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Effect of lighting of *Calceolaria x herbeohybrida* Voss in the flowering phase on leaf injury

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Chillled plants of different cultivars were grown in peat media with different fertilizer levels, and exposed to different kinds of illumination, lighting periods and temperature regime in the flowering period. Use of a culture programme which included supplementary irradiance caused leaf injury. Increased use of light promoted the development of leaf scorce symptoms, discoloration of the leaves and the development of flowers. It was found that a shorter phase between start of lighting and the saleable stage results in a relative reduction in leaf damage. The experiment indicates that a low fertilizer status is preferable at the beginning of the lighting period, but a supply of nutrients throughout the flowering phase is of significance.

Key words: *Calceolaria x herbeohybrida*, fertilizer, leaf injury, lighting, temperature

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Most cultivars of *Calceolaria x herbeohybrida* need a period of low temperature to induce flowering. Further development of the flower bud is enhanced by long photoperiods (Johansson 1976, Rünger 1975) with a critical day length of 14-15 h (Rünger 1975) or 15-16 h (Strømme & Pettersen 1984). The critical day length is influenced by changes in the temperature (Rünger 1978). Under natural light conditions with low light integrals, 15°C is found to be optimal (Johansson 1976, Moum 1976) for a rapid development from the end of the chilling period, followed by 18°C to the marketing stage (Moum 1976).

Supplementary lighting during winter is a common practice in Norwegian greenhouses. For *Calceolaria* too, supplementary lighting is used after the end of the chilling period to enhance flower bud development and to increase plant quality. Unfortunately for the growers, lighting of *Calceolaria x herbeohybrida* often results in leaf injury. The injury can be observed primarily in the leaf margin as a vascular area which advances to become a necrotic leaf margin. Rünger (1975) also described a slight yellowing of the leaves with use of incandescent light, but not with fluorescent light. The purpose of these experiments, was to investigate the effects of supplemental lighting and fertilization after the chilling period on the appearance of leaf injury.

MATERIAL AND METHODS

This investigation includes two experiments carried out in 1988 and 1989. Young plants at the beginning of the chilling period were obtained from a commercial nursery. The plants were grown in low temperature conditions (9°-12°C) under natural light from October/November to January/February, when the photoperiod varied from 4.5 to 11 h. The global radiation levels per day outside the greenhouse in November, December, January and February were 0.7, 0.1, 0.4 and 2.2 MJm^{-2}, respectively. The nutrient solution consisted of Superba 7-4-21 (NPK), calcium nitrate and potassium sulphate calculated to (in mg l^{-1}) 163 N, 42 P, 240 K, 40 Mg, 114 Ca, 53 S, 2.0 Fe, 1.1 Mn, 0.2 Cu, 0.30 Zn, 0.33 B and 0.025 Mo. Sub-irrigation was used as the watering system. Pure liquid CO_2 was injected in the greenhouse and a concentration of 600 vpm CO_2 in the atmosphere was maintained from the start of the supplemental lighting to the end of the experiment, otherwise the CO_2 concentration was normal (345 vpm). Grading of leaf scorce (leaf margin chlorosis and necrosis) and leaf discoloration (a blotchy discoloration) was assessed according to a scale from 0 to 9 where increased numbers indicate a more severe damage.

Observations were subjected to a two-way analysis of variance. The relationships between all variables were determined by single correlations, $P < 0.001$, $P < 0.01$ and $P < 0.05$ indicating a 0.1%, 1% or 5% level of significance, respectively. The letters n.s. indicate no significant effect.

Experiment in 1988

This experiment included the following cultivars, 'Bunter Bikini', 'Gold Bikini', 'Memory Mix', 'White Spots', 'Gem red', 'Portia red', 'Portia yellow' and 'Portia orange'. During the cool period low (ca. 0.5 $mScm^{-1}$), normal (ca. 1.5 $mScm^{-1}$) and high (ca. 3.0 $mScm^{-1}$) levels of electricial conductivity (EC) in the potting medium were established. The different levels of electrical conductivity were established by means of solutions varying from tap water to a nutrient solution with an EC of 3.0. After chilling, only tap water was used.

The supplemental lighting period started on 12 January and lasted for 19 days. At start of lighting, the plants showed visible flower buds. During this period the natural photoperiod increased from 5 h and 24 min to 7 h and 15 min. The supplementary light from high-pressure sodium lamps (SON-T, conversion factor 2.3) was given for 16 h per day and continuously (24 h). The supplementary irradiance (PAR) was 3.5 and 9.0 Wm^{-2} (measured with a lux meter at the top of the plants and estimated). The temperature was set at 15°C ± 0.2. At the end of the experiment, the fertilizer and pH levels in the pots of the cultivars 'Bunter Bikini', 'Gold Bikini', Portia yellow' and 'Portia orange' were measured and the number of flowers per all cultivar was recorded. The experiment was carried out in factorial combinations of cultivars, fertilizer rate, light level and light periods in two replicates with seven plants per plot.

Experiment in 1989

The experiment included the cultivars 'Gem red', 'Portia yellow' and 'Portia red', and the cooled plants were lighted from 23 February to 17 March (22 days). When the lighting period started, the plants were somewhat smaller than those in the previous experiment and the flower buds were correspondingly smaller. The natural photoperiod increased from 9 h and 33 min to 11 h and 52 min through the 22-day period. High-pressure metal halide lamps (HPI-T, conversion factor 2.8) were used for 12 h, 16 h and 24 h a day with an irradiance (PAR) of 7.0, 10.5 and 14.0 Wm^{-2} at plant level (measured with a lux meter and estimated).

The temperature regimes were 15°C ± 0.2 and 18°C ± 0.2. Seven open flowers per plant indicated the marketable stage.

The experiment was carried out factorially with three replicates and six plants per plot.

RESULTS

Cultivars

Highly significant ($P < 0.001$) differences in leaf scorce between cultivars were recorded soon after a 12-h period of supplemental lighting, and these significant differences were maintained throughout all registrations in both experiments. The vascular margin of the damage levels advanced to become a necrotic leaf margin with a chlorotic area within it. The subjective description showed a gradual increase in the damage throughout most of the experimental period. A significant increase in the injury was found between 1.5 and 2 days after start of supplemental lighting in 1988 and between 2 and 3 days of lighting in 1989. A blotchy discoloration of the leaves appeared after a lighting period of about 18 days, especially in the 1988 experiment. This blotchy discoloration, which appeared in the middle of the leaf and only on leaves exposed to illumination from the lamps, was most pronounced in 'Gem red', followed by 'White Spots'.

After 19 days of lighting in the 1988 experiment, the cultivar 'Memory mix' had the lowest average score, 1.1. On the other hand, 'Portia orange' and 'Portia red' each had a score of 1.8, 'Gem red' 1.5 and 'Portia yellow' 1.4. Leaf damage in 'Gem red' increased by 0.7 units between the last two registrations, which was highly significant ($P < 0.001$) compared with that in the other cultivars. Most of the advance in leaf damage in this period is attributed to the blotchy discoloration. In the 1989 experiment, the damage was classified as more pronounced than that in the 1988 experiment. At the end of the experiment, 'Gem red' was given an average score of 3.8, followed by 'Portia red' (3.5) and 'Portia yellow' (3.0). The blotchy discoloration occured more sporadically this time and was not especially connected with the cultivar 'Gem red'. There were highly significant ($P < 0.001$) differences in leaf injury between these three cultivars at each registration in both experiments. In 1989 'Gem red' had the highest score at every registration, followed by 'Portia red' and ' Portia yellow'. There were no significant interactions between cultivars and supplemental light level, cultivars and the duration of daily lighting or cultivars and total artificial radiation.

Supplementary light level

The most pronounced damage was found when high irradiance of supplementary lighting (Figure 1) was used. In 1988, the leaf symptoms were significantly ($P < 0.001$) different between light levels after a 6-7-day lighting period and this trend continued throughout the experimental period. In 1989, the same significant effect occurred with artificial light levels at 7.0 and 14.0 Wm^{-2} after an 11-day period of continuous lighting. With a lighting period of 16 h, the highest light level (14 Wm^{-2}) gave a non significant increase in damage over a 10.5 Wm^{-2} lighting level at each registration period. In the last part of the registration period in 1988 (between 8.5 days and 19 days of lighting), there was a highly significant ($P < 0.001$) effect of increased illumination on

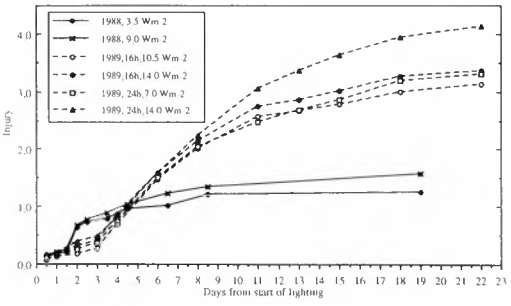

Figure 1. The development of leaf injury in relation to supplemental irradiance of *Calceolonia x herbeohybrida* grown in a light period of 16 h and 24 h in 1988 (average of 16 and 24 h in the figure), 16 h and 24 h in 1989

leaf symptoms. The lowest light level (3.5 Wm^{-2}) increased the scores by 0.04 points in contrast to 0.24 points at the highest light level (9.0 Wm^{-2}).

Daily lighting

Different lighting periods had only a small effect on leaf damage. In 1988 the leaf symptoms were significantly ($P < 0.001$) more pronounced at 16 h lighting compared with continuous lighting after one day and 1.5 days of lighting (Figure 2). The same effect (significant at $P < 0.05$) was found at 2 days, 3.5 days and 19 days of lighting. Continuous lighting increased the leaf injury to a significantly ($P < 0.001$) greater extent in the last part (after 8.5 days of lighting) of the lighting period (0.25 points) compared with 16 h lighting per day (0.03 point). In 1989, the effect of the daily lighting period was recorded as significant ($P < 0.05$) 13 days after the start of lighting. From that time, continuous lighting resulted in a significantly ($P < 0.001$) greater level of injury than daily lighting for a shorter period.

A combination of a 12-h, 16-h and 24-h lighting period with corresponding light levels of 14.0, 10.5 and 7.0 Wm^{-2} (168.0 Wm^{-2} per day) made no significant difference to leaf damage, although the shortest daily artificial lighting period combined with the highest irradiance level gave the highest score at each recorded period.

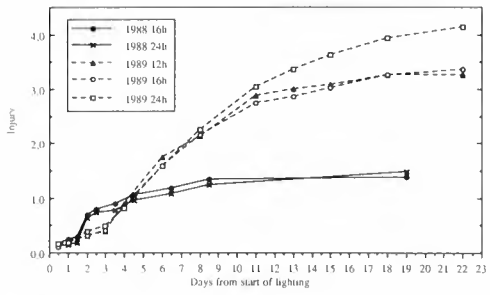

Figure 2. Effect of light period on the development of leaf injury of *Calceolonia x herbeohybrida* grown at a light level of 3.5 Wm^{-2} and 9.0 Wm^{-2} in 1988 (average of 3.5 and 9.0 Wm^{-2} in the figure) and at a light level of 14.0 Wm^{-2} in 1989

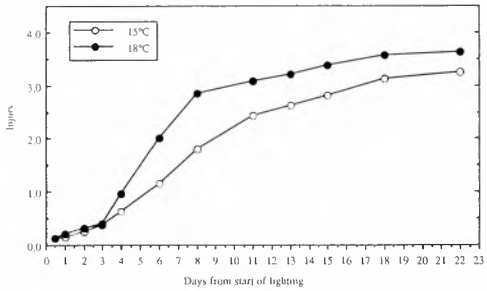

Figure 3. Effects of temperature on the development of leaf injury of *Calceolaria x herbeohybrida*

Temperature

The greatest leaf damage was always found at the highest temperature level (Figure 3). This effect was not significant until 4 days of lighting, after which time the leaf damage was significantly ($P < 0.001$) more pronounced at 18°C than at 15°C. The subjective decription of the symptoms at 4 days of lighting gave a score of 0.6 at 15°C and 1.0 at 18°C, which increased to 3.2 and 3.6 at 22 days of lighting. The difference in leaf damage between 15°C and 18°C was greatest after 6 days of lighting (0.8 points). From that time, the difference decreased gradually, culminating in a difference of 0.4 points after 22 days of lighting. No significant interactions were found between temperature and cultivar, between temperature and the duration of the light period or between temperature and light level.

Fertilizer

Plants which started the lighting period with a high EC status in the pots suffered more severe damage than plants with a low EC status (Figure 4). The development of leaf symptoms in the last phase of the experimental period (between registrations at 8.5 days and 19 days of lighting) showed a highly significant ($P < 0.001$) reduced gradient with increased EC level. In this period the score increased by 0.20, 0.17 and 0.05 for the in-

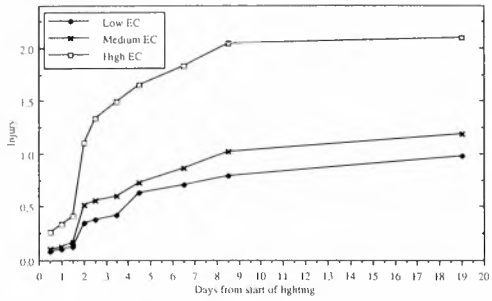

Figure 4. Effects of electrical conductivity (EC) in the pots at start of lighting on the development of leaf injury of *Calceolaria x herbeohybrida*

creased EC levels, respectively. Throughout the development period the EC status, which was established at three different levels, decreased and was found to be at an average of 0.38, 0.43 and 1.51 mSm^{-1} for the four cultivars tested (756 pots analysed). With increasing EC levels, in the pots there was a gradual decrease in pH from 6.2 to 6.1 and 5.6. Each cultivar suffered increased injury with increased level of EC in the pots (Table 1). There was a significant interaction between cultivars and EC level, except at the registrations 4 and 6 days after the start of the lighting period and with the exception of cultivars 'Gem red', 'Portia red' and 'Portia yellow', for which there was no significant interaction at any time of registration.

Analysis of leaves with and without symptoms from comparative plants, showed no difference in the content of nitrogen, phosphorus, potassium, magnesium, calcium, sodium, sulphur, iron, copper, manganese, zinc, boron, molybdenium or aluminium.

Flowering

At the end of the lighting period, there was a significant ($P < 0.001$) difference in number of flowers per plant between cultivars. 'Portia yellow' had most flowers (an average of 22 flowers per plant), followed by 'Portia orange' (19 flowers), 'Gold Bikini' (12 flowers) and 'Gem red' (11 flowers). On the other hand, 'Portia red' had only 2 flowers after 19 days of supplemental lighting in 1988. In 1989, starting the lighting period with smaller plants, resulted in a rapid development of 'Portia red' (50% of the plants at the marketable stage after 22 days of lighting), followed by 'Portia yellow' (34%) and 'Gem red' (18%).

The increase in light level from 3.5 to 9.0 Wm^{-2} in 1988, increased the number of flowers per plant significantly ($P < 0.001$) from 7 to 14. Use of artificial lighting periods of 12 h, 16 h and 24 h in 1989 had a significant ($P < 0.001$) effect on flower development. At the end of the experimental period, 19% of the plants grown under a lighting period of 12 h

Table 1. The effects of electrical conductivity (EC) (L-low, M-medium, H-high), in the pots at start of lighting on leaf injury of different cultivars of *Calceolaria x herbeohybrida* after different lengths of lighting period

Cultivar	2.5 days			6.5 days			19 days		
	L	M	H	L	M	H	L	M	H
Bunter Bikini	0.39	0.38	1.00	0.70	0.66	1.69	0.81	0.83	1.77
Gold Bikini	0.65	0.75	1.06	0.90	1.04	1.69	1.19	1.29	1.92
Memory Mix	0.19	0.58	0.90	0.48	0.79	1.65	0.50	0.94	1.83
White Spots	0.10	0.23	1.42	0.38	0.50	1.75	0.66	0.63	2.13
Gem red	0.08	0.13	1.30	0.25	0.28	1.63	1.13	1.50	1.88
Portia red	0.56	0.79	1.95	0.96	1.23	2.31	1.17	1.69	2.61
Portia yellow	0.44	0.67	1.19	0.85	1.00	1.65	1.15	1.27	1.88
Portia orange	0.58	0.92	1.92	1.02	1.27	2.27	1.27	1.42	2.71
Interaction	$P<0.001$			ns			$P<0.05$		

were marketable, while 35% and 56% of the plants were at the same stage of development when the light period was increased to 16 h and 24 h, respectively, at a light level of 14 Wm^{-2}. Continuous lighting at the highest light level (9.0 Wm^{-2}) in 1988, resulted in significantly more flowers per plant (19 flowers) than other combinations of light level and lighting period with a lower light energy supply (6.5-8.9 flowers per plant). Increasing the light level from 7 to 14 Wm^{-2} continuously in 1989, significantly ($P < 0.001$) increased the propotion of plants at a marketable stage at the end of the experiment from 18% to 56%. Different combinations of light level and lighting period with the same artificial light supply had a significantly ($P<0.001$) positive effect on flower development at a 16-h lighting period with a light level of 10.5 Wm^{-2}. This lighting procedure resulted in 50% marketable plants through the 22-day lighting period, while 19% and 18% of the plants were at the same stage of development when the combinations 12 h/14 Wm^{-2} and 24 h/7.0 Wm^{-2} were used respectively.

An increased air temperature regime secured flower development significantly ($P < 0.001$). At 15°C and 18°C respectively, 18% and 53% of the plants were at the marketable stage at the end of the experimental period. High EC levels in the pots reduced the development of flowers significantly ($P < 0.001$). After 19 days of lighting, the plants with a low or medium EC level at the start of the lighting period had 11 and 12 flowers, respectively, while plants grown with a high EC level had 9 flowers per plant.

DISCUSSION

Calceolaria seemed to be very sensitive to artificial lighting. Little is known about chlorosis and necrosis in *Calceolaria*. Rnger (1975) found a slight yellowing of the leaves when using incandescent light, but no yellowing was observed when fluorescent light was used. Ohlson (1982) mentions a good supply of iron in order to avoid chlorosis. In this investigation neither of these possibilities seemed to be relevant. On the other hand, all contributions that promote the development to anthesis seemed to be conductive to leaf injury.

Transfer of the plants from low temperature (9°C) to a higher temperature (15°C, 18°C) increases the leaf temperature rapidly, but there is a delayed rise in the root temperature. This temperature difference between the root and the leaves in addition to the photosynthetic activity in the leaves could have an influence on the development of the leaf damage.

The promotion of the anthesis by high temperature, long light periods and high light levels is in accordance with Johansson (1974), Moum (1976), Rünger (1978) and White & Biernbaum (1984). From the results of this experiment, it seem to be advantageous to start the flowering period with plants that have not been fertilized too much, but a supply of nutrients must be used in this period, particularly in the last part of it. It might be an advantage to accustom the plants to a low level of artificial light before the end of the chilling period. Selling the plants at an early stage reduces the possibility of the development of the blotchy spots on the leaves.

ACKNOWLEDGEMENTS

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The influence of intercropping and weeds on the oviposition of the brassica root flies (*Delia radicum and D. floralis*)

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Hofsvang, T. 1991. The influence of intercropping and weeds on the oviposition of the brassica root flies (*Delia radicum and D. floralis*). Norwegian Journal of Agricultural Sciences 5: 349-356. ISSN 0801-5341.

The effect of intercropping (cabbage/beans) on the oviposition of *Delia radicum* (L.)/*Delia floralis* (Fallén) (Diptera:Anthomyiidae) was studied during one season. The total number of eggs per cabbage plant was reduced by 29% by intercropping as compared with plants grown in monocultures. The effect of weeds between the cabbage plants on root fly oviposition was observed during two seasons. The total reduction in eggs per cabbage plant in weedy compared with weed-free plots was 63% and 40%, for the two seasons respectively. The mechanisms responsible for the differences in root fly oviposition are discussed in relation to the two current hypotheses: the resource concentration hypothesis and the enemies hypothesis.

Key words: *Delia floralis*; *Delia radicum*; intercropping; oviposition; weeds.

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Individual species of herbivorous insects seem to be less abundant in diverse agroecosystems than in monocultures (Risch et al., 1983, Andow, 1991). Two hypotheses have been proposed to explain the effect of vegetation diversity within a habitat on these insects (Root, 1973): (1) The resource concentration hypothesis predicts that the herbivorous insects can more easily locate the plants, have lower emigration rates and a greater tendency to reproduce in simpler ecosystems/monocultures of their host plants. (2) The enemies hypothesis predicts that the natural enemies of the herbivorous pest are more effective in diverse systems due to more favourable microhabitats and food sources.

The differences in insect abundance between diverse agroecosystems and monocultures seem to be better explained by the host-finding and reproduction behaviour of the herbivorous insects than by the activities of natural enemies (Andow, 1991). However, Russell (1989) concluded that the enemies and the resource concentration hypotheses are complementary mechanisms in reducing numbers of herbivores in diverse agricultural systems.

Several studies have concentrated on the effects of intercropping on a major pest on crucifers, the cabbage root fly (*Delia radicum* (L.)), e.g. Demster & Coaker (1974), O'Donnell & Coaker (1975), Coaker (1980), Ryan et al. (1980), Theunissen & den Ouden (1980), Tukahirwa & Coaker (1982) and Coaker (1988). They all showed a reduction in plant infestation or oviposition in intercropped plots.

In Norway, two species of the genus

Delia are serious pests of cruciferous crops (Rygg, 1988): *D. radicum* and *Delia floralis* (Fallén). In the present study the oviposition of the two species was examined in cabbage intercropped with beans as compared with monocultures, and in weedy cabbage plots as compared with weedfree plots.

MATERIAL AND METHODS

The experiments were located at Ås, in the county of Akershus, in the southern part of Norway during the years 1984, 1985 and 1986. The cabbage cv. Toten Amager Fodstad and the French bean cv. Saxa were used.

Six plots were used each year. In each plot 48 cabbage plants were transplanted in a grid of 8 x 6 plants, 80 cm apart in each direction. A border of 80 cm on the outer side of the grid of the cabbage plants was included in the plots. The transplantings were carried out on 30 May 1984, 3 June 1985 and 2 June 1986.

In 1984 cabbage was intercropped with beans. The beans were transplanted on 30 May. In three randomly selected plots, eight bean plants were planted around each cabbage plant. The distance between the bean and the cabbage plants was about 26 cm, and 384 bean plants were used per plot. In the three remaining plots, the cabbage plants were grown in monocultures. Weeds were removed by hand in all plots during the experiment.

In 1985 and 1986 the effect of having weeds between cabbage plants was studied. At transplanting, all plots were free of weeds. Three plots were kept free of weeds by hand, and in the remaining three plots weeds were allowed to grow freely. On 25 July 1985 (after the cabbage root fly eggs had been counted for that day), and on 10 July 1986, all weeds were removed in the three weedy plots. Thereafter, all six plots were kept free of weeds. The most common weeds were: *Matricariae inodora, M. matricarioides, Taraxacum officinale, Capsella bursa-pastoris, Stellaria media, Atriplex patula, Chenopodium album,* and *Polygonum convolvulus*. The most rapid growth of the weeds was observed in 1985. In the middle of July they completely covered the ground and had reached the same height as the cabbage plants.

To compare the activity of *D. radicum/D. floralis* in intercropping vs. monoculture and in weedy vs. weed-free plots, the number of eggs per cabbage plant was recorded using the Swiss egg trap for cabbage root flies (Freuler & Fischer, 1983). A trap was placed around the stems of about one-third of the plants. The plants were randomly chosen, and 16, 13 and 15 traps per plot were used in 1984, 1985 and 1986, respectively. The eggs were counted every 7-10 days for about two months each year. The eggs of the two *Delia* spp. were not identified to species level. The eggs were removed from the traps after each observation.

On 7 September 1984 and 19 August 1985 the larvae and pupae in the roots and in an approximately standardized soil volume near the roots were counted in 33 and 20 of the cabbage plants per plot, respectively. Egg traps were not used on these plants.

Table 1. Oviposition of *Delia* spp. in intercropping (cabbage/beans) compared with monoculture (cabbage), Ås 1984. Average number of eggs per cabbage plant (SE in parantheses). ANOVA intercropping vs. monoculture: F = 1.91 P = 0.168

Date	Eggs per plant		
	Intercropping	Monoculture	
6 June	1.7 (0.5)	1.8 (0.4)	n.s.*
18 »	5.0 (0.7)	4.6 (0.5)	n.s.
28 »	0.9 (0.2)	3.0 (0.9)	n.s.
10 July	2.2 (0.8)	3.7 (1.4)	n.s.
25 »	21.5 (4.5)	30.8 (6.3)	s.

* sign. P < 0.05 Mann-Whitney

In 1984 a pitfall trap was placed in the middle of each plot. The traps were emptied once a week, and Carabidae and Staphylinidae were identified.

Pesticides were not applied during the three years. The cabbage yields were not recorded because of severe attacks by lepidopterous pests.

RESULTS

The average number of root fly eggs was higher in the monocultures than in cabbage intercropped with beans during the last three observations. The difference was significant only on 25 July, however (Table 1).

Table 2. Oviposition of *Delia* spp. in weedy cabbage plots compared with weed-free plots, Ås 1985. All weeds were removed after the observation of eggs on 25 July. Average number of eggs per cabbage plant (SE in parantheses). ANOVA weedy vs. weed-free (10 June-25 July): $F = 26.60$ $P < 0.001$

Date	Eggs per plant		
	Weedy (until 25 July)	Weed free	
10 June	0.5 (0.2)	1.5 (0.7)	n.s.*
13 »	1.3 (0.4)	3.6 (0.7)	s.
17 »	1.9 (0.4)	3.5 (0.6)	s.
20 »	6.1 (1.0)	3.8 (0.7)	n.s.
27 »	7.0 (0.7)	11.2 (1.5)	s.
4 July	4.5 (1.5)	3.2 (0.6)	n.s.
11 »	6.7 (2.9)	14.3 (3.3)	s.
22 »	40.3 (7.9)	113.9 (11.3)	s.
25 »	6.4 (2.1)	47.6 (9.6)	s.
1 August	75.5 (8.4)	51.3 (10.9)	s.
8 »	49.8 (5.7)	24.5 (5.2)	s.
14 »	27.1 (4.0)	14.8 (3.2)	s.

* sign. $P < 0.05$ Mann-Whitney

Table 3. Oviposition of *Delia* spp. in weedy cabbage plots compared with weed-free plots, Ås 1986. All weeds were removed on 10 July. Average number of eggs per cabbage plant (SE in parantheses). ANOVA weedy vs. weed-free (9 June-7 July): $F = 15.65$ $P < 0.001$

Date	Eggs per plant		
	Weedy (until 10 July)	Weed-free	
9 June	5.0 (1.2)	5.8 (1.2)	n.s.*
16 »	11.5 (1.8)	17.5 (1.8)	s.
23 »	6.3 (1.0)	11.5 (1.4)	s.
30 »	4.8 (1.0)	5.7 (1.3)	n.s.
7 July	3.3 (1.5)	11.4 (2.8)	s.
14 »	3.6 (1.6)	2.5 (1.1)	n.s.
21 »	7.8 (2.5)	4.6 (1.8)	n.s.
30 »	3.7 (0.8)	3.6 (0.9)	n.s.
7 August	6.7 (3.0)	4.7 (1.7)	n.s.

* sign. $P < 0.05$ Mann-Whitney

The average number of larvae and pupae per cabbage plant was 8.7 (SE = 1.3) in the intercrop and 6.7 (SE = 1.3) in monoculture (not significant, $p > 0.05$, Mann-Whitney) on 7 September 1984.

There was a distinct reduction in oviposition in weedy compared with weed-free plots during most of the period from 10 June to 25 July 1985 (Table 2). This effect on oviposition stopped when all the weeds were removed. During the subsequent three observations significantly more eggs were laid in the plots which were now weed-free.

On 19 August 1985, the average number of larvae and pupae per cabbage plant was 4.1 (SE = 0.7) in the weedy plots and 17.9 (SE = 2.5) in weed-free plots (significant, $p < 0.05$, Mann-Whitney).

When all the weeds were removed on 10 July 1986, this affected the number of eggs per plant as in 1985. However, the differences between the treatments were

Table 4. The number of Carabidae and Staphylinidae in pitfall traps in three plots (one trap/plot) of cabbage intercropped with beans and in three plots with cabbage in monoculture, Ås 1984. Start of trapping: 4 june

Carabidae

	Intercrop				Monoculture			
Date	1	2	3	Sum	1	2	3	Sum
12 June	2	9	14	25	7	8	2	17
18 June	17	15	9	41	26	25	7	58
25 June	1	9	2	12	10	8	9	27
2 July	2	1	1	4	6	3	1	14
9 July	4	3	2	9	3	3	4	10
16 July	0	3	2	5	8	6	1	15
23 July	1	2	3	6	0	5	1	6
30 July	1	2	2	5	3	5	2	10
6 Aug.	2	2	0	4	0	3	1	4
13 Aug.	2	4	0	6	1	2	1	4
20 Aug.	0	1	0	1	1	2	0	3
27 Aug.	1	0	0	1	1	0	0	1
3 Sept.	0	0	0	0	0	0	0	0
10 Sept.	0	0	0	2	0	0	0	0

Staphylinidae

	Intercrop				Monoculture			
Date	1	2	3	Sum	1	2	3	Sum
12 June	0	35	31	116	18	28	4	50
18 June	18	10	8	36	19	21	20	60
25 June	13	6	6	25	13	27	15	55
2 July	4	13	5	22	13	22	9	44
9 July	6	5	4	15	18	7	8	33
16 July	6	7	8	21	14	15	7	36
23 July	4	17	6	27	4	13	28	45
30 July	8	5	4	17	3	8	9	20
6 Aug.	2	1	1	4	5	11	3	19
13 Aug.	2	3	0	5	0	3	2	5
20 Aug.	1	2	0	3	1	0	3	4
27 Aug.	3	1	0	4	2	3	1	6
3 Sept.	1	1	0	2	2	1	2	5
10 Sept.	6	5	2	13	0	5	0	5

not significant after the removal of the weeds in 1986 (Table 3).

Table 5. The predominant species of Carabidae and Staphylinidae in pitfall traps in three plots of cabbage intercropped with beans and in three plots with cabbage in monoculture, Ås 12 June-10 September 1984

Species	Percent of total catch
Carabidae	
Bembidion quadrimaculatum (L.)	29.7
Bembidion lampros (Herbst)	28.3
Bembidion tetracolum Say	9.1
Trechus quadristriatus (Schrank)	7.7
Clivina fossor (L.)	7.0
Staphylinidae	
Amischa sp.	41.7
Aloconota gragaria (Erichson)	33.2
Anotylus rugosus (Fabricius)	15.5

With two exceptions, the total weekly number of Carabidae and Staphylinidae in pitfall traps was higher in the cabbage monoculture plots than in the plots with cabbage intercropped with beans (Table 4). Several of the dominating species (Table 5) are known to be important predators on eggs of *D. floralis* in Norway (Andersen et al., 1983).

DISCUSSION

Vegetation diversity in intercropping or in the presence of weeds may influence the oviposition of different herbivorous insects. Throughout Europe, *D. radicum* is a major pest on cruciferous crops, and several studies have shown that diverse agroecosystems reduce the oviposition of this fly (Table 6).

In southern Norway, *D. radicum* is a

Table 6. Studies on the effect of plant diversity (intercropping/undersowing/weeds) on oviposition by *Delia radicum*

Plant diversity	Percent reduction compared with monoculture	Observations	References
Brussels sprouts cauliflower/ clover	29	Eggs	Demster & Coaker (1974)
Brussels sprouts/ clover	60	Eggs	O'Donnell & Coaker (1975)
Brassicas/ beans, spinach, clover, grass	53-77	Eggs	Coaker (1980)
Cabbage/ clover	26-65	Eggs	Ryan et al. (1980)
Brussels sprouts/ spurry	30-99	Infestation	Theunissen & Den Ouden (1980)
Cabbage/ spinach	36-44	Eggs	Tukahirwa & Coaker (1982)
Rape/ clover, weeds	64-89	Infestation	Coaker (1988)

bivoltine species. At Ås the emergence of the first generation starts in the second half of May and lasts throughout most of June (Rygg, 1962). In Scandinavia and Scotland the turnip root fly, *D. floralis*, is also a serious pest on crucifers. This species is univoltine in Norway and emerges at Ås during July (Rygg, 1962). *D. floralis* lays its eggs in larger batches than *D. radicum*. The increase in the number of eggs per trap from the middle of July, most evident in 1985 (Table 2), probably reflects the start of the oviposition of *D. floralis*.

The effect of intercropping cabbage and beans seemed to have little effect on the oviposition of *Delia* spp. (Table 1). The reduction in accumulated number of eggs per plant with intercropping as compared with monoculture was 29%. The low effect of the intercropping may be due to the smallness of the bean plants at transplanting. The area between the cabbage plants was not fully covered with leaves from the beans until the beginning of July.

During the two years when the effect of weeds was studied, observations were usually made every week until the middle of August (Tables 2 and 3). The reduction in accumulated number of eggs per plant in weedy plots up to the day the weeds were removed, was 63% and 40% in 1985 and 1986, respectively. The difference between the two years in oviposition activity (numbers of eggs) and in the effect of weeds on egglaying may be due to climatic conditions. June and July 1986 were very dry months compared with in 1985 (Table 7). The dry conditions probably reduced both the activity of the flies and the growth of weeds. Horn (1987, 1988) demonstrated that the presence of weeds among crop plants influenced the colonization of several pests, aphids as well as lepidopterous larvae.

The criticism has been raised that few studies on plant diversity and insect pests have explored the underlying ecological mechanisms responsible for the observed differences in herbivore abundance (Risch et al., 1983). The most significant predators on eggs of *Delia* spp. in Norway, Carabidae and Staphylinidae (Andersen et al., 1983), seemed not to be affected by intercropping (Table 4). However, the pitfall trap catches should be interpreted with caution. The plots were small, and pitfall traps only measure the activity, not the density of the ground-living beetles.

Table 7. Monthly rainfall (in mm) at Ås during June, July and August 1985 and 1986 (Department of Physics, Agricultural University of Norway, 1985, 1986)

	June	July	August
1985	96.3	98.1	158.4
1986	16.4	63.4 *	129.0

* 30.5 mm on 30 July

The present study indicates that the resource concentration hypothesis may explain the reduced oviposition in weedy plots. After the weeds were removed, either an equal amount or more eggs were observed in these plots compared with the control plots(Tables 2 and 3). In 1985, when the oviposition was large, significantly more eggs were found in the «weedy» plots after the removal of weeds. The root flies now found these plants which had received fewer eggs, more suitable for egglaying. No investigations of the influence of Carabidae and Staphylinidae were carried out in the weedy/weed-free plots in 1985 and 1986. However, the activity of these beetles seemed to be low in this area during the last part of July when the weeds were removed (Table 4, Hofsvang (unpublished): pitfall traps on the same area in intercropping/monoculture 1983). Powell et al. (1985) recorded few large carabids in weedy plots, and the authors suggested that the activity may be reduced by the vegetation.

Two carefully conducted studies of root flies (*D. radicum* and *Psila rosae*

(Fabricius)) in England (Tukahirwa & Coaker, 1982, Uvah & Coaker, 1984) showed that disturbances in host-plant-finding and oviposition behaviour were the main reasons for reduced numbers of root fly eggs in intercropping, not the carabid and staphylinid predation. It can be concluded from the current study that the presence of weeds for several weeks during the oviposition period of *Delia* spp. reduces the number of eggs per cabbage plant. The oviposition was probably reduced as a result of volatiles from the weeds deterring the females, or because the weeds acted as a physical barrier. The possible competition from the weeds on plant growth was not included in this study, but should be investigated before any practical application of this cultural technique is made.

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Neighbour-effects in oat cultivar yield trials

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Interplot competition was studied in 28 yield trials which included two to six oat cultivars of widely different straw length. For each 100 kg/daa higher grain yield the mean straw length increased by 10.9 cm and the mean difference in straw length between cultivars increased by 3.8 cm. The model for the statistical analysis of the data implies that a plot yield comprises a basic cultivar yield and in addition a neighbour-influenced yield component which is usually a function of the difference in straw length multiplied by a factor which varies with the severity of the competition situation. The neighbour effect factor by which the straw length difference should be multiplied to obtain the yield correction is represented by the function $\log y = -0.400065 + 0.0010195x$, where the x is the grain yield in kg per daa. For some cultivar combinations the taller cultivar gained more in grain yield than the shorter cultivar lost in the competition. There were differences between cultivars in aggressiveness of growth, which could bias yield trial results for some cultivars. A formula for correcting bias in yield caused by differences in straw length is proposed.

Key words: Border effects, edge effects, interplot competition.

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Cultivar yield trials are carried out in order to estimate the yield potential of cultivars when grown in farmers' fields. Because of soil heterogeneity and the high cost of large experimental plots, the plot size used in the yield trials is from 10 m^2 and upwards. For breeding material the plot size may even be less.

The techniques and the equipments used to carry out large scale field experiments favour the use of comparatively long and narrow plots as most of the machines for sowing and harvesting the crop are designed for 1.5 m wide plots. This plot shape means that there are large border surfaces in relation to plot areas. Possible bias in yield estimates from cultivar yield trials may in principle be due to three groups of factors. One is the *border effect* of the plot, i.e. differences among cultivars in utilizing the growth factors available from the open alley between the plots. Hulbert et al.(1931) found in their extensive series of experiments that the border effect arising from a two-feet-wide alley between plots could result in biased ranking of the cultivars for yield potential. The border effect and the cultivar x border effect interaction were influenced by the severity of the plant competition, i.e. seed rate, yield level, etc. Gomez (1972) reported on the border effect in rice cultivar experiments and Hadjichristodoulou (1983) on the edge effects in durum wheat and barley trials which could bias yield estimates from cultivar yield trials.

The border row reaction is completely confounded with cultivars and can only be determined in specially designed

experiments. Bias in yield due to the different border reactions of the cultivars can be reduced by use of wider plots, but can only be eliminated by discarding the two border rows adjacent to the alley.

The other reason for biased yield results is the *interplot competition*, i.e. effects of one plot on neighbouring plots across the intervening alley. Given the plot size and shape there are three main factors which may bias the results of yield trials as a result of interplot competition. Straw length is obviously such a character and most investigations on the problem have been related to differences in straw length. It is also obvious that yield level must be of importance. High yield means tall vigorous plants in dense stand where competition for space, light, water and nutrients is strong, to some extent also across the alley between plots. At low yield, i.e. in thin stand of less vigorous plants, however, it can be assumed that the effects of plants across the alley are insignificant.

Mosleth & Dieseth (1985) found that for a part of this material a difference in straw length of 32 cm resulted in a yield depression of 39 kg per daa for the shorter cultivar compared to pure stand and a yield increase of 47 kg for the taller cultivar also compared with the yield in pure stand. Aastveit et al.(1989),in another part of the material, found that grain yield was affected by up to 1-2 kg per daa per cm difference in straw length. Earlier investigations, among which are Jensen & Federer (1964), Fisher (1979), Austin & Blackwell (1980) and Kempton et al.(1986), also have shown that interplot competition may lead to biased results in cultivar yield trials.

A third factor may be the *aggressiveness of growth* of the particular cultivar. Differences in growth habitus, rate of development, etc., may show effects across the alley between plots. This group of characters is difficult to put on scale and can only be estimated in special trials. In yield trials they are completely confounded with cultivars and may therefore bias the yield results of a cultivar compared to its yield potential in farmers' fields. For these reasons the difference in competing ability for most cultivars is assumed to be small compared to other errors in yield trials. However, the results of this investigation show that cultivar differences exist and therefore deserve attention.

The investigations referred to have shown that interplot competition may be a problem in all kinds of yield trials with cereal cultivars and breeding material of different straw length, different competing ability or when treatment strongly affects growth rate and straw length, i.e. growth regulators, fertilizer, etc. None of the investigations have, however, resulted in a formula for routine adjustment of yield bias caused by interplot competition. Such a formula should preferably be based on characters ordinarily recorded in yield trials. Straw length and grain yield are recorded in all yield trials. Therefore, yield adjustment based on these characters, involves no extra cost.

MATERIAL AND METHODS

The material used in the main part of the study included 13 experiments with two cultivars, 7 experiments with three cultivars, 2 experiments with four cultivars and 6 experiments with six cultivars, a total of 28 experiments. The experiments were carried out during the period 1982-1987. The results from five of the two-cultivar experiments have been published earlier by Mosleth & Dieseth (1985) and 13 of the remaining experiments have been published by Aastveit et al. (1989). We believe, however, that use of more efficient statistical methods on the pooled and supplemented material could result in a formula by which the yield of cultivars of different straw length could be adjusted as a part of the routine analysis of yield trials.

The cultivars and some cultivar

Table 1. Cultivars and cultivar characteristics

Cultivar	No.of exp.	Grain yield kg/daa	Straw length cm	Increase in straw length per 100 kg higher yield cm	percent
Puhti	14	568	91	13.3	14.6
Lena	14	579	74	11.5	15.5
Mustang	19	591	84	9.7	11.5
Kapp	4	592	86	12.5	14.5
Svea	4	570	84	10.9	13.0
Dverg	26	561	57	7.4	13.0
Means			79,3	10.9	13.7

characters are listed in Table 1. In the two-, three- and four- cultivar experiments all possible neighbour combinations were included. This means 6 treatments for the two-cultivar experiments, 18 treatments for the three-cultivar experiments and 40 treatments for the four-cultivar experiments. For the six-cultivar experiments only 6 combinations were included.

The width of the plots was 1.50 m, comprising 10 rows 13.3 cm apart and an alley of 30 cm between border rows of the adjacent plots. The length of the plots varied between 4 and 6 m. In two experiments a plot width of 0.75 m comprising of four rows spaced 15 cm apart and an alley of 30 cm between border rows of adjacent plots was used. All experiments were carried out in the same way as routine cultivar yield trials of cereals.

The model applied for the statistical analysis of the data implies that a plot yield is made up of a basic cultivar yield i.e. the yield of the cultivar in uniform pure stand, and in addition a neighbour-influenced yield component which is usually a function of the difference in straw length to neighbouring plots multiplied by a factor which varies with the severity of the competition. In this study the yield level is used as a parameter for the competitive situation.

RESULTS

Straw length and yield

In table 1 the different cultivars included in the experiments are given. The mean grain yield of the cultivars was not significantly different mainly because of high cultivar x yield level interaction.

The cultivars were purposely selected for large differences in straw length. The largest mean difference between the tallest (cv. Puhti) and the shortest (cv. Dverg) cultivar was 34 cm. All cultivars were taller under high yield conditions. The correlation coefficient between straw length and grain yield was $r = 0.83^{**}$ and the mean increase was 10.9 cm per 100 kg higher grain yield. However, the cultivars reacted significantly differently, with an increase of 13.3 cm straw length for the tallest and only 7.4 cm for the shortest cultivar. The different straw length reactions also resulted in varying differences between the cultivars at different yield levels. The *percent* increase in straw length at higher yield, therefore, is less variable and non-significant.

In Figure 1 the mean difference in straw length as a function of yield level is indicated by the function $y = 1.39 + 0.0382x$, i.e. the mean difference in straw length increased by 3.82 cm per 100 kg higher yield. Because of the cultivar differences in straw length reactions the difference between cultivars may also vary with the yield level.

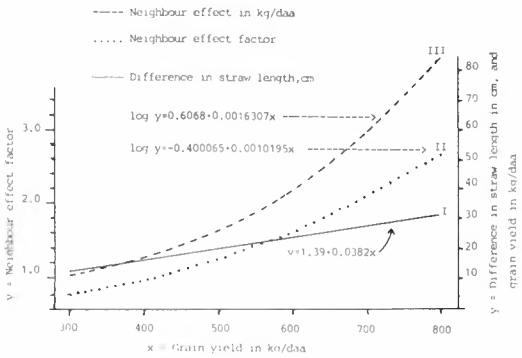

Figure 1. Nighbour effect, neighbour effect factor and difference in straw length as a function of yield level

Neighbour effect and yield level

The curves and equations in Figure 1 were arrived at in the following way:

1. The mean yield of an experiment locates it on the x-axis.
2. The difference in straw length (cm) between two cultivars is marked by a dot for curve I, read on the y-axis to the right.
3. The neighbour effect, BAB - AAA, in kg per daa is marked by a dot for curve III, also read on the y-axis to the right. (The notation BAB means a plot of cultivar A between two plots of cultivar B and AAA means a plot of cultivar A between two plots of the same cultivar).
4. The dot for the curve II is obtained by dividing the dot value of curve III by the dot value of curve I and locating it for curve II according to the scale on the y-axis to the left.
5. The procedure described in steps 1-4 is repeated for all combinations of two cultivars in all experiments.
6. For each of the three dot diagrams an equation is calculated, which describes the curve best fitted to the observations.

Curve I describes the effect of yield on the difference in straw length between two cultivars. The curve is linear, $y = 1.39 + 0.0382x$. The relation between straw length differences and yield based on the mean results of all the experiments did not deviate significantly from a straight line, but combinations of the tallest and the shortest cultivars indicated strongly that the relation in some cases may be slightly logarithmic, i.e. higher neighbour effect factor in cases of large differences in straw length between cultivars. It is assumed, however, that such effects are taken care of by the logarithmic function for the neighbour effect factor.

Curve II describes the effect of yield on the *neighbour effect factor*. The curve is logarithmic, $\log y = -0.400065 + 0.0010195x$. This function is used to calculate the factor by which the difference in straw length should be multiplied in order to obtain the yield correction in kg per daa. As an example the factors at different yield levels are calculated in Table 2.

Table 2. Neighbour effects, straw length differences and neighbour effect factors at different yield levels

Grain yield kg per daa	Neighbour effect kg per daa	Straw length difference,cm	Neighbour effect factor,kg/daa/cm
300	10.3	12.9	0.80
400	16.9	16.7	1.01
500	26.4	20.5	1.29
600	39.9	24.3	1.64
700	58.9	28.2	2.09
800	85.1	32.0	2.66

Curve III describes the sum effects of yield on the neighbour effects. The curve is logarithmic, log y = 0.6086 + 0.0016307x

Neighbour effects in tall and short cultivars

The 13 two-cultivar and the 8 three-cultivar experiments can be analysed for possible differences in neighbour effect on the taller and the shorter cultivars. In the first series of experiments the M (cv. Mustang) had an 85.4 cm straw length and the D (cv. Dverg) a 55.4 cm straw length. The neighbour effects on the taller and the shorter cultivars in the two-cultivar experiments were:

MMM - DMD = – 56.0 kg
DDD - MDM = + 39.9 kg
Difference 16.1 + – 8.6 kg

This shows that, because of its shorter neighbours, the yield increase for cv. Mustang, was 16.1 kg greater than the yield reduction for cv. Dverg because of its taller neighbours.

The straw lengths of the cultivars in the 8 three-cultivar experiments were:

P = Cv. Puhti 89.6 cm
L = Cv. Lena 72.8 cm
D = Cv. Dverg 61.1 cm

The neighbour effects of the different cultivar combinations were:

PPP - LPL = – 54.0 kg
LLL - PLP = + 23.4 kg
Difference 30.6 + – 10.2 kg

PPP - DPD = – 40.6 kg
DDD - PDP = + 43.0 kg
Difference 2.4 + – 14.7 kg

LLL - DLD = 9.0 kg
DDD - LDL = – 6.6 kg
Difference 15.6 + – 15.6 kg

Of the four cultivar combinations analysed the difference in neighbour effect between the shorter and the longer cultivars was significant in one case, close to significant in another and non-significant in the remaining two cases. The interpretation of these results may be that very tall and very short cultivars can react differently, but for most cultivars the differences are assumed to be small. The LLL ---> DLD vs. the DDD ---> LDL combination indicates, however, that differences in aggressiveness which are confounded with cultivars, may in some cases be the reason for differences in neighbour effect reactions of tall and short cultivars.

In the two four-cultivar experiments the six cultivar combinations gave the following mean results.

Effect of shorter cultivars on neighbour plots + 8.7 kg

Effect of taller cultivars on neighbour plots – 21.2 kg.

Because of high experimental errors the differences are not significant.

Cultivar differences in neighbour effects

In chapter I it was postulated that the aggressiveness of growth of the different cultivars could influence the neighbour effect. Ten of the three- and four-cultivar experiments could be used to study cultivar differences in neighbour effects which in this connection are thought to be due to varying degrees of aggressiveness of growth.

The neighbour effect is studied in three cultivar combinations, namely Puhti-Lena, Puhti-Dverg and Lena-Dverg. In order to eliminate the effect of different cultivar straw length on the neighbour effect, the comparisons were based on differences in the ratio: Neighbour effect/differences in straw length, which is indicated by the log y = – 0.400065 + 0.0010195x curve in Figure 1.

The mean of the ratios for the Puhti-Lena combination was 2.14 while for the Puhti-Dverg combination it was 0.93. The 1.21 difference is highly significant. The differences in neighbour effect or aggressiveness of growth between cv.

Lena and cv. Dverg were equivalent to a 13 cm difference in straw length. Cv. Puhti comes closest to cv. Dverg in competing ability per centimetre of straw length. The ranking of the three cultivars in aggressiveness of growth therefore is D > P > L. The material indicates that cv. Lena is a comparatively weak competitor most probably due to its thin straw and non-spreading growth habit. The differences between the other five cultivars in the study seem to be small.

Neighbour effect and plot width

The plot width of the experiments dealt with so far has been 1.50 m. It is obvious that interplot competition declines in proportion to the width of the plots and reaches zero in pure stand.It is also obvious that the neighbour effect in percent of plot yield would increase in more narrow plots. In two experiments a plot width of 75 cm comprising four rows 15 cm apart and an alley of 30 cm was used. The results obtained were close to the expected values, namely twice as high as those for the 1.50 m plot experiments.

Yield corrections for neighbour effects

According to the results of this study a correction of plot yield which is biased because of neighbour effects can be corrected by the formula K = -A*B*C where

A = The difference in straw length in centimetres

B = The neighbour effect factor y where $\log y = -0.400065 + 0.0010195x$

C = The plot width factor which is 150/plot width in centimetres. For plot widths of 150 cm this factor can be omitted.

It is recommended that yield correction is made for each plot. The straw length factor (A) is calculated as half of the difference between the plot straw length and the mean straw length of the two neighbour plots. The yield (the x in the equation for the B factor) is the yield of the plot to be corrected. If the neighbour effect correction is applied to mean results of a series of experiments, the A factor for each cultivar is calculated as its deviation from the mean of all cultivars. If only two cultivars are compared, the yield correction may be applied to one of them based on the full difference in straw length. The yield (x in the equation) may be the yield of the cultivar to be corrected.

The yield corrections described are based mainly on results obtained in experiments with the cvs. Dverg, Mustang, Puhti and Lena (see Table 1). The straw length reactions of the different cultivars to varying growth conditions and yield levels are not very different, as indicated in the last column of Table 1. It is believed, therefore, that the corrections recommended with satisfactory accuracy also apply to oat cultivars in general. In the case of cv. Lena, however, it is shown that cultivars of deviating growth habit may gain or lose in the experiments in relation to most other cultivars.

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Influence of photoperiod and temperature on dry matter production and chlorophyll content in temperate grasses

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Long days (LD), without increase in daily photosynthetic active radiation, stimulated dry matter (DM) production of *Alopecurus pratensis* L. from Grytøy and Ås, *Bromus inermis* Leyss. cvs Løfar and Manchar, *Dactylis glomerata* L. cvs Hattfjelldal and Frode, *Festuca pratensis* Huds. cvs Salten, Løken and Pajbjerg, *Phleum pratense* L. cvs Engmo and Forus and *Poa pratensis* cvs Holt, Lavang and Norma. The basis for this growth stimulation in all these cultivars was the greater leaf area growth in LD than in short days (SD) that more than compensated for reduced net assimilation rate (NAR) in LD. Leaf area ratio (LAR) increased in LD mainly because of higher specific leaf area (SLA), while leaf weight ratio was almost unaffected by daylength. Within species, the northern *D. glomerata* cv. Hattfjelldal responded more strongly to daylength than the southern cv. Frode and the northern *P. pratensis* cvs Holt and Lavang responded more strongly than the southern cv. Norma. Otherwise, there was no difference within species. Chlorophyll levels were measured for *B. inermis* cvs Løfar and Manchar, *F. pratensis* cvs Salten and Pajbjerg, *P. pratense* cvs Engmo and Forus and *P. pratensis* cvs Holt and Norma. Chlorophyll contents per unit leaf area were higher in SD than in LD, and higher at low than at high temperatures. Chlorophyll contents per unit fresh weight were also higher in SD than in LD, while the contents per unit dry weight were little affected by daylength. Chlorophyll a/b ratios increased with decreasing temperature, and the chlorophyll a/b ratio was also slightly higher in SD than in LD. The significance of differences in chlorophyll levels is discussed in relation to LD stimulation of DM production and found to be of minor importance.

Key words: Chlorophyll, dry matter production, grasses, growth analysis, leaf area, photoperiod, temperature.

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Long day (LD) stimulation of dry matter (DM) production has been observed in many temperate grasses (Hay 1990) including *Dactylis glomerata* (Eagles & Østgård 1971), *Poa pratensis* (Hay & Heide 1983, Heide et al. 1985a), *Bromus inermis*, *Phleum pratense* (Heide 1982, Heide et al. 1985b), *Festuca pratensis* and *Lolium perenne* (Ryle 1966). The basis for this stimulation of relative growth rate (RGR) in LD is the increased leaf area ratio (LAR) that more than compensates for a reduced net assimilation rate (NAR) (Hay & Heide 1983, Heide et al. 1985b). Only a few experiments have compared northern and southern cultivars within species. Hay & Pedersen (1986) found a slightly greater LD stimulation of DM

production in northern than in southern cultivars of timothy. There was no significant difference in LD stimulation of DM production between six cultivars of *P. pratense* of latitudinal origin ranging from 69°N to 52°N (Heide 1982).Eagles & Østgård (1971) found that the response of a South-Norwegian population of *D. glomerata* was intermediate that of two North-Norwegian populations and a Portuguese population.

Short days (SD) have been reported to increase the chlorophyll level in grasses cultivated in the field (Foss 1968) and under controlled conditions (Eagles & Østgård 1971). In the field, the chlorophyll level of *P. pratense* was higher in northern than in southern cultivars (Foss 1968). At low temperatures northern populations of *D. glomerata* contained more chlorophyll per unit leaf area than southern ones (Eagles & Østgård 1971). The chlorophyll a/b ratio was higher in SD than in LD in *P. pratense (Foss 1968).* However, the experiments of Eagles & Østgård (1971) were carried out with low light intensity (72 W m^{-1}) and light intensity may affect both the chlorophyll levels and chlorophyll a/b ratios (Anderson 1986).

The aim of the present work was to study LD effects on growth, chlorophyll level and chlorophyll a/b ratio in northern and southern cultivars within each of six temperate grass species.

MATERIALS AND METHODS

Seeds of *Alopecurus pratensis* were collected from natural populations at Grytøy (69°N) and Ås (59°N). Seeds of commercial cultivars were used for the other species. Latitudes of origin are given below.

Poa pratensis: cvs Holt (69°N), Lavang (69°N), Norma (55°N).
Phleum pratense: cvs Engmo (69°N), Forus (59°N).
Dactylis glomerata: cvs Hattfjelldal (66°N), Frode (about 55°N).
Festuca pratensis: cvs Salten (67°N), Løken (61°N), Pajbjerg (about 55°N).
Bromus inermis: cvs Løfar (61°N), Manchar (Pacific Northwest about 55°N).

After germination in the dark at 21°C the plants were cultivated in 8 h photoperiod. At about the two leaf stage the plants were potted singly in 8 cm plastic pots in a standard potting soil (Einheitserde). At about the four to six leaf stage the plants were evenly distributed amongst six treatments in a factorial design for 12, 18, and 24°C × 8 and 24 h daylength in 1986 and 9, 15 and 21°C × 8 and 24 h daylength in 1987. Plant dry weights and leaf areas at the start and duration of the various experiments are given in Tab. 1. An additional experiment for studying time course effects on chlorophyll content and a/b ratio was done in the period from August 22. to October 8. 1986. The experiments were conducted in phytotron compartments with daylight during 8 h and corresponding adjacent rooms that were either dark or illuminated by low intensity incandescent lamps (about 5 µmol m^{-2} s^{-1}). Thus LD- and SD-grown plants received approximately the same total of photosynthetic active irradiation. Because of space limitation the experiments with the various grass species had to be conducted sequentially, and hence under somewhat different daylight conditions.

At harvest the plants were partitioned into three components: green leaf blades (leaves), leaf sheaths and stolons (stems), and roots. Leaf blade area was measured with a Lambda Instruments Corp. Model LI-3000 portable area meter. Dry weights were measured after drying for at least 48 h at 80°C.

Growth analysis

Growth analyses were performed according to Evans (1972). The growth analysis parameters were calculated using pairs of plants consisting of one random

Table 1. Leaf areas and dry weights per plant at start of the experiments. Experiment duration and starting dates are also given

Species	Cultivar	Starting conditions: Leaf area cm^2, $plant^{-1}$	Starting conditions: DW, mg $plant^{-1}$	Starting conditions: Date	Duration days, at temperature levels, °C: 9	12	15	18	21	24
Dactylis glomerata	'Hattfjelldal'	9.1	37.1	10/5-86		25		20		19
	'Frode'	8.6	37.2	10/5-86		25		20		19
	'Hattfjelldal'	4.0	14.8	5/6-87	45		33		28	
	'Frode'	4.6	19.8	5/6-87	45		33		28	
Phleum pratense	'Engmo'	18.4	78.7	10/7-86		31		26		25
	'Forus'	17.3	79.0	10/7-86		31		26		25
	'Engmo'	1.1	5.2	29/7-87	56		41		34	
	'Forus'	1.5	5.8	29/7-87	56		41		34	
Poa pratensis	'Holt'	7.2	67.5	7/7-86		36		32		31
	'Norma'	11.7	76.1	7/7-86		36		32		31
	'Holt'	-	-	11-27/5-87	26		21		21	
	'Lavang'	-		11-27/5-87	26		21		21	
Festuca pratensis	'Salten'	7.9	35.9	6/6-86		32		19		19
	'Pajbjerg'	9.6	46.2	6/6-86		32		19		19
	'Salten'	8.2	50.6	4/7-87	42		23		21	
	'Løken'	13.8	69.1	4/7-87	42		23		21	
	'Pajberg'	10.3	58.6	4/7-87	42		23		21	
	'Salten'	2.0	8.9	29/7-87	55		40		33	
	'Pajbjerg'	1.5	6.6	29/7-87	55		40		33	
Bromus inermis	'Løfar'	11.3	50.8	3/9-86		33		26		19
	'Manchar'	11.3	48.2	3/9-86		33		26		19
	'Løfar'	3.3	14.9	28/8-89	67	53	42	39		
	'Manchar'	2.8	11.9	28/8-89	67	53	42	39		
Alopecurus pratensis	'Grytøy'	5.7	26.4	18/7-86		33		26		25
	'Ås'	4.7	23.5	18/7-86		33		26		25

plant taken at the start of the experiment and one taken at the final harvest. This procedure made statistical analysis of the data possible.

The formulae used for growth analysis were:

$$\text{Relative growth rate (RGR)} = \frac{\ln(W2/W1)}{t}$$

$$\text{Net assimilation rate (NAR)} = \frac{(W2-W1)\ln(A2/A1)}{(A2-A1)t}$$

$$\text{Leaf area ratio (LAR)} = \frac{(A2-A1)\ln(W2/W1)}{(W2-W1)\ln(A2/A1)}$$

$$\text{Relative leaf area growth rate (RLAGR)} = \frac{\ln(A2/A1)}{t}$$

Where: A1 = initial leaf area (cm^2), A2 = final leaf area (cm^2), W1 = initial plant dry weight (mg), W2 = final plant dry weight (mg), t = number of weeks between harvests

$$\text{Leaf weight ratio (LWR)} = \frac{\text{leaf dry weight(mg)}}{\text{plant dry weight (mg)}}$$

$$\text{Specific leaf area (SLA)} = \frac{\text{leaf area } (cm^2)}{\text{leaf dry weight (mg)}}$$

Because leaf blade area only was used in the calculations, NAR is likely to have been overestimated, since leaf sheaths also contribute to photosynthesis. However, Borland & Farrar (1985) estimated

that leaf sheath photosynthesis only contributed toward about five % of the total plant photosynthesis in *Poa annua* and *Poa* × *jemtlandica*. This indicates that the overestimation of NAR per unit leaf blade area will probably be small.

Chlorophyll was extracted with N,N-dimethylformamide and the amount of chlorophyll a and b was calculated according to Moran (1982).

Statistical analysis

Hypothesis within species were tested by means of a three-way analysis of variance with cultivar, daylength and temperature as fixed factors. Hypothesis on effects of daylength and temperature on chlorophyll in *B. inermis*, *F. pratensis*, *P. pratense* and *P. pratensis* were tested by a three-way analysis of variance with species, daylength and temperature as fixed factors. Differences discussed have critical levels of significance of $P \leq 0.05$ unless otherwise stated.

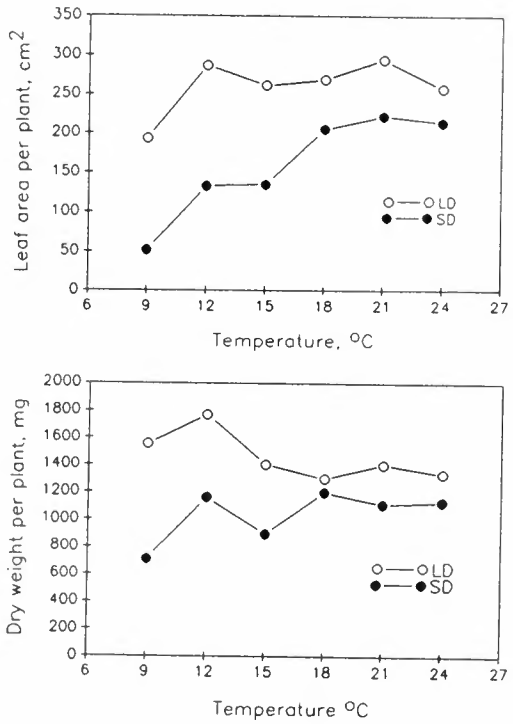

Figure 1. Effects of daylength and temperature on leaf area and dry weight of six grass species. Each point is a mean of all experiments

RESULTS

Dry matter production

In nearly all the cultivars investigated LD stimulated DM production most at low temperatures. On an average for all cultivars LD stimulated DM production by more than 100% at 9°C, by about 50% at 12 and 15°C and by less than 25% at 18, 21 and 24°C (Fig. 1). Within species this LD stimulation was greater in the northern than in the southern *D. glomerata* and *P. pratensis* cultivars. Typically in the southern *P. pratensis* cv. Norma DM production was almost unaffected by daylength. Comparing species, *B. inermis*, *D. glomerata* and *P. pratensis* (except 'Norma') responded more strongly to photoperiod than *P. pratense*, *F. pratensis* and *A. pratensis* (Table 2).

Leaf area

Leaf area was increased more by LD than DM production. At 9°C the leaf area was 275% higher in LD than in SD, at 12 and 15°C the increase was about 100%, and at 18, 21 and 24°C only about 20-30% (Fig. 1). The greatest effect of daylength occurred in the northern cvs Holt and Lavang of *P. pratensis*, cv. Hattfjelldal of *D. glomerata* and cvs Løfar and Manchar of *B. inermis*, in which the leaf areas were 6-9 times larger in LD than in SD at 9°C. Leaf area was less stimulated in *P. pratense*, *F. pratensis*, *A. pratensis* and especially the southern cv. Norma of *P. pratensis*, in which leaf area was hardly increased at all in LD (Tab. 3).

Table 2. Leaf dry weights in mg per plant ± SEM (n = 10) of grass cultivars grown at various constant temperature levels and two daylengths

Species	Cultivar	Day-length, h	Temperature, °C					
			9	12	15	18	21	24
Dactylis glomerata	'Hattfjelldal'	8	623 ± 23	692 ± 62	1172 ± 98	831 ± 104	1407 ± 74	736 ± 47
	"	24	2065 ± 135	1123 ± 80	2216 ± 99	996 ± 87	1538 ± 48	981 ± 60
	'Frode'	8	875 ± 64	762 ± 93	1542 ± 140	805 ± 72	1282 ± 110	842 ± 86
	"	24	1968 ± 191	1232 ± 131	1953 ± 104	865 ± 45	1194 ± 98	912 ± 62
Phleum pratense	'Engmo'	8	422 ± 64	1750 ± 112	487 ± 28	1873 ± 114	753 ± 58	1841 ± 112
	"	24	685 ± 85	2360 ± 112	760 ± 96	1655 ± 96	900 ± 53	2115 ± 121
	'Forus'	8	282 ± 76	1659 ± 118	456 ± 89	1765 ± 115	547 ± 76	1613 ± 117
	"	24	431 ± 82	2296 ± 116	721 ± 96	1650 ± 102	872 ± 94	1920 ± 101
Poa pratensis	'Holt'	8	616 ± 44	1361 ± 86	828 ± 51	1328 ± 122	1383 ± 22	1415 ± 116
	"	24	2094 ± 135	2189 ± 303	1878 ± 164	1721 ± 127	2201 ± 129	2331 ± 143
	'Lavang'	8	692 ± 48		845 ± 68		1252 ± 95	
	"	24	1975 ± 91		1430 ± 99		1949 ± 137	
	'Norma'	8		2331 ± 127		2110 ± 77		2885 ± 112
	"	24		2786 ± 126		2222 ± 70		2581 ± 214
	'Salten'	8	1002 ± 48	1486 ± 52	970 ± 44	879 ± 59	1063 ± 70	1005 ± 72
	"	24	1472 ± 102	1981 ± 107	1007 ± 60	975 ± 55	1207 ± 70	1033 ± 82
Festuca pratensis	'Salten'*	8	882 ± 55		997 ± 73		1214 ± 76	
	"	24	1598 ± 106		1469 ± 61		1749 ± 84	
	'Løken'	8	1159 ± 70		1048 ± 65		1311 ± 86	
	"	24	1894 ± 140		1377 ± 79		1387 ± 79	
	'Pajbjerg'	8	1237 ± 58	1773 ± 115	1047 ± 78	1006 ± 34	1245 ± 110	1159 ± 66
	"	24	2177 ± 124	2125 ± 93	1302 ± 68	937 ± 39	1334 ± 56	1148 ± 82
	'Pajbjerg'	8	483 ± 30		740 ± 26		801 ± 53	
	"	24	1178 ± 95		1453 ± 117		1088 ± 47	
Bromus inermis	'Løfar'	8		707 ± 40		915 ± 106		974 ± 42
	"	24		1399 ± 104		1378 ± 111		953 ± 57
	'Manchar'	8		665 ± 47		993 ± 125		871 ± 117
	"	24		1213 ± 60		1093 ± 64		934 ± 65
	'Løfar'	8	443 ± 35	521 ± 32	675 ± 48	801 ± 38		
	"	24	1387 ± 77	1707 ± 74	1400 ± 95	1295 ± 77		
	'Manchar'	8	520 ± 39	640 ± 65	834 ± 36	1017 ± 67		
	"	24	1278 ± 128	1546 ± 115	1271 ± 77	1232 ± 114		
Alopecurus pratensis	'Grytøy'	8		1497 ± 122		1377 ± 97		1116 ± 150
	"	24		1859 ± 128		1012 ± 124		1489 ± 100
	'Ås'	8		1104 ± 125		1094 ± 94		1109 ± 119
	"	24		1650 ± 176		1138 ± 98		1312 ± 101

* Experiment starting 29/7 87.

Table 3. Leaf-blade areas in cm^2 per plant ± SEM (n = 10) of grass cultivars grown at various constant temperature levels and two daylengths

Species	Cultivar	Day-length, h	Temperature, °C					
			9	12	15	18	21	24
Dactylis glomerata	'Hattfjelldal'	8	46±8	79±8	217±15	161±18	363±18	180±12
	"	24	310±22	242±16	424±14	260±23	420±28	262±12
	'Frode'	8	81±8	102±12	255±24	153±13	278±28	191±18
	"	24	272±18	239±20	356±17	200±12	279±19	204±17
Phleum pratense	'Engmo'	8	30±6	183±13	74±4	373±26	171±14	412±23
	"	24	97±12	418±29	159±27	458±39	214±12	550±22
	'Forus'	8	27±6	180±12	72±14	352±18	120±19	324±26
	"	24	82±12	395±22	144±21	433±31	188±18	381±25
Poa pratensis	'Holt'	8	26±3	107±6	78±4	169±19	208±12	214±20
	"	24	227±13	323±44	299±23	347±31	401±17	444±24
	'Lavang'	8	35±4		86±7		200±16	
	"	24	220±10		251±18		376±24	
	'Norma'	8		273±12		338±11		426±15
	"	24		406±18		384±10		352±27
Festuca pratensis	'Salten'	8	71±5	154±5	138±7	123±7	216±17	150±16
	"	24	149±9	281±17	203±10	155±9	250±15	174±13
	'Salten'*	8	76±7		171±13		207±14	
	"	24	180±12		290±17		338±18	
	'Løken'	8	87±8		153±10		265±18	
	"	24	203±15		264±12		286±15	
	'Pajbjerg'	8	110±5	190±11	159±13	138±7	254±23	173±10
	"	24	260±16	313±13	250±16	153±9	280±18	193±17
	'Pajbjerg'*	8	32±2		125±6		162±12	
	"	24	125±13		293±28		217±11	
Bromus inermis	'Løfar'	8		71±5		167±17		187±1
	"	24		234±18		262±17		199±10
	'Manchar'	8		81±5		200±18		178±18
	"	24		205±8		231±11		193±17
	'Løfar'	8	22±2	41±4	95±6	120±6		
	"	24	195±10	265±10	239±11	231±15		
	'Manchar'	8	29±3	59±7	132±9	179±10		
	"	24	198±14	223±11	222±16	223±19		
Alopecurus pratensis	'Grytøy'	8		178±17		239±15		214±28
	"	24		296±12		209±28		267±24
	'Ås'	8		123±16		164±15		236±25
	"	24		255±29		220±18		227±15

* Experiment starting 29/7 87

Growth analysis

Net assimilation rate was lower in LD than in SD at low temperatures, but this difference decreased with increasing temperature, and at 21 and 24°C there was no difference between LD- and SD-cultivated plants (Fig. 2). Leaf area ratio was higher in LD than in SD-grown plants at low temperatures, but also this difference decreased with increasing temperature, and at 24°C there was no effect of photoperiod (Fig. 2). The stimulation of LAR in LD more than compensated for reduced NAR so the net result was higher RGR in LD (Fig. 2). Long days increased RLAGR more than RGR (Fig. 2). Relative growth rate, LAR and RLAGR increased with the temperature, while NAR was almost unaffected (Fig. 2).

The reduction of NAR in LD was greater in northern cultivars both in *P. pratense* and *P. pratensis* (Fig. 3). In *P. pratensis* LD increased LAR of Holt and Lavang, while Norma was little affected

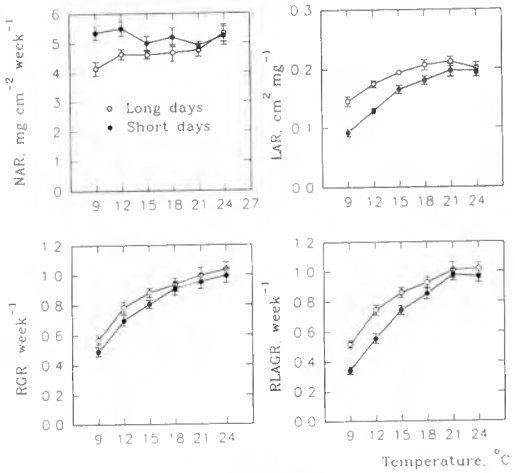

Figure 2. Mean daylength and temperature effects on RGR, NAR, LAR and RLAGR for all grass cultivars. Each point with its ± SEM is weighted mean of all cultivars

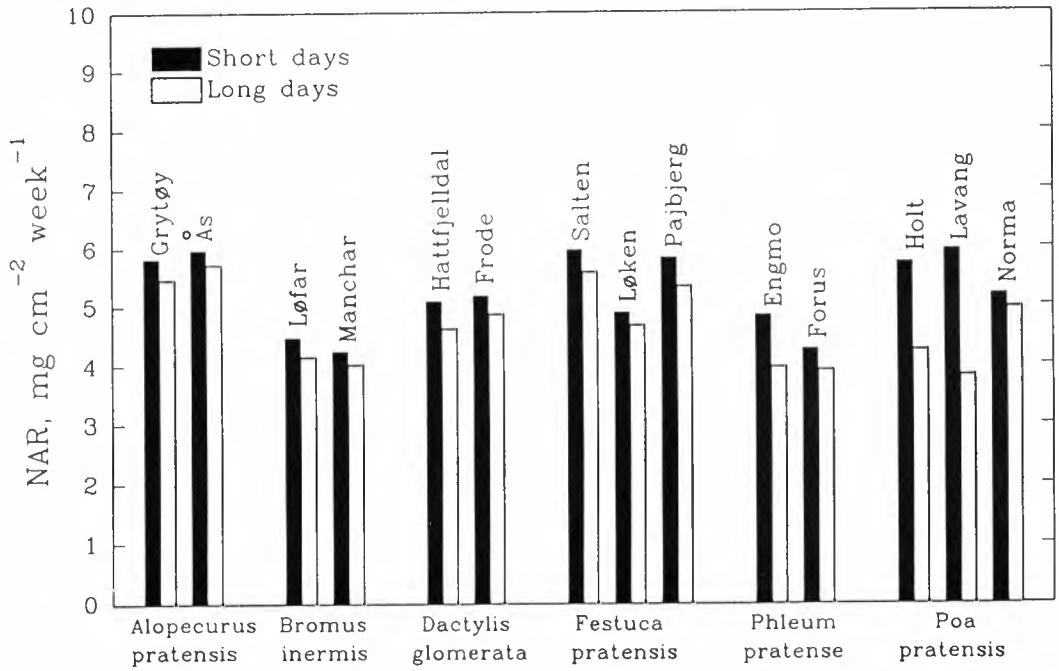

Figure 3. Daylength effects on NAR in northern (left) and southern (right) cultivars of six grass species. The values are averaged over all temperature levels and experiments

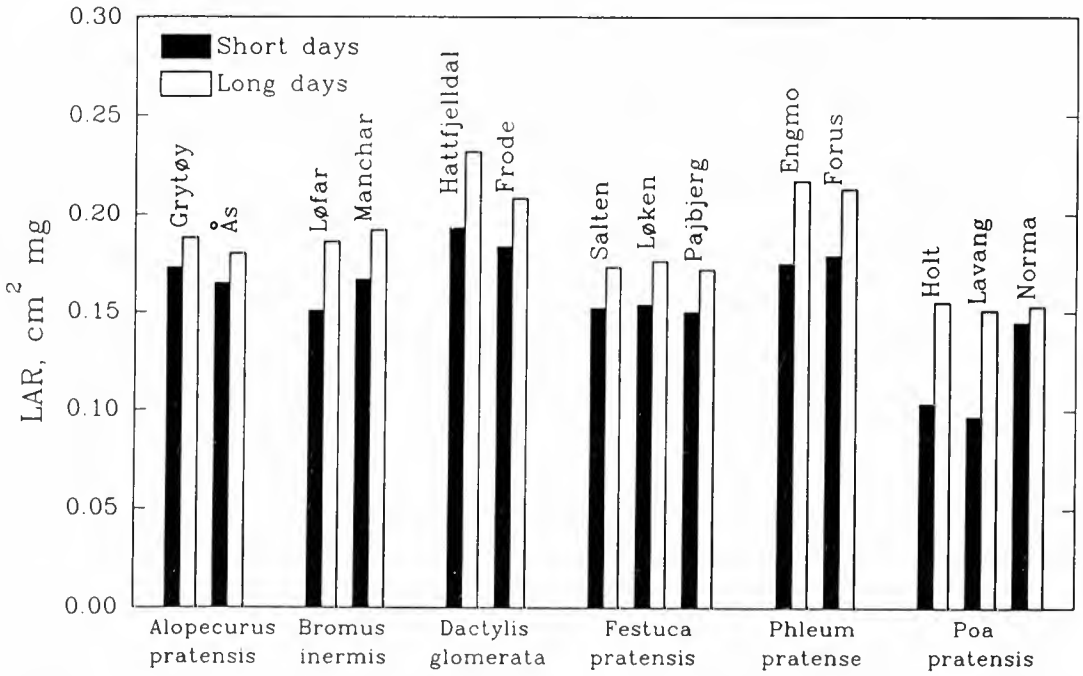

Figure 4. Daylength effects on LAR in northern (left) and southern (right) cultivars of six grass species. The values are averaged over all temperature levels and experiments

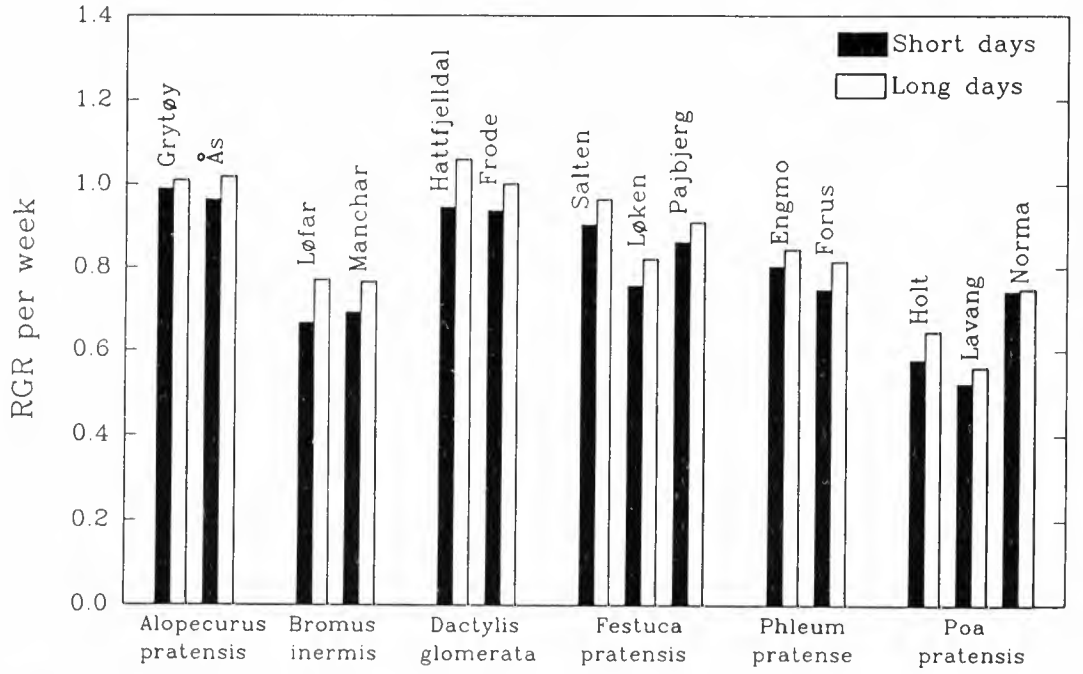

Figure 5. Daylength effects on RGR in northern (left) and southern (right) cultivars of six grass species. The values are averaged over all temperature levels and experiments

(Fig. 4). Also in the northern *D. glomerata* cv. Hattfjelldal, LAR was increased more by LD than in Frode. Otherwise, there was no significant difference in NAR and LAR between cultivars within species as to effect of daylength. Long days increased RGR more in the northern *P. pratensis* cvs Holt and Lavang than in Norma, and in one experiment RGR was more stimulated by LD in *B. inermis* cv. Løfar than in Manchar (Fig. 5). No further significant differences in RGR, NAR and LAR between cultivars of the same species was established.

Specific leaf area (SLA)

Specific leaf area was larger in LD- than in SD-grown plants, and this difference increased with decreasing temperature (Fig. 6). On an average of all experiments, SLA was least at 9°C and maximal at 18-21°C (Fig. 6). Long days increased SLA most in *B. inermis* and the northern *P. pratensis* cvs Holt and Lavang. (Fig. 7).

Distribution of DM between leaves, stems and roots

The effect of daylength on leaf weight ratio (LWR) varied with temperature. At low temperatures LWR was higher in LD than in SD, while at higher temperatures LWR was lower in LD (Fig. 8). The proportion of DM allocated to the leaves increased and the proportion allocated to the roots decreased with increasing temperature, while the proportion allocated to leaf sheaths and stems was not influenced by temperature (Fig. 8). Daylength had a much greater effect on the distribution of DM between leaf sheaths and stems and roots than on LWR. In LD more DM was allocated to leaf sheaths and stems than in SD, while more DM was allocated to the roots in SD (Fig. 8). The greatest effect was found in *B. inermis* in which LD more than doubled the proportion of DM in the leaf sheaths and stems, while reducing the proportion of DM in the roots by nearly 50% (Fig. 9).

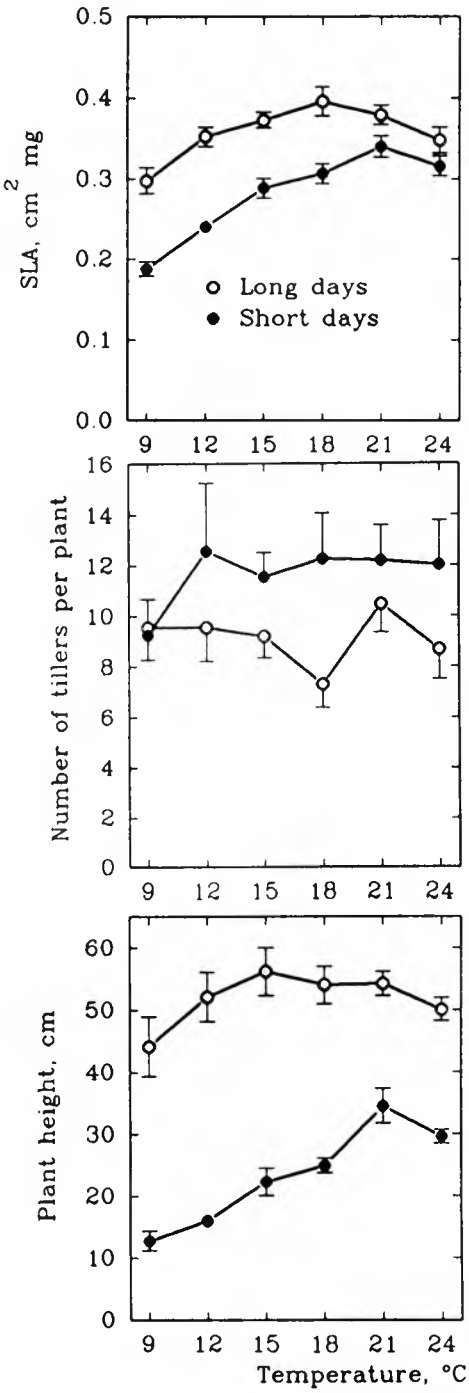

Figure 6. Average effects of daylength and temperature on specific leaf area (SLA), number of tillers per plant and plant height for 14 grass cultivars. Each point with its ± SEM is a weighted mean of all cultivars (n = 11 - 14)

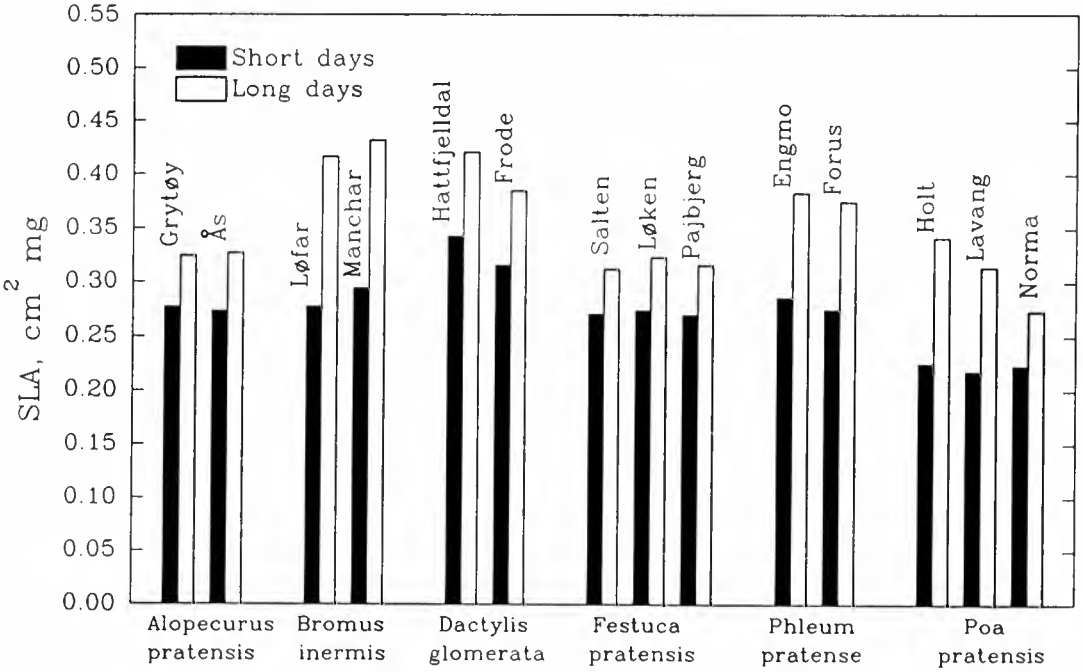

Figure 7. Daylength effects on SLA in northern (left) and southern (right) cultivars of six grass species. The values are averaged over all temperature levels and experiments

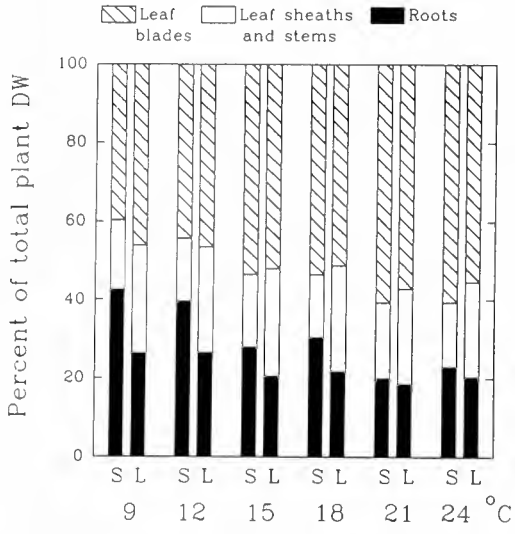

Figure 8. Effects of daylength and temperature on distribution of DM between leaf blades, leaf sheaths and stems, and roots. The values are averaged over species and cultivars within each daylength and temperature combination

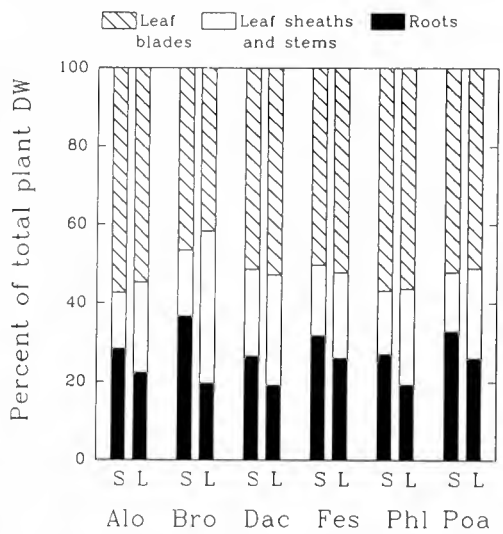

Figure 9. Effects of daylength on distribution of DM between leaf blades, leaf sheaths and stems and roots in *Alopecurus pratensis* (Alo), *Bromus inermis* (Bro), *Dactylis glomerata* (Dac), *Festuca pratensis* (Fes), *Phleum pratense* (Phl) and *Poa pratensis* (Poa). The values are averaged over temperature treatments

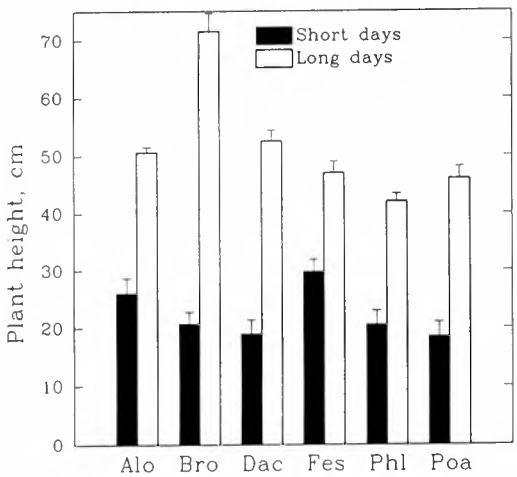

Figure 10. Effects of daylength on plant height in six grass species. Each column with its SEM is an average of temperature treatments and cultivars within species. Abbreviation as in Fig. 9

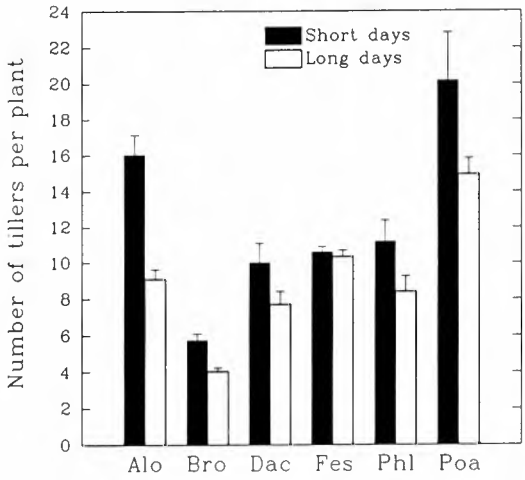

Figure 11. Effects of daylength on number of visible tillers per plant in six grass species. The values are averaged over all temperature treatments and cultivars. Abbreviations as in Fig. 9

Plant height

Plant height to the tip of the longest leaf was greatly stimulated by LD, and the effect increased with decreasing temperature (Fig. 6). Long day stimulation of height growth was greatest in *B. inermis*, and least in *F. pratensis* (Fig. 10). At 9°C *B. inermis* plants were 6-7 times taller in LD than in SD, while *F. pratensis* plants were only two times taller in LD than in SD (data not shown).

Tillering

Short days increased tillering at all temperatures except at 9°C (Fig. 6). In *F. pratensis* daylength had no significant effect on the number of tillers per plant as the mean of all temperatures. In the other species SD increased the average number of tillers per plant (Fig. 11).

Chlorophyll content

Differences between species

There were great differences in both chlorophyll level and a/b ratio between species (Tab. 4). However, these differences are not directly comparable and will not be discussed further since the species were tested sequentially with somewhat varying light conditions during the daylight period. Both chlorophyll level and a/b ratio have probably been affected by this variation in light conditions.

Differences between cultivars within species

There was no significant difference in chlorophyll level between the *B. inermis* cvs Løfar and Manchar. The *P. pratensis* cv. Holt contained more chlorophyll per unit dry weight than 'Norma'. In SD and at low temperatures 'Holt' contained more chlorophyll per unit leaf area, while at high temperatures and LD 'Norma' had the highest content. In SD 'Norma' had the higher chlorophyll a/b ratio, while in LD there was no significant difference. In *P. pratense* cv. Forus had the higher a/b ratio at low temperatures, while in 'Engmo' the ratio was higher at high temperatures ($P < 0.01$). In the *F. pratensis* cv. Pajbjerg the chlorophyll a/b ratio was higher than in 'Salten' (Tab. 4).

Effects of daylength and temperature

Plants cultivated in SD contained about

Table 4. Chlorophyll a/b ratio and chlorophyll content per unit leaf area, unit leaf dry weight and unit leaf fresh weight in six grass cultivars grown at three temparature levels and two daylengths. Values are the means of six plants ± SEM

Species	Cultivar	12°C		18°C		24°C	
		8 h	24 h	8 h	24 h	8 h	24 h
				Chlorophyll a/b ratio			
Bromus	'Løfar'	5.90±0.40	4.81±0.29	3.93±0.10	3.86±0.12	3.93±0.08	3.87±0.18
inermis	'Manchar'	6.32±0.20	5.05±0.56	4.01±0.22	3.80±0.11	4.22±0.20	3.68±0.07
Festuca	'Salten'	2.73±0.06	2.39±0.04	2.23±0.03	2.03±0.04	1.91±0.05	1.75±0.02
pratensis	'Pajbjerg'	3.02±0.05	2.66±0.05	1.96±0.05	2.05±0.03	1.90±0.02	1.95±0.05
Phleum	'Engmo'	2.35±0.06	2.40±0.07	3.23±0.10	3.09±0.05	2.29±0.05	2.42±0.04
pratense	'Forus'	2.56±0.07	2.42±0.06	2.90±0.08	3.12±0.05	2.28±0.05	2.26±0.02
Poa	'Holt'	2.63±0.06	2.68±0.06	2.93±0.10	2.85±0.04	2.36±0.03	2.31±0.03
pratensis	'Norma'	2.62±0.06	2.69±0.04	3.12±0.12	2.86±0.03	2.75±0.03	2.24±0.03
	Mean	3.52	3.14	3.04	2.96	2.70	2.56
				Chlorophyll mg dm^{-2}			
Bromus	'Løfar'	5.95±0.36	3.66±0.08	4.54±0.24	2.87±0.15	3.60±0.17	2.34±0.13
inermis	'Manchar'	5.14±0.24	3.48±0.16	4.20±0.31	2.70±0.21	3.38±0.31	2.55±0.12
Festuca	'Salten'	4.98±0.23	3.22±0.11	4.67±0.40	3.33±0.20	4.47±0.16	3.47±0.20
pratensis	'Pajbjerg'	4.37±0.11	3.75±0.20	5.31±0.52	3.36±0.17	5.12±1.16	3.64±0.16
Phleum	'Engmo'	3.51±0.12	1.91±0.14	3.95±0.22	2.30±0.22	3.80±0.33	2.73±0.17
pratense	'Forus'	3.77±0.28	1.68±0.12	4.04±0.31	2.32±0.22	4.53±0.37	3.12±0.15
Poa	'Holt'	6.58±0.18	3.54±0.07	5.90±0.35	4.05±0.19	6.15±0.48	5.07±0.14
pratensis	'Norma'	5.19±0.39	3.62±0.20	5.75±0.44	4.44±0.17	6.46±0.44	6.27±0.19
	Mean	4.93	3.11	4.80	3.17	4.75	3.65
				Chlorophyll mg/g fresh weight			
Bromus	'Løfar'	3.08±0.10	2.43±0.08	2.54±0.18	2.42±0.14	2.25±0.09	1.89±0.11
inermis	'Manchar'	2.87±0.10	2.37±0.16	3.16±0.29	2.24±0.15	2.12±0.14	2.26±0.07
Festuca	'Salten'	2.14±0.10	1.48±0.07	2.12±0.12	1.55±0.08	1.99±0.08	1.75±0.09
pratensis	'Pajbjerg'	1.82±0.09	1.72±0.08	2.29±0.16	1.54±0.08	2.34±0.03	1.77±0.06
Phleum	'Engmo'	1.88±0.11	1.22±0.08	2.39±0.14	1.49±0.10	2.26±0.13	1.89±0.08
pratense	'Forus'	1.99±0.10	1.16±0.07	2.46±0.13	1.81±0.17	2.80±0.20	2.58±0.15
Poa	'Holt'	3.39±0.16	2.08±0.10	3.23±0.06	2.36±0.11	3.83±0.23	3.03±0.11
pratensis	'Norma'	3.28±0.22	2.27±0.13	2.73±0.14	3.19±0.25	3.82±0.14	3.95±0.10
	Mean	2.56	1.84	2.62	2.08	2.68	2.39
				Chlorophyll mg/g dry weight			
Bromus	'Løfar'	13.98±0.85	14.27±0.31	15.16±0.80	12.57±0.66	12.16±0.57	9.80±0.54
inermis	'Manchar'	13.72±0.64	13.60±0.63	14.78±1.01	12.63±0.98	13.07±1.04	10.50±0.49
Festuca	'Salten'	11.95±0.55	9.60±0.33	12.23±1.05	9.72±0.58	12.07±0.43	11.27±0.65
pratensis	'Pajbjerg'	10.31±0.26	11.62±0.62	13.38±1.38	9.68±0.49	13.51±0.42	11.29±0.50
Phleum	'Engmo'	7.55±0.26	6.55±0.48	13.23±0.74	10.44±1.00	13.49±1.17	12.22±0.76
pratense	'Forus'	8.22±0.61	5.78±0.41	13.25±1.02	10.72±1.02	14.35±1.17	12.01±0.58
Poa	'Holt'	12.17±0.33	10.69±0.21	14.75±0.88	15.55±0.73	16.24±1.27	18.65±0.52
pratensis	'Norma'	10.90±0.82	9.73±0.54	13.92±1.06	13.48±0.52	14.08±0.96	15.55±0.47
	Mean	11.10	10.23	13.84	11.85	13.62	12.66

50% more chlorophyll per unit leaf area than LD-cultivated plants (Tab. 4). The effect of daylength on chlorophyll per unit leaf area increased with decreasing temperatures ($P \leq 0.0005$ for daylength × temperature interaction). Temperature had no significant main effect on the amount of chlorophyll per unit leaf area.

The leaves also had more chlorophyll per unit fresh weight in SD than in LD and again this difference decreased with increasing temperature (Tab. 4). On an average of all grass species the leaves had 39% more chlorophyll per unit fresh weight in SD at 12°C, while the difference was only 12% at 24°C. Since the DM percentage was highest in SD, the chlorophyll level per unit dry weight (DW) was only slightly higher in SD-grown plants (Tab. 4). Temperature had little effect on the amount of chlorophyll per unit leaf DW, in *B. inermis*, while the chlorophyll level increased with the temperature for all the other species ($P \leq 0.0005$).

The mean chlorophyll a/b ratio of all species was higher in SD than in LD ($P \leq 0.0005$, Tab. 4). The effect was greatest in *B. inermis*, *F. pratensis* and *P. pratensis* responded less while *P. pratense* showed the least photoperiodic response in chlorophyll a/b ratio. In *B. inermis* and *F. pratensis* the a/b ratio was much higher at low than at high temperatures, while temperature seemed to have little effect on the a/b ratio in *P. pratense* and *P. pratensis* (Tab. 4).

Time course effects

The chlorophyll level per unit leaf area in *P. pratense* was rather constant during the growing period in LD, while in SD it increased steadily at the lower temperatures until the third harvest after 24 days (Fig. 12). The chlorophyll a/b ratio increased from the first to the second harvest, and decreased from the third to the fourth harvest. This time course was not significantly different between SD and LD. The a/b ratio increased with decreasing temperature in this experiment also ($P \leq 0.0005$). This difference in a/b ratio was found after only four days of treatment (first harvest), and there was a further increase with extended treatment (Fig. 12).

DISCUSSION

Differences in LD stimulation of DM production between and within species

Long-day stimulation of DM production was observed in all temperate grasses in this study. The stimulation was greatest at low temperatures in all species and cultivars. At 9°C mean dry weights over all experiments were more than twice as high in LD as in SD, while at temperatures of 18°C or higher DM production was only slightly enhanced by LD. In a few cases (Tab. 2) dry weights were slightly lower in LD than in SD at high temperatures. Hay & Heide (1984) also found a slight increase in dry weights in SD at high temperatures in *P. pratense* and *B. inermis*.

Long day stimulation of DM production varied among species. Stimulation of RGR in LD compared with SD (Fig. 3) was greater in *B. inermis*, *D. glomerata* and *P. pratensis* cvs Holt and Lavang than in *P. pratense*, *F. pratensis*, *A. pratensis* and *P. pratensis* cv. Norma. In contrast, Hay & Heide (1984) found a greater stimulation of DM production in *P. pratensis* cv. Holt than in *P. pratense* cv. Engmo, while DM production in *B. inermis* cv. Løfar was only slightly stimulated by LD.

Within species, the north-Norwegian *D. glomerata* cv. Hattfjelldal responded more strongly to daylength than the Danish cv. Frode. This agrees with stronger daylength response of north-Norwegian than of south-Norwegian populations of *D. glomerata* reported by Eagles & Østgård (1971). *P. pratensis* cvs Holt and Lavang was strongly stimulated in DM production in LD, while the more southern cv. Norma responded much less. Similar latitude-of-origin effects in ecoty-

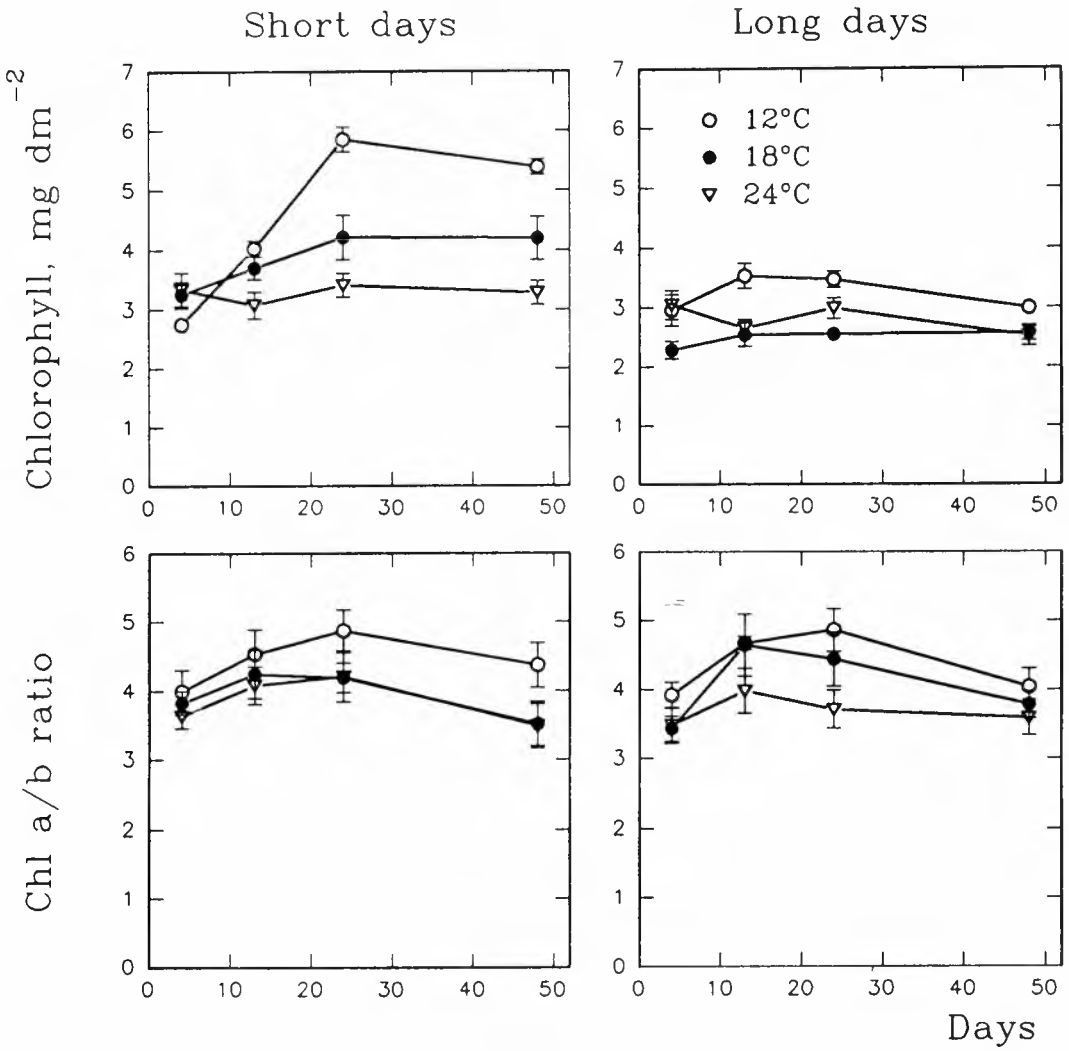

Figure 12. Chlorophyll a/b ratios and chlorophyll levels per unit leaf area of *Phleum pratense* cv. Engmo plants after 4, 13, 24 and 48 days of cultivation in 8 h (SD) or 24 h (LD) photoperiod at 12, 18 and 24°C. Means of 6 measurements ± SEM are given

pes of *P. pratensis* were demonstrated by Håbjørg (1976) in a larger sample of ecotypes.

Similar responses to daylength in northern and southern cultivars of *A. pratensis*, *B. inermis*, *F. pratensis* and *P. pratense* exposed to 8 or 24 h photoperiods in this study do not imply that they will respond identically to natural daylength. Northern cultivars of *D. glomerata* (Hay 1989) and *P. pratense* (Foss 1968, Hay 1989) gave the higher yields in midsummer, while the more southern cultivars yield higher in spring and autumn. These differences in response to natural daylengths and to the extreme photoperiods of 8 and 24 h may be explained by an increasing critical photoperiod for growth in ecotypes with increasing latitude-of-origin. Northern cultivars of *P.*

pratense have longer critical photoperiods for stem elongation and flowering than southern cultivars (Heide 1982). Therefore, growth of northern cultivars is depressed in early spring and autumn. However, depression of growth in autumn may enhance carbohydrate accumulation. Thus northern cultivars have more carbohydrates for rapid leaf area growth when the day reaches sufficient length the next year. A higher capacity for etiolated growth during autumn in northern compared with southern cultivars of *P. pratense* shows that the former ones have more reserves for the start of growth the next year (Klebesadel & Helm 1986, Foss, personal communication 1983). Therefore, northern cultivars may yield higher than southern ones during midsummer under field conditions although they do not perform better in 24 h photoperiods when propagated from seed and grown under partly controlled conditions.

Basis for LD stimulation of DM-production

The experiments in this study confirm earlier results (Hay & Heide 1983, Heide et al. 1985a,b) that temperate grasses increase DM production in LD via increased LAR which more than compensates for reduced NAR in LD. Except at the highest temperatures NAR was higher in SD than in LD. Higher LAR in LD than in SD was mainly a result of the increased leaf area per unit leaf dry weight (SLA) in LD, since the proportion of DM allocated to the leaves (LWR) was almost unaffected by daylength (Fig. 8). When SD-propagated plants are placed in LD, a rapid increase in SLA occurs. In addition, more assimilates are allocated to growth. In small *P. pratensis* plants the fructan level in leaf sheaths and stems was 175% higher in SD than in LD (Solhaug 1991), and fructans are the main storage carbohydrates in temperate grasses. Allocation of more assimilates to growth together with increasing SLA lead to increased leaf area in LD. Since

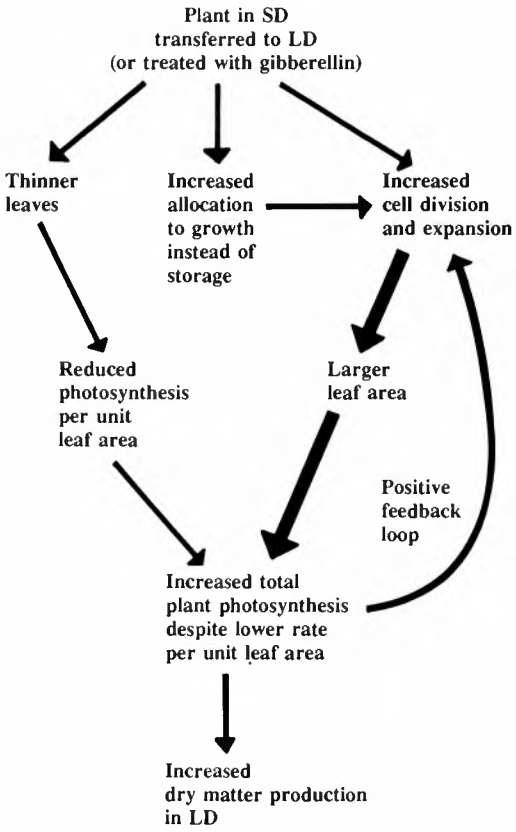

Figure 13. Diagram showing stimulation of DM production in LD

the NAR is only slightly reduced, photosynthetic capacity per plant will increase. This creates a positive feedback system, since more assimilates will be available to leaf growth due to higher photosynthesis per plant. The mechanism of LD stimulation of DM production is schematically illustrated in Fig. 13.

Flowering, and associated stronger sinks in elongating stems and flower heads may be a reason for higher DM production in LD. *P. pratense* is a regular long-day plant that requires only LD for flower initiation (Heide 1982). The other grasses in these experiments require a dual floral induction; primary induction with low temperature or short photoperiods followed by secondary induction

with long photoperiods (Heide 1980, 1984, 1986, 1987, 1988). Therefore, in the present experiments, all species except *P. pratense*, remained vegetative in both LD and SD. The greatest stimulation of DM production was found in *B. inermis*, *D. glomerata* and the northern *P. pratensis* cvs Holt and Lavang, while *P. pratense* responded less. This indicates that DM production in LD is not directly in connection with flower initiation and development. An increase in DM production can be mediated by gibberellins (Hay & Heide 1983, Heide et al. 1985a). Gibberellins may also initiate flowering, but different types of gibberellins seem to be involved in stem elongation and flower initiation in *Lolium temulentum* (Evans et al. 1990). This may also be true for stimulation of DM production and flower initiation in temperate grasses, since an increase in DM production and flower initiation is probably not directly linked.

Light quality influences plant morphology. High far-red/red ratios often promote stem elongation (Morgan & Smith 1981), and red-biased light spectra stimulate DM production compared with blue-biased spectra at equal PAR (Warrington & Mitchell 1976). The effect of photoperiod on DM production in the present study may therefore have been confounded by the spectral quality of the extension light, since daylength extension was given by incandescent lamps with high far-red/red ratios. However, two-hour night break in the middle of the dark period strongly stimulated DM production in *P. pratensis*, while a two-hour extension of the daylight period with the same light source had only a slight effect (Heide et al. 1985a). Therefore, stimulation of DM production in LD extended with incandescent light is mainly a photoperiodic effect, and not an effect of extension light quality.

Effects of latitude of origin on chlorophyll level and a/b ratio

No general differences in chlorophyll level or chlorophyll a/b ratio were found between northern and southern cultivars within species. Northern cultivars have longer critical photoperiods for growth than more southern ones (e.g. Heide 1982), Thus higher chlorophyll levels in northern grass cultivars as observed by Foss (1968), may be a result of such differences in critical daylength manifested under natural conditions in late summer.

Effects of daylength and temperature on chlorophyll a/b ratios

Plants grown in SD tended to have higher chlorophyll a/b ratios than LD-grown plants, although the difference was small. Within plant canopies, sun exposed leaves have been found to have highest chlorophyll a/b ratio (Anderson 1986). Adaptation also may occur across bifacial leaves. In spinach leaves thylakoids adjacent to the upper surface had a chlorophyll a/b ratio of 3.5, while in those adjacent to the lower surface the ratio was 2.6 (Terashima & Inoue 1985). The LD-grown grasses have a relatively great leaf area and therefore more mutual shading (Heide et al. 1985a,b). Reduced chlorophyll a/b ratios in LD may therefore be explained as a shade adaptation. Light quality may be another explanation for lower chlorophyll a/b ratios in LD. The LD plants received 16 h low intensity incandescent light with low red/far-red ratio during the night. Chlorophyll a/b ratios have been reported to be lower in far-red than in red light (see Anderson 1986). Because of canopy filtering of red light by chlorophyll (Morgan & Smith 1981), this effect would be further enhanced by increased leaf shading in LD.

Chlorophyll a/b ratios in most experiments were higher at low than at high temperatures. The effect was large in *B. inermis* and *F. pratensis*, less in *P. pratense*, while the a/b ratio of *P. pratensis* was unaffected by temperature. Enhanced chlorophyll a/b ratios at low temperatures have also been found in spinach, a species which can be acclimated to avoid photoinhibition when grown at low temperature (Schöner & Krause 1990).

High light intensity increases chlorophyll a/b ratio, and plants adapted to high light intensity are more tolerant to photoinhibition also (Björkman & Holmgren 1963). Therefore there may be some connection between high chlorophyll a/b ratios and avoidance of photoinhibition for plants grown at low temperatures.

Chlorophyll content

A general deduction from this and previous experiments is that grasses accumulate more chlorophyll per unit leaf area or fresh weight in SD. However, leaves are very efficient light absorbers, and photosynthesis will probably not be improved by higher chlorophyll levels. Using the equation 'Absorptance = $0.509 + 1.7x - 2.78x^2 + 1.99x^3 - 0.52x^4$', where x = chlorophyll level (mmol Chl m^{-2}) and $0.2 < x < 1.0$ (Evans 1990), absorptance was only about 4% higher in SD leaves than in LD leaves of *P. pratensis*, although the difference in chlorophyll content per unit leaf area was 46%. Thus an increase in plant leaf area is much more important than an increase in the chlorophyll content per unit leaf area for increasing light absorptance. Increased chlorophyll level may actually reduce the photosynthetic rate. When the chlorophyll level is high, almost all light will be absorbed near the leaf surface. Therefore, mesophyll cells lying deep in the leaf will not be light saturated even in strong light and the photosynthesis efficiency may decrease (Terashima & Saeki 1985). This effect depends on irradiance. The light response curve of photosynthesis is affected by the chlorophyll level. At low photon flux density photosynthesis is higher at high chlorophyll level, while at high photon flux density photosynthesis is higher at lower chlorophyll level (Leverenz 1987).

However, electron transport capacity and Rubisco activity are probably more important for photosynthesis than a high chlorophyll level. In LD leaves of temperate grasses are relatively thin with a low DM content per unit leaf area (Hay & Heide 1983, Heide et al. 1985b). They probably also contain less Rubisco protein and have less electron transport capacity than in SD. This reduction can explain reduced photosynthetic rate per unit *P. pratensis* leaf area in LD (Heide et al 1985a). Therefore, the LD reduction of chlorophyll content per unit leaf area in plants cultivated in LD *per se* seems not to be the mechanism causing reduced photosynthetic rate of high-latitude grasses in LD.

CONCLUSIONS

Long days under constant daily photosynthetic active radiation stimulated DM production in all cultivars of the six temperate grasses which were studied. Long days stimulated DM production more in the northern *D. glomerata* cv. Hattfjelldal than in the southern cv. Frode, and it was greater in the northern *P. pratensis* cvs Holt and Lavang than in the southern cv. Norma. Otherwise, there was no significant difference between cultivars within species.

Chlorophyll a/b ratios increased with decreasing temperature and were slightly higher in SD than in LD. Chlorophyll contents per unit leaf area and per unit fresh weight were higher in SD than in LD, while the contents per unit dry weight were little affected by daylength. There was no general pattern as to chlorophyll level and a/b ratio of northern and southern cultivars within species.

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Nitrogen and potassium nutrition of 'Aroma' apples. Effects of different N and K applications on yield, fruit size and fruit quality

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In a nine year study of the response of 'Aroma' apple trees on M26 to different nitrogen and potassium applications it was found that under a soil management system of herbicide strips and grassed alleys soil nitrogen was mineralized in quantities adequate to meet the demand for nitrogen of high-yielding apple trees. Additional nitrogen had no effect on yield, fruit size and the content of fruit soluble solids, but ground colour and surface red colour were affected negatively. There was no increase in yield or fruit size as a result of different potassium applications. The only quality factor affected by differential K fertilization was fruit acidity, where additional K increased the acidity of 'Aroma' apples. Soil non-exchangeable potassium contributed significantly toward meeting the demand for potassium by apple trees in full production.

Key words: Apple, fruit quality, leaf nitrogen, leaf potassium, non-exchangeable potassium, yield.

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Fruit trees have a much smaller need for mineral nutrients than many vegetable and agricultural crops (Greenham 1976). The response to added nutrients may be modified by factors like soil management, water supply and inherent availability in the soil.

The prevailing soil management method employed in Norwegian apple orchards is frequently cut grass in the alleyways and 1-m-wide strips of herbicide-treated, weed-free soil along the tree rows. Root distribution, availability and uptake of major nutrients, particularly nitrogen, are influenced by the herbicide strip treatment compared to overall grass (Atkinson & White 1980). A reassessment of the need for an annual supply of nitrogen and potassium to apple trees of high density planting systems is hence necessary.

An abundant supply of nitrogen affects apple quality negatively in several ways; dark green ground colour, reduced content of soluble solids, reduced storage potential and shelf life (Smock & Boynton 1944, Oland 1955, Ljones & Landfald 1966, Kvåle 1971, Williams & Billingsley 1974). These problems are clearly demonstrated in apple cultivars without a predominantly red surface colour like 'Aroma', an important commercial apple cultivar adapted to Scandinavian growing conditions.

The objective of the experiment was to establish different levels of nitrogen and potassium in the trees in order to get an estimate of the amount of N and K fertilizer needed to produce high yields of high quality apples. A preliminary report on the experiment has already been published (Ystaas 1990).

MATERIALS AND METHODS

A long-term field trial (1980-88) was conducted at Ullensvang Research Station, latitude 60°N, where calcium nitrate was applied at rates of 0 - 60 - 120 kg N ha^{-1} and muriate of potash at rates of 0 - 120 - 240 kg K ha^{-1} to young 'Aroma' apple trees on M26. One-tree plots with guard trees in a completely randomized factorial design with three replications were used.

The trees were spaced at 5 x 2.7 m and were trained as free spindle. The 5-year-old trees had started cropping when the experiment began. The soil was a loamy sand high in organic matter (10,5%). Before the start of the experiment chemical analysis of soil samples from the 0 - 20 cm layer indicated that the soil fertility was satisfactory; on average for all plots the contents of exchangeable K, Mg and Ca were 25, 17 and 214 mg per 100 g soil, respectively. Soil reaction averaged pH 6.0. Soil management combined frequently mown grass in the alleyways with 1-m- wide herbicide strips along the tree rows. Annual data on trunk girth, yield and fruit weight were recorded. Random samples of 20 apples from each tree were kept in cold storage at 4°C for 6-7 weeks until fruit quality examinations took place. Sensoric analysis by a panel of five trained judges was carried out on ground colour (scores 1-9), surface red colour (scores 1-9) and flavour (scores 1-9). The content of soluble solids was measured using an Atago digital refractometer. Titratable acidity was determined by titrating diluted juice samples to pH 8.1 with 0.01 N NaOH.

Leaf samples from mid-shoot leaves of 20 extension shoots per tree were collected during the last week of August for determination of N, P, K, Mg and Ca. Soil samples from all plots were taken from the 0 - 20 cm layer every year in October. Exchangeable cations were extracted with 1N ammoniumacetate (pH 7). Non-exchangeable K was determined according to Reitemeier et al. (1948). For determination of K, Mg, Ca and P in the leaves, the plant material was digested in a 1:2 mixture of perchloric and nitric acids (Oland & Opland 1956). P and N in plant material were determined by generally accepted methods. The determination of cations was carried out by atomic absorption spectrophotometry.

RESULTS

As no significant interaction between nitrogen and potassium was found regarding important parameters like tree size, yield, fruit weight and fruit quality, the effects of different applications of nitrogen and potassium fertilizers will be dealt with separately.

Effects of nitrogen

Tree size, as measured by trunk girth of 13-year-old trees at the end of the experiment, was not affected by differential nitrogen application (Table 1). Leaf nitrogen increased significantly when calcium nitrate was applied. However, no increase in leaf N was found when the annual nitrogen application was increased from 60 to 120 kg N ha^{-1}. Yield and fruit weight were not significantly affected by differential nitrogen applications. The relationship between yield and leaf nitrogen is shown in Fig. 1. Irrespective of differential nitrogen applications the nitrogen content of the leaves fluctuates with crop size; high yields correspond to high leaf nitrogen content and low yields to lower nitrogen levels in the leaves.

The content of soluble solids in 'Aroma' apples was not affected by the

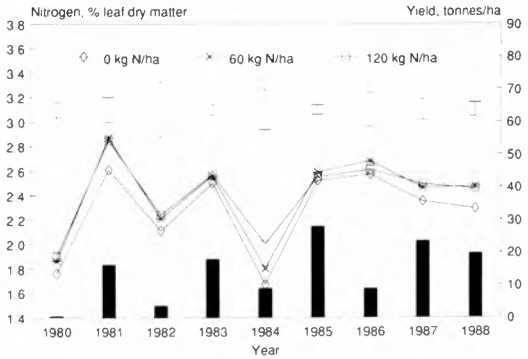

Fig. 1. Relationship between crop load and leaf nitrogen of 'Aroma' apples during nine years. Vertical bars represent LSD (P = 0.05)

different levels of nitrogen established (Table 2). The ground colour, however, was significantly influenced when the nitrogen supply was increased. The ground colour scores indicate that apples from trees that did not receive any nitrogen have a brighter yellow colour than the more green colour of apples from trees where nitrogen is applied. The application of nitrogen significantly reduced surface red colour of 'Aroma' apples (Table 2), while flavour was not significantly affected.

Effects of potassium

Differential potassium applications had no effect on the growth of the trees as measured by trunk girth at the end of the experiment (Table 3).

The different potassium applications established three significantly different levels of potassium in the trees (Table 3). The trees that did not receive any potassium for nine years had normal leaf size with no sign of deficiency symptoms. No significant effect of potassium applica-

Table 1. The effects of different nitrogen applications on trunk girth at the end of the experiment, leaf N, yield and fruit weight of 'Aroma' apples. Average of nine years

Nitrogen applications, kg N ha^{-1}	Trunk girth, cm	Leaf N, per cent	Yield, kg/tree	Fruit weight, g
0	21.7	2.26	17.8	153
60	22.8	2.39	20.1	164
120	22.8	2.41	19.3	164
LSD (P = 0.05)	NS	0.12	NS	NS

Table 2. The effects of different nitrogen applications on fruit quality components of 'Aroma' apples. Average of nine years

Nitrogen applications, kg N ha^{-1}	Soluble solids per cent	Ground colour scores,[1]	Surface red colour scores,[2]	Flavour scores,[3]
0	13.0	6.2	4.2	7.2
60	13.1	5.3	3.5	6.8
120	13.1	4.8	3.2	6.9
LSD (P = 0.05)	NS	0.5	0.4	NS

1) Ground colour scores 1-9, where 1 = dark green and 9 = bright yellow.
2) Surface red colour scores 1-9, where 1 = without any red colour and 9 = whole surface red.
3) Flavour scores 1-9, where 1 = very poor, 3 = poor, 5 = medium, acceptable, 7 = good and 9 = excellent.

tions on yield and fruit weight could be found. Crop size, however, exerted a negative effect on leaf potassium content irrespective of the amounts of potassium fertilizer applied (Fig. 2). Important components of fruit quality like soluble solids, flavour and surface red colour were not affected by differential potassium applications (Table 4). A significant increase in titratable acid in 'Aroma' apples was, however, found by application of 120 kg K ha^{-1}. No further increase in titratable acid was found when larger amounts of potassium were applied.

Exchangeable potassium in the top 20 cm soil layer was significantly affected by the differential potassium applications (Fig. 3). Fluctuation in exchangeable K is mainly due to climatic conditions with high precipitation during mild winters and loss of potassium through leaching. At the end of the experiment non-exchangeable K was found to be significantly lower in the plots where no potassium was applied compared to the plots where the higher amount of potassium fertilizer was given (Table 5).

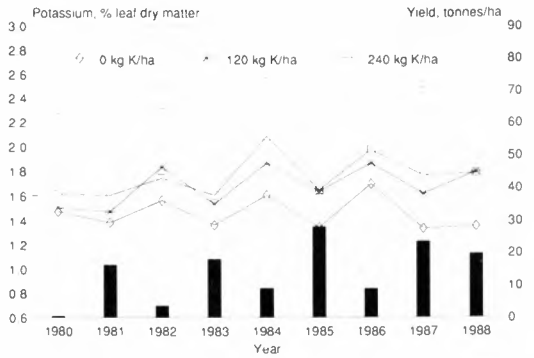

Fig. 2. Relationship between crop load and leaf potassium of 'Aroma' apples during nine years. Vertical bars represent LSD (P = 0.05)

Table 3. The effects of different potassium applications on trunk girth at the end of the experiment, leaf K, yield and fruit weight of 'Aroma' apples. Average of nine years

Potassium applications, kg K ha^{-1}	Trunk girth, cm	Leaf K, per cent	Yield, kg/tree	Fruit weight, g
0	22.2	1.45	19.3	161
120	21.2	1.67	17.2	159
240	23.8	1.75	20.7	162
LSD (P = 0.05)	NS	0.08	NS	NS

Table 4. The effects of different potassium applications on fruit quality components of 'Aroma' apples. Average of nine years

Potassium applications, kg K ha^{-1}	Soluble solids, per cent	Titratable acid, per cent	Surface red colour scores,[1]	Flavour scores,[2]
0	13.1	0.61	3.6	7.0
120	12.9	0.64	3.7	7.0
240	12.9	0.64	3.6	6.9
LSD (P = 0.05)	NS	0.01	NS	NS

1) Surface red colour scores 1-9, where 1 = without any red colour and 9 = whole surface red.
2) Flavour scores 1-9, where 1 = very poor, 3 = poor, 5 = medium, acceptable, 7 = good and 9 = excellent.

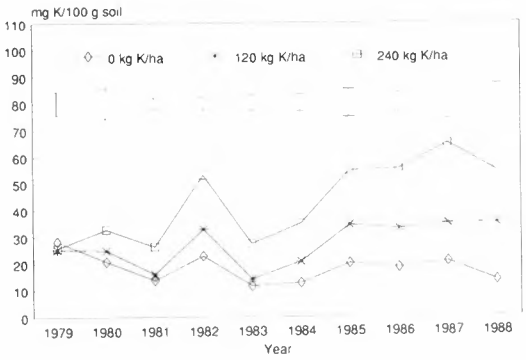

Fig. 3. Effect of differential potassium fertilization on exchangeable potassium in the soil 0-20 cm layer. Vertical bars represent LSD (P = 0.05)

DISCUSSION

After nine years of fertilizer application the nitrogen content of apple leaves was increased by only 0.13-0.15 % compared with an unfertilized control. Although significantly different, the leaf nitrogen levels of fertilized and control trees fall within the optimum range for apple trees (Vang-Petersen et al. 1973, Vang-Petersen & Nikolajsen 1986). This finding indicates that the mineralization of nitrogen from soil organic matter plays an important part in the nitrogen supply of apple trees under the soil management method of herbicide strips and grassed alleyways. The amount of nitrogen released by clean cultivation is found to be 50 - 60 kg N ha^{-1} when soils and climatic conditions are similar to those prevailing in Scandinavia (Dalbro & Nielsen 1958, Aasen 1986). The release of 50-70 kg N ha^{-1} through mineralization of soil organic N under clean cultivation in a long-term experiment with apple trees is reported from England (White & Greenham 1967).

Studies of the root distribution of apple trees grown with herbicide strips and grassed alleys have established that apple trees produce most of their roots and probably obtain most of their mineral nutrients from the soil beneath the herbicide strips (Atkinson & White 1976, Atkinson et al. 1977). This is consistent with the results obtained in this experiment, where young apple trees which had not received any N fertilizer during the 9-year study period sustained a leaf N level of 2.26 % combined with satisfactory yields.

The negative effect of excessive nitrogen supply on important components of apple quality is well established (Kvåle 1971, Williams & Billingsley 1974, Raese & Williams 1974). The present study indicates that when leaf N of 'Aroma' apples lies within 2.26-2.41 % the content of soluble solids is not negatively affected. The ground colour and surface red colour, however, are more easily affected in a negative way by increased nitrogen content of the leaves (Table 2). In order to obtain a satisfactory quality of 'Aroma' apples leaf N should not exceed 2.40 %.

Apple trees respond quickly to differential potassium application (Ljones 1954, Ystaas 1962). Although three sig-

Table 5. The effects of different potassium applications on non-exchangeable K in the 0–20 cm soil layer

Potassium applications, kg K ha^{-1}	K, mg per 100 g soil		
	Year 1	Year 6	Year 9
0	139	134	109
120	139	113	124
240	130	136	145
LSD (P = 0.05)	NS	NS	28.6

nificantly different leaf K levels were established in this experiment, no effect on yield and fruit weight was obtained when the K supply was increased from 0 to 240 kg K ha^{-1}. The results can be explained by the fact that the control trees sustained a leaf K level of 1.45 %, which is within the optimum range (Vang-Petersen et al. 1973, Ystaas 1981). A significant increase in fruit size as a response to potassium fertilization of apple trees has been reported when leaf K lies within the deficiency range of 0.5-0.8 % (Fisher & Kwong 1961, Ystaas 1962).

The soil was well supplied with exchangeable K when the experiment started. Although the control plots showed a significant reduction in exchangeable K over years (Fig. 3), the turnover of potassium from non-exchangeable to exchangeable form has apparently taken place at a rate sufficient to meet the demand for potassium by apple trees in full production. Disregarding the potassium supplying potential of the soil, the application of 120 kg K ha^{-1} has maintained the exchangeable K in the soil or raised it slightly, indicating that 120 kg K ha^{-1} meets the requirement of apple trees in full production. This finding is in agreement with the recommendation by Vang-Petersen (1989) to apply 100 kg K ha^{-1} annually to maintain optimal levels of potassium in Danish apple orchards.

Potassium fertilization increased the acidity of 'Aroma' apples significantly. This is in accordance with results reported by Eaves & Leefe (1955) and Fisher & Kwong (1961).

Crop size is an important factor affecting the chemical composition of the leaves. It is well established that leaves from cropping trees have a higher percentage of nitrogen and a lower percentage of potassium than leaves from trees which are defruited or carry a light crop (Weeks et al. 1958, Emmert 1959, Lamb et al. 1959, Hansen 1971). The explanation for the lower leaf K in the heavy crop years is the relatively large amount of potassium utilized by the fruit. An estimate of the removal of 33.7-40 kg K ha^{-1} through a normal crop of apples has been made (Greenham 1976). The higher leaf N content in a heavy crop year than in a light crop year is not well understood, but is most likely associated with mobilization and utilization of nitrogen and carbohydrate reserves within the tree. The influence of crop on the mineral composition of apple leaves emphasizes, however, the necessity of considering crop size when interpreting leaf analysis data.

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The possible prediction of the degree of infestation of honeybee colonies (*Apis mellifera*) by *Varroa jacobsoni* OUD. by means of its natural death-rate: a dynamic model approach

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Stig W. Omholt & Karl Crailsheim 1991: The possible prediction of the degree of infestation of honeybee colonies (*Apis mellifera*) by *Varroa jacobsoni* OUD. by means of its natural death-rate: a dynamic model approach. Norwegian Journal of Agricultural Sciences 5: 393-400. ISSN 0801-5341

The problem of predicting the degree of infestation by the Varroa mite (*Varroa jacobsoni*) in honeybee colonies in temperate regions in late autumn by means of death-rate data of the mites collected earlier in the season, is analysed by means of an age-structured population dynamic model of the Varroa mite. The state variables of the model are female mite eggs, female juveniles, sexually immature females and sexually mature females. It presumes the population dynamics of the mite to be an autonomous process during the brood rearing period of the infested colony at low to medium degrees of infestation. The model is able to explain why there apparently is no clear relationship between the observed death-rate of the mite in summer/autumn and the infestation in late autumn. Furthermore, it shows how natural death-rate data, when properly related to the brood rearing pattern of the infested colony, may provide a basis for the generation of predictive tables to be used by the beekeeper.

Key words: *Apis mellifera*, dynamic model, natural death rate, *Varroa jacobsoni*

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The development of a simple and reliable technique enabling beekeepers to predict the degree of infestation of their colonies by Varroa mites is recognized to be of importance (Koeniger & Fuchs 1989). Such a technique would have to involve measurements of a few simple parameters, and consultation of a table wherefrom a reliable prediction could be obtained. From a practical point of view a suitable parameter could be the death-rate of the mite expressed by the number of dead mites observed on the bottom board. However, Rademacher (1985) found no clear relationship between natural death-rate in summer and early autumn and infestation level in late autumn. In this paper, such a relationship is sought to be established by the development of a simple age-structured model of the population dynamics of the Varroa mite in colonies in temperate regions with a low to medium degree of infestation. It gives a reasonable explanation of Rademacher's fin-

dings, and it shows that prediction of the degree of Varroa mite infestation by means of natural death-rate data may indeed be possible, provided that these data are interpreted in relation to the brood rearing pattern of the infested colonies. If further testing of the model corroborates the validity of this approach, the model (or probably a more refined version of it) could be used to establish predictive tables for the practical beekeeper, wherefrom he can decide whether a colony needs specific treatment or not.

DESCRIPTION OF THE MODEL

The development of the female Varroa mite population from spring to autumn in non-swarming domesticated colonies in temperate zones at low to moderate infestation levels may be described by

$$V1(t) = \begin{cases} \alpha \cdot V4(t), & Bi < t \leq Bc \\ 0.0, & Bc < t \leq S \end{cases} \quad (1)$$

$$\frac{dV2(t)}{dt} = \iota(t) \cdot V1(t) - \iota(t-q0) \cdot V1(t-q0) \quad (2)$$

$$\frac{dV3(t)}{dt} = \iota(t-q0) \cdot V1(t-q0) - \iota(t-q1) \cdot V1(t-q1) \quad (3)$$

$$\frac{dV4(t)}{dt} = \iota(t-q1) \cdot V1(t-q1) - \iota(t-q2) \cdot V1(t-q2) - M(t) \quad (4)$$

where

$$M(t) = \begin{cases} 0.0 & t \leq t0 \\ V4(0)/(t1-t0) & t0 < t \leq t1 \\ 0.0 & t1 < t; \end{cases} \quad (5)$$

and
V1(t) is the daily egglaying rate of female mite eggs at time t; V2(t) is the number of female juvenile mites in the colony at time t. An egg is classed as a juvenile immediately after it is laid; V3(t) is the number of adult female mites in the colony having not yet started their first egglaying cycle at time t; V4(t) is the number of sexually mature female mites (with regard to age) in the colony at time t; α is the mean egglaying rate per sexually mature female per day; Bi and Bc are the dates of initiation and cessation of the worker brood rearing cycle of the infested colony; S is length of season in days; $\iota(t)$ is the proportion of eggs laid at time t that develops into female juveniles; q0 is the average developmental period from egg to adult for females; q1 is the average length of the sexually immature period for female mites, including their developmental period of q0 days; q2 is the average longevity of female mites, including their developmental period of q0 days; M(t) is the daily death-rate of

the overwintered or initial infesting female mite population; V4(0) is the number of the initial female mite population; t0 and t1 describe the period within which the initial mite population dies off.

Brood rearing of domesticated non-swarming colonies in temperate zones may to a large extent be considered as an autonomous process independent of ambient temperature and forage conditions (Omholt 1986, Wille 1985). As the model is designed in order to study the development of the Varroa mite population at low to medium degrees of infestation, it is reasonable to assume that there will be a surplus of open brood cells available for the mites at any time from onset to cessation of the brood rearing cycle of the infested colony. On the other hand, the effect of the mite infestation on the demographic patterns of the colony, through the impact on individual bees (De Jong et al. 1982, Kovac & Crailsheim 1988, Schneider & Drescher 1987), is likely to be very moderate under such conditions. Thus within the brood rearing period the development of the mite population may be looked upon as an autonomous process independent of the intracolonial dynamics of the infested honeybee colony.

Equation (1) says that the daily laying rate of female mite eggs is proportional to the number of adult female mites older than (q1-q0) days in the colony as long as there is brood available. Taking into account the mite's rather complex reproductive behaviour, this equation may appear oversimplistic. However, presuming the reproductive behaviour of each generation of female mites to be approximately constant, it ought to be valid as a first approximation. This is because the phenomenon of an increasing fraction of non-reproducing females within a given generation from the first to the nth egglaying cycle (Ritter & De Jong 1984, Schulz 1984b), and the time period between each cycle (Schulz 1984b), may be accounted for by proper adjustment of the parameter α.

Empirical data are still too scarce for a reliable independent estimate of α to be made, but, fortunately, an approximate estimate suffices in the present context: Based on the number of eggs a female mite is likely to lay per cycle (Ifantidis, 1984), the length per cycle (Schulz 1984b) and the expected number of reproduction cycles per female, α is estimated to be within the range 0.15-0.25.

Equation (2) says that the time rate of change of the juvenile mite population is given by those eggs that develop into juveniles, minus those eggs laid q0 days earlier that develop into adult mites. The mean developmental time q0 is presumed to be 7 days (Ifantidis 1983, Rehm & Ritter 1989). Concerning the function ι(t), the simplifying assumptions have been made that whether an egg develops into a juvenile or not is determined immediately after the egg is laid, and that no juveniles die during the developmental period. Of course, none of these assumptions are true, but very little is achieved in the present context by relaxing them. Accounting for the fact that the mites strongly prefer to lay eggs on drone brood rather than worker brood (Rosenkranz & Engels 1985, Schulz 1984b), it may be justifiable as a first approximation to express ι(t) as a function of whether the major fraction of egglaying mites stays on worker or drone brood. In this case it may be expressed by the function

$$\iota(t) = \begin{cases} \iota w, & Bi \le t \le Di \\ \iota d, & Di < t \le Dc \\ \iota w, & Dc < t \le Bc, \end{cases} \qquad (6)$$

where Di and Dc are respectively the time of initiation and cessation of drone brood production of the infested colony (Allen 1965, Omholt 1988b, Page 1981). A crude estimate of ιd and ιw may be obtained by dividing the respective reproductive rates on drone and worker brood per female mite per egglaying cycle by the number of eggs laid per cycle. Ifantidis (1983, 1984) reported the number of eggs laid per cycle to be about 6-7, and

Fuchs & Langenbach (1989) have recently estimated the mean reproductive rates on drone and worker brood to be 2.21 and 1.4 respectively. From this, ι_d and ι_w are estimated to be 0.368 and 0.233, which should not be too unrealistic.

Equation (3) is analogous to equation (2), describing the time rate of change of the population of adult females not yet having started their first egglaying cycle. The start of the first reproductive cycle is presumed to occur 13 days (q1-q0) after the mite has become an adult including the expected number of days the adult mite has to stay within the cell before eclosion of the bee (Schulz 1984b). There are, however, considerable variations of this parameter and applying a fixed value may be too simplistic.

Equation (4) expresses the time rate of change of the sexually mature female mite population. Unfortunately, data of female mite longevity seem to be non-existent. Here, a mean longevity of 73 days (q2-q0) will be presumed, which is an estimate above that of Schulz (1984a), but in agreement with the normally cited value of 2-3 months. If the variation in longevity is moderate, the term expressing the death-rate of mites from the summer population in equation (4) ought to be a good description. The function M(t) expresses the death-rate of the female mite population that has survived the winter or has infested the colony in early spring. It suffices in the present context, but it is likely that this term will need considerable revision when more empirical data become available.

A distinction has to be made between short-lived 'summer' mites and long-lived 'winter' mites in order to describe the seasonal death-rate pattern of the mite population. It would seem that the mites are unable to infest brood cells when they have fed on worker bees with a low juvenile hormone titre in their haemolymph, such as winter bees (Hänel & Koeniger 1986). The buildup of the winter bee population is in turn strongly connected with the decline of the brood production (Omholt 1988a). Thus, the time of cessation of the mite's reproduction in the autumn is likely to be rather strictly defined by this twofold process of declining number of bees with a high juvenile hormone titre and declining numbers of open brood. Furthermore, the fact that there is a sharp decline in the death-rate of mites in October (Rademacher 1985), implies that an approximate on/off switch concerning mite longevity is operative. Based on this, it is suggested that only those mites that have not yet started their first egglaying cycle will become long-lived (i.e. V2 and V3) when the number of open brood cells approaches zero ($t = Bc$). This mechanism functions as a switch, and even if there is scant empirical evidence for it at present, it makes sense by virtue of the fact that juvenile hormone is likely to trigger the activation of a whole repertoire of genes responsible for physiological processes related to ageing in honeybees (Fluri et al. 1977, 1982, Rutz et al. 1976). The existence of analogous processes in the Varroa mite would be an excellent strategy in order to synchronize its reproductive period with that of its host (Hänel & Koeniger 1986).

RESULTS

Figure 1 is based on 200 runs of the model where values of Bc, Di, Dc and V4(0) were picked randomly from a uniform probability distribution, so that $Bc \in [120,165]$, $Di \in [30,75]$, $Dc \in [75,120]$, $V4(0) \in [5,65]$. Each of the four subfigures represents 50 runs with a specific seed value of a pseudorandom number generator, and they all show the same pattern: A linear relationship between winter mite population and natural death-rate, but where the variance of the former increases with increasing death-rate. Thus, even within a rather constrained parameter space, the model predicts that above an accumulated death-rate of approximately 3-400 in the period June-

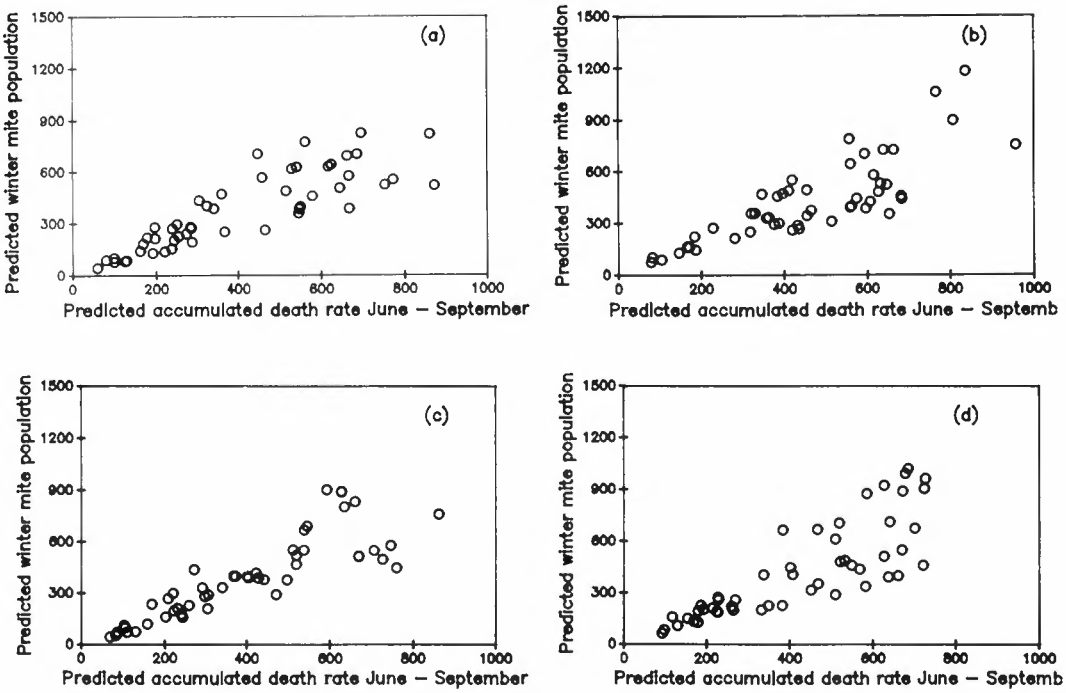

Fig. 1. Predicted winter mite population as a function of accumulated natural death rate of female mites in the period June-September. Each of the 4 subfigures represents 50 runs of the model where, values of Bc, Di, Dc and V4(0) were picked randomly from a uniform probability distribution with a specific seed value of the pseudorandom number generator, so that Bc ε [120,165], Di ε [30,75], Dc ε [75,120] and V4(0) ε [5,65]. The other parameter values were: q0 = 7, q1 = 20, q2 = 80, ιd = 0.368, ιw = 0.233, Bi = 0, t0 = 20 and t1 = 60. t = 0 is supposed to be April 1

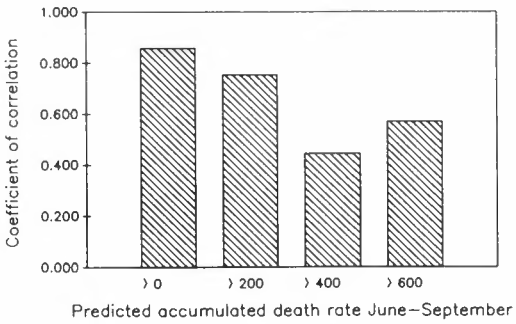

Fig. 2. Calculated coefficients of correlation between predicted winter mite population and natural death-rate by restricting the natural death-rate to be greater than 0, 200, 400 and 600. The calculations are based on the data depicted in Fig. 1a

September, it will be difficult to establish a linear relationship of practical utility (Fig. 2).

Despite its simplicity, the model seems therefore capable of generating the pattern observed by Rademacher (1985), indicating that it has captured the essential features of the population dynamics at low to medium infestation levels. However, by varying only initial mite population number V4(0) and letting Bi, Di and Dc be fixed, the model predicts a strict relationship between natural death-rate and winter mite population (Fig. 3).

DISCUSSION

Figure 3 indicates that the model may become a predictive tool of some utility,

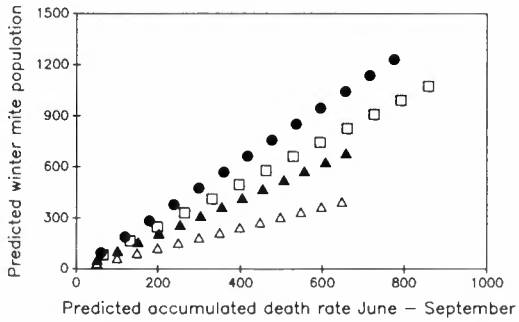

Fig. 3. Predicted relationship between winter mite population level and the natural death-rate in 4 independent runs where Bc, Di, Dc were picked from a uniform probability distribution (within the same ranges as for Fig. 1), and then fixed while V4(0) was looped between 5-65 in increments of 5. All other parameter values are as those listed in Fig. 1

as it may be used to establish a well-defined relationship between death-rate and winter mite population by measuring only Bi, Di and Dc together with the natural death-rate. Note that it is not necessary to know the initial mite population number V4(0). Accumulated death-rate ought to be chosen instead of death-rate in one specific month, because in this way effects from stochastic variations (in the empirical observations) may be reduced. Predictive tables generated by the model will then have to be made for different constellations of Bi, Bc and Dc and natural death-rate. As approximate empirical values of these parameters may be recorded by the practical beekeeper, there is reason to believe that these predictive tables may become of practical utility.

The predictive tables should take into account that it is the size of the winter mite population that is important, not the total number of mites present in the colony in October. For example, if there is a substantial brood rearing in September, and thereby Varroa mite reproduction, many summer mites are still likely to be present in the colony at the end of October.

The effect of reinfestation of colonies is not incorporated into the model. Such reinfestation will influence the population growth rate of the mite. Despite the apparently modest infestation rate of foragers (Schneider 1989), reinfestation as a result of drifting of the foragers (Hüttinger et al. 1981) ought to be considered. In an apiary where most of the colonies have similar infestation levels, and where the drifting pattern is rather uniform, reinfestation will be of minor importance. However, if these conditions are not fulfilled, for example in connection with robbery of heavily infested colonies, reinfestation may cause a considerable impact on the population growth pattern of the mite. If further investigations show that there is a high probability for having colonies with a low natural death-rate of mites but a large winter mite population due to reinfestation, this will have to be incorporated in the model. However, by doing so the practicability of the model will decrease.

It ought to be noted that Rademacher (1985) observed a considerable number of non-pigmented mites on the bottom boards in August and September which were included in her death-rate estimations. These non-pigmented mites are the ones not fully developed upon eclosion of the infested bees, and which therefore die shortly afterwards. They are in fact visible dead juveniles which the model does account for by the function $\tau(t)$, but not in an explicit way. Concerning the predictive ability of the model, the appearance of these dead juveniles on the bottom board does not represent a problem as long as they are omitted from the death-rate estimations. However, it should be noted that sometimes old females remain rather unpigmented (Ifantidis, pers. comm.), and it is important to decide how reliable the pigmentation criterion really is in distinguishing dead juveniles from old females. The model indicates that there is a significant number of female mites that die outside their native colony: when the parameter set is adjusted so that the model generates natural death-

rate patterns in close accordance with those observed by Rademacher (1985) (including non-pigmented mites), the size of the mite population at the end of October is predicted to be considerably less than found by Rademacher (1985) after treating the colonies with an acaricide. If further investigations corroborate this, the predictive tables will have to take this phenomenon into account. However, with a high intercolonial variation of the ratio observed dead mites/total number of dead mites, the practical applicability of the model will be considerably reduced.

The above considerations surely show that the model ought to be more closely tested before it is used as a predictive tool. A natural way of doing this would be to infest colonies with a varying number of mites in early spring and to record the brood rearing patterns of infested colonies together with the natural death-rate of the mite populations during the season. If the model based on these data can predict winter mite population numbers in agreement with estimates obtained by treating the colonies with an acaricide in late autumn, then it will have to be concluded that the model has succeded in capturing the essential features determining the population growth of the Varroa mite. An important task in this connection will be to measure crucial parameters of the model as accurately as possible, so that a good agreement between model results and empirical data due to meticulous manipulation with parameter values may be precluded.

It must be stressed that unless the real natural death- rate can be stipulated from the actually observed one with some confidence, the model will be useless as a predictive tool unless it is improved considerably. It is therefore especially important to test this assumption. Besides, if the autonomy assumption turns out to be oversimplistic, a much more complex model will have to be built, where the intracolonial dynamics of the honeybee colony (Omholt 1986, 1988a, 1988b) will have to be integrated with the population dynamics of the Varroa mite. Such an integrated model must be used at high infestation levels. However, modelling of the mite's dynamics at high population numbers is not very interesting from a practical point of view, as the infested colonies need treatment in any case under such conditions.

Probably, the agreement between model results and empirical test data will not be good enough to allow immediate generation of predictive tables of practical utility. If so, this will not refute the validity of the model approach per se, but rather imply that further refinement of the model is needed.

The present paper shows how a crude dynamic model can be used to elucidate the causal connection between empirical data, thereby providing a basis for a proper transformation of variables to be used in correlation or regression analyses. There is widespread belief that a mathematical model is of no use unless accurate data for all parameters are available. This is not true, as dynamic models may be of considerable importance at all levels in the process of understanding a dynamic phenomenon. In fact, a rapid progression will usually be achieved only if there is a tight feedback link between theoretical and experimental work.

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Field estimation of dry matter, plant nutrients and energy of grass silage effluent by hydrometer

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Synnes, O.M. & S. Tveitnes 1991. Field estimation of dry matter, plant nutrients and energy of grass silage effluent by hydrometer. Norwegian Journal of Agricultural Sciences 5: 401-406. ISSN 0801-5341.

In 1989-90 33 samples of effluent were examined. By means of hydrometers, a close relationship between density and dry matter content was discovered. On one of the hydrometers, a special scale was made in order to take a direct reading of the percentage of dry matter in the effluent. The correlation between the dry matter values read on the hydrometer and those measured in the laboratory was $r = 0.96$ ($P<0.01$). Dry matter estimation by the hydrometer method in the field had almost the same level of accuracy as the oven-drying method in the laboratory. There were also highly significant correlations ($P<0.01$) between dry matter content, and content of Kjeldahl-N ($r = 0.94$), P ($r = 0.86$), K ($r = 0.91$), Mg ($r = 0.80$) and ash ($r = 0.94$). The correlations for NH_4^+-N, NO_3^--N and Ca were not significant ($P>0.05$). The hydrometer method proved to be simple, rapid, cheap and sufficiently exact for field estimation of fertilizer value and feed value of effluent. By this method a better utilization of effluent is achieved.

Key words: Density, dry matter, effluent, hydrometer, nutrients

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There is a great variation in the content of plant nutrients, crude proteins and energy in silage effluent. The main reason for this variation is differences in dry matter content. Investigations in Norway show that the dry matter content in grass silage effluent varies between 2 and 8%. Previous experiments have shown a significant correlation between the dry matter content of plants placed in the silo and the dry matter content of the resulting effluent (Mo 1975, Hole 1985).

Effluent is used as an organic fertilizer, or as a feed for animals. As farmers do not know the content of the effluent, they are unable to apply the correct amounts of plant nutrients to the crop. They are also unable to apply the correct amounts of energy or crude proteins to animals. This lack of knowledge leads to less effective utilization of plant nutrients by crops, more leaching of plant nutrients from the soil, or lower yields. It also leads to less effective utilization of energy and crude proteins by animals.

Previous investigations show a high correlation between dry matter content, and the content of plant nutrients in grass silage effluent (Ilåland 1979). A field method for estimating dry matter

content could provide farmers with a sufficiently accurate information on fertilizer values and feed values of effluent.

Hydrometers measure the density of liquids. Hydrometers are used to estimate the content of sugar, salt or alcohol in water. They are also used for estimating dry matter content of animal slurries and sewage sludge (Tunney & Bertrand 1989, Synnes & Tveitnes 1991). During preliminary experiments with different hydrometers, a relationship between density and dry matter content of effluent was discovered.

The purpose of our experiments was to measure the relationship between density (floating height of hydrometers) and dry matter content of effluent. We also wanted to find and test statistically the regression equations between dry matter content, and content of plant nutrients, crude proteins and ash.

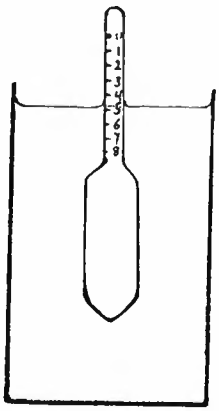

Figure 1. Hydrometer in a bucket with effluent. The bucket should be at least 25 cm deep

MATERIALS AND METHODS

The report deals with 33 samples of grass silage effluent from Møre og Romsdal county, collected in 1989-90. In September-November 1989, 5 preliminary samples were collected at Giske. In 1990 20 samples were collected at Haram, 10 of these shortly after the first cut on June 25-28, and 10 after the second cut on September 3-5. In July 1990 after the first cut, 4 samples were collected at Ørsta and 4 samples at Smøla.

The plant species in the silos were mainly *Phleum pratense* L., *Festuca pratense* L. and *Poa pratensis* L. In all the silos there was less than 10% of clover.

A hydrometer is shown in Figure 1. The principle of a hydrometer is based on the law of Archimedes. The density (g/litre) of effluent dry matter is higher than the density of water. The higher the dry matter content, the higher the density and the floating height of the hydrometer. Two types of hydrometers were used in the experiments. All the results in this report refer to the Herka hydrometer (Tunney 1976). However, the scale on the Herka hydrometer was made for dry matter readings in animal slurries. The density of dry matter in animal slurries is lower than that in effluent, therefore to get correct dry matter readings in effluent, a new scale had to be made.

All samples were immediately frozen, and sent to the Norwegian Agricultural Service Laboratory, or the Chemical Analythical Laboratory at the Agricultural University of Norway, Ås. For all samples dry matter content was measured by oven drying. In addition the 5 preliminary samples from Giske and the 20 samples from Haram were analysed for Kjeldahl-N, NH_4^+-N, NO_3^--N, P, K, Ca, Mg and ash.

The results were tested statistically by correlation analyses and linear regression analyses.

RESULTS

There was a high correlation between the percent dry matter read on the hydrometer, and the dry matter measured by oven drying in the laboratory ($r = 0.96$; $P<0.01$). The regression equation is shown in Figure 2.

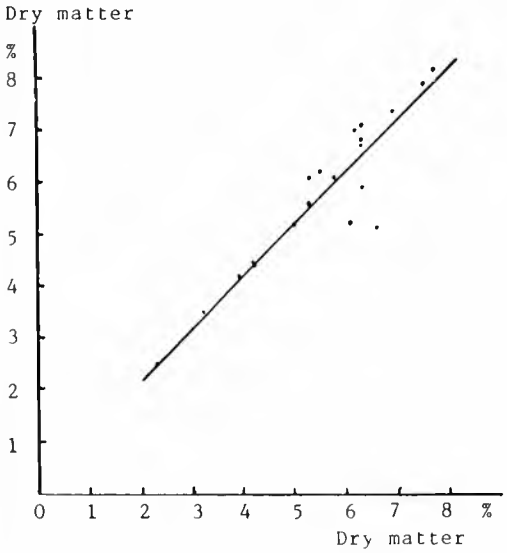

Figure 2. Linear regression equation between dry matter measured by oven drying in the laboratory (Y), and dry matter read on a hydrometer in the field (X). Twenty samples from Haram in 1990 were examined

There was a high correlation between dry matter measured by oven drying, and the content of Kjeldahl-N, P, K, Mg and ash. These regression coefficients were significantly different from 0 ($P<0.01$; Figures 3 and 4). The regression coefficients for NH_4^+-N, NO_3^--N and Ca were not significantly different from 0. These regression lines are therefore not shown in the figures.

There was also a highly significant correlation between the dry matter content read on the hydrometer, and the content of plant nutrients. The correlation coefficient values for dry matter read on the hydrometer were almost as high as those measured by oven drying (Table 1).

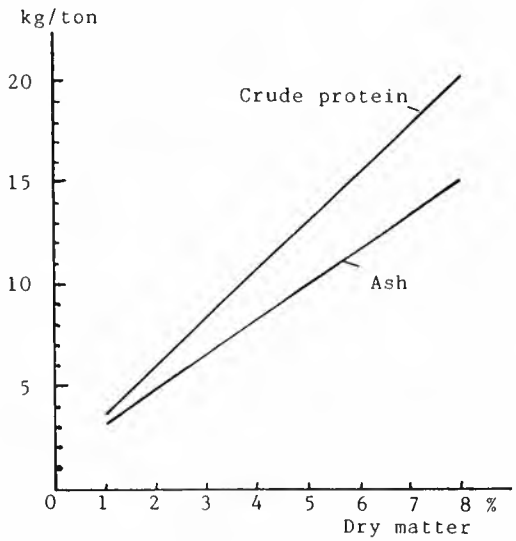

Figure 3. Linear regression between dry matter measured in the laboratory, and Kjeldahl-N, P, K and Mg

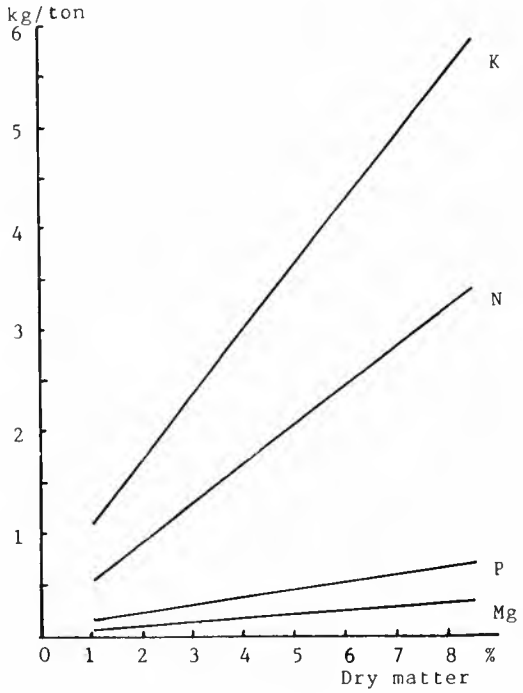

Figure 4. Linear regression between dry matter measured in the laboratory, and crude protein (Kjeldahl-N X 6,25) and ash

Table 1. Correlation (r) between dry matter and nutrients. A: dry matter measured by oven drying in the laboratory. B: dry matter read on a hydrometer

Nutrients	A: laboratory	B: hydrometer	
Kjeldahl-N	0,94	0,89	P<0,01
NH_4^+-N	0,49	0,39	P>0,05
NO_3-N	0,55	0,58	P>0,05
P	0,86	0,82	P<0,01
K	0,91	0,88	P<0,01
Ca	0,45	0,43	P>0,05
Mg	0,80	0,79	P<0,01
Ash	0,94	0,89	P<0,01

DISCUSSION

The experiments proved that hydrometers can be just as accurate as a field test for dry matter estimation of effluent. Only in one out of the 33 samples was the difference between dry matter read on the hydrometer and that measured by oven drying more than one percentage unit. According to the statistical analyses (standard deviation in the t-test of regression coefficients), the hydrometer method appeared to give almost as high an accuracy level as the oven-drying method in the laboratory.

The correlation values between dry matter content and the content of Kjeldahl-N, K and ash, were higher in our samples than those in 68 samples from Western Norway and Trøndelag taken in 1970-78 (Håland 1979). The correlation coefficients for P and Mg were similiar to our samples. Contrary to our samples Håland (1979) found a significant correlation between dry matter and Ca. Also Kemppainen (1987) found a significant correlation between dry matter and nutrients.

The average values for Kjeldahl-N, P, K, Ca, Mg and ash per kg dry matter were in accordance with 68 samples from Eastern Norway and Trøndelag 1970-78 (Håland 1979) and 29 samples from Eastern Norway 1970-74 (Lein 1980). The average values were also in accordance with samples from Finland (Kemppainen 1987).

When effluent is applied to grassland Kjeldahl-N is estimated to be about 40-50% as effective as N in mineral fertilizers (Gilberg & Hammeren 1972, Håland 1979). P and K in effluent seem to have the same efficiency as P an K in mineral fertilizers (Gilberg & Hammeren 1972).

The energy concentration of effluent for cattle and sheep is calculated as 1.1-1.5 kg dry matter per feed unit for fattening (Saue 1975, Pestalozzi 1976, O'Kiely & Flynn 1988, Nordang 1989). For pigs energy concentration is calculated as 0.95-1.3 kg dry matter per feed unit. (Saue 1975, Patterson & Walker 1979).

According to these values from the literature, Table 2 and 3 are suggested as a guide to farmers for predicting fertilizer values and feed values of grass silage effluent at different dry matter levels.

Table 2. Kjeldahl-N, P and K (kg/1000 kg) in grass silage effluent at various dry matter levels

Dry matter	N [1]	P	K
2	1,0	0,26	1,8
4	1,7	0,40	3,1
6	2,5	0,54	4,4
8	3,2	0,68	5,6

1) The effect of Kjeldahl-N in effluent to grassland is about 50% compared to N in mineral fertilizers

Table 3. Crude protein and feed units for fattening in grass silage effluent at different dry matter levels, calculated as 1.2 kg dry matter per feed unit

Dry matter %	Crude protein g/l	l per feed unit
2	6	60
4	11	30
6	16	20
8	20	15

The Herka hydrometer was calibrated at 15.5°C. Tunney & Bertrand (1989) found that in a slurry with 7.5% dry matter, the hydrometer reading at 20°C was 8.0% and the reading at 10°C was 7.0%. Similiar results were obtained in pure water at different temperatures (Synnes unpublished). Hydrometers for effluent should be calibrated at the most common effluent temperature in summer, i.e. about 15°C, in the area in which the particular experiments are being carried out. If the temperature in the effluent is very different from the calibration temperature, the reading should be corrected. The correction can be read directly on the hydrometer as the difference between the zero mark and the surface of pure water. The temperature of the water and the effluent must be similiar. Alternatively, a small sample of effluent can be tempered to obtain approximately the desired temperature.

Fresh grass silage effluent contains approximately 35% sugar, 17% organic acids, 24% crude protein and 24% ash. During storage, sugar will be fermented to organic acids, mostly lactic acid (Saue 1975, Nordang 1989). The density of sugar is about 1.55 g/ml, and lactic acid about 1.4 g/ml. The decrease in density of effluent during storage will consequently be of very little importance.

The experiments carried out prove that the hydrometer method is not only rapid and sufficiently accurate, it is also simple and cheap. These properties makes it advantageous as a field method compared to other known methods.

The hydrometers used in our experiments were made of glass. These proved to be too weak for field work. Plastic or other less fragile materials would be more suitable for field tests.

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