foxtail (*Alopecurus pratensis* L.), timothy (*Phleum pratense* L.), colonial bentgrass (*Agrostis capillaris* L.) and creeping bentgrass (*Agrostis stolonifera* L.). Among the species with particularly deep dormancy, and thus the ability to form persistent seed banks in the soil, are rough bluegrass, annual bluegrass, colonial bentgrass and *Alopecurus geniculatus* L. (Williams 1983a, Synnes 1984, Netland 1985).

The physiological reasons for seed dormancy are complex and not completely understood. A distinction is often made between *embryo dormancy,* in which case the embryo is unable to germinate even when separated from the rest of the seed, and *coat-imposed dormancy*, where the endosperm, testa or pericarp (jointly comprising the seed coat) are responsible for the dormant condition and the embryo germinates when excised (Bewley & Black 1985). Since in many grasses the lemma and palea (often referred to as the hulls) are also attached to the mature caryopsis, any restraint to germination imposed by these structures is often included in the term 'coat-imposed dormancy' as well, but this is imprecise as the hulls are not a part of the seed coat. In the following sections, the term *cover-imposed dormancy* will be used when referring to both the seed coat and the hulls.

Cover-imposed dormancy

According to Bewley & Black (1985), the tissues surrounding the embryo can have the following effects on germination:

1. Mechanical restraint
2. Interference with gas exchange
3. Interference with water uptake
4. Prevention of the exit of inhibitors from the embryo
5. Supply of inhibitors to the embryo.

In the grasses, there is no indication that either the hulls or the pericarp is rigid enough to prevent the protrusion of the radicula or the coleoptile (Simpson 1990). On the other hand, there is considerable evidence that the lemma and palea may restrict the availability of oxygen to the caryopsis. Canode et al. (1963) found that removal of the hulls increased germination by 13-16 per cent units in orchardgrass. Since water absorption

was similar in hulled and dehulled seeds, the authors inferred that the main impact of the appendages was impedance of gas exchange. Increasing the partial pressure of oxygen can partially overcome dormancy in hulled seeds of wild oats and barley (Bewley & Black 1985).

Unfortunately, few anatomical studies have attempted to explain the role of the lemma and palea in seed dormancy. Some investigations suggest that a lipid layer in the inner epidermis of the lemma can interfere with both water and gas exchange. From rice it is known that a high peroxidase activity in the hulls may compete with the embryo for oxygen in the initial stages of germination (Simpson 1990).

In addition to the hulls, the seed coat may also form a barrier to oxygen and water absorption. Puncturing the seed coat, especially adjacent to the embryo, improved germination of naked caryopses of wild oats (Simpson 1990), orchardgrass (Probert et al. 1985c), and reed canarygrass (Junttila et al. 1978). Whether the interference with gas or water movement is the more significant factor is apparently a matter of controversy. Since the water uptake has often been observed to be similar in intact and punctured caryopses, many authors have concluded that oxygen must be the more critical factor (Atwood 1914, Probert et al. 1985c). Soaking dormant seed of reed canarygrass in oxygen-saturated water led to a 73% germination as opposed to only 25% for seed that were soaked in unaerated, still water (Landgraff & Junttila 1979). The authors stressed the importance of oxygen in breaking dormancy. Simpson (1990), on the other hand, argued that differences in embryo water potential and in the water permeability of the seed coat at increasing distances from the embryo could cause various water absorption curves for intact and punctured caryopses. The fact that previously soaked and dried seed of orchardgrass absorbed nearly 70% more water than untreated seed during the first three hours of imbibition (Chippindale 1933), was taken as supporting the latter theory.

The role of germination inhibitors in grass seed dormancy is not clear. Some experiments indicate that the hulls of wild oats contain inhibitors, but there are conflicting reports as to whether these compounds are able to prevent germination in wild oats caryopses or only in other species (Simpson 1990). In a study on germination of various grasses and legumes in leachates from the same or other species, Cope (1982) found that none of the grasses was inhibited by leachate either from its own seed or from other grasses; on the other hand, leachates from ryegrass and orchardgrass hampered germination of many legumes. Although Vose (1962) found evidence for a water-soluble germination inhibitor in reed canarygrass caryopses, Landgraff & Junttila (1979) were unable to discover any dormancy-related inhibitor in extracts from the same species. Conversely, Fendall & Canode (1971) determined that growth inhibitors were present in both hulls and caryopses of one particularly dormant variety of orchardgrass. Seed extracts retarded the growth of seedlings of both lettuce and orchardgrass; however, the variability within treatments was greater for the latter species. This is compatible with Evenari (1949), who noted that most germination inhibitors are non-specific and that there is nearly always an association between germination and seedling growth.

Embryo dormancy

Separation of embryos from the covering structures in wild oats has revealed that this species often possesses some degree of true embryo dormancy. Although some embryos germinated readily after excision, others were still dormant after three years of after-

ripening. Normal germination could be obtained by adding gibberellin to the germination medium which would otherwise contain sugars, amino acids and vitamins (Simpson 1990).

Although there are some indications of embryo dormancy in wheat and barley (Norstog & Klein 1972, Gaspar et al. 1977), it seems probable that the long domestication process has eliminated most of this 'wild' character in the cereals. The forage grasses are more likely to have preserved some embryo dormancy; however, the small seed size makes studies with excised embryos complicated and the literature is therefore meager. In many cases the existence of embryo dormancy has been deduced from the lack of any apparent effect of hulls or seed coat on water absorption or oxygen uptake (Maguire 1969). There is, nevertheless, increasing evidence that the constitution of cell membranes somehow plays a key role in true embryo dormancy (Bewley & Black 1985).

CONCEPTS RELATED TO THE TIMING OF DORMANCY

Primary dormancy, the most universal type of dormancy in the grasses, evolves when the seed is still attached to the mother plant. Usually it is at its deepest before the seed attains maximal dry weight (i.e. well before harvest), and then it dissipates with time until some weeks or months after harvest (e.g. Delouche 1958, Bass 1965). The term *'fresh-seed dormancy'* is frequently used when the primary dormancy is of comparatively short duration; however, there are examples in which grass seed has retained the dormant condition for years (Canode et al. 1963, Fendall & Canode 1971). Such prolonged dormancy may be a special characteristic of populations from high latitudes (Junttila 1977).

The term *afterripening* is often given different interpretations (Simpson 1990), but one reasonable definition seems to be 'the internal processes in the seed that lead to loss of dormancy'. These processes are highly dependent on environment; if conditions are not appropriate, the primary dormancy may, to the contrary, be reinforced.

Under some circumstances, *secondary dormancy* may be induced in seeds which have lost the primary form. According to Bewley & Black (1985), seed may also pass directly from the primary to the secondary state, or the secondary state may be superimposed on the primary one (Simpson 1990). Sveinsson (1987) observed that Icelandic strains of Kentucky bluegrass increased in dormancy during the period from physiological maturity until harvest, quite unlike the normal pattern reported earlier (Delouche 1958, Bass 1965, Phaneendranath et al. 1978). The author suggested that cool and moist weather could lead to secondary dormancy being imposed when the seed was still attached to the mother plant. However, in order to avoid any ambiguity, it seems most consistent to confine 'secondary dormancy' to instances where the dormant condition is reintroduced in non-dormant seed after harvest, in agreement with the definition proposed by Khan (1982). The distinction between primary and secondary dormancy is then reduced to a question of time, as there is no evidence of any difference in physiological mechanisms between the two forms (Bewley & Black 1985).

The state of dormancy, whether primary or secondary, is usually not absolute, but rather just a narrowing of the environmental conditions under which germination will occur. As stated by Simpson (1990), it is not the isolated character of the seed, but the total seed-environment system which prohibits or permits germination. C

this, Vegis (1964) introduced the term *relative dormancy*. Because temperature is the single most decisive factor governing germination in partly dormant seed, a related, but more specific term is *thermodormancy*.

Sometimes, seed may show fluctuations in germination independent of maturity or storage conditions (Kummerow 1965). Maguire (1969) observed that germination of two varieties of Kentucky bluegrass declined sharply three to four months after harvest; then there was an increase followed by a similar decline after six to seven months (Figure 1). Pronounced germination minima in February have been reported for bentgrass (Leggatt 1946) and timothy (Gordon 1951); by contrast, Froud-Williams et al. (1986) observed that germination of rough bluegrass fell markedly in the period between six and 12 months of storage, and Korjakina (1937, cited by Kummerow 1965) found two annual minima to occur in December/January and June/July for a number of grasses. These '*endogenous germination rhythms*' may be interpreted as a special type of 'biological clock' (Maguire 1969), but the way they operate and their relationship to the primary and secondary forms of dormancy remain somewhat fuzzy.

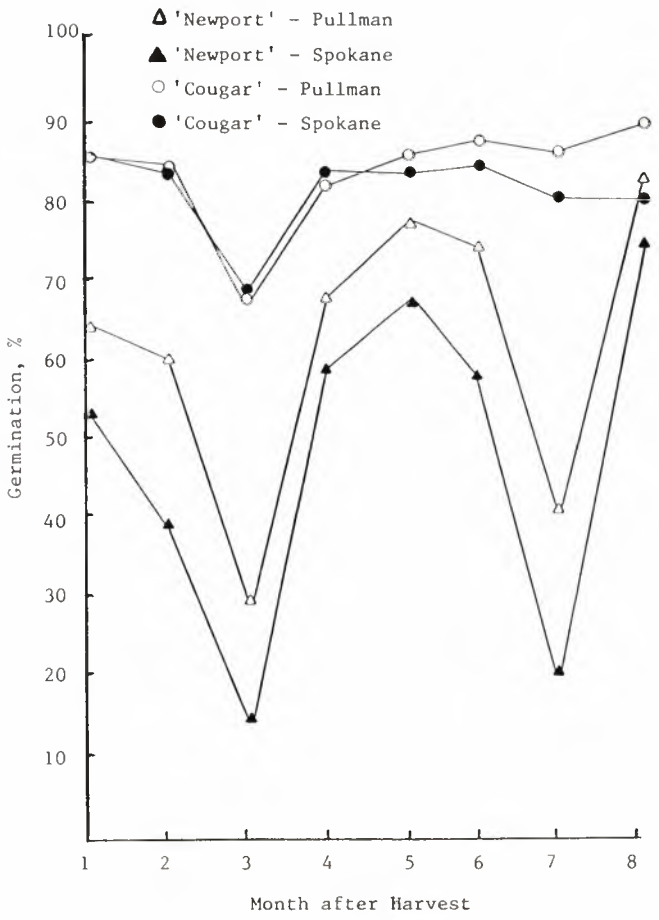

Figure 1. Endogenous germination rhythm in seed of Kentucky bluegrass 'Newport' and 'Cougar' grown at Pullman and Spokane, USA. (After Maguire 1969)

EFFECTS OF TEMPERATURE AND WATER RELATIONS ON THE IMPOSITION OF PRIMARY DORMANCY

Low temperatures during seed maturation induce dormancy in grass seed (Kearns & Toole 1939, Wiesner & Grabe 1972, Boyce et al. 1976, Probert et al. 1985b, Curran & McCarthy 1986). Seed of wild oats was more dormant when subjected to a day/night temperature of 20/15°C than to a constant 20°C during panicle development (Simpson 1990). While a temperature of 9°C during seed maturation caused considerable dormancy in Scandinavian strains of wheat, triticale and barley, seed exposed to temperatures of 15°C and 21°C was virtually non-dormant (Buraas & Skinnes 1985). There is, however, at least one report (Grahl1975) which indicates that excessively high temperatures during the last stages of seed maturation may exacerbate, rather than relieve, seed dormancy in wheat.

Water stress on the mother plant during seed development reduces seed dormancy in barley (Aspinall 1965) and wild oats (Peters 1982). Conversely, a wet climate will often reinforce dormancy, especially if the seed is harvested at a high moisture content (Phaneendranath et al. 1978). Sveinsson (1990) discovered a great disparity in germination capacity of Icelandic varieties of Kentucky bluegrass grown in a warm/dry and a cold/wet season (Figure 2). Since the viability as determined by tetrazolium analyses was the same in the two years, the difference could be entirely attributed to seed dormancy. Despite these obvious relationships, it seems difficult to predict dormancy levels in seed from meteorological data alone (Grahl 1975, Simpson 1990).

EFFECTS OF TEMPERATURE AND SEED MOISTURE ON THE RELEASE, MAINTENANCE AND REIMPOSITION OF DORMANCY AFTER HARVEST

Afterripening of dry seed at high temperatures reduces dormancy in wild oats (Simpson 1990), wheat (Hagemann & Chia 1987) and barley (Strand 1965). Heating at 30-35°C (ISTA 1985) is therefore the most common way of overcoming dormancy in cereals, but similar results have been reported for Kentucky bluegrass as well (Phaneendranath & Funk 1981). Simpson (1990) suggested that the advantageous effect of high-temperature afterripening can largely be ascribed to dehydration, as low temperatures favor high relative humidities and vice versa. This seems reasonable when germination is restricted by the permeability of the hulls or seed coat, but it appears dubious for true embryo dormancy, which is more biochemical in nature. This is substantiated by the numerous reports indicating that low temperatures sustain, rather than alleviate dormancy, even when the seed is kept at very low relative humidities (Kearns & Toole 1939, Phaneendranath & Funk 1981, Probert et al. 1985d). Boyce et al. (1976) in fact prescribed storage in a desiccator at 5°C as a way of preserving primary dormancy in tall fescue seed.

When seed is kept at a high moisture content the effects of high vs. low temperatures on dormancy are reversed. While pre chilling of moist seed at low temperatures will be treated in a separate paragraph, the combination of high temperatures and moist seed often results in secondary dormancy (Grahl 1965, Naylor & Abdalla 1982, Phaneendranath & Funk 1981). Because such dormancy can also be induced by keeping seed under anoxic conditions, for example in an atmosphere of nitrogen, it is probably related to the reduced solubility of oxygen at high temperatures, or alternatively, to a

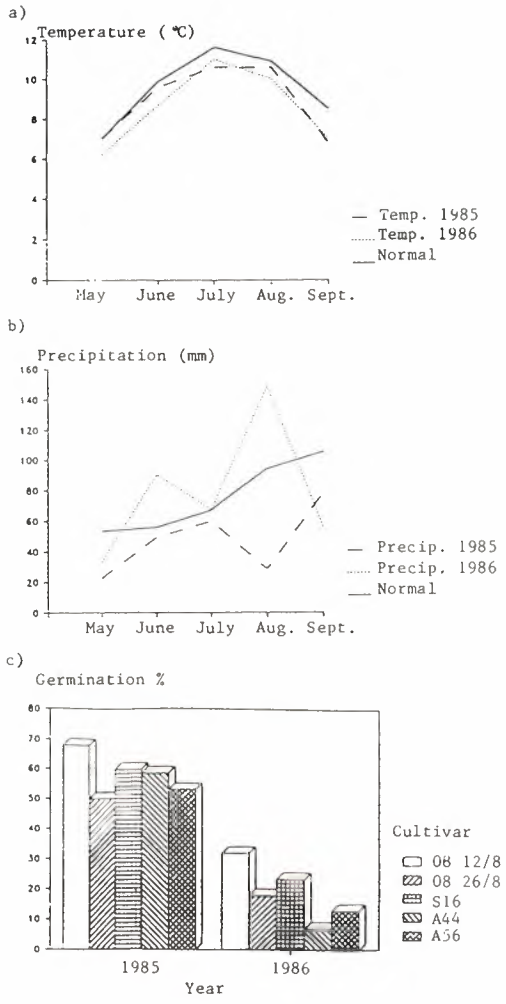

Figure 2. Germination capacity (c) of various Icelandic varieties of Kentucky bluegrass grown in 1985 and 1986; two years with great differences in temperature (a) and precipitation (b). (After Sveinsson 1990)

difference in the demand for oxygen in seed metabolism (Simpson 1990). In wild oats it has been shown that the secondary dormancy directly affects the caryopsis, most likely the embryo, and that the hulls are not involved (Hay 1962, Khan 1982).

To conclude this section, a summary of the combined effects of seed water content and temperature on dormancy after seed harvest is presented in Figure 3.

	Low temperature	**High temperature**
Moist seed	Prechilling Dormancy reduced	Induction of secondary dormancy
Dry seed	Afterripening delayed. Dormancy prolonged	Afterripening enhanced. Dormancy reduced

Figure 3. Combined effects of temperature and seed moisture on the release, maintenance and reimposition of dormancy after harvest

PRE CHILLING

Stratification is an ancient remedy for increasing seed germination in many trees and scrubs. For such seed, a one to 12 months' treatment at 1-5°C might be necessary in order to overcome dormancy. In the case of grasses, a much shorter period is usually required, and the optimum temperature seems to be somewhat higher. For example, Canode et al. (1963), Kearns & Toole (1939) and Curran & McCarthy (1986) concluded that seven days at 5°C was effective in breaking dormancy of orchardgrass, *Festuca spp.* and barley, respectively, and Bass (1955) and Grabe (1955) prescribed five days at 10°C as appropriate treatments for dormant seed of Kentucky bluegrass and smooth bromegrass. There are, nevertheless, also examples that dormancy of tall fescue seed can be broken by 48 days prechilling at 1°C (Boyce et al. 1976), and Junttila (1977) found that a period of at least four weeks at 4°C was required to obtain maximum germination in Norwegian populations of orchardgrass.

From an ecological point of view, it seems quite plausible that dormancy of temperate grasses is broken by frost during the winter months. This may well be the case in the field, where freezing, or repeated freezing and thawing, can increase the permeability of the seed coat and hulls. On the contrary, freezing temperatures during the pre chilling period do not reduce dormancy nearly as much as temperatures above 0°C. Sprague (1940) in fact reported that seven days at -5°C after imbibition diminished both the speed of germination and germination capacity in Kentucky bluegrass.

Provided that light is supplied during the high temperature phase of the subsequent germination treatment, it seems to have little bearing whether pre chilling is carried out in light or darkness (Landgraff & Junttila 1979, Sveinsson 1987, ISTA 1985).

EFFECTS OF CONSTANT AND ALTERNATING TEMPERATURE ON SEED GERMINATION

In most temperate grasses seed dormancy is manifest as the inability to germinate at high temperatures. The deeper the dormancy, the lower the temperature that is required to obtain germination. While non-dormant seed of wild oats has a germination optimum at 18-20°C, a temperature of close to 0°C may be necessary to elicit some germination of freshly harvested seed (Simpson 1990). For red fescue, Kearns & Toole (1939) reported 10°C as the optimum temperature for fresh seed, but some months later, a constant temperature of 15°C or 20°C gave a higher speed of germination and a higher germination capacity.

Many of the early workers on grass seed physiology sought to establish cardinal temperatures for germination (Lehmann & Aichele 1931), but failed to clarify the state of dormancy, and sometimes even the chronological age, of the seed they used. For example, it seems fairly obvious that Haberlandt (1879, cited by Lehmann & Aichele 1931) worked with non-dormant seed of timothy when he determined the minimum, optimum and maximum constant temperatures to be 3-4°C, 26°C and 30°C, respectively. On the other hand, it is just as likely that some dormancy existed in the Kentucky bluegrass material for which Gassner (1930) and Maier (1933) reported the optimum germination temperature to be 12°C. Kreysing (1924) concluded that 4.75°C, 18-20°C and 38°C were minimum, optimum and maximum constant temperatures for

germination of meadow fescue; these can probably be considered as typical for non-dormant seed of most temperate grasses. From Figure 4, which illustrates typical temperature curves for germination of tall fescue (Danielson & Toole 1976), it can be seen that the temperature optimum for germination rate (Maguire 1962) will normally be somewhat higher than that for germination capacity.

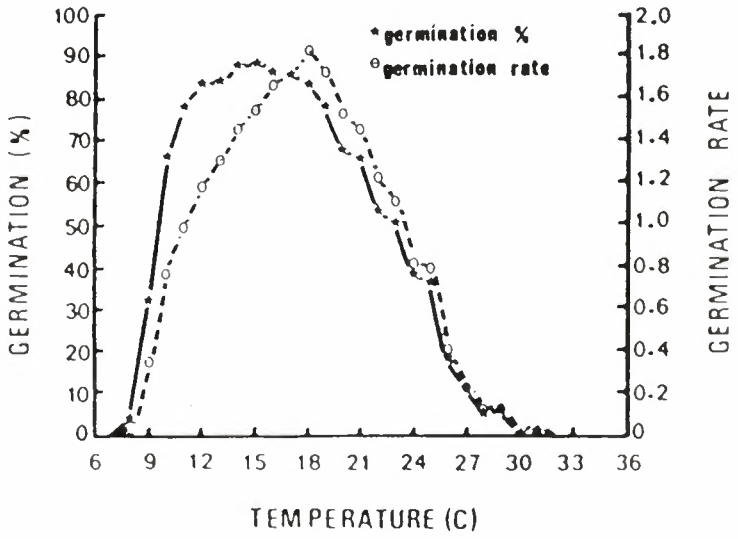

Figure 4. Per cent germination and germination rate (Maguire 1962) of non-dormant seed of tall fescue at various constant temperatures. (After Danielson & Toole 1976)

The promotive effect of alternating temperatures on seed germination has been known for at least 100 years. For example, Liebenberg (1884, cited by Lehmann & Aichele 1931) established that Kentucky bluegrass germinated better when kept at 20°C for 19 h and at 28°C for 5 h each day than at a constant temperature of either 20 or 28°C. Similar results were obtained by Gassner (1930) and Maier (1933), also working with Kentucky bluegrass. Harrington (1923) stated that 'the favorable effect of an alternation of temperatures upon the germination of certain kinds of seed cannot be referred to the specific effect of the extreme temperatures of the alteration or the mean temperature of the alteration, but are the result of the changes in temperature'. This view has later found general acceptance.

With the exception of orchardgrass (Harrington 1923, Sprague 1940) and *Agrostis* spp. (Andersen 1946, Schönfeld & Chancellor 1983), most temperate grasses are less dependent on temperature alterations than Kentucky bluegrass (Lehmann & Aichele 1931, Chippindale 1949). Harrington (1923) in fact found that timothy, smooth bromegrass, meadow fescue, perennial ryegrass and annual ryegrass germinated almost as well at constant as at alternating temperatures. Mention was not made of seed age in Harrington's work, however, and several other investigations have proved that temperature alterations usually enhance germination in freshly harvested seed of these species as well (Kearns & Toole 1939, Andersen 1947, Nakamura 1962, Boyce et al. 1976). For different fescue species, Kearns & Toole (1939) found that both seed age and seed ripeness at harvest influenced the superiority of alternating as compared with constant temperatures.

A number of attempts have been made to model the positive effects of alternating temperatures or to explain them physiologically. The approach taken by Murdoch et al. (1989) seems fruitful in that it systematically splits the temperature effect into different components (Figure 5). Among the seven primary characteristics, most attention has been devoted to maximum and minimum temperature and time per cycle below and above the mean temperature. If the periodic time is considered equal to the diurnal cycles (24 h), the number of cycles designates germination time, which is of course a very essential characteristic as well. The rates of warming and cooling were found by Cohen (1958) to have little or no effect; this explains why consistent results have been obtained both by transferring germinating seeds between chambers maintained at constant temperatures (e.g. Harrington 1923, Junttila 1977), and by heating and cooling a single chamber or germination table. In the latter case, a gradual change lasting up to three hours is generally accepted by ISTA (1985).

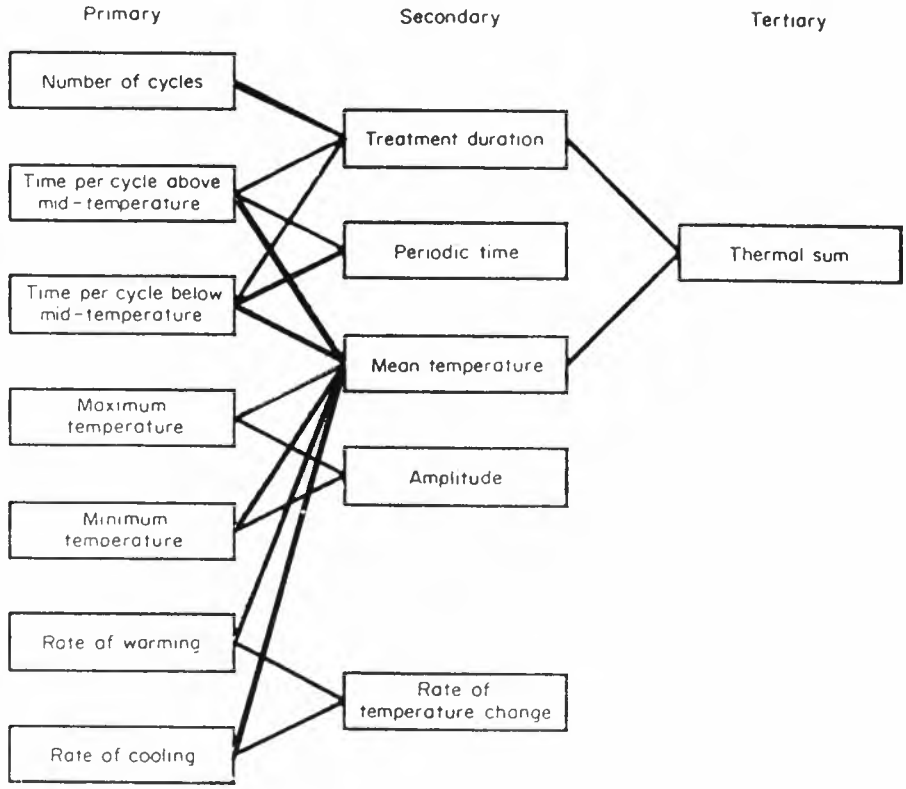

Figure 5. Primary, secondary and tertiary characteristics of an alternating temperature pattern. (After Murdoch et al. 1989)

A particularly useful instrument for evaluating germination response to various temperature regimes is the thermogradient plate (Larsen 1971). This apparatus allows the continuous variation of temperature in two directions, one during the day and the other during the night phase. The results of a germination experiment on such a plate are

illustrated for non-dormant and dormant seed of tall fescue in Figure 6 (Boyce et al. 1976). Under constant temperature conditions (Figure 6D-E), non-dormant seed showed a high germination capacity at 20-25°C constant temperature; by contrast, dormant seed germinated only at 10-20°C, and even then at a rather low percentage. Under alternating temperatures (Figure 6C-A and F-H) the average germination of non-dormant seed declined, whereas the reverse occurred for the dormant seed. For the latter group the effect of low vs. high temperature duration was also spectacular, as higher germination percentages were obtained when the lower temperature was kept for the longer part of the diurnal cycle than vice versa. The germination percentage was thus much higher when 25°C was maintained for 16 or 20 h and 15°C for 8 or 4 h than with the opposite combinations (Figure 6F-G). This is in good agreement with a number of early investigations (Harrington 1923, Gassner 1930, Lehmann & Aichele 1931, Maier 1933). Danielson & Toole (1976) found that germination of tall fescue was significantly reduced when seeds were held longer than 16 h at 25, 8 h at 30 and 4 h at 35°C in daily alternations with 15°C.

From an experiment with different durations of the low and high temperature phases in the germination of dormant orchardgrass populations from North Norway,

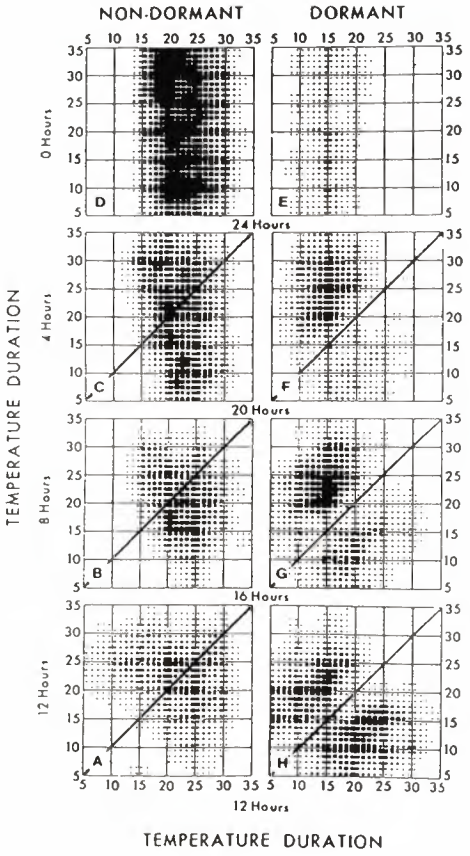

Figure 6. Germination of non-dormant and dormant seed of tall fescue on two-way thermogradient plates with different durations of the two temperature phases. The diagonal lines in A-C and F- H represent areas with constant temperatures. (After Boyce et al. 1976)

Junttila (1977) concluded that even one hour at high temperature increased the germination percentage significantly as compared to the constant temperature control. A further stimulation, especially with regard to speed of germination, was recorded as the high temperature break was extended to two or four hours. For Kentucky bluegrass, Gassner (1930) found that a high + low temperature pattern of 8 + 16 h provided more rapid germination than a 2 + 22 h pattern, although the final germination percentage was the same for the two combinations. The International Rules for Seed Testing prescribe that the higher and lower temperatures be maintained at 8 and 16 h, respectively (ISTA 1985). There are, however, also indications in the literature that an equiperiodic alternation (12 + 12 hours) produces results similar to the 8 + 16 h pattern (Boyce et al. 1976).

Although some reports indicate that certain maximum and minimum temperatures are better than others (Andersen 1941, Bass 1959, Tonkin 1981), many combinations within the range 10-30°C seem equally effective in stimulating germination of temperate grass seed (e.g. Sprague 1940, Bass 1955, Grabe 1955). Consequently, the International Seed Testing Association gives its member laboratories a certain freedom of choice with regard to test temperatures (Table 1 - ISTA 1985). With the exception of ryegrasses, where a constant 20°C is still optional, a prerequisite is always that the temperature amplitude is maintained at 10°C or more. This is in concurrence with early experiments indicating that a 5°C amplitude was too narrow to elicit maximal germination of dormant seed samples (Harrington 1923, Gassner 1930).

Table 1. Temperatures used in germination tests and treatments recommended to break dormancy in some temperate grasses (ISTA 1985)

Species	Temperatures, °C	Dormancy breaking treatment
Agrostis spp.	20-30, 15-25, 10-30	Prechill, KNO_3
Alopecurus pratensis	20-30, 15-25, 10-30	Prechill, KNO_3
Avena sativa	20	Preheat (30-35°C), prechill, GA_3
Bromus inermis	20-30, 15-25	Prechill, KNO_3
Dactylis glomerata	20-30, 15-25	Prechill, KNO3
Festuca spp.	20-30, 15-25	Prechill, KNO3
Hordeum vulgare	20	Preheat (30-35°C), prechill, GA_3
Lolium spp.	20-30, 15-25, 20	Prechill, KNO3
Phalaris arundinacea	20-30	Prechill, KNO_3
Phleum pratense	20-30, 15-25	Prechill, KNO_3
Poa pratensis	20-30, 15-25, 10-30	Prechill, KNO_3
Poa trivialis	20-30, 15-25	Prechill, KNO_3
Secale cerale	20	Prechill, GA_3
Triticum aestivum	20	Preheat (30-35°C), prechill, GA_3

Among the hypotheses explaining the positive effect of temperature fluctuations, the one advanced by Liebenberg (1884, cited by Lehmann & Aichele 1931) still seems quite plausible. According to this theory, the increased respiration during the high temperature break is necessary to facilitate metabolites required for embryo growth in the low temperature phase. As different biochemical reactions within the seed have different

temperature optima, a daily alternation of temperature might be required to attain a favorable balance of the various steps leading to germination (Toole et al. 1956).

LIGHT

The question of whether seed germination of some grass species, notably Kentucky bluegrass, was stimulated by light was strongly debated during the first decades of this century. Many authors, including Nelson (1927), found light to be unnecessary, and Gassner (1930) stated that the apparent light-stimulation of germination in some experiments was an artifact caused by heat radiation with concomitant temperature fluctuations. As pointed out by Lehmann & Aichele (1931), one reason for this confusion must have been a lack of knowledge of the early work by Jönsson (1893), in which light was proved to be necessary only for freshly harvested, dormant seed. This has later been confirmed by at least two reports (Bass 1951, Delouche 1958). Simpson (1990) made the general statement that 'fully after-ripened seed germinate equally well in light and dark over a wide temperature range'.

Light triggers germination of dormant seed, not only in Kentucky bluegrass, but also in annual bluegrass (Roberts & Benjamin 1979, Netland 1985), rough bluegrass (Froud-Williams 1985), bentgrasses (Andersen 1946, Bass 1959, Toole & Koch 1977, Williams 1983a, Thompson 1989), tall fescue (Danielson & Toole 1976), timothy (Gordon 1951, Thompson 1989), and reed canarygrass (Junttila et al. 1977, Landgraff & Junttila 1979). In orchardgrass, populations from northern Europe require light for germination, whereas long photoperiods can induce secondary dormancy in varieties from the Mediterranean area (Probert et al. 1985a). For the ryegrasses, meadow fescue, red fescue and smooth bromegrass there are conflicting reports (Kearns & Toole 1939, Chippindale 1949, Nakamura 1962, Williams 1983a, b, Thompson 1989, Grabe & Bass 1954, Grabe 1955); it seems that these grasses are less influenced by light than those mentioned above, even for freshly harvested seed. Some authors have pointed out that light may lower the speed of germination while increasing the final germination percentage (Kearns & Toole 1939, Leggatt 1946, Andersen 1946). This might be an artifact, however, as seedlings grown in darkness are often longer and more difficult to evaluate because of etiolation. For this reason, ISTA (1985) generally recommends germination in light, even for cereals and other species that germinate equally well in darkness.

For some wild grass species, light has been shown to inhibit germination. The most prominent examples are the annual bromegrasses *Bromus sterilis* L. and *Bromus erectus* L. (Hilton 1984, Thompson 1989).

A very early attempt to determine the effect of light quality on germination was conducted by Cieslar (1883, cited by Lehmann & Aichele 1931) who found that white and yellow light had equivalent effects on germination of Kentucky bluegrass, whilst blue light resembled the influence of darkness. Almost 70 years later, Bass (1950) showed intermediate wavelengths (520-700 nm) to be more promotive to germination of Kentucky bluegrass than light in the blue or red-farred part of the spectrum. However, it was the discovery of the phytochrome system in lettuce seed (Borthwick et al. 1952) that prepared the way for our present understanding of the effect of light on germination (Bewley & Black 1985). The active form of the phytochrome pigment is Pfr, and the Pfr/(Pr + Pfr) ratio must exceed a certain threshold level in order to facilitate ger-

mination of positively photoblastic seeds. Conversely, photoinhibition of germination in *Bromus sterilis* L. is mediated by too high a Pfr/(Pr + Pfr) ratio (Hilton 1984). Repeated radiation with red and farred light proved the key role of phytochrome for germination of dormant seed of Kentucky bluegrass (Toole & Borthwick 1971), reed canarygrass (Landgraff & Junttila 1979) and tall fescue (Danielson & Toole 1976). Various light requirements among orchardgrass populations were explained by Probert et al. (1985a) as differences in the pre-existent level of Pfr. The latter authors also explained the induction of dormancy at high constant temperatures as being due to Pfr reversion to Pr or decay of total phytochrome. Alternatively, synthesis of phytochrome might only occur below a certain temperature threshold, somewhere in the range of 15-25°C (Danielson & Toole 1976).

In 1933 Maier reported that the light quantity required to increase germination of various bluegrasses was remarkably low; even one second of illumination with fluorescent light had a significant effect in *Poa nemoralis* L. This is compatible with current information that the conversion from Pr to Pfr is saturated by as little as 100 J m^{-2} of red light, which is less than one-hundredth of the energy in all visible wavelengths provided by sunlight during a one-minute period (Salisbury & Ross 1985); it is indeed a *low energy reaction* (LER). Some attributes of light germination cannot be explained by the LER, however. While a 10-minute daily illumination with high-intensity fluorescent light strongly promoted germination of Kentucky bluegrass at 20°C constant temperature, continuous light reduced germination to the same level as that of dark controls (Toole & Borthwick 1971). Concurrently, Netland (1985) obtained better germination of annual bluegrass with a 12 h photoperiod than with continuous light, and Landgraff & Junttila (1979) found that more than three days of continuous light lowered the germination capacity in reed canarygrass. Similar effects have been reported for other grasses (Ellis et al. 1986) and are often explained as a *high energy reaction* (HER - Toole 1973).

Unlike the LER, the HER seems to be fairly insensitive to wavelength, but strongly dependent on fluence rate; even red light may inhibit germination provided the photon flux density is high enough (Bartley & Frankland 1982). However, Hendricks et al. (1968) demonstrated that wavelengths of about 720 nm are far more efficient in inhibiting germination than shorter ones. This is close to the 730 nm absorption maximum for Pfr, and it has been argued that the HER is not an independent system, but solely a consequence of Pfr destruction below a critical level or displacement of Pfr from its place of action (Toole 1973).

In a recent paper, Thompson (1989) compared germination of a number of grasses under different photon fluence rates and photoperiods. At a constant temperature of 15°C, red fescue and sheep fescue germinated equally well regardless of treatment, and timothy and rough bluegrass were suppressed only by complete darkness. The most interesting response was obtained with colonial and creeping bentgrass which, at a constant temperature, had a 20-30% germination in a 12 h photoperiod but only 0-3% in continuous light, despite the energy level being the same in both treatments. This result is hard to reconcile with the HER; on the other hand, it suggests that photoperiodism is involved.

KNO_3 AND OTHER CHEMICALS

Although some papers present conflicting results (Kearns & Toole 1939, Froud-Williams 1985), the positive effects of some nitrogen-containing compounds on the germination of grasses have been recognized throughout the last century (e.g. Hite 1920, Lehmann & Aichele 1931, Andersen 1941, Roberts & Benjamin 1979, Netland 1985). As for the light and temperature requirements, many early reports are difficult to interpret because no attention is paid to the afterripening state of the seed. There is appreciable evidence, however, that the same basic dependence on seed age and maturity applies for chemical as for physical stimuli of germination.

In addition to $KN0_3$, $NaNO_3$, $Ca(NO_3)_2$ and other nitrates have been successfully used to overcome dormancy in grass seed (Fykse 1970). Although some hypotheses point to the role of potassium in enzyme activation (Nelson 1927), the prevailing opinion seems to be that the germination impetus of KNO_3 can be ascribed to its anion (Fykse 1970, Simpson 1990).

The promotive effect of KNO_3 on germination typically reaches a maximum at a specific concentration. For example, Maier (1933) reported 31, 39.5 and 28.5% germination after soaking seeds of *Poa nemoralis* L. in solutions of 0.001, 0.01 and 0.1 M, respectively. By comparison, Williams (1983a) found 0.002 M to be sufficient for seed of four out of five grass species; only bentgrass seemed to be encouraged by a tenfold increase to 0.02 M. When KNO_3 is used in official seed testing laboratories, a concentration of 0.2%, corresponding to 0.02 M, is prescribed; however, this solution is only used to saturate the substrate at the beginning of the test, and not for later remoistening (ISTA 1985).

Among other nitrogen-containing compounds, cyanamide (H_2CN_2) and thiourea ($CS(NH_2)_2$) are known to stimulate germination, in some cases equally effective to KNO_3 (Fykse 1970, Simpson 1990). From experiments with lettuce seed, it appears that all these compounds act in the same way, namely by irreversible inhibition of the enzyme catalase, normally known to catalyze H_2O_2 decomposition (Hendricks & Taylorson 1975). This will, in turn, increase seed respiration through the pentose phosphate pathway, a metabolic route commonly associated with the release from dormancy (Bewley & Black 1985). Whether this explanation is also valid for grass seed has not been elucidated.

INTERACTIONS AMONG ALTERNATING TEMPERATURE, PRECHILLING, LIGHT AND KNO_3

From factorial experiments with various treatments known to overcome grass seed dormancy, Williams (1983b) reported alternating temperature to be the most efficient remedy, followed by light and KNO_3. The same order was earlier documented for bluegrasses (Nelson 1927). Although some reports indicate complex two-, three- and four-factor interactions (Andersen 1941, Williams 1983b), many papers indicate a striking additivity between at least two of the factors (Toole & Koch 1977, Netland 1985, Roberts & Benjamin 1979). This is often illustrated by means of so-called Richards' diagrams (Roberts & Benjamin 1979), of which one example is given in Figure 7. In this case, the combination of alternating temperature and light improved germination in

orchardgrass substantially compared with that obtained with either factor applied alone (Probert et al. 1985b). These observations of course indicate that if the factors are not operating through the same mechanism, they must at least be physiologically linked.

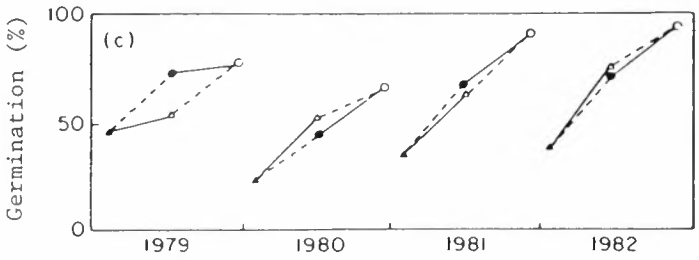

Figure 7. Richards diagram showing the interactive effects of light (——) and alternating temperatures (-----) on germination of one population of orchardgrass grown in four successive years. Treatments: 16°C dark (▲), 16°C light (Δ), 21/11°C dark (•), 21/11°C light (o). (After Probert et al. 1985b)

GIBBERELLIC ACID (GA) AND OTHER GROWTH REGULATORS

In the International Rules for Seed Testing, GA_3 is recommended for promoting germination of dormant cereals (ISTA 1985). There are, however, numerous reports indicating that GA also stimulates germination in smaller grass seed (Nakamura 1962, Junttila et al. 1978, Falkowski et al. 1983). In some experiments, GA has been successfully applied as a last remedy to overcome dormancy, after treatments like alternating temperature, light or KNO_3 have failed (Williams 1983a, b, Schönfeld & Chancellor 1983).

Although most workers investigating the effects of GA on seed germination have used GA_3, some results show that various GAs may have different roles in breaking dormancy (Dathe et al. 1978). In an experiment with mainly non-dormant seed of Kentucky bluegrass, Grimstad (1985) obtained much faster germination with GA_{4+7} than with GA_3. The latter acid was in fact found to reduce the speed of germination in one particular variety ('Nugget').

The concentration of GA required to elicit maximal germination depends on how deep the dormancy is. A solution containing 500 ppm GA_3 is normally used in seed testing, but 1000 ppm may be justified in some cases (ISTA 1985). Junttila (1977) reported that 800-1000 ppm gave maximum response when orchardgrass seed was germinated in solutions of GA_3, but higher concentrations were needed when caryopses were soaked in GA_3 solutions for 24 h, washed and then germinated in water.

The general role of GA in overcoming dormancy in grasses has been largely inferred from its action in mobilization of endosperm reserves in cereals. GA promotes the synthesis of amylase and other hydrolytic enzymes in the scutellum and aleurone tissues, and these enzymes are, in turn, responsible for the breakdown of starch. There is, however, some doubt as to whether this is the primary role by which GA actually subdues dormancy; or whether it is just a secondary event after dormancy is terminated by some other mechanism (Simpson 1990).

Among other growth regulators, cytokinins have been reported to overcome secondary dormancy in wild oats (Filsner & Upadhyaya 1985), but experiments with other grasses indicate no such effect (Junttila 1977, Simpson 1990), and Grimstad (1985) in fact found that cytokinins decreased the speed of germination in Kentucky bluegrass.

Although abscisic acid (ABA) can counteract the positive effect of GA, its exact role in dormancy remains obscure, and auxins are generally believed to have little impact on seed germination (Simpson 1990). Landgraff & Junttila (1979) observed enhanced germination of reed canarygrass after treatment with ethylene, but other reports are not convincing (Simpson 1990).

CONCLUSION

Although various treatments have been used to alleviate dormancy for at least a century, our knowledge about most of them is still fragmentary. This is also the case for the dormancy phenomenon as such, and the great diversity, even within one plant family such as the *Gramineae*, will probably prevent us from ever acquiring conclusive and universal explanations. The fact that Simpson (1990), after having tried to model seed dormancy, concluded that 'every individual seed deserves its own model!', fully illustrates the complexity of this interesting biological phenomenon.

ACKNOWLEDGEMENTS

The author is indebted to Professor Donald F. Grabe, Oregon State University, and Professor Olavi Junttila, The University of Tromsø, for their valuable suggestions and constructive criticism of this manuscript.

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Juvenile period and seedling growth in two micropropagated plum genotypes

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Redalen, G. 1992. Juvenile period and seedling growth in two micropropagated plum genotypes. Norwegian Journal of Agricultural Sciences 6: 241-246. ISSN 0801-5341.

In an experiment at the Department of Horticulture, Agricultural University of Norway, two plum genotypes were multiplied *in vitro* after germination by *in vitro* embryo culture. Thus a number of identical trees were obtained for each genotype. These were subjected to eight different treatments from the first year after germination. Ungrafted trees forced at high temperatures in greenhouse for one additional season flowered one year earlier than those under the control treatment. Practically all the trees, except for 25% of those being replanted after one year in the field, had flowers in the fourth growing season after germination. The grafted trees were smaller than the others at the onset of flowering.

Key words: Breeding, climate and plant development, juvenility, micropropagation, plum.

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Treatments for shortening the juvenile period in seedlings attract considerable attention, since they are known to enhance the efficiency of the breeding work, especially in crops with large plants and a generally long juvenile period.

Several authors have found that grafting apple seedlings onto dwarfing rootstocks shortens the juvenile period (Loewel & Saure 1963; Tydeman 1928, 1961; Tydeman & Alston 1965; Visser 1964, 1973). In the Soviet Union some authors have reported that grafting apple seedlings onto the crowns of cropping trees can reduce the juvenile period to 2-4 years (Kazakov & Kichina 1988; Tikhonov 1957). Recently Verhaegh et al. (1988), after experiments in The Netherlands and Switzerland, concluded that propagation on a rootstock offers no advantage if growing conditions are optimal. Investigations of this kind have not yet been carried out on plums, but Hartmann (1990) has, for example, studied the possibilities for pre-screening in plum breeding.

Since the juvenile phase is normally shorter in plum than in apple seedlings, a natural assumption has been that the grafting of plum seedlings will not have the same positive effect as that in apples.

Traditionally, experiments on juvenility have been done with seedlings from hybrid seeds germinated under normal conditions. The individual tree therefore has its special genetic constitution, and genetic variations within the population cannot be avoided. An exception may be the use of apomictic seedlings, like seedlings of *Malus sikkimensis* or

M. hupehensis, the latter being used in the studies of Zimmerman (1971) where forcing in greenhouse resulted in the shortening of the juvenile period.

In the present study with plums, two genotypes were multiplied *in vitro* after germination by *in vitro* embryo culture. A number of identical trees were obtained for each genotype, and an experiment on juvenility could be started with a low number of trees per treatment, making it possible to compare the results of several treatments. Druart (1991) recently discussed the potentialities of the *in vitro* culture to improve plum-tree breeding, but the potentialities mentioned, did not include the objectives of the present study.

MATERIAL AND METHODS

Two plum genotypes, designated «Genotype 2» and «Genotype 3», from a 'Mallard' x 'Victoria' cross in 1986, were micropropagated after germination by *in vitro* embryo culture in 1987. Thus 40 identical trees were obtained of Genotype 2, and 64 of Genotype 3, and all the trees were grown in greenhouse at about 20°C during the 1987 growing season. Trees of both genotypes were subjected to the following treatments from the first year after germination (eight trees per genotype and treatment) at the Department of Horticulture, Agricultural University of Norway, at a latitude of about 60°N:

A. Control (untopped trees planted in the field the first spring (1988) after germination. Herbicide-treated ground in the tree rows).
B. Topped trees, otherwise like the control.
C. Grafted (scions from the upper part of the seedlings) on St. Julien A rootstock in March 1988, grown in greenhouse (about 20°C) the first year and planted in the field one year later than the control.
D. Trees grown in greenhouse (18°C) the first year and planted in the field one year later than the control.
E. Trees grown in greenhouse (24°C) the first year (otherwise identical with D).

Trees of Genotype 3 were also given the following treatments:

F. Covering the ground with roof paper, otherwise like the control.
G. Bark mulching, otherwise like the control.
H. Replanting the trees after one year in the field, otherwise like the control.

Presence or lack of flowers was recorded on every tree during the years 1989, 1990 and 1991. Trunk circumference 50 cm above the ground and tree height were measured on 6 June, 1989, and on 14 December, 1990. Tree width across the row was also taken on 14 December, 1990.

Statistical calculations were made using the SAS GLM procedure. For comparing the length of the juvenile period a new variable was used: number of years from germination to flowering. Trees which had not flowered by 1991, were all expected to flower in 1992, after five years.

RESULTS

Trees on their own roots grown in greenhouse, in both the year of germination and the following growth season (treatments D and E), had the shortest juvenile period (Table 1). Grafting resulted in the smallest trees (Table 2), but had no statistically significant effect on the length of the juvenile period in these plum genotypes. In Table 2 results for Genotype 3 only are presented, because this genotype was subject to the highest number of treatments. Analogous growth data were found for Genotype 2.

Table 1. Length of juvenile period (years) in two plum genotypes after different treatments

		Genotype 2	Genotype 3	Mean values
A.	Control	3.00 a[1)]	3.13 bc	3.07 c
B.	Topped trees	3.00 a	3.50 abc	3.25 bc
C.	Grafted trees	3.00 a	3.15 bc	3.08 c
D.	Greenhouse (18°C)	2.06 b	3.00 c	2.53 d
E.	Greenhouse (24°C)	2.00 b	2.06 d	2.03 e
F.	Roof paper	-	3.63 ab	3.63 ab
G.	Bark mulching	-	3.25 bc	3.25 bc
H.	Replanting	-	3.88 a	3.88 a
Mean values		2.61	3.20	3.09

1) Different letters indicate significant differences according to Duncan's Multiple Range Test, $\alpha = 0.05$, letters valid only within columns

Table 2. Tree size measured on 6 June, 1989 and on 14 December, 1990, for Genotype 3 after different treatments

		Trunk circumference (cm) 50 cm above the ground		Tree height, cm	
		1989	1990	1989	1990
A	Control	5.09 bc[1)]	12.75 ab	166 b	259 b
B.	Topped trees	4.49 d	9.88 c	139 c	246 b
C.	Grafted trees	2.38 e	6.29 e	123 c	158 d
D.	Greenhouse (18°C)	6.01 a	9.63 cd	201 a	201 c
E.	Greenhouse (24°C)	5.87 a	9.38 cd	193 a	197 c
F.	Roof paper	5.58 ab	11.63 b	170 b	242 b
G.	Bark mulching	4.71 cd	13.25 a	166 b	281 a
H.	Replanting	4.56 d	8.50 d	162 b	190 c
Mean values		4.84	10.16	165	221

1) Different letters indicate significant differences according to Duncan's Multiple Range Test, $\alpha = 0.05$, letters valid only within columns

A direct comparison of the mean values for the two genotypes in Table 1 is not quite right, as the mean values are based on a different number of treatments. The mean value of treatments A-E for Genotype 3 is 2.97 as compared with 2.61 for Genotype 2.

The tree width in 1990 varied from 60.5 cm for the grafted trees to 159.3 cm for the trees with bark mulching. The mean value for all treatments was 102.7 cm, and the

figures for the individual treatments followed the same pattern as those for tree height (see Table 2).

DISCUSSION

The method with micropropagated trees used in this work proved to be very efficient. A large number of treatments could be compared because only a few trees per treatment were needed. Although the number of trees per treatment amounted to only eight, the effects of the different treatments were statistically significant. Of the treatments compared, growing in greenhouse for an additional season, preferably at high temperatures, was the most effective in shortening the juvenile phase. This is in accordance with the results of Aldwinckle (1975) and Zimmerman (1971), who obtained flowering after a short time when growing apple seedlings in the greenhouse, and of Jonkers (1971), who found a close relationship between growing latitude (mainly a temperature effect) and length of the juvenile period.

Grafting on St. Julien A rootstocks did not shorten the juvenile phase of these plum genotypes. This may be due to the fact that even the control trees had a short juvenile period. Grafting might be more relevant for offspring of less precocious parent cultivars.

As might be expected, replanting the trees after one year in the field resulted in the longest juvenile period. Mulching did not result in the positive effect expected but in the same, or an even longer juvenile period than that of the controls. Topped trees showed a tendency towards a longer juvenile period, and this is in agreement with the results obtained by Karnatz (1969) and Verhaegh et al. (1988).

Grafting resulted in reduced tree size, which generally is an advantage for the selection work. Although the differences were substantial in this case, even the trees on their own roots were rather easy to handle. Growing the plum trees in greenhouse for an additional season resulted in the largest trees by the time of planting. Two growing seasons later, however, the control trees, the topped trees, and the trees subjected to mulching, were larger.

CONCLUSIONS

1. *In vitro* multiplied genotypes from *in vitro* embryo cultures give statistically significant treatment differences even with a low number of trees (8) per treatment, and seem to be very useful for juvenility studies.

2. Growing in greenhouse, especially at a relatively high temperature (24°C) was the most effective treatment for shortening the juvenile period in plum genotypes. Grafting on St. Julien A rootstocks had no such effect. Replanting of the trees had the most negative effect.

3. Grafting resulted in smaller fruiting trees than trees on their own roots.

ACKNOWLEDGEMENTS

The author is grateful to the staff at the Department of Horticulture, Agricultural University of Norway, for assistance during the course of the experiment as well as for their statistical handling of the data material.

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Growth and leaf scorce development of *Begonia* x *cheimantha* Everett acclimatized to day length and artificial lighting

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Bævre, O.A. 1992. Growth and leaf scorce development of *Begonia* x *cheimantha* Everett acclimatized to day length and artificial lighting. Norwegian Journal of Agricultural Sciences 6: 247-257. ISSN 0801-5341.

Top cuttings of the cultivars 'Emma' and 'Hanne' were potted in late September and then exposed to different levels of illumination. After the short day flower induction period, the cultivars were also submitted to different day lengths. Increased lighting and day length increased vegetative plant growth and reduced the cultivation period, but promoted and increased the extent of leaf scorce. The cultivar 'Hanne' was more sensitive to intensive lighting than the cultivar 'Emma'. In the experiment there was a somewhat confusing effect between light levels and day length, but the results indicated that the day length was of greater importance than the light level. It is recommended that a day length of 16 h combined with an irradiance of 6-12 Wm^{-2}, or 24 h combined with 4-5 Wm^{-2} be used. It is possible however, that such a programme might induce some leaf scorce, which would have to be removed before sale.

Key words: *Begonia* x *cheimantha*, day length, leaf scorce, lighting.

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Normally, *Begonia* x *cheimatha* Everett is grown over a long period from the time of potting the rooted cuttings to flowering. With such a growing programme, lasting from late July or early August to Christmas, a low temperature and only natural light conditions are used. In the attempts to shorten the cultivation period by means of higher temperature and better light conditions, difficulties have arises with leaf scorce (Moe et al. 1992), often associated with long-lasting intensive lighting.

It is known from experiments and practice on intensive growth programme, that responses in plant growth vary between cultivars. Some cultivars can thrive under conditions which for other cultivars would not be conducive to the production of saleable plants of high quality. Since the change from the short day period to continuous light conditions over night, or a too high lighting regime, was thought to be too severe for the plants, an investigation which included a gradual acclimatization to increased light was started.

MATERIAL AND METHODS

The experiment was carried out in a double layer acrylic greenhouse at Kvithamar Research Station using supplementary artificial light (high-pressure sodium lamp, SON-T) from 21 September to 15 December. In this period day length decreased from 12 h to 4 h 40 min. In the same way, the global radiation per day decreased from about 4 MJm^{-2} at potting to 0.1 MJm^{-2} in December. The total global radiation in the experimental period was 150 MJm^{-2}.

The supplementary light was provided in the natural light period. The cultivars 'Hanne' and 'Emma' were potted in a fertilized peat medium ('Floralux veksttorv') as rooted top cuttings on 21 September and 25 September, respectively. The plants were pinched on 30 September and 2 October, for 'Hanne' and 'Emma', respectively, with 10 h of lighting per day being employed from 9 October.

From potting to the end of the short day period (19 October), the supplementary irradiance levels (PAR) were 4.5, 9.0 and 13.5 Wm^{-2} at the top of the plants, about 25 cm above the top of the pots. The illumination was measured in lux. The conversion factor was 2.3. The lighting programme used before 19 October included all possible combinations with the same lighting after 19 October. The total irradiance used in the calculations comprised natural light (PAR) outside the greenhouse, measured by the sensor of the greenhouse computer, together with the artificial lighting. From potting to the start of the short day flower induction period, the day length was 24 h per day. After short day induction, the day length in hours was differentiated in the following way (week number from end of short day):

Period of day length treatment	Day length treatment					
	1	2	3	4	5	6
1st week (19 Oct. - 25 Oct.)	12	16	24	12	12	16
2nd week (26 Oct. - 1 Nov.)	12	16	24	16	16	24
3rd week (2 Nov. - 8 Nov.)	12	16	24	16	24	24
After the 3rd week	12	16	24	16	24	24

After three weeks, the light period per day until the end of the experiment was the same as in week 3.

The experiment was carried out with two replicates and with six plants in each replicate. Plant density was 25 plants per square metre after 30 October.

The temperature was set at 22°C ± 0.5 (ventilation at 2°C above set temperature) from potting until 31 October, after which time it was set at 18°C ± 0.5. The CO_2 in the atmosphere was 600 vpm. For growth regulation Cycocel (2-chlor-ethyl-three methyl three-methylammoniumchloride) in a concentration of 0.06% active matter was sprayed on the plants to drip point. 'Emma' was sprayed four times from 12 October, and 'Hanne' two times from 30 October. Argylene (silver thiosulphate) was sprayed on

the plants on 2 December. The nutrient solution contained (in ppm): 163 N, 42 P, 240 K, 40 Mg, 114 Ca, 53 S, 2.0 Fe, 1.1 Mn, 0.20 Cu, 0.30 Zn, 0.33 B and 0.025 Mo, made from Superba 7-4-21, calcium nitrate and potasium sulphate. Sub-watering was used.

Grading of chlorotic and necrotic leaves was done according to a scale from 0 to 9. A score from 0 to 3 indicated an increasing chlorosis. Necrosis started at a score of 4. A score of 7 or higher indicated a hard necrosis. Plants with a score of 3 were saleable and those classified at score 4 were saleable after removal of one or two leaves.

After the first registration of chlorotic spots the plants were checked every day. The saleable time of the plants was registered as being when the plant had 15 open flowers. All other registrations took place at the end of the experiment on 14 and 15 December. The number of open flowers included withered flowers.

Observations were subjected to a two-way analysis of variance. The relationships between any variables were determined by simple correlation, $p < 0.001$, $p < 0.01$ and $p < 0.05$ indicating an 0.1%, 1% or 5% level of significance, respectively.

RESULTS

Plant growth

Artificial, supplementary light given before the end of the short day period and after the short day inductive phase, influenced plant growth significantly (Table 1). The greatest effect of supplementary light was found when the lighting was increased from the lowest to the middle level. 'Emma' was significantly ($p < 0.001$) taller than 'Hanne' to the top of the leaves (mean heights were 12.2 cm for 'Emma' and 8.8 cm for 'Hanne'), and had a significantly ($p < 0.001$) greater total height (mean heights were 21.6 cm for 'Emma' and 20.8 cm for 'Hanne') and a significantly ($p < 0.001$) shorter peduncle (mean heights were 9.4 for 'Emma' and 12.0 for 'Hanne'). Plant diameter was significantly ($p < 0.001$) greater for 'Emma' (mean plant diameter 17.0 cm) than for 'Hanne' (mean plant diameter 15.4 cm).

Table 1. The plant size (cm) of *Begonia x cheimantha* (means of 'Emma' and 'Hanne') grown with indicated irradiance supplementary light (SON-T) in addition to natural daylight in different growth periods

Irradiance, Wm^{-2}		Plant height,cm		The height of the peduncle, cm	Plant diameter, cm
before end of short day	after short day	to the top of the leaves	total plant height		
4.5		10.3	20.7	10.4	15.8
9.0		10.6	21.3	10.8	16.3
13.5		10.6	21.5	10.9	16.4
Significance		$p < 0.01$	$p < 0.001$	$p < 0.05$	$p < 0.001$
	4.5	10.2	20.9	10.7	15.7
	9.0	10.5	21.4	10.9	16.2
	13.5	10.7	21.2	10.5	16.6
	Significance	$p < 0.001$	$p < 0.01$	ns	$p < 0.001$

The plant height to the top of the leaves was affected significantly ($p < 0.05$) by the interaction between supplementary light levels after the short day period and the cultivars. The height for 'Hanne' increased more than that for 'Emma', when the supplementary light was increased. On the other hand, with regard to plant diameter there was a significant ($p < 0.01$) interaction between cultivars and the supplementary light levels before the end of the short day period and the supplementary light levels after that time. The diameter of cultivar 'Emma' increased by 1.2 cm when the supplementary light was increased from the lowest to the highest level before the end of the short day period, and by 1.6 cm when the light rate was increased in the same way during the rest of the cultivation period. The corresponding increases in diameter for 'Hanne' were 0.2 cm and 0.3 cm, respectively.

The day length after the flower induction period had a considerable effect on plant growth (Table 2). The significant ($p < 0.05$) effect on plant diameter of interaction between supplementary light levels before the end of the short day induction and day length, gave the greatest increase in plant diameter with increased light levels when using long day periods. The increases in plant diameter were 0.2 cm, 0.8 cm, 1.3 cm, 0.1 cm, 0.7 cm and 0.7 cm from the lowest to the highest supplementary light levels for day length treatments 1, 2, 3, 4, 5 and 6, respectively. The influence of day length on the cultivars was significantly different. Cultivar 'Emma' had a significantly greater increase in height to the top of the leaves with increased day length ($p < 0.01$) than cultivar 'Hanne'. The plant diameter for 'Hanne' was not influenced by day length, while for 'Emma' the diameter increased by 2.3 cm and 3.0 cm when the day length treatments were increased from 1 to 3 and from 1 to 6, respectively. This interaction was significant at the $p < 0.001$ level.

Table 2. Plant size (cm) of *Begonia x cheimantha* (means of 'Emma' and 'Hanne') grown with indicated day length in the first three weeks (w.) after the end of the short day period. The day length for the rest of the cultivation period is the same as in the third week

Day length in hours after end of the short day period			Plant height, cm		The height of the peduncle, cm	Plant diameter, cm
1st w.	2nd w.	3rd w.	to the top of the leaves	total plant height		
12	12	12	9.4	20.7	11.4	15.2
16	16	16	10.7	21.3	10.7	16.3
24	24	24	10.8	21.2	10.4	16.1
12	16	16	10.3	21.4	11.2	16.2
12	16	24	10.9	20.9	10.0	16.6
16	24	24	10.9	21.4	10.5	16.6
Significance			$p < 0.001$	$p < 0.01$	$p < 0.001$	$p < 0.001$

The correlation coefficients between total plant height and the height to the top of the leaves were $r = 0.27$ ($p < 0.01$) for 'Emma' and $r = 0.31$ ($P < 0.01$) for 'Hanne'. A highly significant ($p < 0.01$) correlation coefficient was found between the total plant height and the height of the peduncle for 'Emma' ($r = 0.77$) and for 'Hanne' ($r =$

0.74). For 'Emma' a significant ($p < 0.01$) correlation coefficient was found between the plant diameter and the total light supply throughout the growth period ($r = 0.37$) and the total light supply after the end of the short day period ($r = 0.33$).

Leaf growth

Measurement of the two largest leaves of the plants in two directions and of the length of the petiole showed no significant effects of supplemental lighting. The petiole was significantly ($p < 0.001$) reduced (51 mm, 51 mm, 49 mm, 52 mm, 51 mm, 49 mm for treatments 1, 2, 3, 4, 5 and 6, respectively) with increased day length. The petiole was significantly ($p < 0.001$) longer in 'Emma' (54 mm) than in 'Hanne' (47 mm). The significant ($p < 0.05$) interaction between supplemental light levels before the end of the short day and the day length indicated that the effect of long days in reducing the petiole was greatest at low light levels.

The ratio between the width and the height of the leaves of 'Hanne' was significantly ($p < 0.001$) lower (1.07 and 1.05 for the largest and the next largest leaves, respectively) than that for 'Emma' (ratio 1.13 for both leaves). There was a significant ($p < 0.001$) interaction between cultivars and day length on leaf form. Increased day length had the effect of making the leaves of 'Emma' more rounded (a ratio of about 1.0), while those of 'Hanne' were unaffected by day length.

Flowering

Increasing supplementary light or increasing day length had a marked effect on the cultivation period (Tables 3 and 4, Fig. 1). The significant ($p < 0.001$) interaction between light levels before the end of the short day induction period and the day length later, showed that the greatest effect in reducing the cultivation period was attained when the day length was increased at low light levels or vice versa. Plants of 'Emma' were saleable significantly ($p < 0.001$) earlier than those of 'Hanne' (5.8 days).

Some significant ($p < 0.01$) coefficients of correlation were found between light parameters and the development of flowers on the plants. When natural irradiance and artifical lighting were combined (total irradiance), the correlation coefficients increased over those of artificial lighting alone (Table 5).

Table 3. Plant development of *Begonia x cheimantha* (means of 'Emma' and 'Hanne') grown at the indicated irradiance supplementary light levels (SON-T) in addition to natural daylight in different growth periods

Irradiance, Wm^{-2}		Numbers of days from potting to saleable plant	Number of flowers per plant 84 days after potting
before the end of the short day	after short day		
4.5		77.2	34.8
9.0		77.0	37.5
13.5		75.6	45.5
Significance		$p < 0.001$	$p < 0.001$
	4.5	78.7	28.3
	9.0	76.1	40.2
	13.5	75.0	49.3
	Significance	$p < 0.001$	$p < 0.001$

Table 4. Plant development of *Begonia x cheimantha* (means of 'Emma' and 'Hanne') grown at the indicated day lengths in the first three weeks after end of the short day period. The day length for the rest of the cultivation period is the same as in the third week

Day length in hours after end of the short day period			Number of days from potting to saleable plant	Number of flowers per plant 84 days after potting
1st w.	2nd w.	3rd w.		
12	12	12	78.9	29.6
16	16	16	77.6	34.4
24	24	24	75.2	45.1
12	16	16	77.1	35.6
12	16	24	76.1	43.2
16	24	24	74.8	47.9
Significance			$p < 0.001$	$p < 0.001$

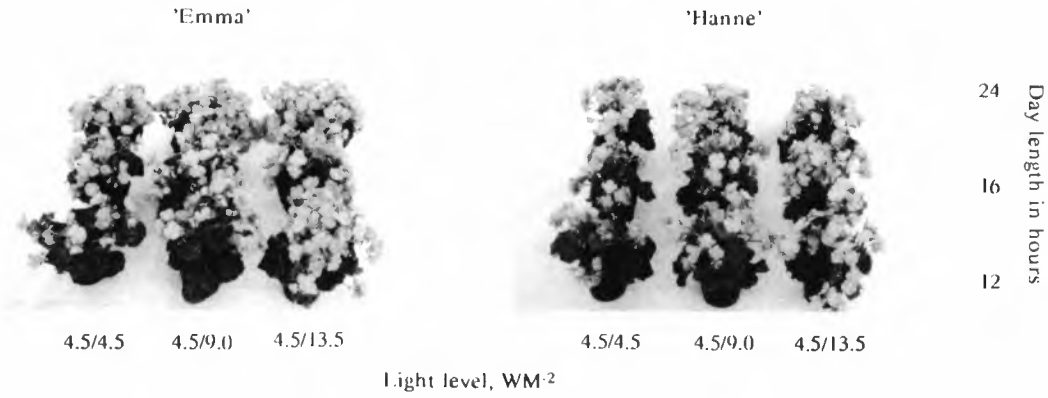

Figure 1. Effects of light level before and in the short day inductive phase (before/in) and daily lighting period with supplementary light on two cultivars of *Begonia x cheimantha*

Table 5. The correlation coefficient between different parameters of lighting and flower development in cultivars of *Begonia* x *cheimantha*

Parameters of lighting	Days from potting to saleable plant		Numbers of flowers 84 days after potting	
	'Emma'	'Hanne'	'Emma'	'Hanne'
Supp. light after end of the short days	- 0.37	- 0.34	0.41	0.44
Total irradiance after end of the short days	- 0.43	- 0.44	0.48	0.51
Total irradiance in the whole cultivation period	- 0.43	- 0.49	0.51	0.57

Leaf scorce

Leaf scorce first appeared as small vascular spots in the leaf margin on the top leaves (Fig. 2). The vascular spots increased along the leaf margin. Later on, these vascular spots developed to become a necrotic leaf margin. Some leaves, especially those hori-

zontally oriented at the top of the plants developed necrotic spots in the middle of the leaf area.

Figure 2. Leaf scorce symptoms on *Begonia* x *cheimantha*

Increased supplementary light after the end of the short day induction and a long lighting period per day promoted leaf scorce markedly (Tables 6 and 7). The period from potting to the chlorosis was seen as being significantly ($p < 0.001$) more reduced with increasing day length at low light levels before and after the end of a short day induction period, or vice versa. 'Emma' was significantly ($p < 0.001$) more influenced than 'Hanne' by the effect of increased day length in shortering the cultivation period until chlorosis was noted. The extent of the damage was significantly ($p < 0.001$) different between 'Emma' (mean 3.1) and 'Hanne' (mean 4.5). Lighting before and after the end of the short day period as well as day length resulted in a significant ($p < 0.001$) interaction on the extent of the damage (Table 8).

Table 6. Days from potting to appearance of leaf spots and the extent of the damage (9 indicates the worst damage) 84 days after potting (15 December) for *Begonia* x *cheimantha* (means of 'Emma' and 'Hanne') grown at the indicated level of supplementary lighting (SON-T) in addition to natural daylight in the different growth periods

Irradiance, Wm^{-2} before end of short day	Wm^{-2} after short day	Number of days to noting of chlorosis	Number of days to noting of necrosis	The damage graded from 0 to 9
4.5		60.2	74.4	3.7
9.0		59.5	74.3	3.7
13.5		59.0	74.7	4.0
Significance		$p < 0.001$	ns	$p < 0.001$
	4.5	62.2	74.8	3.0
	9.0	58.5	74.9	4.0
	13.5	58.0	73.8	4.5
	Significance	$p < 0.001$	$p < 0.001$	$p < 0.001$

Table 7. Days from potting to appearance of leaf spots and the extent of the damage graded from 0 to 9 (9 indicates the worst damage) 84 days after potting (15 December) for *Begonia* x *cheimantha* (means of 'Emma' and 'Hanne'), grown at indicated day lengths in the first three weeks after the end of the short day period. The day length for the rest of the cultivation period is the same as in the third week

Day length in hours after end of the short day period			Number of days to noting of		The damage graded from
1st w.	2nd w.	3rd w.	chlorosis	necrosis	0 to 9
12	12	12	63.1	75.4	1.7
16	16	16	60.9	74.6	2.7
24	24	24	58.2	73.6	5.2
12	16	16	60.1	75.1	3.3
12	16	24	57.7	74.6	5.0
16	24	24	57.8	74.3	5.0
Significanc			$p < 0.001$	$p < 0.05$	$p < 0.001$

Table 8. The extent of the damage graded from 0 to 9 (9 indicates the worst damage) for *Begonia* x *cheimantha* (means of 'Emma' and 'Hanne') 84 days after potting (15 December) grown at different day lengths and different levels of supplemental irradiance before the end of the short day induction (a) and after the short day period (b)

Day length in hours after end of the short day period			Irradiance, Wm^{-2}					
			4.5		9.0		13.5	
1st w.	2nd w.	3rd w.	a	b	a	b	a	b
12	12	12	1.5	1.2	1.7	1.6	2.0	2.5
16	16	16	2.3	1.8	2.0	3.1	3.7	3.1
24	24	24	5.0	4.3	5.1	5.2	5.5	6.0
12	16	16	2.8	2.7	3.1	3.6	4.0	3.6
12	16	24	5.0	3.8	3.4	5.0	4.6	6.3
16	24	24	5.6	4.2	5.2	5.4	4.2	5.3

Concerning the extent of the damage, there was a significant ($p < 0.01$) interaction between supplementary light levels after the end of the short day period and the cultivars. Increasing the light level from 4.5 to 9.0 and 13.5 Wm^{-2} after the end of the short day period increased the damage from 2.3 to 3.1 and 4.9 for 'Emma' and from 3.6 to 4.9 and 5.0 for 'Hanne'.

There was also a significant ($p < 0.001$) interaction between day length and cultivars with regards to extent of the damage. For day length treatments 1-6, the extent of the damage for 'Emma' was 1.4, 1.9, 4.4, 2.3, 4.0 and 4.6 and for 'Hanne' 2.1, 3.5, 5.9, 4.3, 6.0 and 5.4.

Different parameters of lighting and day length showed significant ($p < 0.01$) correlation coefficient with the extent of the damage (Table 9).

Table 9. The correlation coefficients between light and the extent of the leaf scorce in *Begonia* x *cheimantha*

After short day period						Total artificial irradiance throughout the cultivation period	
light level		day length		total irradiance			
'Emma'	'Hanne'	'Emma'	'Hanne'	'Emma'	'Hanne'	'Emma'	'Hanne'
0.41	0.25	0.42	0.31	0.64	0.45	0.62	0.44

The extent of the leaf scorce as a result of artificial supplementary lightning and day length is shown in the following equations:

'Emma': Extent of leaf scorce = -2.172 + 0.168 x + 0.687 y + 1.509 z

'Hanne': Extent of leaf scorce = -2.775 + 0.644 x + 0.754 y + 1.898 z

x = illumination (mWm^{-2}) before the end of the inductive short day phase

y = illumination (mWm^{-2}) after the end of the inductive short day phase

z = day length in hours after the end of the inductive short day phase

These equations are based on constant day length (12, 16, 24 h, day length treatments 1, 2 and 3). The coefficient 0.168 in the first equation was not significant. All other coefficients were significant at the $p < 0.001$ level.

DISCUSSION

The present findings confirm the effect of lighting on leaf scorce development (Moe et al. 1992) and the differences between cultivars. From the viewpoint of fast production of flourishing plants, increased lighting, especially after the short day inductive phase, is a most interesting factor. A day length of 12 h results in plants of loose growth regardless of normal levels of artificial lighting. A greater effort is required in nurturing such plants and they cause more problems with packing and marketability.

Looking exclusively at plant habitus, the highest quality plants were found at a 24 h day length, combined with a high level of illumination. Use of short day lengths after the flower induction period were unfavourable to plant well-being. Gives such treatments, the plants became disproportionate with respect to plant height to the top leaves, plant diameter and peduncle height. The positive influence of increased day length was most pronounced in the cultivar 'Emma'. Using intensive lighting is less viable because of leaf scorce development. On the other hand, Løfvenberg (1984) and Hellgren (1985) did not give any account of chlorosis or necrosis when artificial lighting was used up to

24 h a day. Anderson (1986), working with *Begonia* x *hiemalis* in photoperiods of up to 24 h a day, did not notice any chlorosis or necrosis.

In this experiment it was not easy to discriminate between the effect of lighting and the effect of day length. The increased leaf scorce development with increased day length could be an effect of increased lighting. Nevertheless, the results indicated that day length was of greater importance than light level. The leaf scorce appeared to be specific for this species, and the cultivar effect was mainly registered as a level difference.

Leaf scorce is an old problem in *Begonia* x *cheimantha*. Strømme & Pettersen (1984) connected this damage with effects of climate, irrigation or fertilization. The damage appears on the largest leaves. They say that a too heavy and succulent growth must be avoided. In this experiment, the conductivity in the pots in the flowering phase was about 1.8 $mScm^{-1}$, and leaf scorce was not a problem on the most succulent plants grown at a 12 h day length, combined with low lighting. Leaf scorce described in this investigation also appeared on small leaves, and it is likely that there is a different basis for these leaf symptoms. A temperature effect is a possible association, but it is likely that the increase in temperature in the leaves (Grimstad 1981) is too slight to induce leaf scorce.

This investigation does not clarify the causal relationship between lighting and leaf scorce, but it does give some indication of a connection between lighting and plant development. The appearance of the first symptoms that developed into necrotic scorce was registered about 30 days after the end of the short day period. At this point, immediately before flowering, peduncles began to stretch. Spots developed into necrotic scorce in the phase when the plants began to flower. It may be discussed whether plants with a greater vegetative growth accumulate photosynthetic products, while plants with a slower vegetative growth in a marked generative phase do not. An overoptimal photosynthetic rate could give the leaves a too high content of photosynthetic substances.

If the intention is the rapid development of a high-quality saleable plant, then the chances are that some necrotic spots on the plants will occure, necessitating the removal of one or two leaves. A 24 h day length and a lighting regime of 4-5 Wm^{-2}, or a day length of 16 h and a lighting regime of 6-12 Wm^{-2} could be preferable.

ACKNOWLEDGEMENTS

The author thanks K. O. Leren, G. Ro and J. Brønstad for technical assistance.

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Leaf damage in *Begonia* x *cheimantha* Everett

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Top cuttings of the begonia cultivars 'Emma' and 'Hanne' were potted in mid-September. After the short-day flower inductive period, the plants were exposed to different levels of illumination, photosynthetic active light periods and day-lengthening at low light levels. Increased lighting and day length with photosynthetically active radiation promoted and increased the extent of leaf damage, while day-lengthening at low light levels did not. Pinching-off flower buds delayed and reduced the extent of leaf damage. Chlorophyll a fluorescence was measured using a stress meter. The results indicated that the plant did not suffer from any kind of stress.

Key words: Chlorosis, fluorescence, light, necrosis, photoperiod.

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Abbreviations: D = day, Fm = maximal fluorescence, Fv = variable fluorescence, N = night, PAR = photosynthetic active radiation, PS = photosystem

The introduction of a rapid cultivation programme for Christmas begonia (Moe et al. 1992) has caused problems with leaf scorce (Bævre 1992). The damage was at its most prevalent when high light levels were combined with long lighting periods. Both the light level and the length of photoperiod were shown to increase leaf injury. It was observed that the chlorotic and necrotic leaves occured from the middle of November, when the first buds appeared.

Chlorophyll *a* fluorescence from photosynthetic active tissue is used as a sensitive and intrinsic probe of photosynthetic reactions (Lavorel & Etienne 1977). At room temperature, chlorophyll *a* molecules associated with photosystem II (PSII) are mainly responsible for the fluorescence induction response with a main emission band at 682 nm (Papageorgiou 1975, Krause & Weis 1984).

The primary photochemical events and the activities in the fluorescent PSII and the water-splitting apparatus are sensitive to environmental factors, such as frost, chilling, high temperatures (Öquist 1987) and photon flux densities in excess of the energy turnover in the photosynthetic reactions, including the carbon metabolism (Osmond 1981, Powles 1984, Krause & Laasch 1987).

The object of this study was to investigate the relevance of flower development in leaf damage, especially in combination with lighting (Bævre 1992), and then use chlorophyll *a* fluorescence as a measurement for leaf injury. Work by Hetherington &

Öquist (1988) indicates that there is a linear correlation between the severity of visual leaf damage and a decrease in the induced rise of chlorophyll *a* fluorescence.

MATERIALS AND METHODS

The experiment was carried out with the varieties 'Hanne' and 'Emma'. The rooted cuttings were potted in a fertilized peat medium («Floralux standard veksttorv») on 15 September and the experiment was completed by 19 December. The plants were supplied with a complete nutrient solution through the whole cultural period (Bævre 1992). From potting to the end of the short-day period (10 October), the plants were provided with light from high-pressure sodium lamps (SON-T), 11.5 Wm^{-2}. Until start of short-day treatment (25 September), the day length was 24 h. The daylength in the short-day period was 10 h. The plants were pinched on 20 September.

The plants were sprayed twice with Cycocel (chlormequat) in a concentration of 0.12% active matter, on 19 and 31 October respectively. The temperature was set at 20°C (±0.5°C) D/N until 10 November and thereafter it was lowered to 18°C (±0.5°C) D/N. The CO_2 concentration was at 600 vpm throughout the experimental period.

The experiment was designed as a factorial combination of photoperiod, light level and plants with normal development or plants where the flower buds were pinched off.

From the end of the short days, the plants were exposed to different daylengths and light levels. The daylighting programmes were:

- 10 h photosynthetic light and 14 h night
- 10 h photosynthetic light and 14 h photoregulative light (compact gas-discharge lamps, SL), about 0.25 Wm-2)
- 24 h photosynthetic light

Three different levels of photosynthetic active light were used: 4.5, 9.0 and 13.5 Wm^{-2} (PAR).

One half of the plants flowered as normal, while all the flower buds of the remainder were pinched frequently.

Registration of chlorosis and necrosis was carried out on young leaves (leaves smaller than about 6 cm in diameter) and old leaves (leaves greater than about 6 cm in diameter, i.e. leaves in the periphery of the plants) and recorded as the number of days from potting to the development of visible chlorosis or necrosis. The leaf injury on the whole plant was graded from 0 (no visible symptoms) to 6. This registration (leaf damage index) was carried out on 14 December (90 days after potting). The fluorescence measurements were taken at 20°C on leaves from plants from the lowest and the highest light levels on 13 and 19 December.

A Plant Stress Meter Mark II (BioMonitor S.C.I. AB, Sweden) described by Öquist & Wass (1988) was used. The excitation light was 400 $\mu molm^{-2}s^{-1}$ and the duration of excitation was five seconds. Prior to taking the measurements the leaves were dark-adapted for 10 minutes. The fluorescence parameter measured was Fv/Fm.

The experiment was carried out with two replicates, six plants in each. The data were subjected to analyses of variance. The level of significance is given as follows: *** = $p < 0.001$, ** = $p < 0.01$, * = $p < 0.05$, ns = $p > 0.05$.

RESULTS

Visible chlorosis and necrosis

There was no significant difference between cultivars for number of days until the occurrence of chlorosis (87 days) and necrosis (92 days) on young leaves. On the other hand, the occurrence of leaf injury on old leaves was significantly different ($p < 0.001$ for chlorosis and $p < 0.05$ for necrosis). 'Hanne' reached the chlorotic stage after 82 days, while 'Emma' displayed the same symptoms after 86 days. The corresponding growth period until necrosis was 87 and 89 days. Classification of the leaf injury on the whole plant on 14 December (90 days from potting) showed a significant ($p < 0.001$) higher index for 'Hanne' (2.1) than for 'Emma' (0.9).

The length of the photoperiod or different supplementary light levels appeared to have no significant effect on the number of days until the appearance of chlorosis and necrosis on the young leaves, but photoperiod and light level affected the occurrence of chlorosis and necrosis on old leaves in a significant way (Table 1). The greatest difference in the occurrence of leaf injury was found between 10 h photosynthetic light plus day-lengthening with 14 h low light levels and 24 h photosynthetic light (significance level $p < 0.001$). The interaction between the length of photoperiod and light level on the leaf damage of the whole plants was significant ($p < 0.01$) (Table 2). The leaf injury increased more in proportion to light level at a 10 h daylength than with a longer photoperiod.

Table 1. Effects of length of photoperiod (hours with photosynthetic light level plus the eventual day-lengthening (10 + 14) with low light level, 0.25 Wm^{-2}) and supplemental irradiance level on the number of days from potting to the appearance of chlorosis and necrosis on old leaves and the damage index (0-6, 0 = no damage) of the whole plants of *Begonia x cheimantha*

Leaf damage	Photoperiod (h)				Light level (Wm^{-2})			
	10	10+14	24	Sign.	4.5	9.0	13.5	Sign.
Chlorosis	84	86	83	**	85	83	84	ns
Necrosis	89	90	85	***	90	88	87	***
Leaf scorce	1.2	0.8	2.4	***	1.0	1.5	2.0	***

Pinching-off the flower buds significantly delayed the occurrence of necrosis on old leaves ($p < 0.01$) from 87 days to 90 days. The leaf damage on the whole plant was reduced significantly ($p < 0.001$) from 1.9 to 1.0. The interaction between daylength and flower status of the plants was not significant for number of days to necrosis but significant ($p < 0.01$) for leaf damage (Table 3). The effect of flower bud-pinching was most pronounced when day-lengthening was not employed.

Table 2. Effects of length of photoperiod (photosynthetic light level plus the eventual day-lengthening (10 + 14) with low light level, 0.25 Wm^{-2}) and supplementary light level on the leaf damage index (0-6, 0 = no damage) of the whole plant of *Begonia x cheimantha*

Light level Wm^{-2}	Photoperiod		
	10 h	10 + 14 h	24 h
4.5	0.8	0.5	1.6
9.0	1.2	0.8	2.5
13.5	1.7	1.0	3.2

Table 3. Effects of length of photoperiod (hours with photosynthetic light level plus the eventual day-lengthening (10 + 14) with low light level, 0.25 Wm^{-2}) and plant status (normal flowering plants and plants where all flower buds were pinched off) on number of days from potting to the appearance of necrosis on the old leaves and leaf damage index (0-6, 0 = no damage) on the whole plants of *Begonia x cheimantha*

Plant development	Photoperiod, h					
	10		10 + 14		24	
	days	index	days	index	days	index
Normal flowering plant	88	1.7	89	1.0	84	3.1
Plants without flowers	91	0.8	92	0.6	86	1.7

There was no significant interaction between supplementary light level and flowering status of the plants on days until appearance of necrosis on old leaves or the extent of leaf damage (Table 4).

Table 4. Effects of different supplementary light levels on the number of days from potting to the appearance of necrosis on old leaves and leaf damage index (0-6, 0 = no damage) of the whole plant of *Begonia x cheimantha*

Plant development	Supplementary light level, Wm^{-2}					
	4.5		9.0		13.5	
	days	index	days	index	days	index
Normal flowering plant	89	1.3	86	1.9	85	2.5
Plants without flowers	91	0.6	89	1.0	88	1.5

Fluorescence

The Fv/Fm ratio values ranged from 0.763 to 0.862 for all the treatments and are typical for well-functioning leaves. The results from the chlorophyll *a* measurements indicate that the plants did not suffer from any kind of stress.

DISCUSSION

Pinching-off the flower buds or day-lengthening with a low light irradiance reduced leaf injury in Christmas begonia. The positive effect of day-lengthening on the reduction of leaf damage is also of practical interest.

In earlier investigations, it was found that leaf damage took place from start of flowering (Bævre 1992). The results from the present experiment are in agreement with these findings. Stopping the flower development at the bud stage, reduced the leaf damage, but did not prevent it. Developing flowers are a sink for assimilates in the plant growth, espescially in Christmas begonia with a high percentage of female flowers (Heide 1969; Moe et al. 1992). With no flower development, the requirement of assimilates to the flowering part of the plant and the total requirement were reduced. A less intense flower development may leave more assimilates free for repair processes in the leaf, thus procuring a reduction in leaf damage.

The female flower development is more than likely only part of the explanation for the occurrence of leaf injury. Heide (1969) found a change towards femaleness by long days and high temperature (18-21°C), and from this observation one would expect a high degree of female flowers on plants where the leaf damage index was low. But also in this connection, the flower bud-pinching reduced the leaf injury index and delayed the development of necrosis. There are, then, other underlying factors that also have an influence on leaf injury.

The ratio of variable (Fv) to maximal (Fm) PSII fluorescence, Fv/Fm, is thought to be a direct measurement of efficiency to the primary photochemistry of PSII (Butler & Kitajima 1975). The results from the measurements show Fv/Fm ratios typically for non-stressed leaves in agreement with Björkman & Demmig (1987), who found that the ratio measured under optimal conditions for intact plants of C_3 species was 0.832 $\pm$ 0.004.

ACKNOWLEDGEMENT

The authors express their thanks to Kjell Olav Leren, Guri Ro and Jørn Brønstad for technical assistance. This work was financially supported by Midt-Norden komiteen, group «Greenhouse production of pot plants».

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Predation by selected carabid and staphylinid species on the aphid *Rhopalosiphum padi* in laboratory and semifield experiments

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During May-September 1989-91, 15 carabid and 9 staphylinid species were offered nymphs and adults of the cereal aphid *Rhopalosiphum padi* L. Experiments carried out in petri dishes in the laboratory at 15°C gave the consumption rates as 2.3-19.3 live aphids per beetle per day. In 1 m² outdoor cages under conditions approximating those in the field, the consumption rates were 0.3-7.1 dead aphids per beetle per day. Increases in night temperature led to significantly increased aphid consumption in the semifield experiments. All tested species ate both dead and live aphids. Significant differences occurred between species in both experimental series. Most carabid species ate more than most staphylinid species. *Philonthus* species ate 3-5 times more than the other staphylinids, and they also ate significantly more than most of the carabids. It is concluded that many staphylinid and carabid species are potentially important predators of *R. padi* in the field.

Key words: Carabidae, cereal aphids, polyphagous predators, predation, *Rhopalosiphum padi*, Staphylinidae.

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Most carabid and staphylinid species are polyphagous predators. They are important natural enemies of many pest species on arable crops, including the cereal aphids. This has been confirmed both in the laboratory and in field experiments (i.e. Sunderland 1975, Sunderland & Vickerman 1980, Wratten et al. 1984, Chiverton 1986, Sopp & Wratten 1986, Sunderland et al. 1987, Dennis & Wratten 1991).

In Norway, the bird cherry-oat aphid, *Rhopalosiphum padi* L., is the most serious aphid attacking cereals. The present investigation was carried out to compare consumption rates by some frequent carabid and staphylinid species on nymphs and adult *R. padi* under both laboratory conditions and confined conditions as similar as possible to those in the field.

Polyphagous predators are thought to be of great importance in the immigration phase of the cereal aphids, because they (in contrast to the aphid specific predators) are already in the field and can prey on the first aphid immigrants (Chiverton 1986). The method used in the semifield experiments was devised to simulate the situation in

Norwegian cereal fields in the middle of June, that is, in the immigration phase of *R. padi*.

MATERIALS AND METHODS

The beetles were caught in dry pitfall traps in agricultural fields or by ground search at field edges. They were kept in a darkened room in ventilated plastic boxes with moistened potting soil at +4°C and fed dog biscuits prior to their being used in the experiments. The beetles were normally used in experiments one to three days after they were captured, but in some cases (notably *Bembidion bruxellense* Wesmaël) they were kept for up to four weeks in captivity before being used. In the semifield experiments, because of the low number of *Philonthus* specimens found, the *Philonthus* spp. was a mixture of *P. atratus* (Gravenhorst) (40%), *P. ochropus* (Gravenhorst) (33%), *P. cognatus* Stephens (20%) and *P. carbonarius* (Gravenhorst) (7%).

The aphids were taken from laboratory cultures held on barley plants in a greenhouse at natural daylengths. Aphids used in the experiments always included a mixture of second to fourth instar nymphs and apterous adults.

The laboratory experiments were carried out in plastic petri dishes, diameter 8.7 cm. Each dish contained a moistened filter paper and was equipped with a lid painted with Fluon (polytetrafluoroethylene). The aphids were unable to walk on the fluon and were thus kept within reach of the predators (Chiverton 1988). The beetles were placed individually in petri dishes and were then transferred to a climate chamber set at a constant temperature of 15 ± 2°C and a 16L:8D (2000 lux) photoperiod. After being acclimatized for 24 h, each beetle was offered 20 aphids. Twenty-four hours later the number of aphids eaten was recorded and the experiment stopped.

The semifield experiments were carried out in cages measuring 154 · 65 cm (= 1.0 m^2) and 20 cm high, made of wooden panels and filled with moistened potting soil. On top of the cage was an 0.6-m-high hood of muslin supported by four metal hoops. To approximate field conditions, the cages were placed outdoors, protected from rain by a plastic roof. Each cage contained six rows (22 cm apart), with seven barley plants (8 cm apart) in each. The plants had been raised in a greenhouse and had 3-4 leaves.

In the middle of rows 1, 3 and 5, aphids were put out on so-called «pin-disks» (Fig. 1). A pin-disk consisted of a plastic disk of 7 cm in diameter, covered with 0.5 cm of soil, with three pins pointing upwards. On each of three freshly cut barley tillers with 3-4 leaves, five aphids (killed at ÷20°C for one hour) were glued beside each other using wheat flour and water. Then the tillers were pressed down on one pin each so that the aphids were just above soil level.

Five beetles belonging to the same species were placed in a ventilated plastic box with moistened potting soil. The beetles were placed outdoors near the experimental area for 24 h of acclimatization before being used in the experiments.

At the start of an experiment, each of the three pin-disks in the cage was equipped with three tillers with five aphids each, and the five beetles from one box were released into the cage. After 24 h the number of aphids removed was recorded and freshly cut tillers with new, frozen aphids were offered to the beetles on the pin-disks. This was repeated for four days, at which time the experiment was stopped. The cages were emptied and washed before re-use.

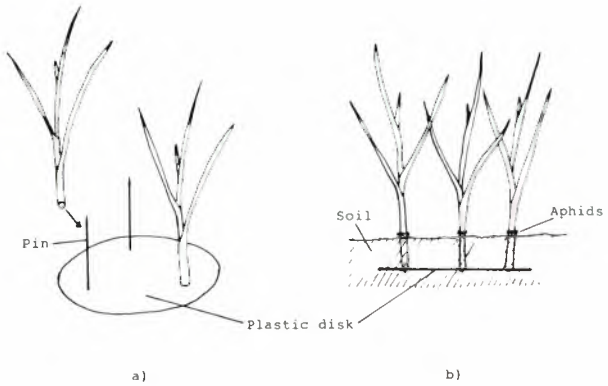

Fig. 1. The «pin-disk». (a) Setting it up. (b) In function in an experiment

To test whether the aphids in the cages could have been removed by anything other than the beetles, an experiment was conducted without beetles. However, during the four days of the experiment none of the 180 glued aphids were missing. Consequently, all aphids removed in the experiments were recorded as having been eaten by the beetles.

The experiments were conducted during May-September 1989-91. Mean day (09.00-18.00 h) and night (21.00-03.00 h) temperatures were calculated from measurements carried out at a meteorological station situated 1.2 km from the experimental area.

The approximation to the normal distribution was tested and found acceptable for the results in both experimental series. The laboratory experiments were tested with an analysis of variance model with nested factors and the semifield experiments were tested with an analysis of covariance model with nested and crossed factors. In all statistical calculations a significance level of 5% was used.

For statistical analysis of the laboratory experiments, the following model was used:

$$y_{ijk} = \mu + \tau_i + \gamma_{j(i)} + \varepsilon_{k(ij)},$$

where i = species, j = month and k = replicates.

For the semifield experiments, the following model was used:

$$y = \mu + \tau_i + \gamma_{j(i)} + \partial_m + x_{ijk1(i)} + x_{ijk2(i)} + \varepsilon_{ijk(i)},$$

where i = species, j = replicates, k1 = night temperature, k2 = day temperature.

RESULTS

In the laboratory experiments there were significant differences in consumption between species, but no significant differences could be observed between different months within each species (Table 1). Consequently, only the mean number of aphids consumed per day was calculated for each species, regardless of when (during May to September)

the experiments had been carried out. The mean number of aphids consumed per beetle per day and the significance of differences between species are presented in Table 2.

Table 1. Statistical analysis of the experiments

Variable	Significance level
a) Laboratory experiments	
Species	0.0001
Months	0.0612
b) Semifield experiments	
Species	0.0001
Replicates	0.0001
Days	0.4079
Night temperatures	0.0003
Day temperatures	0.3086

The results from testing the different variables in the semifield experiments are given in Table 1. Day temperature had no significant effect on the consumption, but an increase in night temperature led to significantly increased aphid consumption. When testing single species, this was shown for *Agonum dorsale* (Pontoppidan), *Harpalus affinis* (Shrank) and *H. rufipes* (Degeer).

There were significant differences in consumption between species and for replicates within each species. Differences between replicates were not tested further. Since no significant differences in consumption could be observed during the four days' duration of each experiment, the mean number of aphids per day was calculated for all four days of each experiment. The mean number of aphids consumed per beetle per day in the semifield experiments and the significance of difference between species are presented in Table 3.

All tested species ate both dead and live aphids, but fewer aphids were eaten in the semifield than in the laboratory experiments. Differences in consumption between species were very much the same in both experimental series (Tables 2 and 3), i.e. most carabid species ate more than most staphylinid species. *Philonthus* species ate 3-5 times more than the other staphylinids tested and they also ate significantly more than most of the carabids.

DISCUSSION

Among the staphylinids tested, *Philonthus cognatus* has previously been shown to be a voracious cereal aphid feeder (Sopp & Wratten 1986, Sunderland et al. 1987). Most of the work has been done with *Sitobion avenae* (F.). Results from the present investigation (Tables 2 and 3) show that *P. atratus* and several other *Philonthus* species also have a high potential as predators of *R. padi*. High consumption rates for several *Philonthus* species combined with their high activity in cereal fields (Andersen 1991) indicate that they can be among the key *R. padi* feeders. However, they normally do not migrate into

Table 2. Mean number of aphids eaten per beetle per day in the laboratory experiments, with significance of differences (Duncan's Multiple Range Test, *:P = 0.05)

Aphids eaten		Species	Statistical Significance																		
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
19.3	1	*Philonthus atratus* (Gravenhorst) [1]	-																			
17.5	2	*Amara apricaria* (Paykull)		-																		
15.8	3	*Calathus melanocephalus* (L.)			-																	
15.5	4	*Agonum dorsale* (Pontoppidan)	*			-																
10.9	5	*Pterostichus melanarius* (Illiger)	*	*	*	*	-															
10.6	6	*Amara bifrons* (Gyllenhal)	*	*	*	*		-														
9.4	7	*Harpalus affinis* (Schrank)	*	*	*	*			-													
9.4	8	*Amara plebeja* (Gyllenhal)	*	*	*	*				-												
9.0	9	*Bembidion tetracolum* (Say)	*	*	*	*					-											
8.9	10	*Trechus secalis* (Paykull)	*	*	*	*						-										
8.6	11	*H. rufipes* (Degeer)	*	*	*	*							-									
8.3	12	*Loricera pilicornis* (Fabricius)	*	*	*	*								-								
6.9	13	*Clivina fossor* (L.)	*	*	*	*	*								-							
5.4	14	*B. lampros* (Herbst)	*	*	*	*	*	*	*	*						-						
4.7	15	*Tachyporus chrysomeliuus* (L.) [1]	*	*	*	*	*	*	*	*	*	*	*	*			-					
4.6	16	*Trechus quadristriatus* (Schrank)	*	*	*	*	*	*	*	*	*	*	*	*				-				
3.9	17	*Tachyporus hypnorum* (Fabricius) [1]	*	*	*	*	*	*	*	*	*	*	*	*					-			
3.5	18	*Tachyporus dispar* (Paykull) [1]	*	*	*	*	*	*	*	*	*	*	*	*						-		
2.5	19	*Aloconota gregaria* (Erichson) [1]	*	*	*	*	*	*	*	*	*	*	*	*	*						-	
2.3	20	*Anotylus rugosus* (Fabricius) [1]	*	*	*	*	*	*	*	*	*	*	*	*	*							-

[1] Staphylinids

Table 3. Mean number of aphids eaten per beetle per day in the semifield experiments, with significance of differences (Duncan's Multiple Range test, *: P=0.05)

Aphids eaten		Species	Statistical Significance														
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
7.1	1	*Philonthus* spp. [1]	-														
6.1	2	*Harpalus affinis* (Schrank)	*	-													
6.0	3	*Agonum dorsale* (Pontoppidan)	*		-												
5.6	4	*Pterostichus melanarius* (Illiger)	*			-											
4.6	5	*Harpalus rufipes* (Degeer)	*	*	*	*	-										
3.9	6	*Amara bifrons* (Gyllenhal)	*	*	*	*	*	-									
3.1	7	*Calathus melanocephalus* (L.)	*	*	*	*	*	*	-								
2.4	8	*Bembidion bruxellense* Wesmaël	*	*	*	*	*	*	*	-							
2.3	9	*Loricera pilicornis* (Fabricius)	*	*	*	*	*	*	*		-						
2.2	10	*Tachyporus hypnorum* (Fabricius) [1]	*	*	*	*	*	*	*			-					
1.6	11	*T. chrysomelinus* (L.) [1]	*	*	*	*	*	*	*	*	*		-				
1.3	12	*B. lampros* (Herbst)	*	*	*	*	*	*	*	*	*	*		-			
0.8	13	*Trechus quadristriatus* (Schrank)	*	*	*	*	*	*	*	*	*	*	*		-		
0.7	14	*Aloconota gregaria* (Erichson) [1]	*	*	*	*	*	*	*	*	*	*	*			-	
0.3	15	*Clivina fossor* (L.)	*	*	*	*	*	*	*	*	*	*	*	*			-

[1] Staphylinids

the cereal fields in large numbers until the middle of June (Andersen 1982), a little later than the first aphid immigrants.

All the *Tachyporus* species in this investigation (except *T. dispar* (Paykull), which probably has been mixed with *T. chrysomelinus* (L.)) have previously been shown to eat cereal aphids to a certain degree (i.e. Dennis & Wratten 1991). The present investigation confirms this, and indicates that their consumption of *R. padi* is only about one-third to one-fifth that by the *Philonthus* species (Tables 2 and 3). The same magnitude of difference was found by Wratten et al. (1984) and Sopp & Wratten (1986) when they tested *P. cognatus* and *Tachyporus* species for predation on *S. avenae*. The adult *Tachyporus* species have their maximum activity in Norwegian agricultural fields in June (Andersen 1982) and are probably among the most important predators of cereal aphids.

Anotylus rugosus (Fabricius) and *Aloconota gregaria* (Erichson), two species which are among the most frequent staphylinids in cereal fields (Andersen 1991), ate some aphids in the experiments (Tables 2 and 3). Their aphid consumption has previously not been tested in confined experiments. Even though *Anotylus* spp. and *Aleocharinae* spp. were found not to react positively to an ELISA test with cereal aphid antiserum, Sunderland et al. (1987) argued that they should not be dismissed as cereal aphid predators. They are very frequent in agricultural fields in May-June (Andersen 1982), the time of the immigration phase of *R. padi*, so even rather small numbers of aphids eaten per beetle per day can make them important in reducing aphid build-up in the field. Consequently, these and other frequent staphylinid species need further investigation before a conclusion can be drawn about their impact on cereal aphids in the field.

Among the carabids tested, *Clivina fossor* (L.) ate very few aphids in the semifield experiments, but relatively more in the laboratory experiments (Tables 2 and 3). This can be explained by its burrowing behaviour, which would make it difficult to find

aphids on the pin-disks in the cages (see also Janssens & De Clercq 1990). This would also reduce its potential value as an aphid predator in the field, even though the species is very frequent in May-June (Andersen 1982, 1990).

Trechus and *Bembidion* species ate relatively few aphids in both experimental series (Tables 2 and 3). This can be explained partly by their small size (Sopp & Wratten 1986). However, large numbers of several *Bembidion* species are often present in cereal fields in May-June (Andersen 1982, 1990) and they can thus be of great importance as predators during the immigration phase of *R. padi*. *Trechus* species, on the other hand, are normally present in low numbers in May-June (Andersen 1982) and are consequently less important as predators on *R. padi* during the immigration phase.

Most of the larger carabids ate more aphids (Tables 2 and 3). Among these, *Agonum dorsale*, *Amara plebeja* (Gyllenhal), *Harpalus affinis* and *Loricera pilicornis* (Fabricius) are the most frequent species in fields in May-June (Andersen 1982). With the exception of *L. pilicornis*, which predominantly feeds on collembola (Sunderland 1975), these species are consequently among the most promising aphid predators.

All species ate less aphids in the semifield than in the laboratory experiments (Tables 2 and 3). This can be explained by the beetles having to use more time to search for aphids in the semifield experiments. Even though dead aphids were used, it is presumed that the present semifield method gives predation rates closer to those in the field than the laboratory experiments and other previously used maximum consumption experiments do (i.e. Sopp & Wratten 1986, Chiverton 1988). In the field, the tested species would probably have eaten fewer aphids, because live aphids have can sometimes escape attack (Chiverton 1988). Alternative food would also be available. Thus, the semifield experiments also probably overestimate the natural field consumption rates.

Predation by polyphagous predators on aphids is correlated with temperature (Scheller 1984, Sopp & Wratten 1986, Chiverton 1988). The many nocturnal species (Luff 1978) used in the semifield experiments explain the increase in aphid consumption with increasing night temperature, while no correlation was found between consumption and day temperature (Table 1).

Carabids and staphylinids mainly search for food on the ground, but many species (including some of the species investigated in the present experiments) climb plants (Luff 1989). The present investigation has only dealt with predation on the ground. When assessing the beneficial value of a predator species, however, one should also take into account its ability to prey on aphids high up on the plants.

The majority of investigations on polyphagous predators and cereal aphids have dealt with carabids and *S. avenae*, although some authors have also investigated staphylinids as predators or *R. padi* as prey. The present investigation shows that both carabids and staphylinids are potentially important predators on the cereal aphid *R. padi*. To find the most important cereal aphid predators in the field, more work is needed on the predatory behaviour of single species under field conditions during the immigration phase of the cereal aphids.

ACKNOWLEDGEMENTS

Øystein Kjos and Stein Winæs gave valuable technical assistance. The investigation was partly supported by The Agricultural Research Council of Norway.

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Short communication

Winter production of cut roses: Effects on keeping quality

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Cut roses constitute an important greenhouse crop in many countries. Since traditionally there is no cut rose production in North-European countries during the winter, supplementary lighting can be used to provide the necessary light conditions for the roses to grow even through the winter months. However, use of supplementary lighting can not be recommended unless the keeping quality of the roses produced under light is satisfactory.

This short communication summarizes some of the results from a preliminary study of rose quality as influenced by supplementary lighting.

MATERIALS AND METHODS

Roses of the cvs Motrea, Fleurop, Kiss, Frisco and Mercedes were grown under natural daylight (NL) with artificial lighting of 70, 130 and 190 µmol $m^{-2}s^{-1}$ from September to April in a double acrylic greenhouse. Supplementary lighting was provided by means of high pressure sodium lamps (Philips SON/T) for 20 h day^{-1}. The plants were watered with a complete nutrient solution with an electric conductivity of 1.7-1.8 $mScm^{-1}$. For further information on growth and climatic conditions, see Mortensen et al. (1992).

Eight roses of each cultivar from each of three flushes were harvested in order to test the keeping quality. The flushes appeared every four to six weeks, depending on irradiance level, and started at the end of October.

After harvest the cut roses were placed in a simulated interior climate (20-21°C, 40-50 % relative humidity and irradiance level of 15 µmol $m^{-2}s^{-1}$) for keeping quality testing. Four roses from each cultivar and irradiance level were put into bottles containing water and chlorine (10 ml l^{-1}).

RESULTS AND DISCUSSION

No significant main effects of irradiance level on vase life were found (Table 1). However, a significant interaction between cultivars and irradiance level was found for vase life (Table 2). When the irradiance level increased from 70 to 190 µmol m^{-2} s^{-1}, vase life in cv. Motrea was not affected, while the vase life of cvs Mercedes and Kiss decrea-

sed by 11%, and the vase life of cvs Frisco and Fleurop increased by 12% and 55%, respectively. Obviously, different cultivars respond differently to supplementary lighting during the winter months.

Table 1. The significance of the main effects and interactions between cultivar and irradiance level (irr.). Significance levels: ns = not significant, * = $P<0.05$, ** = $P<0.01$, *** = $P<0.001$

	DF	Vase life	Stem length	Fresh weight
Cultivar	4	***	***	***
Irr. level	2	ns	***	***
Cultivar x irr.	6	*	*	***
MSrest (error)	359			

Table 2. Effects of irradiance level on vase life (in days) of different cultivars. Percentage of change in vase life between 70 and 190 µmol m^{-2} s^{-1} is given

Cultivars	Irradiance level (µmol m^{-2} s^{-1}) 70	130	190	% change 70->190
Motrea	10.6	10.6	10.6	0
Fleurop	8.5	9.3	13.2	+55
Kiss	6.7	6.8	6.0	-11
Frisco	7.7	7.6	8.5	+12
Mercedes	7.5	6.8	6.7	-11

Scott et al. (1986) reported that they found no differences in keeping quality between lit and unlit plants of the cut rose cv. Samantha. Armitage & Tsujita (1979) reported that supplementary lighting resulted in a poorer vase life in cv. Forever Yours. Different results concerning the effect of supplementary irradiance are likely due to the different responses amongst cultivars. Probably, the cvs. Frisco and Fleurop should be taken into consideration when winter production is planned.

Significant differences in vase life, stem length and fresh weight were found between the cultivars (Table 1). The shortest stems were found in the cvs. Motrea and Fleurop (Table 3). These two cultivars also appeared to have the longest vase life (Table 2). Short stems may offer an easier water uptake, because of the shorter transportation distance from the stem end to the petals. A relatively short transportation distance together with a vase solution containing chlorine might also reduce the vascular blockage by bacteria, since chlorine is a potent bactericide.

The irradiation significantly affected the stem length and the fresh weight of the stems (Table 3). Increasing the irradiance level resulted in increased thickness of the stems. Thick stems increase the quality grading of cut roses, as expressed through the United Nations Economic Commision for Europe (ECE) classification of cut flowers with regard to their appearance (Nowak & Rudnicki 1990). A strong stem affects the keeping quality in a positive way. In the present experiment, increasing the irradiance level resulted in a reduced stem length. This effect has also been reported by Zieslin &

Table 3. Main effects of irradiance level and cultivar on stem length (in cm) and fresh weight (g cm^{-1}). Data are the average of three flushes

	Stem length (cm)	Fresh weight (g cm^{-1})
Irradiance level ($\mu mol\ m^{-2}\ s^{-1}$)		
70	41.6a	0.42b
130	39.8ab	0.47ab
190	39.3b	0.49a
Cultivar		
Motrea	34.9c	0.33b
Fleurop	36.5c	0.49a
Kiss	48.9a	0.47a
Frisco	38.7b	0.51a
Mercedes	38.8b	0.51a

Mor, who claim that the increase in the number of flowers in lit roses derives mainly from an increase in flowers with shorter stems, reducing the average stem length and weight.

In the present experiment the temperature increased when the irradiance level was increased. Inhibition of shoot elongation may therefore also be an effect of high temperature, as reported by Mortensen et al. (1992) and Moe (1972). If the temperature had been kept constant, an increase in irradiance level would probably have increased the stem length.

ACKNOWLEDGEMENTS

This work was supported by the Ragnar J. Svinningen Nursery and the National Agricultural Research Council of Norway.

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La culture de decrue au Gourma, Mali conditions pedologiques, espèces et variétés

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Aune, J. B. 1992. La culture de decrue au Gourma, Mali conditions pedologiques, espèces et variétés. Norwegian Journal of Agricultural Sciences 6: 279-291. ISSN 0801-5341.

La culture de décrue, dans le Gourma au Mali, est effectuée dans les bras du fleuve Niger et dans quelques mares. Les espèces qui se sont avérées les plus adaptées à une telle culture ont été le sorgho et le niébé, alors que le pois chiche et le pois d'angole ont donné des rendements très faibles. Les essais furent menés dans 4 localités, et les rendements ont surtout été faibles dans deux rizières. Les facteurs qui en sont la cause sont une densité apparente du sol élevée (1,57-1,87 kg/dm^3), une faible porosité (30-40%), un pH de 4 à 5, et une teneur en phosphore accessible très faible. La capacité de rétention d'eau dans le premier mètre du sol a varié de 90 mm à 170 mm dans les localités étudiées.

Mots clés: Capacité de rétention d'eau, culture de décrue, denisité du sol, niébe, petit mil, pois chiche, pois d'angole, phosphore, pH, porosité, sorgho.

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Les cultures de décrue du mil et du sorgho sont une ancienne pratique au Gourma. Cette technique consiste à semer sur une plaine au fur et à mesure que l'eau s'en retire. Les plaines qui se prêtent pour la culture de décrue au Gourma sont des mares inondées par de l'eau de pluie, et les bras du fleuve Niger.

Dans les mares, le semis commence à partir d'octobre quand les pluies se sont arrêtées, alors que dans les bras du fleuve Niger, le semis commence à partir de février-mars quand il y a des terrains libres pour y semer. La culture semée dans les mares arrive à maturité avant la saison chaude (avril-mai), et elle est, ainsi, indépendante de la pluie. Les cultures dans les bras du fleuve Niger se développent pendant la saison chaude, mais il faut de la pluie pour que les plantes puissent achever leur cycle. Les cultivateurs empêchent les plantes de fleurir avant l'hivernage, en laissant leurs animaux brouter les plantes ou en coupant les tiges. La moisson est effectuée après l'hivernage, en septembre-octobre, avant que les bras du fleuve ne soient à nouveau inondés.

En semant dans les mares en octobre, la température est bien plus favorable aux plantes pendant leur cycle qu'en semant en février. Les températures deviennent très élevées à partir d'avril (tableau 1) comme montré pour la station météorologique de Tombouctou, située à 50-100 km de ces sites d'expérimentation (Sivakumar et al. 1984).

La culture de décrue dans les mares au Gourma est peu répandue, car ce type de culture peut engendrer des conflits entre agriculteurs et éleveurs, du fait que les éle-

veurs profitent de ces mares pour creuser les puisards qui servent à abreuver leurs animaux. La culture de décrue dans les bras du fleuve cause moins de litiges avec les éleveurs, parce que les animaux partent en transhumance pendant l'hivernage.

Le semis dans les bras du fleuve semble être moins important actuellement qu'autrefois, parce que les surfaces inondées ont diminué et que les pluies pendant l'hivernage ont été faibles pendant la dernière décennie (Gottschalk & Krasovskaia 1987).

Tableau 1. Température moyenne maximale, température moyenne minimale, évapotranspiration potentielle (mm par jour), pluviométrie moyenne par mois à Tombouctou (Sivakumar et al. 1984)

	Temp. moyenne max	Temp. moyenne min	Evapotransp. potentielle	Pluviométrie mm
Janvier	30,0	12,7	4,3	0,0
Février	33,2	15,0	5,0	0,2
Mars	36,6	18,2	6,1	0,4
Avril	39,7	22,0	6,7	0,8
Mai	41,9	25,4	7,4	3,8
Juin	41,5	26,5	7,2	15,6
Juillet	38,3	25,3	6,6	56,2
Août	35,7	24,2	5,2	80,9
Septembre	37,7	24,1	5,6	28,5
Octobre	38,9	22,5	5,8	2,8
Novembre	35,4	18,1	5,0	0,0
Décembre	30,4	13,7	4,1	0,2
Totale				192,3

Une étude morpho-pédologique des plaines de la vallée du Niger du Cercle de Gourma Rharous ont montré que ces sols ont généralement une teneur en phosphore très faible et que le pH est souvent au-dessous de 5 (PIRT 1988). Les besoins en potasse et calcium sont souvent beaucoup mieux satisfaits que celui en phosphore. La saturation en bases est normalement comprise entre 50 et 90%. Les sols argileux, et argilo-limoneux dominent dans les parties basses des plaines inondables, alors que les sols des parties hautes sont généralement caractérisés comme limoneux ou limoneux sableux (PIRT 1988).

Les cultures principales dans les bras du fleuve Niger sont le riz flottant et la plante fourragère bourgo (*Echinocloa stagnina (Retz.) P. Beauv*). Cependant, la culture du riz est très risquée, car elle nécessite de la pluie pour que le riz germe avant que la crue ne survienne. Le but principal de cette étude fut de mettre au point une alternative à la culture du riz en introduisant un système de décrue dans les bras du fleuve Niger comportant des variétés précoces qui peuvent achever leur cycle avant que la saison chaude ne s'installe en avril-mai. En outre, cette étude a eu pour but secondaire d'examiner quels sont les sols qui se prêtent le mieux à ce type de culture.

MATERIELS ET MÉTHODES

Les essais de décrue furent menés dans 4 localités pendant la campagne 1987-1988. Le site de Bambara Maudé est une mare qui se remplit avec de l'eau de pluie, alors que les autres sites sont des bras du Niger. Les cultivateurs ont l'habitude de cultiver le niébé à Bambara Maudé, alors que le sorgho est la culture principale à Sheriffen Rhergo. A Sheriffen Rhergo, le semis est fait à la décrue, mais les plantes profitent de la pluie pour achever leur cycle. Les deux sites à Banguel sont des rizières.

Le dispositif expérimental fut celui du bloc de Fischer à 3 répétitions. Les essais furent conçus de façon à pouvoir faire une comparaison valable entre les différentes espèces et entre les différentes variétés d'une même espèce. Chaque bloc fut divisé en sub-blocs représentants les différentes espèces. Dans les sub-blocs furent représentées les différentes variétés d'une même espèce. Les essais variétaux du niébé ont aussi concerné une variété du pois mung (*Vigna radiata* (L.) Wilczek, variété: celera), pour faire une évaluation, de même, de cette espèce. Cela fut jugé possible, car le comportement du pois mung diffère peu de celui du niébé. Le semis a suivi le retrait de l'eau et s'est étalé de 1 à 2 semaines sur tous les sites. Le pois mung fut semé à raison de 8 grains/poquet alors que les autres légumineuses furent semées à raison de 4 grains/poquet. Toutes les légumineuses furent démariées à raison d'une plante par poquet. Les céréales furent semées à raison d'environ 25 grains et 12 grains/poquet pour le mil et le sorgho respectivement, et démariées à raison de 3 plantes/poquet. Les récoltes furent effectuées au fur et à mesure que la maturité arrivait. Les données expérimentales des essais sont consignées dans le tableau 2.

Tableau 2. Date du semis, largeur des parcelles (m), distance entre plantes (m) et fin de la récolte

	Date du semis	Largeur de la parcelle	Distance entre poquets	Fin de récolte
Bambara Maudé	9/10-21/10	2,7*9,9	0,9*0,9	21/3-88[1]
Banguel, 2 Sites	27/12-6/1[2]	2,1*11,0	0,7*1,0	30/5-88
Sheriffen Rhergo	1/3-12/3	1,8*6,0[3]	0,6*0,6[3]	(début
Sheriffen Rhergo		2,1*7,0[4]	0,7*0,7[4]	octobre)

[1] Récolte du poids d'angole terminée fin avril.
[2] Resemis à Banguel «sable» trois semaines plus tard sur le même site.
[3] Haricot
[4] Autres espèces

La levée des plantes fut enregistrée en comptant les poquets ayant des plantes. Une attaque de Bruche du niébé (*Callosobruchus maculatus*) sur les grains stockés dans le magasin a diminué un peu le rendement du niébé à Sheriffen Rhergo avant la pesée. L'attaque a été estimé à l'oeil nu, et le rendement a été corrigé par cette attaque.

La ppds (plus petite différence significative) 5% est donnée là où elle est trouvée significative. Les niveaux de probabilité à 0,05, 0,01 et 0,001 pour les interactions sont respectivement indiqués par *, **, ***. L'abréviation n.s. signifie non significatif au niveau de probabilité de 0,05.

Les variétés testées furent pour le niébé, le sorgho et le mil les variétés en provenance de la Section de Recherche sur les Cultures Vivrières et Oléagineuses (SRCVO), Bamako, CIPEA (Centre International Pour l'Elevage en Afrique), Bamako et l'ICRISAT Centre Sahélien, Niamey, en plus des variétés locales. Pour le pois d'angole et le pois chiche, toutes les variétés provenaient de l'ICRISAT en Inde.

Les prélèvements du sol pour les analyses physiques furent effectués avec des cylindres ayant un volume de 100 cm^3. Des fosses pédologiques furent creusées et le profil du sol fut divisé en couches suivant la texture. Quatre échantillons de sol furent pris dans chaque couche. Les prélèvements pour les analyses chimiques du sol furent réalisés sur tous les sites, sauf celui de Banguel «sable». Les analyses chimiques du sol furent réalisées dans «le laboratoire des sols» à Bamako, alors que les analyses physiques furent effectuées dans «l'Institut du Sol» à Ås, Norvège.

RESULTATS ET DISCUSSION

Les résultats concernent le comportement des différentes espèces et variétés et les caractéristiques chimiques et physiques du sol.

Comparaison entre espèces

Les essais ont été conçus de façon à pouvoir faire une comparaison entre les différentes espèces. Il est d'abord à souligner qu'une telle comparaison est difficile, car le contenu énergétique ainsi que la valeur nutritive, diffère d'une espèce à l'autre. L'écartement entre les plantes n'est pas toujours optimal pour les espèces considérées. La comparaison entre les espèces est aussi rendue difficile du fait que toutes les variétés des espèces ne sont pas adaptées à la zone. Malgré ces réserves, une comparaison entre les espèces est présentée.

En ce qui concerne la levée, il s'est avéré que la levée sur les deux sites à Banguel a été faible pour toutes les variétés sauf pour le pois chiche. Le semis y a commencé à partir du 28 décembre pendant une période de grand froid, avec des températures nocturnes inférieures à 10 °C. Il a fallu semer à nouveau 3 semaines plus tard le niébé, le pois d'angole, le sorgho et le mil à Banguel «sable». La faible germination obtenue ici pour les espèces citées pourrait être attribuée aux basses températures, car les espèces tropicales germent moins bien avec des températures au-dessous de 20 °C (Fisher 1984, Singh et Dhaliwal 1972). Et, ainsi, pour le pois chiche, qui est adapté à des conditions plus méditerranéennes, aucun problème n'a été observé avec la levée.

Quant aux rendements en grains à Bambara Maudé, ce fut le niébé qui a donné, de loin, les meilleurs rendements (tableau 3). Ce fut surtout le pois chiche qui a produit un rendement faible.

A Sheriffen Rhergo, le rendement du sorgho aurait pu dépassé de loin le rendement du niébé sur ce site, si la crue n'était pas survenue, noyant la récolte du sorgho (tableau 3). Aucun rendement du pois d'angole n'a, ici, été obtenu.

Sur les deux sites de Banguel, les rendements ont été très faibles pour toutes les espèces. Le niébé a ici présenté les rendements les moins faibles. Aucuns rendements du pois d'angole et du pois chiche n'ont été obtenus sur ces deux localités.

Pour l'ensemble des sites, il semble que le niébé, le sorgho, et, éventuellement le mil, sont les espèces qui sont les plus adaptées à la culture de décrue au Gourma.

	Bambara Maudé	Sheriffen Rhergo
Niébé	525	252
Pois mung	198	261
Pois d'angole	190	0
Pois chiche	12	-
Sorgho	90	fort
Mil	109	-

Tableau 3. Rendement en grains (kg/ha) des différentes espèces à Bambara Maudé et Sheriffen Rhergo

Niébé (Vigna unguiculata (L.) Walp.)

Les essais variétaux du niébé comportaient des variétés locales, Mopti et Rouge, et des variétés sélectionnées. C'est la variété Mopti qui semble être la variété la plus répandue dans la zone. La levée a été bonne à Bambara Maudé (tableau 4) alors qu'elle a été trouvée la plus faible à Banguel «argile».

Tableau 4. Levée du niébé (8 variétées) et du pois mung (1 variété) dans les différentes localités

	Bambara Maudé	Sheriffen Rhergo	Banguel sable[1]	Banguel argile	Moyenne
Mopti	100,0	88,9	72,2	60,6	80,4
Rouge		97,7	80,8	58,6	87,5
Suivida 2		58,9	88,3	45,4	72,6
CB-5	89,9	56,7	58,6	21,2	56,6
TN 88-63	71,7	27,7	72,7	38,6	52,6
TVX 32-36	99,0	91,1	77,8	48,5	79,1
Giro 45581	98,0	77,8	93,9	53,5	80,8
IT82D-716	96,0	41,1	37,4	2,0	44,1
Pois mung	99,0	73,3	88,3	42,4	74,4
Moyenne	93,4	68,1	73,8	41,2	69,7
ppds 5%	5,1	21,7	24,9	13,0	18,5
Interaction					**

[1] Deuxième semis

Les rendements en grains ont été très faibles sur les deux sites à Banguel. Aucune différence significative entre les différentes variétés ne s'est dégagée, et les rendements moyens ont été respectivement de 22,2 et de 4,3 kg/ha à Banguel site «sable» et «argile». A Bambara Maudé, la variété Mopti a donné le meilleur rendement, suivie par TN 88-63 (tableau 5). La levée a été de 71,7% et de 100% respectivement pour TN 88-63 et Mopti (tableau 4), et si la levée de TN 88-63 avait été aussi élevée que celle de Mopti, le rendement en grains de TN 88-63 aurait pu atteindre celui de Mopti. Ces deux variétés sont plus tardives que les autres, car la plus grande partie de leur rendement a été obtenue lors de la dernière récolte. Les variétés CB-5 et Giro 45581, ainsi que le pois mung, sont précoces, mais leurs rendements en grains ont été faibles à Bambara Maudé, comparés aux variétés plus tardives. Cependant, il est à souligner que l'écartement entre poquets n'a pas permis aux variétés précoces et érigées, à savoir «pois

mung», CB-5 et Giro 45581 d'atteindre leur potentiel maximal, car elles n'ont pas recouvert le sol aussi bien que les variétés rampantes.

A Sheriffen Rhergo, les variétés Rouge, Suivida 2 et Mopti ont donné les meilleurs rendements (tableau 5). Comme à Bambara Maudé, la variété Mopti n'a pas donné un bon rendement lors de la première récolte; mais lors de la dernière récolte, un meilleur rendement a pu être obtenu, grâce aux pluies tombées en août et en septembre.

Dans des essais menés par l'ICRISAT en Niger, CB-5 et le TN 88-63 se sont montrées assez adaptées à un semis en contre saison, alors que la performance de IT 82D-716 s'est avérée faible pendant cette période (ICRISAT Sahélien Centre 1986, 1988).

Tableau 5. Rendement en grains (kg/ha) (8 variétés de niébe et une variétés de pois mung) dans les différentes périodes, et rendement total Bambara Maudé et à Sheriffen Rhergo

	Bambara Maudé				Sheriffen Rhergo		
	10/12-17/12	18/12-18/1	19/1-21/3	Total	24/5-11/8	11/8-5/10	Total
Mopti	0	56	653	709	134	272	406
Rouge					275	203	478
Suivida 2					185	216	403
CB-5	68	158	201	428	64	0	64
TN 88-63	0	45	574	620	71	163	234
TVX 32-36	0	142	445	587	211	28	239
Giro 45581	67	109	170	346	49	20	69
IT 82D-716	0	66	396	461	116	9	125
Pois mung	64	27	105	198	254	7	261
Moyenne	29	86	364	479	151	102	253
ppds 5%	65	35	283	248	195	144	255

Comme pour les rendements en grains, les rendements en fane se sont révélés très faibles, sauf à Bambara Maudé (tableau 6). Sur tous les sites, Mopti s'est avérée, largement, plus productive que les autres variétés. Les variétés précoces comme CB-5 et Giro 45581, ainsi que le pois mung, ont été nettement moins vigoureuses. Il est à souligner que les rendements en fane sont probablement sous-estimés, parce que le vent avait emporté une partie des feuilles sèches.

A Bambara Maudé, des nodosités sur les racines du niébé ont été recherchées, et des nodosités bien développées ont été trouvées.

Pour le semis en octobre, la variété Mopti semble être le meilleur choix, car, quand elle est semée à ce moment, elle peut achever son cycle avant que la saison chaude ne s'installe. Cette variété a le double avantage de pouvoir donner un bon rendement en grains, ainsi qu'un rendement important en fane.

Un semis en février-mars entraîne le risque que la floraison coïncide avec la saison chaude en avril-mai, et il a été montré que le pourcentage des fleurs qui produisent des gousses diminue considérablement, quand la température commence à augmenter (ICRISAT Centre Sahélien 1988). Le faible rendement de Mopti lors de la première récolte à Sheriffen Rhergo indique qu'elle est trop tardive pour un semis en février-mars si toute la récolte doit être achevée avant le mois de mai (tableau 5). Pour un

semis à ce moment-là, il faut plutôt semer une variété plus précoce comme Suivida 2 ou Rouge. Les résultats de Banguel appuient cette hypothèse, car, ici, les variétés Rouge et Suivida 2 ont eu tendance à être plus performantes pour le rendement en grains que Mopti, bien que ce résultat ne soit pas significatif.

Tableau 6. Rendement en fane (kg/ha) dans différentes localités

	Bambara Maudé	Banguel «sable»	Banguel «argile»
Mopti	1140	203	192
Rouge		70	97
Suivida-2		81	110
CB-5	332	115	39
TN 88-63	565	130	81
TVX 32-36	627	125	169
Giro 45581	371	108	43
IT 82D-716	633	124	19
Pois mung	90	23	0
Moyenne	537	109	83
ppds 5%	259	90	60

Pois d'angole (Cajanus cajan (L.) Millsp.)

Le pois d'angole n'a pas donné de bons résultats au Gourma. Ce fut seulement à Bambara Maudé qu'un faible rendement a pu être obtenu (tableau 7), et le meilleur rendement a été obtenu avec ICPL 83024. Les différentes variétés se sont révélées avoir une précocité identique, et la première récolte a été effectuée 105 jours après le semis. La moisson a duré de fin janvier à fin avril. L'indice de rendement, qui est près de 50%, doit être considéré comme très élevé. Ce résultat est en concordance avec le résultat de Narayanan & Sheldrake (1979), qui ont trouvé que l'indice de rendement est plus élevé en contre saison qu'en saison pluvieuse.

Dans les autres localités, aucun rendement en grains n'a pu être obtenu, et le rendement moyen en fane a été très faible, à savoir 60 et 100 kg/ha respectivement à Banguel site «sable» et site «argile». A Sheriffen Rhergo, le pois d'angole s'est développé de manière satisfaisante, et les plantes ont bien fleuri pendant tout l'hivernage, mais presque aucun développement de gousse n'a été constaté. Ceci est difficile à expliquer, car les plantes ne semblaient pas souffrir de la sécheresse. Les tempêtes de sable sont fréquentes dans la zone, et elles pourraient avoir provoqué la chute des fleurs. Il est aussi possible que les insectes en soient la cause.

Pois chiche (Cicer arietinum L.)

La croissance du pois chiche a été faible sur l'ensemble des sites. A Banguel, sites «sable» et «argile», les plantes se sont très peu développées, et la formation des gousses a été très faible. A Bambara Maudé, les plantes se sont mieux développées, bien que les rendements en grains s'y soient avérés aussi très faibles. La variété ICMH 42 a, ici, présenté le rendement en grains le moins faible (tableau 8).

Tableau 7. Levée (%), rendement et indice de rendement (%) du pois d'angole à Bambara Maudé

	Levée %	Grains kg/ha	Fane kg/ha	Indice de rendement
ICP 148	93,9	191	179	51,6
ICPL 151	98,0	188	179	51,2
ICPL 4	100,0	170	163	51,1
ICPL 83024	99,0	210	201	51,1
Moyenne	97,7	190	181	51,3
ppds 5%	n.s.	24	21	n.s.

A Bambara Maudé, des nodosités sur les racines ont été recherchées, sans donner de résultat positif. Ceci n'est pas étonnant, car le type de rhizobium qui s'associe au pois chiche est très spécifique (Smithson et al. 1985).

Les résultats obtenus, ici, permettent de conclure que le pois chiche ne semble pas être une espèce adaptée pour le Gourma.

Tableau 8. Levée (%), rendement (kg/ha), et indice de rendement (%) du pois chiche à Bambara Maudé

	Levée	Grains	Fane	Indice de rendement
ICCV 2	100,0	3,0	6,7	30,9
ICCV 32	99,0	10,7	61,7	14,7
ICCH 42	99,0	22,7	38,7	36,9
Moyenne	99,3	12,1	35,7	25,3
ppds 5%	n.s.	11,5	n.s.	n.s.

Sorgho (Sorgho bicolor (L.) Moench)

Les essais variétaux du sorgho ont porté sur des variétés locales, Fossa, Djibock et Bambara Maudé, et des variétés sélectionnées. A Bambara Maudé, un faible rendement a pu être obtenu (tableau 9). Les variétés «Djibock» ,«Fossa» et Malisor 84-7 ont donné les rendements en grains les plus élevés, et les deux premières variétés citées se sont avérées aussi être les plus précoces. Les indices de rendement très faibles indiquent que la disponibilité en eau n'était pas suffisante pour que les plantes aient pu achever leur cycle de manière satisfaisante. Les rendements du sorgho sont un peu sous-estimés, car il s'est produit une attaque d'oiseaux lors de la campagne.

A Sheriffen Rhergo, la récolte du sorgho était prometteuse, surtout en ce qui concerne la variété «Rharous», jusqu'à ce que la crue du fleuve ne survienne, noyant une partie des plantes.

Mil (Pennisetum glaucum (L.) R. Br.)

La variété du mil testée fut la variété locale Hombori. A Bambara Maudé, les rendements en grains et en paille ont été de 109,6 et de 567 kg/ha, respectivement. La

Tableau 9. Levée (%), cycle du semis à la première récolte, rendement (kg/ha) et indice de rendement (%) du sorgho à Bambara Maudé

	Levée %	Cycle, jours	Grains kg/ha	Paille kg/ha	Indice de rendement
Bambara Maudé	95,7	129	9,3	1081	0,9
Djibock	98,0	82	165,3	1166	12,4
Fossa	89,9	80	139,7	860	14,0
CE 90	92,9	85	69,3	1028	6,3
Malisor 84-5	88,8	115	14,7	1029	1,4
Malisor 84-7	91,9	105	141,3	798	15,0
Moyenne	92,9	99	89,9	994	8,3
p pds 5%	n.s.	n.s.	92,4	n.s.	3,7

première récolte a été effectuée 82 jours après le semis. Le pourcentage de la levée a été de 79,9%. Comme pour le sorgho, les oiseaux ont diminué légèrement ici les rendements. Le mil a aussi été semé à Banguel et, dans la plupart des poquets, le développement des plantes a été faible, mais quelques poquets ont donné de bons épis.

Conditions pédologiques

La fertilité du sol (tableau 10) est de loin plus favorable à Bambara Maudé qu'à Sheriffen Rhergo et à Banguel «argile». Le pH (KCl) a été trouvé de 4,0 à Banguel «argile» et dans la couche 22-66cm à Sheriffen Rhergo. Un tel pH peut diminuer les rendements parce qu'il a été montré, au Niger, qu'un apport de chaux peut augmenter les rendements du niébé quand le pH (KCl) initial est de 4,5 (Bationo et al. 1989).

C'est le phosphore qui est considéré comme l'élément le plus déficitaire au Sahel (Fussel et al. 1987), et le niveau du phosphore qui permet d'obtenir 90% du rendement maximum (niveau critique) a été estimé à 7,9 ppm avec le test de Bray 1 (Bationo et al. 1989). Cependant, l'analyse du sol utilisée pour le phosphore dans cette étude a été celle de Bray 2. Lorsque ces deux méthodes furent comparées sur 30 différents sols au Nigeria, la quantité de phosphore extraite avec la méthode de Bray 1 et Bray 2 fut respectivement de 22,4 ppm et 27,1 ppm (Enwezor 1977) et la corrélation entre les deux méthodes fut élevée ($r^2 = 0,87$). Cela montre que ces deux méthodes sont proches l'une de l'autre. Les analyses du sol (tableau 10), montrent que le faible niveau du phosphore soluble dans les sols à Sheriffen Rhergo et Banguel «argile» a probablement gravement entravé les rendements. Les teneurs en calcium, magnésium et potasse sont plus satisfaisantes à Bambara Maudé et Banguel «argile» qu'à Sheriffen Rhergo en comparant avec les chiffres donnés dans l'Agricultural Compendium (1981). Il est à remarquer que la saturation en bases à Banguel «argile» est excessivement faible dans la couche 0-20cm. Le niveau de matière organique est faible sur l'ensemble des sites. On remarque que la teneur en argile est de 44,4% à Banguel «argile», ce qui est très élevé.

Les analyses physiques du sol montrent que la densité du sol est élevée, de 1,57 kg/dm^3 à 1,87 kg/dm^3, sur l'ensemble des sites (tableau 11). Au Sénégal, il a été montré que les rendements du sorgho ont diminué de façon linéaire de 450-600 kg/ha avec une augmentation de la densité apparente de 0,1 kg/dm^3 entre des densités de 1,4 kg/dm^3 à 1,6 kg/dm^3 (Charreau & Nicou 1971). Cassel (1983) indique que la limite supérieure de

Tableau 10. Analyses chimiques du sol à Bambara Maudé, Sheriffen Rhergo, et Banguel «argile»

	Bambara Maudé		Sheriffen Rhergo		Banguel argile
	10-20cm	52-60cm	0-22cm	22-66cm	3-55cm
pH eau	6,9	7,8	6,0	5,5	5,3
pH KCl	5,5	5,8	4,8	4,0	4,0
Carbone %	0,27	0,08	0,18	0,22	0,22
P (Bray) ppm	36,4	33,2	0,2	1,0	2,2
CEC méq/100 g	5,2	16,2	4,1	12,6	14,1
Ca éch.méq/100g	3,31	15,85	0,15	4,74	6,27
Mg éch. méq/100g	1,23	5,96	0,06	3,37	3,89
K éch. méq/100g	0,45	0,66	0,02	0,14	0,38
Na éch. méq/100g	0,99	0,14	0,03	0,28	0,57
Saturation%	100	100	6	68	79
Sable%	82,4	45,3	73,5	40,0	37,9
Limon%	5,1	35,2	9,8	21,2	17,9
Argile%	12,4	19,5	16 ,7	38,8	44,4

la densité apparente du sol pour la pénétration des racines dans un sol humide à texture grossière est de 1,75 kg/dm^3, alors que cette limite pour un sol à texture fine est de 1,4 à 1,6 kg/dm^3. A Banguel «sable» la densité apparente dans la couche supérieure fut trouvée de 1,82 kg/dm^3, ce qui fait que la pénétration des racines s'en est trouvée gravement perturbée. Liée à cette densité apparente élevée, se trouve une porosité très faible, de 30,8%. Au Sénégal, il a été montré que l'enracinement est entravé si la porosité baisse de 45% à 38% (Nicou & Charreau 1985). Aux Pays-Bas, il a aussi été trouvé que l'enracinement est difficile au-dessous d'une porosité de 40% (Hidding & Berg 1960). A Banguel «argile», les problèmes liés aux conditions physiques du sol semblent être la densité apparente élevée et le fait que, à la capacité au champs, l'humidité volumique est égale à la porosité (tableau 11). Il en suit qu'à la capacité au champs, toutes les pores sont remplies d'eau, entravant gravement le développement des racines.

La capacité de rétention d'eau est presque identique (avoisinant 170mm dans la couche 0-100cm) à Bambara Maudé, à Sheriffen Rhergo et à Banguel «argile» alors que cette capacité à Banguel «sable» n'est que de 90mm. A Bambara Maudé, il y a une couche de graviers entre 42 et 52cm, qui empêche la remontée capilaire, mais il semble que les racines soient capables de pénétrer cette couche, car des traces de racines ont été trouvées en dessous de celle-ci. Les bons rendements, obtenus ici, indiquent aussi que les racines ont pénétré. A Banguel «sable», il est possible que seule l'eau dans la couche 0-45cm soit disponible. La couche de 45cm à 80cm est une couche de sable pur, car l'humidité volumique à PF 4 est très basse (0,3), et il en suit que les pores, ici, sont plus grosses que celles de la couche supérieure. Quand le stock d'eau dans la couche supérieure est épuisé, l'air rentre probablement dans les grandes pores de la couche sous-jacente, entraînant un drainage de l'eau.

Toute l'eau entre PF 2 et PF 4,2 ne peut pas être disponible aux plantes, à cause de la densité élevée et du manque de porosité qui entravent la pénétration des racines dans le sol. Pour se faire quand même une idée du besoin en eau dans des conditions de décrue au Gourma, les résultats d'une étude réalisée au Niger sur le mil cultivé en

contre saison sur l'eau emmagasinée a été utilisée (Azam-Ali et al. 1984). Il y a été montré que le mil à puisé une quantité importante de son besoin d'eau à une profondeur au-dessous de 1m, et qu'un rendement en matière sèche de 2600 kg/ha a correspondu à une consommation d'eau d'environ 120mm. Cela indique que la quantité d'eau stockée dans le sol n'est pas un facteur limitant les rendements à Bambara Maudé, Sheriffen Rhergo et Banguel «argile», car, ici, la quantité d'eau stocké dans le premier mètre de sol a été d'environ 170mm. A Banguel «sable», il est possible que le manque d'eau puisse compromettre la maturation des plantes, car, là, seuls environ 60mm sont probablement facilement accessibles aux plantes. Une partie de cette eau (10-20%) est aussi perdue par l'evaporation quand la surface du sol sèche (Squire et al. 1987).

Tableau 11. Caractéristiques physiques du sol

	Densité apparente kg/dm^3	% porosité	Humidité volumique (%)		mm d'eau disponible
			PF 2	PF 4,2	
Bambara Maudé					
sable limoneux 0-27cm	1,63	38,2	23,2	5,4	48,1
sable-limoneux 27-42cm	1,66	37,2	13,0	3,8	13,8
gravier 42-52cm					2(1)
limon 52-90cm	1,74	39,5	9,5	18,6	79,4
limon 90-100cm					20,0
mm jusqu'à 100cm					163,3
Banguel argile					
Argile 0-55cm	1,62	40,6	40,6	23,0	91,5
Argile 55-90cm	1,67	41,0	41,0	23,7	60,5
Sable 90-96cm					3(1)
Argile 96-100cm	1,73	35,6	35,6	14,8	6,3
mm jusqu'à 100cm					161,3
Banguel sable					
Sable limoneux 0-45cm	1,82	30,8	26,3	12,9	60,3
sable 45-80cm	1,66	37,2	4,6	0,3	15,1
Sable-limoneux 80-100cm	1,87	28,0	11,6	4,8	13,6
mm d eau jusqu'à 100cm					89,0
Sherrifen Rhergo					
Limon sableux 0-22cm	1,57	39,9	25,2	7,4	39,2
Limon argileux 22-66cm	1,71	36,3	36,3	19,0	76,1
Limon argilo sableux 66-100cm	1,69	32,8	27,3	10,1	58,5
mm d'eau jusqu'à 100cm					173,4

(1) Chiffré estimé

Relations caractéristiques du sol et rendements

Les meilleurs rendements en grains ont été obtenus à Bambara Maudé et à Sheriffen Rhergo. A Bambara Maudé, les conditions sont favorables pour la culture, à savoir un pH élevé, une teneur élevée en phosphore accessible, une capacité de rétention d'eau assez élevée et une porosité du sol satisfaisante. A cela s'ajoute une température favorable pendant la période de croissance. Le niébé y est la plante qui en a le plus profité. A Sheriffen Rhergo, les conditions physiques semblent être satisfaisantes, mais

le facteur principal limitant les rendements semble être la faible teneur en phosphore accessible. Le sorgho a, ici, donné les meilleurs rendements. Sur les deux sites de Banguel, les rendements ont été très faible. A Banguel «argile», les principaux défauts du sol semblent être le manque d'air à la capacité au champs, la densité apparente élevée et la faible teneur en phosphore accessible. A Banguel «sable», les contraintes majeures du sol semblent être la densité apparente élevée et la faible porosité.

Pour la mise en culture des sols à Banguel, il semble nécessaire d'améliorer la structure du sol, rendant l'utilisation de la charrue presque inévitable. Cependant, les moyens dont disposent les cultivateurs sont très limités, rendant un bon labour du sol difficile. Le riz flottant et le bourgou semblent donc les espèces les mieux adaptées pour ces sols.

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Variétés du mil en culture pluviale pour le Gourma au Mali

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Aune, J. B. 1992. Variétés du mil en culture pluviale pour le Gourma au Mali. Norwegian Journal of Agricultural Sciences 6: 293-308. ISSN 0801-5341.

Des essais, en 1988, ont été menés dans quatre localités dans le Gourma au Mali dans des conditions de fertilité naturelle du sol. La pluviométrie a varié de 170 à 290 mm. Le nombre de jours du semis jusqu'à la floraison des variétés testées a varié de 46 à 59 jours. Aucune différence de rendement en grains entre les différentes variétés n'est apparue, quand l'analyse a été effectuée pour l'ensemble des localités. Le principal inconvénient présenté par les variétés les plus précoces semble être leur manque de stabilité en ce qui concerne le rendement en grains. Ces variétés ont néanmoins maintenu un indice de rendement élevé dans l'ensemble des localités. Dans les localités où elles ont produit un rendement faible, c'est surtout le nombre d'épis/plante qui a été réduit.

Mots clés: Pennisetum glaucum, variétés, précocité, indice du rendement, composantes du rendement, adaptation locale.

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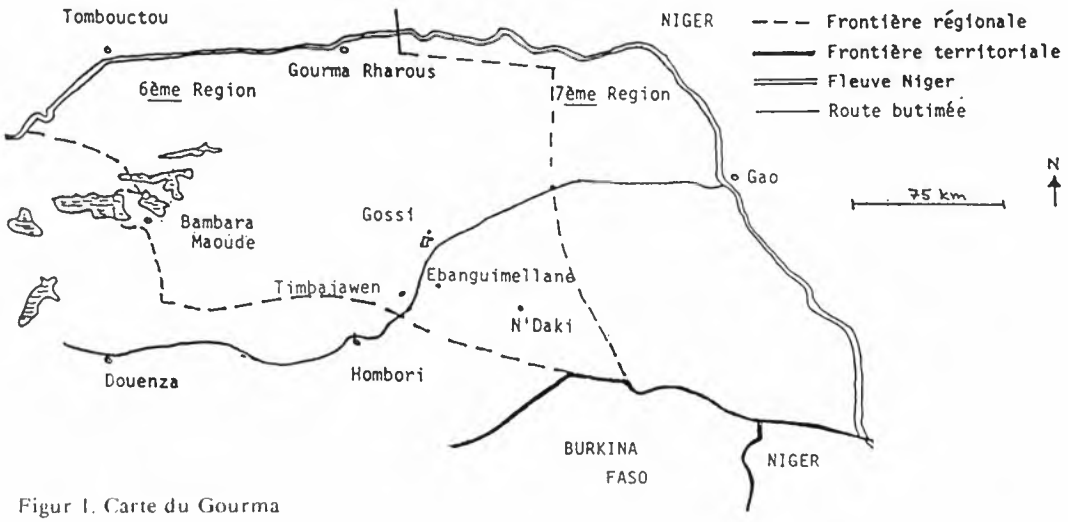
Le mil pennisilaire (*Pennisetum glaucum* (L.) R. Br.) joue un rôle primordial pour l'alimentation de la population au Mali, et il est cultivé presque partout où l'on trouve de l'agriculture pluviale. Souvent, la culture du mil coexiste avec celle du sorgho, mais le mil est plus répandu que le sorgho au nord des isohyètes 700-800 mm (Niagando et al. 1987). La limite septentrionale pour le mil au Mali semble être l'isohyète de 300 mm et cette limite se trouve au Gourma (figure 1) dans la partie sud. En plus de ce facteur, la grande variabilité interannuelle des pluies au nord du Sahel (Sivakumar et al. 1984) rend la culture aléatoire au Gourma. Le mil ne peut donc constituer qu'une source alimentaire complémentaire au Gourma, l'élevage et la cueillette des plantes sauvages représentant le mode d'alimentation principale.

La culture du mil au Gourma se fait sans intrants extérieurs comme de l'engrais ou des produits phytosanitaires. C'est donc une culture extensive. Le semis du mil se fait à partir du début juin, normalement avant le début des pluies, bien que l'irrégularité des pluies soit importante au début de la saison. Le choix de cette période peut se justifier par le fait que les premières pluies déclenchent un processus de minéralisation de l'azote fugace dont la plante peut alors bénéficier (Charreau 1969). L'irrégularité des pluies fait que plusieurs semis consécutifs sont souvent nécessaires. Le mil est ici semé sans aucune préparation préalable du sol, et la distance entre les poquets est d'environ



Figur 1. Carte du Gourma

1m. Dans chaque poquets 20-40 grains sont placés, et le démariage est fait de 2 à 5 plantes/poquet. Le sarclage ne consiste que d'un grattage superficiel du sol.

Du fait que le climat du Gourma n'offre qu'une courte période de croissance, et que les périodes de sécheresse au cours de la saison sont fréquentes, une attention particulière doit être portée à la précocité et à la résistance à la sécheresse lors du choix d'une variété. Bidinger et al. (1987) ont montré que le rendement d'une variété dans des conditions de stress hydrique, dépend de la précocité, du rendement potentiel sans stress, et de l'adaptabilité au stress. Ils indiquent que, parmi ces facteurs, la précocité doit être considérée comme le facteur principal limitant les rendements sous condition de stress hydrique. Cependant, les variétés précoces sont souvent plus attaquées par les oiseaux et les insectes, car leur maturité coïncide davantage avec la période bien arrosée (Niangado et al. 1987).

Bidinger et al. (1987) ont montré que, si une sécheresse intervient entre l'initiation florale et la floraison, les variétés à floraison tardive produisent les meilleurs rendements. Cela peut s'expliquer par une meilleure développement foliaire chez les mils tardifs, permettant une meilleure accumulation de substances nutritives dans les grains. Cette indication peut être étayée par les résultats de Lambert (1983), qui a montré que la formation de l'appareil reproducteur des variétés précoces interfère avec le développement de la touffe, provoquant ainsi une concurrence entre le développement végétatif et le développement reproductif. Les résultats de Dancette (1983) au Sénégal montrent, de même, que les variétés précoces en début de saison ont un besoin plus élevé en eau que les variétés tardives, dû à un développement rapide au début du cycle. En cas de sécheresse post-florale, les variétés à floraison précoce donnent le meilleur rendement, surtout parce qu'elles évitent, alors, le stress hydrique. L'effet du stress sur les composantes du rendement dépend de la phase phénologique de la plante lorsque le stress survient (Bidinger et al. 1987, Mahalakshmi et al. 1987). Dans le cas d'un stress pré-floral, ils ont montré que le nombre des épis augmente alors que le nombre de grains/épi diminue. Le stress post-floral provoque une perte du rendement en diminuant en pre-

mier lieu le nombre des épis/plante, et ensuite en diminuant le poids de 1000 grains et le nombre de grains/epi. Ces résultats sont attribués au tallage asynchrone du mil qui fait que les talles développées les dernières n'arrivent pas à produire d'épis en cas de stress post-floral (Bidinger et al. 1987). Lors d'une sécheresse post-florale, les variétés à floraison précoce donnent les meilleurs rendements, surtout parce qu'elles conservent plus de grains/épi que celles à floraison tardive. Les résultats de l'ICRISAT en Inde indiquent que dans des conditions de stress post-floral, les variétés à gros grains pourraient avoir un avantage, car, alors, la corrélation négative entre le nombre de grains/épi et la taille des grains est moins importante (ICRISAT 1987).

L'amélioration du mil en Afrique de l'ouest vise à mettre au point des variétés ayant un potentiel de rendement élevé et stable dans des conditions de culture améliorées (ICRISAT 1987). Une importance particulière est accordée à la bonne levée et à la survie des jeunes plantes, à la résistance aux sécheresse pré- et post-florales, à la précocité, et à la résistance aux maladies et aux insectes. Les principales maladies en Afrique de l'ouest sont le mildiou du mil (*Sclerospora graminicola*), le charbon (*Tylosporium penicilliae*) et l'ergot (*Claviceps fusiformis*), et les principaux insectes nuisibles sont le foreur des tiges (*Coniesta ignefusalis*) et la mineuse de l'épi (*Heliocheilus albipunctella*) (ICRISAT Centre Sahélien 1986).

Le but de cette étude a été d'examiner les possibilités de trouver des variétés nouvelles qui ont un rendement plus élevé et stable que les variétés locales.

MATERIELS ET METHODES

Les essais menés en 1987 ont échoué en raison du manque de pluies. Ce rapport ne concerne ainsi que les essais menés en 1988. Les variétés testées sont des variétés sélectionnées en provenance de l'ICRISAT Centre Sahélien, et de SRCVO (Section de Recherche sur les Cultures Vivrières et Oléagineuses) à Bamako, et les variétés locales Hombori et Tabi. La variété Hombori semble être la variété locale la plus répandue dans la zone. La variété Tabi provient de la 5ème région dans le pays «Dogon». L'une des variétés sélectionnées, ICMH 88951, est un hybride.

Le dispositif expérimental utilisé a été celui du bloc de Fischer à quatre répétitions. Là où la taille du terrain le permettait, l'on a essayé de diminuer l'effet possible de la parcelle voisine sur le rendement en semant 5 lignes (parcelle élémentaire), et les trois lignes du milieu (parcelle utile) ont fait l'objet des observations ainsi que de la récolte. Les données expérimentales sont consignées dans le tableau 1.

Le semis s'est fait sur le flanc des billons. Sur tous les sites, sauf celui de N'daki, les semis furent réalisés de façon consécutive à une pluie. Environ 25 grains furent semés dans chaque poquet et le démariage fut effectué à raison de trois plantes/poquets à peu près deux semaines après la levée. Deux sarclages à la houe furent effectués au cours de la saison. A Gossi, les plantes ont connu une sécheresse pendant presque tout le cycle et, pour éviter que les plantes ne meurent de la sécheresse, un apport de 6-7 l d'eau/poquet fut donné 6 fois pendant la saison.

Les observations au cours de la saison furent relevées pour chaque parcelle afin de pouvoir réaliser des analyses statistiques. Les observations furent prises de la manière suivante, et les localités où les observations furent prises sont indiquées entre parenthèses.

Tableau 1. Donnés expérimentales des essais variétaux du mil. Dimensions en mètre

	Timbajawen	N'Daki	Gossi	Ebanguimellane
Date du semis	10/7	7/7	10/7	11/7
Parcelle élémentaire	3,6x8,1	4,5x8,1	3,6x6,3	4,5x8,1
Parcelle utile	2,7x8,1	2,7x8,1	3,6x6,3	2,7x8,1
Ecartement entre poquet	0,9x0,9	0,9x0,9	0,9x0,9	0,9x0,9

-la levée: en comptant tous les poquets dans lesquels il y avait des plantes (toutes les localités).
-le nombre de jours jusqu'à 50 % de floraison: en comptant tous les 3 ou 4 jours le nombre de poquets ayant au moins un épi. Le chiffre donné exprime, à partir du semis, le nombre de jours nécessaire pour que 50 % des poquets arrivent à la floraison (toutes les localités, sauf N'daki).
-la verse: en comptant par parcelle les poquets ayant au moins une tige penchée (Timbajawen).
-la résistance à la sécheresse au moment du tallage: en estimant à l'oeil nu les symptômes de stress hydrique, comme le flétrissement et la perte de la turgidité dans le feuillage (Ebanguimellane et Gossi).
-les attaques des oiseaux et la stérilité dans l'épi: en estimant à vue d'oeil, sur 40 épis, le pourcentage de l'attaque et de la stérilité (toutes les localités, sauf Gossi).
-la longueur de la tige jusque au commencement de l'épi: en mesurant dans 20 poquets la longueur de la tige principale (toutes les localités, sauf Gossi).
-poids de 1000 grains: 200 grains furent pesés (toutes les localités, sauf Gossi).
-nombre d'épis/plante: nombre d'épis récoltés par parcelle, divisé par le nombre de plantes par parcelle (toutes les localités).
-le nombre de grains/épi: calculé en se fondant sur le rendement en grains et les autres composantes du rendement (toutes les localités).
-les récoltes en grains et en paille furent séchées au moins pendant 1 mois avant d'être pesées (toutes les localités).
-le pourcentage de protéines a été déterminé avec la méthode de «Near Infrared Reflectance» (NIR) (toutes les localités, sauf Gossi).

Les rendements en grains furent corrigés par le poucentage d'attaque des oiseaux sur les epis. Lors des essais, toutes les variétés n'étaient pas représentées sur tous les sites. Les analyses de variance furent effectuées avec le programme de MSTAT, qui estime les chiffres manquants, permettant ainsi de réaliser des analyses de la variance pour l'ensemble des sites pour les variétés pour lesquelles il y avait des observations dans au moins sur 2 des localités. L'effet de la variété pour les différents paramètres fut testé contre l'interaction variétés(V)* localités(L). L'interaction V*L fut testée contre l'erreur qui fut calculé en effectuant les addition des sum de carrés qui ressortent des différents essais divisé par les degrées de liberté. La ppds (plus petite différence significative) 5% est donnée là où elle est trouvée significative. L'abréviation n.s. signifie non significatif au niveau de probabilité de 0,05.

Sur chaque site, la pluviométrie fut relevée une fois par semaine à l'aide d'un pluviomètre. Pour diminuer la perte d'eau par évapotranspiration, un peu d'huile fut ajoutée à chaque pluviomètre.

Pour les analyses chimiques du sol, des échantillons de sol, chacun contenant 10 sub-échantillons, ont été pris sur chaque site.

LA PEDO-CLIMATOLOGIE DES SITES DES ESSAIS

Les pluies pendant l'année 1987 ont été très déficitaires, ce qui a causé l'échec des essais cette année-là. L'année 1988 a connu une pluviométrie bien plus favorable (tableau 2). Les pluies ont commencé tardivement en 1988, à partir du 9 juillet. Ces pluies ont permit un bon établissement des plantes lors des essais. Le site qui a enregistré la plus faible pluviométrie a été celui de Gossi et, ici, s'ajoute une grave sécheresse pendant le mois de septembre. A Ebanguimellane, les conditions hydriques ont été favorables à partir du 9 juillet, mais les précipitations ont été faibles au mois de septembre. N'daki et Timbajawen ont enregistré la meilleure pluviométrie, mais la répartition des pluies a été irrégulière à partir du 20 août à N'daki. A Timbajawen, les pluies ont été mieux réparties, mais les plantes ont montré, malgré tout, des symptômes de stress hydrique.

Tableau 2. Pluviométrie en 1988 (mm)

	Timbajawen	Ebanguimellane	N'Daki	Gossi
- > 20.6	0	0	12	16
21. 6-30.6	0	3	4	6
1.7-10.7	17	19	16	13
11.7-20.7	9	8	20	17
21.7 -31.7	31	22	42	19
1.8-10.8	53	81	85	28
11.8-20.8	87	15[1]	84	15
21.8-31.8	18	8	4	3
1.9-10.9	31	13	4	50
11.9-0.9	13	7	4	0
21.9-30.9	22	16	19	0
1.10-10.10	0	4	0	0
Totale mm	281	196	294	167

1 observation incertaine

Dans les conditions sahéliennes le phosphore est considéré comme l'élément nutritif qui limite le plus les rendements (Fussel et al. 1987). Bationo et al. (1989) ont estimé, dans les conditions sahéliennes, à 7,9 ppm sol selon la méthode de Bray 1 le niveau du phosphore dans le sol qui permet d'obtenir 90% du rendement maximal. Selon les analyses du sol (tableau 3), la teneur en phosphore a été trouvée au-dessus de ce niveau dans les deux couches à Gossi et dans la couche 40-60 cm à N'daki. Cependant, l'analyse du sol utilisée pour le phosphore dans cette étude a été celle de Bray 2. Lorsque ces deux méthodes furent comparées sur 30 différents sols au Nigeria, la quantité moyenne de

phosphore extraite avec la méthode de Bray 1 et Bray 2 fut respectivement de 22,4 ppm et 27,1 ppm (Enwezor 1977), et la corrélation entre les deux méthodes fut élevée ($r^2 = 0,87$). Cela montre que ces deux méthodes sont proches l'une de l'autre. Il en suit que le besoin en phosphore semble être satisfait seulement à Gossi. Le pH n'a probablement pas limité les rendements dans ces essais, car le pH a été trouvé au-dessus de 5 sur tous les sites. Le mil supporte, aussi, bien le sol acide, et aucune réponse à un apport de chaux n'a été trouvée à l'ICRISAT Centre Sahélien (ICRISAT Centre Sahélien 1988). Dans les conditions sahéliennes, il n'y a, normalement, pas de réponse à l'apport de potasse (Bationo et al. 1989).

Les sols où les essais furent menés sont des sols bien sablonneux avec un pourcentage de sable d'environ 90% (tableau 3). Ceci est un niveau de sable normal pour ce type de sol au Sahel (Stroosnijder 1982, Spencer et Sivakumar 1987). La teneur en matière organique a été trouvée très faible.

Tableau 3. Résultats des analyses des sols dans la couche 0-20 cm (1) et dans la couche 40-60 cm (2)

	Gossi		Ebanguim.		N'Daki		Timbaj.	
	1	2	1	2	1	2	1	2
pH (KCl)	6,2	6,5	5,8	6,1	5,2	5,0	5,6	5,7
% Carbone org.	0,09	0,11	0,12	0,09	0,09	0,07	0,19	0,09
% Azote	0,08	0,14	0,12	0,13	0,14	0,16	0,05	0,10
C/N	1	1	1	1	1	0	4	1
P ass.(Bray2)ppm	21,0	18,3	3,4	1,7	3,2	18,8	2,0	5,6
P total ppm	41	76	111	79	118	121	73	156
CECméq/100g	2,0	1,7	0,5	1,3	0,6	1,3	1,5	3,0
Ca éch, méq/100g	1,41	1,69	0,76	1,17	0,86	1,21	1,09	1,43
Mg éch, méq/100g	0,11	0,14	0,04	0,08	0,05	0,10	0,37	0,78
K éch, méq/100g	0,33	0,27	0,10	0,14	0,08	0,16	0,20	0,18
Na éch, méq/100g	0,00	0,33	0,08	0,03	1,11	0,86	0,60	0,19
Saturation %	93	100	100	100	100	100	100	86
Sable %	89,3	88,0	92,5	90,2	91,9	90,0	89,5	86,3
Limon %	2,3	1,7	1,7	1,8	1,5	1,1	3,1	2,6
Argile %	8,4	10,3	5,7	8,0	6,6	8,8	7,5	11,1

RESULTATS DES ESSAIS VARIETAUX

Là où il y a une interaction (V)*(L), les résultats sont présentés pour chaque localité.

La levée s'est révélée satisfaisante pour l'ensemble des sites (tableau 4). Cependant, elle a été trouvée légèrement inférieure à N'Daki, par rapport à celles des autres sites. Pour l'ensemble des sites, aucune différence entre les variétés en ce qui concerne la levée ne s'est dégagée, mais l'interaction V*L a été significative.

Des différences importantes quant au nombre de jours jusqu'à 50% de floraison sont apparues, et ICMV 87901 et GB 8735 ont fleuri 11-12 jours plus tôt que Hombori (tableau 5). La variété Tabi a été la plus tardive. Les résultats à N'Daki et à Ebanguimellane indiquent que ICTP 8203 et ICMH 88951 sont respectivement 1 et 3 jours plus précoces que ICMV 87901. Comme seules ces deux variétés ont été représentées sur une des localités où les enregistrements de la floraison ont été relevées, la précocité

Tableau 4. Pourcentage de levée dans les différentes localités

	Timbajawen	N'daki	Gossi	Ebanguimellane	Moyenne 88
Hombori	82,8	88,9	98,2	97,4	91,9
Tabi	90,3	87,0	97,5	94,4	92,2
GB 8735	98,1	86,3	100,0	99,2	96,1
ICMV 87901	98,1	80,7	99,3	100,0	94,8
ITMV 8304	98,6	94,4	100,0	99,3	98,1
IKMV 8201	100,0	92,6	99,3		97,7
HKP	97,2	97,4	96,4		97,1
ICMH 88951	98,1	85,2			93,7
So X To			98,2	99,3	100,0
ICTP 8203				100,0	
ICMV 88201				99,3	
Moyenne	95,3	89,3	98,5	98,5	95,4
ppds 5 %	5,2	9,4	n.s.	n.s.	n.s.
Interaction V*L					**

moyenne des variétés ICMH 88951 et ICTP 8203 n'est pas présentée dans un tableau. Les variétés ICMV 87901, GB 8735, ICMH 88951 et ICTP 8203 sont dans cette étude considérées comme les variétés précoces.

L'évaluation de la résistance à la sécheresse pré-florale, à vue d'oeil, a montré que ICMH 88951, Hombori et HKP ont présenté la meilleure résistance (tableau 5).

En ce qui concerne la verse, les résultats de Timbajawen font apparaître que les variétés précoces ont eu une tendance à la verse plus prononcée que les autres (tableau 5).

Tableau 5. Différents paramètres concernant les variétés. Résistance à la sécheresse (échelle 0-5. 5. meilleure résistance)

	Résistance à la sécheresse	verse %	Jours jusqu'à 50 % de floraison	% attaque des oiseaux	% sterilité de l'épi	% protein	Hauteur m
Hombori	3,6	7,8	59	0,8	4,0	14,2	1,40
Tabi	3,3	2,3	62	1,3	8,5	15,2	1,48
GB 8735	2,9	19,8	48	4,9	6,8	14,0	1,31
ICMV 87901	3,0	22,0	47	4,1	7,0	13,1	1,14
ITMV 8304	2,9	7,8	58	0,9	7,1	15,9	1,60
IKMV 8201	3,3	9,8	55	1,1	4,6	14,8	1,58
HKP	3,5	6,0	58	0,1	6,1	16,2	1,57
ICMH 88951	4,2	19,8		4,0	14,6	13,4	1,10
So X To	2,6		58				14,8
Moyenne	3,2	11,9	56	2,2	7,3	14,6	1,40
ppds 5%	0,5	6,4	2	3,5	n.s.	0,8	0,15
Inter. V*L	n.s.	-	n.s.	n.s.	n.s.	n.s.	n.s.
Nbr.de loc.	2	1	3	3	3	3	3

Les variétés précoces ont aussi été plus touchées par l'attaque des oiseaux que les autres variétés (tableau 5). Cette attaque a été la plus marquée à Timbajawen.

Aucune différence quant à la stérilité dans l'épi ne s'est dégagée, mais on remarque malgré tout que ICMH 88951 a montré une stérilité dans l'épi plus aigue que les autres variétés (tableau 5).

Le pourcentage de protéines des grains a différé d'une manière significative selon les variétés. HKP, ITMV 8304 et Tabi ont eu la teneur en protéines la plus élevée (tableau 5).

Les variétés GB 8735, ICMV 87901, ICMH 88951 et ICTP 8203 ont eu des tiges beaucoup plus courtes que les autres variétés (tableau 5).

Aucune différence significative concernant les rendements en grains n'est apparue lorsque l'analyse a été effectué pour l'ensemble des localités, mais la tendance des résultats semble indiquer que HKP, suivi par ICMV 87901 et GB 8735, a donné les meilleurs rendements (tableau 6). Les rendements des variétés précoces ont été faibles surtout à N'daki, mais la même tendance s'est manifestée à Ebanguimellane. Les variétés les plus tardives ont montré une stabilité supérieure aux variétés précoces, expliquant ainsi l'interaction significative V*L.

Tableau 6. Rendement en grains (kg/ha)

	Timbajawen	N'Daki	Gossi	Ebanguimellane	Moyenne
Hombori	842	521	660	641	663
Tabi	615	546	421	466	512
GB 8735	1194	346	676	597	703
ICMV 87901	1216	176	872	563	707
ITMV 8304	874	594	448	559	619
IKMV 8201	883	472	668		652
HKP	998	653	595		726
ICMH 88951	1175	185			634
So X To			564	535	601
ICTP 8203				486	
ICMV 88201				576	
Moyenne	975	436	613	554	647
ppds 5%	265	302	193	n.s.	n.s.
Interaction V*L.					***

Le rendement en paille a différé de manière significative selon les variétés. Pour l'ensemble des essais HKP, ITMV 8304 et Tabi se sont classées en tête dans ce cas, alors que ICMH 88951, ICMV 87901 et GB 8735 se sont avérées peu productives (tableau 7). L'interaction V*L peut être attribuée au fait que les rendements en paille de ICMV 87901, GB 8735 et ICMH 88951 ont été particulièrement faibles à N'Daki.

Les variétés précoces se sont révélées avoir des indices de rendement bien plus élevés, ainsi que plus stables, que les autres variétés (tableau 8).

Les composantes du rendement du mil dans la culture traditionnelle sont le nombre de poquets/ha, le nombre de plantes/poquet, le nombre d'épis/plante, le nombre de grains/épi et le poids unitaire des grains. Si la levée avait eu lieu dans tous les poquets, il

Tableau 7. Rendement en paille (kg/ha)

	Timbajawen	N'Daki	Gossi	Ebanguimellane	Moyenne
Hombori	2898	641	2045	1029	1653
Tabi	3901	915	2081	1052	1987
GB 8735	2178	414	1598	914	1276
ICMV 87901	1612	159	1312	583	917
ITMV 8304	3490	1103	2183	1383	2040
IKMV 8201	2563	683	1956		1548
HKP	3738	1324	2679		2394
ICMH 88951	1492	147			701
So X To			1935	1109	1648
ICTP8203				583	
ICMV 88201				1258	
Moyenne	2734	673	1974	989	1574
ppds 5 %	462	438	397	298	455
Interaction V*L					***

Tableau 8. L'indice de rendement.

	Timbajawen	N'Daki	Gossi	Ebanguimellane	Moyenne
Hombori	19, 0	36,9	19,1	33,0	27,0
Tabi	12,0	31,4	13,2	26,0	20,6
GB 8735	30,9	38,4	24,8	35,4	32,4
ICMV 87901	36,4	45,4	33,9	42,9	39,7
ITMV 8304	17,5	30,8	14,7	25,1	22,0
IKMV 8201	21,8	35,7	21,8		27,7
HKP	18,2	28,0	15,6		21,8
ICMH 88951	36,8	44,7			39,2
SoXTo			19,1	28,6	25,4
ICTP 8203				40,0	
ICMV 88201				28,1	
Moyenne	24,1	36,4	20,3	32,4	28,4
ppds 5 %	5,3	4,6	4,7	4,9	3,3
Interaction V*L					*

y aurait eu 12346 poquets/ha. La deuxième composante fut fixée à trois plantes par poquets lors du démariage. Dans quelques cas, cependant, il est apparu moins de trois plantes/poquet.

En ce qui concerne le nombre d'épis/plante pour l'ensemble les localités, ICMV 87901, GB 8735 et ICMH 88951 ont produit davantage d'épis que les autres variétés. Cependant, à N'Daki, elles ont produit moins d'épis/plante que les autres variétés, la raison pour laquelle l'interaction V*L est fortement significative (tableau 9).

En ce qui concerne le nombre de grains/épi, les variétés précoce ont été moins productives que les autres variétés (tableau 10).

Tableau 9. Nombre d'épis/plante

	Timbajawen	N'Daki	Gossi	Ebanguimellane	Moyenne
Hombori	2,12	1,05	1,69	1,07	1,51
Tabi	2,01	1,15	1,54	0,95	1,46
GB 8735	2,21	1,03	1,91	1,13	1,64
ICMV 87901	2,45	0,74	1,94	1,17	1,68
ITMV 8304	1,58	0,95	1,26	0,95	1,22
IKMV 8201	1,58	1,07	1,52		1,29
HKP	1,67	0,95	1,36		1,23
ICMH 88951	3,15	0,92			2,15
So X To			1,36	0,94	1,29
ICTP 8203				1,22	
ICMV 88201				0,85	
Moyenne	2,12	0,98	1,57	1,04	1,50
ppds 5 %	0,32	n.s.	0,38	0,16	0,41
Interaction V*L					***

Tableau 10. Nombre de grains/épi (calculée en utilisantd'autres composantes du rendement)

	Timbajawen	N'Daki	Gossi	Ebanguimellane	Moyenne
Hombori	2445	1940	1733	2449	1676
Tabi	1794	1890	1461	2202	1431
GB 8735	1767	1102	1096	1526	1236
ICMV 87901	1592	902	1331	1346	1184
ITMV 8304	2227	2133	1392	2459	1866
IKMV 8201	2281	1457	1634		1731
HKP	2485	2410	1879		2179
ICMH 88951	998	646			746
So X To			1655	1774	1571
ICTP 8203				896	
ICMV 88201				2786	
Moyenne	1949	1560	1523	1930	1531
ppds 5 %	459	671	414	n.s.	334
Interaction V*L					n.s.

Les variétés précoces ont produit les grains les plus gros, et pour ces variétés, le poids des grains n'a pas varié beaucoup suivant la localité (tableau 11).

Pour mieux mettre en évidence les relations entre les différents paramètres influençant le comportement de chaque variété, des analyses de régression multiple pour l'ensemble des sites furent effectuées. Aucunes corrélations significatives entre le rendement en grains, d'un côte, et le temps jusqu'à la floraison, la hauteur de la tige et le rendement en paille, de l'autre côte, n'ont été trouvées. Bien que la fonction de 2nd degré entre le rendement en grains et la précocité ne soit pas significative, elle est présentée ici (figure 2).

Tableau 11. Poids de 1000 grains (g)

	Timbajawen	N'Daki	Gossi	Ebanguimellane	Moienne
Hombori	5,3	7,8	6,2	6,8	6,5
Tabi	5,1	7,8	5,2	6,4	6,1
GB 8735	8,4	9,5	8,7	9,4	9,0
ICMV 87901	8,6	8,8	9,2	9,6	9,1
ITMV 8304	6,8	8,4	6,9	6,5	7,2
IKMV 8201	6,6	8,8	7,3		7,7
HKP	6,7	7,9	6,5		7,1
ICMH 88951	10,3	9,9			10,0
So X To			6,9	8,7	8,0
ICTP 8203				12,0	
ICMV 88201				6,6	
Moyenne	7,2	8,6	7,1	8,3	7,9
ppds 5 %	1,0	0,7	1,3	0,9	0,9
Interaction V*L					***

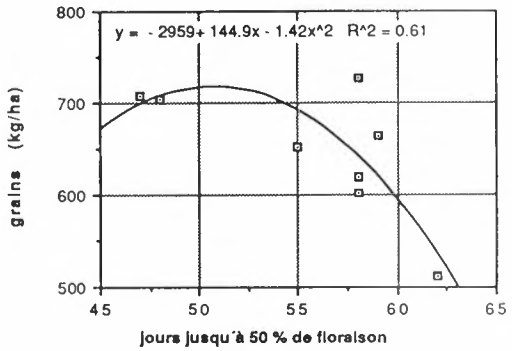


Figure 2. Relation entre rendement en grains et nombre de jours jusqu'à la floraison

Une relation significative (*) pour l'ensemble des sites entre le nombre de jour jusqu'á 50 % de floraison et le rendement en paille est apparue, montrant que le variétés les plus tardives sont aussi celles qui ont les rendements en paille les plus éléves (figure 3).

Les variétés précoces sont celles qui ont produit les grains les plus gros (**) (figure 4).

DISCUSSION

La discussion portera sur les résultats obtenus, et une attention particulière sera accordée au choix des variétés dans cette zone à faible pluviométrie.

L'évaluation de la précocité dans les essais au Gourma fut fondée sur le nombre de jours jusqu'à 50 % de floraison (tableau 5). Cette façon d'estimer la précocité rend bien compte du cycle complet de chaque variété, car Lambert (1983) a montré, en testant des

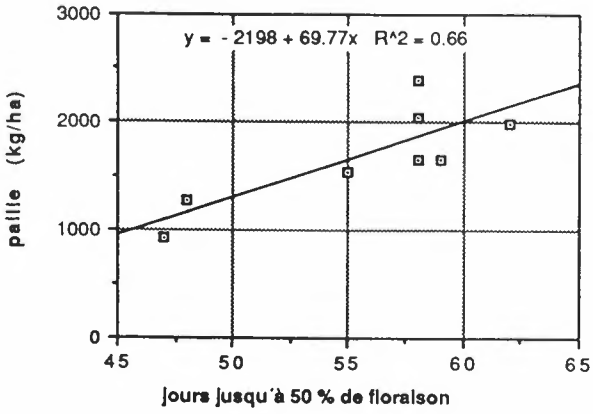


Figure 3. Relation entre rendement en paille et nombre de jours jusqu'à 50 % de floraison

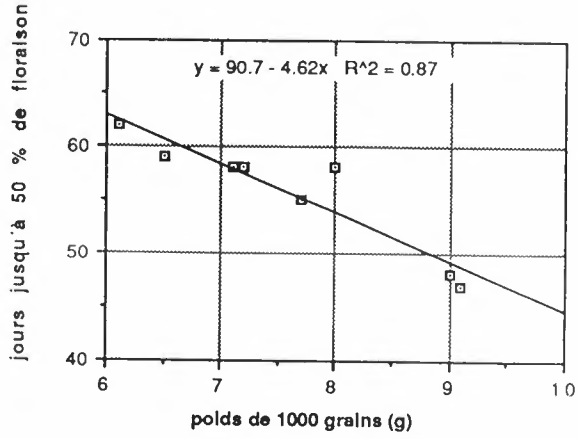


Figure 4. Relation entre le nombre de jours jusqu'à la floraison et le poids de 1000 grains

variétés à cycles très contrastés, que le temps entre la fécondation et la maturité était d'environ 25 jours pour toutes les variétés.

L'attaque des oiseaux a été la plus importante sur les variétés précoces (tableau 5), car quand ces variétés sont arrivées à maturité, le mil cultivé dans les champs aux alentours des essais n'était pas encore arrivé à maturité.

Des différences quant à la résistance à la sécheresse pré-florale ont aussi été constatées, mais ces observations doivent uniquement être considérées comme des indications pour la résistance à la sécheresse post-florale. Une étude plus poussée serait nécessaire pour avoir des résultats plus fiables.

Sivakumar et al. (1984) ont trouvé que le meilleur moment pour semer à Hombori, station météorologique située à 25 km au sud du site de Timbajawen, est aux environs du 7 juillet, en estimant que la meilleure date pour semer est le moment où la précipitation moyenne dépasse la moitié de l'évapotranspiration potentielle. La durée de la période pendant laquelle la précipitation est au-dessus de ce niveau a été estimée à 69 jours à Hombori, et cette période prend fin, ainsi, le 14 septembre. En utilisant le nombre de jours jusqu'à 50 % de floraison (tableau 5) et le fait que la phase entre la

fécondation et la maturité dure environ 25 jours (Lambert 1983), il est possible de déterminer, qu'en semant le 7 juillet, la floraison aura lieu respectivement le 23 août et le 4 septembre pour ICMV 87901 et Hombori. La maturité devrait arriver le 17 septembre et le 29 septembre pour ICMV 87901 et Hombori, respectivement. Une variété ayant un cycle au moins aussi long que celui de Hombori, court alors un risque de stress post-floral, alors que ce risque est moins important pour les variétés précoces. Les possibilités pour un stress entre l'initiation florale et la floraison, en semant le 7 juillet, semblerait moins importantes qu'un stress post-floral, car le mois d'août est le mois le mieux arrosé. Il est cependant à signaler que les cultivateurs ont l'habitude de semer à partir du début juin. Pour les variétés précoces un semis réalisé tôt est à déconseiller, car ces variétés arrivent à compléter leur cycle même si elles ne sont pas semées tôt et, en outre, elles tolèrent peu la sécheresse pré-florale (Bidinger et al. 1987).

Les variétés précoces testées au Gourma sont aussi celles à tiges courtes. L'avantage lié aux variétés à tiges courtes est une efficacité supérieure aux autres variétés en ce qui concerne l'utilisation de l'eau et des éléments minéraux (Dancette 1983, Blondel 1971). Il a, de même, été montré à l'ICRISAT, en introduisant des isogènes de nanisme dans des variétés à tiges longues, que les nains ainsi obtenus ne sont pas plus vulnérables à la sécheresse que les variétés d'origine (ICRISAT 1988). Cependant, en ce qui concerne le rendement en grains, leur performances sont un peu inférieures à celle des variétés à tiges longues, et leur grains sont plus petits (ICRISAT 1988, ICRISAT-Mali 1988).

Quant aux rendements en grains, les rendements à Gossi ont été relativement élevés (tableau 6), compte tenu de la faible pluviométrie qui y a été enregistrée (tableau 2). Cela peut être attribué à la fertilité du sol, et, en particulier, au niveau élevé du phosphore (tableau 3). L'arrosage fourni ici, bien qu'insuffisant, a aussi contribué à augmenter les rendements.

Les variétes les plus tardives ont présenté un rendement en grains plus stable que les variétés précoces. Les variétés précoces se sont révélées avoir un meilleur rendement en grains que les variétés tardives à Gossi et à Timbajawen, et inversement à N'daki (tableau 6). Ce résultat peut, en partie, être expliqué par les conditions hydriques. Les symptômes de sécheresse ont été les plus prononcés pendant la période post-florale à Gossi et à Timbajawen. Le faible indice de rendement et le faible poids de 1000 grains chez les variétés tardives, à Gossi et à Timbajawen, indiquent aussi une sécheresse à la fin du cycle dans ces localités. En étudiant la répartition des pluies du mois de septembre (tableau 2), il ressort que la pluviométrie, ce mois-là, a été très déficitaire, surtout à Gossi, mais aussi à Ebanguimellane et à N'daki. La première partie du mois de septembre a été sèche à Timbajawen, bien que le tableau 3 n'en fasse pas état. Les raisons pour lesquelles les plantes ont connu un stress post-floral plus marqué à Timbajawen qu'à N'daki et à Ebanguimellane pourraient être le fait que le développement végétatif a été beaucoup plus vigoureux à Timbajawen que dans les autres localités (tableau 7), provoquant une transpiration plus importante (Chopart et Nicou 1976). En outre, le terrain expérimental à Ebanguimellane était situé proche d'une mare, ce qui pourrait avoir influencé les conditions hydriques. La fertilité ne peut pas non plus expliquer les faibles résultats obtenus chez les variétés précoces à N'daki, car la fertilité, et surtout le niveau du phosphore, ne se détachent pas de façon négative par rapport aux autres localités (tableau 3). Cependant, bien que les résultats de l'analyse des sols ne fassent pas état des faibles rendements à N'daki, on ne peut pas complètement écarter l'hypothèse que la fertilité du sol a influencé les résultats, car il

est très difficile de prendre des échantillons représentatifs du sol. On ne peut pas non plus attribuer ces résultats aux attaques des insectes, car presque aucune stérilité dans l'épi n'a été observée. Des essais variétaux du sorgho et du mil au Burkina Faso dans des champs de paysans ont aussi montré que le classement des variétés a différé selon les localités (Matlon 1985).

La littérature concernant les variétés étudiées, ici, est faible. Les variétés ITMV 8304 et IKMV 8201 se sont révélées avoir un rendement moyen identique lorsqu'elle ont été testées dans 8 localités en afrique de l'ouest en 1986 (ICRISAT Centre Sahélien 1988). La variété HKP est une variété préconisée au Mali pour la zone de 300-800 mm de précipitation. Elle est considérée comme une variété à rendement stable (SRCVO 1987). Au Niger, ITMV 8304 a dépassé le rendement en grain de HKP (Singh et al. 1986). En Inde, la variété ICTP 8203, d'origine togolaise, est cultivée (Kumar et Rao 1987). Cependant ICMV 87901 a dépassé ICTP 8203 de 10 % pour le rendement en grains quand ces variétés ont été testées sur 15 localités en Inde et au Pakistan (ICRISAT 1989).

En ce qui concerne le rendement en paille, le tableau 5 et le tableau 7 montrent tous deux que les variétés tardives à longue tige se sont classées en tête. Les variétés précoces ont produit un rendement en paille très bas à N'daki, expliquant ainsi l'interaction V*L. Les variétés tardives présentent un rendement en paille beaucoup plus stable. Au Sahel, la paille est hautement appréciée, car elle est utilisée à des fins diverses, comme le fourrage et la construction de clôtures et de paillotes.

Une caractéristique importante du mil est son faible indice de rendement, et les essais réalisés ici, le confirment. Cependant, il est à souligner que les variétés précoces ont pu maintenir, pour l'ensemble des localités, un bon indice de rendement, allant jusqu'à 49,8 % pour ICMV 87901 à N'daki. L'indice de rendement élevé enregistré à N'daki montre aussi que le rendement en paille a, ici, été davantage réduit que le rendement en grains.

Les composantes du rendement ont différé selon que les variétés était précoces ou tardives. Les variétés précoces ont produit plus d'épis/plante (tableau 9), moins de nombre de grains/épi (tableau 10) et des grains plus gros que les variétés plus tardives (tableau 11). A N'daki et à Ebanguimellane, où les rendements des variétés précoces ont été faibles, ce fut tout d'abord le nombre d'épis/plante, puis le nombre de grains/épi qui ont été réduits. Dans ces localités, la baisse de ces composantes de rendement a, en partie, été compensée par une légère hausse du poids unitaire des grains, pour les variétés précoces. Le nombre d'épis/plante a été plus stable pour les variétés tardives expliquant ainsi l'interaction V*L ici. Pour les variétés tardives, le poids unitaire des grains a diminué dans les localités qui ont connu un stress post-floral, à savoir Gossi et Timbajawen. Dans les essais au Gourma, l'effet du stress sur les composantes du rendement a été peu apparent, car lors de ces essais, les plantes ont connu un stress hydrique tout au long de leur cycle.

Les variétés précoces pourraient être intéressantes pour le Gourma du fait de leur période de croissance de courte durée, mais elles semblent présenter le défaut d'être peu stables en ce qui concerne le rendement en grains.

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Norwegian Journal of Agricultural Sciences

Vol. 6 1992 No. 3

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