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The influence of drought and cyst nematodes on potato growth. 4. Effects on crop growth under field conditions of four cultivars differing in tolerance

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Abstract

In field experiments carried out in 3 years with and without fumigation and irrigation 4 cultivars of potato differed in their tolerance of cyst nematodes (*Globodera pallida*). Ground cover, tuber and foliage fresh and dry yields were determined at regular intervals. From these measurements, intercepted radiation, radiation use efficiency for production of total and tuber dry matter and the apparent amount of intercepted radiation at tuber initiation were calculated and compared for all the treatments. The results indicate that cultivars which best maintained ground cover in the absence of nematodes also maintain it best in the presence of nematodes. Such cultivars gave the highest yields at all levels of nematode infestation because the radiation use efficiencies were far less affected by nematodes than was intercepted radiation. The similarity of the responses to nematode infection and to drought and the absence of interaction between these two stress factors facilitated crop simulation modelling. The relationships found here may well be wider used, though they will have to be validated for other cultivars and growing conditions.

Additional keywords: dry matter content, fumigation, *Globodera pallida*, harvest index, irrigation, radiation use efficiency, tolerance of damage.

Introduction

Evans et al. (1975) found that the proportion of ground covered with green foliage declined with increased numbers of potato cyst nematodes with the intolerant cultivar Pentland Dell being affected more than cv. Maris Piper. Trudgill et al. (1975) found no indication that the photosynthetic capacity per unit area was reduced. Yields were decreased because infected plants were smaller and because they senesced earlier than plants infested with few nematodes. Later reports, however indicate that the conversion coefficient between intercepted solar radiation and dry matter yields were negatively affected by potato cyst nematodes (Trudgill (1986). Trudgill (1986), using ground cover data (partly derived from a curvilinear relationship between the fresh weights of potato tops and ground cover) estimated that about two thirds of a 64 % yield reduction with heavily infested 'Pentland Dell' (initial nematode population 105 eggs per g soil) could be accounted for by the effect of potato cyst nematodes on intercepted radiation, the remaining third being due either to differences in harvest index or to a reduction in the efficiency of assimilation. Trudgill et al. (1990) concluded that with 'Pentland Dell', radiation use efficiency for total dry matter production was only slightly affected by potato cyst nematodes and concluded that yield differences were mainly explained by differences in radiation interception. In heavily infested soil the tolerant cv. Cara eventually reached 100 % ground cover and maintained it whereas equivalent cv. Pentland Dell never exceeded 75 % ground cover. It was indirectly estimated that the radiation use efficiency of 'Cara' declined from 1.07 g MJ^{-1} (few nematodes) to 1.03 g MJ^{-1} (many nematodes) whereas with 'Pentland Dell' it declined from 1.30 to 1.18 g MJ^{-1}. However, such estimates did not take account of differences in dry matter losses through lost leaves. The decrease in tuber yield in 'Pentland Dell' was less than that for top growth.

This paper attempts to explain differences in tuber dry matter yields (Y_{tub}) in terms of the effects of *G. pallida* and of drought on the amounts of solar radiation intercepted by the crop (IR_{tot}), the amount of radiation intercepted from tuber initiation ($IR_{tot} - IR_{ti}$), the conversion efficiency for total (E_{tot}) and for tuber (E_{tub}) dry matter production, and the proportion of total dry matter partitioned to the tubers (harvest index, HI). Fresh tuber mass (Y_{tf}) then depends on Y_{tub} and and the tuber dry matter content (DMC). The following linear relationships apply (Haverkort and Harris, 1986, 1987).

$$Y_{tub} = (IR_{tot} - IR_{ti}) \times E_{tub} \tag{1}$$

$$Y_{tot} = IR_{tot} \times E_{tot} \tag{2}$$

$$HI = Y_{tub}/Y_{tot} \tag{3}$$

$$Y_{tf} = Y_{tub}/DMC \tag{4}$$

From the Equation 1-4 follow the simple potato yield models in Equation 5, based on the conversion efficiency for total dry matter production, and Equation 6, based on the conversion efficiency for tuber dry matter production.

$$Ytf = HI \times IR_{tot} \times E_{tot}/DMC \tag{5}$$

$$Y_{tf} = (IR_{tot} - IR_{ti}) \times E_{tub}/DMC \tag{6}$$

The efficiencies for tuber and total dry matter production do not depend on foliar disease such as *Phytophthora infestans* (Haverkort and Bicamumpaka, 1986) as also became apparent from photosynthesis in healthy tissue of late blighted plants (Van Oijen, 1990), but the efficiencies declined at higher ambient temperatures (Haverkort and Harris, 1986).

The objectives of this study were to determine the influences of infestation by *G. pallida* and of drought, and of the two stresses combined on the yield components of Equation 5 and 6. The results may help explain cultivar tolerance differences and they may yield selection criteria for breeders. In addition, they may provide a basis for simulating yield losses due to potato cyst nematodes for use in yield forecasting and crop management systems.

Materials and methods

Field trials were carried out in three years with four cultivars in fumigated and unfumigated soil with and without additional irrigation. Seed potatoes class A or E (35-40 or 45-50 mm) of the cultivars Darwina, Désirée, Elles and Mentor were grown with and without additional irrigation from 1988 through 1990 in soil which was moderately (5-6 eggs per g soil) or heavily (26-58 eggs per g soil, see Table 1) infested with *Globodera pallida*. All cultivars except Désirée are grown for starch production in the North-East of the Netherlands. The experiments were located on a farm with a light sandy soil in Eeserveen at different sites in fields in which potatoes had been grown in the previous season. About 2 weeks prior to planting, the soil was fumigated by spade injection of a double dose of metham sodium (510 g active ingredient per kg) shown in Table 1. A few days prior to planting the soil was mechanically loosened to let escape excess fumes. The top 30 cm of the soil was sampled on the day of planting for the presence of cysts. To this end, 100 g of soil was rinsed with water and adhering organic matter was removed by aceton. The number of cysts was counted under a microscope and then crushed to expose eggs and juveniles in 100 ml water. The number of living eggs and juveniles (viable juveniles with a distinct border between the esophagus and intestinal region (Lamondia et al., 1986) was then counted.

Irrigation where applied, was by overhead sprinkler system at regular intervals to make up for the precipitation deficit (10, 20 or 30 mm a time). Precipitation and irriga-

Table 1. Details of the field trials.

	Year		
	1988	1989	1990
Fumigant metham sodium (kg/ha)	600	500	500
Living juveniles (per g soil)			
Unfumigated soil	28.8	26.1	57.5
Fumigated soil	5.1	6.0	6.1
Planting date	29 April	20 April	17 April
Seed size (mm diameter)			
Darwina	35-50	35-50	35-50
Désirée	35-55	45-55	35-50
Elles	35-50	35-50	35-50
Mentor	35-50	35-50	35-50
Harvest dates			
1	15 June	14 June 20 June	
2	19 July	19 July	18 July
3	6 September	23 August	22 August
4	10 October	16 October	
Plot size at final harvest (m^2)	10.8	5.4	7.2
Irrigation (mm)	50	200	210
Rainfall (mm)	460	295	375

tion data from emergence until the final harvest of the three years are shown in Table 1. The 1988 growing season was so wet that only 50 mm additional irrigation was applied. Henceforward, only reference will be made to the fumigated and unfumigated treatments of 1988. It was drier in 1989 and 1990, and data on the irrigated and unirrigated treatments will be included in the analysis. Late blight control was almost weekly with a fungicide spray and NPK-fertilizer rates were given according to recommendations, after soil sampling, for starch potato production in the area.

A split-split plot design experimental design was used with 2 replicates with varieties in the sub-sub plots, fumigation in the sub plots, and irrigation in the plots. The plot size was 4.5 m wide × 6 m long with six rows spaced 75 cm apart and tubers spaced at 30 cm within the row. At each periodic harvest (3 in 1988 and 4 in 1989 and 1990, dates in Table 1) 8 plants were lifted (2 plants each of the four central rows of the plots) leaving 2 guard plants between the plants used for the next periodic harvest. For the final harvest at complete canopy death, areas as indicated in Table 1 were lifted per plot. At each harvest, tuber and non-tuber parts of the crop were weighed and their dry matter content was determined by drying overnight at 105 °C. The harvest index was calculated as the ratio of final tuber weight to total plant weight. The latter was determined by adding tuber dry matter at the final harvest and the dry matter weight of the non-tuber parts at the harvest (usually the second one) when the foliar weight was at its maximum. At weekly intervals the proportion of the ground covered with green foliage was observed with the aid of a 90 cm × 75 cm grid divided into 100 rectangles viewed directly from above (Haverkort et al, 1991b). Two measurements were taken per plot. Cumulative intercepted radiation was calculated by multiplying the proportion of ground cover (which is a good estimate of the proportion of intercepted solar radiation, e.g. Haverkort et al., (1991b) with global solar radiation from a nearby meteorological station cumulated between emergence and each periodic harvest.

Results

Ground cover development and radiation use efficiencies (E_{tot} and E_{tub}, derived from the slopes between yields and cumulative intercepted radiation) varied between cultivars and treatments. It is shown in Fig. 1 as an example how these crop growth parameters were derived in the 1989 growing season. Total dry matter production (tuber + foliage) is only shown for the first 3 harvests, because from then on, unrecorded leaf drop made assesment of total dry matter accumulation unreliable. Tuber dry matter production is shown for the last three periodic harvests because at the first harvest in general no tubers were present. The cv. Elles shows a relatively minor change of ground cover but its efficiency is more strongly reduced than that of the cv. Mentor whose ground cover was more strongly affected. From the ground cover data it is clear that the more tolerant to cyst nematodes cv. Elles is also a far later cultivar (with a 3.5 weeks longer growing season) than 'Mentor'.

The values of the growth parameters of the control (fumigated and irrigated) plots are shown in Table 2. Fresh actual total tuber yields in 1988 and 1989 were similar, but in 1990 they were lower, possibly due to the higher initial nematode population density, even after a double fumigation in spring. Greatest ground cover with green foliage was obtained in 1989 resulting in the greatest amount of intercepted solar radiation, but

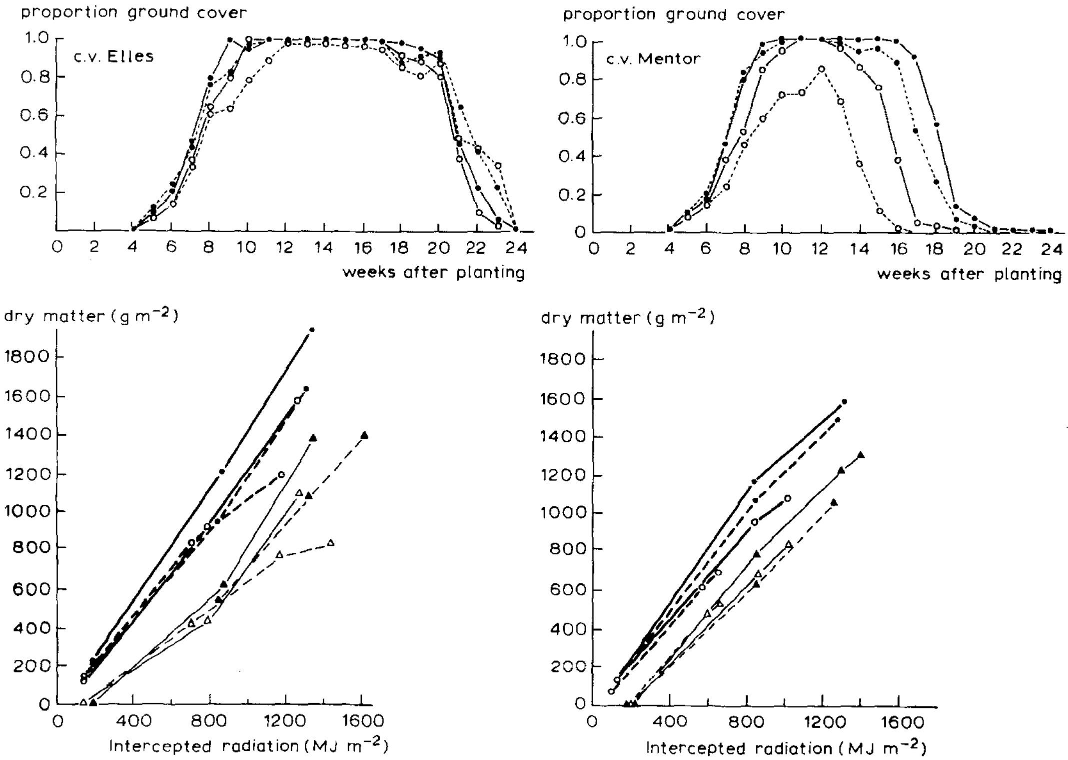

Fig. 1. Ground cover development and relationships between dry matter production and intercepted solar radiation of the cultivars Elles and Mentor in 1989. Closed symbols: fumigated; open symbols: unfumigated; drawn lines: irrigated; broken lines: unirrigated. Dry matter production: circles indicate total dry matter of the first three harvests (towards the fourth leaf drop occurred), triangles indicate tuber dry matter of the last 3 harvests (at the first harvest no tubers were present)

the conversion efficiency for total dry matter production was the least in that year. This might be due to yellowing leaves being included in the green leaf area estimate. This has consequences for these two crop growth parameters within a particular year but has no consequences for the comparison of the effects of drought and nematodes within a year or for comparison of the relative effects as is done in Table 3.The harvest index hardly varied between the three years; it appeared that about 75 % of all dry matter produced by the crop was allocated to the tubers. The dry matter content was lowest in 1989 and highest in 1990. The apparent amount of intercepted radiation at tuber initiation (IR_{ti}) was highest in 1989 and lowest in 1990. This last year was exceptional because a late spring frost killed most of the foliage in early June leading to the low yields and low dry matter contents. Contrary to the radiation use efficiency for total dry matter production (which was lowest in 1989), the efficiency for tuber dry matter production was highest in 1989. Equation 5 allows us to calculate final fresh tuber yields from total intercepted radiation, radiation use efficiency for total dry matter production, harvest index and tuber dry matter content. The result is shown

Table 2. 1988, 1989 and 1990 field data control plots (fumigated and irrigated), tuber weights are actual and calculated (Equations 5 and 6 in text) tuber fresh yields.

Year	Cultivar	Actual tuber weight ($kg\ m^{-2}$)	Total Intercepted Radiation ($MJ\ m^{-2}$)	Light use Efficiency total dry matter ($MJ\ g^{-1}$)	Harvest index ($g\ g^{-1}$)	Dry matter content ($g\ g^{-1}$)	Intercepted radiation at tuber initiation ($MJ\ m^{-2}$)	Light use Efficiency tuber dry matter ($MJ\ g^{-1}$)	Fresh tuber wt. Eq. 5 ($kg\ m^{-2}$)	Fresh tuber wt. Eq. 6 ($kg\ m^{-2}$)
1988	Darwina	5.01	1322	1.43	0.76	0.257	142	1.11	5.59	5.10
	Désirée	5.55	1231	1.50	0.72	0.217	237	1.15	6.13	5.27
	Elles	5.00	1412	1.34	0.71	0.245	378	1.27	5.48	5.36
	Mentor	5.21	1293	1.52	0.75	0.248	253	1.26	5.94	5.28
	Mean	5.19	1390	1.45	0.74	0.242	253	1.20	5.79	5.25
1989	Darwina	5.74	1415	1.15	0.79	0.255	494	1.57	5.38	5.66
	Désirée	5.50	1256	1.07	0.77	0.227	481	1.43	4.55	4.88
	Elles	4.83	1632	1.30	0.71	0.286	520	1.50	5.24	5.83
	Mentor	4.89	1395	1.12	0.76	0.261	368	0.93	4.55	4.66
	Mean	5.24	1424	1.16	0.76	0.257	466	1.36	4.93	5.26
1990	Darwina	4.00	977	1.51	0.77	0.269	113	1.28	4.22	4.12
	Désirée	4.83	1054	1.49	0.76	0.214	76	1.06	5.55	4.84
	Elles	4.69	1261	1.39	0.73	0.272	181	1.18	4.51	4.69
	Mentor	4.42	1060	1.43	0.79	0.279	169	1.27	4.68	4.43
	Mean	4.49	1086	1.46	0.76	0.259	135	1.20	4.74	4.52

in the last but one column in Table 2. Equation 6 makes use of the amount of intercepted radiation at tuber initiation, the light use efficiency for tuber dry matter production and tuber dry matter content to calculate tuber yields. These are shown in the last column of Table 2. The amount of intercepted radiation is calculated through extrapolation of the tuber yield versus intercepted radiation relationship to the abscissae. This is not very accurate (even values of 0 occur) but since the values are relatively low, they do not much influence the final results. The calculated tuber fresh yields from Equation 6 correspond better with the actually observed yields than the yields calculated from Equation 5 which shows the greater potential use of this equation for use in simulation studies.

Differences between cultivars were less obvious with regard to total fresh tuber yields than with regard to the other growth parameters. 'Désirée' showed the lowest total amount of intercepted radiation (except in 1990 because in that year 'Darwina' suffered from an attack by *Rhizoctonia solani*) whereas the very late cv. Elles had the highest amount of intercepted radiation as a result of its long duration of ground cover. The conversion efficiency for total dry matter production (E_{tot}) did not differ much between the cultivars. 'Elles' had the lowest harvest index indicating that this late cultivar partitioned relatively more dry matter to the foliage than the other ones. 'Désirée', which is not normally used as a starch producing cultivar had the lowest dry matter content in the tubers, about 22 % against about 27 % with the starch varieties. The late cultivar Elles had accumulated the highest amount of intercepted radiation, and consequently of dry matter, at the time of tuber initiation. Due to variation in the data between the three seasons, no cultivar effect on the conversion efficiency for tuber dry matter could be demonstrated.

The values of the crop growth parameters of the unirrigated and/or unfumigated plots relative to the fumigated and irrigated control plots are shown in Table 3. Absence of fumigation in the irrigated plots in three years resulted in tuber yields which were only 48 % of the control with 'Darwina' and 'Mentor', 52 % with 'Désirée' and 73 % with cultivar Elles. This strong reduction in yield was mainly attributed to the reduction in ground cover leading to reduced amounts of intercepted radiation (−43 % with cv. Mentor whereas only −14 % with 'Elles'). The efficiency for total dry matter production was reduced by values ranging from 5 % ('Elles') to 14 % ('Désirée'). The harvest index was only slightly reduced by the nematode infection with Darwina and Désirée but not at all with cvs. Elles and Mentor.

The dry matter content of the tubers increased in the absence of fumigation by 1 % ('Mentor') to 7 % ('Elles'). The apparent amount of intercepted radiation at tuber initiation declined strongly, in the absence of fumigation with the cultivars Darwina, Elles and Mentor, whereas De was less affected (−14 %). Lack of fumigation affected the efficiency of tuber dry matter production more than the efficiency of total dry matter production.

Drought, in general, affected the crop growth parameters in ways similar to nematode infection but the average effect on yields (−29 % of all crops in the two years) was less than that due to nematodes (−44 %). Drought mainly led to reduced amounts of intercepted radiation, it only reduced the efficiency of dry matter production with the cultivar Elles (−10%), it only marginally negatively affected the harvest index (−3 % on average), whereas the effect on the tuber dry matter content (+7 %) was greater than that of the nematode infection (+4 %). The efficiency of tuber dry matter

Table 3. Relative values of yield components (1988-1990) as percentage of the control (fumigated and irrigated see Table 2). Irr = irrigated, Fum = fumigated.

Year	Cultivar	Irr	Fum	Actual tuber weight	Total Intercepted Radiation	Light use Efficiency total dry matter	Harvest index	Dry matter content	Intercepted radiation at tuber initiation	Light use Efficiency tuber dry matter
1988	Darwina	+	–	47	51	101	92	102	0	80
	Désirée	+	–	44	63	82	92	92	19	64
	Elles	+	–	65	87	96	101	109	27	65
	Mentor	+	–	49	55	86	99	95	38	83
1989	Astarte	+	–	64	92	82	93	98	77	65
		–	+	84	100	90	99	97	57	71
		–	–	40	62	79	89	104	52	63
	Darwina	+	–	57	72	94	93	107	60	79
		–	+	63	84	96	95	103	66	62
		–	–	48	66	91	93	110	47	42
	Désirée	+	–	55	88	90	87	104	55	63
		–	+	83	98	105	101	109	104	115
		–	–	48	82	78	89	105	93	82
	Elles	+	–	72	93	88	97	104	44	88
		–	+	89	101	83	97	105	29	64
		–	–	59	90	75	92	99	3	39
	Mentor	+	–	57	73	93	98	103	0	74
		–	+	77	92	88	101	107	497	131
		–	–	34	48	80	103	109	249	114

1990	Darwina	+	–	42	61	76	98	105	52	95
		–	+	47	80	101	92	106	88	93
		–	–	40	41	96	109	114	47	108
	Désirée	+	–	58	63	86	101	109	178	113
		–	+	71	78	98	99	110	197	118
		–	–	46	55	86	100	118	215	127
	Elles	+	–	81	78	107	109	107	43	100
		–	+	71	85	97	92	96	67	83
		–	–	62	67	99	110	108	66	92
	Mentor	+	–	41	43	96	102	105	42	109
		–	+	69	82	105	93	114	70	101
		–	–	24	26	99	98	106	34	131
88-90	Darwina	+	–	48	61	90	94	105	37	85 nematode effect
	Désirée	+	–	52	71	86	93	102	84	80
	Elles	+	–	73	86	95	102	107	38	84
	Mentor	+	–	49	57	92	100	101	27	89
	Mean	+	–	56	69	91	97	104	47	85
89-90	Darwina	–	+	55	82	99	94	105	77	78 drought effect
	Désirée	–	+	77	88	99	94	105	77	78
	Elles	–	+	80	93	90	95	101	48	74
	Mentor	–	+	73	87	97	97	111	284	116
	Mean	–	+	71	88	96	95	106	121	86

Table 4 Significancies of the effects of factors and their interactions in 1989 and 1990, NS = non significant, * = $P < 0.10$, ** = $P < 0.05$, *** = $P < 0.01$.

Factor	Actual tuber weight	Total Inter-cepted Radiation	Light use Efficiency total dry weight	Harvest index	Dry matter content	Inter-cepted radiation at tuber initiation	Light use Efficiency tuber dry matter
Year	***	***	**	NS	NS	**	*
Fumigation	***	***	**	*	***	**	***
Irrigation	***	***	*	***	***	NS	**
Cultivar	*	***	NS	***	***	***	*
Year × fumigation	*	***	NS	***	NS	*	***
Irrigation × fumigation	NS	NS	NS	NS	NS	NS	NS
Cultivar × fumigation	***	***	*	**	**	**	*
Cultivar × irrigation	***	***	**	**	**	*	***

production (comparable with that of total dry matter production) was less affected by drought (−4 %) than by potato cyst nematodes (−15 %, mean values of the four cultivars in the last two years). The amount of intercepted radiation at tuber initiation was not significantly affected by drought.

Table 4 shows the levels of significance of the crop growth components of the factors and their interactions. These were only calculated for the two years 1989 and 1990 because in the first year (1988) no drought occurred. The harvest index and the dry matter content were not affected by the growing season. The efficiency for total dry matter production was not affected by cultivar. There was a year × fumigation effect on yield: absence of fumigation led to 10 % lower yields in 1990 than in 1989, which was mainly due to a far lower amount of intercepted radiation (−20 %) but counterbalanced by a higher value of the harvest index in 1990 than in 1989. This indicates that the plants at the final harvest were more mature in 1990 than in 1989. Most strikingly, no interaction was shown between fumigation and irrigation. The effects of drought and nematodes on yield and crop growth parameters were similar. The interaction between cultivar and fumigation was clear. The most tolerant 'Elles' showed far less response than the cv. Mentor, mainly because it maintained its ground cover (hence its total intercepted radiation) and because cvs Elles and Mentor showed unchanged harvest indices. There also was a cultivar × irrigation effect because here 'Désirée' was the only cultivar which did not show a change of harvest index.

Discussion

Fumigation took place only two weeks before planting, which is relatively close. This was done to minimize an increase of nitrogen availability through break-down of dead micro-organisms. It should also be recognized that fumigation with metham-sodium also likely killed other deleterious soil organisms so some care should be taken not to attribute all effects to potato cyst nematode damage. With the high populations present in the unfumigated plots, however, we feel confident that a reduction of the nematode populations following fumigation is the main responsible factor for the observed growth differences.

Fresh tuber yield loss following infection with potato cyst nematodes was mainly due to a reduction of the amount of radiation intercepted by the crop and to a lesser extent to reductions of the radiation use efficiency and the harvest index and to increases in tuber dry matter content. Both the total amount of intercepted radiation and the conversion efficiency of the most tolerant cultivar Elles were least affected by nematodes. Consequently, 'Elles' was the highest yielding cultivar under potato cyst nematode infected conditions, although it did not produce the highest tuber yields in relatively nematode free (fumigated) soils.

The rank order of the four cultivars for drought tolerance, expressed as the lowest proportion of yield loss, was Elles, Désirée, Mentor and Darwina (Table 3 1989 and 1990 data). This was the same order (with the exception of 'Darwina' which was more tolerant to nematodes but less tolerant to drought than 'Désirée') as observed for tolerance for potato cyst nematodes (Table 3, 1988-1990 data). This finding corroborates those reviewed by Evans and Haydock (1990) that a nematode tolerant cultivar proved to be the more drought tolerant. This largely reinforces the hypothesis of Wallace (1987) that selection for drought tolerance may yield genotypes which are tolerant for potato cyst nematodes and vice versa.

Trudgill et al. (1990) suggested that late cultivars which intercept the highest amount of intercepted radiation in the absence of nematodes will also show the highest degree of tolerance. This is partly confirmed by the data presented in this paper: 'Elles' intercepted the highest amount of solar radiation in fumigated and irrigated conditions in each year (Table 2) and it also proved to be the most tolerant. The cultivar 'Désirée', however, was the earliest cultivar with the lowest amount of intercepted radiation, but did not show the lowest tolerance for potato cyst nematodes.

Yields in 1990 were about 4.5 kg per m^2 whereas they were about 5.2 kg per m^2 (mean value of the fumigated and irrigated control plots) in 1988 and 1989. These lower yields were due the killing late frosts in June and to a difference in soil fertility in 1990. Mineralization of nitrogen in these soils is known to vary widely between years depending on temperature and precipitation. The relatively low value of the radiation use efficiency of 1989, only 1.16 g MJ^{-1} whereas it was about 1.45 g MJ^{-1} in the two other years, was due to the inclusion of yellow(ing) leaves in the 1989 count.

The apparent amount of intercepted radiation at tuber initiation was not affected by drought (Table 3) because the drought effect only became apparent after tuber initiation as initially the soil contained sufficient water for unrestricted crop growth. With nematode infection, there was an effect on plant growth from emergence onward, possibly even earlier as nematodes may reduce the number of sprouts developing into stems (Fasan and Haverkort, 1991). Hence, the negative effect of nematode infection on the amount of intercepted radiation at tuber initiation shows that plants are smaller when tubers are initiated in infected plants than in uninfected plants.

A major finding concerns the complete absence of interaction between drought and nematode infection for all the crop growth parameters which were studied. This means that the effects of drought and nematodes are additive. This is contrary to what was expected. We expected nematode infected plants to be more susceptible to drought. Lack of interaction may be partly explained because nematode infected plants deplete soil moisture at a slower rate than healthy plants so that they are subjected to less severe drought conditions. Similar observations were made by Haverkort et al. (1991a). Effects of nematodes and drought being additive are another indication that nematodes cause symptoms which are similar to those of drought as was reported by Fatemy and Evans (1986) and Wallace (1987).

The results shown here indicate that cultivars which best maintain ground cover in the absence of nematodes also maintain it best in the presence of nematodes which leads to the highest yields because the radiation use efficiencies are far less affected by nematodes than radiation interception. The similarity of the response of both stress factors nematode infection and drought and the absence of interaction facilitate crop simulation modelling and the relationships found here may well be used although they have to be validated for other cultivars and growing conditions. Equation 6 should preferrably be used as it more accurately describes the yield function.

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References

Evans, K. & Haydock, P.P.J., 1990. A review of tolerance by by potato plants of cyst nematode attack, with consideration of what factors may confer tolerance and methods of assaying and improving it in crops. Annals of Applied Biology 117: 703-740.

Evans, K., Parkinson, K.J. & Trudgill, D.L., 1975. Effects of potato cyst nematodes on potato plants. III. Effects on the water relations and growth of a resistant and a susceptible variety. Nematologica 21: 273-280.

Fatemy, F, & Evans, K., 1986. Effects of *Globodera rostochiensis* and water stress on shoot and root growth and nutrient uptake of potatoes. Revue Nematologique 9: 181-184.

Fasan, T. & Haverkort, A.J., 1991. The influence of cyst nematodes and drought on potato growth. 1. Effects on plant growth under semi-controlled conditions. Netherlands Journal of Plant Pathology 97: 151-161.

Haverkort, A.J., Fasan, T. & Van de Waart, M., 1991a. The influence of cyst nematodes and drought on potato growth. 2. Effects on plant water relations under semi controlled conditions. Netherlands Journal of Plant Pathology 97: 162-170.

Haverkort, A.J. & Bicamumpaka, M., 1986. Correlation between intercepted radiation and yield of potato crops infested by *Phytophthora infestans* in central Africa. Netherlands Journal of Plant Pathology 92: 239-247.

Haverkort, A.J. & Harris, P.M., 1986. Conversion coefficients between intercepted solar radiation and tuber yields of potato crops under tropical highland conditions. Potato Research 29: 529-533.

Haverkort, A.J. & Harris, P.M., 1987. A Model for potato growth and yield under tropical highland conditions. Agricultural and Forest Meteorology 39: 271-282.

Haverkort, A.J., Uenk, D., Veroude, H. & Van de Waart, M., 1991b. Relationships between ground cover, intercepted radiation, leaf area index and infrared reflectance of potato crops. Potato Research 34: 113-121.

Lamondia, J.A., Rawsthorne, D. & Brodie, B.B., 1986. Methods for reducing experimental variation in *Globodera rostochiensis*. Journal of Nematology 18: 415-418.

Van Oijen, M., 1990. Photosynthesis is not impaired in healthy tissue of blighted potato plants. Netherlands Journal of Plant Pathology 96: 55-63.

Trudgill, D.L., 1986. Yield losses caused by potato cyst nematodes: a review of the current position in Brittain and prospects for improvement. Annals of Applied Biology 108: 181-198.
Trudgill, D.L., Evans, K. & Parrot, D.M., 1975. Effects of potato cyst nematodes on potato plants. Effects in a trial with fumigation and irrigation on the growth and nitrogen and potassium contents of a resistant and a susceptible variety. Nematologica 21: 169-182.
Trudgill, D.L., Marshall, D. & Phillips, M., 1990. A field study of the relationsip between preplanting density of *Globodera pallida* and the growth and yield of two potato cultivars of differing tolerance. Annals of Applied Biology 117: 107-118.
Wallace, H.R., 1987. A perception of tolerance. Nematologica 33: 419-432.