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IMPACT OF CLIMATE AND AGRICULTURAL PRACTICES ON THE PEST STATUS OF *HETERODEROIDEA* NEMATODES IN FINLAND

Selostus: Ilmaston ja viljelytoimenpiteiden vaikutus kysta- ja äkämäankeroisten vahingollisuuteen Suomessa

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Academic dissertation
To be presented, with the permission of the Faculty of Agriculture and Forestry of the University of Helsinki, for public criticism in Auditorium Viikki B2 on May 24th, at 12 o'clock noon.

PREFACE

This research was carried out at the Agricultural Research Centre of Finland, Institute of Plant Protection in Jokioinen, during the period 1978—1989. I am most grateful to Professor Martti Markkula and Miss Katri Tiittanen, M.Sc. for their help from the very beginning of this study and during the preparation of manuscript of the thesis. Their unstinting encouragement has been inestimable help during the process of this research work.

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My dearest thanks I give to my wife Liisa and our children Tero, Jasse and Maria. Without your loving support I would not have been able to carry out this work. I hope that in the future I can give you the love and attention you had to do without when my thoughts were constrained to this research.

Jokioinen, April 1991

Kari Tiilikkala

LIST OF ORIGINAL ARTICLES

The original articles summarized here are:

I TIILIKKALA, K. 1987. Life cycle of the potato cyst nematode in Finland. Ann. Agric. Fenn. 26: 171—179.

II TIILIKKALA, K. 1991. The influence of soil temperature on initial energy reserves of *Globodera rostochiensis*. Rev. Nématol. (in press).

III TIILIKKALA, K. 1991. Effect of crop rotation on potato cyst nematode, *Globodera rostochiensis*, and potato yield. EPPO Bull. 21: 41—47.

IV TIILIKKALA, K. 1985. Influence of sugarbeet and non-host plants on a field population of *Heterodera schachtii*. Ann. Agric. Fenn. 24: 63—69.

V LAHTINEN, A.E., TRUDGILL, D.L. & TIILIKKALA, K. 1988. Threshold temperature and minimal thermal time requirements for the complete life cycle of *Meloidogyne hapla* from Northern Europe. Nematolociga 34: 443—451.

VI TIILIKKALA, K., LAHTINEN, A.E. & TRUDGILL, L. 1988. The pest potential of *Meloidogyne hapla* in northern field conditions. Ann. Agric. Fenn. 27: 329—338.

CONTENTS

PREFACE 127

LIST OF ORIGINAL ARTICLES 128

ABSTRACT 131

INTRODUCTION 132
1. *Heteroderoidea* — a relatively uniform group of phytoparasitic nematodes 132
2. The effect of climate on the distribution of plant parasitic nematodes 133
3. The development—temperature relationship in nematodes 134
4. Object and aims of the study 134

MATERIAL AND METHODS 135
1. Life cycle and energy reserves of the potato cyst nematode 135
2. Population development of the beet cyst nematode 137
3. Temperature requirements of the northern root-knot nematode 137

RESULTS AND DISCUSSION 138
1. Influence of temperature on population dynamics of the nematodes 138
   1.1. Threshold temperatures of cyst and root-knot nematodes 138
   1.2. Accumulated temperature as a tool for predicting nematode development 140
   1.3. Impact of low soil temperature on initial energy reserves of nematode larvae 142
2. Other factors influencing the development of nematode populations 144
   2.1. Abiotic factors other than temperature 144
   2.2. Biotic factors determined by agricultural practices 145
3. Factors affecting the distribution and pest potential of nematodes 149
4. Pest potential of *Heteroderoidea*-nematodes in Finland 151
   4.1. Current situation 151
   4.2. Influence of possible future warming of the climate 152

SUMMARY AND CONCLUSIONS 153

REFERENCES 155

SELOSTUS 159

IMPACT OF CLIMATE AND AGRICULTURAL PRACTICES ON THE PEST STATUS OF *HETERODEROIDEA* NEMATODES IN FINLAND

TIILIKKALA, K. 1991. **Impact of climate and agricultural practices on the pest status of *Heteroderoidea* nematodes in Finland.** Ann. Agric. Fenn. 30: 131—161. (Agric. Res. Centre of Finland, Inst. Pl. Protect., SF-31600 Jokioinen, Finland.)

This study investigates the effect of abiotic factors — especially temperature — and the influence of cultivation methods on the potato cyst nematode *(Globodera rostochiensis)*, beet cyst nematode *(Heterodera schachtii)* and nothern root-knot nematode *(Meloidogyne hapla)*. Particular attention was paid to the effect of low soil temperature on the initial energy reserves of the developing larvae. For the estimation of the energy reserves a computer aided image analysis was developed.

The result showed that the development, distribution and pest potential of the nematodes may be predicted by comparing their temperature requirements with the prevailing temperatures in the growing areas. The effect of cultivation methods on temperature accumulation was also found to be important. To predict the development of cyst nematodes a base soil temperature of 4.4 °C can be applied, while for the northern root-knot nematode a base temperature of 8.3 °C is appropriate. The development of cyst nematodes requires about 598 ± 24 day-degrees above 4.4 °C, while the first new larvae of *M. hapla* hatch when about 553 ± 2 day-degrees above 8.3 °C have accumulated. The results of the laboratory experiments indicated that low soil temperature during development led to low initial energy reserves of the larvae.

In present climatic conditions in Finland the beet cyst nematode can rarely exceed the economic threshold of 10 larvae/g soil, since the heat accumulation over the growing season permits the complete development of only one generation per season. For the potato cyst nematode the heat sum is sufficient to develop new larvae throughout the country as far as the Arctic circle, but the development of population densities to high numbers is only possible in southern Finland. The potato cyst nematode was controlled succesfully by the crop rotation of potatoes, growing potatoes once every three years with susceptible and resistant cultivars being used alternately. The northern root-knot nematode failed to reproduce outdoors on annual carrots which accumulated 554 day degrees, but new larvae developed on perennial white clover in a case when the accumulated soil temperature was 631 day-degrees above 8.3 °C. About 10 % of the larvae overwintered in field plots. The risk that *M. hapla* could become a seriuos outdoor perst was found to be small.

The results indicated that the predicted warming of the climate may advance the distribution of the nematodes and increase their pest potential in Finland.

Index words: cyst nematodes, root-knot nematodes, *Globodera rostochiensis, Heterodera schachtii, Meloidogyne hapla,* soil temperature, temperature requirements, development, initial energy reserves, distribution, pest potential, integrated pest management, image analysis.

1. *Heteroderoidea* — relatively uniform group of phytoparasitic nematodes

As plant parasites the nematodes of the super family *Heteroderoidea* have an extremely high pest status. Root-knot nematodes (*Meloidogyne* spp.) are distributed more widely than any other plant parasitic nematode and they are economically very important throughout the world (SASSER 1977). Cyst nematodes also have a wide distribution; for example the potato cyst nematode (*Globodera* spp.) and beet cyst nematode *(Heterodera schachtii)* are established in all of the main growing areas of potato and sugar beet (MAI 1977, WILLIAMS 1978). Because of the great need to prevent the spread of the cyst and root-knot nematodes, they are classified as quarantine pests by the European Plant Protection Organization (ANON. 1978), and the nematodes of this study *G. rostochiensis, H. schachtii* and *M. hapla* — were in 1982 defined as quarantine pests under the Finnish plant quarantine law (ANON. 1982).

There are three factors linking cyst nematodes (Heteroderidae) and root-knot nematodes (Meloidogynidae) as plant parasites, namely a taxonomic connection, similar life cycles and great economic importance. The heteroderids originate from a common tylenchid ancestor (COOMANS 1979) and they are limited to abursate male forms with a short tail, usually less than half the body width long and didelphic female forms in which enlargement usually begins by the third juvenile stage. Because the Meloidogynidae and Heteroderidae share this unique combination of characters they are placed in the same super family, *Heteroderoidea* share this unique combination of characters they are placed in the same super family, *Heteroderoidea* (STONE 1986). There are more than 80 different species of cyst nematode from six different genera: *Afenesrata, Cactodera, Dolichodera, Globodera, Heterodera* and *Punctodera* (STONE 1986). The recognized genera in the family Meloidogynidae are: *Meloidogyne, Hypsoperine, Meloidorella* and *Meloinema* with the type genus *Meloidogyne* having 36 species (FRANKLIN 1979). The most typical feature of the Heteroderidae nematodes is the development of the females to thick walled cysts filled with eggs. The distinguishing characteristic for the Meloidogynidae nematodes is the induction of gall-formation root-knots around the developing females. The females of Meloidogynidae do not develop to cysts and the eggs are left free in the soil or embedded in a gelatinous matrix.

The heteroderids are endoparasites and they all have a broadly similar life cycle. Second-stage larvae hatch from the eggs and invade the roots. They penetrate the cortex and establish themselves with the anterior end in contact with the vascular cylinder where they induce the formation of the giant cells upon which they feed. During their further development the larvae gradually assume a flask shape and undergo three further moults. Finally the males appear as a long filiform nematode folded inside the cuticle of the fourth larval stage. In the amphimictic species the males copulate after escaping from the last larval exuviae. *Meloidogynidae* females secrete a gelatinous matrix into which they extrude a large number of eggs. Heteroderidae females swell up to form a spherical, sub-spherical or lemon-shaped cyst containing the eggs. Cyst nematodes do not induce gall formation but the cyst walls shelter the eggs for long periods of time. Many species of the Meloidogynidae are parthenogenetic, obligate or facultative. Most of the cyst nematodes are sexual.

2. The effect of climate on the distribution of plant parasitic nematodes

The environmental factors which are known to be instrumental in the biology of soil and plant nematodes are of a physical, chemical and biological nature. DAO (1970) has listed them as follows:

- climatic influences, related to temperature, moisture, light and other types of radiation, periodicity;
- soil influences, related to soil composition and structure, moisture, the chemistry of the soil solution and soil air;
- food influences, related to host characteristics, the quantity and quality of organic material;
- the effect of other organisms, related to interspecific competition, predation, parasitism and diseases, other complex relationships;
- intraspecific factors, related to competition and cooperation.

According to DAO (1970) climate appears to have a determining effect in limiting the range of any species of animal or plant. This effect may be direct, or it may be indirect, for example via food or via the soil. The main climatic factors for flora and fauna are temperature, moisture and light. As long ago as 1938, HOPKINS attempted to relate plant response to geographic location and elevation, working out a 'bioclimatic law' that covered a response to climate, especially temperature. The rate of development of poikilothermic animals such as nematodes is related to the temperature of their environment which for the cyst and root-knot nematodes is soil. For this reason accumulated soil temperatures has been used to predict the development of nematodes (e.g. by JONES 1975 a). Recently BOAG and CRAWFORD (1990) have suggested that global warming may change the geographical distribution and pest potential of nematodes. The use of accumulated temperatures to predict the development of nematodes may increase in years to come, as a result of the possible warming of the climate, and also the adoption of more liberal plant quarantine regulations in Europe. Low winter temperatures are critical for some species (BERGESON 1959, DAULTON and NUSBAUM 1961) but many of the heteroderids, including the potato cyst nematode, can withstand very low temperatures (ÖYDVIN and HAMMERAAS 1973). The population densities of many poikilotherms depend mainly on their ability to multiply during the growing season (DOWNES 1964).

QUICKLEY (1980) suggested that the accumulated temperature in Finland at the Arctic Circle would be sufficient for potato cyst nematode females to develop to maturity and produce some eggs with embryos. In contrast, MAGNUSSON (1986) argued that temperature requirements of the potato cyst nematode are so high that the nematode will fail to complete its life cycle in the climate of the Arctic Circle, but will be able to survive in central and southern Finland. The success of many other cyst nematodes adapted to cool climatic conditions may be comparable with that of the potato cyst nematode. The root-knot nematodes is known to have adapted to temperate climate in central Europe (RITTER 1972), the USA (DAULTON and NUSBAUM 1961) and Sweden (ANDERSSON 1970). In Canada, *M. hapla* is able to overwinter in the Ontario region (JOHNSSON and POTTER 1980), where the winter is as cold as or even colder than in Finland. Thus, the adaptive capacity of this species may be good enough for its survival in Finnish climatic conditions.

3. The development-temperature relationship in nematodes

Nematodes are poikilothermic animals, and their metabolism, activity and behaviour follow the temperature in the environment with very little delay. The environmental temperature is therefore one of the most important factors in nematode biology. For endoparasitic nematodes the effect of temperature is more marked than it is for free-living nematodes (JONES 1975 a, 1983). Soil and plant nematodes are active and thriving at temperatures between 15 °C and 30 °C, but become motionless in the ranges 5—15 °C and 30—40 °C. The minimum temperature for some essential activities can be as low as +2 °C for the emergence of the cereal cyst nematode *(Heterodera avenae)*, +5 °C for invasion by the stem nematode *(Ditylenchus dipsaci)* and northern root-knot nematode *(M. hapla)* and +5—10 °C for activity in the potato cyst nematode *(G. rostochiensis)* and beet cyst nematode *(H. schachtii)* (DAO 1970). If the temperature fluctuates about a mean the mean rate of development may be greater than that indicated by the mean temperature alone because of these nematodes can sometimes be active when average temperatures are below what might be considered the minimum for activity. In general, nematodes from warmer regions have higher minimum temperatures than those known from temperate climates (DAO 1970).

The three characteristic temperatures that describe the development-temperature relationship are the minimum temperature, the optimum temperature and the maximum temperature for different activities. The minimum temperature indicates the time of the season or the geographical region in which the nematode can be active. The optimum temperature expresses the condition in which development and reproduction is rapid and population densities can rise to high levels. The maximum temperature indicates the extreme limit at which nematode populations can survive. One of the most widely used figures for development-temperature relationship is the accumulated temperature (JONES 1975 a), which is calculated in day-degrees (or hour degrees) using the degrees above the basal temperature. The basal development temperature can be found by the rate of development (expressed as the reciprocal of the time taken); in the middle range of useful temperatures the rate of development is linearly correlated with the temperature, and the intersection of the correlation line and the temperature axis gives the base development temperature (ALLEE et al. 1949). It is known that the effective temperature sum for the development of one generation is not constant, and will vary according to many other factors and the extent to which they differ from the optimum. Typical of these factors are the quality and resistance of the host plant, which will have an effect on the rate of nematode development (WALLACE 1973, FERRIS and van GUNDY 1979). Nevertheless, in simulations of the development of endoparasitic nematodes heat sums have proved to be useful. Heat sum calculations have been used to estimate the development of nematodes and nematode population densities, and the need for and timing of control measures (DAO 1970, JONES 1975 a, SASSER 1977, FERRIS et al. 1978, JONES 1983). The effect of temperature has been simulated most successfully by computer-aided models in which many factors, biotic and abiotic, can be controlled simultaneously (e.g. WAGNER et al. 1984, BAKER and COHEN 1985, WARD et al. 1985).

4. Objects and aims of the study

The nematode species of the family *Heteroderidae* studied in this research project were the beet cyst nematode, *H. schachtii* (Schmidt) and the potato cyst nematode, *G. rostochiensis*

(Wollenweber). The beet cyst nematode was first found in Finland in the late 1950s (ROIVAINEN 1962) and it is established only on some fields near sugar factories. The beet cyst nematode has hardly ever caused yield loses in Finland, except in 1977, but every year permanent populations can be found in some fields with continuously grown sugar beet. The potato cyst nematode was first found in 1946 (VAPPULA 1954) and by the early 1980s it had spread throughout the southern parts of the country to some areas in central Finland (TIILIKKALA and AAPRO 1980). The northernmost discovery of the potato cyst nematode has been made near the town Rovaniemi, close the Arctic Circle (SARAKOSKI 1976). At present, the potato cyst nematode is the most noxious animal pest in commercial potato production, although *Globodera pallida* has not been established. The *Meloidogynidae* species of this study was the northern root-knot nematode, *M. hapla* (Chitwood). None of the root-knot nematodes has been established in open fields in Finland, but *M. hapla* occurs frequently on roses grown under glass. The infested peat-based growth media from the greenhouses is generally spread on adjacent fields making the spread of *M. hapla* to field crops possible.

The main objects of this research were:

1) to determine the effect of temperature (especially low temperature) on the development of cyst and root-knot nematodes and on their initial energy reserves;
2) to find out the accumulated temperatures required for the complete development of the three nematode species;
3) to estimate the pest potential of root-knot and cyst nematodes in Finland;
4) to study the impact of cultivation methods on the nematode populations.

In addition to the practical aims the research had a theoretical purpose, namely to test whether the hypothesis of RICHARDS (1964) is valid for nematodes. According to this hypothesis, relatively more energy is required for the complete development of larvae at minimal temperatures. RICHARDS showed that the phenomenon was present in insects, but suggested that it would also apply to other organisms.

MATERIAL AND METHODS

1. Life cycle and energy reserves of the potato cyst nematode

The development of the potato cyst nematode populations in two fields was studied over the period 1981—1984 (I) in Jokioinen (60°50′ N, 23°30′ E). The density of the encysted nematode population was monitored each year from soil samples taken at 7-day intervals during the growing season. The numbers and colours of the nematode females on the roots were recorded for the years 1981 and 1982. The numbers of invading larvae, third and fourth stage larvae, males, females, new eggs and embryonated larvae were recorded for the years 1983 and 1984. The temperature sums required for the development of the different stages were determined.

Soil temperatures were obtained from routine measurements made by the Finnish Meteorological Institute of Jokioinen (4 km from the experimental field) and at Sodankylä, Lapland (67°25′ N, 26°40′ E). The mean soil temperatures/day were calculated from the minimum and maximum temperatures at a

Table 1. The cropping systems used in the field study conducted in southern Finland 1981—1989. S = susceptible potato, R = H1 resistant potato, Sn = susceptible potato protected with a nematicide, O = oats grown as an intermediate crop.

Cropping system	Year								
	1981	1982	1983	1984	1985	1986	1987	1988	1989
1	S	O	O	O	O	S	O	O	O
2	S	O	O	O	S	O	O	O	S
3	S	O	O	R	O	O	S	O	O
4	S	O	R	Sn	O	S	O	R.	Sn
5	S	Sn	O	Sn	S	O	Sn	S	O
6	S	S	S	S	S	S	S	S	S

depth of 10 cm. At Jokioinen the temperatures were measured with a mercury thermometer in clay soil under permanent grass. At Sodankylä the temperature was recorded from sandy soil under lichen. The temperature accumulation was counted in day-degrees (henceforth referred to as dd) above the basal development temperature of 4.4 °C. The basal temperature was chosen to be the same (4.4 °C = 40 °F) as that used for cyst nematodes by JONES and PARROT (1969) and JONES (1975 a) because it fitted well with the observed start of migration in the field.

The effect of temperature on initial energy reserves of newly developed larvae was studied in a laboratory experiment carried out in 1989 (II). A computer-aided image analysis was used to estimate the lipid content of potato cyst nematode larvae reared at four soil temperatures and over three developmental periods. At the beginning of the experiment, four-week-old potato plants were infected by 1 000 larvae per pot. After an incubation period of one week at 15 °C, the temperatures of the pots were set to 12, 16, 20 and 24 °C (fifteen pots per temperature). Five pots per temperature at a time were moved from the water bath 59, 69 and 79 days after the incubation period to a cold-storage room with an air temperature of + 3 °C. Cysts were extracted from the soil, and larvae counted and stained with Oil Red O. Analysis of the stained fractions of the larvae was carried out using an image-analyser (IMAGIST, Princeton Gamma-Tech). The size of the larvae was estimated and the final population density/pot determined. The accumulated soil temperatures of the pots were compared to field data from the years 1981—1989. The soil temperature data were obtained from routine measurements made by the Finnish Meteorological Institute of Jokioinen.

The effect of cultivation methods on the population density of the potato cyst nematode was studied (III) on a farm specializing in potato production in Renko (60°50′ N, 24°15′ E). The cropping systems studied are shown in Table 1. A soil sample was taken from each plot before planting and harvesting. Population densities were determined and the Pf/Pi (final population/initial population) values calculated using the spring population of one year as Pi and the spring population of the following year as Pf. The soil mixing effect of tillage on population estimates was thus the same for both estimates. Soil temperatures indicating developmental conditions for the nematode during the experimental years were obtained from the measurements made at Jokioinen (36 km from the experimental field). The effective heat accumulation was calculated in day-degrees above the basal temperature of 4.4 °C. The year 1987 was exceptionally cold and unfavourable for plant growth and the development of the nematode. The growing season of 1988 was, in contrast to 1987, one of the warmest ever recorded in Finland (ANON. 1988, 1989.)

2. Population development of the beet cyst nematode

The field experiment (IV) for population studies of *H. schachtii* was conducted in a field near the town of Salo (60°30′ N, 23°00′ E), where the beet cyst nematode had damaged sugar beet exceptionally severely in the summer of 1977. The field had previously been used for sugar beet production for more than five years. Sugar beet and non-host plants (alfalfa, barley, broad bean and rye) were grown in the years 1978—1980. Population densities were determined from soil samples taken from six plots per plant in the spring after tillage of the soil, and in the autumn after harvesting.

Rainfall per day was taken from the measurements of the Finnish Meteorological Station at Piikkiö (30 km from the experimental field) and the soil temperature from the measurements of the station at Jokioinen (50 km from the experimental field). The effective accumulated soil temperature was calculated using the methods described by GRIFFIN (1981) using two different base temperatures, 10 °C and 4.4 °C.

3. Temperature requirements of the northern root-knot nematode

The temperature requirements of three populations of *M. hapla* were tested; these originated from a greenhouse in Finland and from fields in Sweden and the Netherlands (V). The populations were maintained on tomatoes, initially in greenhouse in Finland and, then in Scotland. The test plants, tomato and cabbage, were infected by juveniles and after the incubation placed in controlled-temperature water baths at 16, 20, 24 and 28 °C. Newly hatched juveniles were collected, identified and counted. The number of juveniles progressively increased in all the experiments, and collection and counting was continued for several days to help confirm the date when juveniles were first produced. Five experiments were carried out (V). On the basis of the first findings of newly hatched juveniles at different temperatures and the linear relationship between development and accumulated temperature (ALLEE et al. 1949), the threshold temperature for *M. hapla* was calculated and the thermal-time requirements above the base threshold estimated.

During 1985—1987, the development of an outdoor Finnish population of *M. hapla* was studied in Finland and the predictive value of the laboratory result tested in field conditions (VI). The nematode population originated from infested peat in a commercial rose growing greenhouse. The peat was removed in October 1984 and piled up to a height of about 5 m. In spring 1985, two similar field experiments were commenced: one at Tuusula, 20 km north of Helsinki, and the other at Toholampi (63°45′ N, 24°15′ E). At each site thirty plots were established by removing the top 10 cm of the soil and replacing it with peat taken from the infested peat heap. The host plant grown in the plots was carrot, with Timothy grass being grown as a non-host. A certain number of the plots were left unseeded and allowed to be colonized by the wild vegetation of the experimental sites.

The nematode densities in each plot were determined during the sowing and harvesting of the carrots. Samples were taken from the surface of the peat heap and at depths of 1 m and 2 m in December 1986, May 1985 and May 1986. The free larvae in the samples were extracted, counted and their infectivity tested in the spring of 1985 and 1987. The development of the females was monitored in Tuusula during the summer of 1986.

Soil temperature records were obtained from routine measurements made at Jokioinen (90 km northwest of Tuusula) and at Ruukki

(90 km north of Toholampi). At Ruukki the temperatures at 20 cm were recorded and the 10 cm values estimated using the 10 cm/20 cm ratio from the Jokioinen measurements. The effective air temperature at Ruukki is very similar to that at Toholampi (MUKULA and RANTANEN 1987).

The sites of the experiments had to be chosen so that the continuous cropping of susceptible plants could be officially approved by the Plant Quarantine Office.

RESULTS AND DISCUSSION

1. Influence of temperature on the population dynamics of the nematodes

1.1. Threshold temperatures of cyst and root-knot nematodes

Cyst nematodes

At the beginning of the growing season the temperature has an effect on the migration of the infective stages on nematodes. In Finland the first migrating larvae of potato cyst nematode were found during the first week of May when the soil temperature was 4—5 °C (I). FELDMESSER and FASSULIOTIS (1950) have reported similar results, but FRANCO (1979) did not notice any hatching at 5 °C. FOOT (1978) found larvae to emerge at 7 °C and INAGAKI (1977) reported that the potato cyst nematode in Japan hatches when the soil temperature is 10 °C. Adaptation to low temperatures has been found to be possible (HOMINICK 1979) and based on differences in temperature requirements populations have been graded as belonging to different thermotypes (DAO 1970) or ecotypes (MUGNIERY 1982). SIGGEIRSON and QUICKLEY (1983) suggested that the lower threshold for development of potato cyst nematode is about 5 °C for populations adapted to cool climatic conditions, and that the temperature requirements of nematodes do in general correspond to the requirements of the host plant. The base temperature of 4.4 °C used by JONES and PARROT (1969) and JONES (1975 a) corresponds well with the data of this study and can be used as a threshold for the calculation of accumulated temperatures. The base temperature of 6 °C used by MAGNUSSON (1986) for studies on Scandinavian population was an arbitrary choice without any experimental work to find the lower threshold temperature and is somewhat too high for potato cyst nematode in Finland.

In the soil the number of migrating larvae was low until the soil temperature exceeded 10 °C and the peak of migration was noticed at 15 °C. In general, the peak emergence and invasion of cyst nematodes has been reported to occur at 15—16 °C (CHITWOOD and BUHRER 1946, WILLIAMS et al. 1977 and INAGAKI 1977). In Finland, the soil temperature in June may be critical for migration; in some years the peak of migration is possible as early as the last week of May, but if it is cool in spring, the peak may occur four weeks later. This kind of variation may affect the multiplication of nematodes and yield losses caused by the nematode.

In 1983 the first L2-larvae in the roots were found five days after planting when only 62 dd had accumulated since the planting. A difference between soil types was encountered in 1984. In sandy soil the peak was on the 6th of June but in clay soil two peaks were found, on the 6th and 27th of June. The soil temperature was very low (below 10 °C) between these two dates and the second peak of invasion was found at the time when the soil temperature had increased again to 15 °C. It seems that 10 °C is too low for a mass invasion. MUGNIERY (1978) found the first larvae to invade the roots 3 days after planting, but STOREY (1982) found it to be two weeks after. According to JONES and PARROT (1969) the invasion starts when 167 dd have accumulated following planting. There are differences among populations from different localities, and it seems that in Finland the potato cyst nematode invades the roots as soon as root growth begins. The main invasion occurred over a brief period, as observed by INAGAKI (1977), at the soil temperature of about 15 °C.

The laboratory experiments showed that the optimum temperature for the development of cyst nematodes in Finland is close to 20 °C, because all of the measured qualities of potato cyst nematode: reproduction, size and initial energy reserves of the larvae reached the maximum values at 20 °C (II). In general, the optimum varies between 15—27 °C. For example the optimum of *H. schachtii* is about 27 °C in the California region (THOMASON and FIFE 1962), and in Europe *H. schachtii* reproduces most rapidly at soil temperatures of 23—27 °C (COOKE and THOMASON 1979). For potato cyst nematode the optimum temperature is lower; FOOT (1978) proved that the optimum temperature lay between 15 and 20 °C in New Zealand and in England it is 18—24 °C (FERRIS 1957). The highest reproduction was recorded at 20 °C in Japan (INAGAKI 1984), and also FENWICK (1951) estimated the optimum to be at 20 °C. In Finland, one of the key factors is that the soil temperature during the growing season is 4 to 5 °C lower than the optimum for the development of potato cyst nematode.

Root-knot nematodes

The laboratory experiments showed that the temperature threshold of the northern root-knot nematode in Finland is 8.3 °C (V). The threshold was the same for outdoor populations from Southern Sweden and Holland as for the Finnish population from a greenhouse. None of the tested populations have had the possibility to adapt to low outdoor temperatures such as are typical in Finland. The work of others suggest that hatching and invasion by the nematode may have base temperatures close to 8 °C; VRAIN et al. (1978) reported a base temperature of 8.8 °C for invasion and development. For embryogenesis VRAIN and BARKER (1978) reported an even lower threshold of 6.74 and STARR and MAI (1976) suggested that in New York the lower threshold is closer to 5—7 °C than to 10 °C. In the laboratory experiment (V) hatching was delayed at the lowest temperature of 17 °C, but it is unlikely that 17 °C is close to the base temperature for hatching or invasion. The delay may be caused by a short diapause induced at 17 °C.

In this study the development time of the larvae was shorter at 28 °C than at 24 °C or the lower temperatures. The result indicates that the temperature optimum for the population which originated from the greenhouse was closer to 28 °C than 24 °C (IV). Others have reported that the optimum temperatures for development of the northern root-knot nematode are 25 °C for hatching, 20 °C for mobility, 15—20 °C for invasion and 20—25 °C for growth (BIRD and WALLACE 1965). THOMASON and LEAR (1961) and FINLEY (1981) recorded the maximum egg mass reproduction at 25—30 °C. Many other *Meloidogyne* species have a higher optimum than *M. hapla* except *M. chitwoodi*, which is better adapted to low soil temperatures (SANTO and O'BANNON 1981, INSERRA et al. 1983).

Overwintering

In the present study the root-knot nematode population from the greenhouse overwintered well in the peat heap and about 10 % of the field population could overwinter and remain infective. In Canada about 25 % of the nematodes of the same species can overwinter yearly (SAYRE 1963), and in Sweden the nematode is able to overwinter upto the Stockholm region but not in the northern part of the country (BANCK 1985). The soil temperature during the winter time is critical for many *Meloidogyne* species (BERGESON 1959, DAULTON and NUSBAUM 1961). At Ontario, *M. incognita* did not overwinter below the frost line in a moderate year, but by comparison, the *M. hapla* survived well (JOHNSON and POTTER 1980).

The effect of winter temperatures on cyst nematodes was not studied in this research project, because it is well known that cyst nematodes can endure extremely low temperatures (DAO 1970). For example potato cyst nematodes were able to hatch after 4-weeks storage at —35 °C (ÖYDVIN and HAMMERAAS 1973). In Finland the soil temperature at depth of 10 cm in winter time is 0 to —5 °C which is easily tolerated by cyst nematodes.

1.2. Accumulated temperatures as a tool for predicting nematode development

Cyst nematodes

In this study the effective heat sum required for the development of the first new larvae of cyst nematodes was 598 ± 24 dd above the base of 4.4 °C. The heat sum was calculated as the mean of soil temperatures which accumulated after the planting of potatoes and an invasion period of five days. The temperature requirement is consistent with that of other populations which have adapted to low soil temperatures (SIGGEIRSON and QUICKLEY 1983). QUICKLEY (1980) suggested that if 5 °C is used as the lower threshold, the day-degrees for Rovaniemi confirm that 690 units are about right for the completion of one generation of cyst nematodes in northern Europe. Quickley used air temperatures in contrast to this study which is based on soil temperatures. The comparison of air and soil temperatures is complicated in areas below the frost line, because in spring, during the melting of the ice, the soil temperature does not correspond to the rise in air temperature (KARVONEN 1988). However, the air temperature accumulation of 690 dd may be close to the accumulation of 598 ± 24 dd of soil temperature (10 cm).

MAGNUSSON (1987) suggested that potato cyst nematode requires about 1 000 day-degrees above the threshold of 6 °C to complete the life cycle. The heat sum is much higher than found in this study (I) or reported by QUICKLEY (1980), SIGGEIRSON and QUICKLEY (1983) or INAGAKI (1984). There are at least three possible explanations for the differences. Firstly MAGNUSSON used the ratio Pf/Pi as the criteria for development. The multiplication of nematodes on pot-grown plants depend on a variety of factors other than temperature (VAN DER WAL and VINKE 1982) and thus the ratio Pf/Pi is poorly suited to studies on temperature requirements. Secondly, the estimated initial population was inaccurate, because the nematodes were inoculated as cysts collected from the field. Soil samples taken from a field contain cysts from a long period of time, and thus the infectivity of the larvae is variable, and hardly ever equal to that of the total number of encysted larvae. In this kind of experiment nematodes should be inoculated as larvae freely hatched from cysts, although their infectivity too may be variable (REVERSAT 1980). Finally the lower threshold temperature of 6 °C appears slightly too high to be used for potato cyst nematode population established in northern Europe.

The temperature requirements of the beet cyst nematode are about the same as that of the potato cyst nematode; MÜLLER (1978) reported that at 25 °C one generation of the beet cyst nematode developed in 28 days, and the accumulation above 4.4 °C was thus 576 dd. The result is consistent with the temperature requirements of the potato cyst nematode in this study (I). Thus, it can be argued that one generation per growing season can fully complete its life cycle in Finland. Three generations develop in central Europe (MÜLLER 1979) and five in the California region (THOMASON and FIFE 1962). When using accumulated temperatures the effect of soil temperature during the development of every generation must be taken into consideration, because THOMASON and FIFE (1962) proved conclusively that the heat accumulation of development of one beet cyst nematode generation varied from 319 to 1 255 dd depending on the time of the year the beet was grown. The variation was caused by the fact that in winter time the nematodes had to develop at minimal temperatures of development and during the growing season in summer time the development of nematodes took place at the optimum temperatures of development.

Root-knot nematode

The total thermal time requirements for development of the first newly-hatched larvae of the northern root-knot nematode was found to be 553 ± 2 dd above the threshold of 8.3 °C. The maximum rate of output of the larvae occurred when the host plants had accumulated between 700 and 900 dd, although new larvae were still being collected when plants had accumulated 1 100 dd. In Canada, the northern root-knot nematode produced egg masses at 20 °C after 30—40 days (STEPHAN and TRUDGILL 1982), and the accumulated soil temperature above 8.25 °C was 352—470 dd. VRAIN et al. (1978) reported that 450 dd above 8.8 °C is needed for reproduction to begin. They also showed that the accumulated temperature depended on the date of planting i.e. on the rearing temperature. MERCER (1990) reported completion of development of the first generation as the appearance of distinct juveniles within the eggs; for *M. hapla* this occurred when 407 dd had accumulated above 10 °C. This is equivalent to 491 dd above 8 °C. In our study (V) the estimated heat requirement included dd needed for the hatching of the larvae, whereas MERCER's estimate did not. Taking into account the difference in the method of calculations, our results are quite consistent with those in MERCER (1990).

Although BAKER (1980) encountered many problems in using assumed lower temperature thresholds and averaged meteorological data when calculating accumulated temperatures for predictions of expected developments, in this study accumulated temperatures were found to be a useful tool for predicting the possibility and time of development of cyst and root-knot nematodes. JONES (1983) has also argued that despite the difficulties of assumed basal development temperatures and average soil temperatures, the development of endoparisitic nematodes can be effectively predicted by means of accumulated temperatures. Soil temperatures at 10 cm fluctuate less than air temperatures and the amplitude of fluctuation decreases with depth. In addition, the weather has not such a complex effect on nematode behaviour as it has on that of insects (BAKER 1980). Accumulated temperatures have been widely used for predicting the development of nematodes (FERRIS et al. 1978, QUICKLEY 1980, WEBLEY and JONES 1981). In the use of accumulated temperatures there are at least three important prerequisites: i) the right threshold temperature needs to be found, ii) the difference between optimum temperature for the nematode development and the average temperature of places where nematode occurs needs to be known iii) the possibility of adaptation of the nematode to new environmental conditions has to be taken into account. In addition, the effect of the cultivation method may also be essential as was found in our field experiment (VI).

In Finland, the average accumulated soil temperature above 4.4 °C is 1 200—1 400 dd in southern parts and 740—870 dd in northern parts of the country. Heat accumulation is thus sufficient for development of one generation of cyst nematodes upto the Arctic Circle, but in the northernmost part of Finland only a small number of individual nematodes are able to complete their entire life cycle. Although MAGNUSSON (née SARAKOSKI) 1986 argued that potato cyst nematode fails to complete its life cycle in temperatures corresponding to conditions at the Arctic Circle, SARAKOSKI (1976) has already reported the northernmost discovery of potato cyst nematode at a place located a few kilometers north of the Arctic Circle. Also ANDERSSON (1987) has discovered high population densities of potato cyst nematode in northern areas where MAGNUSSON (1987) considered the development to be impossible. This example proves that in the use of accumulated temperatures the calculations must be based on correct parameters, otherwise, even already established populations may be seen as a "remarkable finding" as with MAGNUSSON (1987) and control strategies may be based on incorrect conclusions. Because of the poor multiplication of the nematodes on pot-grown plants MAGNUSSON (1986) was even unable to get a population increase in treatments adjusted to simulate the conditions of central and southern Finland, although in southern Finland the potato cyst nematode is known to have caused yield losses annually since the 1970s. However, the present result on heat requirement: 598 ± 24 dd above 4.4 °C for the development of cyst nematodes, is consistent with the northernmost discoveries of potato cyst nematode

For cyst nematodes, which may have several generations per season, the accumulated soil temperature in Finland is inadequate. For example. the development of two generations of cyst nematodes would require about 1 200—1 300 dd above 4.4 °C In Finnish field conditions perfect development of two generations is virtually impossible and this might be the main reason why population densities of the beet cyst nematode remain below the economical threshold even in fields with continuous cropping of sugar beet (IV). It may also be an explanation why cereal cyst nematode has not become established in Finland although it is common in southern Sweden.

For the development of the northern root-knot nematode the heat accumulation during a growing season was critical. After the laboratory experiments, development of new larvae required 553 ± 2 dd above 8.3 °C. Correspondingly, in the field experiments newly-developed larvae were found only on the plants which had accumulated 631 dd. The critical heat sum was barely reached in carrots but well fulfilled on perennial white clover. In 1987, which was an exceptionally cold year, the field populations of the nematode disappeared totally when the heat accumulation for all plants was below 553 dd (VI). Thus the results of the field experiment proved that the thermal requirement estimated by the greenhouse experiments was useful for predicting the development of the root-knot nematode out-of-doors.

When using the accumulated temperatures as a tool for predictions, it must be remembered that: (i) maximum output of new larvae needs about 200—300 dd more than development of the first larvae (VII), (ii) ecotypes from separate areas may have different thermal requirements, (iii) heat units at optimum temperatures are not equal to units at extreme temperatures, and (iv) temperature records of meteorological stations are never totally representative for variable micro climates. It is known that at both ends of the temperature range the response of a nematode to temperature is distorted and one dd is not as effective in promoting growth as in the optimal range (THOMASON and FIFE 1962). This phenomenon is important especially in highlatitude climatic conditions.

1.3. Impact of low soil temperatures on initial energy reserves of nematode larvae

The present study (II) showed that nematodes which developed at minimal soil temperatures have lower initial energy reserves than those developed at higher temperatures. The hypothesis presented in RICHARDS (1964) that "relatively more energy is required for the complete development of insect larvae at minimal temperatures" apparently concerns nematodes, too. The amount of energy reserves depended on temperature and accumulated temperature, but the effect of developmental time alone was insignificant (II). The lipid content of potato cyst nematode larvae reached its maximum at 20 °C, and was at the same level at 24 °C. At 12 °C and at 16 °C the energy reserves were significantly lower than at 20 °C. An increase of 100 dd in accumulated soil temperature raised the reserves by about 3 %. The interaction of temperature and time of development was significant also in the size of the larvae. DAO (1970) had also found that the rearing temperature affected the size and other morphological characters of nematodes.

Infectivity of plant parasitic nematodes depends on their energy reserves (van GUNDY et al. 1967, CROLL and MATTHEWS 1973, STOREY 1984, STOREY and ATKINSON 1984) which mainly consist of neutral lipid reserves (BARRET 1976). ROBINSON et al. (1987 a, 1987 b) have described how lipid reserves influence the activity of potato cyst nematode larvae; the 65 % level of the initial lipid content was critical to infectivity. Energy reserves may also affect the susceptibility of larvae to control methods (ALPHEY 1983). Nematode energy metabolism is described in detail for example by ROLLA (1980).

The results of this study suggested that in Northern Europe a part of nematode larvae of field populations may no be infective at all, or their infective life is short. Correspondingly FERRIS (1985) suggested that low levels of initial food reserves may result in a reduced capacity to survive overwintering in root-knot nematodes. The initial energy reserves of the potato cyst nematode developed at the typical Finnish soil temperature of 16 °C were distinctly lower than the reserves of the larvae developed at 20 °C. The critical energy reserve for infectivity ROBINSON et al. 1987 b) was reached by 46 % of the larvae developed at 12 °C, by 60 % at 16 °C, by 73 % at 20 °C and by 76 % developed at 24 °C. The low level of initial energy reserves of potato cyst nematode larvae might be one of the reasons why potato cyst nematode has been controlled successfully be means of short crop rotation cycles (III) in Finland.

The present result also supported STOREY's (1984) suggestion that measurement of lipid reserves is of value for modifying the economic thresholds. In addition, the estimation of lipids can possibly be used as qualitative test for the assessment of population densities and infectivity instead of the biotest, which was described for example for the beet cyst nematode by MÜLLER et al. (1990). So far, because of the complicated methods, the estimation of lipid reserves has not been widely used. The computer-aided image analysis, used in this study, was found to be a useful method for routine work. In the image analysis, both the size and the density of stained lipid are included in the estimation and the analysis can be done from one individual or for many larvae at a time.

In addition to planning control strategies, the effect of minimal temperatures on initial energy reserves could possibly be applied in the predictions of distribution and pest potential of nematodes in new areas. The phenomenon, that population density of the potato cyst nematode declines faster in northern Sweden than in the southern part of the country (ANDERSSON 1987), may be related to lower energy reserves of the northern populations. Low energy reserves may also increase the susceptibility of nematodes to soil antagonists and cause higher fungal parasitism of the northern potato cyst nematode populations as was described by ANDERSSON (1987) and DACKMAN (1988).

Although in many cases the infective life time of nematodes depends on energy reserves it is not the only factor affecting infectivity. CROLL and MATTHEWS (1973) warned, that the loss of lipid has often been related to a reduction of larval infectivity and it has almost become a parasitological dogma that the physiological age of a nematode larva may be determined by an examination of its lipid reserves. CROLL and MATTHEWS (1973) showed that the aging of hookworm (a parasite of cats) is related directly to a decreased metabolic rate, and not primarily to lipid levels. Infectivity of entomophilic nematodes has often been related to factors other than energy reserves. MOLYNEUX (1985) and FAN and HOMINICK (1991) have argued that energy reserves are critical for different species to differing extents because of the behavioural differences of nematodes.

2. Other factors influencing the development of nematode populations

2.1. Abiotic factors other than temperature

Soil structure

In addition to temperature, the main climatic factors affecting the development of nematodes are moisture, light and cyclic influences (DAO 1970). Moisture affects nematodes via the soil, and light via the host plant. Soil factors include soil structure, moisture, chemistry and soil air content. Of these, soil structure and moisture are the two most important ones in Finnish conditions. In the present study (I) a higher proportion of potato cyst nematode larvae invaded potato roots in sandy soil than in clay soil. The peak numbers of migrating larvae were similar, 314 and 375/100 ml soil, in clay soil and sandy soil, where the peak numbers of invaded larvae were different, 41 and 312/g of root, respectively. The two peaks of root invasion found in clay soil in 1984 indicate that migration takes longer in clay than in sandy soil. The longer the time of migration, the more energy is used. In the case of larvae with low initial energy reserves, the energy spent during migration may lower their capacity for invasion.

The soil environment affects the activity of cyst and root-knot nematodes only for a short period during the invasion process. Nematodes in soil pores are influenced by pore morphology and size, the amount of water in the pores, surface tension forces and the oxygen concentration in the pore the amount of water in the pores, surface tension forces and the oxygen concentration in the pore (JONES 1978). Studies in graded sands show that nematodes move fastest when the particle size is about one-third of the nematode body length i.e. when particles fit into the wave pattern of the nematode when moving in water (WALLACE 1958). For the motility of cyst nematodes coarse sand is best (WALLACE 1956). Correspondingly, the larvae of northern root-knot nematode migrate faster and produce more root knots, in loamy sand than in sandy loam, and no migration occurred in sandy clay loam STEPHAN and ESTEY (1982). In general, yield losses caused by cyst nematodes are most severe in light soils (JONES 1975 b), and FERRIS & van GUNDY (1979) reported that root-knot nematodes occur in greater numbers in sandy soils than in clay soils.

Considering soil type, the risk of yield losses caused by heteroderids in Finland is much higher on potato than on sugar beet or cereals, because 50 to 80 % of potato fields (depending on the region) are on sandy soils and very few on clay soils. The soil used for growing cereals is in most cases clayey, and sugar beet is often grown on heavy soils, too. Soil type may thus have been one of the factors preventing the developments of cereal cyst nematode populations in Finland; this nematode is relatively common on southern Sweden, for instance.

As far as root-knot nematodes are concerned the light soils used for production of carrots and potato may favour population development. In this study, neither of the experimental fields infested with the root-knot nematode had the optimal soil type for the development of the nematode, and thus the pest potential of the nematode might be higher on fields with lighter soil. The experimental fields had to be chosen so that there was no risk of the nematode spreading to the surrounding fields.

Soil moisture

In all kinds of soil, the movement of nematodes is dependent on the presence of a water film around soil particles (WALLACE 1958). The results of this study suggest that the exceptionally severe nematode damage encountered on sugar beet in 1977 was caused by the unusually rainy and warm spring weather which favoured the movement of beet cyst nematode larvae and their invasion of plant roots (IV). It is known that rain in spring improves larval motility (JONES 1983) and that successful larval migration is reflected as yield losses (BELAIR 1987, BROWN 1987). During dry springs and summers, nematodes are more or less inactive except after occasional rain when the soil pores are briefly filled with water. It follows that accumulated rainfall is a crude measure of the duration of activity (JONES 1975 b). In Finland it is obvious that in areas with plenty of snow melting in the spring, soil moisture is rarely a limiting factor after the hatching of nematodes.

Daylight length

The discovery of potato cyst nematode in the far north of Finland indicates that it is well adapted to long daylight. It has been suggested that day length may have an influence on the multiplication of cyst nematodes and may affect their development and distribution (ELLENBY 1958, EVANS, et al. 1975). In addition, studies on root-knot nematodes have shown that the photoperiod influences the migration of the nematodes by determining the host plant's production of attractive substances which stimulate larval movement (PROT and van GUNDY 1981). In the climatic conditions of high latitudes, the plant vigour brought along by the overwhelming solar radiation might improve the host quality of plants and affect the development of endoparasitic nematodes.

2.2. Biotic factors determined by agricultural practices

Effect of host plant in crop rotation

The development, distribution and economic importance of nematodes is dependent on many agricultural variables of which the number and relative suitability of available hosts is the most important (SASSER 1977). In agroecosystems the frequency of occurrence of host plant on a field depends on crop rotation. This study (III) showed that growth of populations of the potato cyst nematode, which has only one host plant, can be effectively prevented by crop rotation. When potatoes were grown once in three years on a site, alternating between a susceptible and a resistant cultivar, the population density of potato cyst nematode fell below the detectable level. In warmer climatic conditions than those prevalent in Finland longer rotation cycles are needed (TRUDGILL et al. 1987). The present results on the control of beet cyst nematode suggest that if climatic factors restrict the development of a nematode as effectively as they do in Finland, even one non-host crop can reduce the nematode population density to an economically acceptable level (IV). In the case of polyphagous species such as the root-knot nematode, however, it is more difficult to find a type of crop rotation which would prevent the development of nematode populations (SANTO et al. 1980).

During one growing season, host plants affect phytoparasitic nematodes in many ways, starting from the hatching process to the development of new larvae. In this study the hatching rate of potato cyst nematode was found to be related to the crop of the preceding season. In the first year after potato, the spontaneous hatching rate was 80—90 %, or as high as hatching on potato. This percentage is higher than that normally reported for spontaneous hatching (WARD et al. 1985). The result supports the suggestions that soil micro-organisms (ELLENBY and SMITH 1967) or remnants of the host plant might produce hatching factors (PERRY et al. 1981). In the second and subsequent years after potato, the spontaneous hatching rate was about 50 %, which corroborates previous findings.

Once the larvae have invaded the roots, their multiplication depends on the growth and host status of the plant; the host location is governed by root exudates (e.g. MOLTMANN 1990), and the rate and time of development depend on host quality (MILNE and DU PLESSIS 1964, FASSULIOTIS 1970). In the present study, the multiplication of potato cyst nematode on continuously grown potato ranged from 0.2 to 31.4 per season, depending on the initial population density of the nematode and growth vigour of the potato. In the infection process, the host-parasite interaction determines how many larvae are able to enter and become established at each infection site. In some cases the host status affects the sex ratio of the developing nematode population (GUIRAN and RITTER 1979) and thus also its multiplication; it is further known that the higher the population density, the greater the proportion of males. TRUDGILL (1967) suggested that the competition for giant cell sites was a determining factor in sex determination. Sex ratios were not investigated in the present study, but a clear population decline was found in the field when initial population densities were high and the growth of host plant was poor (III).

In the laboratory studies on the root-knot nematode, no difference in developmental time was found between cabbage and tomato although more larvae developed on tomato (V). TRUDGILL (1972) has suggested that juveniles receiving a poor supply of food may take longer to reach the point at which moulting to next stage is possible, and hence nematode development may take longer on a poor host plant. Thus, the value of the invaded plant as host must be considered when accumulated temperatures are used to predict the development and pest potential of nematodes.

Use of resistant cultivars and non-host plants

Plant resistance to nematodes is widely used to control nematode multiplication. In this study, it was found that resistant potato cultivars reduced the population density of potato cyst nematode by 70—80 % annually when used after a non-host crop (III). The same rate of population decline has been found in many previous studies (e.g. TRUDGILL et al. (1987). In the field experiment reported by MAGNUSSON (1984), the population density of potato cyst nematode decreased 66 % on average per season when resistant cultivars were grown for four years. During the first years after susceptible potato the density decreased 70—90 %.

Varieties resistant to beet cyst nematode and root-knot nematode also exist (FASSULIOTIS 1979, COOKE 1985) but these are not used in Finland. STEPHAN and TRUDGILL (1982) studied the resistance of cucumbers against *M. hapla* and suggested that the durability of this resistance is unknown, because many populations will possess the capacity to adapt and may develop resistance breaking pathotypes. The possibility of favouring the selection of aggressive pathotypes had limited the use of resistant cultivars especially for the control of potato cyst nematode in many European countries. To avoid this type of selection in Finland, plant quarantine regulations require that the H1-resistant potato cultivars are alternated with susceptible varieties on fields officially declared as infested by the potato cyst nematode. On non-infested fields, resistant cultivars are allowed to be grown without limitations.

Although the use of resistant cultivars as a method of controlling the potato cyst nematode does not cause environmental problems, it is an expensive and short-lasting method of ensuring monoculture cropping of one plant.

A non-host crop decreased the population density of beet cyst nematode by 40 % and that of potato cyst nematode by 60 % annually (IV). The first non-host crop after potato reduced the potato cyst nematode population by 90 % but the subsequent reduction was 50 % annually. MAGNUSSON (1987) observed a 87 % decrease of the potato cyst nematode population under barley in the first year after potato. Barley is hardly more attractive to the potato cyst nematode than any other non-host plant for potato cyst nematode, although MAGNUSSON (1987) proposed that this might be the case. It appears more likely that the sharp decline in the first year after potato was due to hatching factors remaining in the soil, as many other workers have suggested (ELLENBY and SMITH 1967, TSUTSUMI 1978, PERRY et al. 1981).

ANDERSSON (1987) reported that in central and northern Sweden the population decline of potato cyst nematode in the first year after a potato crop is 80—90 % independent of the species of the non-host plant. The same situation is apparent in the results of MAGNUSSON (1987), too, but she did not use this information in her conclusions. The present study (III) supports ANDERSSON's (1987) statement that the control effect of resistant cultivars is mainly wasted if they are used in the first year after susceptible potato, because the population density of the nematode declines sharply anyway.

Timing of cultivation practices

The present study showed that in Finland the increase of potato cyst nematode populations can be prevented by harvesting the potatoes before the first week of August, i.e. before the accumulated soil temperature (10 cm) above 4.4 °C exceeds 600 dd counting from time of planting of potatoes. It was also found that some newly developed larvae hatch in mid August and thus harvesting at that time might have an effect on the final population density of the nematode. The effect of haulm killing on the population increase of the potato cyst nematode was studied in a preliminary field experiment. It was found that the final population density was lower in plots where the stems of the potato plants were cut in the middle of August than in plots where the potatoes were allowed to grow four weeks longer (TIILIKKALA 1983). In general, any cultivation practices, which enhance the early maturation of host plants are beneficial from the point of nematode control in high latitudes.

There have been some reports of problems with repeated early harvesting. HOMINICK (1979) showed that repeated cultivation of early potatoes favours the selection of nematodes which hatch at lower temperatures, and WEBLEY and JONES (1981) suggested that early harvesting might favour *G. pallida* because of its ability to develop faster than *G. rostochiensis* in cool soils. In Finland, *G. rostochiensis* is already well adapted to low soil temperatures (I), and further adaptation is not likely, as potato is hardly ever planted when the soil temperature is below 4 °C. On the other hand, the probability that *G. pallida* might thrive in Finland is high, and therefore the spread of *G. pallida* to Finland should be prevented by all available means.

In the field studies (I), a low secondary peak of free-living potato cyst nematode larvae occurred in August concurrently with a reduction in the numbers of encysted larvae. The significance of the hatching of new larvae from yellow cysts, reported previously by ELLENBY and SMITH (1967) and STOREY (1982), requires further study before the phenomenon can be availed of in control strategies. Harvesting during the third week of August may be useful for the control of potato cyst nematode in Finland.

For root-knot nematodes, the normal harvesting time of annual plants in Finland is early enough to control nematode population increase (VI). Perennial host plants, however, may accumulate a temperature sum high enough for complete development of the nematode and may maintain permanent populations for some years. This would appear to offer a good chance for the nematode to adapt to low soil temperatures. In the case of the beet cyst nematode, the normal harvesting of sugar beet stops the development of the second generation and is sufficient to keep population densities at an economically acceptable level.

The effect of organic manuring on the population development of the potato cyst nematode was studied in a microplot experiment in 1985—1987. Microplots were made of concrete drain pipes (diameter 40 cm) placed upright in soil and filled with soil of one of four types: sand, mould, peat and clay, 16 plots/soil type. Every other plot was manured with commercial chicken manure (BIOLAN, 2 500/ha) and the rest with chlorine-free NPK fertilizer (800 kg/ha). One hundred cysts of *G. rostochiensis* were mixed in the soil of each plot. Susceptible potato cultivar was grown during three years, and after the third year population densities of the nematode were in average more than double in the plots with chemical fertilizer compared with those in the plots with organic manure (Fig. 1).

It is well established that organic manuring affects the development of cyst nematodes. The possible mechanisms include the alteration of attractive compounds in the soil, an increase in soil organisms antagonistic to nematodes, changes in vesicular arbuscular mycorrhizae (VAM) and enhancement of the activity of many indigenous soil microbes (KERRY 1990). HOESTRA and HARSHHAGEN (1981) reported that softwood bark added to the soil reduced the number of newly formed cysts of the potato cyst

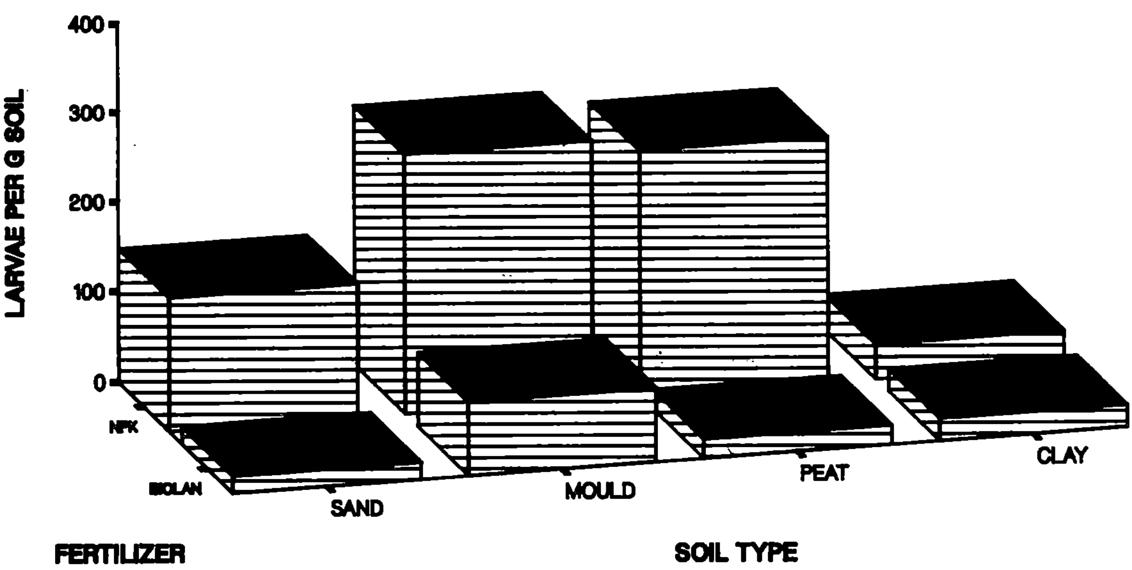

Fig. 1. Population density of the potato cyst nematode after three susceptible potato crops in microplots in four different soil types. The plots were manured with commercial chicken manure (BIOLAN) or chlorine-free NPK fertilizer.

nematode considerably compared with untreated soil; however, NICOLAY et al. (1990) failed to establish stimulation of the activity of fungal egg parasites of the beet cyst nematode by green manuring.

The existence of fungi which prey on nematodes has been known for a long time (ZOPF 1888), but it was not until DRESCHLER (1937) reported 17 antagonistic species that it was realized that they were fairly common. KERRY (1984) was able to refer to 145 scientific publications in his review on nematophagous fungi. Fungal parasites of cyst nematodes are also known to occur in northern conditions (DACKMAN and NORDBRING-HERTZ 1985, DACKMAN 1990). Bacterial infections of plant parasitic nematodes may also have potential as a biocontrol agents (CHANNER et al. 1990), and nematodes have many natural enemies among invertebrate animals (SCHAEFFENBERG 1950, MURPHY and DONCASTER 1957).

Future trends in crop protection may favour the use of cultural methods in nematode control instead of chemicals KERRY (1990), which can be expected to encourage ecological studies of soil organisms. In Finland, where the soils are cool and moist such studies should be focused on finding control agents from among fungi, some of the most important of which may be VAM fungi (CARON 1989). OSMAN et al. (1990) have already shown that the final population of nematodes and the amount of damage decreases when plants are treated with VAM fungus. In general, the role of all organisms of the rhizosphere should be better known before biological control can be applied in practice. In high latitude climatic conditions, the low level of energy reserves of nematode larvae may increase their susceptibility to biological control agents; it has been found that the proportion of naturally parasitized potato cyst nematode larvae is the higher the more northerly the nematode's geographical distribution (ANDERSSON 1987, DACKMAN 1988).

3. Factors affecting the distribution and pest potential of nematodes

SASSER (1977) divided biological and environment influences in three phases: in transit phase, establishment phase and economic importance phase. The present study showed that especially at high latitudes abiotic factors determine the establishment and economic importance of nematodes. Agricultural practices may be important in the transit phase and may also have influence on nematode establishment and pest potential in areas where nematodes are subject to extreme climatic conditions.

Data on the geographic distribution of plant parasitic nematodes is far from comprehensive, and knowledge of factors determining it are fragmentary. Based on studies of nematode populations in relation to their environment, DAO (1970) published a functional scheme of factors important for the development of nematodes (Fig. 2). DAO's results on the direct effects of locality, soil, plant and growth factors are consist with the findings in the present study and show that the distribution range of nematodes is determined to a large extent by climate, especially by temperature. DAO (1970) argued that the climatic or geographic range of a nematode species appears to be closely related to lethal temperatures on the one hand, and optimum temperatures for activity on the other. In Finland, as in other high latitude areas, the most important factor limiting the establishment and pest potential of nematodes is the shortness of summer (DOWNES 1964). Even the duration of daylight may, in some cases determine nematode establishment (EVANS et al. 1975).

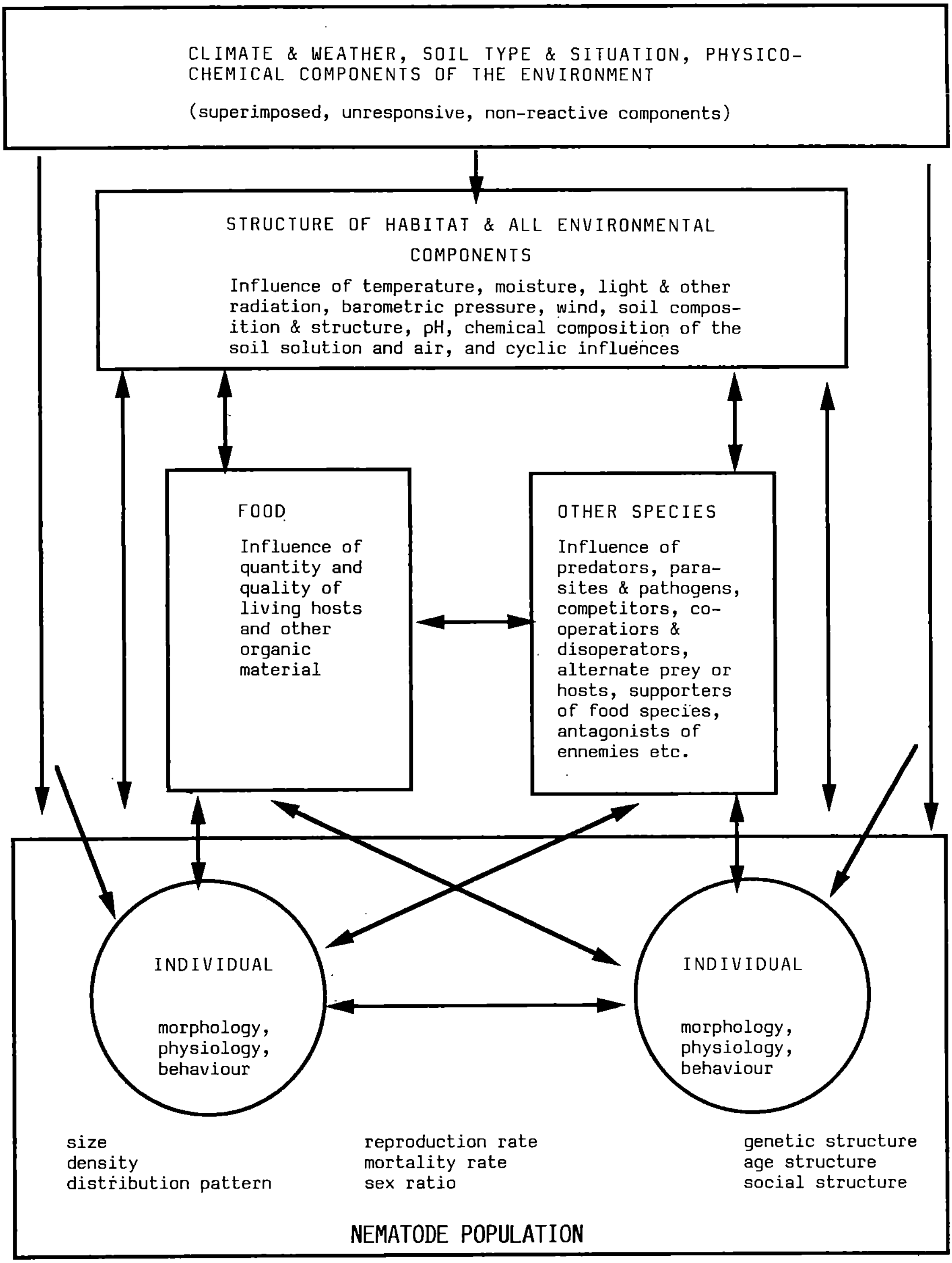

Fig. 2. Scheme of the relation of a nematode population to its environment according to DAO (1970).

4. Pest potential of *Heteroderoidea* nematodes in Finland

4.1. Current situation

Cyst nematodes

Based on present knowledge, it can be argued that the potato cyst nematode in Finland is well adapted to high latitude conditions and agricultural practices. The nematode is common up to 62° N latitude where it is able to cause crop losses every year. Temperature requirements do not seem to limit the spread of the nematode (QUICKLEY 1980), which is consistent with the discovery of the nematode north of the Arctic Circle (SARAKOSKI 1976) and its reported distribution in Sweden (ANDERSSON 1987) and Iceland (SIGGEIRSSON and QUICKLEY 1983). Quite recently (1990) Finnish agricultural advisors found a potato cyst nematode population causing distinct yield losses in Sotkamo (64° N). The heat accumulation during the growing season in Sotkamo area is the same as in Tornio, about 30 km south of the Arctic Circle (MUKULA and RANTANEN 1987). This indicates that the nematode population encountered by SARAKOSKI (1976) is no isolated finding and that population densities of the potato cyst nematode can become economically relevant even in Lapland if potatoes are grown continuously in the same fields for a long time.

The pest potential and economic importance of the potato cyst nematode is reduced in Finland because of low soil temperature. Population decline is relatively fast even in southern Finland possibly because of the low initial energy reserves of the larvae. The nematode can be controlled by cultural methods, and no nematicide is needed (III). In the northern parts of the potato growing area, the risk of potato cyst nematode populations reaching economically meaningful numbers is low. Even short crop rotation cycles (1 : 2) may be sufficient if combined with other agricultural methods such as early harvesting and the use of resistant cultivars.

The risk of *G. pallida* thriving in Finland is high, as it is better adapted to cool climatic conditions (FOOT 1978, MUGNIERY 1978, FRANCO 1979) than *G. rostochiensis* and its pest potential in Finland would be higher. In 1986 the Plant Quarantine Office of Finland started a survey of the distribution of potato cyst nematodes in Finland and so far all the species found have been identified and no *G. pallida* has been detected. It is nevertheless possible that it will be encountered at a later stage because the fields with the highest population densities have not yet been thoroughly investigated.

The pest potential of the beet cyst nematode in Finland is very low owing to only one generation per growing season. The beet cyst nematode has been present for a long time on farms with continuous growing of sugar beet and thus its adaptation to low soil temperatures is, no doubt, complete. The increased cultivation of oil seed rape could in some cases increase beet cyst nematode populations to levels causing economically significant losses (HORN 1961), and thus the presence of beet cyst nematode has to be taken into account when planning crop rotations.

Root-knot nematodes

The risk posed by the northern root-knot nematode *(M. hapla)* on outdoor fields in Finland is very small. Some populations may survive the winter provided that they are better adapted to low soil temperature than the populations of this study. In southern Sweden, this nematode has been present for a long of time (ANDERSSON 1970) without causing any great economic losses. BANCK (1985) found that in the Uppsala region (temperature accumulation equivalent to that in southern Finland) root-knot nematode populations gradually disappeared if distributed outdoors. The pest potential of *M. chitwoodi* would be much higher be-

Table 2. Some factors affecting the pest potential of *Heteroderoidea* nematodes in Finland. Adapted from SASSER (1977).

Biological/Environmental factors	Probability index		
	PCN	*H. schachtii*	*M. hapla*
In transit phase			
1) Endo- or Ectoparasitic	8	7	6
2) Developmental stage(s) involved in transit	10	9	6
3) Amount of inoculum and frequency of transport	4	2	10
4) Type and conditions of carrier soil, root, seed, leaves	8	8	8
5) Sensitivity to desiccation	10	9	5
Establishment phase			
1) Numbers and relative suitability of available hosts	3	5	10
2) Amount of inoculum and frequency of transport	9	4	6
3) Temperature requirements	8	2	1
4) Moisture requirements	9	8	8
5) Soil requirements	9	7	7
6) Mode of reproduction	7	7	8
7) Survival mechanisms	10	8	4
8) Capacity to change and adapt to new situation and cultivation	2	4	8
Economic importance phase			
1) Host range and economic importance of crops attacked	3	4	9
2) Number of life cycles and reproductive capacity under prevailing environmental conditions	7	2	1
3) Pathogenicity	7	2	6
4) Ability to interact with other soil borne pathogens	7	7	9
5) Cropping systems and land management practices	8	8	8

PCN = potato cyst nematode
Probability index scale of 0—10. 0 = highly unfavourable, 10 = highly favourable

cause of its better adaptation to cool climatic conditions (SANTO and O'BANNON 1981). In addition, the host range of *M. chitwoodi* is wider than that of *M. hapla* (SANTO et al. 1980, SANTO and O'BANNON 1981). According to KURPPA (1985), 12 % plant material imported to Finland in 1980 was infested by root-knot nematodes showing that the risk of *M. chitwoodi* spreading to Finland is a real one. In greenhouses, *M. hapla* is able survive and reach high numbers especially on roses, which are grown in the same growth media for many years. Although lowering of the greenhouse temperature for the winter season decreases the soil temperature under roses to 4—6 °C, the nematode is not killed, but its development is distinctly delayed. In modern cropping systems, isolation of the growth medium from the ground soil prevents invasions by nematode larvae. In greenhouses with ebb and flow systems, nematodes can spread rapidly (AMSING 1990) and the yield losses may be as severe in Finland as in any other country.

The results of the present study and rough estimates of the critical factors affecting the outdoor pest potential of root-knot and cyst nematodes can be incorporated within a hypothetical scheme (Table 2) adapted from that of SASSER (1977).

4.2. Influence of possible future warming of the climate

Under the scenario of a long-term climatic change caused by a doubling in the atmospheric carbon dioxide concentration, the average annual temperature in Finland will be 4—5 °C higher than at present (KETTUNEN et al. 1988);

precipitation could be expected to rise by about 25 mm at the beginning, 35 mm at the middle and 15—20 mm at the end of the growing season. An increase of one degree in air temperature causes the soil temperature to rise by 0.71 °C at the depth of 1 cm and by 0.47 °C at 10 cm (MacLEAN and AYRES 1985). Changes such as increases in soil temperature and accumulated temperature and an increase in precipitation in the spring may lead to increased pest potential of nematodes in Finland. The effective growing season of soil organisms may lengthen relatively more than that of many other organisms, as there would be no soil frost and heat would not be spent on melting the frozen soil pores in the spring. In addition, shorter and milder winters may also enhance the overwintering of many cold-sensitive nematode species.

The results of the present study indicate that even a modest warming of the climate might improve the success of nematodes; in addition, the predicted changes in the cultivation of crops in Finland (KETTUNEN et al. 1988) might also render the agriculture-related factors more favourable for nematode spread and development. In the future, the species pattern of nematodes in Finland may resemble that now prevailing in Denmark or the Netherlands.

In the speculated warmer climate, the pest potential and economic importance of the potato cyst nematode would be high in southern Finland, and in the northern potato growing areas the problems would resemble the present situation in southern Finland. Special attention would have to be paid on maintaining the area of seed potato production free from potato cyst nematode. The beet cyst nematode would be able to produce two generations per year and its population densities might reach economically harmful numbers, making the continuous growing of sugar beet on the same fields uneconomical. Root-knot nematodes *(M. hapla, M. chitwoodi)* might become established as outdoor pests and plant quarantine regulations would have to be focused on limiting the spread of these polyphagous nematodes.

In general, any warming of the climate would require much more attention on nematode control, including improved knowledge about the antagonistic potential in soils in order to allow successful integration of this phenomenon into nematode control systems. There would be no sense in starting chemical control in Finland after avoiding it for such a long time. The danger of ground water contamination and other adverse environmental effects caused by soil fumigants and nematicides, experienced to day in the Netherlands (LISTER and BOESTEN 1989), for example, should be reason enough to pursue ecologically acceptable solutions to the possibly increasing nematode problems in Finland.

SUMMARY AND CONCLUSIONS

The influence of temperature and cultural practices on potato cyst nematode, beet cyst nematode and the northern root-knot nematode was studied in 1978—1989.

In the present climatic conditions in Finland the pest potential of cyst and root-knot nematodes is relatively low compared with that in central Europe. The population densities of beet cyst nematode remain mostly under the level of economic impact, 10 larvae/g soil, because complete development of only one generation per season is possible. The lack of nematode damage has allowed ecologically inadvisable continuous cultivation of sugar beet on the same fields without crop rotation.

The potato cyst nematode is able to complete

its life cycle in the whole potato growing area in Finland upto the Arctic Circle, although in northern Finland only a small proportion of nematodes produce new larvae before the end of the growing season. Monoculture growing of susceptible potato varieties can increase the populations to economically significant densities in all parts of the country. Yield losses and multiplication of the nematode can be controlled by crop rotation; good results were obtained in a field study by growing potatoes once in three years, alternating susceptible and resistant cultivars. Early harvesting can be used to restrict the multiplication of the nematode. No nematicide is registered for the control of potato cyst nematode in Finland and none is needed.

Summer and winter temperatures both affect the northern root-knot nematode in field conditions in Finland. About 10 % of the nematode population was able to overwinter outdoors when transferred in infested peat from a greenhouse to a field. The nematode failed to produce new larvae on carrots, but new larvae were found on white clover during a summer when the clover accumulated 631 dd above 8.3 °C. During the exceptionally cool summer of 1987, all the field populations of the northern root-knot nematode vanished. The risk *M. hapla* becoming a serious pest on open fields in Finland is low, whereas *M. chitwoodi* might survive and thrive in case it spreads to Finland. If growth media infested with *M. hapla* are used for growing crops, they should be spread on open fields in the autumn and the fields fallowed for one year before growing host plants on them.

Accumulated soil temperature was found to be a useful tool for predicting the development, distribution and pest potential of the nematodes in high latitude climatic conditions. For the predictions, accurate base temperature of development and the temperature requirements of a complete life cycle are required. A useful base temperature for predicting the development of cyst nematodes was found to be 4.4 °C and development of new larvae required 598 ± 24 dd above 4.4 °C. The temperature requirement of cyst nematodes estimated by field studies in southern Finland is consistent with the northernmost locations of the potato cyst nematode in the Nordic Countries and with the multiplication rate of cyst nematodes in southern Finland.

In laboratory experiments, the base temperature for the development of the northern root-knot nematode was found to be about 8.3 °C and the first new larva was found to hatch when 553 dd had accumulated above the base temperature. The temperature requirements were found to be the same for a Finnish population originating from a greenhouse and field populations from southern Sweden and the Netherlands. In a field study, newly hatched free larvae were found only on plots growing perennial white-clover which accumulated 631 dd per season. In contrast, carrots grown as an annual host plant accumulated 554 dd and no free larvae were detected in the soil at the time of harvest. The results show that accumulated soil temperatures can be used to predict the development of nematodes, provided that modifying effect of various cropping variables are taken into account.

Previous studies indicated that insects require more energy for complete larval development in low temperature environment. Laboratory studies to test whether the same was true in the case of the potato cyst nematode showed the lower the soil temperature during development, the smaller the initial energy reserves of larvae. The results indicate that in Finland the infective life span of nematodes may be shortened and their pest potential lowered because of the low energy reserves of larvae developing at temperatures 4—6 °C lower than the optimum.

The speculated warming of the climate would improve the success of the phytoparasitic nematodes and increase their pest potential in Finland. Beet cyst nematode populations would increase to such an high extent that the continuous growing of sugar beet on the same fields would no longer be possible. The problems caused by potato cyst nematode would increase and the situation would resemble that currently experienced in Denmark or the Netherlands. Special attention would have to be paid on maintaining the area of seed potato production free from the nematode. Milder winters and longer growing seasons might enable the root-knot nematodes and some other species to spread to fields in southern Finland and cause yield losses and quality problems in plants such as potato and carrot. In general, more attention would have to be focused on nematodes and more knowledge about the interaction of soil organisms would be needed if the worsening nematode problems are to be controlled without pesticides.

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SELOSTUS

Ilmaston ja viljelytoimenpiteiden vaikutus kysta- ja äkämäankeroisten vahingollisuuteen Suomessa

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Maatalouden tutkimuskeskus

Lyhyt ja viileä kasvukausi rajoittaa ankeroisten kehitystä

Ankeroisten aiheuttamat kasvinsuojeluongelmat ovat olleet varsin vähäisiä Suomessa verrattuina esimerkiksi Keski-Euroopassa todettuihin ongelmiin. Tärkeimpiä ankeroisten menestymistä rajoittavia tekijöitä ovat tämän tutkimuksen mukaan kasvukautemme lyhyys ja maan lämpötilan alhaisuus kasvukauden aikana. Esimerkiksi juurikasankeroisella on meillä vain yksi täydellisesti kehittyvä sukupolvi vuodessa, kun se tarvitsisi vähintään kaksi sukupolvea, jotta toukkien määrä nousisi haitallisen suureksi. Keski-Euroopassa juurikasankeroisella on kolme sukupolvea kasvukaudessa. Juurikasankeroisen on todettu esiintyvän jatkuvasti muutamilla Salon seudun ja Turengin juurikasviljelmillä aiheuttamatta selvää sadonalennusta kesää 1977 lukuunottamatta. Silloin havaitut poikkeuksellisen näkyvät vioitukset johtuivat todennäköisesti ankeroisten kehitystä edistäneistä säistä. Maan korkea lämpötila toukokuun alussa ja samanaikaiset runsaat sateet edistivät ankeroistoukkien liikkumista niin, että suuret toukkamäärät saattoivat tunkeutua normaalia aikaisemmin taimien juuriin aiheuttaen selviä kasvuhäiriöitä. Ankeroisten aiheuttama vioitus on yleensä sitä vahingollisempaa, mitä aikaisemmassa kasvin kehitysvaiheessa toukat tunkeutuvat juuriin.

Peruna-ankeroisella on Euroopassa yleensäkin vain yksi sukupolvi vuodessa kasvukauden aikana, joten sen edellytykset muodostua tuholaiseksi pelloillamme ovat suhteellisesti paremmat kuin juurikasankeroisen. Etelä-Suomessa peruna-ankeroisen toukkamäärät nousevatkin helposti yli tuhokynnyksen, 10 toukkaa/g maata, jos perunaa viljellään jatkuvasti samalla paikalla. Uusien toukkien kehitys kasvukauden aikana on mahdollista koko perunanviljelyalueella aina napapiirille saakka, joskin Pohjois-Suomessa vain pieni osa munista ehtii kehittyä toukiksi ennen sadon korjuuta. Pohjoisin peruna-ankeroisesiintymä on todettu Apukassa, lähellä Rovaniemeä. Kasvukauden lämpösummalla mitattuna kylmin viljelypaikka, jossa ankeroisen on todettu alentavan perunasatoa, on Sotkamossa.

Jokioisilla tehdyissä kenttäkokeissa todettiin, että ensimmäiset peruna-ankeroistoukat lähtevät liikkeelle keväällä, kun maan lämpötila on 4—5 °C, ja pääosa toukista tunkeutuu perunan juuriin juhannuksen aikoihin, kun maan lämpötila on noin 15 °C. Heinäkuussa ankeroiset kehittyvät nopeasti ja ensimmäiset uudet toukat kypsyvät heinä—elokuun vaihteessa, kun tehollinen lämpösumma ylittää 600 dd (day-degrees). Tehollinen lämpösumma on 10 cm:n syvyydestä mitattu maan lämpötila (°C) kerrottuna niiden perunan istutuksen jälkeisten päivien lukumäärällä, joina maan keskilämpötila ylittää kehityksen peruslämpötilan 4,4 °C. Uusien toukkien kypsyminen on nopeinta elokuun puolivälissä ja syyskuussa toukkamäärä voi olla yli kymmenkertainen kevään ankeroismäärään verrattuna.

Juuriäkämäankeroinen (*Meloidogyne hapla*, josta NJF-Utredning/Rapport no. 37 käyttää nimeä pohjanäkämäankeroinen) on sopeutunut pohjoisiin viljelyoloihin kystaankeroisia huonommin, ja siksi se on toistaiseksi ollut vain kasvihuoneviljelmien ongelma. Lajin leviäminen peltoviljelyksille on kuitenkin hyvin mahdollista, koska kasvihuoneista poistettuja juuriäkämäankeroisen saastuttamia turvemaita on yleisesti käytetty maanparannusaineena avomaalla ja viheralueiden kasvualustana. Tämän tutkimuksen tulokset osoittavatkin, että kasvihuoneista ulos siirretyt juuriäkämäankeroiset voivat vioittaa viljelykasveja avomaalla, jos alttiita kasveja viljellään turpeella katetussa maassa heti maan siirron jälkeen. Kasvihuoneista poistettavat turpeet tulisikin aina tutkituttaa ennen niiden käyttöä viljelytarkoituksiin. Mikäli turpeessa on haitallinen määrä juuria vioittavia ankeroisia, voidaan ne torjua kesannoimalla maata yhden kasvukauden ajan. Vain noin 10 % juuriäkämäankeroisen toukista talvehtii avomaalla, joten yhden kesannon ja talven jälkeen on ankeroisten aiheuttama sadonmenetysriski olematon. Turvekasassa juuriäkämäankeroisen toukat voivat säilyä elinvoimaisina kaksikin vuotta, joten vanhojenkin turvekasojen ankeroistilanne kannattaa tutkia ennen turpeen käyttöä viljelytarkoituksiin.

Juuriäkämäankeroisen kehitys on mahdollista kun maan lämpötila on yli 8,3 °C, ja uuden sukupolven kehitys edellyttää 550 dd:n tehoisaa lämpösummaa. Tämän tutkimuksen kenttäkokeissa ei em. kriittinen lämpösumma ylittynyt yksivuotista porkkanaa viljeltäessä eikä uusia toukkia kehittynyt porkkanaa kasvaneissa koeruuduissa. Sen sijaan monivuotisella valkoapilalla lämpösumma oli 631 dd, ja uusia toukkia kehittyi ja kuoriutui näyteanalyyseissäkin löytyviä määriä. Monivuotisen valkoapilan juuristo on ankeroisten käytettävissä huomattavasti aikaisemmin kuin siemenestä kasvaneen porkkanan, minkä johdosta lämpösummat ovat erilaiset. Kenttäkokeiden tulos todisti selvästi, että laboratoriokokeisiin perustuvia laskelmia ankeroisten lämpötilavaatimuksista voidaan käyttää hyväksi arvioitaessa ankeroisten menestymistä ja vahingollisuutta uusilla alueilla tai ilmaston muuttuessa. Laboratoriotutkimuksissa todettiin myös, että juuriäkämäankeroisen maksimaalinen lisääntyminen edellyttää 700—900 dd:n. Käytännössä Suomen kasvukauden pidentyminen noin kuukaudella riittäisi juuriäkämäankeroisen maksimaaliseen lisääntymiseen avomaalla.

Alhaisessa lämpötilassa kehittyvien toukkien energiavarasto on vähäinen

Ankeroisten kehityksen aikana vallitsevan maan lämpötilan todettiin vaikuttavan uusien toukkien sisältämän vararavinnon määrään; mitä alhaisempi kehityslämpötila, sitä vähäisemmäksi jäävät toukkien energiavarat. Energia on pääasiassa varastoituneena neutraaleihin lipideihin, jotka toimivat "polttoaineena" toukkien lepovaiheen ajan sekä niiden liikkuessa ja tunkeutuessa kasvien juuriin. Vähäinen energiavarasto lyhentää toukan infektiivisyysikää sekä huonontaa sen kykyä tunkeutua kasvin sisään. Täten on mahdollista, että esimerkiksi kasvinvuorotuksen hyvä teho peruna-ankeroiseen Suomessa johtuu ainakin osittain toukkien energiavaraston pienuudesta ja tämän aiheuttamasta infektiivisyyden laskusta. Energiavarojen vaikutusta toukkien infektiivisyyteen on tutkittu useissa maissa; sen sijaan alhaisten kehityslämpötilojen vaikutus energiavarastoon on jäänyt vähemmälle huomiolle. Toukkien energiavarastoa ei myöskään ole otettu huomioon arvioitaessa ankeroisten menestymismahdollisuutta tai vahingollisuutta uusilla viljelyalueilla. Energiavarojen mittausta on kyllä pidetty tärkeänä ankeroisten torjuntatarvetta arvioitaessa, mutta aikaisemmin käytetyt lipidimäärien mittausmenetelmät ovat olleet niin työläitä etteivät ne ole soveltuneet rutiinikäyttöön. Tämän tutkimuksen yhtenä osana kehitettiin tietokoneella tehtävään kuva-analyysiin perustuva toukkien lipidipitoisuuden mittausmenetelmä, jota voidaan käyttää rutiininomaisesti ankeroisten energiavarojen arviointiin.

Peruna-ankeroinen voidaan torjua viljelyksellisin menetelmin

Tutkituista ankeroislajeista peruna-ankeroinen on toistaiseksi ainoa, jonka torjunta on Suomessa otettava huomioon sekä valtakunnallisia että tilakohtaisia tuotantosuunnitelmia laadittaessa. Maan käyttö, kasvinvuorotus, lajikevalinta ja viljelytoimenpiteet on suunniteltava siten, ettei peruna-ankeroinen voi lisääntyä, jatkettiinpa perunantuotantoa tilalla miten pitkään tahansa. Torjunnan kannalta on olennaista, että pitkä kasvupäivä hyödyttää ensisijaisesti kasveja ja vasta kasvien kautta niissä loisivia ankeroisia. Pitkään päivään sopeutuneet viljelykasvimme kehittyvät nopeasti ja "karkaavat" helposti niiden juuria vioittavilta ankeroisilta, joiden kehitys ja lisääntymisnopeus ovat lähes täysin maan lämpötilasta riippuvaisia. Tätä kasvien hyvää kilpailuasemaa tulee viljelijän tukea, joten kaikki toimenpiteet, joilla nopeutetaan perunan kehitystä nostokuntoon, ovat osa ankeroistorjuntaa.

Rengossa tehdyt kenttäkokeet osoittivat, että ankeroinen voidaan torjua ja hyvä satotaso säilyttää kasvinvuorotuksella, jossa viljellään kerran kolmessa vuodessa vuoroin ankeroisenkestävää ja vuoroin altista perunalajiketta. Alttiiden lajikkeiden viljely kerran kuudessa vuodessa on välttämätöntä, jotta uusien, kestävissäkin lajikkeissa lisääntyvien ankeroistyyppien valikoituminen vallitseviksi voidaan estää. Kestäviä lajikkeita ei kannata myöskään viljellä heti alttiiden perunoiden viljelyn jälkeen, koska noin 90 % toukista kuoriutuu ja tuhoutuu seuraavana vuonna luonnostaan mitä tahansa kasvia viljeltäessä. Kuoriutumisen saavat aikaan ilmeisesti edellisen vuoden perunakasvustosta maahan jäävät kuoriutumistekijät, joita erittyy vanhoista juurijätteistä tai mikrobeista. Kasvinvuorotus on tarpeen myös maan rakenteen sekä perunan laadun säilyttämisen kannalta, joten ankeroistorjunnan edellyttämä kasvinvuorotus on järkevän perunanviljelyn perusasia.

Peruna-ankeroisen lisääntymistä voidaan rajoittaa myös maan luontaista vastustuskykyä parantamalla. Alustavat pienruutukokeet ja monet ulkomaiset tutkimustulokset ovat osoittaneet, että orgaanisen aineksen lisäys maahan rajoittaa ankeroisten lisääntymistä ja määrää. Torjuntavaikutuksen syitä ja mekanismia ei ole kyetty selvittämään, mutta on ilmeistä, että hyvin monet pieneliöt ja maan mikrobit vaikuttavat ankeroisten menestymiseen ja kasvien vastustuskykyyn. Orgaanisen aineksen lisäys parantaa myös maan rakennetta, ravinteiden pidätyskykyä sekä kasvien vesitaloutta. Maan kyky torjua ankeroisten lisääntyminen on tällä hetkellä yksi tutkituimpia aiheita nematologiassa.

Varhaisen noston vaikutuksen peruna-ankeroisen lisääntymiseen saatiin tässä tutkimuksessa selvät tulokset. Peruna-ankeroinen ei ole varhaisperunatuotannon ongelma Suomessa, koska ankeroinen ei ehdi lisääntyä, jos peruna nostetaan ennen heinäkuun loppua. Sopiva nostoaika lasketaan kasvinsuojelun tutkimuslaitoksella vuosittain lämpösummien perusteella, ja nostokehotus julkaistaan mm. videotex-järjestelmän kasvinsuojeluohjeissa. On hyvä muistaa, että katteet lisäävät maan lämpösummaa samoin kuin kasvupaikan sähköinen lämmmittäminen. Lämmitettyjen kasvualustojen lämpösummat tulisi mitata ja laskea jokaisella viljelypaikalla erikseen, ja ankeroistilanne tulisi tutkia vuosittain otettavien maanäytteiden avulla.

Suomen ankeroisongelmiin ei kannata hakea ratkaisumalleja Keski-Euroopasta, sillä siellä peruna-ankeroisen torjunta kasvinvuorotuksella edellyttäisi, että perunaa viljellään vain joka kahdeksas vuosi samalla paikalla. Tällaisen vuorotuksen järjestäminen on esimerkiksi Hollannissa ollut mahdotonta, ja maan ankeroistorjunta on jo pitkään perustunut kestävien lajikkeiden ja torjunta-aineiden käyttöön. Hollannissa torjunta-aineiden käyttö viljelypinta-alaa kohti laskettuna on noin 20 kertainen Suomen käyttöön verrattuna, ja 60 % käytetyistä torjunta-aineista levitetään peltomaahan ankeroisten torjumiseksi. Näitä ympäristövaikutuksiltaan haitallisimpia torjunta-aineita ei Suomen pelloilla ole käytetty koskaan, eikä esimerkiksi peruna-ankeroisen torjuntaan ole yhtään valmistetta Suomessa edes kaupan.

Kasvihuoneilmiö lisää ankeroisten aiheuttamaa sadonmenetysriskiä

Monet ilmastoskenaariot ennustavat keskilämpötilan nousevan Suomessa, sateiden lisääntyvän, kasvukauden pidentyvän ja talvien lauhtuvan. Tämän tutkimuksen perusteella voidaan arvioida, että kaikki ennustetut muutokset parantaisivat olennaisesti kasviparasiittisten ankeroisten menestymistä ja vahingollisuutta maassamme. Ankeroistilanne voi tulevaisuudessa muistuttaa hyvinkin nykyistä Tanskan tai Hollannin tilannetta. Juurikasankeroisen populaatiotiheydet lisääntyisivät yli tuhokynnyksen, ja sokerijuurikkaan jatkuva viljely samoilla pelloilla kävisi kannattamattomaksi. Myös muiden *Heterodera*-suvun ankeroisten, kuten kaura-ankeroisen *(H. avenae)* aiheuttamat ongelmat voisivat muodostua meillä esim. nykyisin Etelä-Ruotsissa esiintyvien ongelmien kaltaisiksi. Peruna-ankeroisen menestyminen olisi siemenperunakeskusta ympäröivillä siementuotantoalueilla yhtä hyvä kuin Etelä-Suomessa nykyään, ja vastaavasti Etelä-Suomessa tulisi viljely suunnitella Hollannin kaltaisten ankeroisongelmien torjuntaa varten. Juuriäkämäankeroinen *(M. hapla, M. chitwoodi)* menestyisi hyvin Etelä-Suomessa ja aiheuttaisi todennäköisesti sato- ja laatutappioita peruna- ja vihannesviljelmillä.

Ilmaston lämpenemisen ja mahdollisesti lisääntyvien ankeroisongelmien myötä myös ankeroisten torjuntaan kehitettyjen torjunta-aineiden käyttötarve lisääntyisi. Ilmastomuutosten hitautta tulisi käyttää hyväksi ekologisen tietouden lisäämiseksi siten, että kasviparasiittisten ankeroisten torjunta olisi myös tulevaisuudessa mahdollista viljelyksellisin keinoin sekä maan antagonistisuuteen eli luontaiseen vastustuskykyyn perustuvan biologisen torjunnan avulla. Pohjavesien puhtautta ja peltomaan välttämätöntä pieneliötoimintaa ei tulisi vaarantaa maandesinfiointiaineilla. Valitettavasti peltoekosysteemien mikrobiston ja pieneliöstön perustutkimus on ollut toistaiseksi niin puutteellista, ettei nykyinen tietämys anna kunnollista pohjaa biologisen torjunnan kehittämiselle tai kasvien juuriston vastustuskyvyn lisäämiselle.

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Seria AGRICULTURA N. 99 — Sarja PELTOVILJELY n:o 99

FACTORS AFFECTING PANICLE PRODUCTION OF COCKSFOOT (*DACTYLIS GLOMERATA* L.) IN FINLAND

IV. RESPONSE TO FROST AT PANICLE GROWTH PHASE

OIVA NIEMELÄINEN

NIEMELÄINEN, O. 1991. **Factors affecting panicle production of cocksfoot (*Dactylis glomerata* L.) in Finland. IV. Response to frost at panicle growth phase.** Ann. Agric. Fenn. 30: 163—172. (Agric. Res. Centre, Inst. Crop and Soil Sci., SF-31600 Jokioinen, Finland.)

Frost treatment after floral initiation decreased the number of panicles in cocksfoot. The effect was strongest by a −10 °C frost treatment but treatments at −6 °C and −3 °C also had a significant negative effect on panicle number. Panicle production of cocksfoot was more sensitive to frost injury at the late stage of development than at the early developmental stage.

The production of above ground phytomass was not as sensitive to frost injury as panicle production. It was difficult to detect the immediate injury caused by frost even in the small pots.

At the panicle in boot stage a −7.9 °C (soil surface) natural frost occurred destroying about one half of in boot panicles in an undense first year stand, and about one-third in a dense second year stand.

Because of the early development of cocksfoot panicles and the frequent occurrence of spring frosts in Finland, frost is an important risk to cocksfoot seed production in Finland. The extent of frost damage to seed yield depends on the likelihood of new tillers substituting panicle production in frost-damaged tillers.

Index words: *Dactylis glomerata,* orchard grass, seed production, stress, frost bite, risk, floral initiation.

INTRODUCTION

Spring frosts occur in Finland long after the onset of the growing season (SOLANTIE 1987). Such frosts have damaged, for example, rye (MUKULA et al. 1976, MUKULA and RANTANEN 1989 a) and barley (LALLUKKA 1979, MUKULA and RANTANEN 1989 c). The most serious frosts for cereals in Finland occur, however, in the fall because of the short growing season (PESSI 1958, MUKULA and RANTANEN 1989 b, c, d).

Only a few observations and experiments on the effect of frost on herbage seed production are available. KÖYLIJÄRVI (1983) reported that spring frost caused a nearly total loss of the cocksfoot and meadow fescue seed yield in 1975. A reduction in the panicle production of cocksfoot due to frost damage has been reported also from Denmark (NORDESTGAARD 1982, ANON. 1983). In NIKOLAESKAYA's (1973) trial with cocksfoot, a −6 °C frost treatment at the flowering phase destroyed all caryopsies. According to HUOKUNA (1989) cocksfoot is sensitive to frosts and its leaf tips are often damaged by spring frosts in Finland.

In the experiment of HEIDE (1980) with *Poa pratensis* frost treatment decreased strongly the number of panicles per plant. Treatments at −5 °C and at −10 °C decreased panicle number, and at −15 °C all flower heads were destroyed. The damage was specific to flower primordia as otherwise the plants survived the frost treatments and the fresh weight of plants and the length of the leaves were similar in the frost treatments with those found in the control treatment (HEIDE 1980).

VALMARI A. and VALMARI I. (1966) studied the effect of frost on the seed yield of red clover in field conditions in Finland. The early fall frost caused damage to seed yield both by destroying the branches of red clover with flower heads and by damaging individual flowerheads. Frost from −6 to −7 °C was the mildest frost causing noticeable injuries.

In this study frost treatments of various degree of severity at different stages of panicle development were performed in growth chamber experiments. Observations on the effect of natural frost on the panicle production of cocksfoot are presented.

MATERIAL AND METHODS

Results are presented from three separate pot trials. In all trials samples (15 cm long section of a row) were dug up from a field grown cultivar Haka row stand. The samples were taken on 26 November 1987 in Trial I, on 4 May 1988 in Trial II, and on 15 November 1988 in Trial III. The samples were planted in 5 l pots and fertilized with 5 grams of mixed fertilizer (17-6-12 NPK) per pot. Then the samples were grown in a glasshouse at about +18 °C at continuous light both prior to and after frost treatment. Growing time in the glasshouse and effective temperature sum (degree days, above +5 °C) prior to frost treatments in the different trials were follows:

Time of frost treatment	Trial I		Trial II		Trial III	
	Days	Temp. sum °C	Days	Temp. sum °C	Days	Temp. sum °C
I	13	170	7	130	10	110
II	20	260	13	210	20	240
III			16	250	24	290
IV			19	290	28	350

The stage of panicle development at treatment was analyzed by uncovering the growing point of additional sample tillers and checking the stage of development by microscope, if necessary. The stage of panicle development of main tillers varied at different treatment times from the vegetative stage to panicle emergence. The stage of development of the largest tillers at treatment is presented in Tables 2—4. Because of the uneven development of the cocksfoot stand tillers in various stages of development were subjected to frost during each treatment. The assigned stage of development describes the status of the most advanced tillers.

Frost treatments were conducted either in growth chambers or in freeze rooms. The decrease of temperature to minimum temperature was carried out gradually in all trials. The duration of the whole treatment and the duration at minimum temperature varied for the different trials. The duration of the minimum temperature in Trial I lasted 4 hours, in Trial II 11 hours, and in Trial III 4 hours. Maximum time for the whole treatment was 29 hours in Trial II. Frost treatment was performed in darkness.

The frost temperatures used in the present study −3, −6, and −10 °C were chosen based

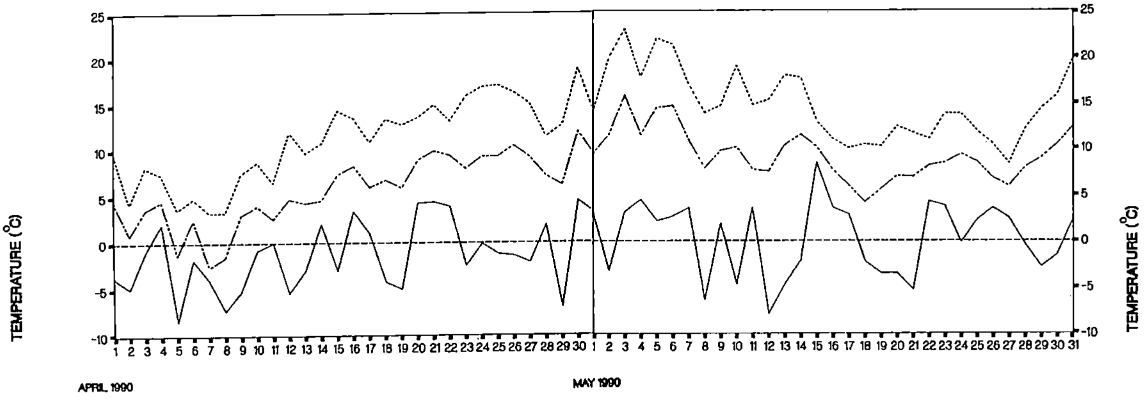

Fig. 1. Daily average (— -- —) and daily maximum (----) temperature of weather cage at 2 meters height, and daily minimum (———) temperature at soil surface at Jokioinen Observatory in April and May in 1990 (ANON. 1990, and unpubl. data).

on experience from a preliminary trial where a −15 °C frost treatment caused the total failure of panicle production in cocksfoot and had a strong effect also on the above ground phytomass production at an early stage of panicle development. Treatment at −7 °C negatively affected panicle and phytomass production, especially at the late stage of panicle development (NIEMELÄINEN unpubl.).

The number of pots per treatment was 9 or 10, depending on the trial. The location of the pots in the glasshouse was according to randomized block design in Trials I and III and according to split plot design in Trial II. Control plants were kept at +3 °C during frost treatments.

After each frost treatment the immediate effect of frost was observed. At the end of the experiment the number of panicles and the number of main tillers per pot were counted, and the dry weight of panicles and that of the above ground phytomass measured. In Trial III the emergence of panicles was counted every two days from the start of panicle emergence throughout the growing period.

Natural frost occurred in Jokioinen on the night between the 11 and 12 May in 1990. The minimum temperature at the soil surface was −7.9 °C at the Jokioinen Observatory (ANON. 1990) which is situated about 1000 m from the experimental field. The growing season began on 15 April and the effective temperature sum (above +5 °C) from the onset of the growing season was 123 °C before the above mentioned night frost. The daily average and daily maximum temperatures at 2 meters- height, and the daily minimum temperature at soil surface at the Jokioinen Observatory in April and May in 1990 are presented in Fig. 1. In addition to above mentioned frost also a −5.3 °C frost (soil surface) occurred between 20 and 21 of May.

The most advanced tillers were at the panicle emergence stage when the frost occurred. The following observations were made. Four days after the frost 100 tillers were sampled (in the panicle in boot stage), both from 1st and 2nd year stands, and the panicle revealed and rated to be either healthy, injured or destroyed. At the same time 110 tillers from the first year stand both in the panicle emergence stage and in the panicle in boot stage were marked with strings of different colour. The condition of the marked tillers was analyzed in July when the stand was maturing. In 1990 June and July were frostless in Jokioinen.

In the statistical analysis the significance of the effect of frost treatment in Trials I, II and III was tested first using a contrast test (ANON. 1986) subjecting the control treatment against all frost treatments. If the frost treatments as a group had a significant effect, the significance of the difference of the means was tested by variance analysis according to randomized block (Trials I and III) or to the split plot design (Trial II) using Tukey's multiple comparison test (SNEDECOR and COCHRAN 1978).

RESULTS

The frost treatments had a significant negative effect on the panicle production in all three trials according to the contrast analysis (Table 1). The frost treatments had a significant negative effect also on above ground phytomass production and on the number of large tillers per pot in Trials I and II.

The number of panicles in the −10 °C frost treatment was less than 10 per cent of the number of panicles in the control treatment in Trial II (Table 3). In Trial I the number of panicles after a −10 °C treatment was about 30 per cent of the control treatment (Table 2). The effect of the −10 °C frost treatment was the stron-

Table 1. Contrast comparisons for effect of frost treatment on number of panicles, dry weight of panicles and above ground phytomass, and number of large tillers in Trials I, II and III. Control treatment was tested against all frost treatments for different characteristics.[z]

Trial	Number of panicles	Dry weight of panicles	Dry weight of above ground phytomass	Number of large tillers
Trial I, stage of development I, d.f. 32 control vs. −3, −7, −10 °C	*	*	***	*
Trial I, stage of development II, d.f. 32 control vs. −3, −7, −10 °C	**	***	***	*
Trial II, all stages of development control vs. −3, −6, −10 °C	***	***	***	***
Trial III control vs. frost (−10 °C) at four stages of development	**	*	ns	ns

[z] Significance of the effect of frost treatment is expressed as follows: * $P<0.05$, ** $P<0.01$, *** $P<0.001$, ns nonsignificant.

Table 2. Effect of frost treatments at two stages of panicle development on the production of panicles and on the growth of cocksfoot. The stands were analyzed after 6 weeks subsequent to growing in a glasshouse. n = 9. The results of the same control treatment were used in statistical analysis in both developmental stages. Trial I.

Frost treatment	Number of panicles		Dry weight of panicles (g)		Dry weight of above ground phytomass (g)		Number of large tillers	
Stage[z]	I	II	I	II	I	II	I	II
A. + 3 °C	22.0^{a}	22.0^{a}	3.4^{a}	3.4^{a}	66.4^{a}	66.4^{a}	44.6^{a}	44.6^{a}
B. − 3 °C	18.8^{ab}	16.3^{ab}	3.2^{a}	2.3^{ab}	56.6^{a}	46.3^{b}	32.9^{b}	36.4^{a}
C. − 7 °C	15.9^{ab}	11.0^{bc}	2.7^{ab}	1.9^{bc}	56.7^{a}	52.7^{b}	39.8^{ab}	36.0^{a}
D. −10 °C	9.6^{b}	4.9^{c}	1.4^{b}	0.7^{c}	43.1^{b}	43.7^{b}	33.3^{ab}	33.3^{a}

[a—c] Means with a different superscript letter within a column are significantly different ($P<0.05$).
[z] Stage of panicle development I panicle of largest tillers 0.5—2 cm
II panicle of largest tillers 3—5 cm

gest, but also treatments at −3 and −6 °C had a significant negative effect in Trial II.

The panicle production of cocksfoot was more sensitive to frost damage when the treatment was conducted at the late stage of the stand's development than at the early stage (Tables 2, 4). Frost had a significant negative effect on the production of above ground phytomass in Trials I and II. The decrease in the dry weight of phytomass due to frost was proportionally not, however, so strong as that in the number of panicles. This is partly clarified by the observation that when tillers died during frost treatment new tillers arose from the axillary buds at the base of the dead tillers, but these tillers remained vegetative.

Table 3. Effect of at different stage of panicle development performed frost treatment of various severity on the panicle production and growth of cocksfoot. n = 10. Trial II.

Stage of development*	Number of panicles/pot					Dry weight of panicles (g)/pot				
	Frost treatment °C					Frost treatment °C				
	+3	−3	−6	−10	X̄	+3	−3	−6	−10	X̄
A Panicles 5—10 mm	22.3	21.4	12.8	2.7	14.8^{a}	4.7	4.2	2.9	0.9	3.2^{a}
B Panicles 2—3 cm	17.9	13.0	9.6	2.3	10.7^{b}	3.7	2.8	1.9	0.6	2.3^{b}
C Panicles 5—9 cm	19.0	7.2	11.5	0.0	9.4^{b}	3.3	1.0	2.0	0.0	1.6^{b}
D At panicle emergence	18.4	13.9	14.6	0.9	12.0^{ab}	3.4	1.5	1.9	0.4	1.8^{b}
X̄	19.4^{a}	13.9^{b}	12.1^{b}	1.5^{c}		3.8^{a}	2.4^{b}	2.2^{b}	0.5^{c}	

* Stage of development of most advanced tillers in a pot.

Treatments	d.f.	F	d.f.	F
A Stage of development	3	5.1^{**}	3	13.4^{***}
F Frost treatment	3	54.4^{***}	3	48.6^{***}
A × B	9	1.8^{ns}	9	2.0^{*}

Stage of development*	Dry weight of above ground phytomass (g)/pot					Number of large tillers/pot				
	Frost treatment °C					Frost treatment °C				
	+3	−3	·6	−10	X̄	+3	−3	−6	−10	X̄
A Panicles 5—10 mm	45.8	43.6	41.3	24.6	38.8^{a}	32.8	30.6	23.7	11.9	24.8^{a}
B Panicles 2—3 cm	45.7	41.2	33.9	23.2	36.0^{a}	28.9	20.6	22.6	12.3	21.1^{ab}
C Panicles 5—9 cm	41.1	33.6	36.4	12.7	31.0^{b}	28.8	17.5	24.2	10.0	20.1^{b}
D At panicle emergence	45.1	37.2	36.2	15.2	36.0^{a}	30.1	24.6	23.4	9.3	21.9^{ab}
X̄	44.4^{a}	38.9^{b}	37.0^{b}	21.4^{c}		30.2^{a}	23.3^{b}	23.5^{b}	10.9^{c}	

* Stage of development of most advanced tillers in a pot.

Treatments	d.f.	F	d.f.	F
A Stage of development	3	7.2^{***}	3	2.7^{*}
F Frost treatment	3	65.0^{***}	3	43.8^{***}
A × B	9	1.4^{ns}	9	1.2^{ns}

a—c Means not having the same superscript letter within a column or a row are significantly different (P < 0.05).

Table 4. Effect of −10 °C frost treatment on the production of panicles and on the growth of cocksfoot. The stands were analyzed after 6 weeks subsequent growing in a glasshouse. The −10 °C frost lasted 4 hours. n = 10. Trial III.

Stage of panicle development at frost treatment	Number of panicles	Dry weight of panicles (g)	Dry weight of above ground phytomass (g)	Number of large tillers
A. Control	13.7[a]	3.1[a]	48.5[a]	12.8[a]
I. Vegetative	11.3[a]	2.7[a]	47.1[a]	13.6[a]
II. Panicle 2—3 cm	11.0[a]	3.0[a]	44.6[a]	10.6[a]
III. Panicle 4—9 cm	7.4[ab]	1.8[ab]	39.5[a]	8.2[a]
IV. Panicle emergence	3.6[b]	1.0[b]	42.0[a]	12.5[a]

[a—b] See Table 2.

The immediate injury caused by frost was difficult to detect even in the small pots. At that stage of the stand's development growth was very rapid and other elongating tillers rapidly covered those tillers which had been either damaged or died. The dead tillers dried out soon and were thus difficult to detect. When tillers in various stages of development were marked before the frost treatment it was not possible to identify a certain sensitive phase of development for frost injury. On the one hand, tillers of various size died and, on the other hand, tillers at just the identical stage of development died while similar ones remained uninjured.

Panicle emergence took place over a long period. Most of the panicles emerged within the two weeks-period from the appearance of first panicles, but panicle emergence continued for the whole four-week period until the termination of the trial III (Fig. 2). At a late stage of development the frost treatment performed delayed the proliferation of panicle emergence.

The −7.9 °C natural frost destroyed a great

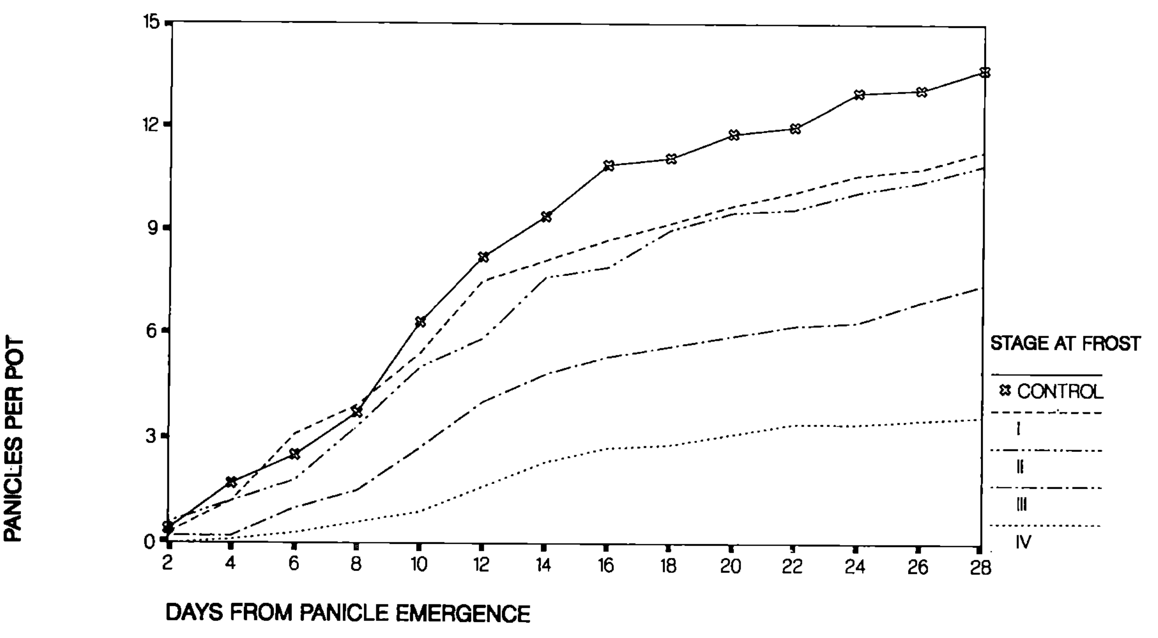

Fig. 2. Panicle emergence of cocksfoot when −10 °C frost treatment was performed at different developmental stages of a stand. Stage of development of most advanced tillers at frost treatment I) vegetative, II) panicle 2—3 cm, III) panicle 4—9 cm, IV) at panicle emergence.

Table 5. Condition of cocksfoot panicles 4 days and 2 months after natural frost −7.9 °C in severity at soil surface.[z] The frost occurred between 11th and 12th of May in 1990. Condition of 100 panicles at boot stage was studied 4 days after the frost both from first year and from a second year stand. At the same time tillers were marked with strings from the first year stand. Condition of marked tillers was analyzed 17.7.1990.

Condition[y] of panicles	Panicles analyzed 15th of May 1990						Panicles analyzed 17th of July 1990	
	Second year stand			First year stand			First year stand	
	Number of panicles	Length of panicle cm	Length of panicle s[x]	Number of panicles	Length of panicle cm	Length of panicle s[x]	Panicles in boot when marked Number of panicles	Panicles at ear emergence 15th of May Number of panicles
A. Healthy	63	3.0	1.6	39	9.1	3.0	54	45
B. Destroyed	8	3.5	1.2	41	10.4	3.0	46	55
C. Injured	29	3.6	2.2	20	11.4	1.9		

[x] s means standard deviation.
[z] The weather data was obtained from the Jokioinen Observatory, situated about 1000 m from the experimental field. See also Fig. 1 for weather data.
[y] Condition of a panicle was rated as healthy, injured, or destroyed (completely darkened). On 17th of July analyzed panicles were rated only either as healthy or destroyed.

proportion of the most advanced tillers. Sixty-one of the 100 panicles studied were either completely or partially destroyed in the first year stand (Table 5). In the second year stand, 37 of the 100 panicles were completely or partially destroyed. The developmental stage of the tillers studied was more advanced in the first year stand since the length of healthy panicles in first year stand was 9.1 cm (s 3.0) and 3.0 (s 1.6) in the second year stand in the samples analyzed on 15 May, 1990. When the condition of the tillers marked shortly after frost was analyzed at maturity stage many of the panicles had remained in the boot or had stopped their growth at the panicle emergence stage (Table 5). It was not possible to identify partially injured panicles and therefore the panicles were classified as either healthy of destroyed. About 50 per cent of the marked tillers were destroyed (Table 5).

DISCUSSION

The frost treatment negatively effected the number of panicles as in the trial of HEIDE (1980) with *Poa pratensis*. The results affirm the possibility of total seed yield failure in cocksfoot due to frost as KÖYLIJÄRVI (1983) has reported. The seed production failure at the Southwest Finland Research Station in 1975 (KÖYLIJÄRVI 1983) occurred due to a −8.2 °C frost at soil surface (−3.8 °C at 2 m height) on 30 May (ANON. 1975 a). The damage to cocksfoot seed production was so strong that the trial was not harvested for seed but only for green matter (ANON. 1975 b).

The growing season started on 19 April at the Southwest Finland Research Station in 1975 and the effective temperature sum (above +5 °C) from the beginning of growing period to the night frost was 208 °C (ANON. 1975 a). A comparison of the effective temperature sum before the frost treatment in the present study and in field conditions may, however, not be justified because the same stage of development has been attained with a smaller effective temperature sum in field conditions than in laboratory conditions. In the seed production trials cv. Haka reached the panicle emergence stage at the effective temperature sum of 184 °C from the beginning of the growing season (NIEMELÄINEN 1991), but in the present laboratory trials the same stage of development was attained at the temperature of 290 °C in Trial II and 350 °C in Trial III. One reason for the difference may be that the direct transfer of the plants to + 18 °C temperature from the field delayed the start of growth and so led to some lost effective temperature sum in the laboratory experiments. On the other hand, + 5 °C may not be the best base temperature for calculating the effective temperature sum in Finnish conditions (see PULLI 1980).

In the present study the most advanced tillers died after the −10 °C treatment and growth continued from axillary tillers. Such an activation of axillary tillers after frost damage has been observed in rape (TORSSEL and JOHANSSON 1962) and in barley (LALLUKKA 1979). In both rape and barley new axillary tillers compensated the seed yield to some extent, but in cocksfoot axillary tillers mainly produce vegetative growth. However, also in rape the effect of frost was weaker on the total phytomass production than on seed yield.

The loss of panicles due to the occurrence of natural frost varied from about one-third to about one half of the sample tillers. This does not, however, describe the situation on the stand basis because only tillers from a certain stage of development were studied. Nevertheless, the results indicate that a considerable loss of panicles was obvious due to the −7.9 °C frost, supporting the findings of the growth chamber experiments. The difference in the number of destroyed panicles between the first and second year stands may depend, on the one hand, on the different location of stands (1 km from each other), and on the other hand, on the different structure of the stand. In the first year stand the most advanced tillers grew individually and the cold air probably had good contact with tillers. The second year stand was dense and the tillers were probably protected from direct frost. The developmental stage of the tillers studied was more advanced in the first year stand, too.

The loss of tillers in the spring is a normal situation in a cocksfoot sward. For example, HUOKUNA (1964) determined that about 60 % of the young tillers died evidently as a result of shading caused by the uncut growth from the previous year. The extent of damage caused by frost depends on the total number of tillers able to produce panicles. If that number is so high that all tillers cannot produce panicles even in favourable conditions due to strong competition, the negative effect of frost is weakened. However, in Finnish conditions the total number of tillers able to produce panicles is usually so low that probably all frost-destroyed panicles are in fact also panicles which could have contributed to the seed yield. This makes the frost damage a more serious problem in conditions where the floral evocation requirements are critical compared to situations where floral evocation requirements are well met, and the potential number of panicle bearing tillers is high.

The variation in the developmental stages of different tillers of grasses at a particular time makes it difficult to identify precisely the effect of frost on panicles at different stages of development. The data indicates that frost treatment at a late developmental stage caused a delay in the panicle emergence. However, there appeared no clear step at the emergence of panicles in each treatment time which could have demonstrated the existence of a sensitive phase.

The frost treatments had a negative effect on the number of panicles but the damage to the total above ground phytomass was small and it was difficult to detect the injured tillers even in the small pots. Frost damage may be one factor causing a situation such that panicle production of a stand is small but phytomass production is average. It is probable that a considerable loss of panicles due to frost damage may remain unnoticed in seed production fields.

Because of the early development of the panicles of cocksfoot and the frequent occurrence of spring frosts in Finland, frost is an important risk factor in cocksfoot seed production. According to KÖYLIJÄRVI (1983), cocksfoot, meadow fescue and red fescue are the most frost sensitive herbage crops because the development of panicles is earliest in those crops. Spring and early summer frosts have probably decreased the seed yield in several seed production trials of cocksfoot between 1977—1990 in Finland (NIEMELÄINEN 1991). The risk of frost should be taken into consideration when the location of a cocksfoot seed production field is decided. The fields should be located on such areas where the risk is minimal. RANTANEN and SOLANTIE (1987) and SOLANTIE (1987) have studied the risk of frost in different regions of Finland.

This article is the fourth and last article in the series on factors affecting panicle production of cocksfoot in Finland. The role of cultivar in panicle and seed production of cocksfoot in Finland is presented in a separate article by NIEMELÄINEN (1991).

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SELOSTUS

Koiranheinän (*Dactylis glomerata* L.) röyhynmuodostukseen vaikuttavista tekijöistä Suomessa

IV. Röyhynkasvuvaiheessa esiintyvän hallan vaikutus

OIVA NIEMELÄINEN

Maatalouden tutkimuskeskus

Kasvukauden alkamisen jälkeen esiintyneet keväthallat ovat aiheuttaneet ajoittain vahinkoja ruis- ja ohrakasvustoille maassamme. Havaintoja keväthallan tuhoista koiranheinän ja nurminadan siemenviljelyksiltä on myös olemassa.

Tässä tutkimuksessa selvitettiin kontrolloiduissa olosuhteissa ankaruudeltaan erilaisen hallan vaikutusta eri röyhynmuodostusvaiheissa olleen koiranheinän röyhynmuodostukselle. Myös havaintoja luonnonhallan vaikutuksesta röyhynmuodostukseen esitetään.

Kymmenen asteen hallan vaikutus oli voimakkain, mutta myös −6 ja −3 asteen halla vähensi röyhynmuodostusta merkitsevästi. Koiranheinäkasvuston röyhynmuodostus oli arempi hallavioitukselle myöhäisellä kuin varhaisella kehitysasteella.

Hallan negatiivinen vaikutus koko maanpäällisen kasvimassan kasvuun ei ollut niin voimakas kuin röyhynmuodostukseen. Hallan aiheuttama välitön vahinko oli vaikea havaita pienissä astiakasvustoissakin. Pelto-olosuhteissa suuri osa hallan aiheuttamista vaurioista jää todennäköisesti havaitsematta, koska kevään nopeassa kasvuvaiheessa uudet versot peittävät pian tuhoutuneet versot.

Jokioisissa esiintyi vuoden 1990 toukokuun 11 ja 12 päivän välisenä yönä −7.9 asteen halla (maan pinnan lämpötila). Halla tuhosi noin puolet tupessa olleista koiranheinän röyhyistä koiranheinän ensimmäisen nurmivuoden kasvustossa, joka oli harva ja jossa pitkälle kehittyneet versot olivat yksittäisiä. Tiheässä toisen nurmivuoden kasvustossa halla tuhosi noin kolmasosan tupessa olleista röyhyistä.

Koska koiranheinän röyhynkehitys on aikainen ja Suomessa esiintyy usein ankariakin keväthalloja huomattavasti kasvukauden alkamisen jälkeen, muodostaa halla merkittävän riskitekijän koiranheinän siementuotannolle. Hallan vahingollisuutta lisää se, että koiranheinäkasvustossa röyhynmuodostukseen kykenevien versojen lukumäärä on Suomessa pieni, ja kaikki hallan tuhoamat suuret versot vaikuttavat suoraan kasvuston siemenmuodostuskapasiteettiin. Halla on yksi tekijä, jonka vaikutuksesta siemenviljelykasvustoon muodostuu röyhyjä vain vähän vaikka kasvusto tuottaa vegetatiivista kasvimassaa kohtuullisesti.

Koiranheinän siemenviljelykasvustot tulisi sijoittaa maassamme alueille, joilla myöhään kasvukauden alkamisen jälkeen esiintyvän hallan todennäköisyys on pieni.

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VARIATION IN SEED YIELD OF COCKSFOOT (*DACTYLIS GLOMERATA* L.) IN FINLAND

OIVA NIEMELÄINEN

NIEMELÄINEN, O. 1991. **Variation in seed yield of cocksfoot (*Dactylis glomerata* L.) in Finland.** Ann. Agric. Fenn. 30: 173—189. (Agric. Res. Centre of Finland, Inst. Crop and Soil Sci., SF-31600 Jokioinen, Finland.)

Variation in seed yield of cocksfoot was studied by using data from trials on seed production of cultivars conducted at the Agricultural Research Centre in 1977—1990. Totally 32 trials of cv. Haka were available from three research sites in Southern Finland. Six cultivars were included in the study.

The seed yield ranged from 0 to 697 kg ha^{-1} for cv. Haka. The average seed yield for cv. Haka was 258 kg ha^{-1} for the 32 harvests. Second year stands produced on average a higher seed yield (343 kg ha^{-1}) than first (208 kg ha^{-1}) and third (216 kg ha^{-1}) year stands. In ten out of the total 32 harvests, seed yield was 150 kg ha^{-1} or less.

The average seed yield of cocksfoot was low compared to seed yield of cocksfoot in Sweden, Norway and Denmark, and compared to seed yield of timothy, meadow fescue and perennial ryegrass in Finland. The reasons for the low seed yield were inadequate floral evocation in the first harvest year when the stand was established with a cover crop, high winter damage due to freezing and/or ice cover and early summer frosts at the panicle growth stage. Early summer drought and pre-harvest shedding also reduced the seed yield in some trials.

Cv. Haka had a significantly higher density of panicles and produced significantly higher seed yield than cvs. Tatu, Hera Daehnfeldt, Fala and Frode. The difference between cvs. Haka and Tammisto was neither significant in terms of seed yield nor in panicle density. The correlation coefficient between seed yield and visually evaluated (scale 0—100 %) density of panicles ranged from 0.74 to 0.98 for different cultivars and was significant for all cultivars. The correlation coefficient between density of panicles and ground cover in the spring was significant only in cvs. Haka and Tammisto. The data suggest that differences between cvs. Haka and Hera, Fala, Tatu and Frode in seed yield and in density of panicles were due to differences in the fulfilment of floral evocation.

Index words: *Dactylis glomerata,* orchard grass, seed production, wintering, frost, ice cover, freezing, varieties, cultivars, stress, drought.

INTRODUCTION

Commercial seed production of cocksfoot in Finland is small compared to seed demand. A factor contributing to that is the frequently observed poor panicle production in cocksfoot seed production stands which has lead to low average yield per hectare (KÖYLIJÄRVI 1983). A laboratory study on factors affecting panicle production of cocksfoot was recently completed in Finland. The results suggest that incomplete floral evocation, damage due to cold temperature and/or exhaustion of carbohydrate reserve of the plant during winter may decrease the production of panicles (NIEMELÄINEN 1990 a, b, c). In addition, late spring frosts at the panicle growth stage can decrease the panicle production (NIEMELÄINEN 1991). In the present study, the results of trials conducted at the Agricultural Research Centre on seed production of cocksfoot cultivars were studied in relation to factors which are critical for panicle production. In addition, the role of cultivar in the seed production of cocksfoot in Finland was studied.

MATERIAL AND METHODS

The Agricultural Research Centre has tested both fodder production and seed production of new forage cultivars. The present study is based on the results of cocksfoot seed production cultivar trials. The data were collected from three locations in Finland. The trials were conducted at the Institute of Crop and Soil Science in 1977—1978 in Tikkurila (latitude 60°19′ N), in 1983—1990 in Jokioinen (latitude 60°49′ N) and at the South-West Finland Research Station in Mietoinen in 1979—1989 (latitude 60°38′ N).

The trials were conducted according to the guidelines of the Agricultural Research Centre set for herbage seed production experiments (ANON. 1982). The experimental design was a randomized block with 4 or 3 replicates. The seed rate was 1000 germinating seeds per m^{-2}, and the row width was 12.5 cm. The plots were 1.5 m wide and 10 m long.

The trials were established mainly with a companion crop (barley, 70 % of normal seed rate). Some trials were sown without a companion crop (Table 1). Nitrogen fertilization of the companion crop was 80 % of the normal fertilization to avoid lodging. When cocksfoot was established without a companion crop, the nitrogen fertilization rate ranged from 20 to 60 kg N ha^{-1} in the establishment year. During seed harvest years 54 to 120 kg N ha^{-1} of nitrogen was applied in spring (Table 1). In the beginning of September, nitrogen was applied at a rate 30 kg ha^{-1}. Phosphorous and potassium fertilization was adjusted to the fertility values of the soil. Phosphorous application ranged from 20 to 54 kg P ha^{-1} and potassium application from 12 to 78 kg K ha^{-1} per season. An appropriate herbicide treatment was given when necessary in the establishment year and/or in the spring of the first harvest year. The experimental soil was heavy clay or clay loam soil, pH 5.9—6.9. Only in Mietoinen in 1979 the trial was established on loam soil. In that particular trial, the pH of the soil was 5.3. The fertility values of the soils were good.

The ground cover percentage of the plot was evaluated visually both in the fall and spring. This was done to reveal possible winter damage. The density of panicles was evaluated visually at the maturing phase on a scale of 0—100 % (100 = abundant panicle production). The seed yield was harvested by a Hege or Wintersteiger plot combine. The yield per ha^{-1} is presented at 88 % dry matter.

When the yield was low, no quality assessment was performed. The thousand seed weight was analyzed for 18, germination for 15 harvests. The date of panicle emergence was observed only in five trials in Jokioinen.

In the cultivar testing system, new cultivars are annually accepted for testing, and older cultivars are excluded. Therefore, only the standard cultivar Haka was included in all 12 trials. These 12 trials yielded totally 32 results. Each trial covered (in principle) the establishment year and three seed production years, and a complete trial thus gave three results. The data are presented so that one result (n in Tables 2—4 and 6) is a mean value of replicates in one trial in one growing season. The statistical significance of the differences between means of the standard cultivar Haka and other cultivars were tested in pairs by Student's t-test (ANON. 1986). Therefore n varies in different cultivars in the analyzes in Tables 3 and 4.

All five cultivars which were recommended for cultivation in Finland in 1991 (ANON. 1990) were included in the study. In addition, the oldest Finnish cocksfoot cv. Tammisto was included. Cultivars Haka (description by RAVANTTI 1981) and Tatu (description by KAJASTE 1989) are later Finnish cultivars. Cv. Hera Daehnfeldt is of Danish, cv. Fala of Polish, and cv. Frode of Swedish origin (ANON. 1989 a).

The climatic observations were done at weather stations at respective research locations. The data from Mietoinen and Jokioinen were obtained by using the climatic data register prepared by the Meteorological Institute for use at the Agricultural Research Centre (see ANON. 1988 a). However, in Jokioinen the snow cover values used were those measured in field conditions at Jokioinen Observatory (unpubl. records). The climatic observations from Tikkurila were obtained from the original recordings at the Institute of Crop and Soil Science. Number of snow cover days in winter seasons for Mietoinen were obtained from the weather statistics of the research station (ANON. 1989 b).

Monthly precipitation, evaporation and mean temperature in May, June and July and precipitation deficiency in May and June as well as the length of snow cover period in winter seasons at the research locations are presented in Table 2. The depth of snow cover and minimum temperature at soil/snow surface in certain winter seasons are presented in Figures 1 and 2. The snow cover value is the average for a five-day period but the minimum temperature is the lowest temperature measured at the soil/snow surface during that period.

RESULT AND DISCUSSION

Climatic factors affecting cocksfoot seed production

Performance of cocksfoot as a species was studied by examining the results of cv. Haka in relation to critical factors for panicle production. The average yield of cv. Haka was 258 kg ha^{-1} (Table 3). In ten out of the 32 harvests the yield of Haka was 150 kg ha^{-1} or less (Table 1). The second year stands produced on average higher seed yield (343 kg ha^{-1}) than first (208 kg ha^{-1}) and third (216 kg ha^{-1}) year stands (Table 4). However, the conditions in different years affected wintering and seed production strongly, which interfere with the effect of age of the stand (Table 1).

The average seed yield was low in comparison to average yields in Sweden 576 kg ha^{-1} (CEDELL 1990), in Norway 520 kg ha^{-1} (AAMLID 1990), and in Denmark 824 kg ha^{-1} (SØRENSEN and BORGGAARD 1990). However, yields above 600 kg ha^{-1} were attained occasionally also in this material (Table 1). The seed yield of cocksfoot was low in comparison to other important fodder grass species in Finland i.e. *Phleum pratense, Festuca pratensis,* and *Lolium perenne* (see MUSTONEN et al. 1987).

The results from previous experiments suggested that the floral evocation of cocksfoot is not amply fulfilled in Finnish conditions especially if the stand is sown late in the previous season (NIEMELÄINEN 1990 a and b). In the present study, the data indicate that inadequate floral evocation was probably the main reason for low yield in seven trials in the first harvest year (Table 1). In those trials the ground cover was so high in spring (above 85 per cent) that the stand produced vegetative phytomass normally, but panicle production was poor.

In order to produce a high number of panicles, the stand should be well developed in the previous fall (NORDESTGAARD 1988, NIEMELÄINEN 1990 b). Because the stands were estab-

Table 1. Age of stand, nitrogen fertilization in spring, ground cover percentage in spring and seed yield of standard cv. Haka in seed production cultivar trials in Tikkurila, Mietoinen and Jokioinen in different growing seasons. Probable reason(s) for yield reduction is presented.

Location	Year	Age of stand	N fert. spring kg ha^{-1}	Ground cover in spring (%)	Seed yield kg ha^{-1}	Probable reason(s) for yield reduction
Tikkurila	1977	1	80	85	61	Inadequate floral evocation, frost damage
Tikkurila	1978	2	80	42	0	Winter and frost damage, drought
Mietoinen	1979	1	60	85	58	Inadequate floral evocation[cc]
»	»	2	60	46	218	Poor ground cover[x]
Mietoinen	1980	1	60	100	218	Inadequate floral evocation[cc], frost damage
»	»	2	60	93	244	Frost damage, drought
»	»	3	60	29	300	Poor ground cover[x], frost damage
Mietoinen	1981	2	60	2	0	Winter damage
»	»	3	60	1	0	Winter damage
Mietoinen	1982	1	54	96	230	Inadequate floral evocation[cc]
»	»	3	54	60	120	Poor ground cover[x], frost damage
Mietoinen	1983	1	90	91	340	Seed shedding, (inadequate floral evocation[wcc])
»	»	2	90	97	480	Seed shedding
Mietoinen	1984	2	90	40	130	Winter damage
»	»	3	90	61	150	Winter damage
Mietoinen	1985	1	72	87	220	Inadequate floral evocation[cc]
»	»	3	90	37	300	Poor ground cover[x]
Mietoinen	1986	1	79	99	300	Inadequate floral evocation[cc]
»	»	2	72	81	620	
Mietoinen	1987	2	100	95	300	Cool season
»	»	3	92	49	180	Poor ground cover[x]
Mietoinen	1988	3	90	68	370	Winter damage
Mietoinen	1989	1	80	90	440	Seed shedding
Jokioinen	1983	1[y]	64	94	697	
Jokioinen	1984	2[y]	96	81	74	Frost damage
Jokioinen	1985	3[y]	96	74	247	Frost damage
Jokioinen	1986	1	100	100	182	Frost damage, drought, (inadequate floral evocation[wcc])
Jokioinen	1987	2	120	—	459	Cool season
Jokioinen	1988	1	120	95	31	Inadequate floral evocation[cc], frost damage
»	»	3	120	99	267	Frost damage, seed shedding
Jokioinen	1989	2	120	99	626	
Jokioinen	1990	3	120	95	398	Frost damage

[x] Poor ground cover in the spring was due to damage earlier than the previous winter.
[y] The stand was sown on 24 August, 1981, but the age of stand in 1983, 1984 and 1985 is assigned to be 1, 2 and 3 because no seed yield was expected in 1982 due to the late sowing date.
[cc] The stand was established in a cover crop in the previous year.
[wcc] The stand was established without a cover crop in the previous year.

lished in a cover crop, the plants were probably not developed enough in the fall, and as a consequence floral evocation was not adequate for optimum panicle production in the first harvest year. The negative effect of a late harvested cover crop on seed production of cocksfoot in the first harvest year in Finnish conditions is reported in the studies of VALLE (1963), HAKKOLA (1967) and ANTILA (1971).

The optimal period for floral evocation is relatively short in northern localities after the daylength is shortened to optimal level (HEIDE 1990). The optimal flowering of three Nordic cocksfoot cultivars required 10 weeks of exposure to short days at temperatures ranging from 9 to 21 °C in the study of HEIDE (1987). Therefore the evocation may be incomplete even in older cocksfoot stands before winter and the beneficial conditions for evocation in the winter and spring become important (NIEMELÄINEN 1990 a).

Great winter damage decreased the yield in six trials (Table 1). The ground cover ranged from 1 to 68 % in the spring, and both phytomass and panicle production was poor. A critical period for wintering is when the snow cover is absent or thin, and temperatures are low (YLIMÄKI 1962, LÜTKE-ENTRUP and SCHRIMPF 1964, NIEMELÄINEN 1990 c). Cocksfoot is sensitive also to ice cover (HUOKUNA 1958, TEITTINEN 1958, RAVANTTI 1960, GUDLEIFSSON et al. 1986, RAVANTTI and MIETTINEN 1989). Low temperatures (< −15 °C) and absence of snow cover, with severe winter dam-

Table 2. Monthly precipitation P (mm), evaporation E (mm), and mean temperature t (°C) in May, June and July, the precipitation deficiency Pd (mm, precipitation — evaporation) in May and June, and the number of snow cover days in the pervious winter in Tikkurila, Mietoinen and Jokioinen.

Season	May			June			July			Pd in May and June	Snow cover period (d) in previous winter
	t °C	P mm	E mm	T °C	P mm	E mm	T °C	P mm	E mm	mm	
					Tikkurila						
1977	9.6	25	94	14.2	48	132	14.6	125	92	(−153)	145
1978	10.5	5	134	14.7	44	147	15.6	65	98	(−232)	134
					Mietoinen						
1979	9.8	32	118	15.3	13	174	14.7	92	84	(−247)	116
1980	8.1	12	119	16.9	64	146	17.2	122	122	(−189)	88
1981	11.4	13	144	13.2	117	94	16.4	68	98	(−108)	139
1982	8.3	53	94	11.7	15	135	16.5	72	148	(−161)	124
1983	10.9	30	85	13.5	65	117	16.7	35	134	(−107)	79
1984	12.7	36	123	14.2	70	116	15.0	44	80	(−133)	127
1985	8.6	44	108	13.9	49	108	15.7	109	109	(−123)	116
1986	10.4	38	117	16.2	25	144	16.4	149	121	(−198)	130
1987	7.4	45	78	11.7	91	110	15.0	142	110	(− 52)	117
1988	11.0	42	123	16.3	45	118	19.1	127	124	(−154)	123
1989	10.1	40	117	15.1	48	132	16.4	106	132	(−161)	90
					Jokioinen						
1983	11.0	44	92	13.3	84	117	16.6	41	149	(− 81)	100
1984	12.6	66	141	13.1	113	113	14.8	91	95	(− 75)	143
1985	8.6	43	110	13.2	41	121	15.3	55	115	(−147)	149
1986	10.5	52	109	16.3	11	178	16.2	65	123	(−224)	134
1987	7.6	38	92	12.1	82	88	14.8	68	143	(− 60)	131
1988	11.4	44	133	16.5	25	147	19.0	128	150	(−211)	157
1989	10.4	41	133	15.4	30	154	16.3	85	145	(−216)	110
1990	14.8	22	114	14.4	20	157	15.2	85	114	(−229)	110

ages, were recorded in Tikkurila in winter season 1977—78, and in Mietoinen in the winter seasons 1980—81, 1983—84 and 1987—88 (Fig. 1, Table 1). It is difficult to attribute the damage to low temperature or to ice cover. In some winters, an ice cover was formed on the stands after the snow had melted.

Exceptionally difficult ice cover was ob-

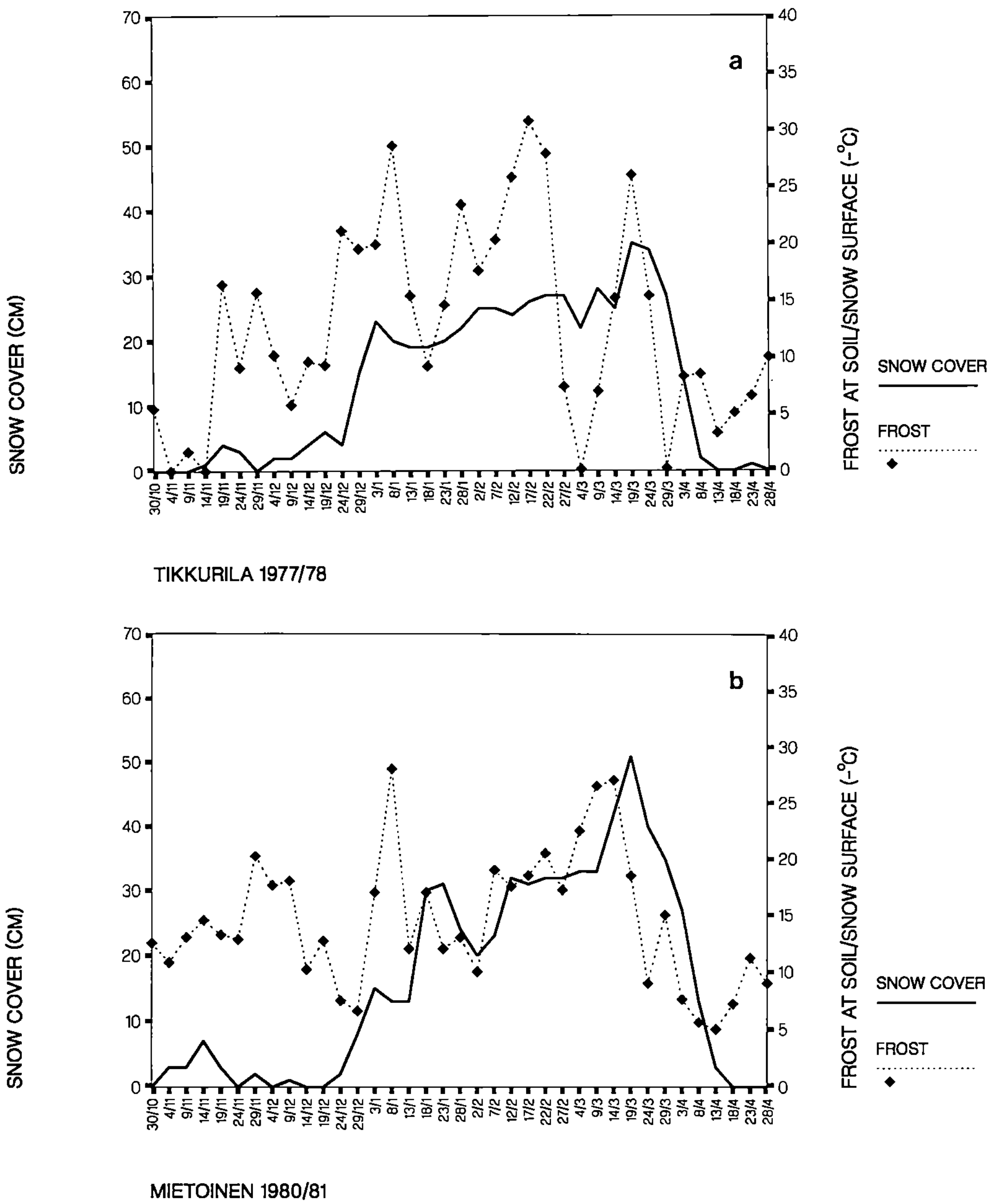
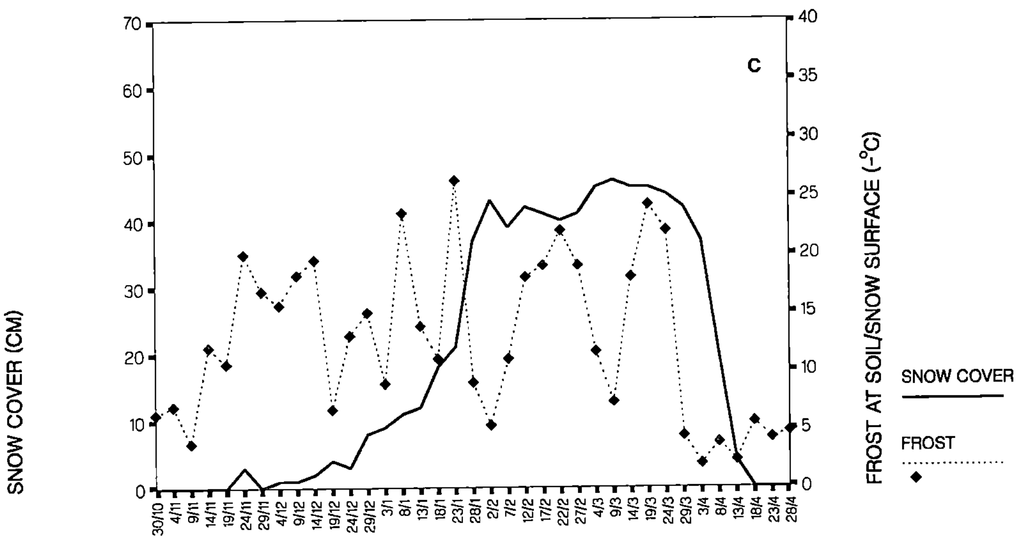


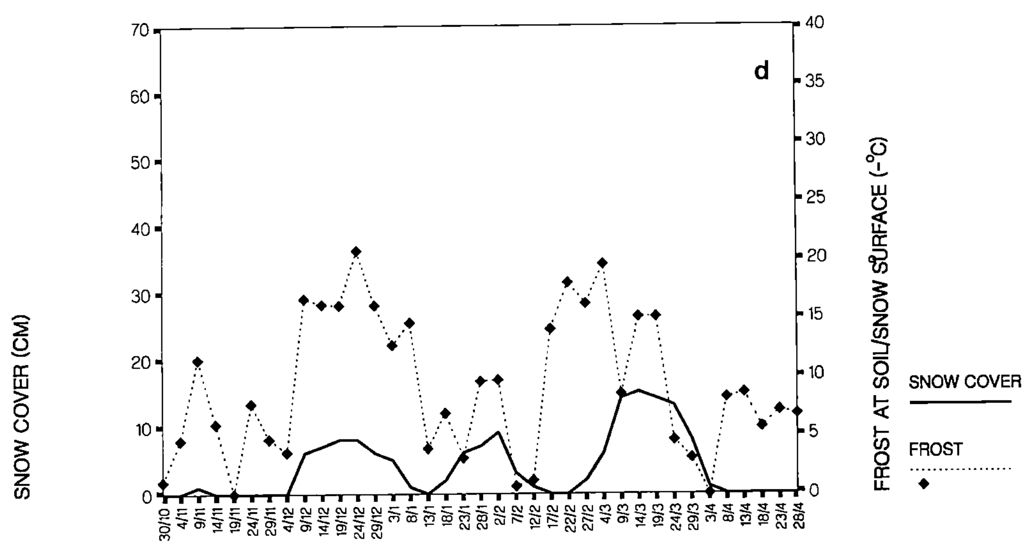
Fig. 1. Average depth of snow cover (________) and minimum temperature (-◆--◆--) (°C) at soil/snow surface in five-day periods during winter seasons in Tikkurila in 1977/78 (a), and in Mietoinen in 1980/81 (b), 1983/84 (c), and 1987/88 (d). Date of the middle day of the five-day period is assigned. Factors during these winters decreased wintering and/or seed yield.

served in the winters of 1980—81 and 1983—84 in Mietoinen (ANON. 1981 and 1984). Low temperatures in the absence of snow cover caused damages at least in the winter season of 1987—88 in Mietoinen (ANON. 1987).

A laboratory experiment showed that exhaustion of plants reserve carbohydrates decreased the ability of the plant to produce panicles (NIEMELÄINEN 1990 c). In the present material based on field trials it is difficult to distinguish between the effect of exhaustion of carbohydrate reserves and other factors, e.g. in-



MIETOINEN 1983/84



MIETOINEN 1987/88

adequate floral evocation and injury due to low temperature. The ground is snow-covered to a relatively short period in Southern Finland. Freezing and ice cover are therefore more important factors causing winter damage to cocksfoot in Southern Finland than a long period of snow cover (JAMALAINEN 1978, RAVANTTI and MIETTINEN 1989). According to the laboratory studies, however, the panicle production is more sensitive to exhaustion of carbohydrate reserves than the phytomass production of cocksfoot. Therefore the long snow cover period may have a negative effect on panicle production although the effect is not apparent in phytomass production (NIEMELÄINEN 1990 c).

The snow cover period ranged from 79 to 157 days in the winter seasons. The seed yield was not high when the snow cover period of the preceding winter was longer than 140 days (Tables 1 and 2). In general seed yield tended to be high when the snow cover period was shorter than 120 days. A high seed yield (620 kg ha^{-1}) after a snow cover period of 130 days obtained in Mietoinen 1986, however indicated that the effect of the length of snow cover period is not clear. The winter damage evaluated by ground cover percentage in spring was low in winters of long snow cover period except for the winter season 1980—81 in Mietoinen (Tables 1 and 2). However, ice cover and freezing were the reasons for the winter damage in that particular season (ANON. 1981).

The evocation of cocksfoot has been shown to occur at 0. . . +2 °C (BLONDON 1972) and +3 °C (HEIDE 1987), both at short and long daylength. Thus, although the main period for evocation is fall, the floral evocation can be enchanced also during winter and spring. Therefore a long snow cover period may affect the panicle production by exhausting carbohydrate

Table 3. Seed yield, density of panicles, and ground cover in spring for cocksfoot cultivars in the seed production cultivar trials in Finland in 1977—1990. Haka is the standard cultivar, and the other cultivars are tested one by one with Haka.

Cultivar	Seed yield kg/ha			Density of panicles %			Ground cover in spring %		
	n[z]	Significance[x]		n[z]	Significance[x]		n[z]	Significance[x]	
Haka (all trials)	32	258		27	43		31	73	
Haka	28	242	ns	23	40	ns	27	70	*
Tammisto		234			40			67	
Haka	10	342	***	8	63	*	9	88	ns
Tatu		223			57			80	
Haka	20	243	***	19	38	***	20	69	ns
Hera		143			20			65	
Haka	20	230	***	17	42	***	20	70	**
Fala		151			32			65	
Haka	8	146	*	7	22	*	8	52	ns
Frode		28			7			46	

[z] n = the number of comparisons between cv. Haka and the cultivar studied.
[x] According to Student's t-test, the means of the two varieties differ significantly from each other at $P<0.05$ = *, $P<0.01$ = **, $P<0.001$ = ***. ns = not significant.

Table 4. Seed yield in the first, second and third harvest year for cocksfoot cultivars in the seed production cultivar trials in Finland in 1977—1990. Haka is the standard cultivar, and the other cultivars are tested in pairs with Haka.

Cultivar	Seed yield (kg ha^{-1})					
	First harvest year		Second harvest year		Third harvest year	
	n	Significance[x]	n	Significance[x]	n	Significance[x]
Haka (all trials[z])	10	208	11	343	10	216
Haka		302		252		215
	9	ns	10	ns	9	*
Tammisto		279		245		178
Haka		218		568		282
	3	*	3	ns	3	**
Tatu		136		398		164
Haka		263		254		216
	6	*	7	ns	7	ns
Hera		169		146		118
Haka		180		313		191
	7	*	7	ns	6	ns
Fala		111		232		102
Haka		138		154		140
	2	—	3	ns	3	ns
Frode		0		40		33

[x] According to Tukey's t-test, the means of the two varieties differ significantly from each other at $P<0.05$ = *, $P<0.01$ = **, $P<0.001$ = ***. ns = not significant.

[z] The age of the stand sown in Jokioinen in 1981 is assigned to be on this line 2 in 1983 and 3 ih 1984. The zero yield from the first year stand in 1982 is not included. See Table 1.

Table 5. Occurrence of spring and summer frosts in 1977—1990. After the frost temperature the date and in parentheses the degree days (above +5°C) from the beginning of growing season is presented.

Year	Frost temperature[z]	Frost date	Onset of growing season	Degree days at frost date	Frost temperature[z]	Frost date	Onset growing season	Degree days at frost date
		Tikkurila				Mietoinen		
1977	−4,0 °C	29/5	26/4	143 °C*	no trial			
1978	−6,5 °C	8/5	3/5	7 °C	no trial			
»	−3,6 °C	18/6	»	334 °C*				
1979	no trial				−5,0 °C	21/5	9/5	51° C
1980	no trial				−7,0 °C	20/5	23/4	100 °C*
1981	no trial				−5,7 °C	4/5	5/5	0 °C
1982	no trial				−4,0 °C	21/5	4/5	39 °C
					−5,2 °C	11/6	»	186 °C*
		Jokioinen						
1983	−4,5 °C	8/5	18/4	56 °C				
1984	−6,5 °C	12/5	28/4	49 °C	−3,8 °C	12/5	29/4	46 °C
»	−4,7 °C	11/6	»	354 °C*				
1985	−6,4 °C	22/5	7/5	48 °C	−4,7 °C	16/5	8/5	30 °C
»	−4,6 °C	4/6	»	145 °C*	−3,0 °C	4/6	»	142 °C
1986	−6,3 °C	19/5	23/4	133 °C*				
1987	−7,8 °C	25/5	28/4	90 °C	−5,5 °C	25/5	28/4	66 °C
1988	−7,3 °C	20/5	30/4	86 °C*	−5,1 °C	20/5	»	91 °C
»	−3,7 °C	3/6	»	206 °C*				
1989	−5,0 °C	12/5	19/4	78 °C	−4,8 °C	1/5	11/4	55 °C
1990	−7,9 °C	12/5	15/4	123 °C*	no trial			

* Frost is probably one cause for poor seed yield (see Table 1).

[z] Frost temperatures measured at soil surface. Only the most severe frosts in May and June are mentioned. Frosts milder than −3.0 °C are not mentioned.

reserves, but also by preventing the enhancement of floral evocation. A too long snow cover period may be one factor decreasing the seed yield of cocksfoot in Southern Finland, but the question needs further investigation, especially when seed is produced on areas of even longer snow cover periods.

Frost may destroy the panicles of coksfoot (ANON. 1983, NIEMELÄINEN 1991) and decrease the number of seeds per panicle (NIKOLAEVSKAYA 1973). KÖYLIJÄRVI (1983) reported of a total failure in cocksfoot panicle production and seed yield due to frost in Mietoinen in 1975. In the present material, frost decreased the seed yield in 12 trials (Table 1). Late after onset of the growing season severe frosts caused remarkable yield reduction in Tikkurila in 1978, and in Jokioinen in 1984 and 1988 (Tables 1 and 5). In Tikkurila in 1978 a frost of —3.6 °C caused total failure of the seed yield of cocksfoot, and decreased considerably seed yield of other grasses, too. For example, the seed yield of timothy cv. Tarmo was only 313 kg ha^{-1} and that of meadow fescue cv. Kalevi 182 kg ha^{-1} in second year stands which had overwintered without problems (ANON. 1978). Frost caused severe damage also to cereal fields in Tikkurila in 1978 (LALLUKKA 1979). Yield reduction in Jokioinen in 1984 was also nearly complete when a —4.7 °C frost occurred late after onset of the growing season (Tables 1 and 5). The immediate damage caused by frost may easily remain unnoticed in field conditions (NIEMELÄINEN 1991).

Cocksfoot has an extensive root system and it has a good drought tolerance in general (JUNG and BAKER 1985, PULLI 1986). In the study of JONASSEN (1986), drought prior to flowering had a negative effect on the seed yield of cocksfoot in Norway, but drought during the seed development and maturing phase had a positive effect. In this respect drought in May and June may have a negative effect on the seed yield of cocksfoot in Finland. Precipitation deficit in May and June is a common phenomenon in Southern Finland. Early summer drought has been the most important cause of yearly variation in silage yield in Southern Finland (MUKULA et al. 1981). However, hay production, especially the yield of first cut, was not sensitive to drought. The difference was due to the ability of the stand to utilize the ample spring moisture content of soil better in hay production than in silage production (MUKULA et al. 1981).

The effect of early summer drought on the seed yield of cocksfoot is difficult to evaluate in the present study, because of the interference of several factors, e.g. winter damage, frost, inadequate floral evocation and drought.

Precipitation deficiency in May and June, which ranged from 52 to 247 mm, in the present study (Table 2), was greater than in the experiment of JONASSEN (1986). However, in the present study the experimental soil was heavy clay, which keeps the moisture better than does the sand in JONASSEN's (1986) study (HEINONEN 1954). Immediately after winter the moisture content of the soil is high due to the melting snow.

The high yield obtained in the second year stands in Mietoinen in 1986 and in Jokioinen in 1989 despite the great precipitation deficiency in May and June, indicates that drought has not been the primary reason for yield reductions in the present material. However, drought may have decreased the yield in some trials, e.g. in Tikkurila in 1978, in the second year stands in Mietoinen in 1979 and 1980, and in the first year stands in Jokioinen in 1986 (Tables 1 and 2).

Poor ground cover and pre-harvest seed shedding also contribute to low seed yield. Inferior establishment of the trial sown in 1977 in Mietoinen caused total seed failure in 1978 (zero yield is not included in the calculations) and a considerable yield reduction also in the second year stands in 1979 and in the third year stand in 1980. Poor ground cover, due to damages from earlier winters, decreased the seed yield of third year stands in Mietoinen in

1982 and in 1985 in third year stand (Table 1).

Cocksfoot sheds seed easily. ARNOLD and LAKE (1966) reported that seed shedding is severe at a moisture content of 30 %, but they did not recommend earlier direct combine harvesting due to an increased risk of germination damage to seed. However, WØLNER (1986) recommended double threshing and early first combining at a seed moisture content of 35—37 % in order to eliminate severe pre-harvest shedding. According to WØLNER (1986) a considerable amount of seed is shed if the first threshing is done at a seed moisture content below 34 %.

In the present material, the seed moisture content of cv. Haka averaged 30.2 % in the 12 harvests where moisture content was analyzed. If the values for the extremely cool season of 1987 are excluded, the average for the remaining 10 analyses was 27.4 % which gives a rough estimate of the maturity level of the crop at harvest time. The low moisture content indicates that several trials were harvested so late that seed shedding losses were considerable. The yield loss due to pre-harvest shedding may have been as much as one-third in some trials when the results of WØLNER (1986) are used as a basis for estimation.

The nitrogen application varied greatly in the trials (Table 1). According to fertilizer experiments, nitrogen application above 100 kg N ha^{-1} in spring is advantageous to the seed yield of cocksfoot in Finnish conditions (HAKKOLA 1967, NIEMELÄINEN unpubl.). Thus the application levels in spring were not optimal in all trials in the present study. However, the two seed yields above 600 kg ha^{-1} with spring nitrogen applications of 64 and 72 kg N ha^{-1} (plus 30 kg N ha^{-1} in the previous fall) show that high seed yield can be attained with quite low levels of nitrogen application (Table 1). Therefore, nitrogen deficiency cannot be the primary reason for poor panicle production and seed yield in the present material.

It can be pointed out that the highest yields were attained in the absence of the above mentioned negative factors. Exceptionally high yields were obtained in Mietoinen in 1986 and in Jokioinen in 1983 and in 1989. High yields were obtained in Mietoinen also in 1983 and in 1989, if the obvious loss of seed by pre-harvest shedding in those trials is taken into consideration (Table 1). With the exception of Mietoinen in 1988/1989 (Fig. 2 c) when a temperature of -21.5 °C was measured in the absence of snow cover, in these seasons, no severe frost late after onset of the growing season or low temperatures (< -15 °C) in the absence of snow cover were reported (see Table 5 and Fig. 2 a—e). However, it is possible that there was some snow cover on the field also in Mietoinen 1988/89, although the value at the measuring point was 0 cm according to the climatic data register. According to the weather statistics, the precipitation due to snowing was 4.4 mm during two days prior to the -21.5 °C temperature (ANON. 1988 b). This precipitation usually means a snow cover of about 4 to 5 cm.

Effect of cultivar

Cultivar Haka produced significantly higher seed yield than cvs. Tatu, Hera, Fala and Frode. The difference between cvs. Haka and Tammisto was small and not significant. The density of panicles was also significantly higher in cv. Haka than in cvs. Tatu, Hera, Fala and Frode. However, the differences between cv. Haka and other cultivars were small in terms of ground cover in the spring. In terms of ground cover values, only cvs. Fala and Tammisto differed significantly from cv. Haka (Table 3).

The correlation coefficient between seed yield and density of panicles ranged from 0.74 to 0.98 for different cultivars and was significant for all cultivars (Table 6). The values are similar to those reported by NORDESTGAARD and LARSEN (1974) for the correlation coefficient between seed yield and number of panicles per square meter. The coefficient ranged from 0.62 to 0.88 in different years and was significant in all years (NORDESTGAARD and LARSEN 1974). The correlation coefficient between seed yield and ground cover in the spring was significant for cvs. Haka, Tammisto, Hera and Fala, ranging from 0.51 to 0.38. In the present material, the correlation coefficient between den-

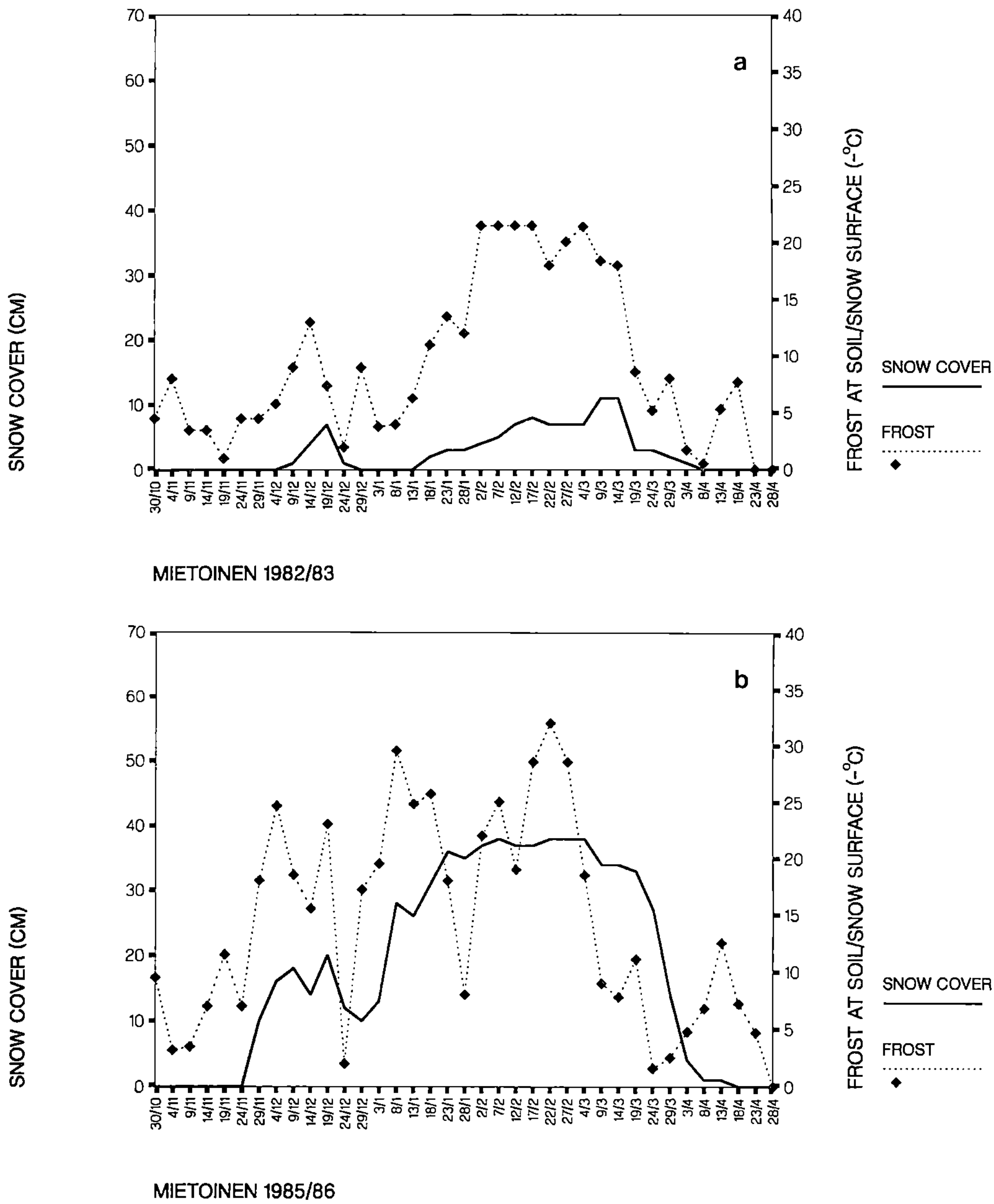
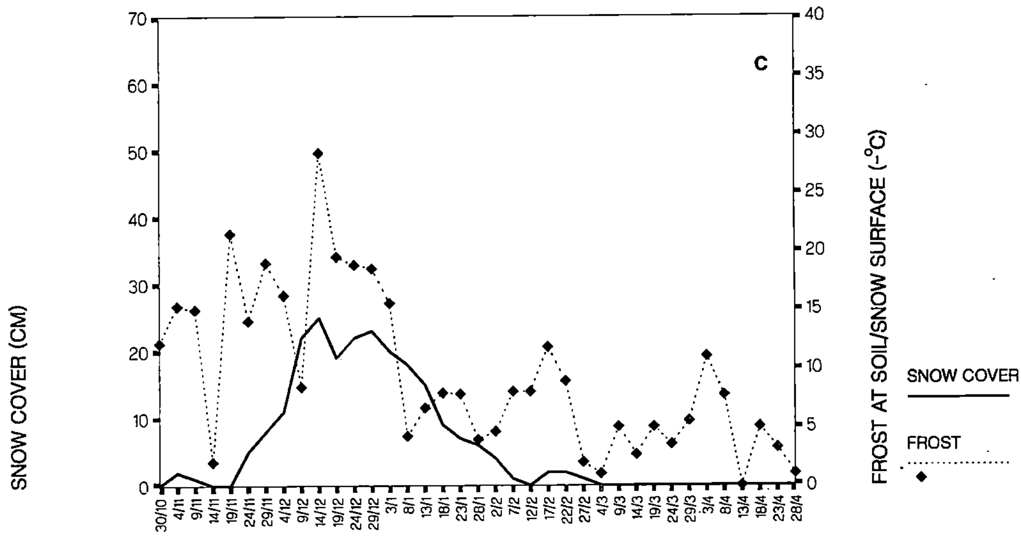


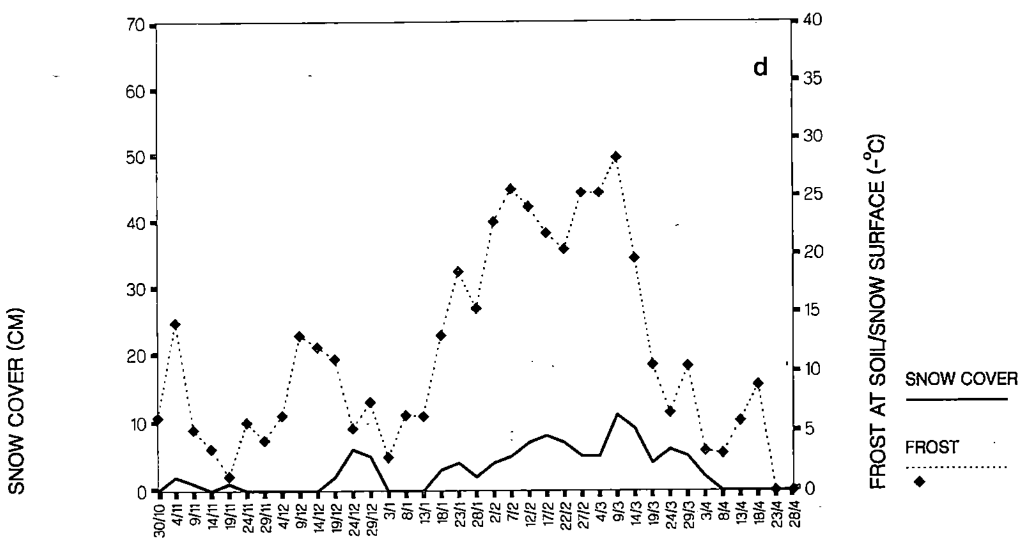
Fig. 2. Average depth of snow cover (________) and minimum temperature (- ◆ -- ◆ --) (°C) at soil/snow surface in five-day periods during winter seasons in Mietoinen in 1982/83 (a), in 1985/86 (b), 1988/89 (c), and in Jokioinen in 1982/83 (d) and 1988/89 (e). Date of the middle day of the five-day period is assigned. Exceptionally high seed yields were obtained after these winters.

sity of panicles and ground cover in the spring was significant only for cvs. Haka (0.34) and Tammisto (0.61) (Table 6).

The difference in panicle density and seed yield was significant between cv. Haka and cvs. Tatu, Hera, and Frode. As the difference in ground cover was not, however, significant in spring, the data suggest that differences between cv. Haka and cvs. Hera, Tatu and Frode in seed yield and in panicle density were due to differences in the fulfilment of floral evocation. Differences probably exist also between



MIETOINEN 1988/89



JOKIOINEN 1982/83

Table 6. Correlation coefficient[z] between seed yield, density of panicles and ground cover in the spring for cocksfoot cultivars in the seed production cultivar trials in 1977—1990.

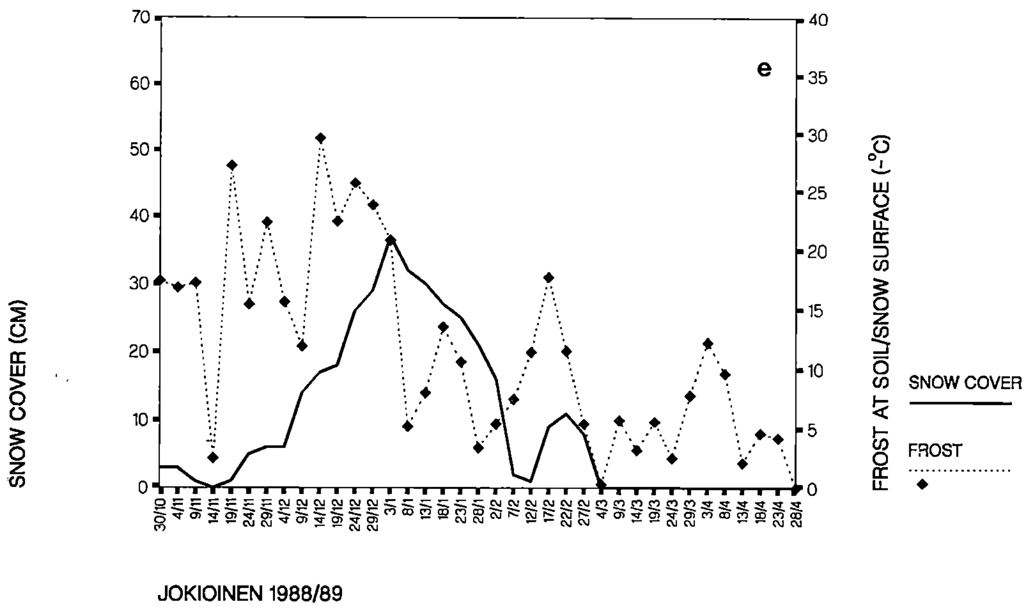
Cultivar	Correlation coefficients between different variables					
	Seed yield/ density of panicles		Seed yield/ ground cover in spring		Density of panicles/ ground cover in spring	
Haka	0.74***	(n = 27)	0.42**	(n = 32)	0.34*	(n = 27)
Tammisto	0.81***	(n = 23)	0.51**	(n = 28)	0.61**	(n = 23)
Tatu	0.76*	(n = 8)	0.04ns	(n = 10)	0.34ns	(n = 8)
Hera	0.94***	(n = 19)	0.39*	(n = 20)	0.30ns	(n = 19)
Fala	0.92***	(n = 17)	0.38*	(n = 20)	0.35ns	(n = 17)
Frode	0.98***	(n = 7)	−0.02ns	(n = 8)	−0.07ns	(n = 7)

[z] The correlation coefficient is statistically significant at * $P<0.05$, ** $P<0.01$, *** $P<0.001$. ns = correlation coefficient is not statistically significant.

cvs. Haka and Fala, although the significantly lower ground cover of cv. Fala in spring has further increased the difference in seed yield (Table 3).

There can be remarkable differences in the floral evocation requirements between ecotypes of the same species (HEIDE 1990). In the study of HEIDE (1987) the differences were small between three Nordic cultivars of cocksfoot in the short day or low temperature treatment on floral evocation, but the number of panicles per plant differed significantly in response to number of long day cycles after floral evocation. The difference in the origin of cultivars was greater in the present study than in the study of HEIDE (1987).

The fulfilment of floral evocation of cultivars of even wider origin was studied in a small trial in Jokioinen. An Italian cv. Dora and the Finnish cv. Haka were sown in field (31 May, 1989) and were transferred into a glasshouse, just prior to onset of winter. There they were



grown for eight weeks under conditions favourable, for instance, to panicle growth. Cv. Haka produced a significantly greater number of panicles (14.2) per pot than cv. Dora (1.6), but the difference was not significant in the production of above ground phytomass (64.2 and 68.5 g per pot, respectively) (NIEMELÄINEN unpubl.). This indicates that the floral evocation requirement of cv. Haka was more completely fulfilled before the onset of winter than of that of cv. Dora.

In spite of the great difference in the average seed yield between cultivars, also cvs. Hera, Tatu and Fala, in addition to cvs. Haka and Tammisto, produced occasionally high seed yields. The maximum yields were 697 kg ha^{-1} for cv. Haka, 661 kg ha^{-1} for cvs. Tammisto and Hera, 570 kg ha^{-1} for cv. Tatu, 560 kg ha^{-1} for cv. Fala. Cultivar Frode was included only in trials of very low yields, and the maximum yield for cv. Frode was only 120 kg ha^{-1}.

The quality characteristics of seed must be considered cautiously, because the results are from a cultivar trial of a cross-pollinated crop. Cross-pollination of cultivars is inevitable. The average thousand seed weight for cv. Haka was 1.34 g for the 18 harvests analyzed. Cultivars Tatu and Tammisto had significantly lower 1 000 seed weight (relative figure for cv. Haka 92 and 94), and cv. Hera had a significantly higher 1 000 seed weight than cv. Haka (relative figure 112). The average germination percentage for cv. Haka was 77 for the 15 harvests studied.

The average date for panicle emergence was 4 June for cv. Haka. The difference between cultivars in date of panicle emergence was less than two days. The average degree days (above +5 °C) from the onset of growing season to emergence of panicles was 184 °C for cv. Haka in Jokioinen (average of five observations). However, the right base temperature for calculating degree days in Finnish conditions may be lower than +5 °C (PULLI 1980). Unfortunately the data available are not sufficient to approximate the ideal base temperature for degree days for cocksfoot in Finnish conditions.

In conclusion, the reasons for the failures in seed yield and for low average yield were inadequate floral evocation in the first harvest year stands, great winter damage caused by freezing and/or ice cover, and frost damage. In addition, preharvest seed shedding caused in several trials an obvious decrease in seed yield. The effect of drought and a long snow cover period remained unclear. A prerequisite for high seed yield is the use of an appropriate cultivar. When measures are taken to eliminate the effect of the negative factors, the chances for considerably higher average seed yields are good. The highest yields exceeded 600 kg ha^{-1}, which indicates that cocksfoot has potential for high seed yields also in Finnish conditions.

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SELOSTUS

Koiranheinän (*Dactylis glomerata* L.) siemensadon vaihtelu Suomessa

OIVA NIEMELÄINEN

Maatalouden tutkimuskeskus

Tutkimuksessa tarkasteltiin koiranheinän siemenviljelyn onnistumista Maatalouden tutkimuskeskuksen siemenviljelyn lajikekokeissa. Tuloksia oli käytettävissä kasvinviljelylaitokselta Tikkurilasta vuosilta 1977—1978, Lounais-Suomen tutkimusasemalta Mietoisista vuosilta 1979—1989 sekä kasvintuotannon tutkimuslaitokselta Jokioisista vuosilta 1983—1990. Tarkasteltavina lajikkeina olivat Haka, Tammisto, Tatu, Hera Daehnfeldt, Fala ja Frode.

Mittarilajike Hakan kaikkiaan 32:n koetuloksen keskimääräinen siemensato oli 258 kg ha^{-1}. Kymmenessä kokeessa Hakan siemensato oli korkeintaan 150 kg ha^{-1}. Hehtaarisato oli keskimäärin korkeampi toisen vuoden nurmessa (343 kg ha^{-1}) kuin ensimmäisen (208 kg ha^{-1}) tai kolmannen (216 kg ha^{-1}) vuoden nurmessa. Suurimmat yksittäiset sadot olivat yli 600 kg ha^{-1}.

Siemensatoa alentavat tekijät voitiin jakaa kolmeen ryhmään. Ensinnäkin vähäinen kukinnan virittyminen vähensi röyhynmuodostusta etenkin ensimmäisen nurmivuoden kasvustoissa. Suojaviljaan perustettujen kasvustojen röyhynmuodostus oli ensimmäisenä nurmivuonna vähäistä vaikka kasvustot olivat keväällä täystiheitä.

Toiseksi jääpolte sekä ankarat pakkaset lumettomaan aikaan aiheuttivat niin suuria talvituhoja, että siemenmuodostus jäi pieneksi kasvuston vähäisyyden vuoksi. Kolmanneksi myöhään kasvukauden alkamisen jälkeen esiintyneet hallat vähensivät sekä röyhyn- että siemenmuodostusta useissa kokeissa. Näiden tekijöiden lisäksi joissakin kokeissa hehtaarisatoa alensivat alkukesän kuivuus, siementen variseminen ennen puintia ja heikosta kasvuston taimettumisesta johtuva kasvuston vähäisyys. Lumipeiteajan keston vaikutus siemensatoon ei ollut selkeä. Yleensä lyhyt lumipeiteaika (alle 120 vrk) oli edullinen siemensadon muodostumiselle. Typpilannoitus oli eräissä kokeissa optimilannoitusta pienempi.

Siemensadon ja röyhyjen suhteellisen tiheyden välinen korrelaatiokerroin oli tilastollisesti merkitsevä kaikissa lajikkeissa ja vaihteli välillä 0.74—0.98. Korrelaatiokerroin siemensadon ja keväisen kasvuston tiheyden välillä oli pienempi (−0.02—0.51) ja merkitsevä lajikkeissa Haka, Tammisto, Hera Daehnfeldt ja Fala. Kasvuston tiheyden ja röyhyjen suhteellisen tiheyden välillä oli merkitsevä korrelaatiokerroin vain lajikkeilla Haka (0.34) ja Tammisto (0.61).

Haka -lajike muodosti merkitsevästi enemmän röyhyjä ja sen siemensato oli suurempi kuin lajikkeiden Tatu, Hera Daehnfeldt, Fala ja Frode siemensato. Tammiston ja Hakan välillä ei ollut merkitsevää eroa röyhynmuodostuksessa eikä siemensadossa. Ainoastaan Fala ja Tammisto lajikkeiden kasvuston peittävyys keväällä oli merkitsevästi pienempi kuin Hakan. Tulokset viittaavat siihen, että Tatun, Hera Daehnfeldtin ja Froden puutteellisempi kukinnanvirittyminen Hakaan verrattuna oli syynä niiden Hakaa vähäisempään röyhyn- ja siemensadonmuodostukseen.

ANNALES AGRICULTURAE FENNIAE, VOL. 30: 191—198 (1991)

Seria AGRICULTURA N. 101 — Sarja PELTOVILJELY n:o 101

SUITABILITY OF GLUTEN INDEX METHOD FOR EVALUATION OF WHEAT FLOWER QUALITY

LEENA HÖMMÖ, ELISA PIETILÄ and YRJÖ SALO

HÖMMÖ, L., PIETILÄ, E. & SALO, Y. 1991. **Suitability of gluten index method for evaluation of wheat flour quality.** Ann. Agric. Fenn. 30: 191—198. (Agric. Res. Centre of Finland, Inst. Pl. Breed., SF-31600 Jokioinen, Finland.)

The suitability of Perten's gluten index method for the determination of gluten quality was studied using Finnish spring and winter wheat varieties and breeder's lines. A very high positive correlation was found between the tensile properties of the dough as determined by extensograph and gluten index values. The gluten index also turned out to be well suited for estimating the stability of dough determined by farinograph. On the other hand, on the basis of our results the gluten index could not be used for predicting the properties of bread, especially loaf volume. The reasons for this are briefly discussed.

Index words: baking quality, dough quality, gluten index, wheat quality.

INTRODUCTION

It has long been recognized that the gluten fraction of total protein is mainly responsible for the viscoelastic property of wheat dough and also for the final baking value of the flour. The usual method of using wet gluten as an indicator of the quality of wheat protein has turned out to be too imprecise, as flours with the same amount of wet gluten often behave quite differently during the baking procedure. Thus not only the quantity, but also the quality of gluten determines the baking behaviour of flour.

Since the late 1970's it has been known that various gluten subunits with both high and low molecular weights are mainly responsible for the baking quality of wheat (PAYNE et al. 1979, BURNOUF and BOURIQUET 1980, SOZINOV and POPERELYA 1980 and GUPTA et al. 1989). These subunits can be determined by electrophoretic or by chromatographic methods. Many sophisticated methods have been developed for these determinations, but they are all quite laborious and time-consuming.

For breeding purposes, it would be important to have a fast and reliable method for gluten quality selections from a small amount of seeds. This would enable a breeder to select for quality already during early generations.

The gluten index method has been proposed by PERTEN (1989) to be a rapid method for determining both the quantity and quality of wet gluten simultaneously. This method is based on centrifugal force causing a part of the wet gluten sample to pass through a specially constructed sieve.

In this study, we determined the gluten index for a number of spring and winter wheat varieties and breeder's lines, and compared it with various flour quality indicators as determined by farinograph and extensograph and with the final baking results.

MATERIAL AND METHODS

The materials for experiments were obtained from spring and winter wheat field trials in Jokioinen, Southwestern Finland, in 1988 and from spring wheat trials only in 1989. The samples consisted of both varieties and breeding lines of spring and winter wheat. The numbers of samples were 84 (1988) and 25 (1989) for spring wheat and 78 (1988) for winter wheat.

Seed samples were milled on a Bühler laboratory mill MLU 202 with flour fractions 1—6 combined. The flour thus obtained was used in all procedures. The only exception was the determination of gluten index in 1989, in which whole meal, ground in a Falling Number laboratory mill 3 100 was used.

A Technicon 400R infrared-reflectance analyzer was employed for the determination of total proteins in the samples.

Dough properties were determined by Brabender's farinograph and extensograph, ICC procedures 115 and 117, accordingly (ANON. 1987). Wet gluten was separated from wheat flour by a Glutomatic 2200 system (Falling Number AB) according to ICC procedure 137 (ANON. 1987). The gluten index was determined according to the method described by PERTEN (1989). In this method, after being washed the gluten is centrifuged on a special sieve. From the part of the gluten remaining on the sieve and passing through the sieve, the gluten index can be calculated in the following way:

$$\text{Gluten Index} = \frac{\text{gluten remaining on the sieve (g)}}{\text{total gluten (g)}} \times 100$$

The gluten index is expressed on the scale 0—100. A low gluten index indicates weak (extensible or soft) gluten and a high gluten index indicates strong (short) gluten.

Baking quality was estimated on the basis of experimental laboratory bakings carried out according to the recipe of the Finnish State Granary. The dough is composed of:

250 g flour (moisture content 15 %)
7.5 g yeast
5.0 g salt
5.0 g sugar
5.0 g margarine
6.0 ml 1 % ascorbic acid solution
malt flour, if necessary, to get falling number down to 250
the amount of water is determined farinographically

After being mixed with the farinograph the dough is left to rest for about 45 minutes at the temperature of 28—30 °C. This is followed by rolling out the dough twice and another resting period as before. Some properties such as the hardiness and stickiness of the dough are estimated, and the dough is weighed. After this, the dough is rolled out as before and put in the mould into the fermentation chamber (temperature 32 °C, humidity 80 %) for 90 minutes. The bread is baked first 10 minutes at 150 °C with steaming and then another 10 minutes at 200 °C without steam.

The results were analysed statistically using Pearson's correlation (ANON. 1985).

RESULTS

Total proteins in the spring wheat samples varied between 14.4 and 19.3 % with mean 17.0 % in 1988 and between 15.8 and 20.2 %, mean 17.3 % in 1989. In winter wheat the level of total protein was somewhat lower, varying between 11.5 and 16.7 % with a mean of 13.4 % (in 1988).

The amount of wet gluten in the spring wheat samples varied between 32.7—48.4 %, mean 38.8 % in 1988 and between 38.4—53.8 %, mean 44.9 % in 1989. The gluten index varied between 45 and 98, mean 77 in 1988 and between 31 and 88, mean 57 in 1989. In 1988, the corresponding values in winter wheat were 21.1—39.3 %, mean 30.9 % for wet gluten and 7—96, mean 65 for the gluten index.

In this study, we found a very clear negative correlation between the gluten index and the quantity of wet gluten in both spring and winter wheat (Table 1 and Fig. 1).

When studying the correlations between the tensile properties of the dough as determined by extensograph and wet gluten or by gluten index we found that wet gluten correlated slightly negatively or not at all with the resistance to extension or with the energy of the dough. On the other hand, there was a very significant positive correlation between the gluten index values and the extensograph properties mentioned above (Table 1 and Figs. 2 and 3).

There was essentially no correlation between the water binding capacity of the flour and wet gluten or gluten index (Table 1). Only in 1988

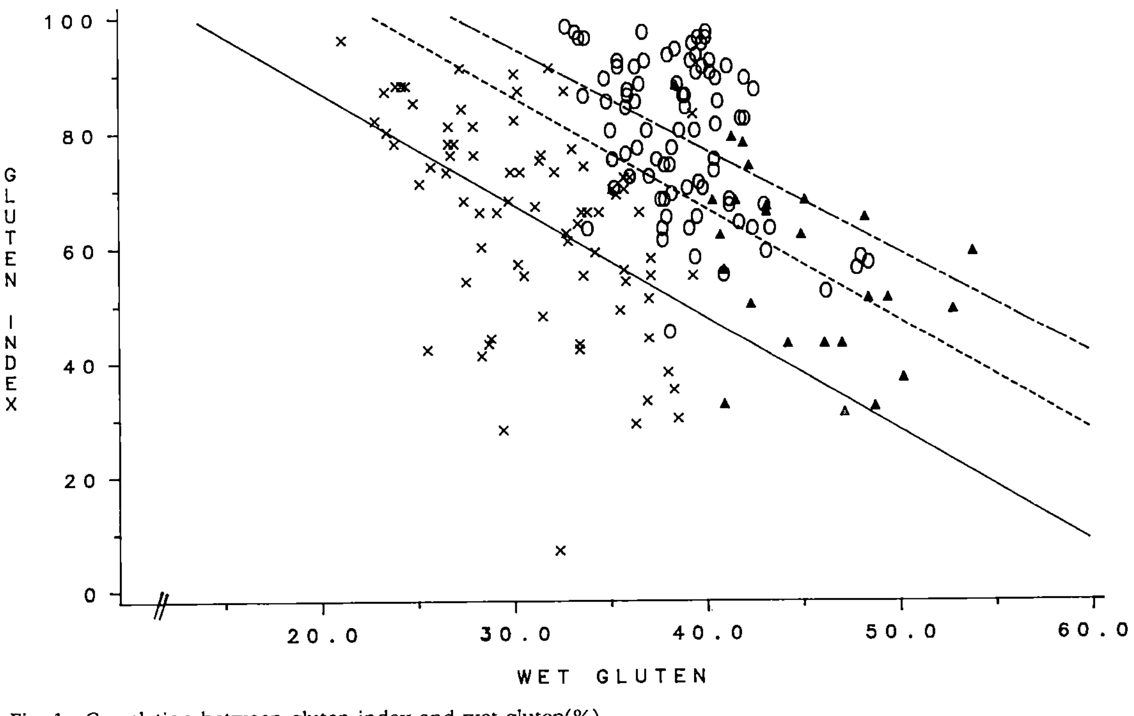

Fig. 1. Correlation between gluten index and wet gluten(%).

Spring wheat 1988 — — — OOOO

Spring wheat 1989 — — — ▲▲▲▲

Winter wheat 1988 ——— XXXX

did the wet gluten content of spring wheat correlate clearly positively with water absorption.

Development time of the dough and the valorimeter value correlated significantly positively with the amount of wet gluten of spring and winter wheat in 1988. The gluten index did not correlate with the above mentioned properties as clearly as wet gluten.

The stability of the dough correlated positively with the gluten index. This correlation was very significant in 1988 in winter wheat and in 1989 in the spring wheat results (Table 1).

When studying the results from the experimental bakings, a clear positive correlation was found between bread volume and wet gluten. With the gluten index this correlation was negative (Table 1).

In the winter wheat trial there was a strong negative correlation between the porosity of bread and wet gluten. Between the gluten index and porosity the correlation was clearly positive. In the spring wheat trials no correlation was found between these traits (Table 1).

Table 1. Correlations of wet gluten and gluten index of some Finnish spring and winter wheat varieties and breeder's lines with wet gluten, some extensograph, farinograph and experimental bread-values. Statistical significance: * $p<0.05$, ** $p<0.01$ and *** $p<0.001$.

Material	Number of samples	Wet gluten	Extensograph		Farinograph				Experimental bread	
			Energy	Resistance to extension	Water absorption	Develop-ment time	Stability	Valori-meter value	Loaf volume*	Porosity
Spring wheat 1988	84									
Wet gluten			−0.148	−0.226*	0.313**	0.448***	0.069	0.376***	0.257*	−0.147
Gluten index		−0.430***	0.635***	0.502***	−0.194	−0.123	0.196	−0.065	−0.036	0.162
Spring wheat 1989	25									
Wet gluten			−0.201	−0.340	0.227	0.196	−0.183	0.158	0.509**	0.065
Gluten index		−0.514**	0.739***	0.716***	−0.276	0.232	0.638***	0.419*	−0.508**	−0.063
Winter wheat 1988	78									
Wet gluten			0.119	−0.282*	0.133	0.570***	0.160	0.417***	0.722***	−0.490***
Gluten index		−0.495***	0.443***	0.344**	0.036	0.078	0.414***	0.292**	−0.564***	0.392***

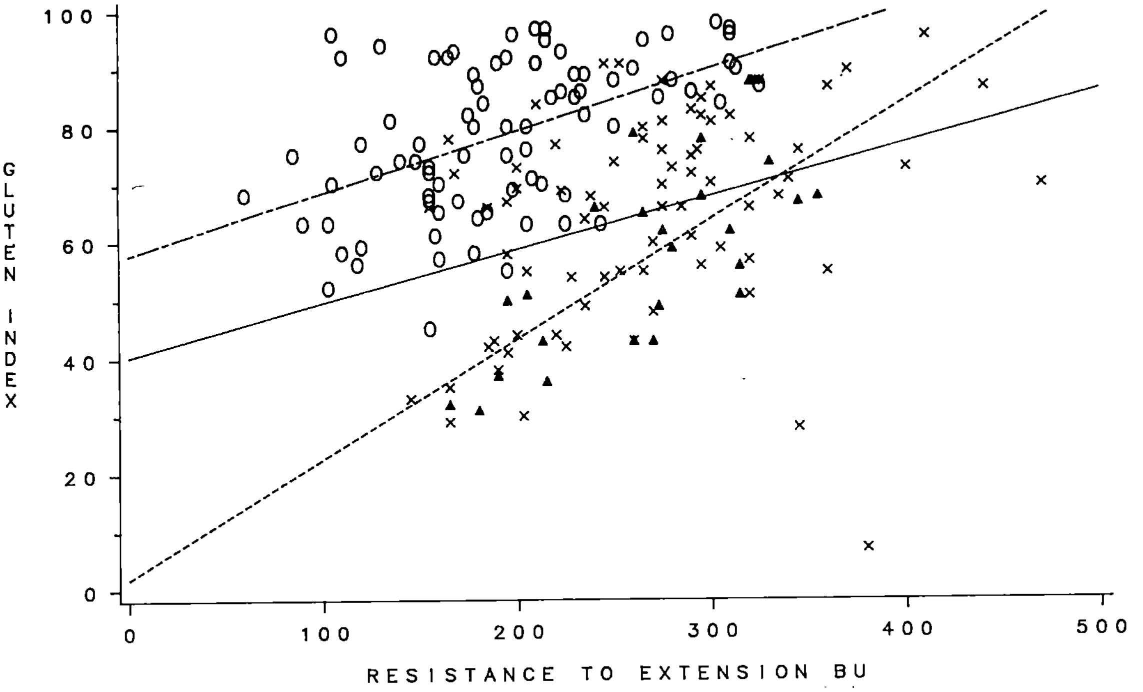

Fig. 2. Correlation between gluten index and resistance to extension (BU).

Spring wheat 1988 — – — 0000 Spring wheat 1989 – – – ▲▲▲▲ Winter wheat 1988 ——— XXXX

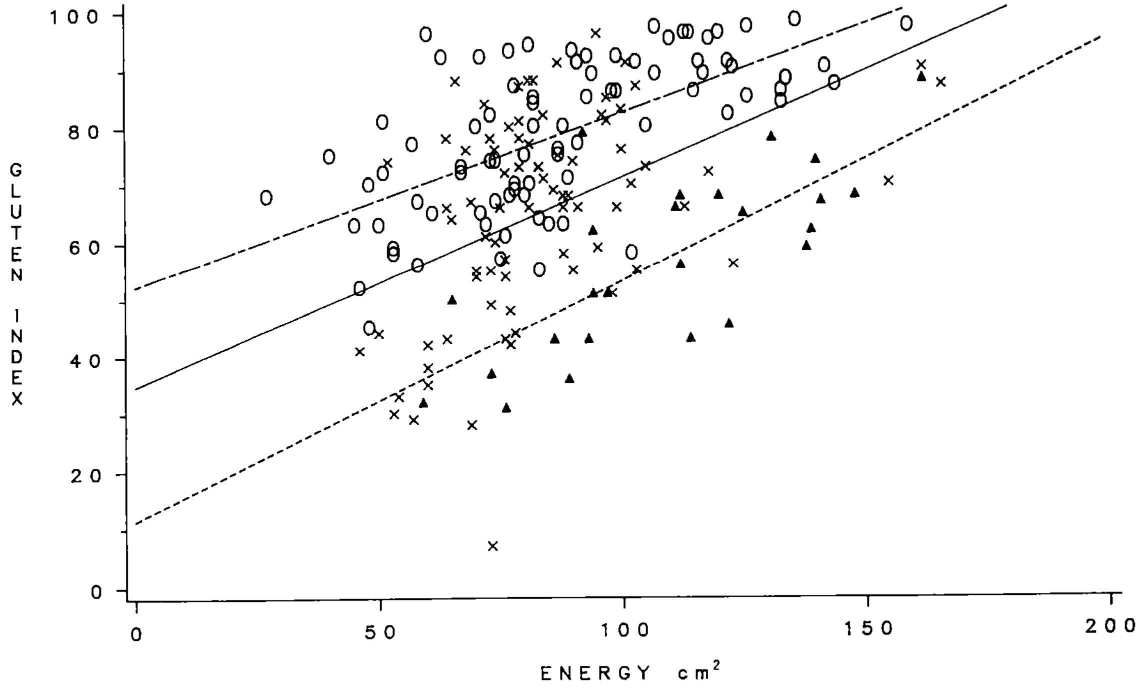

Fig. 3. Correlation between gluten index and energy (cm²).

Spring wheat 1988 — – — 0000 Spring wheat 1989 – – – ▲▲▲▲ Winter wheat 1988 ——— XXXX

DISCUSSION

Since the summers of 1988 and 1989 were both very hot and dry in Finland, the plant stands suffered quite badly. Because of this, the total protein, especially in spring wheat, rose to a very high level. This could have caused some error not only in the experimental baking results, but also in the other methods used for determining wheat flour and dough quality (TIPPLES and KILBORN 1974, HIBBERD and GRAS 1989).

According to PERTEN (1989) there should not be any correlation between wet gluten and gluten index. However, in our study we found a very clear negative correlation between these traits. This could partly be explained by the unusually high protein content mentioned above. This also resulted in a high wet gluten quantity that could have obscured the quality differences. The picture would perhaps have been very different, if only wet gluten values between 30.0 % and 40.0 % had been taken into consideration.

In 1989 the wet gluten and gluten index determinations were carried out on whole meal. Our results are in accordance with Perten's results: whole meal is very well suited to gluten quality estimations by the gluten index. This yields many advantages, as whole meal gluten represents the whole grain, no just a part of it. There is also no need for large amounts of seed or time-consuming gridings to obtain extracted flours.

One of the most frequently used methods for estimating the elasticity and extensibility of gluten is to do it by extensograph (WEIPERT 1989). In this study a very significant positive correlation was found between gluten index and extensograph values in both the resistance to extension and energy. On the other hand, there was no correlation between wet gluten and extensograph values. Thus these results support the idea of the gluten index being superior to wet gluten for describing gluten quality.

While studying the correlations between farinograph values and wet gluten and the gluten index, we found that both the capacity of binding water and dough development time depended more on the amount of wet gluten, than on the quality of gluten measured by the gluten index. On the other hand, the stability of dough seems to depend more just on the quality and less on the quantity of gluten. The valorimeter value is a combination of dough development and stability values, so it depends on both the quantity and quality of gluten.

According to PERTEN (1989), there is no direct correlation between loaf volume and gluten index, but the loaf volume is only dependent on the quantity of gluten. On the other hand, he has presented that the optimum gluten index values for baking purposes should be between 60—90. This optimum level was confirmed also by JOHNSSON (1990). SCHÖGGL (1989) found that when using wheat flour with a good gluten index (80.2) the resulting test bread was very good, with a high loaf volume. The use of flour having an excessively high gluten index (95.5) resulted in bread of poor quality.

Our results support the idea of wet gluten being more important in determining loaf volume, since we found a very significant positive correlation between these traits. Somewhat surprisingly, we found a very significant negative correlation between gluten index and loaf volume. The extremely high protein and wet gluten content could perhaps explain a part of this result. There could also have been some inaccuracy in the experimental baking procedure employed. The high amount of ascorbic acid used, the processing of dough and the use of a mould during fermentation and baking should be studied more carefully.

Some other explanations could be brought up for discussion also. First, perhaps the results would possibly have been more informative if only the optimum or "more normal" wet gluten and gluten index values had been taken into consideration. Second, there could be one quite hypothetical explanation for these results. It is based on behaviour of different gluten subunits.

It would be interesting to find out if there are some differences in the composition of HMW-gluten subunits in the part of gluten that stays on the sieve and that which is passed through when determining the gluten index. There could also be some differences in the behaviour of both HMW- and LMW-gluten subunits during the baking procedure which could explain the observed inconsistency between the quality of gluten as expressed by gluten index or by extensograph values as well as the final baking results, especially loaf volume.

Perten's gluten index is quite an interesting new method for the determination of gluten quality. It still has some shortcomings, but according to our results it can provide more information about the quality of wheat flour than the use of wet gluten determinations only.

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SELOSTUS

Gluteeni-indeksimenetelmän soveltuvuus vehnän laadun määrittämiseen

LEENA HÖMMÖ, ELISA PIETILÄ ja YRJÖ SALO

Maatalouden tutkimuskeskus

Vehnän proteiineista gluteeni vaikuttaa eniten taikinan leivontalaatuun. Jauhon leivontalaatu määräytyy sekä gluteenin määrän (ilmoitetaan yleensä märkägluteenina) että gluteenin laadun perusteella. Äskettäin kehitetyn menetelmän (PERTEN 1989) avulla on mahdollista määrittää samanaikaisesti sekä märkägluteeni, että gluteenin laatua kuvaava gluteeni-indeksi. Gluteeni sentrifugoidaan erityisen sihdin päällä, jolloin osa gluteenista menee sihdin läpi. Gluteeni-indeksi saadaan jakamalla sihdin päälle jäänyt gluteenin osa gluteenin kokonaismäärällä ja kertomalla tämä osamäärä sadalla.

Tutkittaessa gluteeni-indeksimenetelmän soveltuvuutta suomalaisten kevät- ja syysvehnien leivontalaadun määrittämiseen, gluteeni-indeksin havaittiin korreloivan märkägluteenia paremmin ekstensografin antamien taikinan venyvyyttä kuvaavien venytysvoiman ja venytysvastuksen kanssa. Farinografituloksista vain taikinan stabiliteetti korreloi tilastollisesti merkitsevästi gluteeni-indeksin kanssa. Gluteenin määrä näyttää vaikuttavan laatua enemmän taikinan vedensitomiskykyyn ja muodostumisaikaan.

Gluteeni-indeksin ei havaittu korreloivan koeleivontatulosten kanssa. Syynä tähän saattaa olla esimerkiksi koeleivonnassa käytettävä suuri askorbiinihapon määrä tai pitkitetyt nostatusajat.

Gluteeni-indeksimenetelmä sopii kuitenkin märkägluteenin ohella hyvin kuvaamaan jauhon sitko-ominaisuuksia. Koska gluteeni-indeksi voidaan määrittää myös sakolukurouheesta, sitä voidaan käyttää pienenkin siemenmäärän laadun selvittämiseen. Lisäksi menetelmä on nopea ja yksinkertainen, joten se soveltuu erityisen hyvin kasvinjalostajan tarpeisiin.

ANNALES AGRICULTURAE FENNIAE, VOL. 30: 199—206 (1991)

Seria AGRICULTURA N. 102 — Sarja PELTOVILJELY n:o 102

PROFITABILITY OF CHEMICAL WEED CONTROL IN SPRING CEREALS

LEILA-RIITTA ERVIÖ, TIMO TANSKANEN and JUKKA SALONEN

ERVIÖ, L-R., TANSKANEN, T. & SALONEN, J. 1991. **Profitability of chemical weed control in spring cereals.** Ann. Agric. Fenn. 30: 199—206. (Agric. Res. Centre of Finland, Inst. Pl. Protect. SF-31600 Jokioinen.)

The profitability of chemical weed control in the cultivation of spring cereals was studied in 1982—1984 on several locations of Finland. The economic return varied considerably between years, localities and fields. Chemical control was profitable in 60 % of fields. Generally the net economic return rose with increasing weed density but was also related to the yield level of the crop.

Chemical weed control increased grain yield by 123 kg ha^{-1} on average which meant a net profit of FIM 121 ha^{-1} in 1985. The return/cost ratio averaged 3.1. Of the herbicides used, those containing MCPA and dichlorprop or mecoprop gave the best economic benefit.

Linear regressions indicated that the reduction of crop yield per one weed plant m^{-2} was 1.8 kg ha^{-1} and that the increase of crop yield per one destroyed weed plant m^{-2} was 0.5 kg ha^{-1}. The threshold values for economical weed control were 52 and 101 weeds m^{-2}, respectively.

Index words: profitability, chemical control, weeds, weed control, spring cereals, threshold values of control, economic return, Finland.

INTRODUCTION

As reported in a previous paper (ERVIÖ and SALONEN 1987), the number and dry weight of weeds in spring cereal fields are at present about one-third compared to the situation in the early 1960s. This obviously has an influence on both the necessity and the economy of chemical weed control which is a common practice in Finnish cereal cultivation. The area treated with herbicides in 1989 was about 1 million hectares, equivalent to 87 % of total cereal acreage in that year (HYNNINEN and BLOMQVIST 1990). Several studies (a.o. NIEMANN 1982, ERVIÖ and HIIVOLA 1986, HEITEFUSS et al. 1987) have revealed that the economic return from herbicide treatments varies between occasions and is often dependent on weed density (WALLGREN 1980). The present study was carried out in order to estimate the profitability of chemical weed control in the cultivation of spring cereals.

MATERIAL AND METHODS

The material is based on a weed survey conducted on spring cereal fields in ten localities in Finland (Fig. 1.) in 1982—1984. Of a total of 267 fields surveyed, 253 were included in the present study with four pairs of untreated and treated sample plots per field. All the plots were similarly managed except for herbicide application. A detailed description of the material is given in previous publications (ERVIÖ and SALONEN 1987, SALONEN and ERVIÖ 1988).

Yield samples were taken at harvest from four plots of 0.5 m^2 in size, located on previously marked untreated and treated plots in each field. The crop was cut at soil surface and dried in the laboratory. The grain moisture at harvest was determined immediately after sampling from a sample of 10 ears/plot. After drying the yield was threshed, sorted and certain quality factors affecting the price of grain yield were determined.

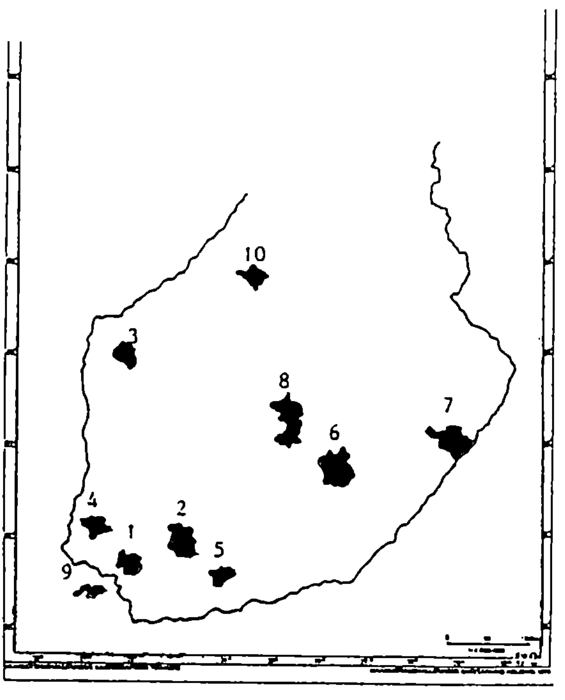

Fig. 1. Surveyed localities in 1982—84.

The effect of chemical control on the financial return from the cereal crop was determined according to the increase and price of yield and to the price of control measures by: 1) deducting the value of yield difference between treated and untreated plots from control costs and 2) by counting the benefit/cost ratio. In September 1985, the price of bread wheat was FIM 2.20 kg^{-1}, feed barley FIM 1.63 and oats FIM 1.50 kg^{-1}.

Control costs consisted of herbicide prices and spraying expenses including labor and machinery. Herbicides were classified according to prices as follows:

			FIM ha^{-1}
1. MCPA	35 %	of treatments	20—80
2. dichlorprop or mecoprop + MCPA	50 %	»	30—126
3. "broad-spectrum" compounds	10 %	»	67—121
4. others	5 %	»	25—405

Spraying costs were FIM 21 ha^{-1} when a farmer's own equipment was used.

The objective of this study was also to determine the minimum number of weeds which was profitable for chemical control. This threshold value was calculated by the regression coefficient in the equation between weed number and yield difference of treated and untreated plots.

The statistical significance of weed occurrence and yield results was tested by analysis of variance and by regression coefficients with Student's T-test. Square root transformation was used to reduce the observed skewness in the experimental data concerning weed density.

RESULTS

Crop yield

Chemical control did not increase the grain yield in all instances. On the contrary, treated plots gave a smaller yield than untreated areas in 38 % of the fields studied (Table 1). However, chemical weed control increased the yield on average by 123 kg ha^{-1}.

The yield increase by herbicide treatment varied between localities and years more than between cereal species. The highest average yield increases were observed in localities 9 and 10 where the majority of herbicide treatments were profitable (Table 1). Weeds occurred most abundantly in locality 9, but the lowest number of weeds m^{-2} in this study occurred in locality 10 (Table 2), where the density of weeds seemed not to be the only reason for profitable control. Annual variations between yield increases were not statistically significant.

The quality of yield was not affected by chemical weed control in this study.

Economic return

The economic return of herbicide treatment varied from field to field for many reasons which could not be explained in detail in this

Table 1. Effect of herbicide treatment on grain yield in different localities in 1982-1984. +/− percentage of observations with yield increase or decrease.

Year	Locality	Yield difference kg ha^{-1}		Percentage of observations		Total number of observations
		Average	Standard deviation	+	−	
	1	−13	308	53	47	34
	2	29	363	58	42	33
1982		8	335	55	45	67
	3	155	625	65	35	23
	4	113	331	48	52	23
	5	128	324	70	30	23
	6	192	435	61	39	23
1983		147	439	61	39	92
	7	164	689	64	36	22
	8	22	446	60	40	25
	9	251	490	75	25	24
	10	301	415	74	26	23
1984		182	520	68	32	94
Total		123	452	62	38	253

Table 2. Average weed density and profit or loss by chemical control in different localities and years.

Year	1982		1983				1984			
Locality	1	2	3	4	5	6	7	8	9	10
Profit FIM ha^{-1}	−97	−47	196	129	153	171	179	−46	340	316
Years on average	−73		137				218			
Weed density plants m^{-2}	106	186	146	166	246	222	210	119	271	67

study. After deducting costs, the net profit averaged FIM 121 ha^{-1}. On 40 % of fields, no positive return was achieved by weed control. In these cases the density of weeds was generally low.

Chemical control gave the best financial return in localities 9 and 10, corresponding to the yield increase. In localities 1, 2 and 8, chemical control caused economic loss (Table 2).

Average annual differences varies from a loss of FIM 73 to a profit of FIM 218 ha^{-1}.

Factors influencing the economic return

In order to determine individual factors influencing the financial outcome of weed control, the material was studied both by classified groups and by regression models.

Herbicides

Herbicides were classified into four groups according to their active ingredients. The best return was achieved with mixtures of MCPA/dichlorprop and MCPA/mecoprop (Table 3). These herbicides are commonly used in cereal cultivation, and they were frequently encountered also in this study. Products containing MCPA alone gave nearly similar results. In the group consisting of other herbicides the material was so small that no obvious difference could be observed between products.

Weed density

When the material was classified according to weed number, the results showed a rising profit from control with an increasing number of weeds (Table 4). However, due to considerable variation within the classes, only the first and last groups differed from each other significantly at the 0.05 % level. Control measures yielded economic losses when less than 50 weeds grew per square metre.

The return/cost ratio for weed control determined according to the profit was 3.1, on aver-

Table 3. Economic return of herbicide treatment in different herbicide groups.

Herbicide class	Profit FIM ha^{-1}	Significance, with Students t-test	Weeds m^{-2}	Number of observations
1. MCPA	117	1.46	193	89
2. dichlorprop/MCPA mecoprop/MCPA	186	2.82**	158	126
3. "broad-spectrum" compounds	134	0.89	188	24
4. others	−103	0.52	121	14

Table 4. Outcome of chemical weed control at different weed denisties.

Density	Yield difference kg ha^{-1}	Profit FIM ha^{-1}	Ratio return/cost	Percentage of observations
below 50	−18	−130	0.2	14
50—99	58	16	2.3	25
100—149	126	106	2.0	18
150—199	206	262	5.1	15
200—299	101	132	2.4	13
300 or more	299	401	6.9	15
Total	123	121	3.1	100
F-value	2.45*			

Table 5. Interaction between weed density and the outcome of chemical control on different yield levels studied with linear regression.

Yield	Constant term	Regression coefficient b	R^2	Number of observations	F-value
below 2000	−316	1.58	0.11	14	1.47
2000—2999	−352***	0.92***	0.34	30	14.64***
3000—3999	−176	1.05	0.05	72	3.94*
4000—4999	73	1.24*	0.05	76	4.05*
5000 or more	145	0.59	0.004	61	0.25
Total material	−19	0.81**	0.03	253	7.95**

age (Table 4), which means that one Finnish mark invested in weed control yielded about three Finnish marks. When weed density was below 59 plants m^{-2}, the ratio was <1.0, indicating unprofitable weed control. The ratio tended ro rise with increasing weed density.

According to the linear and exponential regression models studied, weed density alone did not explain the final result of weed control. The explanation rates in the total material were only 3 % and 4 %, respectively.

When the significance of weed density was studied at different yield levels, the highest explanation rate was seen in the second yield class (Table 5). Regression coefficients in this class and in the total material were very similar. They showed that weed control returned FIM 0.81—0.92 ha^{-1} per each weed plant grown in a square metre. The return in relation to weed density seemed to rise more sharply at the lower (b = 1.58) than at the higher (b = 0.59) yield level.

Interaction between weeds and crop yield

The importance of weeds to crop yield was determined with two linear regression models. The first one described the relation between crop yield and weed number in untreated stands. The variables in the second model were yield differences between treated and untreated crop areas and the weed density in these areas, respectively.

Table 6. Equations between weed density and crop yield in untreated plots.

	a	b	N	r
Wheat	4029	−0.94	52	−0.174
Barley	4326	−2.22*	105	−0.221
Oats	4503	−2.12**	96	−0.264
1982	4106	−1.06	67	−0.154
1983	5130	−4.02***	92	−0.376
1984	3958	−1.30*	94	−0.223
Total	4330	−1.82***	253	−0.234

In the first case, the equation was y = 4 330—1.82*** X (R^2 = 0.06). According to this model, one weed plant m^{-2} would decrease crop yield by 1.8 kg ha^{-1}. The results varied considerably between different cereal species and between years (Table 6).

The second model included both weed density and the effect of herbicide treatment. It gave the equation y = 40 + 0.49** X (R^2 = 0.03), indicating that the yield increase per one destroyed weed plant m^{-2} was 0.5 kg ha^{-1}. This was less than could be expected on the basis of the first model. The increase of crop yield did not correlate with weed density as well as with crop yield level. The explanation rate remained low, but the regression coefficient was significant at the level of 0.01.

Thresholds for economical weed control

On the basis of previous models, the thresholds for economical weed control in barley were calculated as follows:

1) When considering yield decrease per one weed plant grown in a square metre the result was:

$$\frac{81}{1.82 \times 1.63 \times 0.53} = 52 \text{ weeds m}^{-2} \text{ where}$$

81 = cost of chemical weed control FIM ha^{-1}
1.82 = yield decrease ha^{-1} by one weed m^{-2}
0.53 = percent of weeds killed on average
1.63 = price of barley yield FIM kg^{-1}

This model indicated profitable chemical control at a weed density of at least 52 weeds m^{-2}.

2) Calculation of yield increase by chemical control gave the following threshold:

$$\frac{81}{0.49 \times 1.63} = 101 \text{ weeds m}^{-2}$$

where 0.49 = yield increase per one weed plant m^{-2} by chemical control.

Table 7. Threshold values with different costs and crops calculated by models 1 and 2 (p.).

Cost of control FIM ha^{-1}	Model	Wheat	Barley	Oats
65	1	31	41	45
	2	60	81	88
80	1	38	51	55
	2	74	100	108
100	1	47	64	69
	2	93	125	136
120	1	56	76	83
	2	111	150	160
150	1	71	95	103
	2	139	188	103
200	1	94	127	138
	2	185	250	271

Different calculation criteria gave different threshold values (Table 7). Additionally, costs of herbicide treatments, yield levels and yield prices modified the values in the different crops.

DISCUSSION

In this study, the economic return from chemical control was mainly attributable to the increase of cereal yield as the control costs were relatively invariable. Herbicide treatment increased crop yield on average by 123 kg ha^{-1}, or about 3 %. This result was slightly lower than in some earlier studies (MUKULA and KÖYLIJÄRVI 1965). A decline in weed number (ERVIÖ and SALONEN 1987) and a rising crop yield level observed during the last decades have probably diminished the influence of herbicide treatment on yield increase.

Crop yield varied considerably between fields in this study, because growth conditions, occurrence of weeds and herbicide treatment differed from field to field. This variation was reflected also between localities in yield results and the financial return of chemical control. Another reason for the variation in yield size may have been the relatively small sample size taken from the fields.

Chemical control was profitable in 60 % of the treatments which is comparable to some other results (a.o. GEROWITT et al. 1984, MÜLLVERSTED 1986). Herbicides were applied in very different circumstances in terms of year, locality and field but no specific reasons for the unprofitable control were observed. Some common factors in practical cultivation such as incorrect choice of compound in relation to weed flora or improperly adjusted spraying equipment (LUOMA and LAVONEN 1987), may be at fault. Additionally, the material included fields with low weed density, which could lead to uneconomical chemical control, as shown in several experiments (a.o. WALLGREN 1980, ERVIÖ and HIIVOLA 1986).

Several studies have indicated that weed density or weed cover are useful means to determine the need and profitability of chemical weed control (GEROWITT et al. 1984, WAHMHOFF and HEITEFUSS 1984, SPRINGER 1985). In our study the financial return from weed control rose with increasing weed density, but no unambiguous threshold values could be determined.

The thresholds were calculated with different criteria which gave variable results (Table 4 and 7). These values rose fairly high, especially with expensive herbicides compared to some other studies. For example, SCHIETINGER (1987) reported unprofitable chemical control in weed stands with fewer than 40 to 60 plants m^{-2}. On the contrary, MÜLLVERSTEDT (1986) and WAHMHOFF (1986) considered such densities adequate for economical weed control. The lower threshold values calculated in our study corresponded to those. In Finnish conditions the thresholds for economical weed control have generally been relatively high, varying according to treatments as seen in some previous studies (ERVIÖ 1983, ERVIÖ and HIIVOLA 1986).

The present study clearly revealed that chemical weed control in practical cultivation on Finnish spring cereal fields is not always profitable. In order to obtain financial return, herbicide treatments should be adjusted according to weed density and the conditions prevailing in a crop stand. In favourable circumstances it is advantageous to diminish the chemical control of weeds.

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SELOSTUS

Rikkakasvien kemiallisen torjunnan kannattavuus kevätviljoissa

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Maatalouden tutkimuskeskus

Rikkakasvien kemiallisen torjunnan kannattavuutta tutkittiin käytännön kevätviljapelloilla vuosina 1982—84. Torjunnan tulos vaihteli huomattavasti vuosittain, alueittain ja peltokohtaisesti. Käsittely oli kannattavaa 60 prosentilla pelloista. Yleensä nettotuotto nousi rikkakasvimäärän myötä, mutta kannattavuus kytkeytyi myös viljan satotasoon.

Torjuntakäsittely lisäsi viljan satoa keskimäärin 123 kg ha^{-1}. Siitä saatu nettotuotto oli 121 mk ha^{-1}. Tuoton ja kustannusten suhteeksi tuli keskimäärin 3.1. Paras taloudellinen tulos saavutettiin MCPA:n seoksilla diklorpropin tai mekopropin kanssa.

Lineaarisen regressioanalyysin mukaan yksi neliömetrillä kasvanut rikkakasvi vähensi viljan satoa 1.8 kg ha^{-1}. Toisaalta viljan sadonlisäys yhtä neliömetriltä hävitettyä rikkakasviyksilöä kohti oli 0.5 kg ha^{-1}.

Erilaisin perustein lasketut torjunnan kynnysarvot vaihtelivat huomattavasti ja osa niistä nousi varsin suuriksi. Luokiteltuun rikkakasvitiheyteen perustuva laskelma antoi kynnysarvoksi 50—99 rikkakasvia m^{-2}. Satotappion perusteella laskettu arvo vaihteli 31:stä 138:aan yksilöön m^{-2} sadon hinnoittelun ja käytetyn herbisidin mukaan. Vastaavasti torjunnalla aikaansaatuun sadonlisäykseen perustuva kynnysarvo vaihteli välillä 60—271 kpl m^{-2}.

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Seria ANIMALIA NOCENTIA N. 152 — Sarja TUHOELÄIMET n:o 152

YELLOW STICKY TRAPS IN MONITORING AND CONTROL OF CARROT RUST FLY IN HOME GARDENS

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HOLOPAINEN, J.K., HAVUKKALA, I., KNUUTTILA, T. and KETTUNEN, S. 1991. **Yellow sticky traps in monitoring and control of carrot rust fly in home gardens.** Ann. Agric. Fenn. 30: 207—214. (Univ. Kuopio, Dept. Environ. Sci., SF-70210 Kuopio, Finland.)

Fly populations of *Psila rosae* F. (Psilidae) were monitored with two-sided yellow sticky traps in southern and central Finland in 1983—1985. An optimum trapping system was sought by using yellow boards at different heights and positions.

The first flies were caught in the traps in early June, when the accumulated temperature sum was about 300 day degrees over the base 5 °C. The peak occurrence of the first generation of *P. rosae* was between June 20 and July 10 at a temperature sum of ca. 480 day degrees. In central Finland the peak was usually one week later than in southern Finland. The second generation of *P. rosae* occurred in southern Finland in mid-August, but totalled only one-third of the first generation catches.

The first generation flies were caught more often at a height of 1—30 cm, the second generation at 40—60 cm. Vertical traps were easier to use and slightly more effective than inclined or horizontal traps. More flies were caught on the southern side of the trap than on the northern side. Usually there were no differences between the catches of upper and lower sides of the vertical traps.

In small home gardens in southern Finland, where a second generation occurred, yellow sticky traps appeared to reduce slightly the number of damaged carrots compared to control plots. Yellow sticky traps combined with fiber covers provide a suitable non-chemical control method for carrot rust fly in home gardens.

Index words: Yellow traps, carrot rust fly, Psilidae, *Psila rosae,* temperature sum, monitoring, non-chemical control.

INTRODUCTION

In Finland, carrot rust fly (*Psila rosae* F.) (Diptera: Psilidae) occurs locally (VARIS and TIITTANEN 1982), and usually it is not an economically important pest. However, in home gardens the carrots are sometimes heavily attacked (KETTUNEN et al. 1988), mainly because the fly prefers sheltered places (WAKERLY 1963), and the flying distance is short (STÄDLER 1972).

In this paper the flying periods as well as the monitoring and control of carrot rust fly by yellow sticky traps in home gardens are reported.

MATERIAL AND METHODS

The flying periods of carrot rust fly were monitored in 1983—1985 using yellow sticky traps in 10 localities in southern and central Finland (Fig. 1).

In central Finland, the cultivated plots varied between 4 to 6 m^2 in size the plots including 2 m double rows of carrot in four to eight replicates. The cultivated varieties were Nantes 20 and Sytan. Two sticky traps were used per plot, except for Kuopio in 1985 where one trap was used per plot. In southern and southwestern Finland the areas of the cultivated carrot plots ranged between 3 and 1600 m^2. The varieties were mostly Nantes 20, Nantes Fancy, Nantes Duke, Nantes Tip Top, Nantes Lontoontori and Feonia Fina Hunderup. One trap was used in small plots; in bigger plots two to four traps were used.

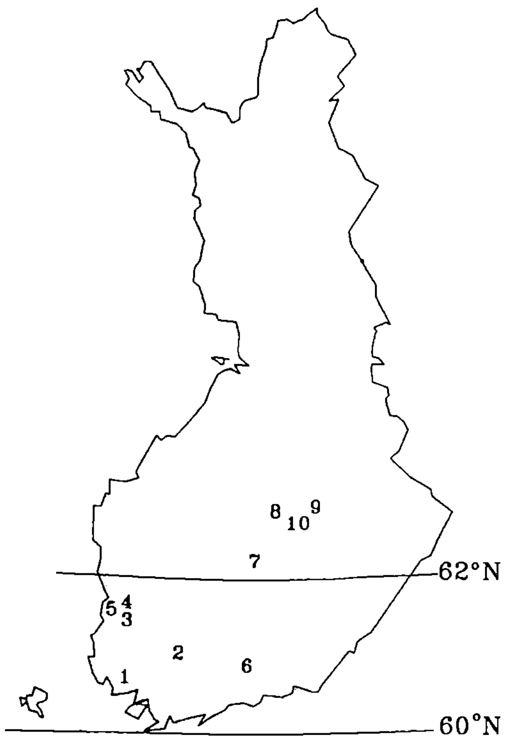

Fig. 1. Trapping localities. 1 = Turku 1984, 2 = Ypäjä 1984, 3 = Ulvila 1984 and 1985, 4 = Noormarkku 1985, 5 = Pori 1985, 6 = Pukkila 1984, 7 = Toivakka 1984, 8 = Vesanto 1983, 1984, 9 = Kuopio 1984, 1985, 10 = Karttula 1983.

In 1983 the sticky traps used were 15 cm × 21 cm in size (Rebell E:FA, CH-8820 Wädenswil), in 1984 15 cm × 30 cm (Sticky Strips, Norsk-Alkali A/S, Malmö) and in 1985 they were yellow laminated cardboard traps (whitefly trap Kelta-ansa, Kemira Oy), 15 cm × 30 cm in size. The traps were sprayed on both sides with a special glue (SOVEURODE®, Sovilo Ltd, France).

In central Finland, except for Vesanto in 1984, the traps were positioned horizontally on the level of the tips of the carrot tops and they were raised, as the plants grew. In southern Finland, and in Vesanto in 1984, the traps were positioned vertically, the flat sides facing south-north and the midpoint of the board at the level of the tips of the carrots.

The trapping efficiency of the traps at different heights was studied in localities 1, 3 and 6 in 1984 and in localities 3, 4 and 5 in 1985. The vertical traps were placed at five distances from soil surface: the midpoints of the boards were at the heights' of 15, 20, 30, 50 and 70 cm in 1984 and at 15, 30, 50, 70 and 90 cm in 1985.

The efficiency of trap position was studied in localities 2 and 7 in 1984, in localities 3 and 4 in 1985. Three positions were used; vertical, horizontal and inclined 45° with the midpoints of the board at the level of the carrot tops. The trapping period varied between 1,5 and 3,5 months in 1984 and was 3,5 months in 1985. The flying height of the carrot rust flies was determined by measuring the position of the fly caught in the trap.

The number of damaged carrots was counted in plots where yellow sticky traps had been placed and in nearby (within 100 m) control plots with no traps. At least 600 carrots were checked in each locality. The day degrees were calculated from the daily mean temperature using a +5 °C base.

The weather data (air temperature) were collected from the meteorological stations of Turku, Kokemäki and Kuopio for southern, south-western and central Finland, respectively (ANON. 1983, 1984, 1985).

RESULTS

The phenology of *P. rosae*

The flight of *P. rosae* starts in early June both in southern (Fig. 2) and central (Figs. 3 and 4) Finland. The peak usually occurs in late June or in early July, in the central parts of the country usually one week later than in the southern parts. In southern Finland there is also a small second generation, the flight peaking in late August.

The first flies were caught in the traps when the yearly temperature sum had reached 274—314 day degrees. Regression analysis of the carrot fly catches from southern Finland (locality 1) in 1984 and from south-western Finland in 1985 (localities 3—5), as well as the pooled material from central Finland (localities 8—10) in 1983—1985 showed that peak catches and 50 % of the total catch had been caught at ca. 480 day degrees. Temperature sum explained 85 % to 97 % of the fly catch variation (Table 1).

Table 1. Linear regression equations between the relative proportion of the total carrot fly catch in traps and cumulative temperature (day degrees, base +5 °C).

Locality	Year	Equation	r^2	p
Southern	1984	y = 0.19x — 29.86	0.968	< 0.001
South-western	1985	y = 0.20x — 39.16	0.904	< 0.001
Central	1983	y = 0.18x — 33.00	0.853	< 0.001
Central	1984—85	y = 0.21x — 34.87	0.927	< 0.001

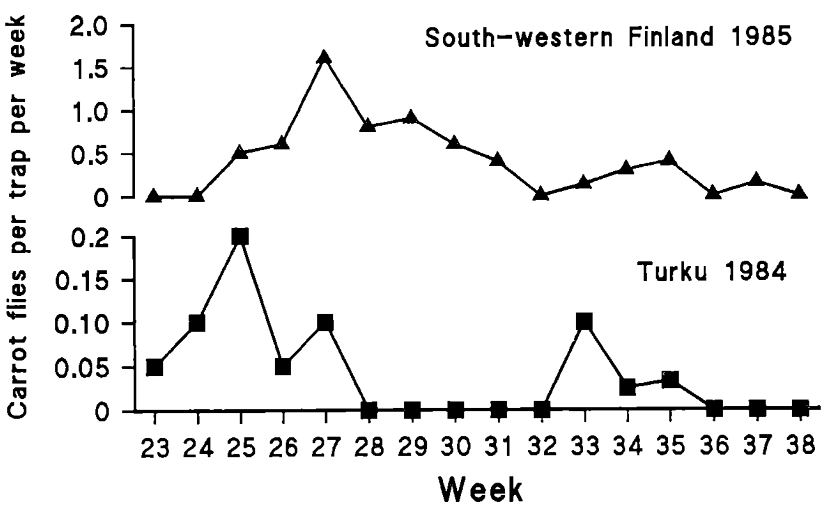

Fig. 2. Flying periods of *P. rosae* in southern (locality 1) and south-western Finland (localities 3—5) in 1984 and 1985.

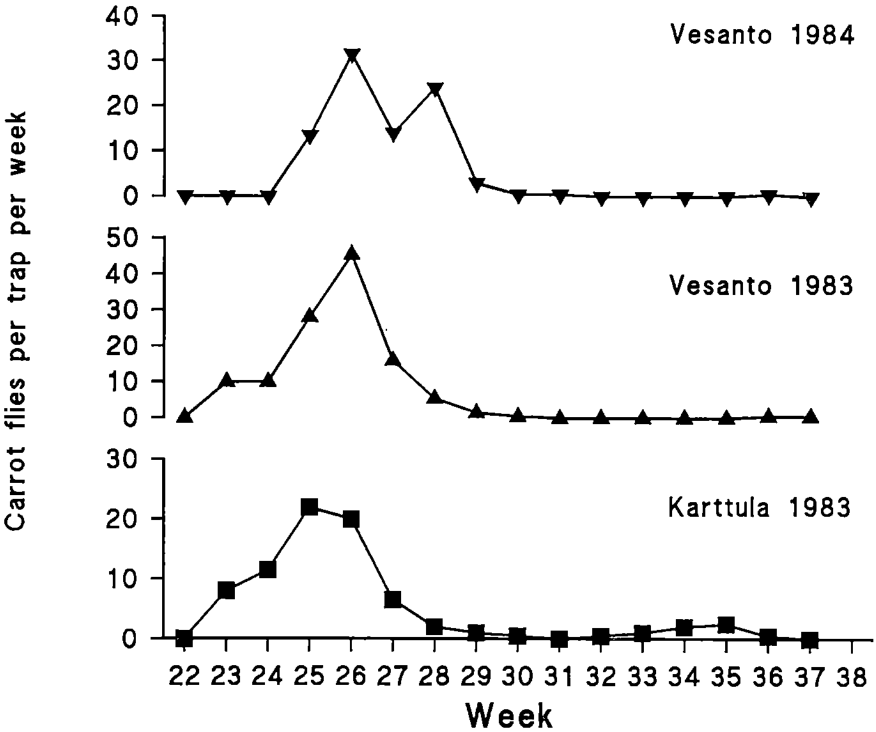

Fig. 3. Flying periods of *P. rosae* in central Finland (localities 8 and 10) in 1983 and 1984.

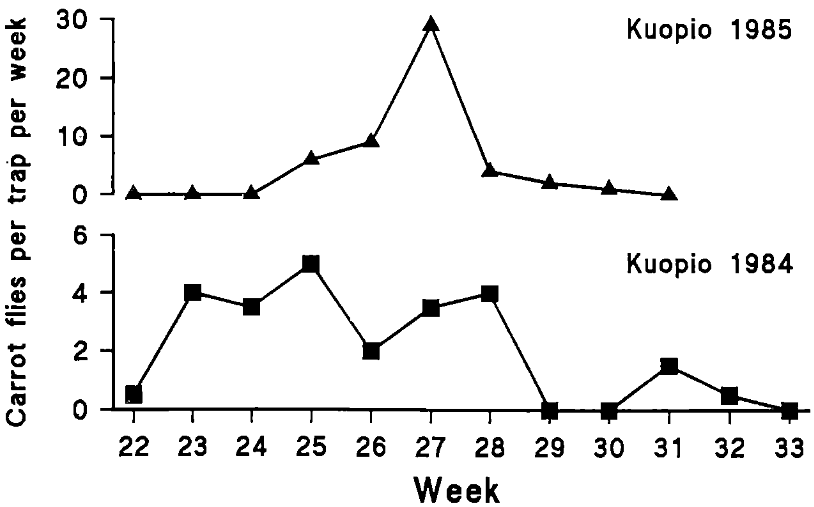

Fig. 4. Flying periods of *P. rosae* in central Finland (locality 9) in 1984 and 1985.

The effect of trap position and trap side on the trapping efficiency

In 1984—1985, the traps positioned in southern Finland vertically and horizontally caught more flies than the inclined traps (Fig. 5). The brighter side of the vertical traps facing south caught significantly more flies than the side facing north both in 1984 ($\chi^2 = 6.77$, df = 1, $p < 0.01$) and in 1985 ($\chi^2 = 10.02$, df = 1,

Table 2. Mean number of carrot rust flies caught per trap side per week in central Finland.

Locality	Year	n	Upper side x + S.E.	Lower side x + S.E.	Z-value[1]	p
Vesanto	1983	30	4.10 + 1.03	3.80 + 1.53	—0.781	n.s.
Karttula	1983	30	2.37 + 0.59	2.97 + 0.97	—0.971	n.s.
Kuopio	1984	24	0.63 + 0.17	1.38 + 0.29	—2.830	< 0.05
Kuopio	1985	20	3.00 + 1.96	2.00 + 0.85	—0.070	n.s.

[1] Wilcoxon's matched-pairs, signed-ranks test

$p < 0.01$). As for the upper and lower side of the traps, there were no significant differences between catches.

In central Finland (VESANTO 1984), the mean number of carrot rust flies per trap side per week for the vertical trap was 3.85 ± 1.3 (S.E.), n = 25) on the southerly side and 2.77 ± 0.90, n = 25) on the northerly side, but the difference was not significant. In the horizontal traps the number of carrot rust flies caught per trap side per week did not differ significantly, except for Kuopio in 1984 (Table 2).

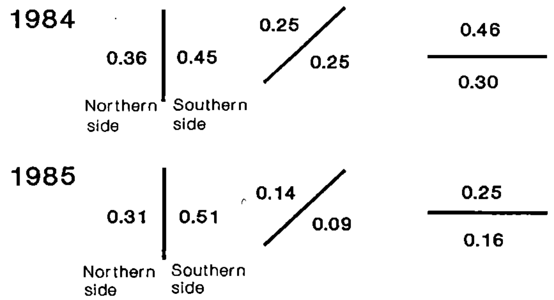

Fig. 5. Effect of position and side of the trap on carrot fly catches in 1984—1985. Average numbers of flies caught per trap side are given.

Flying height of *P. rosae*

In 1984, slightly more flies of the first generation were caught at lower heights, but there were no statistically significant differences between traps at different heights (Fig. 6). In 1985, the lowest trap, on the other hand, caught flies most efficiently, and the trap height had a

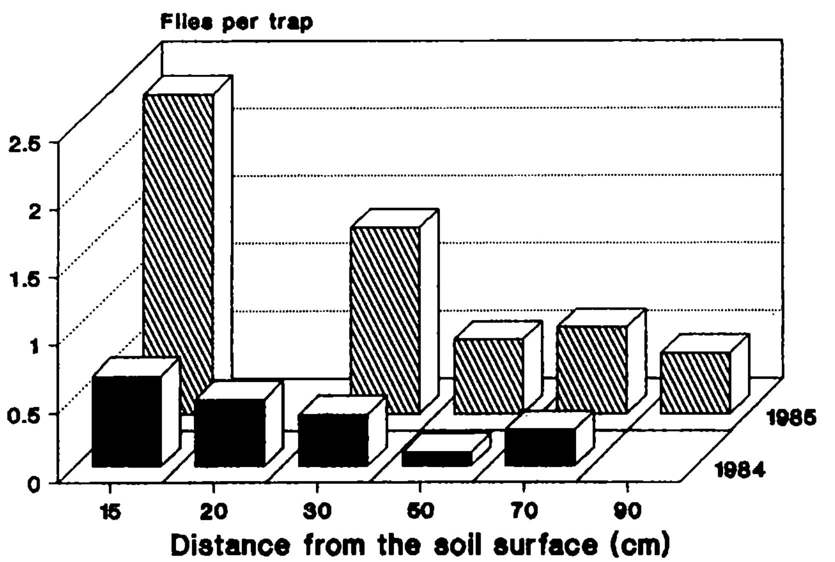

Fig. 6. Effect of trap height on catches of the first generation carrot flies in 1984 and 1985.

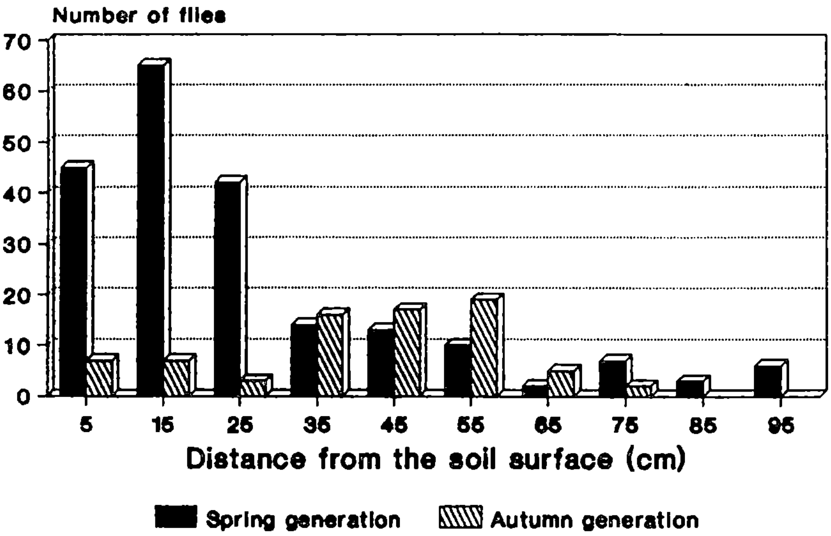

Fig. 7. Flying heights of trapped carrot flies of the first (1984) and the second (1984, 1985) generation.

significant effect on the carrot rust fly catches (χ^2 = 33.34, df = 1, p < 0.001).

A flying height of 1—30 cm of the first generation of *P. rosae* in 1985 was significantly more common (χ^2 = 53.26, df = 1, p < 0.01) than the higher heights (Fig. 7). In contrast, the second generation in 1984 and 1985 was caught more frequently (χ^2 = 20.43, df = 1, p < 0.001) at the height of 40—60 cm than at the lower heights (Fig. 7).

The influence of traps on the carrot damage

The percentage of damaged carrots was higher in control plots in each year of the study. In 1984, the mean percentages were 26.7 % for control plots (n = 6 plots) and 13.2 % (n = 6) for trapped plots. The difference is statistically significant (χ^2 = 35.02 df = 1, p < 0.001). In 1985, the mean percentages did not differ much, being 10.8 % for control plots and 7.5 % for trapped plots.

The number of carrot rust flies in traps correlated with the percentage of damaged carrots (regression equation: y = 0.08x — 3.73, R = 0.55, p < 0.05), but the density of traps did not affect the percentage of damaged carrots (r.e: y = —0.03x — 3.73, R = 0.46, p > 0.05).

The percentage of damaged carrots in the current year correlated highly significantly with the damage in the previous year (r.e: y = 0.93x — 3.73, R = 0.93, p < 0.001).

DISCUSSION

P. rosae has two distinct generations in southern Finland, but in central Finland the second generation is very small and obviously does not cause any great damage to carrot. The northernmost report of a second generation of *P. rosae* (63° 28') is from Norway (AUSLAND 1954). Vesanto and Kuopio (62° 53') are situated slightly further south.

The temperature sum (air measurements) has been used fairly successfully to forecast the emergence of cabbage and carrot fly populations (ECKENRODE and CHAPMAN 1972, STEVENSON 1981, COLLIER and FINCH 1985). Local, on-site measurements from soil at pupation depth might improve the accuracy of such forecasts.

STEVENSON (1981) used +2 °C as a base temperature in day degree calculations in laboratory experiments and found 368 day degrees for the 50 % emergence of *P. rosae*. On the basis of our results it seems possible to predict the flying activity of *P. rosae* using yellow sticky trap catches. The sum of 480 day degrees or slightly earlier seems to be the best time to evaluate the possible need for *P. rosae* control.

In Norway, a threshold of five flies per trap per week was proposed for control measures to be economical (HOFSVANG and LIEN 1986). This threshold was exceeded in central Finland each year in 1983—1985. The highest catches per trap per week in Vesanto (46 in 1983 and 32 in 1984) were even higher than the highest value (29) per trap reported in Sweden by FORSBERG (1981). It is possible that the small garden plots studied here have much higher densities of flies than windswept commercial carrot cultivations.

As for the method of trapping, we found that traps placed low caught most of the first generation flies, as also found by COLLIER and FINCH (1990). However, the second generation seemed to land higher in the traps, perhaps due to the higher carrot foliage making the insects fly higher and/or affecting the apparency or catching efficiency of the lower traps.

FINCH and COLLIER (1989) reported that with one-sided traps inclined at eight different angles of an octagon most carrot flies (59 %) were caught when inclined 45°, with the glued surface downwards. With two-sided traps we found no such preference between horizontal, inclined and vertical traps. This discrepancy might be explained by the fact that the flies, after landing on an unglued inclined surface, often fly or walk to the lower surface of the same trap, getting caught there. A possible source of error here is a differential drying/stickiness of the glue on the upper and lower surfaces of the traps.

The efficiency of the traps in reducing root damage was not high (e.g. in 1985 reduction of damaged carrots 27 to 13 %). Thus this control method should be supplemented with other measures. In home gardens, in addition to moving the site of the plot annually (c.f. KETTUNEN et al. 1988), fiber covers seem to provide the most feasible control method (HOUGH-GOLDSTEIN 1987).

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SELOSTUS

Kelta-ansojen käyttö porkkanakärpäsen tarkkailussa ja torjunnassa kotipuutarhoissa

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Porkkanakärpäsen *Psila rosae* F. esiintymistä tarkkailtiin kummaltakin puolelta liimapinnoitetuilla kelta-ansoilla vuosina 1983—1985 Etelä-Suomessa (Turku, Ypäjä, Ulvila, Noormarkku, Pori ja Pukkila) ja Keski-Suomessa (Toivakka, Vesanto, Karttula ja Kuopio). Optimaalista pyydystysmenetelmää selvitettiin sijoittamalla keltaisia pyydyslevyjä eri korkeuksille maanpinnasta pystysuoraan, vaakasuoraan tai kallistettuna 45°.

Ensimmäiset kärpäset saatiin pyydyksiin kesäkuun alussa, jolloin lämpösumma oli n. 300 astepäivää. Porkkanakärpäsen ensimmäisen sukupolven esiintymishuippu sijoittui ajalle 20. 6.—10. 7., jolloin lämpösumma oli keskimäärin 480 astepäivää. Keski-Suomessa kärpästen esiintyminen oli runsaimmillaan noin viikon myöhemmin kuin Etelä-Suomessa. Porkkanakärpäsen toista sukupolvea tavattiin Etelä-Suomessa elokuun keskivaiheilla, mutta pyydyksiin saatu kärpäsmäärä oli vain n. yksi kolmasosa ensimmäisen sukupolven määrästä.

Ensimmäisen sukupolven kärpäsiä saatiin pyydyksiin useimmin 1—30 cm:n korkeudelta ja toisen sukupolven kärpäsiä 40—60 cm:n korkeudelta. Pystysuorat pyydykset ovat helpommin käsiteltäviä ja hieman tehokkaampia kuin vaakasuorat ja kallistetut pyydykset. Pystysuorien pyydysten valoisammalle eteläpuolelle saatiin enemmän kärpäsiä kuin pohjoispuolelle. Vaakasuorien pyydysten ylä- ja alapuolen kärpässaaliit eivät yleensä poikenneet toisistaan.

Etelä-Suomen pienissä kotipuutarhoissa, joissa porkkanakärpäsen toista sukupolvea esiintyi, kelta-ansat alensivat hieman vioittuneiden porkkanoiden määrää ilman pyydyksiä olleisiin verranneruutuihin nähden. Kelta-ansat käytettynä yhdessä kateharsojen kanssa ovat kotipuutarhoille sopiva ei-kemiallinen porkkanakärpäsen torjuntamenetelmä.

CONTENTS

TIILIKKALA, K. Impact of climate and agricultural practices on the pest status of *Heteroderoidea* nematodes in Finland 125

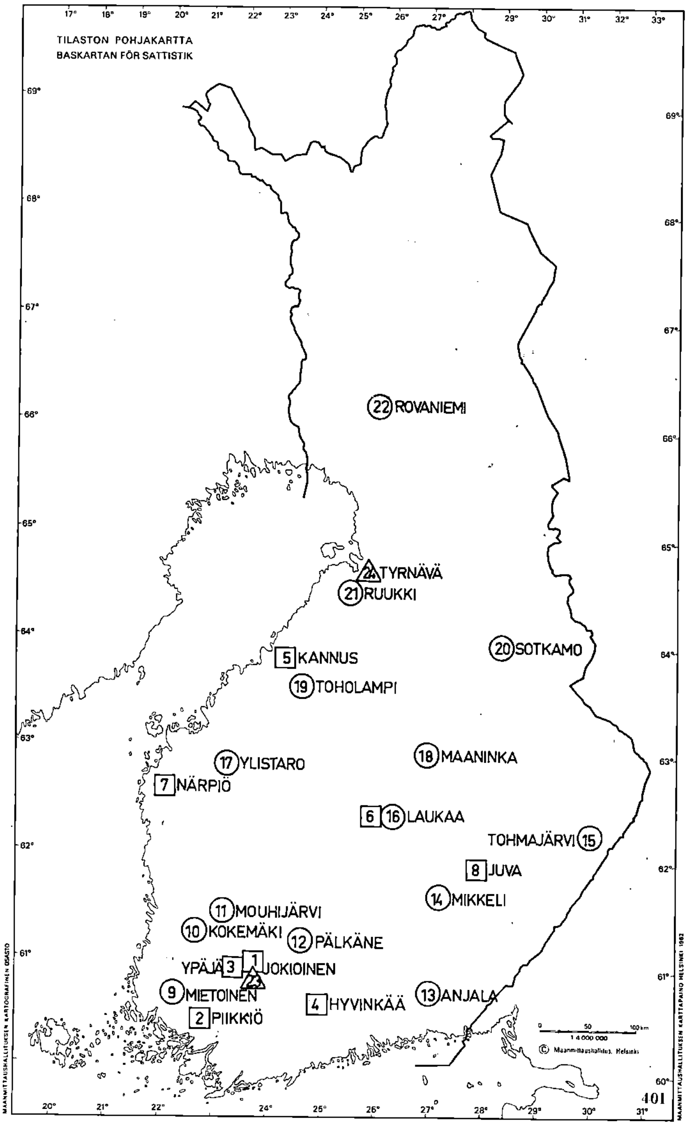
NIEMELÄINEN, O. Factors affecting panicle production of cocksfoot (*Dactylis glomerata* L.) in Finland. IV. Response to frost at panicle growth phase . . 163

— Variation in seed yield of cocksfoot (*Dactylis glomerata* L.) in Finland . . . 173

HÖMMÖ, L., PIETILÄ, E. & SALO, Y. Suitability of gluten index method for evaluation of wheat flour quality 191

ERVIÖ, L.R., TANSKANEN, T. & SALONEN, J. Profitability of chemical weed control in spring cereals 199

HOLOPAINEN, J.K., HAVUKKALA, I., KNUUTTILA, T. & KETTUNEN, S. Yellow sticky traps in monitoring and control of carrot rust fly in home gardens 207



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SISÄLLYS — CONTENTS

TIILIKKALA, K. Impact of climate and agricultural practices on the pest status of *Heteroderoidea* nematodes in Finland 125
Selostus: Ilmaston ja viljelytoimenpiteiden vaikutus kysta- ja äkämäankeroisten vahingollisuuteen Suomessa 159

NIEMELÄINEN, O. Factors affecting panicle production of cocksfoot (*Dactylis glomerata* L.) in Finland. IV. Response to frost at panicle growth phase .. 163
Selostus: Koiranheinän (*Dactylis glomerata* L.) röyhynmuodostukseen vaikuttavista tekijöistä Suomessa. IV. Röyhynkasvuvaiheessa esiintyvän hallan vaikutus 172

— Variation in seed yield of cocksfoot (*Dactylis glomerata* L.) in Finland ... 173
Selostus: Koiranheinän (*Dactylis glomerata* L.) siemensadon vaihtelu Suomessa 189

HÖMMÖ, L., PIETILÄ, E. & SALO, Y. Suitability of gluten index method for evaluation of wheat flour quality 191
Selostus: Gluteeni-indeksimenetelmän soveltuvuus vehnän laadun määrittämiseen 198

ERVIÖ, L-R., TANSKANEN, T. & SALONEN, J. Profitability of chemical weed control in spring cereals 199
Selostus: Rikkakasvien kemiallisen torjunnan kannattavuus kevätviljoissa .. 206

HOLOPAINEN, J.K., HAVUKKALA, I., KNUUTTILA, T. & KETTUNEN, S. Yellow sticky traps in monitoring and control of carrot rust fly in home gardens 207
Selostus: Kelta-ansojen käyttö porkkanakärpäsen tarkkailussa ja torjunnassa kotipuutarhoissa 214