Tolerance of the potato to stress associated with potato cyst nematodes, drought and pH.

An ecophysiological approach

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A. Mulder

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Proefschrift
ter verkrijging van de graad van doctor
in de landbouw- en milieuwetenschappen
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dr. C.M. Karssen,
in het openbaar te verdedigen
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The studies presented in this thesis were performed at

H.L. HILBRANDS LABORATORY for SOIL-BORNE PESTS and DISEASES

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Contents

Stellingen.

1. De betrekkelijk eenvoudige vergelijking van Oostenbrink beschrijft de aaltjesdichtheid/schade relatie op adequate wijze en leent zich bovendien uitstekend voor uitbouw in ecofysiologische zin.
   Oostenbrink, 1966: Mededelingen Landbouwhogeschool Wageningen 66/4.
   Dit proefschrift.

2. De verzuchting van CAIUS PETRONIUS (AD 66), in het Nederlands neerkomend op: "*We hebben ons best gedaan, maar het leek er op dat, telkens als wij als team begonnen te functioneren, we werden gereorganiseerd. Ouder geworden leerde ik dat wij er toe neigen iedere nieuwe situatie het hoofd te bieden door reorganisatie. Welk een wonderbaarlijke methode om de illusie van vooruitgang te wekken, terwijl slechts verwarring, inefficiëntie en demoralisatie het gevolg zijn!*" was 2000 jaar geleden actueel, maar had ook vandaag geschreven kunnen zijn.

3. Tolerantie uitsluitend baseren op relatieve schade mag eenvoudig lijken, maar gaat voorbij aan het feit dat de praktijk vraagt naar opbrengst in tonnen per ha en niet naar schade in procenten.
   Dit proefschrift.

4. De opbrengst van aardappelen en de schade door het aardappelcysteaaltje kunnen aanzienlijk worden verhoogd door op gronden met een geringe waterretentie regelmatig en per keer matig te irrigeren.
   Dit proefschrift.

5. Bij toenemende droogte doen aaltjes in absolute zin minder schade.
   Dit proefschrift.

6. Tolerantie tegen aardappelcysteaaltjes en droogte zijn verschillende fenomenen; beide eigenschappen verdienen een plaats in de Beschrijvende Rassenlijst voor Landbouwgewassen.
   Dit proefschrift.

7. De in de opeenvolgende Beschrijvende Rassenlijsten voor Landbouwgewassen vermelde cijfers voor "droogteresistentie" van aardappelrassen dienen uiterst tolerant te worden geïnterpreteerd. Dat pH-tolerantie cijfers in deze lijsten node worden gemist moet niet worden opgevat als een zure opmerking.

8. Akkergroenten kosten de boeren geld en de tuinders gaan er aan kapot.

9. Vergrassing van de heidevelden is geen nieuw probleem. Naast de schaapskudde heeft grazend rundvee eeuwenlang het beeld van de Drentse heide bepaald.
   Jan Bieleman, Geschiedenis van de landbouw in Nederland, 1500-1950 (1992).

10. Omstreeks 1650 werd in Dwingeloo geklaagd dat "onse heijdevelt geheel tot zandt verstoft" was en dat de zuid-es "merendeels met sant overwaeyt" werd. Deze verstuiving was een gevolg van slecht beheer. Nu wordt deze situatie door het overheidsbeleid nagestreefd en "hoogwaardige natuur" genoemd.
    Jan Bieleman, Geschiedenis van de landbouw in Nederland, 1500-1950 (1992);
    Plan Goudplevier, Natuurbehoud 23/2 (1992): 4-7.

11. Iemands waarheden worden vervelend als hij ze aan een ander opdringt; ze worden rampzalig als hij ze aan een ander oplegt.
    Boerenwijsheid.

12. In Wageningen houdt promoveren meer in dan innoverend citeren.
    Naar aanleiding van een voordracht van Dr. P.T. Smit, oud Directeur-Arts van de Provinciale Raad voor de Volksgezondheid in Drenthe.

Stellingen behorend bij het proefschrift van A. Mulder:
Tolerance of the potato to stress, associated with potato cyst nematodes, drought and pH.
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Wageningen, 30 mei 1994.

Voorwoord

Het voorliggende onderzoeksverslag is de neerslag van vijftien jaar onderzoek naar schade door het witte aardappelcysteaaltje, *Globodera pallida* Stone, 1973, aan aardappelplanten resp. aardappelgewassen en naar verschillen in schadegevoeligheid tussen aardappelrassen.
De mate waarin de plant schade lijdt door aaltjes wordt mede bepaald door omgevingsfactoren die van invloed zijn op de fysiologie van de aardappelplant en daarmee op groei en ontwikkeling van aardappelgewassen. Omdat aardappelrassen zo verschillend op omgevingsfactoren als weersgesteldheid en bodemcondities reageren kan inzicht in deze materie vooral worden verkregen door onderzoek met een breed rassen-assortiment gedurende voldoende lange tijd onder natuurlijke omstandigheden uit te voeren. Voor de aardappelteelt ten behoeve van de zetmeelindustrie zijn dat de typische omstandigheden van de zand- en dalgronden in noordoost en middenoost Nederland. Deze gronden worden gekenmerkt door een redelijk goede en vrij stabiele textuur en zijn van nature mineralogisch zeer arm en zuur.

Het proefschrift wordt opgedragen aan mijn ouders en mijn leermeesters. Mijn ouders brachten hun kinderen liefde en eerbied bij voor de natuur, wezen hen op haar lieflijkheid, op haar aanpassingsvermogen aan al dan niet door de mens veroorzaakte veranderingen zoals die in het huidige landschap tot uiting komen, als ook op haar meedogenloosheid. Zo werd de kiem gelegd voor de latere behoefte in en met die natuur te werken en er een bestaan in op te bouwen.
In de veel te vroeg overleden dr. ir. M. Oostenbrink, bij leven lector in de Nematologie, en ir. L.J.P. Kupers, emeritus hoogleraar in de Leer van de Landbouwplantenteelt, wil ik allen danken die hebben bijgedragen aan mijn praktische en wetenschappelijke opleiding en vorming, en ontwikkeling tot op de praktijk gerichte wetenschappelijk onderzoeker.
De eerste ervaringen met de landbouwpraktijk werden opgedaan in het laatste oorlogsjaar. In het najaar van 1944 werd de schooljeugd ingezet bij de aardappeloogst. Die kennismaking beviel zo goed dat te beginnen met de zomer van 1945 alle vakanties tijdens lagere school- en HBS-tijd werden doorgebracht op het gemengde bedrijf van de familie G.H. Hidskes te Kloosterveen bij Assen. Om als niet-boerenzoon te worden toegelaten tot de toenmalige Rijks Middelbare Landbouwschool (thans Agrarische Hogeschool, het "Van Hall Instituut") te Groningen was een aaneengesloten

praktijktijd van een jaar vereist. Die leertijd, en de latere vakanties/praktijkperiodes werden doorgebracht op het akkerbouwbedrijf van de familie G. van Hoorn te Kloosterburen op het Groninger Hoge Land.

In Oostenbrink, stammend uit het Drentse boerenland, verloor de landbouw een eminent wetenschapper met een open oog voor de problemen van de praktijk, een uitstekend leraar en een goede vriend.
Hooggeleerde Kupers, tijdens lange gesprekken op uw kamer kwamen destijds vele zaken aan de orde die buiten de collegestof omgingen en waarin mijn interesse voor de fysiologie van landbouwgewassen sterk werd gestimuleerd. Opgegroeid in een gebied waar de aardappelteelt van oudsher een belangrijke plaats inneemt richtte die belangstelling zich als vanzelf op de fysiologie van het aardappelgewas. Als het specifiek om het aardappelgewas ging fungeerde uw medewerker ir. F.J.H. van Hiele als wetenschappelijke vraagbaak en steun en toeverlaat.
De latere vakgroepen Nematologie, Fytopathologie en Landbouwplantenteelt zijn door de jaren heen mijn wetenschappelijke thuishaven gebleven, en het is de gecombineerde kennis van deze vakgebieden die het schrijven van het voorliggende werkstuk heeft mogelijk gemaakt.
Hooggeleerde Van der Wal, beste Ton, onze contacten dateren van 1976/1977 toen bleek dat ieder van ons met de hem ten dienste staande middelen en mogelijkheden een deel van zijn onderzoekscapaciteit besteedde aan het probleem van verschillen in gevoeligheid voor schade door aardappelcysteaaltjes tussen aardappelrassen. Het was logisch beider onderzoek zo in te richten dat kon worden bezien of er een goede correlatie bestond tussen de resultaten van het kasonderzoek van de Stichting voor Plantenveredeling (SVP) en van het veldonderzoek van het (Hilbrands) Laboratorium voor Bodemziekten (HLB). In de volgende jaren zijn de onderlinge verstandhouding en samenwerking steeds goed geweest. Het doet me daarom genoegen dit proefschrift als afsluiting van het meer fundamentele deel van het tolerantieonderzoek onder jouw leiding te hebben kunnen schrijven.
Zonder hulp van anderen, waaronder staf en medewerkers van het Hilbrands Laboratorium, zou dit proefschrift niet tot stand zijn gekomen. Zonder iemand te kort te willen doen wil ik enkelen met name noemen: ing. Jans Roosjen, die mij de afgelopen twee jaren extra veel werk uit handen heeft genomen waardoor er ruimte en tijd kon worden gevonden voor het vele extra werk dat het schrijven van een proefschrift nu eenmaal met zich mee brengt; de oud HLB medewerkers Geert Garming, ing. Henk Jan Lutgert en Jan Renting voor de uitvoering van de eerste grote, op tolerantie gerichte veldproeven in de jaren 1976 - 1980; ing. Margriet Boerma en ing. Roland Velema voor het in het kader van het Tolerantie-project uitvoeren van de

vele zeer arbeidsintensieve proeven in kas en veld gedurende de jaren 1986 tot en met 1991; de heer Jan S. Zwiers van het Instituut voor Bodemvruchtbaarheid te Haren voor de bepaling van de pF-curves van de verschillende gronden; mevrouw Jenny van der Wal-Leeuwis van het C.P.R.O. voor haar hulp bij het opsporen van "oude" literatuur over de effecten van de zuurgraad van de bodem op groei en ontwikkeling van wortelstelsels; ing. Roland Velema voor het met veel inzicht, inzet en geduld uitgevoerde reken- en tekenwerk en de hulp bij het ontwikkelen van modellen; dr. ir. Anton J. Haverkort van het C.A.B.O. en dr. ir. Lo J. Turkensteen van het I.P.O. voor het kritisch doorlezen van het manuscript en hun vele op- en aanmerkingen en suggesties ter verbetering van inhoud en leesbaarheid en Mrs. Josie M. Dutton voor de correcties van de engelse tekst en haar suggesties deze ook voor "leken" leesbaar en begrijpelijk te maken.

Een bijzonder woord van dank is hier op zijn plaats voor het Bestuur van de Stichting Interprovinciaal Onderzoekcentrum voor de Akkerbouw op zand- en veenkoloniale grond in Middenoost- en Noordoost Nederland (SIO) en de Begeleidingscommissie van het Hilbrands Laboratorium voor Bodemziekten (HLB) voor de gelegenheid en de medewerking die werden gegeven voor het schrijven van dit proefschrift.

Tenslotte gaat mijn dank in het bijzonder uit naar Lies, die het de laatste jaren heeft moeten stellen met een vaak afwezige echtgenoot die, indien thuis, tot in de kleine uurtjes druk was met boeken en paperassen en dan veelal slecht aanspreekbaar was.

Samenvatting

Aardappelcysteaaltjes (*Globodera rostochiensis* en *G. pallida*) vormen in veel landen een bedreiging voor de aardappelteelt. In Hoofdstuk I wordt een overzicht gegeven van de biologie van het aardappelcysteaaltje in relatie tot de aardappelplant en van de mate van gevoeligheid voor schade door aardappelcysteaaltjes van de aardappelplant. Tolerantie is die eigenschap van een cultivar, waardoor deze bij aantasting in verhouding tot andere cultivars minder schade lijdt. Tolerantie wordt besproken in relatie tot resistentie tegen nematoden, en in afhankelijkheid van andere biotische en abiotische factoren. Tolerantie lijkt in eerste instantie te worden bepaald door de mate waarin de groei van het wortelstelsel, en vervolgens ook van de bovengrondse delen van de plant wordt geremd na een invasie van grote aantallen jonge alen. De mate waarin aardappelplanten door aardappelcysteaaltjes worden geschaad wordt niet alleen bepaald door de hoogte van de besmetting, maar wordt mede bepaald door andere factoren, zoals de kwaliteit van het pootgoed, de pH van de bodem, droogte, en andere pathogenen van de aardappel.

Diverse modellen zijn ontwikkeld om de relatie tussen opbrengst en aaltjesdichtheid te beschrijven. De modellen ontwikkeld door Brown, Oostenbrink, Seinhorst en Elston *et al.* worden besproken en hun eigenschappen geanalyseerd in Hoofdstuk II. Het blijkt dat over de jaren, en in het initiële dichtheidsbereik (P_i) van 1 tot 100 aaltjes per g grond Oostenbrink's vergelijking: Opbrengst = $a + b \cdot \log(P_i)$ beter voldoet dan de lineaire relatie $Y = a + b \cdot P_i$, en even goed of beter was dan meer gecompliceerde relaties (Hoofdstuk III). De hoeveelheid neerslag in de kritische periode van het groeiseizoen beïnvloedde de opbrengst / aaltjesdichtheid relatie in hoge mate. In jaren met een geringe hoeveelheid neerslag en dus ook een betrekkelijk laag opbrengstniveau, was de absolute toename van de schade door aaltjes bij toenemende dichtheid geringer dan in jaren met overvloedige regenval.

In de jaren 1979 en 1980 werden op de toenmalige Stichting voor Plantenveredeling (SVP) in een kas een groep van 52 rassen driemaal getoetst op hun groeireactie bij een hoge aaltjesdichtheid gedurende de eerste 10 weken. Hieruit werden 20 rassen gekozen om door het Laboratorium voor Bodemziekten (thans HLB) ook in het veld gedurende twee jaren (1978 en 1979) te worden getoetst op opbrengst bij hoge besmettingen met *G. pallida*.

De schade te velde bleek sterk gecorreleerd met de initiële groeivertraging van de planten, zoals die in de kas was bepaald (Hoofdstuk IV). Dit gegeven was aanleiding om van een aantal rassen de groei van het gewas te velde in verschillende jaren, dus onder wisselende omstandigheden te onderzoeken bij diverse aaltjesdichtheden. De resultaten van grootschalige proeven met vier rassen gedurende drie opeenvolgende jaren worden beschreven in Hoofdstuk V. Het bleek dat de opbrengst op eenvoudige wijze met de door het gewas opgevangen zonnestraling in verband kon worden gebracht, en dat deze relatie zeer goed wordt weergegeven door een rechte lijn. Deze relatie bleek over de jaren, cultivars en behandelingen niet te veranderen. Het aantal uitgegroeide knollen bleek te worden bepaald door de hoeveelheid opgevangen straling in de eerste helft van het groeiseizoen. De sortering wordt bepaald door de ingevangen straling gedurende zowel de eerste als de tweede periode van het groeiseisoen. Een kwantitatieve basis voor deze relatie wordt gegeven in Hoofdstuk V.

Teneinde deze relaties te toetsen voor een groot aantal rassen en mogelijke interacties vast te kunnen stellen werd daarop een veldproef aangelegd met 18 fabrieksaardappelrassen. De grondbedekkingscurven van alle rassen, behorende tot vijf rijptijdsklassen werden bepaald voor zowel zwaar als licht besmette grond. Het bleek dat de mate van initiële groeivertraging van de rassen, in reactie op de invasie van de juvenielen niet gerelateerd was aan rijptijdsklasse. Door de waarden voor grondbedekking op de zwaar besmette grond af te trekken van die op licht besmette grond werden curven voor het verschil in grondbedekking verkregen. De late cultivars vertoonden een duidelijk herstel van de groei, hetgeen tot uiting kwam in tweetoppigheid van de verschilcurven. Naarmate de cultivars vroeger waren bleken deze tweetoppige curven geleidelijk over te gaan in verschilcurven met slechts één top. Door de kortere groeiperiode van deze laatste groep rassen is het blijkbaar niet mogelijk erg lang van hun herstel van de infectie gebruik te maken, in tegenstelling tot de late cultivars. Deze verschillen kwamen ook tot uiting in de opbrengstcijfers.
Op dezelfde wijze werden per rijptijdsklasse de curven voor verschil in opbrengst op geirrigeerde en niet geirrigeerde grond bepaald. Opvallend is dat zowel op de licht besmette als op de zwaar besmette grond droogte nagenoeg een zelfde effect had op cultivars van alle rijptijdsklassen. Op zwaar besmette grond worden wederom voor vroege en middenvroege rassen eentoppige verschilcurven gevonden, terwijl de tweetoppigheid weer verschijnt voor de late - en de zeer late rassen, zij het dat de verschillen kleiner zijn dan zonder droogte.
Wanneer de opbrengsten worden uitgezet tegen de hoeveelheid opgevangen straling wordt voor alle rassen en behandelingen een constante verhouding tussen de knolopbrengst en de opgevangen straling gevonden. De groeipatronen van de

cultivars kunnen verschillen als gevolg van stress, veroorzaakt door droogte of cysteaaltjes en verschil in rijptijdsklasse. Toch bleek de conversiefaktor, de toename van droge stof vastgelegd in knollen per MJ, niet te verschillen. Deze wordt berekend op 1.08 g "knoldrogestof" per additionele MJ opgevangen straling.
De cultivars vertoonden grote verschillen in zowel tolerantie tegen aardappelcysteaaltjes als tegen droogte. Beide eigenschappen waren niet gecorreleerd (Hoofdstukken V en VI).

De relatie tussen opbrengst en initiële aaltjesdichtheid bleek ook sterk te worden beïnvloed door het type grond, waarop de gewassen groeiden. Dit werd bepaald in proeven over vele jaren op vijf locaties. Bij pH_{KCl}-waarden < 5,2 worden deze verschillen toegeschreven aan het effect van de waterretentie van de bouwvoor. Deze factor leek in belangrijke mate zowel het opbrengstniveau over de jaren als de hellingshoek van de curve die de relatie tussen opbrengst en aaltjesdichtheid beschrijft te bepalen. De beschikbaarheid van water uit de ondergrond droeg belangrijk bij aan de opbrengst en was van invloed op de relatie tussen de knolopbrengst en de dichtheid van de aaltjespopulatie (Hoofdstuk VII).

Bij afwezigheid van aardappelcysteaaltjes blijkt de zuurgraad van de bodem bij pH_{KCl}-waarden van 5,5 en hoger in het algemeen negatief gecorreleerd met de opbrengst. De verschillende cultivars blijken echter niet in gelijke mate op een hoge zuurgraad van de grond te reageren; een enkele cultivar leed zelfs geen schade bij $pH_{KCl} = 6,3$ (Hoofdstuk VIII).
De interactie tussen aardappelcysteaaltjes en pH bleek significant, evenals de interactie tussen cysteaaltjes, pH en cultivar. Bij aanwezigheid van aardappelcysteaaltjes treedt de schade reeds bij een lagere pH op. Dit wordt mogelijk verklaard doordat het wortelstelsel van aardappelplanten, zowel in massa als in bewortelingsdiepte, bij toenemende pH-waarden vermindert, zonder dat dit onder gunstige omstandigheden leidt tot opbrengstvermindering. Er is kennelijk een overcapaciteit aan wortelmassa, die echter bij aaltjesaantasting op zodanige wijze wordt aangesproken dat toch schade optreedt.

Oostenbrink's vergelijking, $Y = a + b \cdot \log(P_i)$ werd als basis gebruikt om de gegevens van de voorgaande proeven met elkaar in verband te brengen. Op grond van bodemfactoren en tolerantie-eigenschappen van aardappelcultivars kan nu een zodanige keuze uit de beschikbare cultivars kan worden gemaakt, dat de kans op schade minimaal is (Hoofdstuk IX). Het model heeft als bodemparameters nodig: de

initiële besmetting met aardappelcysteaaltjes (P_i), de water-retentie van boven- en ondergrond, en de pH_{KCl} van de grond. Als cultivareigenschappen zijn vereist: de relatieve opbrengst, en de tolerantiegraad van de cultivars voor aardappelcysteaaltjes, voor droogte en voor pH.
In niet besmette grond wordt de verwachte opbrengst (a) van een ras voor een bepaald perceel geschat uit het opbrengend vermogen, de droogte- en pH tolerantie van de cultivar en de waterretentie en pH van de bodem. De hellingshoek (b) van de curve wordt geschat uit de tolerantie van het ras voor aardappelcysteaaltjes en de interactie tussen besmettingsniveau (P_i) en pH. Significante kleine interacties tussen P_i en beregening (droogte) werden waargenomen voor geïntegreerde bodembedekking met groen loof en ingevangen straling. Voor de knolopbrengst daarentegen zijn tot nu toe geen interacties tussen P_i en droogte waargenomen (Hoofdstukken V en VI), en deze zijn daarom niet opgenomen in het model. De structuur van het model is zodanig dat het invoegen van deze en eventuele andere interacties goed mogelijk is. Ook kunnen betere schattingen van parameterwaarden, die uit vervolgonderzoek naar voren kunnen komen, gemakkelijk worden ingepast. Bovengenoemde benadering maakt een goede cultivarkeuze, gericht op een minimaal risico op schade, mogelijk.

Informatie over de opgevangen straling in de eerste helft van het groeiseizoen is van belang voor de telers van pootgoed in verband met het knolaantal. Voorts kan de meting van de opgevangen straling van een gewas in de eerste twaalf weken van het groeiseizoen (gerekend vanaf de pootdatum) worden benut om in een vroeg stadium tot een redelijke schatting van de eindopbrengst te komen. Deze schatting zal bij opeenvolgende metingen in de rest van het groeiseizoen steeds nauwkeuriger worden. Deze gegevens kunnen worden gebruikt bij de planning van transport en opslag van de aardappeloogst, bij de capaciteitstoewijzing bij de verwerking, en het in- en verkoopbeleid van de industrie.

In dit proefschrift is een methode ontwikkeld, om getalswaarden toe te kennen aan de toleranties ten aanzien van het witte aardappelcysteaaltje, droogte en pH, de "Tolerantie Waarden".
Naast het voordeel dat deze waarden direct een vergelijking tussen cultivars mogelijk maken, kunnen zij ook worden ingevoerd in het model en de akkerbouwer ondersteunen bij het bepalen van de beste cultivars, gegeven de gesteldheid van zijn grond. Het opnemen van dergelijke "Tolerantie Waarden" in de Nederlandse Beschrijvende Rassenlijst voor Landbouwgewassen wordt aanbevolen.

Voor de veredeling lijkt het toetsen van toleranties voor aardappelcysteaaltjes, droogte en pH in een vroeg stadium van veredelingsprogramma's mogelijk, omdat met geringe aantallen planten kan worden volstaan. De programma's kunnen daardoor sterk aan efficiëntie winnen.

Abstract

The impact of Potato Cyst Nematode (PCN) soil infestations on the growth and development of potato cultivars was investigated in greenhouse and field trials. PCN effect on yield was almost totally explained by reduced integrated ground cover, and hence, less light interception. There was no indication for any specific PCN effect other than reduced ground cover. The damaging effect of PCN was also studied in combination with soil type, drought and soil pH. In addition to the considerable effects of the main factors PCN, drought and pH, interaction between PCN and soil pH was found, but none was found between PCN infection and drought. However, it should be considered that the last mentioned events occurred separately in time.

With respect to the yield capacity of potato cultivars the following parameters appeared to be of major importance: PCN infestation level, water retention and pH of the soil. With soil pH_{KCl} values over 5.0, the vulnerability of the potato to PCN infection increases with decreasing acidity. The cultivar characteristics, resistance to PCN and tolerance to PCN, and the characteristics tolerance to PCN and tolerance to drought, were not correlated.

In nematology, tolerance to PCN is presented as percentage yield under PCN infestation. Quantifying the yielding capacity by means of tuber production, large numbers of plants are needed for accurate assessment and hence can not be done in early stages of breeding-programmes. Therefore, a screening method for tolerance to PCN was developed, allowing screening for this character to take place in a greenhouse at an early stage of a breeding programme. Also, integrated ground cover can be assessed with few plants, and offers a tool to assess tolerance under field conditions for breeding purposes.

Four descriptive equations, relating PCN infestation and yield, were studied. Based on experimental data over a number of years, Oostenbrink's equation described this relation simply, accurately and consistently. A decision-making model was developed to assist farmers in making the best cultivar choice, with respect to yield, based on prevailing soil factors (PCN infestation, water retention of top and subsoil, and pH) and cultivar characteristics. The same model is able to predict final yield with increasing precision with time during the current growing season. For this purpose Tolerance Values of cultivars for these stress factors were introduced. A procedure for estimation of tuber number and tuber dry matter yield is discussed, based on their relationships with intercepted radiation in the course of the season. Such estimates are useful to seed growers in order to set harvest dates and to the potato industry to obtain yield estimates in order to adapt logistics, storing and marketing.

Additional keywords: *Globodera pallida*, growth, ground cover, ground cover duration, intercepted radiation, soil type, soil water retention, cultivars, genotypes, maturity, root growth, yield, grade, tuber number, breeding, screening, Tolerance Values.

Introduction

The geological history of north western Europe gave rise to the mineralogically very poor and acid sandy and sandy peat soils in the north-eastern parts of the Netherlands (ter Wee, 1962, 1972; van Heuveln, 1965a,b; Stolp, 1977), northern Germany and eastward into Poland and Russia (Edelman, 1947; van der Lijn, 1986). As a consequence, agriculture could develop well in these regions only after fertilisers became available. Even then, only a limited number of crops could be grown on these acid soil types. The main crops were buckwheat, rye and oats. During the last century, these soils also proved suitable for growing potatoes. During the twentieth century, potatoes became the main arable crop and provided the basis for the potato starch industry. By using alkaline reacting fertiliser, acidity gradually decreased until pH_{KCl} values reached 4.8 to 5.2 during the sixties. Then, sugar beet became a second high yielding, profitable cash crop on these soils.

The texture and structure of the sandy and sandy peat soils in these regions make them a good biotope for many nematode species, including a number of economically important plant parasitic nematodes, such as the potato cyst nematodes, *Globodera rostochiensis* and *G. pallida*.

In the temperate regions throughout the world where potatoes are grown intensively, these nematode pests pose one of the most serious threats to potato production. They are easily spread by all processes where movement of soil is involved and on seed tubers from infested fields. They are very persistent and difficult to control (Southey, 1965).

Before World War II, potatoes were grown very intensively in the starch potato region of the Netherlands. In some years, up to 70 % of the arable acreage was used for potato growing. In this region, potato cyst nematodes were first found in 1948, five years after potato production was prohibited on infested fields and restricted to one crop in three years on uninfested fields (Oostenbrink, 1950). This legislation, however, did not prevent the further spread of the then predominant yellow potato cyst nematode, *G. rostochiensis*. In the sixties, integrated control schemes were developed and introduced in 1968. These schemes were based on crop rotation, the use of resistant potato cultivars (resistance based on the H_1-gene derived from *Solanum andigena*, CPC 1672) and chemical control by soil fumigation. Since 1968, the most commonly used scheme in the starch potato region was: one potato crop every two years, resistant and susceptible cultivars used alternately and in combination with one soil fumigation in four years, preferably carried out one or two years before the resistent cultivar was planted (Nollen and Mulder, 1969). This scheme was very successful; the number and levels of infestation decreased rapidly in the following years, often resulting in undetectable infestation levels. After the 1979 crop, the number and levels of infestation started to increase again; *G. rostochiensis* had lost its predominant position to the white potato cyst nematode *G. pallida* (Mulder and Veninga, 1988a). Polygenic resistance to this nematode was found in *Solanum vernei*. Breeding for resistance to this nematode resulted in the cultivars Darwina (1981) and Atrela (1983), both resistant to pathotype Pa-2 (Mulder and Jellema, 1990) and both very susceptible to damage caused by potato cyst nematode attack (Velema and Boerma, 1991). This last characteristic often resulted in total crop failure and made farmers reluctant to use these cultivars. Also, it raised the interest of research workers and management in the phenomenon of tolerance to potato cyst nematodes in potatoes.

In this thesis, data collected over an eighteen year period in the north-east of the Netherlands are analyzed to determine the relationships between cultivar, soil, weather and yield losses due to potato cyst nematode infections. An attempt is made to understand the effect of various soil factors and weather conditions on tuber yield and tolerance of potato cultivars to potato cyst nematodes, and finally, to use the results:
- to reduce the farmer's risk of crop damage caused by potato cyst nematodes,
- to design a monitoring method for growth, tuber number and tuber yield,
- to provide potato breeders with a screening method for tolerance in the early stages of a breeding programme.

Chapter I

Relationship between potato cyst nematodes and their principal host

Introduction

Potato crops can be severely damaged by the two potato cyst nematodes, *Globodera rostochiensis* (Wollenweber, 1923) Skarbilovich, 1959 and *Globodera pallida* Stone, 1973 (Loof and Bakker, 1992). Both nematode species are specialized on potato and some other *Solanaceae*, and have evolved very complex and specialized relationships with their hosts. The ability of these sedentary nematodes to feed for a long time without impairing the food source requires an exact match between products in nematode saliva and in the transfer cell (Stone, 1979).
These nematodes are named after their persistent soil borne structure, the so-called cyst (Photo 1.1), which consists of the toughened integument of the dead female body, filled with embryonated eggs. The cyst remains in the soil after the crop has been harvested. Encysted dormant eggs may persist for many years, withstanding drought and frost (Stone, 1979). In the absence of hosts, some eggs may survive up to thirty years within the cyst (Winslow and Willis, 1972).

Biology

Embryogenesis ends with a first stage juvenile. As the embryo increases in length, it starts to move within the egg shell and three flexures develop. The first moult occurs within the egg shell, giving rise to a second stage juvenile (J_2). During this first moult, the stylet is formed. These J_2s are the only migratory stage of cyst nematodes. They respond to specific root exudates produced by their hosts, commonly called hatching agents (Baunacke, 1923; Triffit, 1930; O'Brien and Prentice, 1930; Fenwick, 1949; Oostenbrink, 1950; Winslow, 1954; Janzen and Tuin, 1956). Recently, the formula of one of these, a small molecular agent (M = 498) produced by potato roots, has been identified. It is named Solano eclepin A, with the formula $C_{27}H_{30}O_9$ (Nieboer *et al.*, 1994).

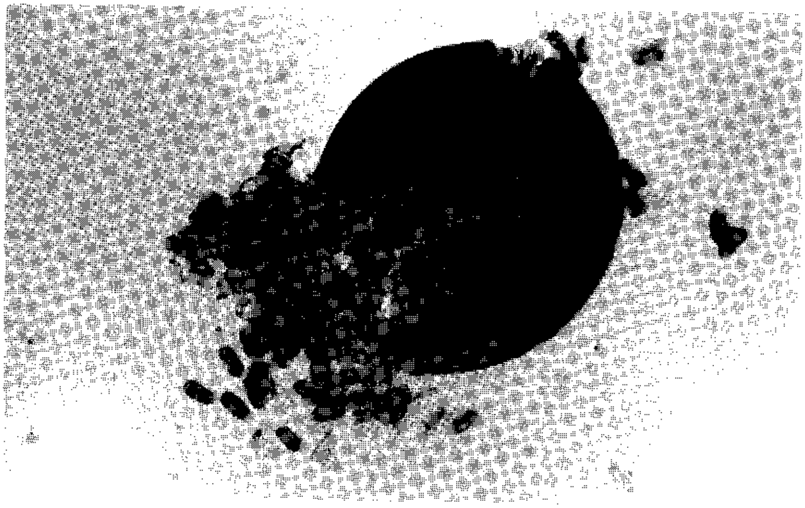


Photo 1.1. Four months old cyst of Globodera pallida with ruptured wall and extruded contents. The coiled up second stage juveniles are visible inside the transparent egg shells; egg size: 103 x 47 μ.

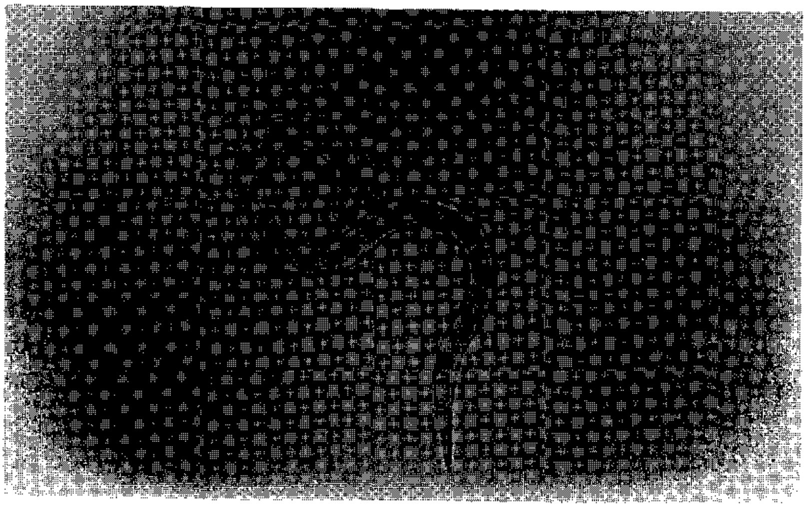


Photo 1.2. The second stage juvenile of *Globodera pallida* is a slender, slowly moving nematode; length 463 - 509 μ, width 19 μ (Stone, 1973).

The J_2s (Photo 1.2) emerge from the eggs, using their stylet to cut a slit in the shell. They leave the cyst through the natural openings of the vulva and head end, and migrate to host roots. They usually congregate at and penetrate just behind the root tip, the area of root cell elongation and differentiation. Penetration can also occur at sites where lateral roots emerge (Steinbach, 1968; Widdowson *et al.*, 1958; Williams, 1978). They invade the roots, passing from cell to cell by cutting through the cell walls with their stylets. They migrate through the cortex to the region of cell differentiation and to the periphery of the vascular tissue, causing extensive damage by rupturing and destroying cells on the way. Reaching the pericycle, the juveniles settle and start to feed by piercing adjacent cells close to the stele (Steinbach, 1968). The injection of saliva induces the formation of an extensive feeding structure. Adjacent cell walls become partly dissolved and a large multi-nucleate syncytium with dense granular cytoplasm develops. Wall ingrowths increase the surface area of the syncytium in the region where nutrients pass from the stele into the feeding structure (Steinbach, 1968; Huijsman *et al.*, 1969; Endo, 1971; Hoopes *et al.*, 1978; Stone, 1979; Jones, 1981; Hussey, 1985). The nematode feeds on the gradually expanding syncytium which has the characteristics of a transfer cell (Jones and Northcote, 1972). These feeding structures enable the sessile stages of the nematode to develop and to mature. Depending on the temperature, the second juvenile stage is completed about seven days after invasion.

During the third stage, which is completed in about ten to eleven days after invasion, the juveniles differentiate into females with paired ovaries, and males with a single testis (Franklin, 1951).

The fourth-stage female juvenile is flask-shaped and about 0.4 mm long. The body cavity becomes almost completely filled with the developing ovaries. During the fourth moult, the reproductive system opens to the exterior via the formation of the vulva. The young mature females stay sessile, the swollen body, about 0.5-0.8 mm across, protruding through the epidermis.

The males elongate within the cuticles of the third and fourth juvenile stages and emerge, as filiform adult males, about 20 days after juvenile entry, and migrate to the root surface. Attracted by exudates (sex-pheromones) they move towards young mature females (Green and Greet, 1972), with which they mate. Many males may surround each female and multiple mating occurs. (Green *et al.*, 1970). Males are short lived, only remaining active for nine to ten days (Evans, 1970).

Ovaries of fertilized females increase rapidly in size, ultimately filling almost the whole of the swollen body. About four weeks after fertilization, the cyst is full of embryonated eggs (Franklin, 1951; Williams, 1978).

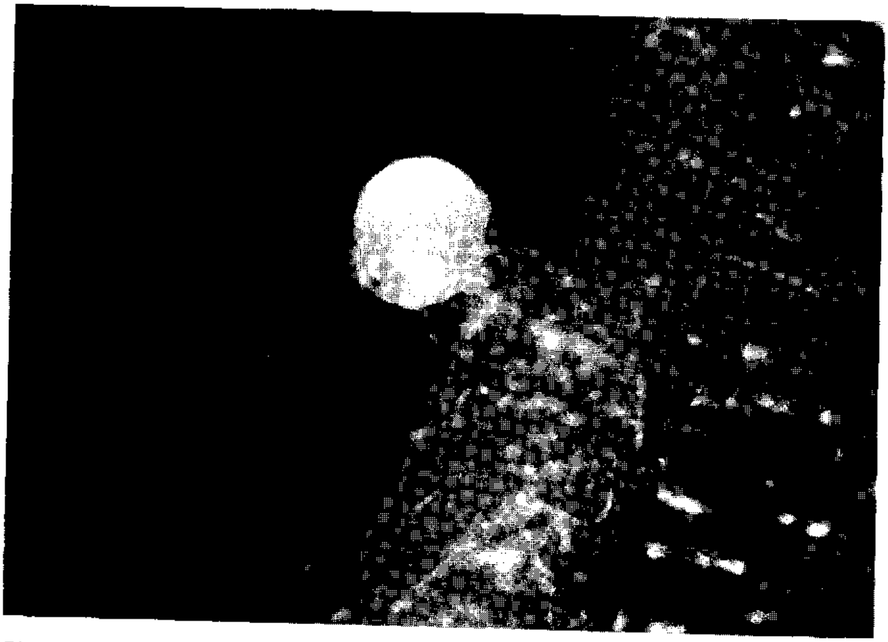


Photo 1.3. Young mature female of *Globodera pallida* protruding through cortex and epidermis of a potato root.

Photo 1.4. Symptoms of patchy infestations with potato cyst nematodes, locally causing total crop failure.

In infested fields, mature females may be found on potato roots (Photo 1.3) within six to seven weeks after crop emergence, and fully developed eggs in cysts a month later (Miles, 1930; O'Brien and Prentice, 1930). Males can also be found six to seven weeks after crop emergence (O'Brien and Prentice, 1930). At death, the female body wall tans and hardens to form a tough brown cyst, enclosing the eggs (Photo 1.1).

Symptoms

Above-ground symptoms of potato plants to nematode attack are not specific to potato cyst nematodes. Growth delay at the beginning of the season, poor plant growth, reduction of leaf expansion, reduced ground cover, retarded flowering and premature haulm senescence are not characteristic of a nematode attack.
The most obvious reactions of the potato plant to invasion of the roots by potato cyst nematodes (PCN) are abnormal branching and stunting of the root system (Oostenbrink, 1950; Evans, 1982; Evans *et al.*, 1977). All these effects lead to a considerably reduced ground cover duration (Haydock, 1989; Haverkort *et al.*, 1992; Schans, 1993). Plant development is delayed and the formation of tubers and flowering of infected plants is later than that of uninfected plants. In a potato field, a group of late flowering plants often marks a heavily infested patch. When fields are uniformly infested, these symptoms are not so obvious when compared with more recent patchy infestations (Photo 1.4).
The nematodes' effect on plant growth varies with years, even when nematode densities are comparable. When drought occurs early in the season, cell elongation and thus stem growth and leaf expansion seem to be much more affected by nematode infestation than under humid conditions. Whereas senescence is accelerated by dry spells later in the season. Such plant reactions to potato cyst nematode attack are neither specific for potato, nor for the potato cyst nematode (Oostenbrink, 1950). Similar effects have been observed in several crops attacked by other nematode species, e.g. potatoes attacked by *Pratylenchus penetrans* (Olthof, 1986), *Trichodorus* spp. and *Paratrichodorus* spp. (Kuiper, 1977). Similar effects on growth and development have been recorded on wheat attacked by *Heterodera avenae* (Wilson *et al.*, 1983) and oats attacked by *H. avenae* (Kort, 1972).
Detailed studies on the response of potato cultivars to potato cyst nematode infection revealed large differences in yield, as well as in histological response of the root tissue to invasion by second stage juveniles of PCN (Huijsman *et al.*, 1969).

Tolerance and resistance

History of resistance and tolerance research. When Ellenby (1948, 1952, 1954) found resistance to potato cyst nematodes in *Solanum tuberosum* subsp. *andigena* Salaman & Hawkes, 1949 and *S. vernei* Bitt et Wittm., 1914, it appeared that the resistant plants provided inadequate feeding sites for the females. Females did not develop, or did so in very small numbers (Toxopeus and Huijsman, 1952, 1953). Many nematodes died, or only males appeared. First reports on the existence of biological races or pathotypes of PCN which were able to multiply in roots of the resistant clones and cultivars derived from *S. tuberosum* subsp. *andigena* were published, starting in 1956 in the Netherlands, the United Kingdom and Germany (Toxopeus, 1956; Jones, 1957; Van der Laan and Huijsman, 1957; Huijsman, 1958; Goffart, 1960; Toxopeus and Huijsman, 1960; Kort, 1962, 1963). In the Netherlands, breeding for resistance has been given a high priority. Resistant cultivars, introduced in the Netherlands since 1962, have proved able to effectively control potato cyst nematode populations (Huijsman, 1956; 1958; 1961; 1963; Cole and Howard, 1959; 1962), especially when included in integrated control systems (Nollen and Mulder, 1969; Hyink, 1972; Mulder and Veninga, 1988a).
In the late sixties and early seventies, it became apparent that the genetically diverse population of the nematode yielded races able to overcome the resistance derived from *S. tuberosum* subsp. *andigena*, CPC 1673 (Huijsman, 1970; 1972; Huijsman and Lamberts, 1972; Nollen and Mulder, 1969; Mulder and Veninga, 1988a). Extensive studies of a number of *Solanum* species followed in a search for additional sources of resistance (Huijsman, 1972, 1974; Scurrah and Van der Wal, 1978). The type of hypersensitive resistance was used to keep the level of PCN far below damage levels. However, where this resistance failed because of new pathotypes, PCN populations built up and damage occurred.
Results of field trials, as well as data collected by growers, showed that the newly developed Pa-2 resistant *ex Solanum verneï* cultivars (cvs Activa and Darwina) were marked by high yield losses when exposed to moderate to high density levels of non-compatible nematode populations (see also Chapters IV and VI). It became clear that in the old *Solanum andigena* (CPC 1673) derived cultivars, the hypersensitivity resistance went along with some level of tolerance, which was almost completely absent in the *ex S. verneï*, $(VT^n)^2$ 62-33-3, derived cultivars. Therefore, if potatoes are to be grown in infested fields, some level of tolerance seems to be a prerequisite, for resistant cultivars also. A policy of combining resistance and tolerance (*ex Solanum tuberosum andigena* and *S. phureja*) in an early stage of a breeding programme was outlined for potato growing in the Andes (Van der Wal, 1978), where local cultivars

must be able to withstand obviously unavoidable high nematode densities.
In the late sixties policies to control potato cyst nematodes in the starch potato growing area were no longer exclusively aimed at eradication, as was the intention in the fifties (Kort, 1970). Instead, procedures were developed to keep the nematode populations at very low levels, once infestations were detected. As tolerant cultivars did apparently not comply with the policy aimed at keeping nematode levels low, the development of tolerant cultivars was initially disencouraged. However, since some tolerance appeared to be necessary, interest in tolerance to PCN revived in the eighties, and a research programme to combine resistance and tolerance was implemented (this Thesis).

The main tools to control potato cyst nematodes in the past 30 years were rotation with non host crops, chemical control and the use of resistant cultivars. Brought together in an integrated control scheme in the sixties, this combination proved very effective. But from 1979 onwards, evidence accumulated that the resistance sources used so far, based mainly on the H_1-gene derived from *S. tuberosum* subsp. *andigena* (CPC 1673), were becoming less effective against an increasing number of PCN populations (Mulder and Veninga, 1988a), many of them now dominated by *G. pallida*. The breeding was started of cultivars with new and complex resistance to both PCN species, using *S. verneï* and *S. andigena* as progenitors for resistance and tolerance. Research was carried out on the rate of change in potato cyst nematode populations induced by the use of resistance (Van der Wal, 1987; Spitters and Ward, 1988). It was shown by pot experiments, that many populations could overcome resistance in 3 to 5 generations (Nollen and Mulder, 1969). Similar results were obtained through field data, collected from 1968 to 1984 (Mulder and Veninga, 1988a). This phenomenon of selection of "new" pathotypes by growing resistant cultivars makes the search and breeding for resistance a continuing process.

Mechanisms of tolerance. The negligible mobility of juveniles, the limited length of the life cycle and only one generation per year, make preplanting density the determining factor for the level of damage (Oostenbrink, 1966). In fact, the number of juveniles actually invading the root system is relevant for damage. However, this information is difficult to obtain and in most experiments the initial density is defined as numbers of viable eggs and juveniles per unit soil.

Huijsman *et al.* (1969) screened 118 potato clones for tolerance to *G. rostochiensis* in a field trial and found that the cultivar Multa out-yielded all others. Examination of root anatomy showed a difference in the degree of necrosis between more and less tolerant cultivars. Tolerant cultivars showed little necrosis and vigorously growing callus around the syncytia, thus compressing the feeding sites, leading especially to starvation of the female nematodes. Besides Arntzen (1993) stated that tolerant cultivars, which showed partial resistance to pathotype Pa-2, were found to be characterized by reduced necrosis after invasion, which seems to be associated with limited disturbance of root growth. Pronounced necrosis around invading juveniles may be the main reason for the extreme intolerance of some *ex S. verneï* cultivars (Evans and Haydock, 1990).

Cultivars differ in root growth reaction following nematode invasion, as well as in the resumption of growth by the formation of new roots (Van der Wal, 1981b), which, since most juveniles hatch earlier, hardly become infested. Matos and Franco (1981, cited by Evans and Haydock, 1990) explained the tolerance of the cultivars Huaytapallana and Revolucion by the ability of these cultivars to develop and maintain an abundant root system in heavily infested soil. The author's experience with potato production on heavily infested soils in the Andes is that local cultivars produce very extensive root systems, able to carry high numbers of PCN cysts without apparent damage (Dees and Mulder, unpublished data). Most European, high yielding cultivars are characterized by a restricted root system. In the case of nematode attack, there is little or no compensation, which consequently leads to poor foliar development and also tends to lead to premature senescence of the crop. This further decreases leaf area duration and yield (Trudgill and Cotes, 1983b, Fasan and Haverkort, 1991; Haverkort *et al.*, 1991a; 1992). Based on experimental evidence the relationship between nematode attack, initial root growth and yield is elucidated in Chapter IV.

Damage initially induced by nematodes, can be enhanced by soil-borne pathogenic fungi and bacteria, as well as by abiotic stress factors such as drought. A number of cases have been well documented in which interactions have been found between various organisms in conjunction with nematodes at the expense of plant growth and yield (Evans, 1987; Jatala and Turkensteen, 1977; Rowe *et al.*, 1985; Scholte and 's Jacob, 1989; Storey and Evans, 1987). Experiments to investigate the relationship between drought and nematode attack are dealt with in Chapters V and VI.
When drought occurs in the Netherlands, it is seldom within eight weeks after planting, whereas PCN attack occurs shortly after planting. Both events rarely coincide and therefore effects of drought and effects of potato cyst nematode are not likely to show interaction. Consequently, when drought occurs, in most cases its effects are additional to those of the nematodes.

Tolerance versus resistance. Caldwell *et al.* (1958) defined tolerance to disease as the quality that enables a susceptible plant to endure severe attack by a pathogen without suffering severe yield loss . Wallace (1987) reviewed tolerance, not only in nematology, but in plant pathology in general. He concluded that tolerance must be perceived as a function of the physiology of the whole plant interacting with its environment. Schäfer (1971) defined tolerance as the capacity of a cultivar that leads to less yield or quality loss relative to disease severity compared with other cultivars. In the present study, tolerance of a cultivar is defined as the capacity to regenerate after nematode attack and resume growth, which ultimately results in less yield (or quality) loss, relative to nematode density compared with a number of other cultivars. Environmental conditions, such as soil structure and texture, water retention of the soil and soil pH, may contribute to the expression of tolerance of various genotypes, since interactions between genotype and environment cannot be excluded.

Absolute yield (tons of dry matter per ha) is most important to starch potato growers. It depends on the yielding capacity of the cultivar, and its tolerance, relative to infection. As tolerance may strongly differ between cultivars, lower yielding cultivars with a high tolerance may exceed that of high yielding cultivars with a lower tolerance on heavily infested soil. Therefore, these two factors mainly determine the cultivar choice of the farmer.

Both resistant and susceptible potato plants are invaded by juveniles. Resistant plants slow down population increase and in many cases reduce the nematode population. Dalmasso *et al.* (1992) summarized several defence mechanisms of plants: physical barriers to nematode penetration by thickened root tissues, biochemical defences by root excretion of toxins and hypersensitivity. Resistance to PCN in potatoes is based on hypersensitivity.

However, the resistance incorporated so far in tetraploid cultivars is mainly the ability of the plant to block, in a hypersensitive way, the development of females. This results in localized necrosis and restricted (female) nematode development at the infection site (Kaplan and Keen, 1980), either in the number of females and/or in egg content per female. Plant growth or yield are not considered when resistance is measured. Resistance refers to the multiplication of PCN populations on a host crop and is expressed by the multiplication factor P_f / P_i, in which P_f is the population density after harvest, and P_i is the population density just before planting.

Although the distinction of the terms "tolerance" and "resistance" seems clear, it may need some reconsideration. Root growth of some genotypes ceases almost immediately after massive invasion by juveniles, and many roots die rapidly, giving the juveniles no chance to develop into females. Such genotypes are considered "resistant" with respect to PCN multiplication, but at the same time "intolerant" because of yield loss. However, when grown at low nematode densities, these genotypes might prove good hosts and consequently, the multiplication rates might be high. Hence, these genotypes are considered "susceptible". Therefore, in screening for resistance, attention has to be paid to root development to ensure that no multiplication is found under conditions where "non-resistant" plants show a high rate of PCN multiplication. In extreme cases of intolerance, as was found for the cultivars Activa, Appassionato and Darwina, the level of resistance was difficult to determine in field and laboratory experiments conducted in 1983 - 1986 (Hendriks, 1988) and 1986 - 1990 (Boerma and Velema, 1991; Velema and Boerma, 1991).
Tolerant plants usually show a well developed root system with ample opportunity for the nematodes to develop. Therefore one might conclude that the higher the tolerance level, the higher the multiplication of the nematode. Therefore, resistance to PCN is needed to prevent build up of the PCN population levels to such an extent that tolerance also fails. With respect to multiplication of PCN, differences between cultivars have been found both in presence and in absence of the hypersensitivity reaction (Huijsman, 1974; Kort, 1970; Dale and Phillips, 1985). How important these differences are between such cultivars can be evaluated in terms of their contribution to the build up of the nematode population in the field. Apart from extreme situations, it is justifiable to consider tolerance independently of resistance. This applies also to methods of assessing both characteristics in breeding programmes and in farming practice. This view is confirmed by the findings of Arntzen (1993).

At present, there is pressure from society to diminish the use of pesticides (Anonymous, 1991c). Reduction in the use of chemical control agents will allow the populations of a range of nematode species to build up to damaging levels. Strategies have to be developed to meet this "new" situation. Most questions raised today, have already been brought up in the fifties and sixties, but to date, not all have been answered. There is no doubt that resistance and tolerance form an important part of the answer.

Chapter II

Comparison of regression curves used to describe the relationship between potato yield and potato cyst nematode density

Introduction

In this chapter an attempt is made to make the equations, developed to describe the relation between PCN density and tuber yield, more accessible to researchers, layman and interested farmers. Preplanting density of potato cyst nematodes determines the amount of damage suffered by a potato crop (Oostenbrink, 1966; Photo 3.1). Four equations describing the relation between potato tuber yield and initial PCN density are found in the literature (Brown, 1969; Oostenbrink,1966; Seinhorst, 1965; Elston *et al.*, 1991). The aim of this chapter is to show the differences in the way they respond to the same data. This Chapter in fact is an introduction to Chapter III, where these equations will be evaluated, using field data.

The most simple equation describes a linear regression curve,

Brown (1969): $$E(Y) = a + b \cdot P_i \quad (1)$$

where E(Y) is the expected yield, P_i is the nematode density before planting (numbers of encysted eggs and juveniles per unit soil, g or ml), "a" presents the yield at density zero $\{E(Y)=a\}$ and "b" the rate of decrease in yield per unit increase of nematode density $\{b=\Delta E(Y) \cdot \Delta P_i^{-1}\}$ respectively.

In this equation yield reduction by additional numbers of nematodes is independent of PCN density, each additional nematode per g soil induces the same yield reduction, regardless as to whether there are 10 or 100 nematodes per g soil. Brown (1969) demonstrated, using a range of field data, that in many cases regression can be represented equally well by the equations $Y = a + b \cdot P_i$ and $Y = a + b \cdot (\log P_i)$. Based on his data, in which large experimental variations existed in yield and in P_i data, the correlation coefficients appeared relatively low. In fact, too low to decide for one of the two equations and since there was not much difference between both resulting curves, he proposed the most simple one.

A log linear regression curve was introduced by Oostenbrink (1966) to describe nematode damage relationships with the equation:

Oostenbrink (1966): $$E(Y) = a + b \cdot (\log P_i) \qquad (2)$$

where E(Y) is the expected yield, log P_i is the logarithm of the nematode density before planting, and a and b are constants obtained from experimental data by regression (a = yield at density zero; b = rate of yield reduction). In this equation the damaging effect per nematode is larger at lower densities than at higher ones, since from 1 to 10 nematodes damage increases in the same way as from 10 to 100 nematodes. This relation appeared valid in the range of densities frequently occurring in the field. Oostenbrink stated that the relationship might deviate at very low and at very high nematode population densities. Considering extreme low and high densities, the curve concerned is a sigmoid one. Oostenbrink argued that the effect of such low densities are rarely seen in naturally infested fields, especially, since such low densities are not normally detected. Very high densities, at least under Dutch growing conditions, are also rare, since they will be avoided by farmers in practice. Hence, the log-linear regression (2) adequately describes the yield/PCN density relationship in the field for most purposes.

Tammes (1961) suggested that the relationship between disease incidence and yield loss can be divided into three stages. In the first stage, the injurious factor (here nematodes) has hardly any influence on the yield because of "compensation". The second stage shows a yield loss correlated with increase of the injurious factor. In the third stage, the effect of the injurious factor may be the level of maximum possible injury (which may be zero yield), or the self limiting effect of the injurious factor (competition for invasion and feeding sites), or both.

Seinhorst (1965) introduced the concept of a nematode threshold density below which no yield loss exists and named it the tolerance limit (T), and also defined the minimum yield (m), a value below which yield will not further decrease with increasing nematode density.
Based on this concept he developed the equation $y = m + (1-m)\, z^{Pi-T}$ (Seinhorst, 1982), which can be formulated as:

Seinhorst (1965, 1982):

$$E(Y) = Y_{max} \qquad \text{if } P_i \leq T$$
$$E(Y) = Y_{max} \cdot \{m + (1\text{-}m) \cdot z^{P_i\text{-}T}\} \qquad \text{if } P_i > T \qquad (3)$$

Where Y_{max} is the yield at densities lower than T, the tolerance limit, m is the minimum yield, and z is a variable. These four parameters have to be determined from experimental data. This model has two equations, one for densities equal or smaller than T and one for densities greater than T. The first part of the curve is density independent, the second equation has a density independent component (m), and a density dependent part. For densities greater than T, the exponential relation results in a gradually diminishing effect per nematode with increasing densities. The maximum yield reduction per additional juvenile occurs at an initial PCN density (P_i) of T+1. When z=0.95 this amounts to 5% of 1-m, the density dependent yield range. With P_i = T+2 the density dependent fraction of yield is 0.95 · 0.95 of 1-m (a reduction of 9.75% of 1-m). When P_i = 100, the additional reduction by increasing nematode densities comes close to zero, hence the value of m is being approached. The rate of yield reduction depends on the value of z, which is field and year dependent and can also be considered as a cultivar parameter for tolerance. Hence, the value of parameter z is the resultant of season, field and cultivar characteristics, which cannot be disentangled in this equation. For z = 0.99 the rate of yield reduction is much slower than with z = 0.95.
Seinhorst's equation expresses that plants might be suffering more or less by nematode attack due to variation in the parameters T, z and m. However, Seinhorst (1986) later concluded that most differences in tolerance to nematode attack between crops are due entirely to variation of m.

Elston *et al.* (1991) introduced an inverse linear regression curve to describe the relation between yield and preplanting initial nematode density, formulated as:

Elston *et al.* (1991)

$$E(Y) = Y_{max} \cdot \{1\text{-}(1\text{-}m) \cdot P_i / (c + P_i)\} \qquad (4)$$

Tolerance, $\{1\text{-}(1\text{-}m) \cdot P_i / (c + P_i)\}$, is expressed here with three parameters: Y_{max}, the expected yield at density zero; "c", a constant determining yield decrease with increasing PCN density, and "m" the minimum yield as fraction of the yield without PCN infestation, as in equation 3, (Elston *et al.*, 1991).
The attractive feature of the inverse linear regression is that it only needs three parameters, of which two, c and m, determine tolerance. When m=0, equation 4 may be written as:

$$E(Y) = Y_{max} / \{1+(P_i / c)\} \tag{4a}$$

leaving c as the sole parameter to be assessed, the yield decrease per unit increase of the nematode density P_i.

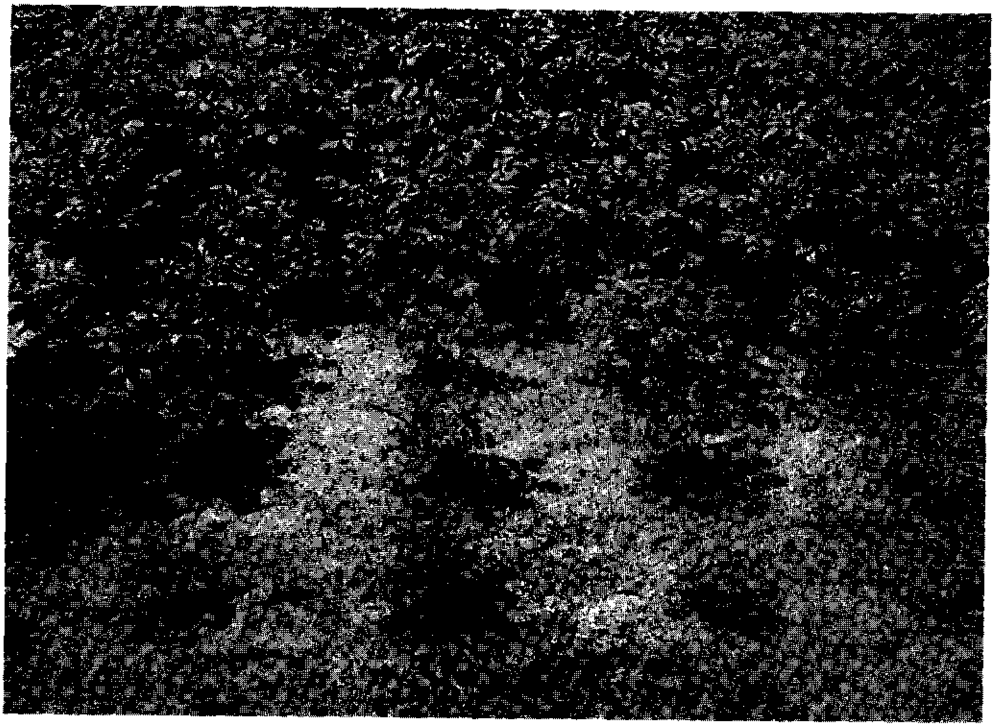


Photo 2.1. Gradient of growth of potato plants in a nematode infested patch.

Method

To demonstrate similarities and differences of the four equations, the corresponding curves were calculated for nematode densities from 0 to 260 eggs per g soil. The highest yield (Y_{max} = yield at nematode density zero) was set at 50 tons per ha, and the minimum yield (m) was set at 15 tons per ha, which was to be obtained in any case at an initial PCN density of 260 eggs per g soil. The four equations were plotted on a linear and a log nematode density scale. To cope with densities smaller than 1, the log transformation of the densities was computed after adding 1 to the density values.

Results

These assumptions yield the following equations.

1. Brown: $E(Y) = 50 - 0.1346 \cdot P_i$

2. Oostenbrink: $E(Y) = 50 - 14.482 \cdot \log P_i$

3. Seinhorst: $E(Y) = 50 \cdot \{0.3 + (1-0.3) \cdot 0.965^{P_i}\}$ T=0 and m=0.3

4. Elston: $E(Y) = 50 \cdot \{1 - P_i / (111.45 + P_i)\}$ m=0

The value of T of Seinhorst's equation was set to zero to make a better comparison with the other three equations, in that all three include a nematode effect starting at the lowest nematode density (here 0). The introduction of values in the order of two to five nematodes per g soil in the Seinhorst approach would shift the Seinhorst curve slightly to the right, at least at the lower densities.
In Equation (4), the value of m was set to 0, since any non-zero value of m caused the equation to fit with the given yield of 15 tons per ha at density 260 nematodes per g soil, only when c = 0. It follows from equation (4) that only in that situation is *m* reached, all other values increase the yield at higher densities. The simplified equation has therefore only one parameter c to be estimated, which appeared to be 111.45, given the yield of 15 tons per ha at P_i of 260 nematodes per g soil.

Plotted on a linear scale equation (1) yields a straight line (Fig. 1A). The log linear equation (2) leads to a strong yield decrease at low nematode densities, and a reduced yield decrease at high densities.

Equation (3) in figure 1 describes yield reduction to be somewhat less strong at low densities, but it reaches the minimum yield much sooner than equations (1) and (2). It is insensitive to density increase above circa 100 eggs per gram, which is inherent in the way that Pi is taken as a power function in Seinhorst's equation.

Equation (4) shows the smallest deviation from the linear relationship between yield and initial nematode density, and a more gradual yield decrease with increasing density, when compared to equations (2) and (3).

When the data are plotted on a logarithmic scale (Fig. 1B), equation (2) shows a straight line, and the linear model (1) shows hardly any yield decreasing effect of nematodes at lower densities, up to 15 eggs per g soil. Then a rapid yield reduction is plotted at the higher densities. It should be stressed here that this optical impression

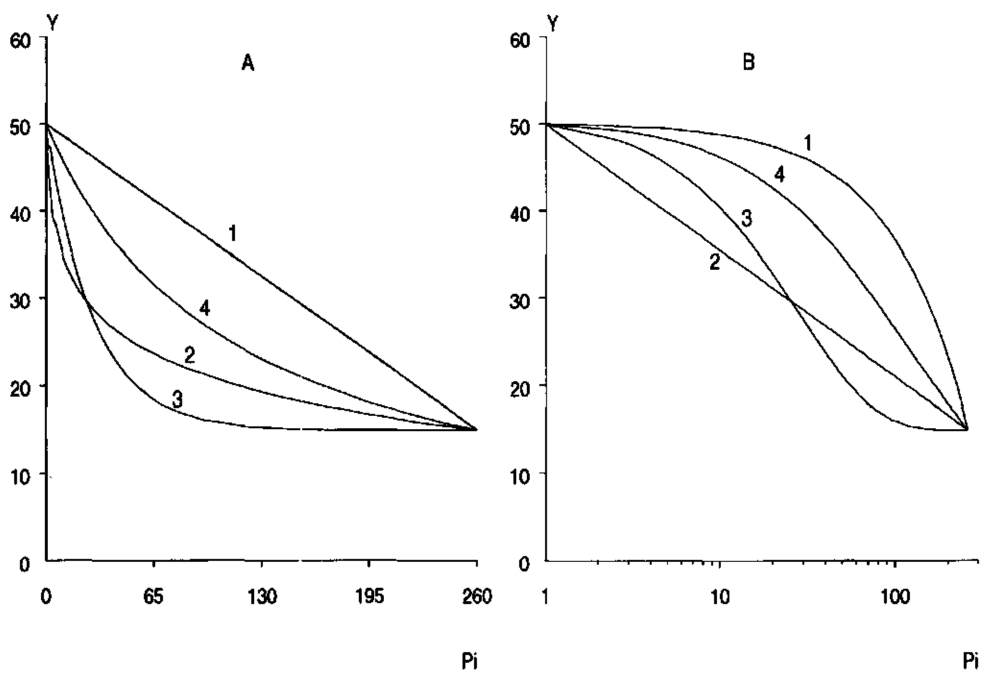


Fig. 1 Yield (Y) versus densities (P_i) as computed by the four equations of Brown (1), Oostenbrink (2), Seinhorst (3) and Elston *et al.* (4) respectively, in the range of 0 to 260 eggs per g soil, Y_{max} set at 50 tons per ha, the lowest yield at 15 tons per ha at 260 eggs per g soil, and plotted on a linear density scale (A) and on a log density scale (B).

is just a matter of scale, since the data in Fig. 1A and 1B are exactly the same. Equation (4) also shows a reduced rate of yield reduction at the lower densities followed by an increased reduction at the higher ones. Equation (3) shows, as compared to the log linear equation (2) a slower reduction increase at the lower densities, followed by a faster reduction increase than in any of the other equations, leading to a flat part in the curve at the higher densities, above about ninety eggs per g soil.

By changing the scale from linear to log linear, the yield/nematode density curves look different. No conclusions on the biological significance of any of these curves can be drawn, since what is shown are just the effects of the equations themselves, and not of the data. The differences in yield values created by the various equations are shown in Fig. 2A and 2B, again on a linear and log linear scale respectively. Fig. 2A shows

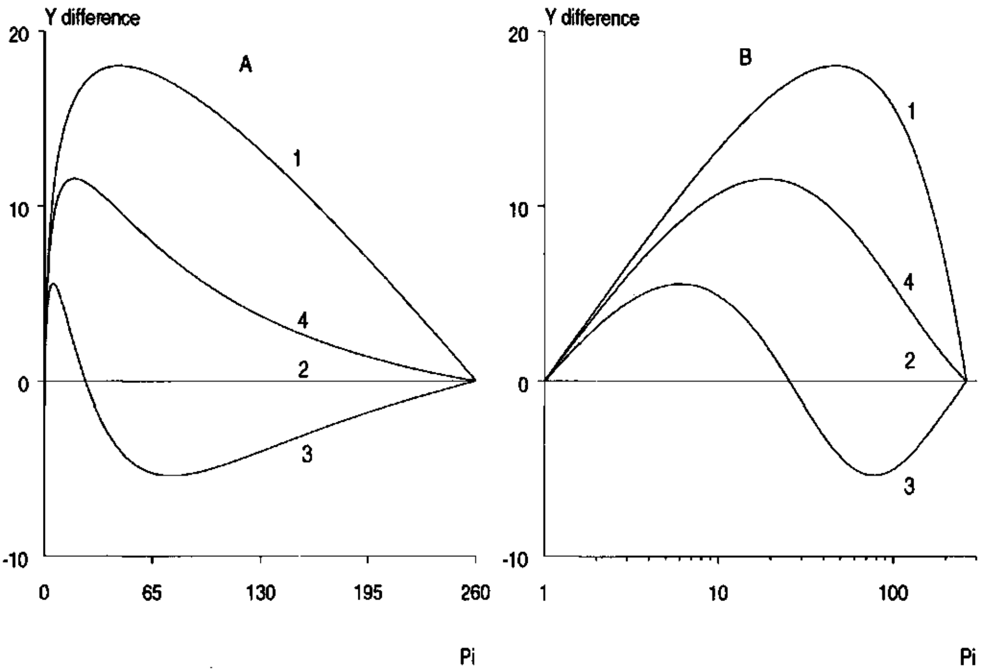


Fig. 2 The computed differences in yield (Y difference) between the equations versus densities (P_i) are plotted on both linear (A) and log linear (B) scales as in Fig. 1. The yield values computed with the log linear equation (2) were subtracted from the values computed by the linear equation (1), the Seinhorst equation (3) and the Elston *et al.* equation (4).

a rapid deviation from the 0 line (the log linear equation (2)) for all three equations. The largest deviation reached for the linear equation (about 18 tons per ha at $P_i = 65$), followed by the Elston *et al.* equation (4) with about 11 tons per ha at $P_i = 40$. Then the differences of both decrease gradually, but the curves are shaped differently. At low densities, the Seinhorst equation (3) shows a similar pattern to that of Brown's and Elston's models. Then, the difference from Oostenbrink's equation reduces rapidly and sinks below 0 at 25 eggs per g soil, to raise again at nematode densities higher than 75 eggs per g soil. When plotted on a log scale (Fig. 2B) the shapes of the curves change, but the responses are similar.

Discussion

The equations mentioned reflect regression curves, relating nematode densities to yields. How well an equation describes the relationship between nematode densities and yield is a statistical problem, opting for that equation with the smallest deviation of the experimental data from the line generated by the equation. More than one equation may fit the same data properly.

The basic question already put forward by Wallace (1973), is whether sigmoid curves for the relation yield/PCN density really exist. After all, there has to be a minimum yield for high PCN levels, which, in the most severe cases, is zero. At low initial nematode densities, a horizontal part in the yield/nematode density curve can easily be created by plotting (relative) yield against the log of the PCN densities. However, when yield is plotted against untransformed initial nematode densities on a linear scale, no sign of a "horizontal" part in the curve at the lower densities is found. It is therefore invalid to assess a tolerance level 'by eye', from graphs where log numbers of nematodes are plotted against yield (Wallace, 1973). In addition, very low levels of disease incidence often result in a slight increase in yield (Oostenbrink, 1966). This phenomenon was also found for plant/nematode interactions at very low nematode densities, e.g. the potato/PCN relation (Wallace, 1973).

None of the reviewed equations is valid to explain or forecast yield damage caused by PCN, which is clearly demonstrated in Figs 1 and 2 of Chapter III. The damaging effect of PCN is not only determined by PCN density, but also by such factors as cultivar, crop husbandry and environmental conditions such as soil type and season. This view was expressed by Wallace (1973) and is repeatedly found in discussions of other authors (Trudgill, 1986 ; Evans and Haydock, 1990; Elston *et al.*, 1991) and was experimentally and theoretically further investigated by Fasan and Haverkort (1991), Haverkort *et al.* (1990a, 1991a, 1992), Schans (1991) and Schans and Arntzen (1991).

Chapter III

Variation of potato yield and potato cyst nematode relationships between seasons

Introduction

In farming practice, and also in experimental fields, the damaging effect of PCN on potato crops was found to differ greatly between cultivars (Huijsman *et al.*, 1969; den Ouden, 1973), sites and seasons (Nollen and Mulder, 1969). To gain more insight into this phenomenon, twenty one cultivars were grown on infested fields over three years, viz. 1976, 1978 and 1979. The responses of the individual cultivars to PCN infection are dealt with in Chapter IV, together with results of greenhouse trials.
The aim of the research described in this chapter was to investigate the effects of different years on the relationship between tuber yield and the initial population density (P_i), and to examine the way several equations describing these relationship (Brown, 1969; Oostenbrink, 1966; Seinhorst 1965, 1982; Elston *et al.*, 1991), fit the collected data.

Materials and methods

Field experiments were conducted to study the effect of various PCN densities on the yield of 21 cultivars in the three years; in 1976 to evaluate the experimental design and in 1978 and 1979 to obtain more data. The 21 cultivars of starch potatoes were chosen from different maturity classes, maturity values ranging from 3 (very late) to 7.5 (early). All classes of the then available cultivars resistant to *Globodera rostochiensis* and *G. pallida* were present in the series (Table 1).
The fields used were moderately to heavily infested with *G. rostochiensis* (Ro3) in 1976 or *G. pallida* (Pa-2) in 1978 and 1979. The sandy soils were (moderately) drought sensitive (water retention estimated at about 30 mm), and no irrigation was applied. The acidity of the topsoils varied from $4.8 < pH_{KCl} < 5.1$.

Photo 3.1. Overview of the field experiment in 1978.

The experiments were laid out in a randomized block design with four replicates. Within each replicate the twenty one cultivars were present in quadruple, each plot consisted of two plants. The blocks were arranged in such a way that the 16 two-plant plots per cultivar were exposed to different density classes of the PCN populations. Fertilizer rates were determined by soil analysis, and applied as recommended locally for growing starch potatoes. The various cultivars were widely spaced to avoid mutual interference. Each plot had a gross size of 150 · 165 cm and a nett size of 75 · 66 cm. Two tubers of each cultivar were planted 33 cm apart in the same ridge. The distance between ridges was 75 cm and between two cultivars in the ridge 99 cm. As only every other ridge was planted, the distance between two planted ridges was 150 cm. The initial PCN population density just before planting (P_i) was determined by taking 15 cores, 16 · 25 cm apart, of circa 15 ml soil per core, brought together in a bulk sample of 225 ml soil per plot. The 'low' PCN density plots were achieved by applying metham sodium (300 l per ha twice within a fortnight) to one quart of each block. The fumigations were carried out in spring to avoid nitrogen effects (Kolenbrander, 1969a, b, c).

Table 1. List of 21 cultivars in alphabetical order, their maturity values and resistance to potato cyst nematode (Anonymous, 1977; Joosten and Van der Woude, 1985).

Cultivar	Maturity value	Resistance factors to PCN	Cultivar	Maturity value	Resistance factors to PCN
Amigo	4	Ro 1,4	Mentor	5	none
Arjan	5	Ro 1,4	Pansta	5^5	Ro 1,2/3,4 Pa-2
Astarte	3	Ro 1,2/3	Prevalent	4	Ro 1,4
Aurora	7	Ro 1,4	Procura	3^5	Ro 1,4
Eba	4^5	none	Prominent	4^5	Ro 1,4
Ehud	7^5	Ro 1,4	Provita	7^5	Ro 1,4
Element	6	Ro 1,4	Rector	5	Ro 1,4
Elkana	4^5	Ro 1,2/3,4	Satelliet	5	Ro 1,2/3,4, Pa-2
Krostar	7	Ro 1,2/3	Saturna	5^5	Ro 1,4
Mara	3^5	Ro 1,2/3	Ultimus	6^5	none
Marijke	5	Ro 1,4			

Cysts were extracted by using the modified Fenwick apparatus (Oostenbrink, 1960). The viable cyst content was estimated by staining eggs and juveniles with New Blue R (Shepherd, 1962). The number of living eggs and juveniles was determined in samples of at least 250 g dry soil, and P_i was expressed as the number of viable eggs and juveniles per gram of dried soil, as required by the Seinhorst equation.

Pre-sprouted tubers (35-45 mm) were planted at the end of April. After the haulm died, the tubers were harvested. Tuber yields, fresh weight and underwater weight were determined. The dry matter content and tuber dry matter yield were calculated from these data (Bernelot Moens, 1973).

Precipitation (mm per 10 day period) and the average air temperature in °C were obtained from the meteorological station of the Royal Netherlands Meteorological Institute at the airport Eelde in the North East of the Netherlands, at a distance of eighteen to twenty km from the field locations (Table 2).

Table 2. Summary of the precipitation and temperature in 1976, 1978 and 1979 at the weather station Eelde. Source: Royal Netherlands Meteorological Institute (KNMI) De Bilt (Anonymous, 1976; 1978; 1979).

month	10 day	precipitation (mm)				mean temperature (°C)			
	period	1976	1978	1979	N	1976	1978	1979	N
April	I	4	1	12		6.3	5.5	4.9	
	II	0	14	15		8.5	5.1	8.7	
	III	2	7	49		5.6	7.5	7.2	
	M	6	21	76	46	6.8	6.1	6.9	7.5
May	I	7	5	41		13.5	11.9	5.7	
	II	14	22	11		12.5	8.9	13.2	
	III	26	2	38		11.7	13.3	14.0	
	M	47	29	89	52	12.5	11.4	11.0	11.5
June	I	16	17	32		14.0	17.1	15.9	
	II	20	5	32		15.0	13.1	12.9	
	III	1	50	19		20.1	12.5	15.3	
	M	37	72	83	55	16.4	14.5	14.7	14.5
July	I	0	47	9		20.0	12.6	14.1	
	II	15	5	16		18.7	12.6	14.8	
	III	24	10	59		15.2	17.8	15.6	
	M	39	62	83	87	17.9	14.5	14.8	16.3
August	I	18	44	38		15.1	15.3	15.5	
	II	0	10	7		17.7	15.0	16.4	
	III	12	21	17		17.3	13.7	13.7	
	M	30	75	62	87	16.7	14.7	15.1	16.3
September	I	28	39	14		13.3	13.3	15.8	
	II	13	31	26		12.9	13.4	13.1	
	III	16	47	9		13.7	12.4	10.2	
	M	57	117	49	69	13.3	13.0	13.0	13.7
total/mean		216	376	442	396	13.9	12.4	12.6	13.3

I 1st - 10th day
II 11th - 20st day
III 21st - last day

M Total of the three 10 day periods
N Normal value (mean precipitation/temperature of 30 years (1931-1960).

In addition to the four equations introduced by Brown (1969), Oostenbrink (1966), Seinhorst (1965, 1982) and Elston *et al.* (1991), a quadratic and a log quadratic function were used to describe the yield / density relations.

Results

Emergence was not found to vary significantly between cultivars, but initial development and growth were clearly different and related to the initial nematode density. Tuber yield, expressed as dry matter in g per plant, of 21 cultivars, was plotted against nematode density (Fig. 1). The 336 P_i / yield-combinations per year were sorted and grouped into eight classes of nematode density, characterized by their mean values and are presented in Fig. 1. In Figures 1.A1 and 1.A2 the densities are given on a linear scale, in the figures 1.B1 and B2, a log scale is used. The extremely dry year, 1976 with its warm growing season (Table 2), is shown separately to compensate for scale differences in both yield and initial nematode density. The equations with their parameter values and their fits (R^2) are given in Table 3.

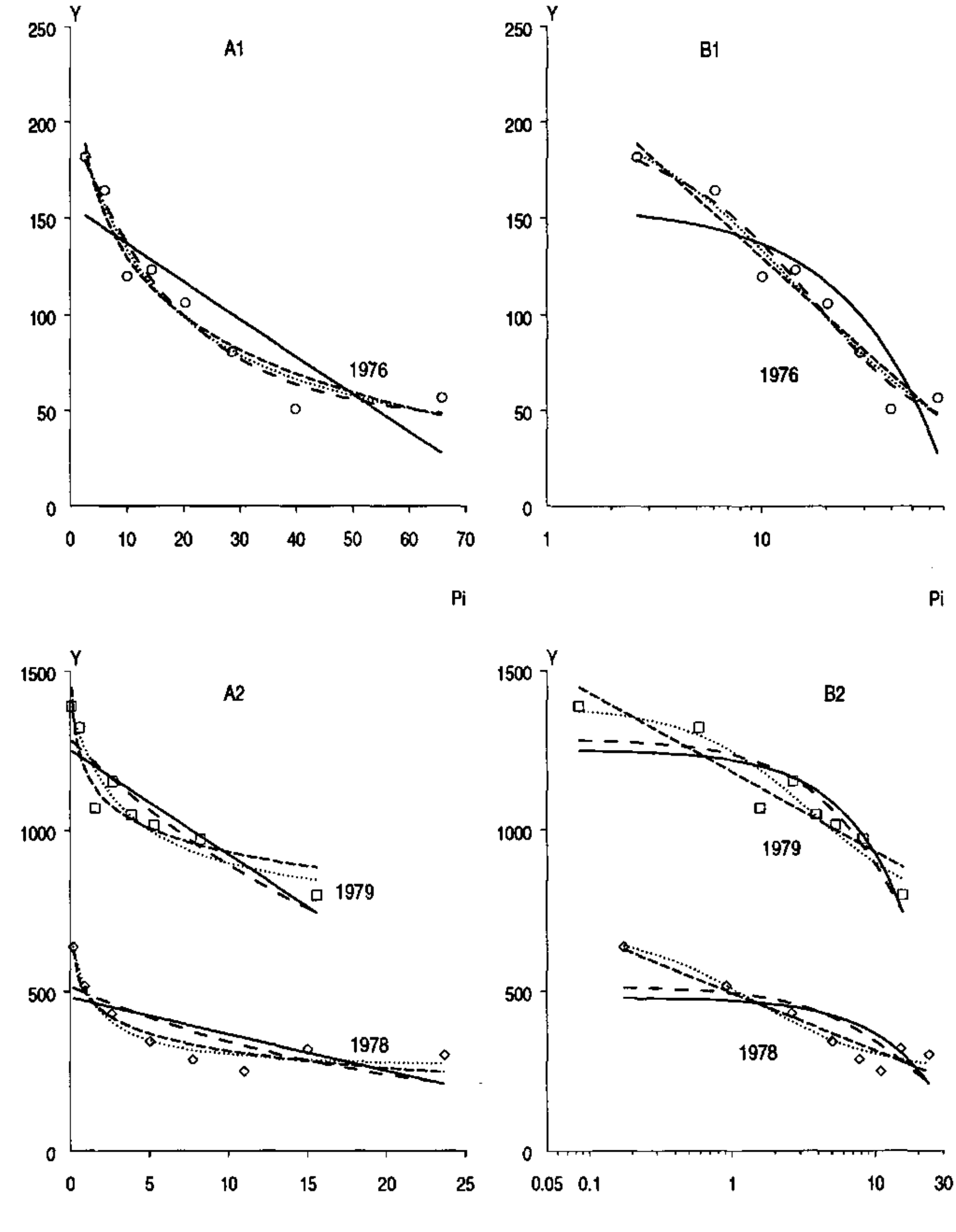


Fig. 1 Yield/density relations in three years based on data of the 21 cultivars. Y = Tuber yields, expressed as g dry matter per plant, P_i=initial nematode density as viable eggs per g soil. ——— = Brown – – – – = Seinhorst - - - - - = Oostenbrink ·········· = Elston *et al.*

Table 3. Equations, their parameter values and their fits, applied to describe the yield/density relations for 21 cultivars found in the experiments of 1976, 1978 and 1979.

model	Parameter	Parameter values 1976	1978	1979	mean [1]
Brown	a	157	482	1250	
$E(Y) = a + b \cdot P_i$	b	-2.0	-11.46	-32.6	
	R^2	0.72	0.39	0.73	0.61 a
Oostenbrink	a	231	494	1181	
$E(Y) = a + b \cdot \log P_i$	b	-100.9	-179.4	-248.8	
	R^2	0.93	0.90	0.87	0.90 c
Seinhorst	Y_{max}	203	516	1284	
$E(Y) = Y_{max} \cdot \{m + (1 - m) \cdot z^{P_i T}\}$	m	0.23	0.17	0.21	
	z	0.945	0.950[2]	0.952	
conditions: $z < 1$; $0.9 < z^T < 1.0$	T	0	0	0	
	R^2	0.93	0.35	0.69	0.66 ab
Elston *et al.*	Y_{max}	213	688	1388	
$E(Y) = Y_{max} \cdot \{1 - (1 - m)P_i / (c + P_i)\}$	m	0.04	0.36	0.52	
	c	15.75	1.44	3.67	
	R^2	0.94	0.93	0.88	0.92 c
quadratic	a	0.053	1.42	2.41	
$E(Y) = a \cdot P_i^2 + b \cdot P_i + c$	b	-5.5	-43.7	-69.9	
	c	191	571	1317	
	R^2	0.95	0.79	0.81	0.85 bc
log-quadratic	a	-7.10	36.50	-78.10	
$E(Y) = a \cdot (\log P_i)^2 + b \cdot (\log P_i) + c$	b	-85.0	-202.2	-242.0	
	c	223	479	1223	
	R^2	0.92	0.90	0.91	0.91 c

[1]) R^2 followed by the same letter do not differ significantly ($P \leq 0.01$), according to two way anova after angular transformation.

[2]) To comply with the second condition, the z-value is set on 0.95.

The best fit is by the equations of Elston *et al.*, Oostenbrink, and the quadratic and log quadratic equations. Significantly less so are the equations of Brown and Seinhorst.

Discussion

All equations fitted relatively well in 1976, with R^2 values well over 0.90, except for Brown's equation, which gave a $R^2 = 0.72$. The low yield figures in this year apparently obscured the differences between the models (Fig. 1). At higher yield levels, in 1978 and 1979, both Brown's and Seinhorst's equations fitted poorly (Table 2). This is in agreement with Trudgill's (1986) findings, when he reviewed the differences between Brown's and Seinhorst's equations. He concluded that, up to initial PCN densities of 75 viable eggs and juveniles (J_2) per gram soil in crops with low potential yield levels (30 tons per ha), only small differences in yield loss could be demonstrated. Whereas in crops with high potential yield levels (60 tons tuber fresh weight per ha), the differences between both equations increased to a maximum at 75 J_2s per gram soil, where with Seinhorst's equation a yield loss of 34 tons per ha was calculated and with Brown's equation 25.5 tons. With further increasing initial PCN densities the differences diminished gradually till both equations predicted a yield loss of about 45 tons at 150 J_2s per gram dried soil (Trudgill, 1986). The equation of Elston *et al.*, the log equation of Oostenbrink and the log-quadratic equation showed hardly any difference in R^2-values between years. Findings by Elston *et al.* (1991) are in agreement with these data. The Oostenbrink equation is the most simple, and in fact no substantial improvement is achieved with the more complex descriptive equations.
The yield levels on the infested plots differed markedly between years (Table 3). This is partly due to differences in levels of infestation, but seems more probably to be the result of differences in precipitation between growing seasons (Table 2). The slopes of the regression lines differed markedly and significantly in the various years (Fig. 2). The slopes became steeper with increasing potential yield levels between years. This means that additional nematodes have a more damaging effect on high yielding plants than at low production levels. As can be seen from Fig. 2, the degree of damage due to nematodes is less than damage by drought.
Considering Fig. 2, in which the Oostenbrink equation is used to describe the relation between yield and the initial PCN density in the three years, the differences in slope of the regression lines, presented in Table 3, become apparent.

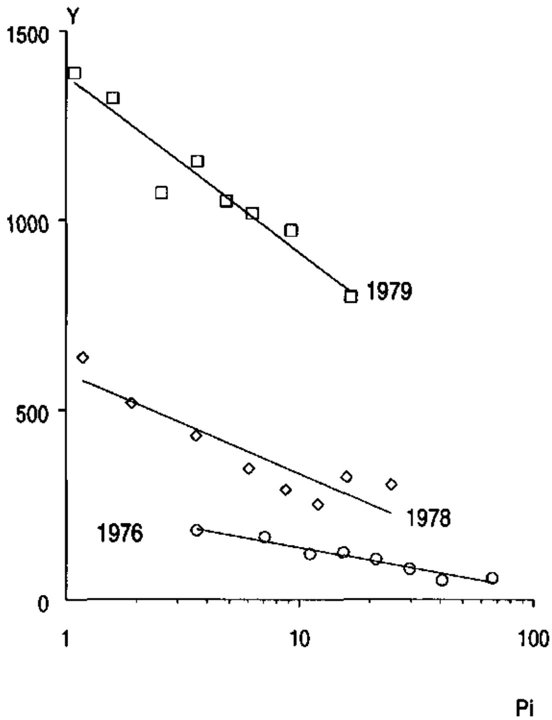


Fig. 2 Yield as tuber dry weight (g per plant) versus P_i = initial density of PCN (viable eggs and juveniles per g dry soil) in 1976, 1978 and 1979.

To avoid distortion of the curves in the range from 0 to 1 egg per g soil, when the log transformations are used, 1 is added to the initial nematode densities in Fig. 2. The regression equations are:

1976:	E(Y)	=	$248 - 111 \cdot \log(P_i+1)$	$R^2 = 0.95$
1978:	E(Y)	=	$596 - 265 \cdot \log(P_i+1)$	$R^2 = 0.83$
1979:	E(Y)	=	$1380 - 465 \cdot \log(P_i+1)$	$R^2 = 0.92$

The R^2 values for the curves concerned are nearly the same as those given in Table 3. Comparing the different regression lines, the intercept as well as the slope of the curves differ significantly ($P \leq 0.05$) between the three curves.
To compare tolerance between years, the intercept was set to 100. It was found that these relative curves did not differ significantly ($P \leq 0.05$) with a slope of about - 40.

Hence, the potential production level for a certain year has no bearing on the test for tolerance in the field. This is in agreement with results of Evans and Russell (1990) and with results presented in Chapter VI, were statistically no interaction was found between damage caused by PCN and by drought, when drought is the main production limiting factor.

Conclusions

Potato cyst nematodes have a significantly more damaging effect on high yielding plants than on low yielding ones.

The equations, given by Oostenbrink (1966) and Elston *et al.* (1991), and the log-quadratic equation describe the relationship between yield and initial potato cyst nematode density consistently over the three experimental years in a highly accurate way. The least consistent equations were the ones given by Brown and by Seinhorst.

Oostenbrink's equation is the most simple one to describe the relationship between yield and PCN density. It describes the relationship as well as the other best fitting equations. Hence, there is no need to use the more complex equations for this relationship.

There is a clear correlation between nematode density and yield within years. However, year effects on yield levels exceeded the effect of PCN. These high yield effects between years are accounted for by differences in precipitation (See also Chapter V).

The annual yield level does not interfere with tolerance; therefore testing for tolerance can be adequately done in any single year.

Chapter IV

Relationship between tolerance of cultivars and the effect of potato cyst nematode on initial plant growth

A.F. van der Wal, A. Mulder and R.A.J. Velema

Introduction

Interest in tolerance of plants to nematode attack became marked in the 1970's. This can be seen by the number of papers published on tolerance to the 15 major genera of plant parasitic nematodes, including potato cyst nematodes (Evans and Haydock, 1990). In the Netherlands, interest declined after the initial interest in the 1970's, only to increase again towards the end of the 1980's.

In the last decade, some resistant cultivars planted in infested fields showed severe yield losses. Their resistance (hypersensitivity) is marked by severe damage to the root system when used on soils with moderate to high levels of PCN infestation. Hence, there is a demand for cultivars which can be used in moderately infested fields, and which suffer relatively little damage.

Tolerance is defined as the capacity of a cultivar to reduce yield (or quality) loss relative to nematode density, when compared with other cultivars (Schäfer, 1971). However, when tolerance to potato cyst nematodes is included in a breeding programme, yield tests can not be performed in the early stages of the programme, due to the lack of sufficient planting material and to the high costs of testing many clones in sufficient replications.

As early as in the sixties, characteristics other than yield were investigated to indicate differences in tolerance (Huijsman *et al.*, 1969). Growth, as well as plant development, appears to slow down after infection by potato cyst nematodes, at least during the first weeks. Afterwards, growth may resume, even to a level similar to that of uninfected plants. Poor initial growth is a loss factor which is not fully compensated for later in the season. It also contributes to the vulnerability of the crop to other stresses (Anonymous, 1981; Van der Wal, 1981b). Senescence of the plant usually starts earlier in the season and the crop dies sooner. Both these effects result in a

shorter growing period and, hence, reduced light interception, and largely explain the yield loss induced by potato cyst nematodes. Initial growth response to infection can be tested relatively simply and quickly in the green-house, and seems also suitable for large scale screening. Pilot experiments in the greenhouse showed that the difference in growth between plants grown in heavily infested soil and the controls grown in uninfested soil, were at a maximum eight to ten weeks after planting.
The aim of the experiments reported in this chapter is to evaluate the relationship between tolerance of potato cyst nematodes based on yield losses in the field and initial growth of plants in pots with infested soil in the greenhouse. Most experiments in greenhouses are done in off season periods. As an interaction between seed age and reaction to PCN might exist, experiments were conducted in the spring and autumn, using the same seed source.

Materials and Methods

Two greenhouse experiments with seed of good vigour from 52 cultivars, originating from Germany, Spain, the United Kingdom and the Netherlands, were carried out in early spring (March to Mid-May of 1979 and 1980: Experiments 1 and 2). A third experiment was carried out in the autumn (end August to October 1980), using seed which had been stored for over a year at 2 °C. All cultivars used are known to be susceptible to *G. pallida*, but a few have resistance to *G. rostochiensis*.
Field experiments were carried out in 1978 and 1979 with 20 of these 52 cultivars.

Greenhouse experiments

Root medium and inoculum. Potting soil with a high organic matter content (TRIO 17 Special: organic matter content 44%, pH_{KCl} = 5.2; Van der Wal and Cowan, 1974) was thoroughly blended to obtain a homogeneous loose soil. Vintage cysts of a mixture of *Globodera pallida* populations, multiplied in a greenhouse on susceptible *ex Solanum tuberosum* cultivars, were mixed with the soil in a concrete mixer to give a density of 1500 cysts per litre soil. Soil samples taken after mixing showed a density of 1509 (s.e. 61) cysts per litre, yielding 322 (s.e. 29) juveniles per ml soil.

Transparent rectangular containers sized 20 x 2 x 25 cm (length, width, height) were arranged in blocks of 10, and each container was filled with 1 litre of the heavily infested soil. The transparent walls served to observe the growing roots without disturbing the system. The container bottoms were perforated to allow moisture exchange with the cotton capillary matting on the greenhouse bench. The matting was kept moist and when needed, plants were watered from the top.

Plant growing. Eyepieces of 2 cm diameter were taken from the mid-region of non pre-sprouted tubers. Only one stem per eyepiece was allowed to develop. Each experiment contained two blocks with plants in infested soil. Final screening was 10 weeks after planting. One replicate with uninfested soil served as a control to compare the growth of the different cultivars.
Day-length was between 14 and 16 hours, using additional light from HPI/T 400 W lamps in the morning and at the end of the day, when needed (Van der Wal and Vinke, 1982).

Root and stem development. Root mass was estimated ten weeks after planting, using a simple scale developed in several pilot experiments: score 1: root mass similar to the one as formed by cv Record at this high nematode density; score 3: idem for the roots formed by cv Irene, and score 5: the maximum root mass found in these experiments, as formed by cv Multa (Photo 4.1).
Regrowth, the presence of newly formed white roots, was also estimated on a scale from 1 to 5. Stem length and maximum stem diameter (at maximum about 30 cm above soil level) of all plants were measured 10 weeks after planting. Tuber formation and flowering were also recorded.

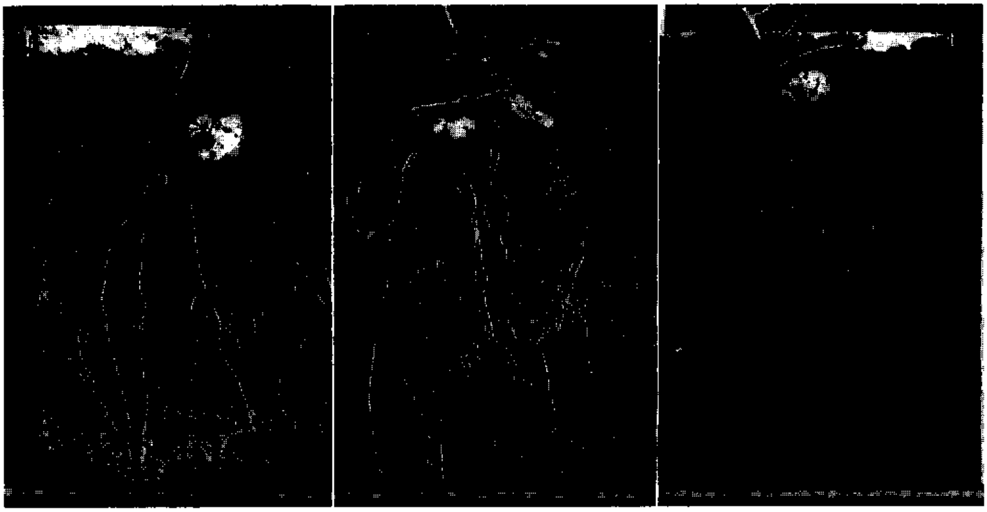


Photo 4.1. The root masses of, from left to the right: cv Multa (score 5), of cv Irene (score 3) and cv Record (score 1), ten weeks after planting.

Field experiments

The experiments were carried out on heavily infested sandy and sandy-peat soils. The initial PCN population density just before planting was determined by taking fifteen ml soil cores per plot, 16 · 25 cm apart, which were bulked to form a sample of c 225 ml of soil. The samples were air dried and weighed. Cysts were extracted using the modified Fenwick apparatus (Oostenbrink, 1960) and the living cyst content was estimated by staining eggs and juveniles with New Blue R (Shepherd, 1962).
PCN infestation in these fields was identified as *Globodera pallida* (Pa-2), density levels ranged from < 0.2 - 24 eggs per g soil in the field used in 1978 and < 0.1 - 15 eggs per g soil in the field used in 1979. The low PCN density plots were obtained by applying metham sodium (300 l per ha) twice within a fortnight. Fumigations were carried out in early spring to avoid nitrogen effects (Kolenbrander, 1969a,b,c).
The experiments were arranged in a randomized block design in four replicates. Each block was subdivided again into four sub-blocks, and within each sub-block, two plants of each cultivar were grown. Fertilizer was applied on the basis of results of soil analysis. The twenty cultivars chosen (Table 1) ranged in maturity value from 3 (very late-maturing) to 7.5 (early-maturing).
The plants of the various cultivars were widely spaced so as to avoid mutual interference. Each plot had a gross size of 150 cm · 165 cm and a nett size of

75 cm · 66 cm. Two tubers of each cultivar were planted in ridges 75 cm apart, and the distance between plants in the ridge was 33 cm. The distance between two cultivars in the ridge was 99 cm and only every other ridge was planted. Thus the distance between two planted ridges was 150 cm.
Planting of pre-sprouted tubers of 35-45 mm took place at the end of April. Emergence was evaluated and growth and development of the plants were periodically recorded. After plant senescence, tuber fresh weight and under water weight were determined. The dry matter content was calculated from these data, as was the dry matter yield (Bernelot Moens, 1973).

Comparison of the field and greenhouse trials results.

The yield data of the 20 cultivars planted in the field experiments of 1978 and 1979 (Chapter III, Table 1, all cultivars except cv Arjan) were compared with the growth response of the same cultivars in the greenhouse. The relative yields of these cultivars, defined as:

$$100 \cdot \text{(yield at high PCN density)/(yield at low PCN density)} \qquad (1)$$

were ranked with three parameters for initial growth response in the greenhouse experiments: Root = root-mass · regrowth, RootDiam = root-mass · regrowth · stem-diameter and RootStem = root-mass · regrowth · stem-diameter · length. These parameters of initial growth were calculated per experiment by first averaging the assessments of the two infested blocks per cultivar, followed by ranking per experiment. Then the ranked values of the three experiments were averaged and ranked again.

Results

Greenhouse experiments. From the fourth week after planting onwards, the plants grown in infested soil in the greenhouse clearly differed from the uninfested control. They were shorter, the leaves were a darker green, and the root systems were less developed. Examination of root samples revealed a massive invasion of the roots by PCN juveniles.
Measured ten weeks after planting, infected plants were shorter than the control plants, especially in the two spring experiments (an average of 55% and 12%

reduction respectively, significant at P=0.01). In the autumn experiment, where old seed was used, only a non significant 4% reduction of length was found with infected plants.

Stem-diameter was reduced by 42% in Experiment 1, 23% in Experiment 2, and 25% in Experiment 3, averaged over all cultivars, and in all cases significant at P=0.01.

Young seed produced slightly more vigorous roots in uninfested soil in the spring than old seed did in the autumn.

Regrowth of roots was also slightly better in both spring experiments than in the autumn one, but the difference was not significant. Only a few cultivars were negatively affected by the long storage period of Experiment 3. Cv Krostar, for example, grew poorly in the autumn compared to its growth in the spring. This cultivar is known to be affected by prolonged storage.

The tuber numbers of infected plants were significantly ($P \leq 0.001$) less than that of the uninfected control plants. Averaged over the three greenhouse experiments, 0.9 tubers were found per infected plant, compared with 2.2 tubers per control plant. Also, flowering of infected plants was less, 0.3 flowers per infected plant and 0.6 flowers per control plant ($P \leq 0.01$).

The growth parameters were found to be correlated, but the correlation with maturity value was in all cases low and only significant for length (Table 1).

Table 1. Matrix of correlation coefficients of ranks of the scores of rootmass and regrowth, maximum stem diameter and stem length (averages of three greenhouse experiments) and maturity value of 52 cultivars.

Correlation coefficients	Root mass	Regrowth	Diameter	Length	Maturity value
Root mass	---				
Regrowth	0.86 ***	---			
Diameter	0.87 ***	0.79 ***	---		
Length	0.61 ***	0.57 ***	0.64 ***	---	
Maturity value	-0.21	-0.24	-0.23	-0.39 *	---

*** $P \leq 0.001$ (1-tailed) * $P \leq 0.05$ (1-tailed)

Results of greenhouse and field experiments compared. Emergence did not vary very much in the field experiments but growth was slower, development retarded and senescence started earlier in relation to increasing nematode density. In Table 2, the relationship of the yield data of the 20 cultivars with the data of the greenhouse experiments is presented.
The relative yield of the field grown cultivars correlated very well with the initial growth response in the greenhouse, as based on the parameter RootDiam. The correlation of the parameters with maturity value of these cultivars was low, negative, and not significant. All other correlations were very high (Table 2).

The 20 field grown cultivars covered the whole range for RootDiam of the 52 cultivars used in the greenhouse experiments (Table 3). RootDiam showed the strongest correlation with yield (r = 0.86).

Table 2. Matrix of correlation coefficients of ranks of relative field yield (Rel.Yield) averaged over two years, compared to three combinations of growth parameters in greenhouse experiments (Root, RootDiam, RootStem) and maturity value of 20 cultivars.

Correlations	Rel.Yield	Root	RootDiam	RootStem
Rel.Yield	---			
Root	0.77 ****	---		
RootDiam	0.86 ****	0.97 ****	---	
RootStem	0.83 ****	0.96 ****	0.98 ****	---
Maturity value	0.07	-0.25	-0.25	-0.27

**** $P \leq 0.0001$

Table 3. Ranking of the 52 glasshouse grown cultivars for initial growth response to *Globodera pallida* infection (RootDiam = rootgrowth · regrowth · stem-diameter), their maturity value MV (Joosten and Van der Woude, 1985) and Relative Yield of the 20 field grown cultivars.

Cultivar	MV	mean ranks		
		52 cvs	20 cvs	
		RootDiam (greenhouse)	RootDiam (greenhouse)	Relative yield (field)
Record	7	1		
Marijke	5	2	2.0	1.5
Satelliet	5^5	3	3.0	2.5
Pentland Beauty	8	4		
Woudster	5	5		
Provita	7^5	6	4.0	9.0
Pimpernel	3^5	7		
Parel	7^5	8		
Ackersegen	4	9		
Element	6	10	4.7	6.0
Maris Peer	6^5	11		
Welcome	6	12		
Saturna	5^5	13	6.0	10.0
IJsselster	6^5	14		
Irene	5^5	15		
Ambassadeur	5	16		
Aurora	7	17	7.3	8.5
Allerfr. Gelbe	7	18		
Up to date	5	19		
Patrones	5^5	20		
Rector	5	21	8.0	10.5
Amigo	4	22	9.3	10.5
Bevelander	6	23		
Kathadin	6	24		
Bintje	6^5	25		
Krostar	7	26	9.7	7.5
Romula	8	27		

Table 3. Continued

Cultivar	MV	mean ranks		
		52 cvs	20 cvs	
		RootDiam (greenhouse)	RootDiam (greenhouse)	Relative yield (field)
Acresta	5	28		
Ari	6^5	29		
Amera	6	30		
Procura	3^5	31	11.0	6.5
Prevalent	4	32	10.7	12.5
Resy	7^5	33		
Eba	4^5	34	10.7	11.0
Lori	6^5	35		
Mara	3^5	36	12.5	16.0
Ollala	6	37		
Astarte	3^5	38	14.0	13.5
Ultimus	6^5	39	14.3	18.0
Palma	6^5	40		
Mentor	5	41	13.3	10.5
Pansta	5^5	42	14.3	13.5
Zenith	5	43		
Prominent	4^5	44	15.2	16.5
Ostara	8	45		
Elkana	4^5	46	16.5	17.5
Veenster	6	47		
Ehud	7^5	48	16.3	17.5
Voran	4	49		
Pruceres	4	50		
Kennebec	6	51		
Multa	3^5	52		
LSD (P = 0.05)				9.0

Correlation RootDiam/Rel Yield (20 cultivars) = 0.86. $R^2 = 0.74$ ($P \leq 0.0001$).

The high correlation between the rankings of RootDiam and Rel.Yield with R^2=0.74, indicates that yield loss in the field is, to a large extent, dependent on the initial growth response to PCN infection.

Discussion

Potato cultivars differ in initial growth response to PCN infection. Rel.Yield was found to be highly correlated with root development in the greenhouse trials in heavily infested soil, but was only weakly correlated with differences in root and stem growth of the uninfected control (r = 0.30). Therefore, it is not necessary to include the uninfected control for all cultivars in this type experiments. These findings were confirmed by Arntzen (1993).

The high correlation of the ranking of RootDiam (= rootmass · regrowth · stem-diameter) with the rank of the relative yield (Rel Yield) seems to be a consequence of the way PCN inflicts damage to potatoes. Damage to the root system can be directly translated to a reduced asssimilation apparatus in time and volume (see Chapter V and VI).

Growth delay causes losses in two ways: firstly fewer tubers develop, and secondly, the shortened growing period due to initial growth delay and early senescence results in less light interception (Chapters V and VI).

The correlation of maturity class to all growth parameters was weak, and only significant for stem length (Table 1). The yield figures also confirm that tolerance to PCN can occur in early as well as in late cultivars. Maturity does not determine tolerance. Hence, breeding for tolerance is not only feasible for late, but also for early cultivars (see also Chapter VI).

It is obvious that recovery of the root system can be adequately assessed in pot trials. However, early senescence which is also a cultivar dependent reaction to PCN infection, is better assessed in the field.

Since the response to storage of new breeding material is generally unknown, it is better to conduct experiments with vigorous young seed tubers, rather than with seed stored for a long period.

Conclusions

The responses of root growth parameters to PCN infection all showed high and significant correlations with each other and with yield. The highest correlation was given by RootDiam (= rootmass · regrowth · stem-diameter) and yield (R^2 = 0.74). This parameter can be assessed early and is an useful parameter for determining tolerance.

A rather simple greenhouse test, only assessing root growth response to PCN, gives a good insight of the cultivar's tolerance performance in the field, in the early stages of the growing season.

Early senescence, as a cultivar dependent reaction to PCN infection, is better assessed in the field.

Provided that growing conditions, seed and inoculum quality are optimal, screening for initial growth response of genotypes to nematode infection is possible with only a few plants per genotype in early stages of a breeding programme.

As some cultivars (e.g. cv Krostar) do not stand long storage periods, it is recommended to use vigorous young seed tubers to determine the root growth response to PCN infection.

Chapter V

Ground cover, development, intercepted radiation and yield of four potato cultivars as influenced by potato cyst nematode and drought

Introduction

PCN inflicted damage to individual plants in the field correlated (r=0.87) with initial growth retardation of the plants in the greenhouse.
This chapter is focused on the damaging effect of PCN to the crop, in relation to growth and development, affecting tuber number and tuber yield, and on the interaction of PCN with drought. PCN attack affects the ability of the crop to assimilate, and hence to produce. There are two mechanisms involved through which assimilation may be reduced. The first one concerns the growth and development of the crop. When ground cover is affected, light interception is affected. The lower the ground cover, the lower the assimilation per unit of ground surface, and the lower the dry matter production. The second one concerns the ability of the plant to effectively use intercepted radiation when affected by PCN, a response which may differ for cultivars. Drought may affect the potato crop by reducing the amount of productive foliage, by decreasing the rate of photosynthesis per unit of leaf area and by shortening the vegetative period (Van Loon, 1986). Four cultivars, which respond differently to PCN infection, were used to investigate whether (under Dutch growing conditions) the effects of PCN and drought were mainly caused by reduced light interception or other factors, and whether interactions between PCN and drought occurred.

Materials and methods

The experiments, realized in 1988, 1989 and 1990, were located on adjacent parts of the same field at Eeserveen. The soil concerned is sandy and drought-sensitive and had an organic matter content of about 6.5 %, and a pH_{KCl} of 5.2. Prior to planting, PCN density was determined by taking duplicate soil samples (250 cc) of each plot to the full depth of the tillage layer. The field was deep cultivated to a depth of 1.25 m in 1975 and found to be heavily infested with *Globodera pallida*, pathotype

Pa-2 (Table 1). Low levels of infestation were achieved by soil fumigation with metham sodium, 500 l per ha, 510 g a.i. per litre, applied by a rotary spading injector (Mulder *et al.*, 1990a). Non-fumigated plots were treated mechanically in the identical way, except that the fumigation equipment ran idle. In order to avoid differences in N-content of the soil at planting, fumigations were carried out in early spring (Kolenbrander, 1969a,b,c), four weeks prior to planting. Three weeks later, the field was cultivated, and five days later ploughed to a depth of 25 cm, allowing residual fumes of methylisothiocyanate (MITC) to escape.
The experimental design was a split-split plot scheme with two replicates, with supplemental irrigation of plots, fumigation of subplots and cultivars in sub-sub plots. Plots consisted of 6 ridges, spaced 75 cm apart, with a length of 7.5 m each, with a total area of $4.5 \cdot 7.5$ m.
The cultivars used were Désirée, Mentor, Darwina and Elles, with maturity values of 5, 5^5, 4^5 and 3^5, and values for drought resistance of 8, 7, 7 and 8 respectively (Joosten, 1988; Anonymous, 1988a). Cv Mentor is especially highly appreciated by farmers for its good performance on drought-sensitive soils. The first two cultivars (*ex Solanum tuberosum*) are susceptible to all pathotypes of both PCN species, while the other two show resistance to *G. pallida* pathotype Pa-2, (*ex Solanum vernei*, $(VT^n)^2$ 62.33.3) and to all pathotypes of *G. rostochiensis* (Anonymous, 1989a). Cvs Mentor and Darwina are considered to be intolerant, whereas the other two are reported to possess some degree of tolerance to PCN (Velema and Boerma, 1988). Cv Désirée is used for both fresh consumption and industrial purposes, while the three other cultivars are grown for starch. The seed, size 35 - 50 mm, was treated against *Rhizoctonia solani* by dipping the tubers in a 3% solution of validamycine (Solacol). Fertiliser (NPK) was applied in accordance with a soil fertility analysis. Planting was carried out by hand in the second half of April; the arrangement of plants was 75 by 30 cm and details are summarized in Table 1. Control of late blight and weeds were according to standard farming practice. Soil moisture content was recorded weekly. To prevent drought stress (pF values exceeding 2.8), 25 - 30 mm water was applied by overhead irrigation (Photo 5.1, page 72) each time when pF-values exceeded 2.6 (Table 1).
The proportion of ground covered by green foliage was assessed at weekly intervals with the aid of a 90 by 75 cm grid divided into 100 rectangles. Viewed directly from above (Photo 5.2, page 78), the number of rectangles estimated to exceed 50% ground cover with green leaves was counted, and this value was used as percentage ground cover (Haverkort *et al.*, 1991b). Two assessments per plot were made.

Table 1. Details of the field trials at Eeserveen.

Experimental year	1988	1989	1990
Infestation level, viable eggs per g dry soil			
heavily infested plots	28.8 ± 4.4	26.1 ± 4.3	57.5 ± 9.3
lightly infested plots	5.1 ± 1.7	6.0 ± 1.9	6.1 ± 1.0
Planting date	April 29	April 20	April 17
Harvest dates	September 6 October 11	August 23 October 10	August 22 October 16
Plot size harvested	10.8 m^2 48 plants	5.4 m^2 24 plants	7.2 m^2 32 plants
Overhead irrigation (mm)	50	200	210
number of rounds	2	8	8
Precipitation (mm) *	328	216	171

* during the last 10 days of May, June, July and August (derived from Anonymous, 1988b; 1989b; 1990b).

Tubers were harvested in October, after the haulm of all cultivars had died. Tubers were counted, and fresh and dry weights were determined. In 1989, two interim harvests prior to crop senescence were performed to follow tuber development and growth, and tubers were graded at the final harvest (Table 3).
Data on regional weather conditions were obtained from the reports of the station of the Royal Netherlands Meteorological Institute at the airport Eelde, 30 km from the experimental sites.

Statistical analyses.

Although these experiments were set up to assess cultivar effects, they were laid out according to a split-split plot design for practical reasons. The soil of the experimental field was very homogenous. In a series of field experiments conducted in the period 1972 - 1992, only minor, non-significant effects of soil type and soil conditions were experienced. With respect to variability in nematode density, only small differences were measured. No significant soil type differences were to be expected between field locations. Therefore results have not only been submitted to a split-split plot based analysis of variance, but in addition, have also been submitted to three and four-way orthogonal analyses of variance, irrespective of the split-split plot field lay out.

Results

Weather conditions in general.

The weather in these three years was characterized by extremes in solar radiation and temperature.

1988. The first three months of 1988 were extremely mild and wet, with over 320 mm precipitation (normally: 157 mm). In contrast, weather conditions in April and May were bright and very dry, and so the seed was planted in well prepared soil. June, July and August were generally overcast, with 100 hours less sunshine than normal for June. In addition, these summer months had an excess of rainfall. Thus, the growing season of 1988 was characterized by a good start in April and May, followed by a generally dull, rather cool and exceptionally wet summer season with c. 200 hours less sunshine than normal. The weather conditions of 1988 were in sharp contrast to those of the following year.

1989. The 1989 growing season was characterized by bright weather, with over 50 hours sunshine above normal, and the highest average daily temperatures in 250 years.

1990. After an extremely mild winter, the growing season of 1990 started with a bright and warm March and a rather cool first half of April. May was also bright and warm, but with frost in the nights of the 23rd, 27th and 29th, when the plants were 10 to 15 cm high. The first half of June gave rather dull, cool weather, but weather conditions during July and August were warm and dry. The growing season of 1990 was characterized by dry and warm weather conditions with 75 hours sunshine less than "normal" in July and August (derived from Anonymous, 1988b; 1989b; 1990b), see also Table 4 page 79.

In May, plants were only lightly frosted. Since damage was very light and uniformly distributed, no significant differential effects were to be expected concerning the experimental design.

Irrigation.

Climatic conditions in the early summer of 1988 were such that irrigation was applied twice. Both irrigations were followed by sufficient precipitation within 12 hours, thus preventing drought stress in the non-irrigated plots as well. Hence, in 1988 no drought stress was experienced on the unirrigated plots. In 1989 and 1990, irrigations were necessary to avoid drought stress. In 1989, the first irrigation was needed in the last week of June, which is normal for this region. In 1990, drought spells started early and a first irrigation was necessary on the 5^{th} of June, before the canopy closed.

Analysis of variance.

Both analyses of variance, according to the experimental split-split plot design and a simulated three and four-way orthogonal analyses of variance, yielded very similar results, not differing more than 0.2%. Only the significance of the difference between years, which is not calculated with the split-split plot based variance analyses, could not be compared (Tables 2, 3, 5 and 6).

Ground cover.

In all three years, emergence was normal and completed within seven days for all cultivars. Results on ground cover for 1988 are represented in Figs 1 and 2. In the lightly infested plots, ground cover for all cultivars increased rapidly to 100%, eight to nine weeks after planting. For cultivars Mentor and Désirée, ground cover decline started at 16 weeks after planting, and the foliage was dead after 22 weeks. For cvs Darwina and Elles, ground cover reduction started in week 17 and 20, and the foliage was dead 23 and 24 weeks after planting respectively (Fig. 1).

At the high infestation level, all cultivars showed retardation of haulm growth, development and flowering. Cv Désirée showed less retardation, compared with the other cultivars and came close to 100% ground cover, whereas cvs Mentor and Darwina never achieved more than 95% ground cover. From week 13 after planting, cvs Désirée, Mentor and Darwina rapidly senesced. Cv Elles maintained 100% ground cover up to 17 weeks after planting, followed by a relatively slow reduction in ground cover (Fig. 1). Compared with lightly infested plots, cv Elles started to senesce about three weeks earlier and was 100% senescent about one week earlier (23 weeks after planting).

The reaction patterns for 1989 and 1990 were similar to the one of 1988 and therefore are not presented separately. Instead, results for integrated ground cover of the four cultivars in all three years are presented in Table 2 and Figs 4 and 5. Integrated ground cover was calculated as the sum of weekly measured ground cover percentages during the various periods of the growing season.

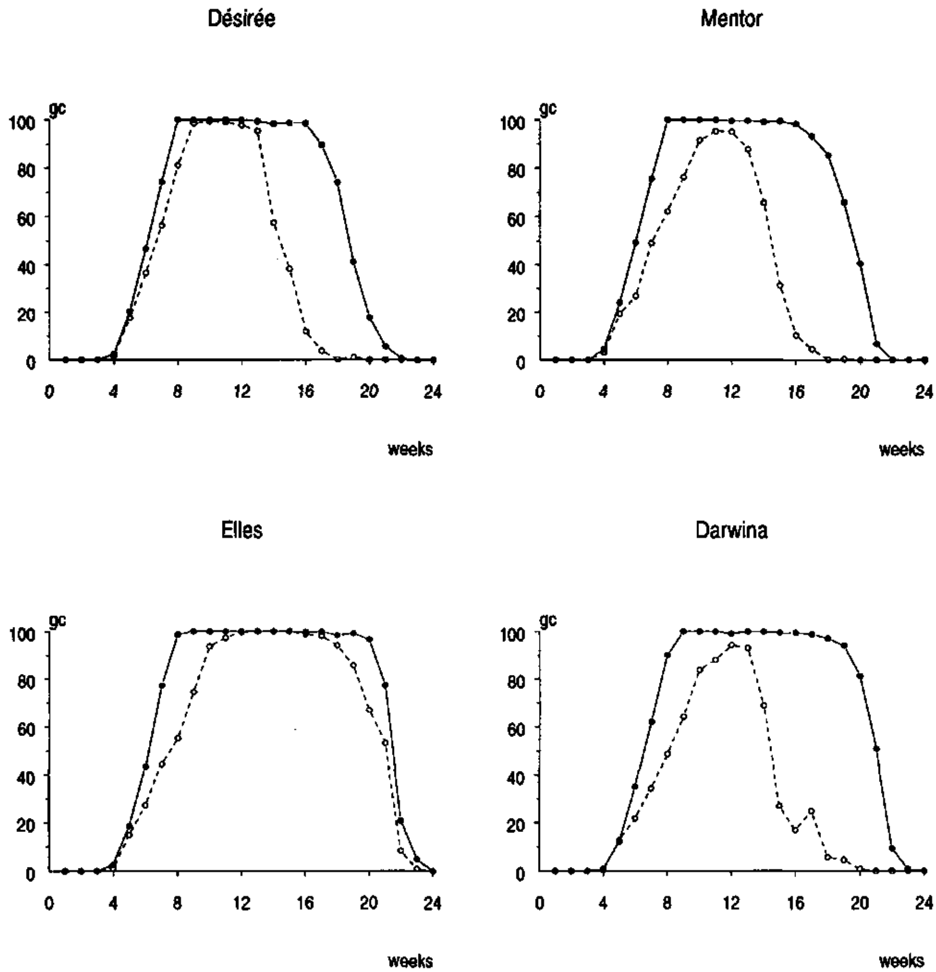


Fig. 1 Percentage ground cover (gc) during the growing season of 1988 (weeks after planting) of the four cultivars Mentor, Désirée, Elles and Darwina, grown at low and high PCN densities (closed and open symbols respectively).

For the period week 4 to week 24, the weekly differences in ground cover in 1988 for the lightly and heavily infested plots are presented in Fig. 2. These curves show two distinct and very prominent tops. The first one coincides with the period of canopy build up and tuber initiation, the second one with the bulking period. In the first part of the growing season, up to 10 weeks after planting, cv Désirée showed a minimal reduction in ground cover, indicating an almost normal growth pattern in the heavily

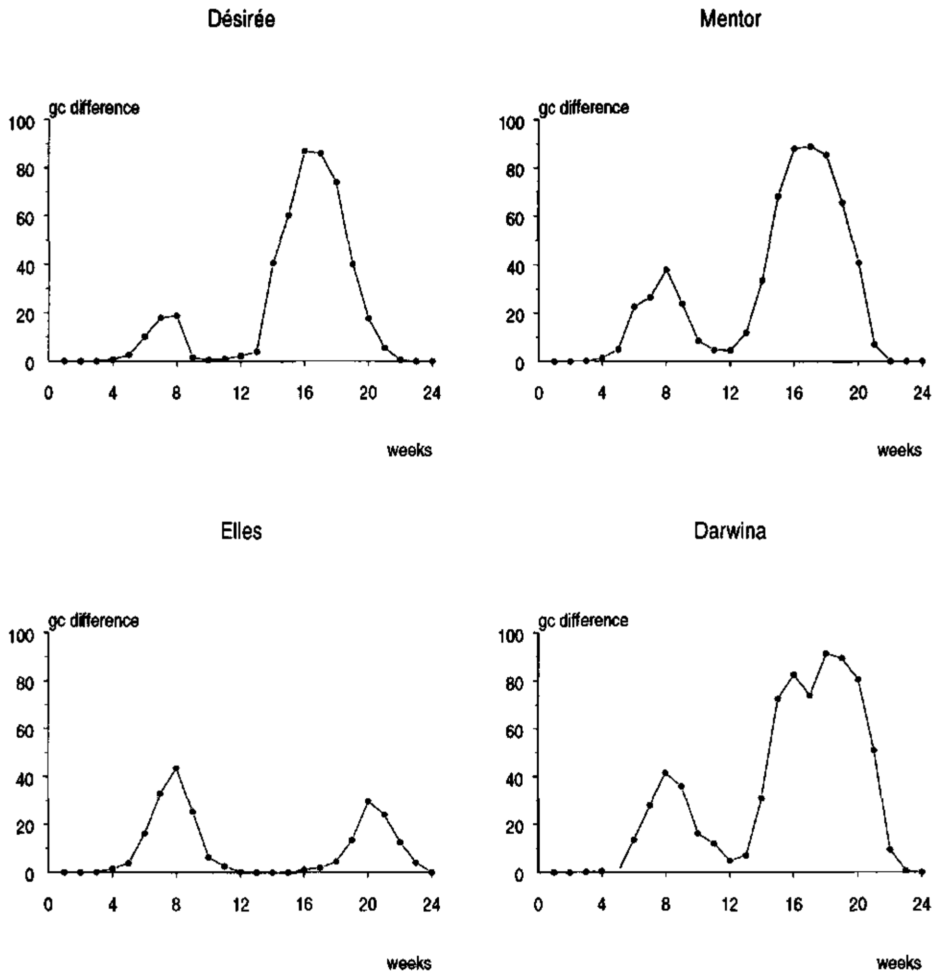


Fig. 2 Difference in percentage ground cover (gc difference) between the lightly and heavily infected crop during the growing season (weeks after planting) of the four cultivars in 1988.

infested plots. The other three cultivars showed considerable retardation of initial growth. In the second part of the growing period, cv Elles showed little difference in ground cover between the two PCN infestation levels compared with the other three cultivars, all of which showed marked reduction of the duration of ground covered with green foliage, due to infection; cv Désirée a little less than cv Mentor, cv Darwina considerably more (Fig. 2).

Table 2. Results and anova for integrated ground cover for the first growing period of 12 weeks (GC_1), and for the following weeks (GC_2), for three successive years, with and without supplemental overhead irrigation, on lightly (L) and heavily (H) infested sandy soil. *** = $P \leq 0.001$, ** = $P \leq 0.01$, * = $P \leq 0.05$; % dv = % declared variation.

Year	Cultivar	GC_1				GC_2			
		irrigated		not irrigated		irrigated		not irrigated	
		L	H	L	H	L	H	L	H
1988	Darwina	541	450	557	352	865	340	897	239
	Désirée	587	558	595	517	742	334	605	179
	Elles	595	505	581	410	989	841	905	872
	Mentor	600	524	598	413	767	306	710	190
	Mean	581	509	583	423	841	455	779	370
1989	Darwina	470	377	388	358	698	455	598	385
	Désirée	486	444	487	449	503	429	483	339
	Elles	500	452	486	396	891	860	951	915
	Mentor	498	437	501	333	617	350	511	158
	Mean	489	428	466	384	677	524	636	449
1990	Darwina	395	269	381	212	414	182	230	109
	Désirée	451	343	473	398	410	186	204	119
	Elles	492	350	448	317	611	462	427	380
	Mentor	474	239	455	186	410	132	241	45
	Mean	453	300	439	278	461	241	276	163
Total mean		508	412	496	362	660	407	564	327

Factors	GC_1 F-values	GC_1 % dv	GC_2 F-values	GC_2 % dv
Main effects: Year	-.-	39.1	-.-	27.9
Infestation level	470.82 ***	31.6	322.69 ***	19.8
Irrigation	27.03 *	2.3	23.01 *	2.5
Cultivar	39.79 ***	9.9	185.96 ***	33.3
2-way interactions:				
Year x Inf.level	21.97 **	2.9	31.51 ***	3.9
Year x Irrigation	1.40	0.2	1.51	0.3
Year x Cultivar	2.83 *	1.4	6.26 ***	2.2
Inf.l x Irrigation	13.61 **	0.9	0.40	<0.1
Inf.l x Cultivar	13.11 ***	3.3	21.89 ***	3.9
Irrig x Cultivar	4.99 **	1.2	2.14	<0.1
3- and 4-way interactions:				
Yr x Inf.l x Irrigation	5.51 *	0.7	2.81	0.3
Yr x Inf.l x Cultivar	2.34	1.2	4.17 **	1.5
Yr x Irrig x Cultivar	0.36	0.2	1.37	0.5
Inf.l x Irrig x Cultivar	1.92	0.5	0.52	0.1
Yr x Inf.l x Irr x Cv	1.25	<0.1	0.58	0.2
Coefficient of variation	6.5		13.5	

For integrated ground cover, the analysis of variance (Table 2) shows large and highly significant effects for *Years*, *PCN Infestation level* and *Cultivars*. For *Irrigation*, a significant but small effect is shown during the first and the second part of the growing period. The Cultivar effect is more pronounced in the second part of the growing period. Most of the variation for ground cover (82.9 % in period 1 and 83.5 % in period 2) is explained by the effects of these four main factors.

Also, there are highly significant but rather small, two-way interactions, together explaining 9.9 % of the variability for integrated ground cover during the first part of the growing period (period 1) and 10.3 % during the second part (period 2):

A. *Year x Infestation level* is highly significant for both parts of the growing period;
B. *Year x Irrigation* is not significant in both growing periods.
C. *Year x Cultivar* is small but significant for the first part of the growing season and highly significant for the second part;
D. *Infestation level x Irrigation* is small but very significant on ground cover in the first part of the growing period only;
E. *Infestation level x Cultivar* is highly significant for both parts of the growing period;
F. *Irrigation and Cultivar* is very significant but small in the first part of the growing season only.

Finally, the significant but small three-way interactions explain 0.7 % of the variation of ground cover during the first part of the growing period, and 1.5 % during the second part:

G. *Year x Infestation level x Irrigation* is significant but small in the first part of the growing period;
H. *Year x Infestation level x Cultivar* is small but very significant for the second part of the growing period only;
I. There is no interaction shown between *Year, Irrigation and Cultivar*, between *Infestation level, Irrigation and Cultivar*, and between *Year, Infestation level, Irrigation and Cultivar*.

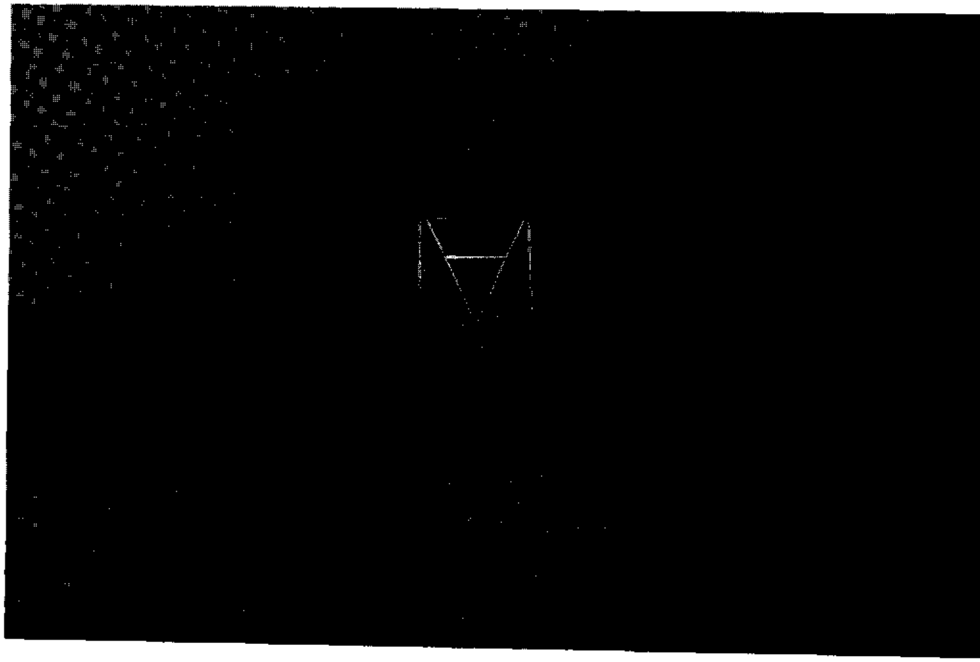
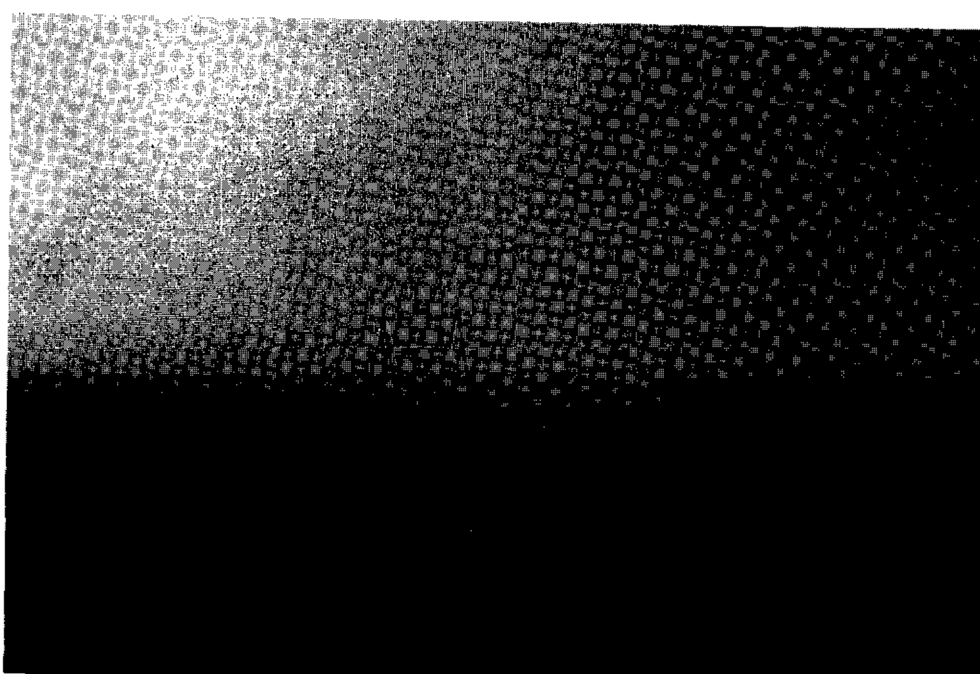


Photo 5.1. Supplemental irrigation was applied by an overhead irrigation system (working width 63 m) when soil pF-values exeeded 2.6.



Tuber yield and tuber number.

Results on tuber yield are presented as tuber number per m^2, tuber fresh weight (kg per m^2), tuber dry matter yield (g per m^2) and mean tuber dry weight (g per tuber) in Tables 3a and 3b.

In 1989, tuber number and mean tuber dry weight differed considerably with those of 1988 and 1990 for all four cultivars and all treatments. Tuber number was 1.63 times higher than those for 1988 and 1990, which at 49 and 44 respectively, were very similar. However, tuber dry matter production was only 1.15 times higher in 1989. Since mean tuber dry weight is dry matter yield divided by tuber number, the mean tuber dry weight was much lower in 1989.

At low nematode densities and without water stress, cvs Darwina, Désirée, Elles and Mentor yielded 5.03, 5.47, 4.73 and 4.87 kg tuber fresh weight per m^2, averaged over the three years. The corresponding tuber dry matter yields were 1297, 1138, 1238 and 1223 g tuber dry matter per m^2 respectively. For the non-irrigated plots these figures were 1007, 884, 1095 and 1084 g tuber dry matter per m^2. At the high nematode densities, cv Elles on average, out-yielded ($P \leq 0.01$) the other three cultivars, in fresh and dry weight by 33% and 56% respectively (Table 3). The dry matter yields of cvs Darwina, Désirée and Mentor were similar when averaged over the three years. They yielded approximately 595 g dry matter per m^2 in plots with supplementary irrigation, and 537 g dry matter in the non-irrigated plots.

Mean tuber dry weight.

The relationship between mean tuber dry weight (w_t) and weekly measured, cumulated ground cover in the second part of the growing season (gc_2) is presented in Fig. 5. This relationship is best described by a linear regression equation. Similarly, the relationship between intercepted radiation and mean tuber dry weight is best presented by linear regression (Fig. 7). Fitting the curves for the years gives two separate curves, one for the years 1988 and 1990, and the other one for 1989. The differences are totally explained by differences in tuber number (averaged 49 in 1988; 44 in 1990 and 76 in 1989). Tuber number had no impact on total dry matter production, which mainly depends on intercepted solar radiation. Hence, dry matter produced during the second part of the growing season is divided over the number of tubers formed in the first part of the growing season.

Table 3a. Results and anova for tuber number per m² and tuber fresh weight (kg per m²) of four cultivars in three successive years, with and without supplemental irrigation on lightly (L) and heavily (H) *Globodera pallida* infested soil at the final harvest.
*** = $P \leq 0.001$, ** = $P \leq 0.01$, * = $P \leq 0.05$; % dv = % declared variation.

Year	Cultivar	tuber number per m²				tuber fresh weight (kg per m²)			
		irrigated		not irrigated		irrigated		not irrigated	
		L	H	L	H	L	H	L	H
1988	Darwina	50	37	52	29	5.3	2.5	4.8	1.7
	Désirée	64	52	64	49	5.7	2.6	5.4	2.0
	Elles	54	38	52	35	4.9	3.4	5.1	3.1
	Mentor	60	47	62	34	5.2	2.6	5.2	1.8
	Mean	57	43	58	37	5.3	2.8	5.1	2.2
1989	Darwina	86	69	73	66	5.7	3.3	3.6	2.8
	Désirée	99	62	97	71	5.5	3.0	4.6	2.6
	Elles	86	52	78	58	4.8	3.5	4.3	2.9
	Mentor	98	70	90	56	4.9	2.8	3.8	1.7
	Mean	92	63	85	63	5.2	3.2	4.1	2.5
1990	Darwina	44	34	40	27	4.1	2.2	3.1	1.5
	Désirée	45	36	35	46	5.2	2.6	2.6	2.4
	Elles	61	44	52	42	4.5	3.1	3.2	2.3
	Mentor	67	40	63	29	4.5	2.5	3.5	1.2
	Mean	54	39	48	36	4.6	2.6	3.1	1.9
	Total mean	68	48	64	45	5.0	2.9	4.1	2.2

Factors	tuber number: F-values	tuber number: % dv	tuber fresh weight: F-values	tuber fresh weight: % dv
Main effects: Year	-.-	52.2	-.-	7.5
Infestation level	106.44 ***	24.0	1033.20 ***	64.1
Irrigation	48.46 **	1.0	72.59 **	9.7
Cultivar	14.86 ***	4.2	10.82 ***	2.2
2-way interactions:				
Year x Inf.level	3.55	1.6	26.25 ***	3.3
Year x Irrigation	0.54	<0.1	5.81	1.6
Year x Cultivar	8.13 ***	4.6	2.46 *	1.0
Inf.l x Irrigation	0.14	<0.1	4.80	0.3
Inf.l x Cultivar	6.47 ***	1.8	10.00 ***	2.1
Irrig x Cultivar	2.68	0.8	1.51	0.3
3- and 4-way interactions:				
Yr x Inf.l x Irrigation	1.41	0.6	7.41 *	0.9
Yr x Inf.l x Cultivar	4.34 **	2.5	1.93	0.8
Yr x Irrig x Cultivar	0.43	0.2	1.68	0.7
Inf.l x Irrig x Cultivar	3.42 *	1.0	4.06 *	0.8
Yr x Inf.l x Irr x Cv	0.42	0.2	2.44 *	1.0
coefficient of variation	10.3		9.5	

Table 3b. Results and anova for tuber dry matter yield (g per m²) and mean tuber dry weight (g per tuber) of four cultivars in three successive years, with and without supplemental irrigation on lightly (L) and heavily (H) *Globodera pallida* infested soil at the final harvest. *** = $P \leq 0.001$, ** = $P \leq 0.01$, * = $P \leq 0.05$; % dv = % declared variation.

Year	Cultivar	tuber dry matter yield (g/m²)				mean tuber dry weight (g/tuber)			
		irrigated		not irrigated		irrigated		not irrigated	
		L	H	L	H	L	H	L	H
1988	Darwina	1289	607	1199	424	25.6	16.6	23.0	14.9
	Désirée	1068	494	1043	377	16.7	9.6	16.2	7.7
	Elles	1154	833	1231	829	21.4	22.1	23.6	23.6
	Mentor	1230	604	1249	408	20.5	12.8	20.1	12.0
	Mean	1185	635	1181	510	21.1	15.3	20.8	14.6
1989	Darwina	1465	888	942	774	17.0	12.8	13.1	11.5
	Désirée	1217	677	1021	619	12.3	10.9	10.5	8.6
	Elles	1336	1023	1219	818	15.5	19.9	15.7	14.2
	Mentor	1260	693	1019	452	12.9	9.9	11.3	8.1
	Mean	1320	820	1050	666	14.4	13.4	12.7	10.6
1990	Darwina	1138	641	879	405	26.4	18.9	21.8	16.6
	Désirée	1129	582	509	558	25.3	16.4	16.7	12.1
	Elles	1224	936	835	711	20.1	21.6	15.8	16.8
	Mentor	1180	690	983	321	17.7	16.9	15.5	11.0
	Mean	1168	712	801	498	22.4	18.5	17.5	14.1
	Total mean	1224	722	1011	591	19.3	15.7	17.0	13.1

Factors	F-values	% dv	F-values	% dv
Main effects: Year	-.-	4.6	-.-	24.7
Infestation level	640.90 ***	60.4	253.72 ***	13.8
Irrigation	68.61 **	8.8	56.84 **	6.0
Cultivar	29.82 ***	7.7	85.43 ***	24.8
2-way interactions:				
Year x Inf.level	12.71 **	2.4	30.29 ***	3.3
Year x Irrigation	7.72	2.0	12.82 *	2.7
Year x Cultivar	1.92	1.0	14.33 ***	8.3
Inf.l x Irrigation	1.64	0.4	0.33	<0.1
Inf.l x Cultivar	13.77 ***	3.5	27.30 ***	7.9
Irrig x Cultivar	1.07	0.3	0.97	0.3
3- and 4-way interactions:				
Yr x Inf.l x Irrigation	5.07	1.0	0.99	0.1
Yr x Inf.l x Cultivar	2.00	1.0	2.40 *	1.4
Yr x Irrig x Cultivar	1.24	0.6	1.54	0.9
Inf.l x Irrig x Cultivar	3.65 *	0.9	2.48	0.7
Yr x Inf.l x Irr x Cv	2.26	1.2	1.54	0.9
coefficient of variation	10.0		9.3	

The analyses of variance (Tables 3a and 3b) indicate highly significant effects for all main variables (*Year, PCN Infestation level, Irrigation* and *Cultivar*) concerning tuber number, tuber fresh weight, tuber dry matter yield and mean tuber dry weight. Most of the variation (81.4, 83.5, 81.5 and 69.3 % respectively) is explained by these factors.

Also there are significant two-way interactions, explaining 6.4 % of the variability of tuber number, 6.4 and 5.9 % of variability of tuber fresh weight and tuber dry matter yield and 22.2 % of the variability of the mean tuber dry weight:

A. *Year x Infestation level* is highly significant for tuber yield, either fresh or dry matter yield, and for mean tuber dry weight;
B. *Year x Irrigation* over all years is significant for mean tuber weight only;
C. *Year x Cultivar* is highly significant for tuber number and mean tuber dry weight, and is not significant for tuber yield;
D. *Infestation level x Irrigation* (drought) is not significant for tuber number, for tuber fresh yield and tuber dry matter yield, and for mean tuber dry weight;
E. *Infestation level x Cultivar* is highly significant for tuber number, tuber yield and mean tuber dry weight; and
F. there was no significant interaction between *Irrigation and Cultivar.*

Finally, there are significant but small three-way and four-way interactions, explaining 3.5, 2.7, 0.9 and 1.4 % of the variation of tuber number, tuber fresh weight, tuber dry matter yield, and mean tuber dry weight respectively:

G. *Year x Infestation level x Cultivar* is significant for tuber number and mean tuber dry weight
H. *Infestation level x Irrigation x Cultivar* is small and just significant for tuber number and tuber yield, and not significant for mean tuber dry weight and the four-way interaction, and
I. *Year x Infestation level x Irrigation x Cultivar* shows small and just significant effects at the 5% significance level on tuber fresh weight only.

Tuber size distribution.

In 1988, tuber size distribution was also determined. All cultivars showed similar tuber size distributions for the lightly infested soil. However, they responded differently in heavily infested soil (Fig. 3). With PCN attack, cultivars Désirée, Mentor and Darwina showed a shift in tuber grade towards the smaller sizes. Very few tubers over 55 mm were present and those over 45 mm were severely reduced in number. For cv Elles tuber grade was almost unaffected (Fig. 3).

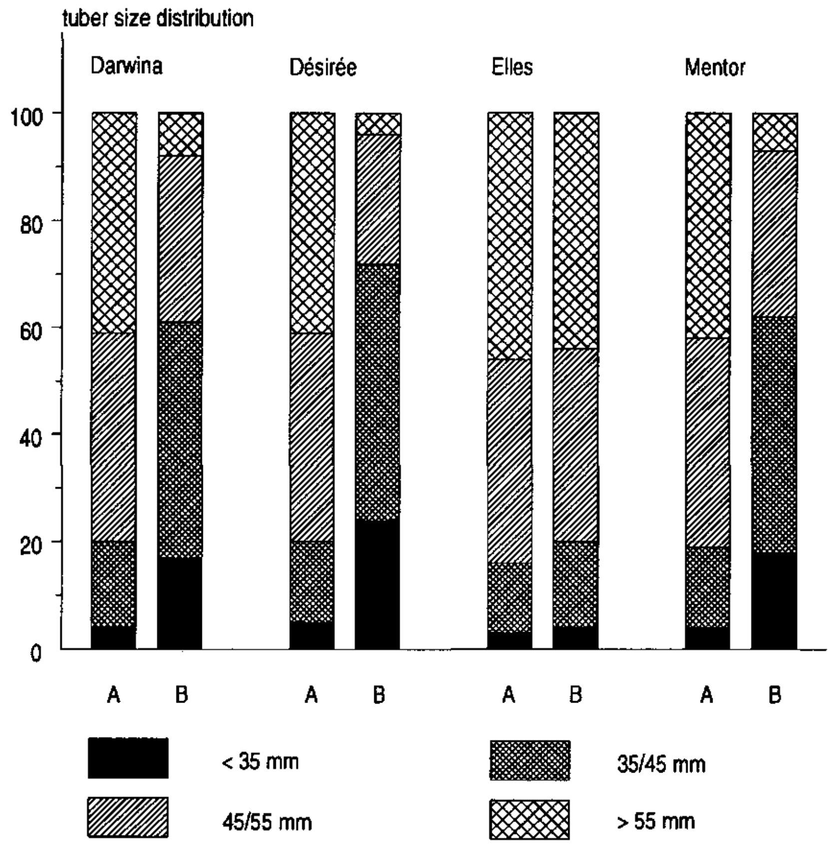


Fig. 3 Tuber size distribution in percentages of total tuber yield of the four cultivars at final harvest. Yield on lightly (A) and heavily (B) infested soil.

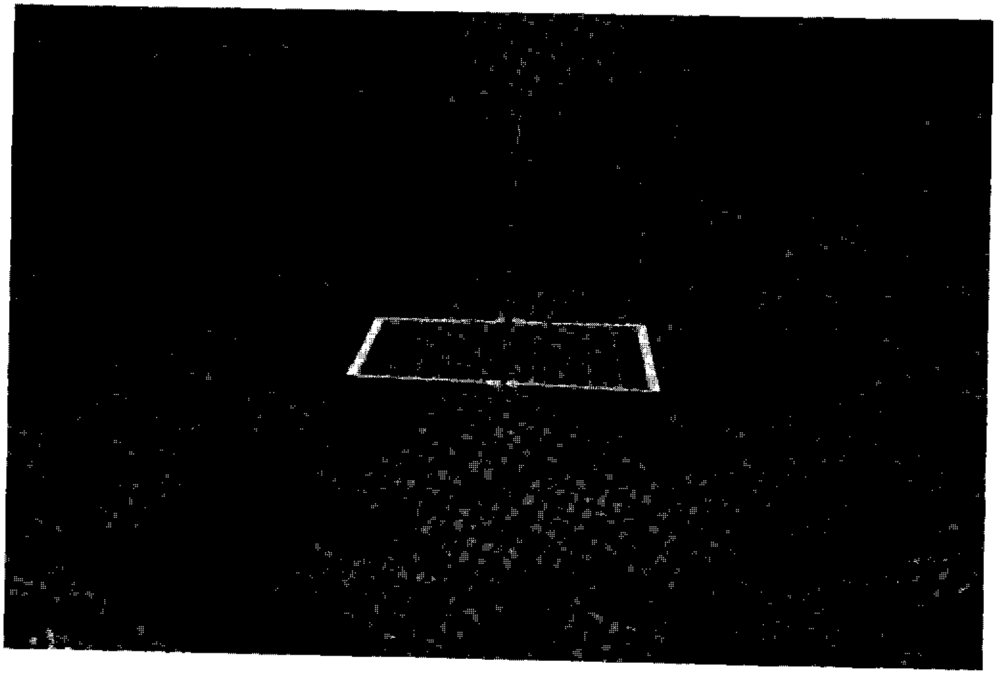
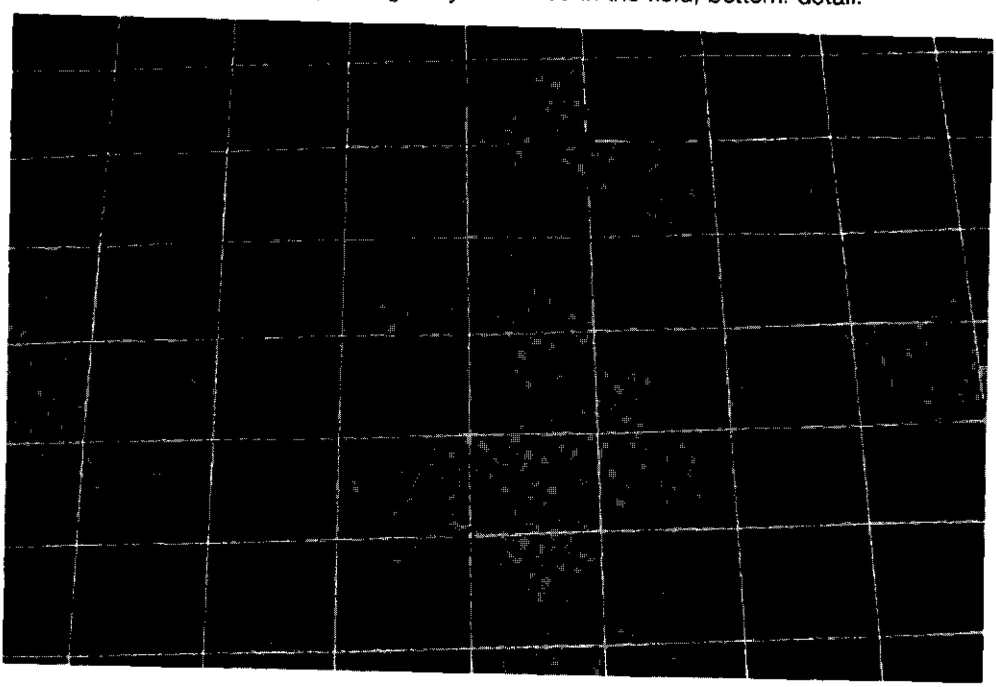


Photo 5.2. Percentage ground covered with green foliage was estimated by means of a grid system, measuring 75 by 100 cm and divided in a hundred rectangles of 7.5 by 10 cm. Top: the grid system used in the field, bottom: detail.



Effect of solar radiation and water supply.

Large and highly significant differences between years were found for ground cover (Table 2) and tuber number, tuber fresh weight, tuber dry matter yield and mean tuber dry weight (Tables 3a and 3b). Also, considerable differences were found in solar radiation (Table 4) and precipitation (Table 1).

Table 4. Solar radiation (MJ per m^2) in May, June, July, August and September of 1988, 1989 and 1990 at the nearby airport of Eelde (derived from Anonymous, 1988b, 1989b and 1990b).

Month	Solar radiation			
	1988	1989	1990	Normal
May	578	674	597	533
June	410	662	429	567
July	422	502	551	536
May till August	*1410*	*1838*	*1577*	*1636*
August	456	437	473	483
September	273	245	245	316
Aug till Oct	*729*	*762*	*718*	*799*
Total	2139	2600	2295	2435

Intercepted radiation.

Intercepted solar radiation is calculated as the sum of the products of the weekly assessed proportion of ground covered with green foliage and the corresponding amount of solar radiation for the weeks concerned.

For each cultivar and each treatment, the amount of intercepted radiation was calculated for the period from emergence to 12 weeks after planting, and for the period 12 weeks after planting to complete canopy death. The results are presented in Table 5.

Table 5. Results and anova for intercepted radiation for the first 12 week growing (IR_1) and the following period, until canopy death (IR_2), in three successive years, with and without supplemental irrigation, on lightly (L) and heavily (H) infested sandy soil.
*** = P ≤ 0.001, ** = P ≤ 0.01, * = P ≤ 0.05; % dv = % declared variation.

Year	Cultivar	IR_1				IR_2			
		irrigated		not irrigated		irrigated		not irrigated	
		L	H	L	H	L	H	L	H
1988	Darwina	518	427	533	332	813	339	838	229
	Désirée	565	534	574	492	722	346	610	165
	Elles	576	483	560	388	885	793	846	815
	Mentor	580	505	579	397	747	314	699	182
	Mean	560	487	562	402	792	448	748	348
1989	Darwina	720	567	586	537	710	477	614	400
	Désirée	748	683	745	688	522	450	506	358
	Elles	771	691	744	600	886	858	928	894
	Mentor	766	666	772	509	647	371	535	171
	Mean	751	652	712	584	691	539	646	456
1990	Darwina	423	286	412	222	527	235	298	143
	Désirée	487	370	510	426	523	239	265	156
	Elles	525	375	483	339	736	576	513	488
	Mentor	506	260	486	201	529	172	315	58
	Mean	485	323	473	297	579	310	348	211
	Total mean	599	487	582	428	687	432	581	338

Factors	IR_1 F-values	IR_1 % dv	IR_2 F-values	IR_2 % dv
Main effects: Year	-.-	61.3	-.-	17.4
Infestation level	592.43 ***	20.4	302.96 ***	25.6
Irrigation	25.63 *	1.7	35.96 **	3.9
Cultivar	47.70 ***	7.0	169.91 ***	36.5
2-way interactions:				
Year x Inf.level	10.79 ***	0.7	18.80 **	3.1
Year x Irrigation	1.81	0.2	3.60	0.8
Year x Cultivar	2.85 *	0.8	2.82 *	1.2
Inf.l x Irrigation	15.42 **	0.5	0.25	<0.1
Inf.l x Cultivar	13.96 ***	2.1	25.62 ***	5.5
Irrig x Cultivar	5.67 **	0.8	2.44	0.5
3- and 4-way interactions:				
Yr x Inf.l x Irrigation	4.32	0.3	4.62	0.7
Yr x Inf.l x Cultivar	1.77	0.5	3.21 *	1.4
Yr x Irrig x Cultivar	0.42	0.1	1.13	0.5
Inf.l x Irrig x Cultivar	2.80	0.4	0.44	<0.1
Yr x Inf.l x Irr x Cv	2.31	0.7	0.38	0.2
coefficient of variation	6.1		12.9	

The analysis of variance shows large and highly significant effects for *Years, PCN Infestation level* and *Cultivars*. There is a small but significant effect for *Irrigation* during the first part of the growing season, and a very significant but small effect on intercepted radiation during the second part. Most of the variation (90.4 % for period 1, and 83.4 % for period 2) is explained by these four factors.

There are significant and highly significant two-way interactions for both parts of the growing period, explaining 4.9 % and 9.8 % of the variation for period 1 and 2 respectively.

A. *Year x Infestation level* is highly, respectively very significant for the first and second part of the growing period, but very small for period 1;
B. *Year x Irrigation* is not significant for both periods of the growing season ;
C. *Year x Cultivar* is just significant, but very small;
D. *Infestation level x Irrigation* (drought) is very significant but also very small for period 1 and not significant for period 2;
E. *Infestation level x Cultivar* is highly significant for both parts of the growing season, and
F. *Irrigation x Cultivar* is very significant but also very small for period 1 only.

There is one significant but small three-way interaction, explaining 1.4 % of the variation for the second part of the growing season:

G. *Year x Infestation level x Cultivar* is only significant for the second part of the growing period;
H. The interactions *Year x Infestation level x Irrigation, Year x Irrigation x Cultivar* and *Infestation level x Irrigation x Cultivar* and the four-way interaction *Year x Infestation level x Irrigation x Cultivar* are not significant.

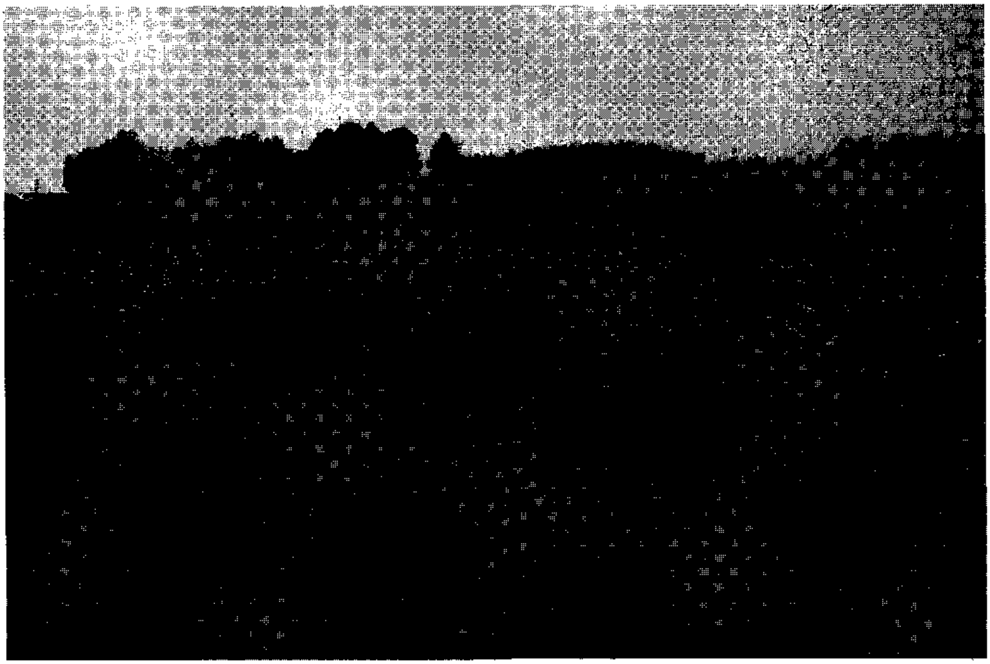


Photo 5.3. Growth and development of cv Mentor affected by *Globodera rostochiensis* on a soil fumigation experiment on a heavily infested sandy peat soil near Witteveen. Left: untreated, right: treated with 150 litre 1,3-dichloropropene per ha.

Tuber number.

Tuber number is dependent on the cumulated weekly measured ground cover during the first twelve weeks after planting (Fig. 4), while mean tuber dry weight is dependent on the cumulated weekly measured ground cover from twelve weeks onwards (Fig. 5). The curves for both tuber number and mean tuber weight versus ground cover differ significantly and profoundly for the three years (Figs 4 and 5), indicating a strong year effect. The number of tubers per m^2 at harvest in 1989 was much higher than in 1988 and 1990 (Fig. 4). A noticeable difference between these years concerns the quantity of solar radiation, especially in the first part of the growing season. It was substantially higher than normal in 1989, and lower than normal in the other two years (Table 4).

To evaluate whether tuber number is directly related to intercepted radiation, the proportion ground covered, which is considered to be a good estimation of the proportion of intercepted solar radiation (Haverkort *et al.*, 1991b), is multiplied by global solar radiation for each year. These results are represented as intercepted radiation plotted against corresponding tuber number and mean tuber dry weight in Figs 6 and 7[1].

Regression analysis (Snedecor and Cochran, 1991) shows that the relationship between tuber number for all four cultivars with intercepted radiation in the first 12 weeks after planting is best described with the following quadratic equation:

$$n_t = 0.000137 \cdot ir^2 - 0.0281 \cdot ir + 30.3 \qquad (r = 0.96)$$

When fitted to a straight line (in the range of 300 - 800 MJ per m^2), the equation :

$$n_t = 0.129 \cdot ir - 12.51 \qquad (r = 0.95)$$

was obtained. Both equations explain this relationship quite well.

[1] To enhance the graphic presentation and to facilitate regression analysis, the 32 points obtained for ground cover resp. intercepted radiation per year over all treatments are pooled, ranked from low to high and grouped in subsequent not overlapping quartets. The average group values are used for regression and statitical analysis (Snedecor and Cochran, 1991).

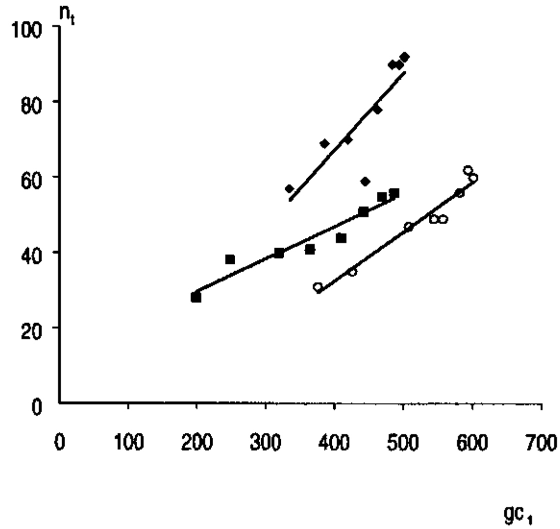


Fig. 4 Number of tubers (n_t) per m² versus cumulated weekly measured ground cover during the first 12 weeks after planting (gc_1) in 1988(o), $n_t = 0.13 \cdot gc_1 - 24.8$ (r = 0.98), 1989(♦), $n_t = 0.20 \cdot gc_1 - 19.9$ (r = 0.92) and 1990(■), $n_t = 0.08 \cdot gc_1 + 12.3$ (r = 0.98).

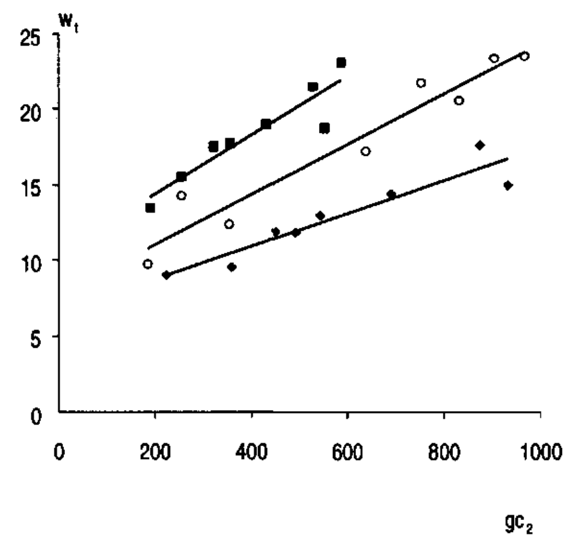


Fig. 5 Mean tuber dry weight (w_t) in g per tuber versus cumulated weekly measured ground cover from 12 weeks after planting (gc_2) in 1988(o), $w_t = 0.017 \cdot gc_2 + 7.7$ (r = 0.98), 1989(♦), $w_t = 0.011 \cdot gc_2 + 6.5$ (r = 0.97) and 1990(■), $w_t = 0.020 \cdot gc_2 + 10.5$ (r = 0.96).

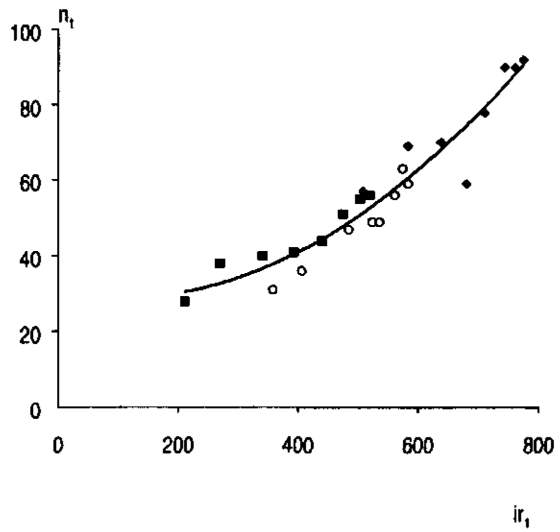


Fig. 6 Tuber number (n_t) per m² versus intercepted radiation during the first 12 weeks after planting (ir_1) in MJ per m² in 1988 (o), 1989 (♦) and 1990 (■), $n_t = 0.000137 \cdot ir_1^2 - 0.0281 \cdot ir_1 + 30.3$ ($r = 0.96$).

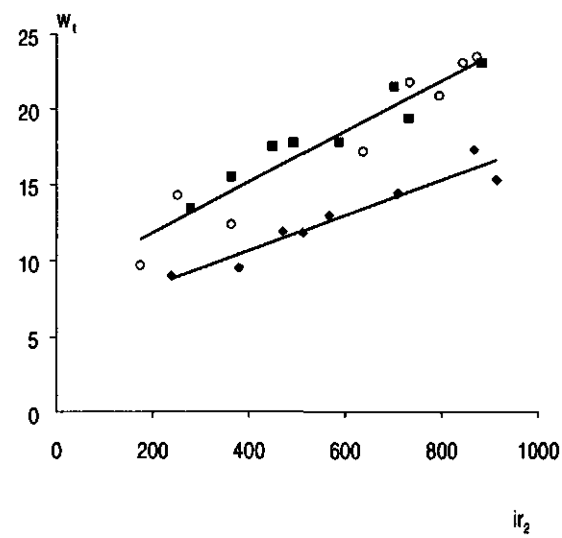


Fig. 7 Mean tuber dry weight (w_t) in g dry matter per tuber versus intercepted radiation from 12 weeks after planting till harvest (ir_2) in MJ per m² in 1989 (♦), $w_t = 0.012 \cdot ir_2 + 7.3$ ($r = 0.96$) and 1988 (o)/1990 (■), $w_t = 0.017 \cdot ir_2 + 8.5$ ($r = 0.95$).

Tuber yield.

Percentage of ground cover assessments and solar radiation from the date of emergence to the date of complete canopy death, were transformed into "total integrated ground cover" and "total intercepted radiation" (Table 6).

For both, total integrated ground cover and total intercepted radiation, the analyses of variance produce almost identical results. Large and highly significant effects are shown for *Years, PCN Infestation level* and *Cultivars.* The effects of *Irrigation* are significant for integrated ground cover and very significant for total intercepted radiation, but relatively small for both. Most of the variation (> 85 %) is explained by the effect of these four main factors.

Also there are significant two-way interactions, explaining 7.4 % and 6.9 % of variation of total integrated ground cover and total intercepted radiation respectively:

A. *Year x Infestation level* is highly, respectively very significant, but small;
B. *Year x Irrigation* over all years is not significant;
C. *Year x Cultivar* is very significant but small for total ground cover only, but is not significant for total intercepted radiation;
D. *Infestation level x Irrigation* (drought) is not significant;
E. *Infestation level x Cultivar* is highly significant for total integrated ground cover and for total intercepted radiation, and relatively large;
F. there was no interaction between *Irrigation and cultivar.*

One of the three-way interactions is significant but very small, explaining only 1.0 % of the variation for both total integrated ground cover, and total intercepted radiation:

G. *Year x Infestation level x cultivar* is significant but very small for total ground cover and total intercepted radiation;
H. *Year x Infestation level x cultivar, Year x Irrigation x Cultivar* and *Infestation level x Irrigation x Cultivar,* and the four-way interaction *Year x Infestation level x Irrigation x Cultivar* are not significant.

When plotting the total intercepted radiation from emergence to harvest (ir_{tot}) against tuber dry matter yield (Y) for the three years, three straight lines were obtained. As the curves for each year did not differ significantly, the whole data set was well described by one regression line (Fig. 8). This figure was obtained by ranking all data on total intercepted radiation (ir_{tot}) for each year, irrespective of treatments and

Table 6. Results and anova for total integrated ground cover and total intercepted radiation from emergence until canopy death for four cultivars and three successive years with and without supplemental irrigation, on lightly (L) and heavily (H) infested sandy soil.
*** = P ≤ 0.001, ** = P ≤ 0.01, * = P ≤ 0.05; % dv = % declared variation.

Year	Cultivar	total integrated ground cover				total intercepted radiation			
		irrigated		not irrigated		irrigated		not irrigated	
		L	H	L	H	L	H	L	H
1988	Darwina	1406	790	1455	590	1331	766	1371	561
	Désirée	1329	892	1200	696	1287	881	1184	658
	Elles	1584	1346	1486	1282	1461	1276	1406	1202
	Mentor	1367	830	1308	603	1327	819	1279	579
	Mean	1422	963	1362	793	1352	936	1310	750
1989	Darwina	1168	832	985	743	1430	1044	1200	937
	Désirée	989	874	970	789	1270	1133	1251	1046
	Elles	1390	1312	1437	1311	1656	1548	1672	1493
	Mentor	1115	787	1012	491	1413	1036	1307	680
	Mean	1166	951	1101	834	1442	1190	1358	1039
1990	Darwina	809	450	611	321	950	520	710	365
	Désirée	861	529	677	517	1010	609	774	582
	Elles	1102	812	874	696	1261	951	996	827
	Mentor	885	371	696	230	1034	432	801	259
	Mean	914	541	715	441	1064	628	820	508
	Total mean	1167	818	1059	689	1286	918	1163	766

Factors	F-values	% dv	F-values	% dv
Main effects: Year	-.-	34.8	-.-	15.7
Infestation level	482.38 ***	26.8	449.51 ***	37.5
Irrigation	24.76 *	2.9	34.84 **	4.9
Cultivar	148.06 ***	22.9	132.20 ***	27.1
2-way interactions:				
Year x Inf.level	24.25 ***	2.7	10.56 **	1.8
Year x Irrigation	0.51	0.1	0.88	<0.1
Year x Cultivar	3.79 **	1.2	2.26	0.9
Inf.l x Irrigation	0.45	<0.1	0.63	<0.1
Inf.l x Cultivar	22.41 ***	3.5	24.78 ***	5.1
Irrig x Cultivar	1.53	0.2	1.78	0.4
3- and 4-way interactions:				
Yr x Inf.l x Irrigation	3.73	0.4	4.88	0.8
Yr x Inf.l x Cultivar	3.08 *	1.0	2.41 *	1.0
Yr x Irrig x Cultivar	1.34	0.4	1.17	0.5
Inf.l x Irrig x Cultivar	0.92	0.1	1.04	0.2
Yr x Inf.l x Irr x Cv	0.87	0.3	0.93	0.4
coefficient of variation	8.3		7.3	

cultivars. For the relationship between total intercepted radiation and tuber dry matter yield (Fig. 8)[2], linear regression according to the equation:

$$Y = 0.85 \cdot ir_{tot} - 49$$

gives the best fit (r = 0.96).

The Year effect is explained, to a large extent (R^2 = 93%), by differences in intercepted radiation. Therefore, the effects of PCN attack can be directly translated in reduced light interception due to reduced ground cover. In addition to radiation, effects of temperature may also play a role. Temperature effects can not be separated from radiation, as these factors are tangled. Especially in the first cool part of the growing season increased temperatures have a relatively stronger effect than in the warmer part of the growing period, as temperatures are then, on average, far below the optimum for growth (Van der Zaag, 1984).

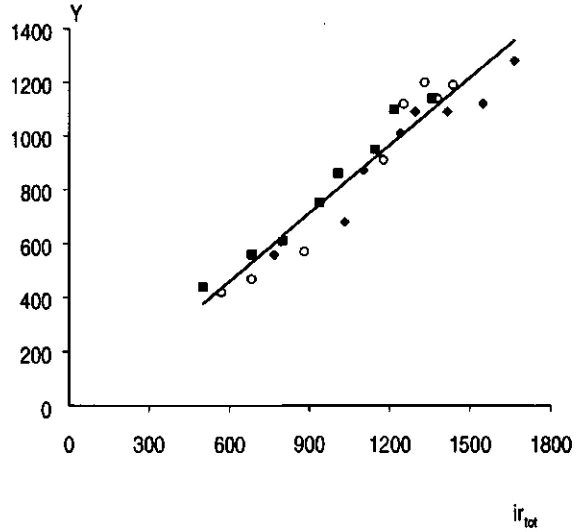


Fig. 8 Tuber yield (Y) in g dry matter per m^2 versus total intercepted radiation (ir_{tot}) in MJ per m^2 from emergence to harvest in 1988 (o), 1989 (♦) and 1990 (■), $Y = 0.85 \cdot ir_{tot} - 49$ (r = 0.96).

[2] see footnote on page 83.

Also, the transportation of assimilates from the foliage to tubers may be affected by temperature (Midmore, 1992). As most of the variation (93%) is explained by reduced canopy, there is no evidence that there are other major effects due to PCN attack interfering with production or assimilation.

Differences in light use efficiency between cultivars?

When the cultivar effect is calculated (mean values per treatment over the years), linear regression analysis shows that three cultivars, Darwina, Désirée and Mentor, fit the same regression line, with a slope of 1.14 g per MJ (Fig. 9)[3]. Averaged over the three years, the curve of cv Elles deviated by a constant of about 250 MJ per m^2 (ir_{tot}), but the difference between the slopes was not significant ($P \leq 0.05$). The aberration of cv Elles is largely due to its performance in 1989, when it failed to increase tuber yield in the period from August 23 onwards (Fig. 10).

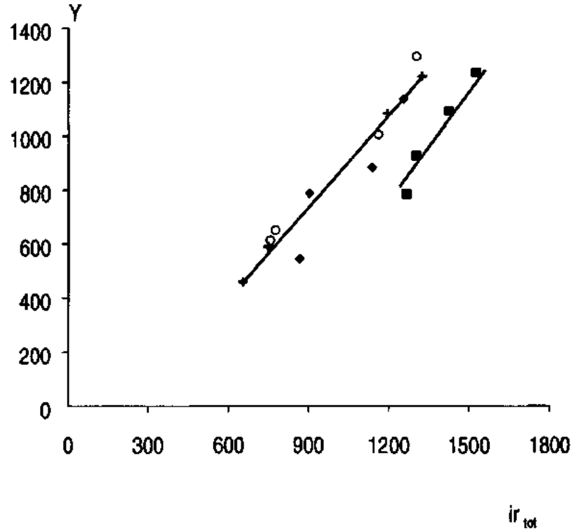


Fig. 9 Tuber yield (Y) in g dry matter per m^2 versus total intercepted radiation (ir_{tot}) in MJ per m^2 from emergence to harvest of the four treatments and the four cultivars Darwina (o), Désirée (♦) and Mentor (+), $Y = 1.14 \cdot ir_{tot} - 287$ ($r = 0.97$) and Elles (■), $Y = 1.34 \cdot ir_{tot} - 849$ ($r = 0.99$).

[3] see footnote on page 83.

As expected, the most tolerant cultivar (Elles) gave not only high yields in the lightly infested plots, but also the least yield reduction in the heavily infested ones. With increasing ir_{tot}, tuber yield increased proportionally, but yields of the irrigated plots with low PCN infestation levels were similar to those of the other three cultivars (Fig. 9). Cv Elles differs from the other three in maturity class, in that it is late-maturing, and shows a prolonged period of ground cover (Fig. 1).

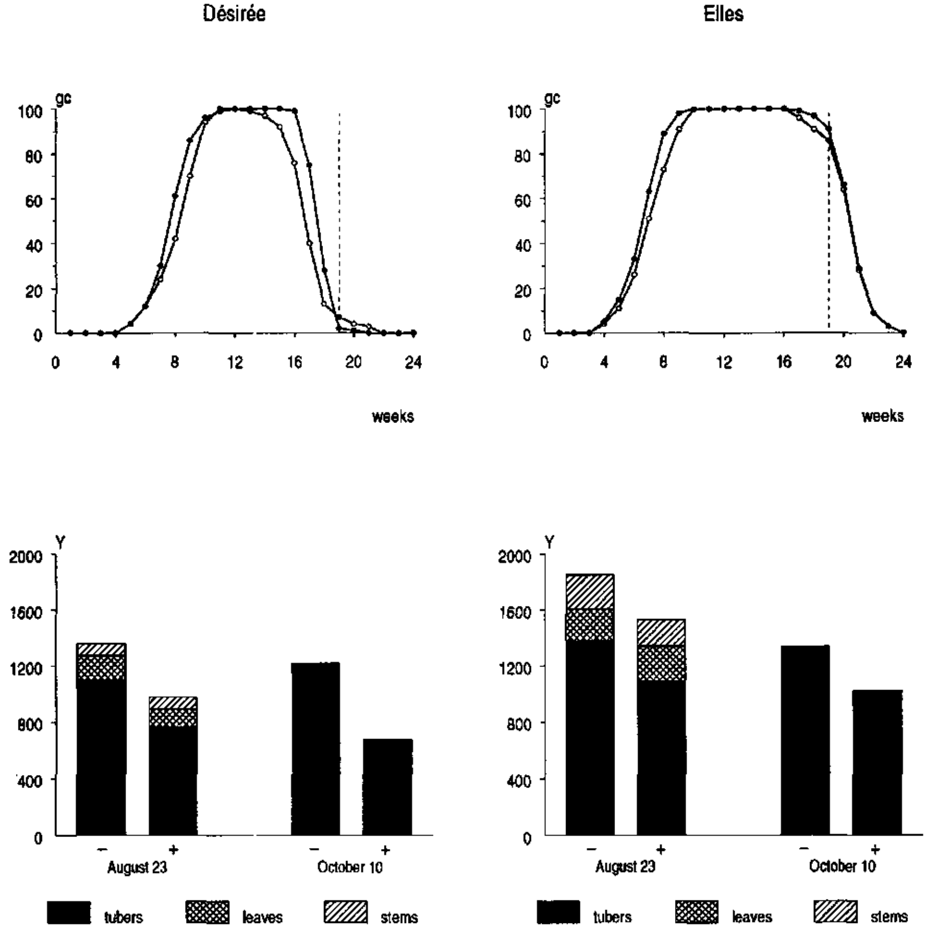


Fig. 10 Top: Ground cover (gc) during the growing season of 1989 (weeks after planting) for cultivars Désirée and Elles on lightly and on heavily infested soil (resp. closed and open symbols). The dotted vertical lines indicate the harvest of August 23.

Bottom: Total dry matter yield (Y), divided in tubers, leaves and stems, for the cultivars Désirée and Elles on lightly (-) and heavily (+) infested soil at the harvest of August 23 and October 10, 1989.

Nevertheless, light-use efficiency of cv Elles appeared to be considerably less than that of the other cultivars. Compared with the other three cultivars, cv Elles showed a considerable and significant discrepancy between calculated intercepted radiation and dry matter yield in 1989. For 1988 and 1990, the differences were small and insignificant. When the dry matter distribution of the crop at intermediate harvests is examined, it appears that, after the harvest on August 23, 1989, the tuber dry weight of Elles did not increase any more on the lightly infested plots, in spite of the still-green canopy. Apparently, no contribution was made by the intercepted radiation to tuber dry weight from August 23 onwards (Fig. 10). This explains the difference of about 400 MJ per m² in 1989, compared with the other cultivars. When the data of this year for cultivar Elles are omitted from the data set, the results fit (r = 0.97) the linear regression curve

$$Y = 0.96 \cdot ir_{tot} - 155$$

as represented in Fig. 11. Therefore, it can be concluded that, with comparable intercepted radiation, light-use efficiency did not differ between these three years.

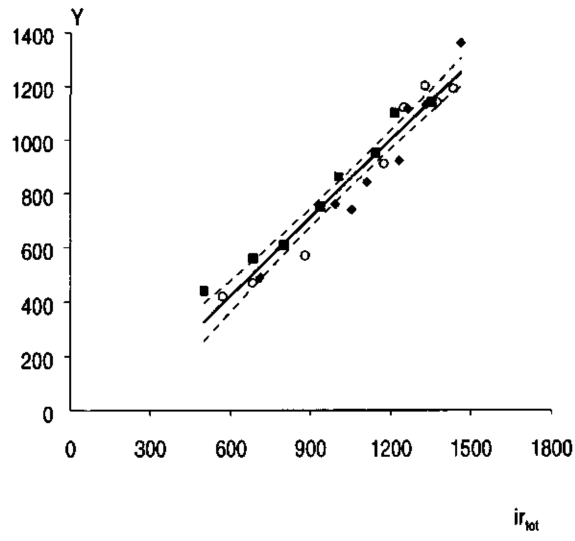


Fig. 11 Yield (Y) in g dry matter per m² versus total intercepted radiation (ir_{tot}) in MJ per m² from emergence to harvest in 1988 (o), 1989 (♦), data of cv Elles included and 1990 (■), data Elles 1989 excluded; $Y = 0.96 \cdot ir_{tot} - 155$ ($r = 0.97$); the thin broken lines indicate the confidence interval ($P \leq 0.95$).

Discussion

Tuber number

Tuber initiation is realized in the first weeks of the growing period. Irrigation showed a significant but very small effect on tuber number, responsible for only 1% of total variation (Table 3a). These findings concur with those of Krug and Wiese (1972), MacKerron and Jefferies (1986) and Jefferies and Mackerron (1987), who found that tuber number was only negatively affected when drought occurred before the onset of tuber initiation. Based on the results of three years of experiments under controlled conditions with the cvs Radosa and Bintje, and the data of the "growth curve experiments", spanning thirteen years of field trials with cv Bintje on a sandy loam soil in the most northern part of the Netherlands, Haverkort *et al.* (1990b) concluded that the mechanism through which tuber numbers are reduced is through reduction of stolons per stem and not through a reduction of the number of tubers per stolon.

PCN attack severely delays development in the first part of the growing period, depending on cultivar. It is expected that tuber number is the more affected, the more severely initial development is delayed. The relationship between tuber number per m^2 and ground cover up to 12 weeks after planting is well described by a linear curve. Between years, these curves differ significantly in range, level and slope. When, however, ground cover is combined with solar radiation and then integrated in the respective periods for the three years, all data fit a second order equation (Fig. 6). The number of harvestable tubers increased with increasing light interception in the first part of the growing season. A similar experience is reported by Sale (1973 a and b). Working with cv Sebago in a region with high radiation (23 MJ per m^2 per day in mid summer, New South Wales, Australia) he found decreasing tuber numbers (from 67 to 55 per m^2) with progressive shading (up to 34%) of his potato crop. In the experiments described here, the average daily radiation in May and June 1989 was comparable to those in New South Wales, 22 versus 23 MJ per m^2 per day. In 1988 and 1990 daily radiation varied from 15 to 20 MJ per m^2 per day (Table 4), up to - 32% and tuber number (averaged over treatments and cultivars) varied from 76 in 1989 to 49 in 1988 and 44 in 1990 (- 35%, a much larger effect than Sale reported in 1973 for his experiments with cv Sebago).
The value of the intercept of the quadratic equation of page 83, 30.3 tubers per m^2, may be explained as the number of tubers formed in absence of foliage. This value is in accordance with the number of premature tubers, referred to by British growers as "little potato" (Burton, 1989), formed from physiologically "worn out" seed, about 6 to 7 per mother tuber, thus approximately 30 per m^2.

In most cases, were intercepted radiation during the first 12 weeks after planting exeeds 300 MJ per m^2, the linear equation of page 83 describes the relationship between intercepted radiation and tuber number adequately.

Mean tuber weight

After tuber initiation, young tubers increase in size during the remaining part of the growing period. PCN infection leads to reduced intergrated ground cover, which affects tuber growth (bulking) accordingly. The relationship between cumulated ground cover and mean tuber dry weight from 12 weeks after planting till harvest, closely fits a linear one. The linear curves obtained for 1990 and 1988 differed in level, but not in slope. The slope of the curve for 1989 was half that of the value of the other two years, corresponding to 1.6 times as many tubers per m^2 in this year (cf. Figs 4 and 5). When the solar radiation in the second part of the growing period was combined with ground cover and then integrated, the intercepted radiation and mean tuber dry weight were linearly related. However, the effect of the year 1989 remained, reflecting the high number of tubers in this particular year (Figs 6 and 7).

Dry matter yield

Total intercepted radiation (MJ per m^2) from emergence to harvest was calculated and plotted against tuber dry matter yield (g per m^2) for these three years. This relationship was well described by a linear curve (Fig. 8), with a slope of 0.85 g per MJ, or 1.18 MJ per g tuber dry matter. This relationship was obtained for the range from 500 to 1650 MJ, with corresponding yields from 0.40 to 1.35 kg tuber dry matter per m^2. These values reflect a range of fresh weight yields of 16 to 54 tons per ha. The conversion of MJ into dry matter is lower than that found by Allen and Scott (1980), who found about 1.1 g tuber dry weight per MJ. After correction for the apparently ineffective green foliage of cv Elles in the period from August 23, 1989 (Fig. 10), the conversion factor increased to 0.96 g per MJ (Fig. 11).

In 1989, from August 23 onwards (Fig. 10), tuber dry matter yield for cv Elles did not increase further, inspite of the still green canopy on the lightly infested plots. Apparently, there was no further contribution of the intercepted radiation to tuber dry weight during this part of the 1989 growing season (Fig. 10).
In 1992 also, a similar behaviour concerning tuber dry matter production was found for the very late maturing cvs Karnico and Elles (Anonymous, 1992a,b,c). Similarly to 1989, the first period of the growing season was exceptionally bright and warm. Thijn (1957) reported that potato crops, although still having green canopies, stopped tuber growth, their foliage apparently 'running idle'. This feature seems to be

associated with exposure of late-maturing cultivars to high temperatures and/or radiation earlier in the season. In 1992, cv Karnico, which is an extremely late-maturing cultivar (2^5), reacted like cv Elles (Anonymous, 1992a,c). Krug (1965) found that, under long day conditions and high temperatures, tuber production of especially late-maturing cultivars came to a halt. It seems that cvs Elles and Karnico also failed to recuperate after a hot spell earlier in the season. Hence, for late-maturing cultivars, care is needed in interpreting ground cover data at the end of the growing season, as experienced in the growing seasons of 1989 and 1992; see also Appendices I to III. Using an infra-red reflection meter (see Chapter VI) may be a better procedure to avoid this type of aberration in assessing yielding capacity of the potato crop.

Tuber dry matter yield can be explained as a highly correlated linear function of the total intercepted radiation (Fig. 11), explaining 94% of the variation. No indication was found of any specific effect of PCN infestation level or drought stress other than through reducing integrated ground cover. Hence, both stress factors, PCN and drought, affect light interception through ground cover, but, apparently, do not interfere with the physiology of production.

It seems that reduction of ground cover during the "pre-bulking" period determines the number of harvestable tubers, whereas ground cover reduction during the bulking period, mainly determines the bulking of the tubers. Grades are determined and therefore, affected by both phenomena.

The data did not indicate any relationship between resistance factors and tolerance. The cvs Darwina and Elles both have hypersensitivity resistance to the local *G. pallida* population, but reacted differently for yield, and hence, differ in tolerance to this population.
Cvs Désirée and Mentor, both susceptible to the local PCN population, clearly reacted differently in ground cover pattern in the first part of the growing season and consequently in tuber number on heavily infested soil at the final harvest. Final tuber yield did not differ significantly (Table 3), as was already indicated by a similar ground cover pattern during the second period (Figs 1 and 2), and a similar bulking (Fig. 3).

The Pa-2 resistant cultivar Darwina did not differ in tolerance from the susceptible cultivars Désirée and Mentor, while the Pa-2 resistant cultivar Elles showed a high level of tolerance.

Drought and PCN attack did not coincide in these trials. This phenomenon is normal for Dutch potato growing conditions. Hence, the small interactions found between PCN infestation level and irrigation for ground cover and intercepted radiation during the first twelve weeks after planting do not imply that there could not be a substantial interaction when drought and PCN attack do coincide. Therefore, the conclusions on drought and PCN interaction can not be extrapolated to other potato growing areas where PCN is a problem and growing seasons start with drought stress.

Conclusions

Ground cover and solar radiation in the first part (12 weeks) of the growing period were found to determine the number of harvestable tubers. Ground cover reduction due to PCN infestation resulted in lower numbers of tubers at final harvest. Cultivar effects were highly significant and considerable.

Integrated ground cover and solar radiation in the second part of the growing period appeared to determine mainly the bulking. Also in this case cultivar effects were significant.

Ground cover and solar radiation in the first as well as in the second part of the growing season determine the grade.

Tuber dry matter production (g per m^2) was linearly related to total intercepted *radiation from emergence to haulm death, data for all years fitting the same curve.* Apart from reduction of ground cover, no indication was found of other specific effects of PCN, whether or not followed by drought.

Tolerance was not found to be related to resistance to PCN, at least not for this group of four cultivars.

For tuber dry matter yield no interaction was found between PCN infestation level and irrigation; effects were additive only.

Chapter VI

Relationship between maturity class, tolerance to potato cyst nematode and to drought, of eighteen potato cultivars

Introduction

The potato plant responds to PCN attack by retardation of growth at the beginning of the season, by delayed tuber initiation and flowering, and by premature senescence of the crop (cf. Chapter I). Within years, apart from infestation level most of the declared variation for tuber dry matter yield was attributed to effect of cultivar and irrigation. The year effect was significant and large, and especially so for groundcover and tuber number (Chapter V). A considerable part of variation in yield between years (Chapter III) might be explained by variation in water supply at critical stages of crop development, interacting with nematode attack, when present. Since cultivars differ in rate of growth and development, and in tolerance to drought (Van Loon 1981, 1986; Beekman and Bouma, 1986), the time of onset and the duration of the drought period have a varying effect on yield (Van der Wal *et al.*, 1978).
The work described here was initiated to determine differences in growth, development and yield of 18 cultivars of varying maturity classes when exposed to PCN infection and drought.

Materials and methods

The experiment was realized in 1990 on a sandy soil with an organic matter content of 5.9 % and a pH_{KCl} of 4.7. The field was naturally infested with potato cyst nematode, identified as *Globodera pallida*, pathotype 2 (Pa-2). The initial density was 53 eggs per g soil. A reduced level of 6 eggs per g soil was achieved by soil fumigation with metham sodium (500 l per ha, 510 g active ingredient per litre), applied on March 14th 1990 with a spade injector (Mulder *et al.*, 1990a). Unfumigated plots were treated with the fumigation machinery in the same way as the fumigated plots, but without applying the nematicide. To avoid differences in the amount of available nitrogen to the crop, soil fumigations were carried out in early spring (Kolenbrander, 1968a,b,c). To allow residual methylisothiocyanate (MITC) to escape, the tillage layer was worked by a rigid-tine cultivator three weeks after fumigation and ploughed five days later to a depth of 25 cm. The unfumigated plots were treated in the same way.

The experiment was designed as a split-split plot with supplemental irrigation of plots, fumigation of sub-plots and cultivars in sub-sub plots. Eighteen cultivars were planted, 30 plants per cultivar in three ridges of ten plants (inter-row distance 75 cm and 30 cm between plants).

Fertilizer (200 kg N, 120 kg P_2O_5 and 180 kg K_2O per ha) was applied according to the advice, based on soil sampling, from the Laboratory for Soil and Crop Analysis, as recommended for starch potato production in the area (Anonymous, 1986).

The cultivars used, represented five maturity classes ranging from early to very late. Maturity class and value (Joosten, 1990) and type of resistance to PCN are given in Table 1.

The seed tubers weighed 50 - 55 g each, and were treated against *Rhizoctonia solani* by dipping in a 3% solution of validamycine (Solacol). They were then pre-sprouted under natural daylight conditions during the four weeks prior to planting. At the time of planting, the seed tubers had reached a stage of development indicated as 212 (Jefferies and Lawson, 1991). Planting was carried out by hand on the 17th of April. Control of late blight and weeds were according to standard farming procedures.

The weather during the growing period, as recorded at the nearby airport of Eelde, was characterized as dry and warm. During the last week of July and in August, temperatures frequently rose to 28 °C and during the growing season, periods of 14 days without rainfall occurred four times (Anonymous, 1990b). Soil moisture content was recorded weekly and when the moisture content of the irrigation plots reached a value equivalent to pF = 2.6, irrigation by an overhead sprinkler system was used at regular intervals to make up for the precipitation deficit, applying 25-35 mm at a time, 210 mm total. In 1990, drought spells started early and a first irrigation was already needed before the canopy closed (25 mm applied on June 5th). Six additional irrigations were needed during June, July and August.

Starting in the fourth week after planting, crop development was periodically measured, using an infra-red reflection meter (Uenk, 1982; Haverkort *et al.*, 1991b), from emergence until maturity (Photo 6.1). The readings were transformed to percentage ground cover, according to the equation $GC = \alpha + \beta \cdot WDVI$[1], given by

[1] WDVI, the Weighted Difference Vegetation Index, is calculated from the readings of the reflection meter, according to: $WDVI = IR - (IR_s/GR_s) \cdot GR\%$, in which IR and GR stand for infra-red and green refections of the crop, and IR_s and GR_s for infra-red and green reflection of the bare soil, measured before emergence.
Until maximum ground cover the percentage ground covered was calculated according to $GC = 1.966 \cdot WDVI$ and thereafter according to $GC = - 8.050 + 2.285 \cdot WDVI$.

Table 1. Maturity class, maturity value and type of resistance to PCN of eighteen cultivars. MV = maturity value: 10 = very early; 1 = extremely late (Anonymous, 1989a; Joosten, 1990). *) = some level of resistance present for the marked factor, but not meeting Dutch standard for resistance.

Maturity class		Cultivar	MV	PCN resistance type
Early	1	Appassionato	7^5	Ro 1,3,4 Pa 2,3
	2	Krostar	7	Ro 1,3 *
	3	Ehud	7^5	Ro 1,4
Mid-early	4	Element	6	Ro 1,4
	5	Belita	6^5	Ro 1,3,4
Mid-late	6	Mentor	5	
	7	Karida	5	Ro 1,3,4
Late	8	Darwina	4^5	Ro 1,3,4 Pa 2
	9	Elkana	4^5	Ro 1,3,4
	10	Prevalent	4	Ro 1,4
	11	Prominent	4^5	Ro 1,4
	12	Vebeca	4^5	Ro 1,3
Very late	13	Astarte	3	Ro 1,3 *
	14	Elles	3^5	Ro 1,3,4 Pa 2
	15	Kardal	3	Ro 1,3 *,4
	16	Karnico	2^5	Ro 1,3
	17	Producent	3^5	Ro 1,3,4 Pa 2 *
	18	Astol	3^5	Ro 1,3,4

Uenk *et al.* (1992). By multiplying these data for the individual cultivars with time (weeks) followed by summation, integrated ground cover was calculated and presented in Figs 3a and 3b.

On October 16, three plants per plot were harvested, the tubers were counted and tuber fresh weight was determined. Tuber dry weight was calculated on the basis of underwater weight (Bosch and de Jonge, 1989).

Results

Ground cover

Emergence was regular for all cultivars, and completed within 7 days. However, immediately after emergence, differences in growth and development became apparent between the two nematode infestation levels. These differences reached a maximum approximately 10 weeks after planting, when ground cover was maximal. Effects of irrigation on growth became apparent in June, when the transpiration levels increased with increasing leaf area, radiation and temperature. These differences in ground cover diminished gradually during the next period of two to three weeks. Later, in the second part of the growing period, differences between treatments increased again due to early senescence, especially in the heavily infested plots. Lack of water, in addition to the effect of nematode infection, accelerated senescence of many cultivars.

Differences between cultivars

Ground cover curves of the eighteen individual cultivars, grouped in the five maturity classes, are shown in the appendix IV. Below, in Fig. 1, ground cover curves are given for the early cultivars only, on lightly infested as well as on heavily infested soil, both with supplemental irrigation (graphs A) and under drought stress (graphs B).

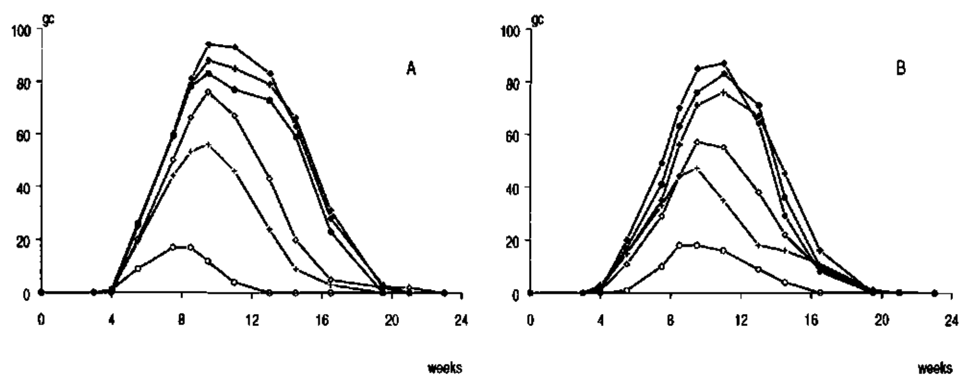


Fig. 1 Percentage ground cover (gc) of the early-maturing cultivars Appassionato (-•-), Krostar (-+-) and Ehud (-♦-) on lightly infested soil (solid symbols) and on heavily infested soil (open symbols). A: irrigated , B: non-irrigated.

The ground cover curves of the three early-maturing cultivars were very similar under light infestation, but those on the heavily infested soil were markedly different. Ground cover of cv Appassionato was strongly reduced by nematode attack, whereas that of cv Ehud was comparatively little affected. Cv Krostar showed an intermediate response. Under drought stress, the initial growth of the three cultivars differed noticeably on lightly infested soil, indicating a different response to drought. Cv Krostar seemed to suffer more from drought than cvs Appassionato and Ehud.

Effect of maturity class

Irrigated plots: Soil water potential was kept sufficiently high so as not to limit growth. On the lightly infested plots, ground cover for all cultivars of all maturity classes increased rapidly, as expressed by an almost straight line between week four and week nine (Fig. 2). Maximum ground cover was realized between 9 and 13 weeks after planting, depending on maturity class. The later maturing cultivars maintained a high degree of ground cover for a longer period than the early- maturing ones (Figs 2 and 3). On heavily infested soil, canopy development was severely retarded and ground cover strongly reduced. Large differences for ground cover between maturity class averages existed, but also differences between cultivars within maturity groups were evident (see Appendix IV). However, ground cover was generally maintained better by later maturing cultivars than by earlier ones (Figs 2A and 2B).

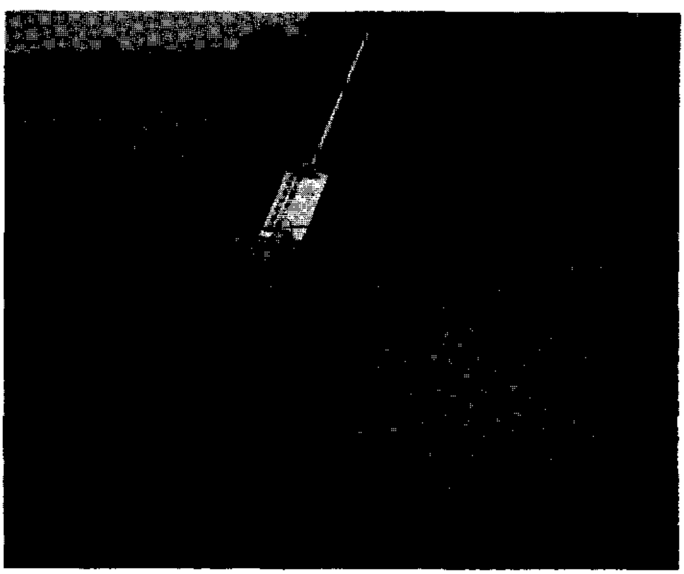


Photo 6.1. Infra-red reflection meter in use.

Non-irrigated plots: Ground cover was significantly lower in non-irrigated plots than in plots under irrigation. The dip in the ground cover curve in week seven (Figs 2C and 2D) reflects the effect of drought stress, in early June, on canopy development. In the second part of the season, lack of water considerably accelerated senescence independently of nematode infection. On the lightly infested plots, senescence of the crops of all maturity classes was accelerated by drought stress (Fig. 2C). All cultivars reached maximum ground cover on approximately the same

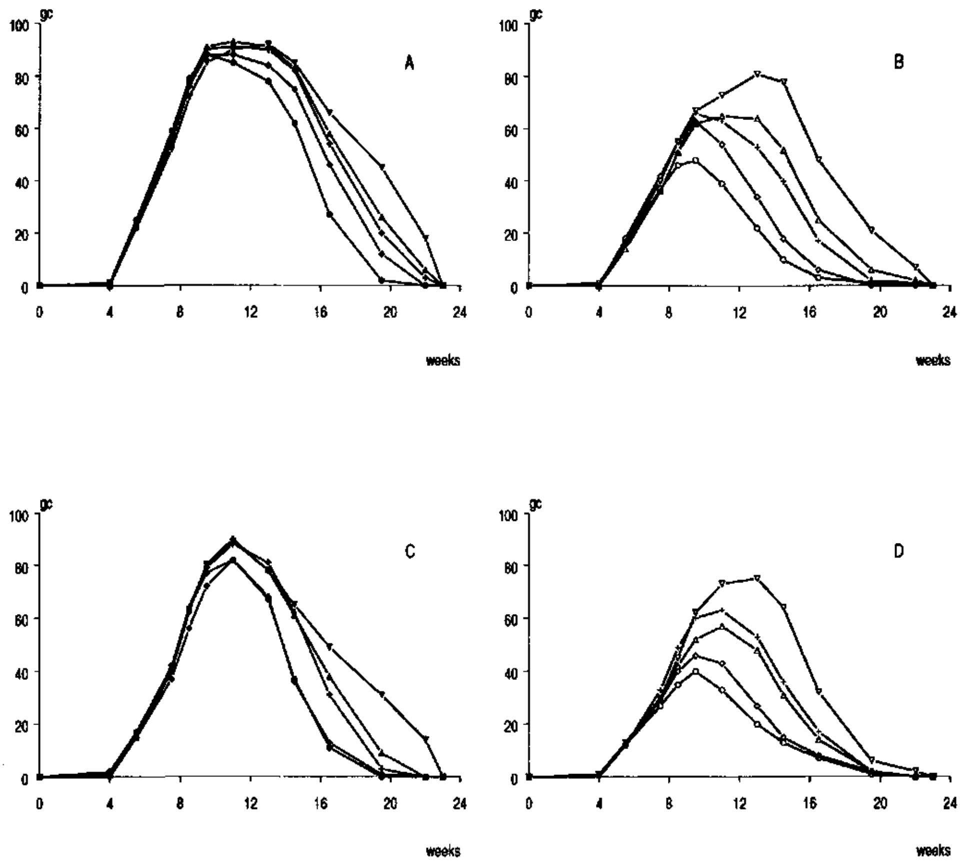


Fig. 2 Average percentage ground cover (gc) per maturity class during the growing season of 18 cultivars, grouped in 5 maturity classes: early (-•-), mid-early (-♦-), mid-late (-+-), late (-▲-) and very late (-▼-); solid symbols lightly infested, open symbols heavily infested.
A: lightly infested, irrigated B: heavily infested, irrigated
C: lightly infested, non-irrigated D: heavily infested, non-irrigated

date, regardless of maturity class. However, at the highest infestation level, maximum ground cover for later maturing cultivars was reached later than for the early and mid early cultivars. This effect was most obvious on the non-irrigated plots (Fig. 2D), but was also observed on the heavily infested, irrigated plots (Fig. 2B).

Intergrated ground cover

Integrated ground cover values have been calculated for each cultivar. These values are given for cultivars grown with and without supplemental irrigation, Figs 3A and 3B respectively. The analysis of variance was performed according to the experimental split-split plot design. The results are shown in Table 2.

Table 2. Results of the analysis of variance for total integrated ground cover from emergence until canopy death for eighteen cultivars, with and without supplemental irrigation, on lightly and heavily infested sandy soil.
*** = P≤0.001, ** = P≤0.01, * = P≤0.05, %dv = % declared variation.

Factors		F-values	%dv
Main effects:	Block	-.-	<0.1
	Infestation level	2639.87 ***	41.7
	Irrigation	2309.74 *	10.8
	Cultivar	19.64 ***	33.5
2-way interactions:			
	Inf.I x Irrigation	68.90 *	1.1
	Inf.I x Cultivar	2.41 **	4.1
	Irrig x Cultivar	0.56	1.0
3-way interaction:			
	Inf.I x Irrig x Cv	0.54	0.9
coefficient of variation		13.7	

Variance analysis shows large and highly significant differences for PCN Infestation level and Cultivar, and a significant and considerable effect for Irrigation (drought). Most of the variation for total integrated ground cover (86%) is explained by the three main factors.

Also there are significant two-way interactions, explaining 5.2% of the variation for total integrated ground cover.

A. *Infestation level x Irrigation* is significant, but small;
B. *Infestation level x Cultivar* is very significant and explains 4.1% of the variability, and
C. *Irrigation x Cultivar*, and the three-way interaction *Infestation level x Irrigation x Cultivar* are not significant.

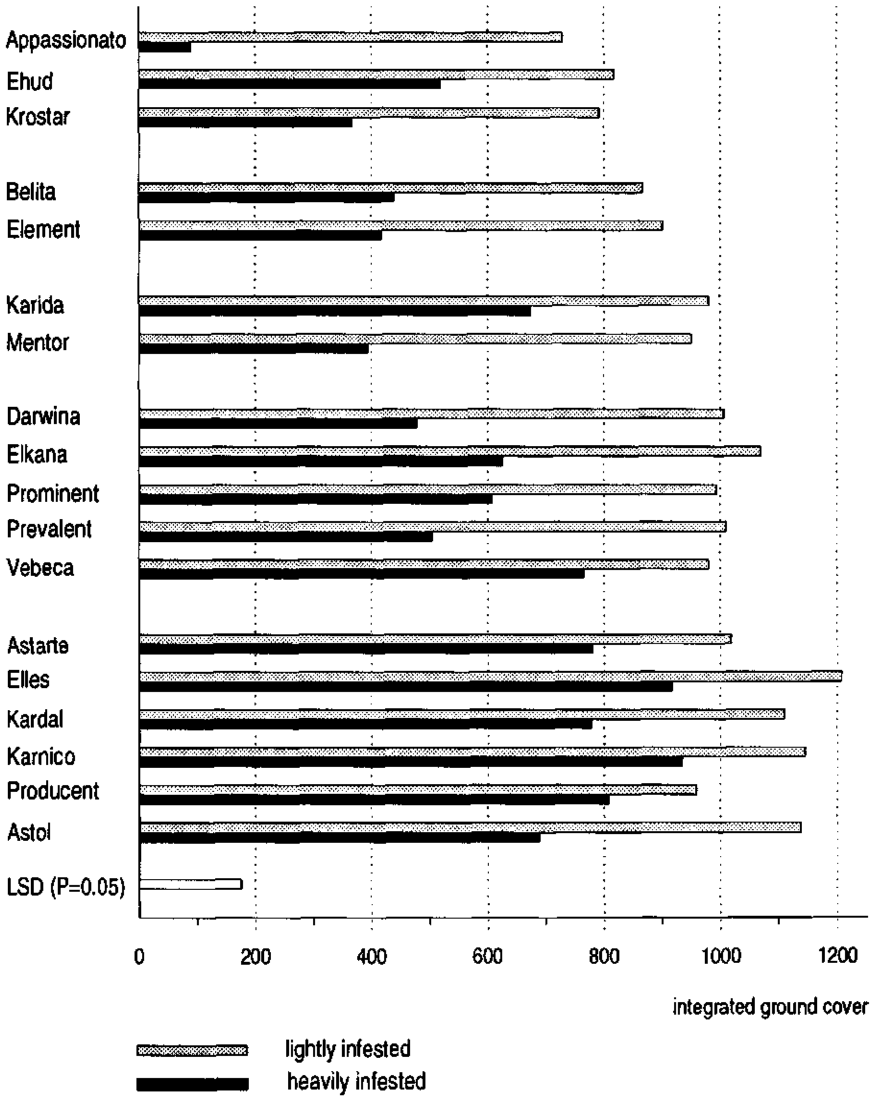


Fig. 3A Integrated ground cover (accumulated percentage ground cover, assessed at weekly intervals during the growing period) for 18 cultivars, grouped according to maturity from early to very late (Table 1), planted on lightly and heavily infested plots with supplemental irrigation.

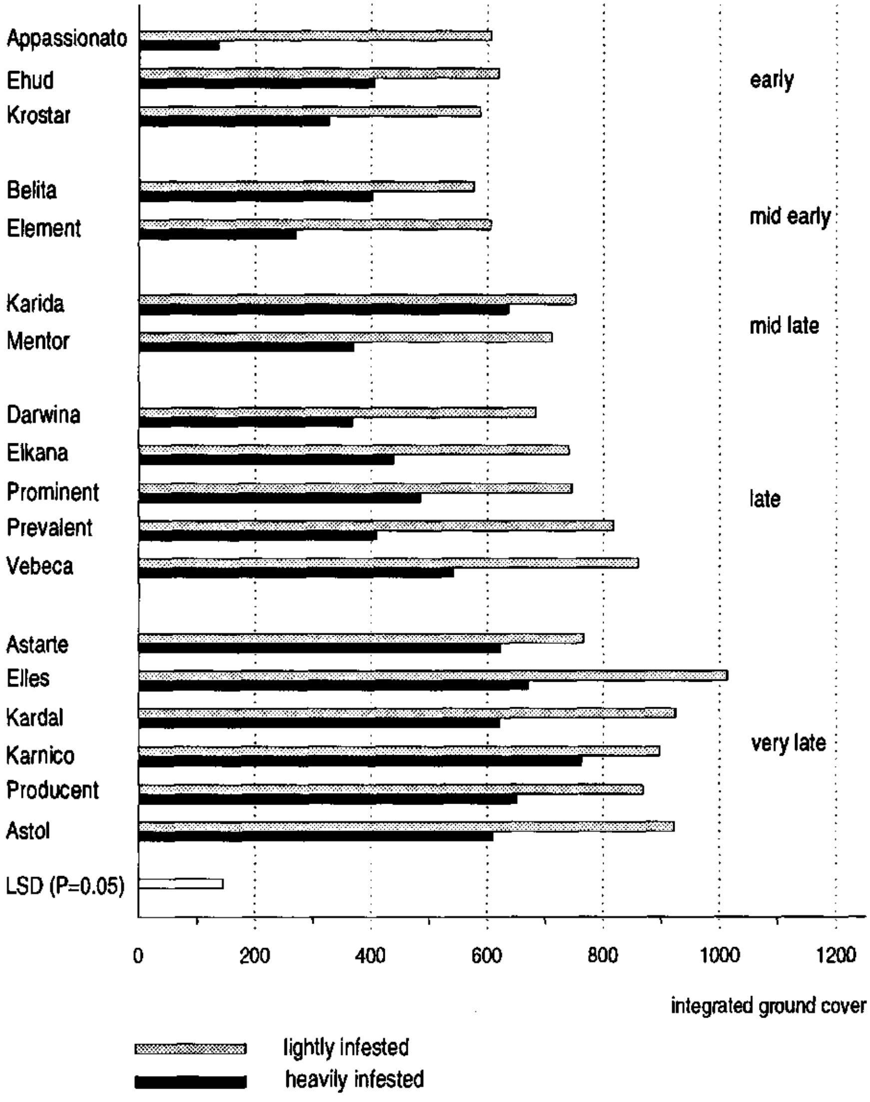


Fig. 3B Integrated ground cover (accumulated percentage ground cover, assessed at weekly intervals during the growing period) for 18 cultivars, grouped according to maturity from early to very late (Table 1), planted on lightly and heavily infested plots without supplemental irrigation.

Effect of PCN infestation levels on crops in irrigated and non-irrigated plots

The differences in area between the ground cover curves on lightly and on heavily infested soil are presented according to the 5 maturity classes for the irrigated plots (Fig. 4A) and the non-irrigated ones (Fig. 4B). The surface of these areas reflects the impact of PCN infection on ground cover, the larger the area, the larger the impact.

On average, ground cover and integrated ground cover of the early- maturing cultivars were more markedly reduced by PCN than those of later maturing cultivars both under irrigation and drought stress. The difference between lightly and heavily infested plots of the early cultivars reached a maximum at about 13 weeks after planting. The differences gradually declined with increasing lateness of the cultivars.
The shape of the curves changes with maturity class from a single topped (early cultivars) to a two topped one (very late cultivars).

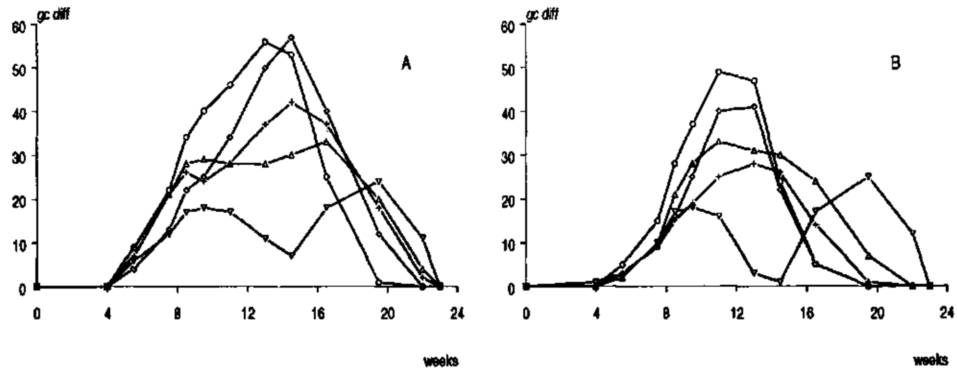


Fig. 4 Differences in ground cover curves between the canopy on lightly infested and on heavily infested soil of the 5 maturity classes (early -o-, mid-early -◇-, mid-late -+-, late -△- and very late -▽-). A: irrigated, B: non-irrigated.

For the early-maturing cultivars, the curve shows a relatively steep increase, a maximum after 13 weeks, and a gradual decrease to zero at harvest. However, the curve for the group of very late-maturing cultivars shows two distinct peaks. At first the difference increases slowly, with the first peak about 9 weeks after planting. It then declines to a minimum value of only 8% under irrigation, and less than 1% under drought stress, both 14 weeks after planting. In the second part of the growing period, differences increase again and reach a second maximum 19 weeks after planting under both irrigation regimes. During the last four weeks of the growing season, differences diminish and become zero, 23 weeks after planting.

The curves of the other three maturity classes fit into this pattern of gradual change from a single peaked, rather steep curve of the group of early-maturing cultivars, via a relatively flat curve of the mid early/mid late-maturing group of cultivars into two peaked curves for the groups of late and very late-maturing cultivars. It must be realized that the curves presented in Figs 4A and 4B reflect average patterns for groups of cultivars. Individual cultivars may deviate considerably from these average patterns, as is shown for the various cultivars within the 5 maturity classes in the figures in Appendix IV.
Summarizing the ground cover data, it became evident that although a clear pattern was found of PCN and drought effects when cultivars are classified according to maturity (Fig. 2), cultivars within maturity class may differ greatly in their response to these stress factors (Fig. 1 and Appendix IV, Figs 1 to 5).

<u>Effect of drought on crops on lightly and heavily infested plots</u>

Differences in area between ground cover curves on irrigated and non-irrigated soil are presented for the five cultivar maturity classes grown on lightly and on heavily infested plots (Fig. 5). On lightly infested soil (Fig. 5A), cultivars of all maturity classes showed an increase in the difference in ground cover from week four onwards. Differences in ground cover reached a maximum at week eight, then diminished to almost zero by week eleven. Subsequently, differences increased again, reflecting the earlier senescence of the plants in non-irrigated plots. After week fourteen, the rate of senescence for most cultivars was higher in the irrigated plots than in the non-irrigated, and is shown here as a decreasing difference in ground cover.
The curve for the mid-early cultivars shows a markedly greater difference than the others, which may be attributed to the relatively greater susceptibility to drought of both cultivars in this group (Appendix IV, Fig. 2).
The early-maturing cultivars showed a maximum difference in ground cover at week fourteen. This was followed by a rapidly diminishing difference in ground cover, due to the faster senescence of the haulm in the non-irrigated plots from week eleven to week fourteen, followed by an accelerated senescence of the crops in the irrigated plots from week fourteen onwards, resulting in a rapid reduction of the difference.

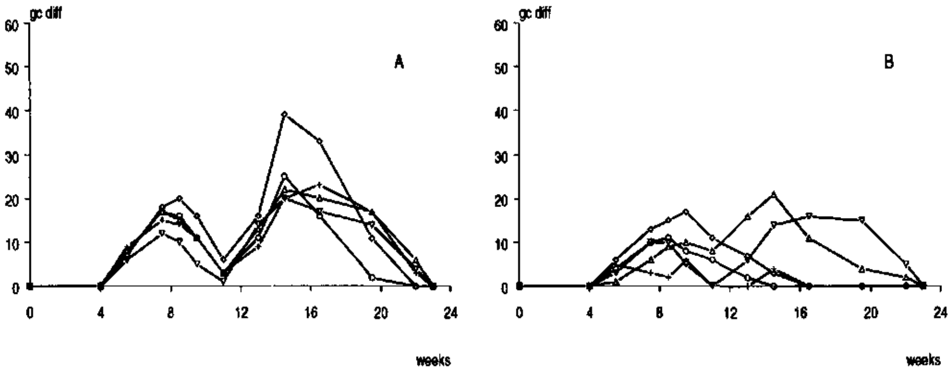


Fig. 5 Differences in ground cover curves between the canopy of potato crops grown with and without supplemental irrigation, of the 5 maturity classes (early -o-, mid-early -◇-, mid-late -+-, late -△- and very late -▽-) on lightly (A) and heavily infested (B) plots.

For the heavily infested plots (Fig. 5B), supplemental irrigation produced a ground cover difference curve for the group of early-maturing cultivars, with a maximum at nine weeks, and for the mid-early-maturing group with a maximum at ten weeks after planting. At week fifteen and sixteen, the differences are reduced to zero.

The group of mid-late-maturing cultivars showed only a small difference in response to irrigation. The ground cover difference curves of the late and very late-maturing cultivars show two peaks: a small peak at week nine, induced by irrigation at the beginning of June, and a larger one, later in the growing season, as this difference becomes much greater. The crops in the irrigated plots maintained ground cover much better than those in the non-irrigated plots. So, the effect of irrigation on ground cover is greater with later maturing cultivars, and this effect is even more pronounced at high PCN infestation levels.

Tuber yield

Tuber yields in g dry matter per m^2 and the results of the analysis of variance are presented in Table 3.

Table 3. Results and anova for tuber yields in g dry matter per m² of the 18 cultivars on irrigated and non-irrigated and on lightly (L) and heavily (H) infested soil. Cultivars are grouped in maturity classes. *** = P≤0.001, ** = P≤0.01, * = P≤0.05, %dv = % declared variation.

Maturity class	Cultivar	tuber yield			
		irrigated		non irrigated	
		L	H	L	H
Early	Appassionato	1153	88	716	152
	Krostar	1223	481	655	385
	Ehud	1227	606	844	455
Mid-early	Element	1397	440	929	233
	Belita	1215	597	938	547
Mid-late	Mentor	1383	460	1245	464
	Karida	1321	836	825	664
Late	Darwina	1211	590	874	459
	Elkana	1100	712	913	391
	Prevalent	1369	611	765	334
	Prominent	1265	733	814	501
	Vebeca	1284	823	899	577
Very late	Astarte	1662	883	809	695
	Elles	1322	1018	949	574
	Kardal	1472	944	1062	553
	Karnico	1370	942	873	752
	Producent	1645	1117	846	824
	Astol	1123	1080	821	673
Mean		1319	720	877	513

Factors		F-values	%dv
Main effects:			
	Block	-.-	0.4
	Infestation level	129.24 **	43.3
	Irrigation	413.06 *	18.4
	Cultivar	6.54 ***	14.1
2-way interactions:			
	Inf.l x Irrigation	10.54	2.4
	Irrig x Cultivar	3.25 ***	7.0
	Inf. l x Cultivar	1.12	2.4
3-way interaction:			
	Inf.l x Irrig x Cv	1.28	2.8
coefficient of variation		18.3 %	

The analysis of variance shows a very significant and large effect for *Infestation level*, a smaller but highly significant effect for *Cultivar*, and a significant and considerable effect for *Irrigation*. Most of the variation (75.8 %) for tuber dry matter yield is explained by these three main factors.

Also, there is a highly significant two-way interaction for *Irrigation x Cultivar*, explaining 7.0 % of the total variation. The two-way interactions *Infestation level x Irrigation*, *Infestation level x Cultivar* and the three-way interaction *Infestation level x Irrigation x Cultivar* are not significant.
With 18.3 % the coefficient of variation is rather high.

Therefore, tuber dry matter yield was greatly affected by PCN infestation, cultivar and irrigation ($P \leq 0.01$), and there is a considerable interaction between Irrigation and Cultivar. For this group of cultivars, with considerable and significant differences for tolerance to PCN and to drought, no two-way interaction was found between PCN and irrigation, indicating that these characters for tolerance to PCN and to drought are additive only and not correlated.

The highest yields were recorded for the fumigated, irrigated plots, averaging 1319 g dry matter per m^2. With 1200 g dry matter per m^2, the early-maturing cultivars all yielded slightly less than average, but the yield differences between cultivars in other maturity classes were relatively small. Only the very late cultivars Astarte, Kardal and Producent yielded substantially above average.
On the heavily infested soil the average yield loss was about 600 g dry matter per m^2, which is over 45%.

Under irrigation, but at high infestation levels, cv Appassionato showed the highest yield loss (Table 2). The cvs Krostar, Element and Mentor also yielded significantly below average under high infestation levels. Although yield losses were recorded for cvs Ehud, Belita, Darwina and Prevalent, these losses were not significant. Significantly better than average yielded cvs Elles, Producent and Astol. The latter being the least affected by PCN, suffering only a 43 g dry matter per m^2, less than 4% under a heavy infestation.

Under drought stress, the pattern changed totally. On lightly infested soil, the average yield was 877 g dry matter per m^2. Only cv Krostar yielded significantly less than average, and only cv Mentor yielded significantly better, followed by cv Kardal. On heavily infested soil, most damage was done to cvs Appassionato and Element, followed by Prevalent and Elkana. Under these conditions cvs Karnico and Producent yielded the best.

The relationship between intercepted radiation and tuber dry matter yield

By multiplying ground cover data of the individual cultivars from emergence to harvest with solar radiation during the growing season (Chapter V, Table 4), total intercepted radiation is obtained. All data on total intercepted radiation from emergence to harvest (ir_{tot}) in MJ per m^2 are ranked from low to high, irrespective of treatments and cultivars, and the mean values of subsequent not overlapping quartets are plotted against tuber dry matter yield (Y) in g per m^2. The relationship is best expressed by a linear curve (Fig. 6).
Consequently, the range of the total intercepted radiation directly reflects the range in yield. Apparently, both PCN and drought affect with ground cover, and hence

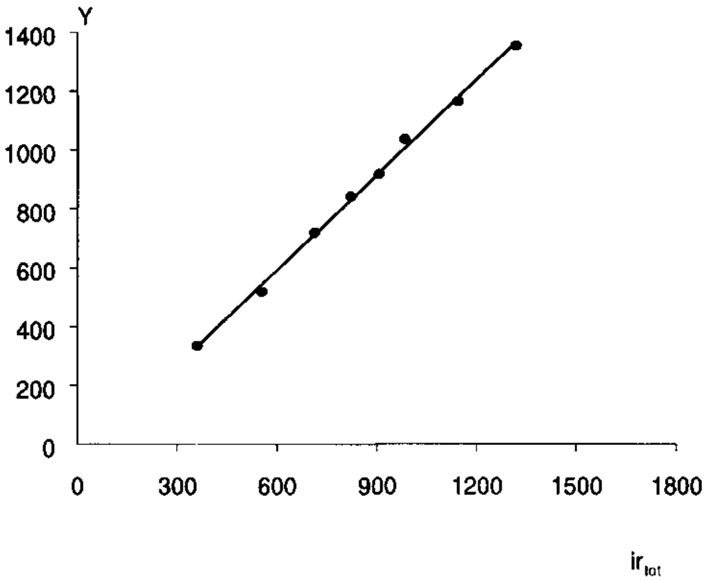


Fig. 6 Yield (Y) in g dry matter per m^2 versus total intercepted radiation (ir_{tot}) in MJ per m^2 from emergence to harvest. $Y = 1.08 \cdot ir_{tot} - 52.6$ ($r = 0.99$)

reduce light interception, explaining the yield reduction almost completely (R^2= 0.99). No indication of other yield-reducing factors were found.

Discussion

Integrated ground cover is found to be related to PCN infestation, irrigation, cultivar and maturity class (Figs 3A and 3B). When the differences of ground cover between high and low PCN infestation are plotted, for both irrigated and non-irrigated plots, a double peaked curve is found for the very late-maturing cultivars, whereas the early cultivars show a single peaked curve. Cultivars belonging to the mid-early, mid-late and late maturity classes show intermediate responses. The curves for differences in ground cover under water stress show slightly lower values for non-irrigated versus irrigated plots, but the patterns are similar (Fig. 4). This phenomenon can be explained by the fact that very late-maturing cultivars recover from infection mainly by forming new uninfected roots over a relatively long period, whereas early-maturing cultivars fail to do so. Growth, reflected as increase in ground cover, was restored and at about 15 weeks after planting the difference of ground cover between lightly and heavily infested plots disappeared. As early-maturing cultivars are already senescent at 15 weeks, a similar recovery is not to be expected for such cultivars. Cultivars, belonging to other maturity classes display an intermediate response.

Differences in response to PCN of cultivars related to maturity class do not mean that all cultivars within a maturity class react similarly to high nematode densities. The early cultivar Ehud showed a markedly better response than mid-early cv Element and the mid-late cv Mentor, and was as severely damaged as the late cvs Darwina and Prevalent.

Although the chances of finding higher levels of tolerance are greater the later the cultivar, the only conclusion can be that, irrespective of maturity class, there is a wide range of cultivar response to high PCN levels. Hence, it is worthwhile also to look for tolerance even in the group of early-maturing cultivars. Since late maturity is not a guarantee of tolerance, clones and cultivars of these maturity classes have to be checked for damage response at high infestation levels. This conclusion unites the often opposing opinions on the relationship between tolerance and maturity class (Evans and Haydock, 1990).

Tolerance to PCN and drought are subject to recurrent discussion. In many experimental designs, the effects of both are entangled and are often confused.

In Fig. 7, the yield losses by PCN are plotted against the losses induced by drought for the 18 cultivars planted in this experiment. The losses are expressed as percentages of the control, viz. the plants on the lightly PCN infested and irrigated plots. The yield loss data were obtained from Table 3, and the numbers in the graph refer to the cultivar numbers in Table 1. Cv Appassionato (1), almost killed by PCN, appeared only moderately damaged by drought, whereas cv Mentor (6), over 60% damaged by PCN, was only slightly affected by drought. This agrees with previous experience with this cultivar and explains why it is popular for its yield stability on drought-sensitive soils. It is, however, severely damaged by PCN. Cv Astol (18) was hardly affected by PCN, but showed a yield loss due to drought of 30%. Cv Astarte (13), a high yielding very late cultivar, lost almost 40% of yield to PCN and over 40% to drought, and cv Elles (14) lost just over 30% to PCN, and also over 30% to drought.

For this group of 18 cultivars, the analysis of variance shows a significant but small interaction between PCN infestation level and irrigation. Therefore it follows, that in this experiment the effects of drought and PCN infection are additive. In general, it can be stated that no significant correlation was found for tolerance to PCN and to drought, ($r = -0.21$; $R^2 = 0.04$). Although the impression might be obtained from Wallace (1987) that selection for drought tolerance implies selection for PCN tolerance, the data presented here contradict such an opinion entirely. Tolerance to drought and tolerance to PCN are two distinct plant characteristics.

The cultivars can be grouped according to maturity class. The early cultivars (1,2,3) show a close-to-average tolerance to PCN and drought, except cultivar Appassionato (1), which is extremely intolerant to PCN and which reacts averagely to

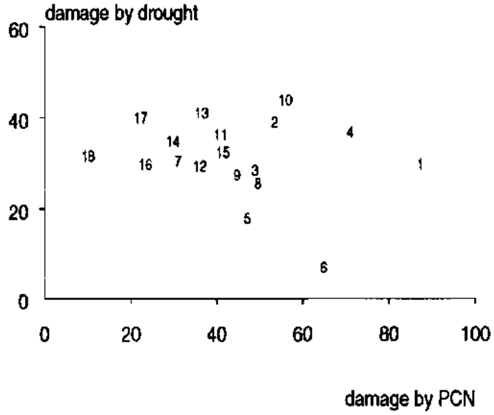


Fig. 7 Damage in percentage caused by PCN (X) versus damage in percentage caused by drought (Y), for the 18 cultivars, given as relative values. Numbers indicate cultivars according to Table 1. $Y = -0.099X + 35.7$ ($r = -0.21$; $R^2 = 0.04$).

drought. The mid-early cultivars (4 and 5) show less tolerance to PCN than to drought. The mid-late cultivar Mentor (6) is well known for its drought tolerance, but is highly intolerant of PCN. Cv Karida (7) shows an intermediate response for both characteristics, as do the late cultivars (8 to 12), except, perhaps, cv Prevalent (10). In this experiment the relative damage by drought was the most severe for cv Prevalent. As expected, the very late cultivars (13 to 18), as a group, are more tolerant to PCN than average. However, their relative yield loss induced by drought does not deviate from the mean.

It is concluded that tolerance to PCN infestation is not related to drought tolerance. On physiological grounds such a relation is not likely to exist. The damage induced by PCN seems merely based on the ability to first 'carry' the load of juveniles inside the root system and sequentiallly to recover and maintain root growth. Some cultivars, such as Appassionato, respond with a total collapse of root growth; consequently growth of the haulm stops, followed by a premature senescence, resulting in yield loss close to 100%. Other cultivars, such as cv Elles, show a temporary reduction in growth, but resume growth after recovery of the root system.

The ability to withstand drought is a different feature. Under the climatic conditions of the Netherlands' starch potato area, drought starts relatively late, when the root system has largely been formed. When cultivars are screened for drought tolerance of the foliage about 10 weeks after planting (Beekman and Bouma, 1986), they differ greatly in recovery from low leaf water potentials. Since intercepted radiation, and thus ground cover, is the main determinant of yield and yield loss (Chapter IV), the ability of the foliage to recover from low water potentials seems essential for tolerance to drought. Here, the root system is not directly so much affected, as with PCN infection, but rather the foliage, which has to recover from low leaf water potentials (Van der Wal, 1981a).

According to Schans (1991), a root system weakened by PCN will predispose the plant to water stress, since the roots do not penetrate the deeper soil layers, and therefore the root system's capacity to take up water is reduced. A high transpiration demand imposed by the environment, even for short periods of drought, might cause a severe reduction of leaf water potential in PCN infected plants. Cultivars sensitive to drought, such as cvs Astarte (13) and Producent (17), will then lose ground cover easily, and suffer yield loss. Others, such as cv Mentor (6), might recover, since their foliage can withstand low leaf water potentials (Van der Wal, unpublished data). However, in our series of field experiments no effects of such predisposition were observed. This may be explained because PCN attack results in reduced canopy development, which is therefore less sensitive to drought than a fully developed canopy of a healthy PCN free crop. Moreover, PCN affected crops show a recovering root system which may be better able to supply the reduced canopy with water than a crop with normal root- and canopy development.

As yield loss inflicted by both PCN attack and by drought is directly related to reduced light interception due to reduced integrated ground cover, tolerance for these cultivar characteristics can be directly obtained by assessing ground cover under stress free and PCN stressed and drought stressed conditions separately. For this procedure only a few plants are needed. It makes early screening for breeding purposes possible.

Conclusions

The disadvantageous impact of PCN and of drought can be directly translated into reduced intercepted radiation, due to reduced percentage soil covered with photosynthetically effective foliage.

With respect to ground cover and associated intercepted radiation, PCN infestation and drought showed a significant but small interaction component; with respect to tuber yield only additive effects were found to be present.

Tolerance to drought and tolerance to PCN were shown to be independent cultivar characteristics.

In general, early-maturing cultivars suffered more from PCN-attack than late- and very late-maturing cultivars. However, cultivars within each maturity group differ considerably in tolerance to PCN.

Production potential on lightly and heavily infested soil can be assessed in field experiments by determining integrated ground cover, from which tolerance can be directly and easily calculated.

A similar procedure can be applied to assessing drought tolerance in field experiments.

Chapter VII

Potato yield on different soils infested with potato cyst nematodes

Introduction

Information on the effect of soil type in relation to PCN damage and tolerance is scarce. Trudgill *et al.* (1978) and Trudgill and Cotes (1983a,b) stated that losses are most severe in sandy soils, more than in peaty soils, as measured by greater yield response to non-volatile nematicides. This lesser response in peat soils, however, could also be due to a greater adsorption of the active ingredients by the organic matter. Gurr (1987) found that the expression of tolerance was strongly influenced by soil type and water availability. However, he did not give details on soil type or water retention.

In this chapter, data collected in a series of fumigation experiments, conducted in the years 1973 to 1984 on sandy and sandy peat soils in the North East of the Netherlands, are analyzed to reveal soil parameters which influence potato yield and yield loss by potato cyst nematodes.

Materials and Methods

Long term experiments were carried out on five sites with different soil types. Soil type, organic matter content (omc), pH_{KCL}, pore volume and specific density (s.d.) are given in Table 1, and the pF-curves of the top soils in Fig. 1.

Sites Rolde (LS1) and Odoorn (S1) are reclaimed heathland; the soil of LS1 is a loamy sand, containing 20.1 % silt (≤ 50µ) in the topsoil, and the soil of S1 is sandy with a low organic matter content. Site Borgercompagnie (S2) is an old sandy peat soil, reclaimed about 300 years ago, which has lost most of its organic matter; site Smilde (SP1) is an old sandy peat soil, reclaimed about 150 years ago, and site Bergentheim (SP2) is a relatively young sandy peat soil, reclaimed about 70 years ago.

Table 1. Characteristics of the top soil of the five experimental fields (for sites see Table 2).

field code	soil type	omc (%)	pH_{KCL}	pore vol. (%)	specific density (g/ml)
LS1	loamy sand	4.4	5.3	45.3	1.56
S1	sand	4.8	5.2	45.9	1.40
S2	sand	7.2	5.1	47.1	1.32
SP1	sandy peat	12.4	5.0	55.1	1.10
SP2	sandy peat	21.9	5.2	63.4	1.08

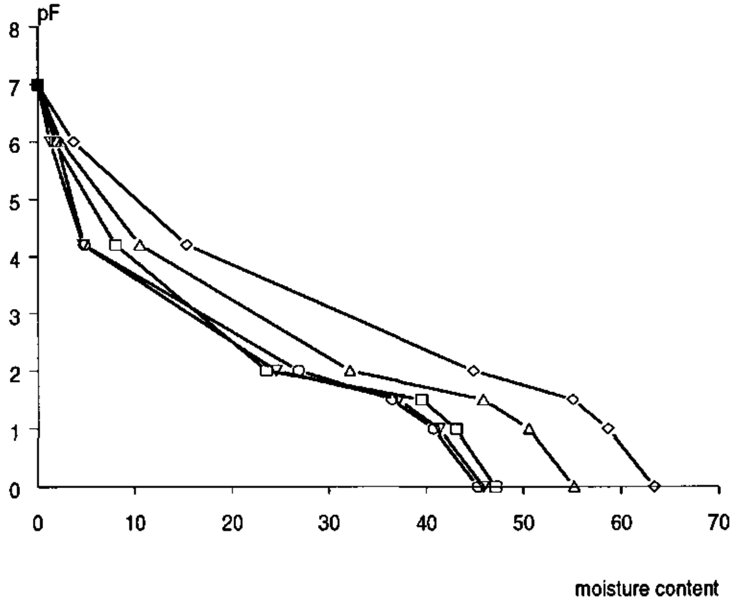


Fig. 1 The pF-curves of top soils of fields LS1 (-o-), S1 (-▽-), S2 (-□-), SP1 (-△-) and SP2 (-◇-). Moisture content as % by volume.

The pF-curve of the topsoil of field SP2 differed clearly from the other four in its slope in the range from pF-2 to pF-3, indicating a greater water retention of this soil compared with the other fields. In this pF-trajectory, the topsoils of the other four fields did not differ much from each other in water retention. The maximum amount of available water in this pF-trajectory is equivalent to 28 mm water (28 l per m^2) for SP2, for the other four fields it was approximately 18 mm.
The subsoil of field S1 was too compact for penetration by potato roots. The relatively loose subsoils of the four other fields allowed root penetration.

With the exception of field S1, which was infested with *Globodera rostochiensis* (Ro-1), all fields were infested with *G. pallida* (Pa-2). The initial densities ranged from almost 0 to over 100 eggs per g dry soil. Fields LS1, S1, S2 and SP1 were in use from 1973 to 1984 and field SP2 from 1981 to 1984 only. An overview of more detailed information is given in Table 2.

On all fields, potatoes were grown every year. On field S1, cv Mentor was grown for nine out of the twelve years and cv Eba for the other three years, 1978, 1979 and 1980. Both are susceptible to *G. rostochiensis* and *G. pallida.* The Ro-1,4 resistant cv Prominent was grown on fields LS1, S2 and SP2. On field SP1, the Ro-1,4 resistant cultivars Ehud (1980 and 1983) and Prumex (1976), and the Ro-1,3 resistant cv Astarte were planted, of which cvs Prumex and Astarte are considered to be more tolerant than cvs Prominent and Mentor (Chapter VI). All cultivars are susceptible to *G. pallida*.

Table 2. Fieldcode and site, the prevailing nematode species, the experimental period and the cultivars used.

field code	Site	*Globodera* species	Experimental period	Cultivars used
LS1	Rolde	*G. pallida*	1973 - 1984	Prominent
S1	Odoorn	*G. rostochiensis*	1973 - 1984	mainly Mentor
S2	Borgercie	*G. pallida*	1973 - 1984	Prominent
SP1	Smilde	*G. pallida*	1973 - 1984	mainly Astarte
SP2	Bergentheim	*G. pallida*	1981 - 1984	Prominent

The experiments were laid out in split-plot designs, in four replicates, sized at least 100 m^2, in average 200 m^2 per plot.
Different nematode densities were achieved by fumigation with a range of dosages of metham-sodium and 1,3-dichloropropene, and by using differences in density of PCN in the field. The fumigations were carried out in autumn, between the first of

October and the sixteenth of November. To counterbalance the differences in nitrogen losses by leaching, due to the inhibition of nitrification on the fumigated plots (Kolenbrander, 1969a,b,c), the unfumigated plots were compensated with an additional amount of 20-40 kg fertiliser N per ha, depending on the organic matter content of the topsoil and the fumigant used.

At least two subplots of 4 m^2 were assigned per plot, for which soil samples were taken and crop development and yield were analyzed. Initial nematode densities were determined by sampling the soil just before planting, taking 200 - 800 ml bulk samples, consisting of 16 cores of 25 cm, taken from the full depth of the tillage layer. The core diameter varied between 1 - 2.5 cm. Preliminary soil sampling per replicate yielded global information on PCN density. For the ultimate sampling sample size was adjusted in such a way that each soil sample contained at least 100 cysts, which was achieved by using different core diameters.
The viability of the cyst contents was determined by staining with New Blue R (Shepherd, 1962).
After senescence of the crops, the tubers were harvested, and the tuber fresh weight and tuber dry matter weight were then determined.

Results

As results for all fields were obtained only for the period 1981 - 1984 and not for the whole period, a test was run to see whether the curves available for both the period 1973 - 1980 and for the period 1981 - 1984 differed on the various sites. No differences were found between periods, but they were found consistently between fields. Regression analysis (Snedecor and Cochran, 1991) of the data collected in both periods on the experimental fields LS1, S1, S2 and SP1 showed that for both periods, the intercepts, as well as the slopes of the curves, did not differ ($P \leq 0.05$). Consequently, the results of field SP2 can be compared with the data for the other fields, pooled over the years. The data of each field over the years were arranged according to increasing nematode densities and grouped into eight P_i classes. The means of these classes were used for further analysis.

The relationship between tuber dry matter yields and initial nematode densities on the three fields LS1, S2 and SP2, planted with cv Prominent, are presented in Fig. 2, as well as of fields SP1 and S1, with other cultivars. Results of analysis of these curves

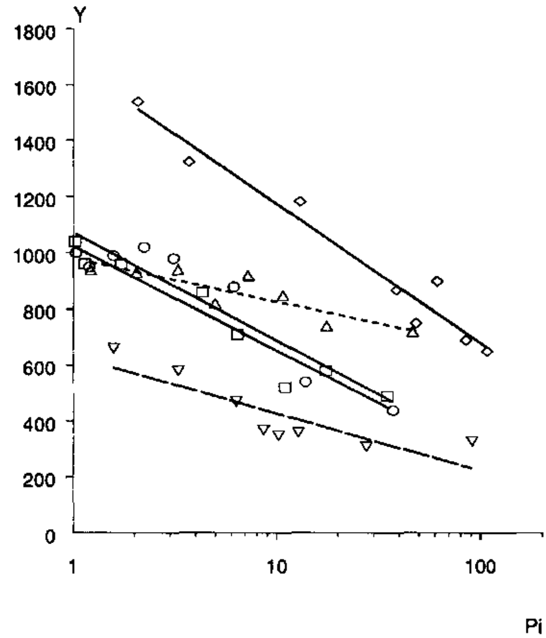


Fig. 2 Tuber yield (Y) of cv Prominent in g dry matter per m² on fields SP2, LS1 and S2 (solid lines), of more PCN-tolerant cvs on SP1, and of cvs Mentor and Eba on S1 (broken lines) in relation to nematode density (P_i) in eggs per g soil, using Oostenbrink's (1966) descriptive equation. Legends: LS1 (-○-), S1 (-▿-), S2 (-□-), SP1 (-▵-), SP2 (-◊-).

Table 3. Field code, intercept (g tuber dry matter per m²) at 1 egg per g soil, slope (g tuber dry matter per log P_i) and R^2 of the curves relating tuber yield (dry matter in g per m²) and maximum nematode density (P_i max as eggs per g dry soil), using Oostenbrink's equation: Y = intercept + slope · Log P_i.

field code	intercept [1] g dm/m²	slope [1] g dm/log P_i	R^2	P_i max eggs/g soil
LS1	1070 b	-380 b	0.86	27
S1	630 c	-200 a	0.74	90
S2	1020 b	-370 b	0.93	33
SP1	980 b	-150 a	0.76	45
SP2	1670 a	-490 c	0.96	106

[1]) Values followed by different characters differ significantly ($P \leq 0.05$).

are given in Table 3. In Fig. 3 the same results are presented as relative yield compared with calculated yields for uninfested soils.
The curves of the fields LS1, S2 and SP1 had almost the same intercepts, ranging from 980 to 1070 g tuber dry matter per m². The curve of field SP2 had a larger intercept (1670), probably related to the high water retention of this soil type (Fig. 1). Field S1 differed from LS1 and S2 in PCN-species, in cultivars used and in subsoil.

Discussion

PCN-species

With respect to the different PCN species on field S1, Schans (1993) indicated, on the basis of experiments carefully designed to study the population dynamics of both species under controlled conditions, that "yield loss due to *G. pallida* could have been slightly greater than that due to *G. rostochiensis*". His findings are consistent with those of Trudgill (cited by Evans and Haydock, 1990), who showed a consistently, slightly greater yield increase due to nematicides for fields infested with *G. pallida* than for fields infested with *G. rostochiensis*. Therefore it is admissible to impute the differences in yield response between field S1 and the other fields to soil type and not to PCN species.
Effect on yield of the nematode species involved is considered to be low (Schans, 1993). The cultivar used on field S1 was Mentor. From field experiments in the past no differential yield interaction to PCN species was found to be present for this cultivar. Apparently, cv Mentor is as susceptible to yield reduction caused by *G. rostochiensis* as it is by *G. pallida*. PCN-species have hardly any different effects on yield levels at the same PCN densities, certainly not at low nematode densities (Schans, 1993). At these low PCN densities, potential yield levels of cvs Mentor and Eba are similar to that of cv Prominent, when not exposed to drought stress (Joosten and Van der Woude, 1985; cf. Chapter VI, Table 2).

Soils

The figures of LS1, S2 and SP2 reflect yields of the cultivar Prominent over a number of years. On SP2 (with 22 % organic matter) the maximum yield was higher than on fields LS1 and S2. Differences in the slopes can be explained mainly by differences in soil characteristics (Table 1 and Fig. 1). Although LS1 and S2 clearly differed in organic matter content, the lower value of LS1 is compensated by a considerable silt fraction of 20.1 % (Table 1).

Soil pH

Soil pH is also known as a factor affecting yield (see Chapter VIII). However, for this series of experiments the pH-range (5.0 - 5.3) was too small to be considered as a significant factor.

Water retention

The poor yield at S1 of 630 g tuber dry matter per m^2, is not fully explained by water retention of the topsoil, since LS1 and S2 had almost similar pF-curves but yielded better, about 400 g dry matter per m^2. The main feature that explains the low yield of field S1 is to be found in the difference of subsoil. The low yield must be largely accounted for by the shallow rooting of the plants, as, contrary to the other fields, the subsoil is very compacted.

Rijtema and Endrödi (1970; cited by Van der Zaag, 1991) found that in the period 1959 - 1966 well irrigated potato crops of four cultivars transpired on average about 275 mm water to produce about 12 tonnes total plant dry matter per ha, which is equivalent to about 230 l water per kg dry matter. This, combined with an average precipitation of some 400 ml during the growing season (cf. Chapter III, Table 2), means that the potato crop on field S1 had the equivalent of 90 mm less water than the crops on the other fields during the growing season.

Water retention characteristics of the soil of field SP1 are similar to those of field LS1 and S2, in the range pF 2 to pF 3. In this field, various cultivars were used. The early-maturing cultivar Ehud has a lower yield potential than the very late-maturing cultivars Prumex and Astarte. The mean yield at low PCN densities of those cultivars hardly differed from the yield potential of cv Prominent. Therefore the intercepts of the curves of the fields S2, LS1 and SP1 were nearly the same.

PCN density / yield regression lines

In Fig. 2, the slopes of all regression lines, except the one of field SP1, are steeper with increasing yield potential at low PCN densities. A similar phenomenon was found earlier (Chapter III, Fig. 2).

The cultivars used on field SP1 were more tolerant to PCN than the cvs Prominent, Mentor and Eba. As with more tolerant cultivars less yield reduction is suffered by PCN attack, the less steep slope of the curve of field SP1 is therefore explained.

Comparison of the regression lines for relative yield (Snedecor and Cochran, 1991; Fig. 3) showed that the slope of the curve of field SP1 differs ($P \leq 0.05$) from the ones for the other fields (Fig. 3). The slopes of the curves for fields SP2, S1 and S2 and

LS1 do not differ significantly. This means that the percentage yield loss per unit increase of log P_i of the fields SP2, S2, LS1 and S1 do not differ significantly. In these fields, cultivars with similar tolerance to PCN were grown, cv Prominent in fields SP2, LS1 and S2 and mainly cv Mentor and sometimes cv Eba in field S1 (see also Chapter X, Table 1). The difference between the curve for SP1 and the other four curves reflects the use of more tolerant cultivars in this field.
The drought tolerance of the cultivars (Mentor and Eba) used in field S1 results in a higher intercept "a" (= absolute yield at low PCN densities), but no effect on the slope of the curve Y_{rel}/P_i was found.

With drought stress, however, cv Mentor suffers less than cv Prominent. With cv Prominent instead of cvs Mentor and Eba, the value of the intercept would have been even lower (Chapter VI, Fig. 8).

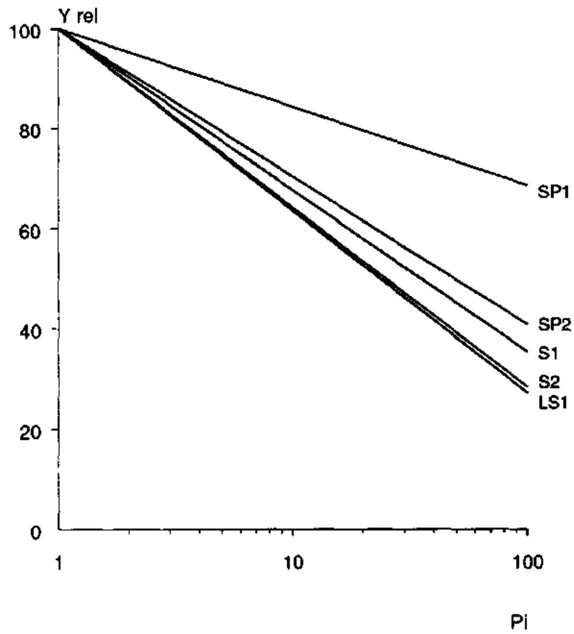


Fig. 3 Relative yield (Y_{rel}) on the five fields in relation with the nematode density (P_i) in eggs per g soil.

Conclusions

In addition to the yielding capacity of the cultivars and tolerance to PCN and drought, the water retention of the top and subsoil largely determines the potential yield level of the fields concerned.

Water retention of both top and subsoil largely determine the yield level (intercept "a" of the yield/PCN density curves) in the different fields.

The slopes of the curves are steeper with increasing yield level. Hence, the higher the yield level, the higher the absolute yield loss.

Increasing tolerance of cultivars to PCN is reflected in less steep slopes of the yield/density curves.

When yield is expressed as percentage of maximum yield, yield reduction related to PCN density does not differ in a significant way, except when tolerant cultivars are used.

Chapter VIII

Effect of soil pH on degree of damage to potatoes by potato cyst nematodes

Introduction

The sandy and sandy peat soils in the North Eastern part of the Netherlands are relatively acid. Traditional crops in this area are potatoes, rye and oats, which tolerate low pH_{KCl} values.
The relationship between pH_{H_2O} and potato yield was already established in the forties by Goedewaagen and De Willigen (1947) and by Schippers (1962).
In the nineteen sixties and seventies, the most common pH_{KCl} values were between 4.5 and 5. The aspiration to grow crops with a higher pH demand, such as sugar-beet, field beans, and peas, resulted in measures to increase the pH. At present, it is advised to maintain a pH_{KCl} for sandy soils of 5.7, when potatoes, sugar-beet and cereals are included in a crop rotation scheme (Anonymous, 1985; 1986). This advice is considered a compromise, balancing unfavourable effects of higher pH level on certain crops, such as potatoes, with favourable effects on others, such as sugar-beet and peas (Loman, 1974).
Preliminary results of crop-rotation trials gave the impression that potatoes were more severely damaged by PCN than expected at pH_{KCl} values over 5 (Wilting, 1990). The first mention of a relationship between pH and damage by PCN was made by Mulder (1990), and the relationship was corroborated by the results of Haverkort *et al.*, (1993).
The aim of the experiments described in this chapter was to obtain data on the magnitude of the effect of soil pH_{KCl} on yield loss of potatoes due to PCN infestation.

Materials and methods

In 1988 and 1989, two field experiments were laid out on PCN-infested sandy soils with a naturally occurring acidity range, with three cultivars, and a cultivar/pH_{KCl} trial with seven cultivars in 1991, on a sandy peat soil.

Field experiments in 1988 and 1989

The first two experiments were laid out on sandy soils, with an organic matter content of 5.0% in the field planted in 1988, and 6.5% in the field planted in 1989.

Four blocks were devised with a range of nematode density plots with 0.1 to 50 viable eggs per g dry soil. The PCN populations were identified as Pa-2. The range of nematode densities was created in previous years by growing cultivars with different degrees of PCN multiplication rates, in combination with the application of nematicides. Densities were determined by sampling the tillage layer of 25 cm of each individual plot prior to planting, followed by hatching tests, to determine the numbers of viable eggs and juveniles. Data were ^{10}log transformed after adding 1, to account for PCN densities < 1 viable egg or juvenile per g soil.

The pH_{KCl} values were measured for each individual plot. In the field of 1988 pH_{KCl} values ranged from 4.9 to 6.1, and in the field of 1989 from 4.7 tot 5.6.

In both years, cultivars Astarte, Darwina and Elles were planted. Tubers, sized 35-45 mm, were treated against *Rhizoctonia solani* with validamycine (Solacol), pre-sprouted, and planted by hand in the third week of April. The arrangement of plants was 75 · 30 cm. Fertiliser (NPK) was applied according to the recommendations for starch potato production in the area, as given by the Laboratory for Soil and Crop Analysis (Anonymous, 1986). Cultural, weed and late blight control measures were according to standard farming procedures. During the growing season of 1988, irrigation was not necessary. In 1989, the crop was irrigated seven times by an overhead sprinkler system, 25 - 30 mm per round. In October, after senescence of the crops, 40 plants (9 m^2) were harvested, and tuber fresh weight and underwater weight of 5000 g of tubers were determined. Based on these data tuber dry matter weight was calculated according to Bosch and De Jonge (1989).

Field experiment in 1991

The experimental site planted in 1991 was a sandy peat soil with an organic matter content of 11.7%, and a very light regularly distributed *G. pallida* infestation, not exceeding 2.0 eggs per g soil. In preceding years, pH_{KCl} levels ranging from 4.7 to 6.3 were established in a trial aimed at testing the effect of pH_{KCl} on the growth of sugarbeet, starch potatoes and cereals (Wilting, 1990, 1991; Houtman and Wilting, 1992). In addition to cvs Astarte, Darwina and Elles used in the prior experiments, also cvs Elkana, Karnico, Mentor and Producent were planted by hand on April 20, 1991. The experiment was executed in the same way as the 1988 and 1989 experiments.

Results

Experiments in 1988 and 1989 with three cultivars.
Results of the analysis of variance on effect of the factors *Experimental field, Cultivar, Soil pH* and *Infestation level* on tuber dry matter yield are presented in Table 1.

Table 1. Results of the analysis of variance for the effect of soil pH on yield of three potato cultivars on PCN infested fields. *** = P≤0.001 * = P≤0.05 %dv = % declared variation.

Factors		F-values	%dv
Main effects:			
	Experimental field	0.12	<0.1
	Cultivar	12.66 ***	10.9
	Soil pH	49.04 ***	21.1
	Infestation level	110.41 ***	47.6
2-way interactions:			
	Exp. fld x Cultivar	0.31	0.3
	Cultivar x Soil pH	0.27	0.2
	Cultivar x Inf. level	4.10 *	3.3
3-way interaction:			
	Cv x pH x Inf. level	3.96 *	3.1
coefficient of variation		15.2	

The analysis of variance shows no effect on tuber dry matter yield of the factor *Experimental field*, and highly significant and large effects of the factors *Cultivar, Soil pH* and *Infestation level.* Most of the variation (79.6%) for tuber dry matter yield is explained by these three main factors, being 10.9, 21.1 and 47.6% respectively.
Also, there is a significant but small two-way interaction for *Cultivar x Infestation level* which explains 3.3% of the total variation. The two-way interactions *Experimental field x Cultivar* and *Cultivar x Soil pH* are not significant.
Finally, there is a significant but small three-way interaction *Cultivar x Soil pH x Infestation level* which explains 3.1% of the total variation.

The significance of the two-way interaction between *Cultivar* and *Infestation level* expresses the differences for tolerance to PCN between the three cultivars. The absence of an interaction between *Experimental field* and *Cultivar* and between *Cultivar* and *Soil pH* indicates that the three cultivars used react in the same way to the experimental field and to soil pH.

The significance of the three-way interaction between *Cultivar*, *Soil pH* and *Infestation level* indicates that the tolerance expression of the cultivars does not only depend on PCN infestation level, but also on soil pH.

As the analysis of variance shows that the factor *Experimental field* had no effect on the way the cultivars responded to the different fields (in two years) and to soil pH-values, it is permissible to combine the data of the 1988 and 1989 experiments. They were grouped into three pH classes, $4.7 \leq pH_{KCl} \leq 5.0$, $5.0 < pH_{KCl} \leq 5.5$ and $5.5 < pH_{KCl} \leq 6.1$. In each class, the yield/Pi-combinations were sorted according to increasing nematode densities and grouped into four mean values. Averaged over the three cultivars there are large and significant effects of soil pH (Figs 1 and 2, Table 2).

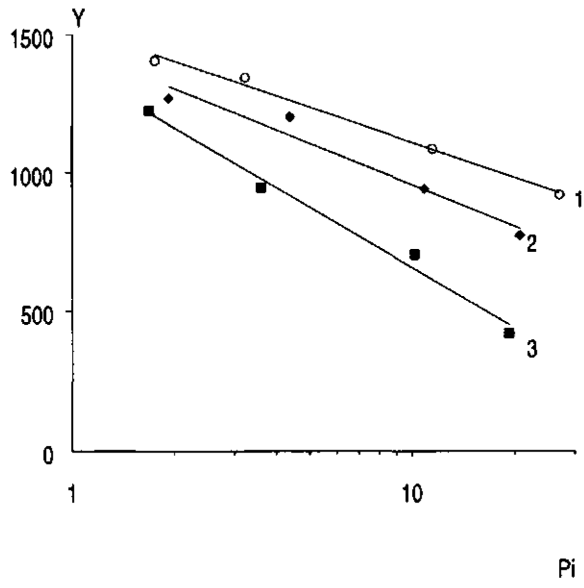


Fig. 1 Relationship between tuber yield (g dry matter per m²) and initial PCN densities (P_i = eggs per g soil) at three pH_{KCl} levels. 1) $pH_{KCl} \leq 5.0$, 2) $5.0 < pH_{KCl} \leq 5.5$ and 3) $pH_{KCl} > 5.5$. Data based on averaged yields of cvs Astarte, Darwina and Elles in the 1988 and 1989 experiments.

Table 2. Effect of PCN density, log (P_i), on yield for three soil pH_{KCl} ranges. Y = yield.

pH_{KCl} range	equation	correlation (r)
$4.7 \leq pH_{KCl} \leq 5.0$	$Y = 1530 - 421 \cdot \log(P_i)$	0.995
$5.0 < pH_{KCl} \leq 5.5$	$Y = 1452 - 497 \cdot \log(P_i)$	0.986
$5.5 < pH_{KCl} \leq 6.1$	$Y = 1378 - 722 \cdot \log(P_i)$	0.995

With increasing pH values, the damaging effect of PCN infestation becomes greater as is shown by the slopes of the three regression lines (Fig. 2).

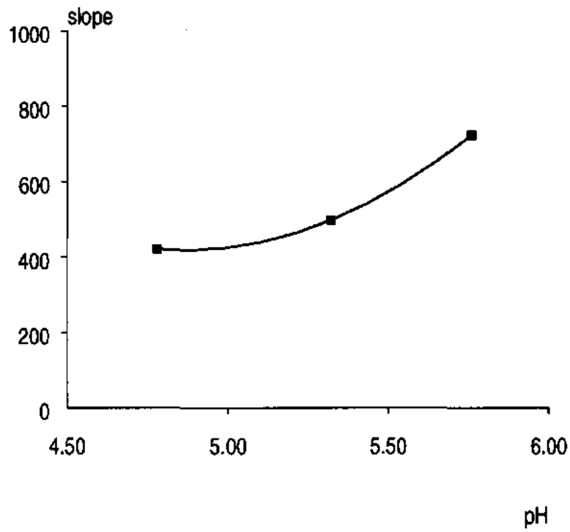


Fig. 2 The relationship between the slopes of the yield/density curves and the mean pH_{KCl} value of the three classes. Slope = $9365 - 3679 \cdot pH_{KCl} + 378 \cdot pH_{KCl}^2$ [$g \cdot m^{-2} \cdot \log Pi^{-1}$]

In conclusion, the 1988 and 1989 experiments on the sandy soils showed a highly significant effect on yield by PCN, cultivar and pH_{KCl}. Tolerance expression of cultivars does not only depend on PCN infestation level, but depends also on soil pH.

The 1991 experiment with seven cultivars

The results are presented in Table 3.

Table 3. Effect of pH_{KCl} on tuber yield (g dry matter per m^2) at low PCN densities (P_i=1.6 eggs per g soil) of seven cultivars on a sandy peat soil. Different letters indicate significant ($P \leq 0.05$) differences.

cultivar	pH_{KCl}		
	4.7 - 5.5	5.8	6.3
Astarte	1108 b	1111 b	901 c
Darwina	938 c	868 c	703 d
Elkana	1119 b	1054 b	1062 b
Elles	1085 b	959 bc	883 c
Karnico	1294 ab	1323 a	1309 ab
Mentor	1177 ab	1109 b	907 c
Producent	1187 a	1188 ab	1122 b
mean	1119 ab	1087 b	984 bc

LSD = 143 ($P \leq 0.05$); coefficient of variation = 15.1.

Within the group of seven cultivars no pH_{KCl} effect on yield was found within the pH_{KCl} range of 4.7 - 5.5. At pH_{KCl} = 5.8 cvs Darwina and Elles showed a significant yield reduction. Cvs Astarte and Mentor showed a significant reduction only at the highest pH_{KCl} = 6.3, and cvs Elkana, Producent and Karnico showed hardly any response to pH_{KCl} with respect to yield. The results show that there exists a clear *cultivar x pH* interaction for this set of seven cultivars ($P \leq 0.05$) at pH_{KCl} levels above pH_{KCl} = 5.5.

Discussion

A clear effect of pH_{KCl} on tuber yield, as indicated by Goedewaagen and De Willigen (1947), Schippers (1962) and Loman (1974), was also found in our experiments in all years. Goedewagen and De Willigen found that damage to the root system occurs at lower pH_{KCl} values than those reducing tuber yield. The results of twelve field experiments in the province of Drenthe with cvs Aristo, Irene, Libertas and IJsselster, carried out on sandy soils with pH_{KCL} values ranging from 4.2 - 5.2, indicated a marked negative effect of increasing pH_{KCl} values on tuber dry matter yield of ware potatoes (Schippers, 1962), and Loman (1974) found, on average, maximum tuber yields in

the pH_{KCl} range between 4.6 and 5.0. All their data apply to potato crops grown under PCN-free conditions. In our experiments, in the absence of PCN or at very low infestation, all cultivars tended to yield less at pH_{KCl} > 5.5 than they did in the pH_{KCl} range of 4.5 - 5.5, but the yield reduction response was highest at the highest pH_{KCl} = 6.3. Data obtained from experiments conducted in 1991 showed a *cultivar x pH* interaction, in agreement with results of Goedewaagen and De Willigen (1947).
With PCN present in the soil, pH_{KCl} affected yield at lower values than it did in the absence of PCN. Goedewaagen and De Willigen (1947) found that the root system, root mass, as well as rooting depth, is already adversely affected by increasing pH_{KCl} before yield reduction is observed. Hence the root system has a buffering capacity to compensate for damage. Both increasing pH_{KCl} values and PCN reduce this buffering capacity, with the ultimate result that damage is more severe with increasing pH_{KCl} and shows up at lower pH_{KCl} values than without PCN infection and visa versa. This effect of pH_{KCl} on root growth and yield was confirmed by Groenwold and Bus (1985). As indicated by the three way interaction components, it seems likely that the combined effect of PCN and pH_{KCl} on yield is cultivar specific. The data collected until now are insufficient to assign these interaction values to each cultivar individually.

Conclusions

On average there is a considerable negative effect of increasing soil pH_{KCl} on yield.

However, cultivars differ greatly in pH_{KCl} tolerance. Cvs Darwina and Elles are sensitive to increasing soil pH_{KCl}, whereas cv Karnico shows no sensitivity.

PCN infection aggravates the effect of pH_{KCl} concerning yield depression. Both PCN infection and increasing pH_{KCl} values reduce the buffering capacity of the root system.

Testing for yield as well as for tolerance to PCN infestation should be realized at a range of pH_{KCl} values, as found in the target area. This refers to breeding as well as cultivar trials.

In trials for tolerance knowledge of pH_{KCl} values of the soil is indispensable.

Chapter IX

Model for yield estimation of cultivars under various soil conditions and PCN infestation

Introduction

Reviewing the results in the previous chapters, the various components which determine potato yield on PCN infested fields can be formulated quantitatively. It seems straightforward to express the tolerance of cultivars as a proportion of yield loss due to PCN under comparable conditions (Schäfer,1971). The yield is of utmost importance to farmers, and in this respect relative yield loss due to PCN is not the only determining factor. Yield depends on the production level of a cultivar without PCN minus loss due to PCN. As a consequence, a higher yielding cultivar with a higher relative yield loss may yield better than a less productive cultivar with a low relative loss. This phenomenon is also described by Evans and Russell (1990). For starch potato growers, only tuber dry matter yield is of importance.

The aim of this chapter is to incorporate the aspects of PCN infestation, drought and soil pH (including the interactions of the various stress factors on yield) in a model for yield estimation, using an adapted Oostenbrink equation, as presented in Chapter III.

Predictability

Some factors, such as those related to the weather (amount and distribution of precipitation and solar radiation) are unknown and unpredictable at the time of planting. Others can be determined, or are known beforehand, such as those related to soil condition and cultivar. They form the basis for choosing the best cultivar for a given set of conditions. The analysis does not predict growth and yield, since the weather can not be forecast for the entire growing season. The approach presented here is, therefore, essentially a risk analysis. It is based on a set of characteristics of soil and cultivar (known at planting) and their various relationships which have been determined over many years.

Proposed basic model

The relationship between yield and nematode density is adequately described by Oostenbrink's (1966) equation. Yield effects due to PCN densities less than 2 eggs per g soil are insignificant concerning yield reduction, and values of $P_i < 1$ are cumbersome for the implication of the model. Therefore, for practical purposes this formula is slightly adapted by replacing log P_i by $\log(P_i+1)$:

$$E(Y) = a + b \cdot \log(P_i+1) \qquad (1)$$

in which: E(Y) is the estimate of tuber yield in g dry matter per m^2,
P_i the initial PCN population density in eggs per g soil,
a represents the potential yield level, and
b yield loss per unit log of PCN infestation (eggs per g soil).

Yield potential (a)

The value of parameter a, the yield under stress-free conditions (potential yield), is mainly influenced by yield potential level of the cultivar, soil water retention, soil pH and soil fertility, hence the yield under the described conditions.

Cultivar

Tuber dry matter yield is directly related to the amount of intercepted radiation during the growing period, and therefore to earliness of ripening of the cultivars. For cultivars of all maturity classes, listed in the Dutch Cultivar List for Arable Crops, tuber dry matter production is given as a relative figure (Y_{rel}), ranging from 60 for cv Minerva to 120 for cv Kardal (Anonymous, 1991a). In this value, the effect on yield of the earliness of the cultivars is included, and similarly the effect of the duration of the growing period on yield. Experimental evidence of yield maximizing trials for starch production over three successive years resulted in a possible yield for cv Astarte (Y_{rel}=115, and an estimated 24% dry matter) of approximately 80 ton per ha (Van der Zaag, 1984). For the purpose of this model the average relative tuber dry matter yield (Y_{rel}=100) under stress-free conditions is calculated at 1650 g tuber dry matter per m^2 for the sandy and sandy peat soils in the north eastern parts of the Netherlands.

Soil water retention (WR)

Yield depends on the potential yield of the cultivar for the soil concerned, the water retention of the soil and the water supply. The better the water retention and the water supply and the more drought-tolerant the cultivar, the less the cultivar suffers from drought.

Potential yield and water retention of the soil are known parameters. The quantitative effect of drought and the resulting yield reduction can be obtained by calculating average yields for the cultivars concerned over a number of years on soils which differ in water retention. With the help of such parameters, a cultivar's drought tolerance can be calculated for use in potato growing advisory systems and for associated decision-making models. With the limited data available at present, an example is given showing how such parameters can be calculated. For this purpose the results are used from Chapters VI and VII.

The best soil found (field SP2) in the experiments described in Chapter VII, had a water retention of 30 mm in the topsoil, with an estimated additional 10 mm available from the subsoil: 40 mm in total. The soil with the poorest water retention was field S1 with 20 mm available water, obtainable from the topsoil only, since the subsoil was impenetrable for roots.

The cultivar's reaction to drought stress influences the yield and, therefore, its response to drought must be considered for the purpose of advisory systems. As such data were not yet available, drought tolerance values (TV_{dr}) were calculated from the data of Chapter VI as the ratio of tuber yield under non-irrigated conditions to tuber yield of a crop free of drought stress (Chapter VI, Table 1).

The best soil (SP2) was assigned a yield response factor of 1.00 (point A in Fig. 1). On medium type soils with WR=30 mm (LS1 and S2), a yield response value of 0.63 (point B in Fig. 1) was obtained for cv Prominent (TV_{dr} = 0.66). For the poorest soil, a yield response factor of 0.38 (point C in Fig. 1) was calculated as relative yield for cv Mentor (TV_{dr} = 0.93) on field S1, compared with its obtainable yield on field SP2. These last two values are based on the average yield over twelve years without PCN (Chapter VII) and/or soil pH (Chapter VIII) interaction.

After sufficient data are obtained the real shape of the curves can be calculated. For the present exemplifying approach the curves concerned are dealt with as if they are straight lines, from point A through point B and from point A through point C respectively.

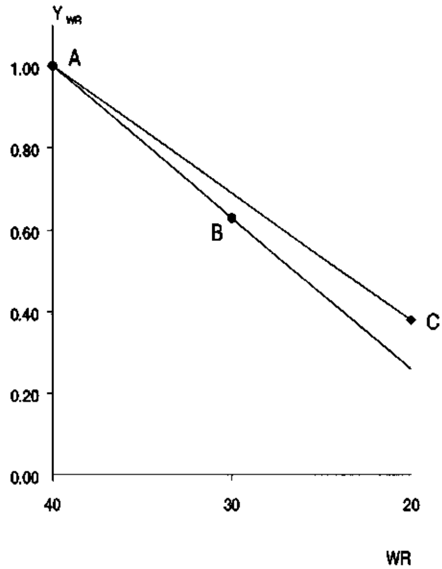


Fig. 1 The effect of the water retention (WR in mm) of the soil on the relative yield for the cvs Mentor (upper line) and Prominent (lower line).

The corresponding equations for the cvs Mentor and Prominent are:

$$\text{cv Mentor:} \quad Y_{WR} = 1.00 - 0.031 \times (40 - WR) \qquad (2)$$

$$\text{cv Prominent:} \quad Y_{WR} = 1.00 - 0.037 \times (40 - WR) \qquad (3)$$

Since cv Prominent is more drought-sensitive than cv Mentor the corresponding points for the ultimate curve for cv Prominent will always be situated below the one for cv Mentor.

The water retention factor (F_{WR}) is now introduced. This factor indicates which part of the potential yield remains at a known water retention of the soil and a given drought tolerance value of the cultivar. It is necessary to use this factor because the drought tolerance characteristic of a cultivar becomes more important the lower water-retention of the soil. On a soil with a water-retention of 40 mm it does not make any difference whether a drought-tolerant or a drought-sensitive cultivar is used. The water-retention factor (F_{WR}) depends on the steepness of the Y_{WR}/WR curves, values of which are given in Fig. 2.

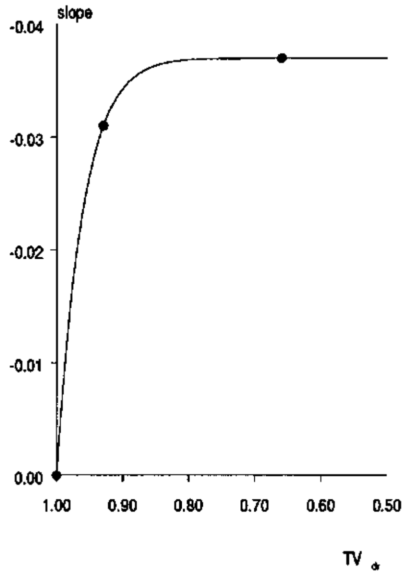


Fig. 2 The effect of the cultivar's drought tolerance value on the slope of the Y_{wr}/WR-curve.

For the present approach, with a linear relationship, the best fit was calculated with the curve fitter option in the graphical programme "Slide Write Plus" version 5 (Daniele and Wittering, 1992), yielding the following equation:

$$\text{slope} = a + b \cdot x^{c} \qquad (4)$$

in which: x = TV_{dr} of the cultivar concerned, and
a, b and c are, with this linear approach, constants with values of - 0.037, 0.037 and 25.07 respectively.

Now the water-retention factor can be calculated according to the equation 5:

$$F_{WR} = 1.00 - (a + b \cdot x^{c}) \cdot (40 - WR) \qquad (5)$$

Soil acidity

From pH_{KCl} 4.7 to 5.5, pH has no effect on yield, although root growth is reported to be affected at lower pH values (Goedewaagen and de Willigen, 1947). In the pH_{KCl}-range (4.7 to 6.3) encountered in the field, soil pH values above 5.5 reduced yield levels. Cultivars appear to differ in tolerance to pH (Chapter VIII, Table 3).
The pH tolerance value (TV_{pH}) is the yield proportion realized at $pH_{KCl} = 6.5$ compared with the yield at $pH_{KCl} = 5.5$.

The pH tolerance values of the cultivars[1] are derived from Table 3 of Chapter VIII, and are calculated according to the equation:

$$TV_{pH} = 1 - \frac{1 - Y_j / Y_i}{pH_j - 5.5} \qquad (2)$$

in which: Y_i is the yield for $4.7 \leq pH_i \leq 5.5$ and Y_j is the yield for $pH_j > 5.5$.
This Tolerance Value for pH indicates the yield that remains when soil pH increases by one unit above pH_{KCl}=5.5.
To formulate the effect of pH tolerance of a cultivar (TV_{pH}) at a given pH_{KCl} the pH tolerance factor (F_{pH}) was developed:

for $5.5 \leq pH_{KCl} \leq 6.3$,

$$F_{pH} = 1 - (1 - TV_{pH}) \cdot (pH_{KCl} - 5.5) \qquad (3a)$$

and for $4.7 < pH_{KCl} < 5.5$

$$F_{pH} = 1.0 \qquad (3b)$$

This pH tolerance factor, F_{pH}, determines the effect of pH on the yield of the cultivar (TV_{pH}, Table 1) at a given pH. It is expressed as yield decrease per unit pH_{KCl}.
pH values below 4.7 and over 6.3 were not present in the experimental fields, hence no conclusion on effects of these pH ranges on yield can be given.

[1] In this report, such values refer exclusively to cultivars bred and used for starch production in sandy and sandy peat soils in the north-eastern parts of the Netherlands.

Soil fertility

Plant nutrients (N,P,K,Ca,Mg) are applied according to the recommendations for starch potato production in the area. The amounts added are based on the results of soil sample analysis by the Laboratory for Soil and Crop Testing. Hence, soil fertility is considered here to be optimum.

Cultivar characterization

The cultivars can be characterized by their yield potential, and tolerance to PCN, drought and pH, expressed as relative yield (Y_{rel}) and their respective tolerance values TV_{PCN}, TV_{dr} and TV_{pH}. These factors have been determined for seven cultivars (Chapters VI and VIII, Table 1.

Table 1. Relative yields (Y_{rel}) and tolerance values for PCN (TV_{PCN}), drought (TV_{dr}) and pH (TV_{pH}) of seven cultivars.

Cultivar	Y_{rel}	TV_{PCN}	TV_{dr}	TV_{pH}
Astarte	1.15	0.72	0.59	0.83
Darwina	0.95	0.49	0.74	0.70
Elkana	1.10	0.64	0.72	0.90
Elles	1.10	0.81	0.76	0.73
Karnico	1.15	0.79	0.72	1.00
Mentor	1.00	0.55	0.93	0.74
Producent	1.10	0.84	0.60	0.95

Parameter 'a', the potential yield for cultivar and field concerned, may yet be formulated as:

$$a = Y_{pot} \cdot Y_{rel} \cdot F_{WR} \cdot F_{pH} \tag{6}$$

in which: Y_{pot} = 1650 g tuber dry matter per m², the estimated yield under stress-free conditions for a cultivar with Y_{rel} = 100% in an average year;

Y_{rel} = relative yield, given as a percentage (Anonymous, 1991a), and used as proportion;

F_{WR} = the soil water retention factor;

F_{pH} = the soil pH factor.

In the absence of PCN, a = Y_{pot} for a cultivar with an average yield level (Y_{rel} = 1.00), grown on a soil with pH_{KCl} < 5.5 and with a good water retention (WR = 40 mm). On this type of soil the cultivar's level of drought tolerance has no impact, at least not over a number of years. However, in extremely dry years, even on these soils, absence of drought tolerance will show its effect in reducing yield loss; but for the present "risk analysis", drought tolerance is not considered a prerequisite for potato growing on such soils.

e.g. *A cultivar with a Y_{rel} = 1.15, grown on a soil with a water retention of 40 mm and a pH_{KCl} = 5.0, will yield, averaged over the years, 1650 · 1.15 = 1900 g tuber dry matter per m^2, equivalent to about 80 tons tuber fresh weight per ha (with 23.7% dry matter, equivalent to an underwater weight of 455 g per 5000 g tuber). On average, tolerance of drought, pH and PCN are of no consequence for yield, since soil conditions are optimal, and $log(P_i)$ = 0.*

Yield reduction due to PCN (b)

The extent of absolute yield reduction depends on the potential yield (a), the slope of the yield/PCN density (Y/P_i) curve of equation (1) and the level of PCN infestation of the soil.

The value of parameter b, the (expected) slope of the curve is mainly determined by:
- the potential yield (a),
- the tolerance of the cultivar to PCN,
- the interaction between P_i and drought, and
- the interaction between P_i and pH

PCN infestation level, the cultivar's tolerance to PCN infection and the interaction between P_i and pH can be known before planting, but drought remains an unknown factor, since, in addition to the water retention of the soil, it is dependent on the amount and distribution of precipitation during the growing season.

Potential Yield (a)

The higher the potential yield, the higher the absolute loss the crop suffers by PCN infection. This is expressed by a steeper slope of the Y/P_i-curve with increasing yield levels (Chapters III and VII).

Tolerance to PCN (TV_{PCN})

The use of tolerant cultivars results in a less steep slope (b) in the yield/PCN density relationship, compared with more sensitive cultivars, grown under the same conditions (Chapter VII, Fig. 2, curve for field SP1 versus curves for field LS1 and field S2).

In accordance with equation (1), tolerance is now expressed as the proportion of the yield remaining after an increase of PCN population density with one unit $\log P_i$, in the range of $0 \leq \log P_i \leq 2$. The tolerance value for a cultivar is calculated by equations (7) to (10). Given a PCN infestation level of Pi_i and a second level of Pi_j ($Pi_i < Pi_j$), and the corresponding yields of Y_i and Y_j ($Y_i > Y_j$), the slope b_1 is the factor determined by the tolerance of the cultivar used (TV_{PCN}), and is calculated according to equation (7):

$$b_1 = \frac{Y_i - Y_j}{\log(Pi_j) - \log(Pi_i)} \qquad (7)$$

Then Y_0, the yield at log $(P_i) = 0$, is calculated according to the equation:

$$Y_0 = b_1 \cdot \log(Pi_i) + Y_i \tag{8}$$

and the fraction yield loss per unit log (P_i) is then:

$$b_1 / Y_0 \tag{9}$$

The cultivar's tolerance value to PCN (TV_{PCN}) is the remaining yield fraction:

$$TV_{PCN} = 1 - b_1 / Y_0 \tag{10}$$

The PCN tolerance value (TV_{PCN}) is a relative value, but using equation 1, in which the relative yield of the cultivar is included as well as the potential yield, the absolute yield of any cultivar at any initial PCN population density (P_i) can be estimated.

Interaction between Drought and PCN

Interaction between drought and PCN may only occur when both stress factors act simultaneously. PCN affects a potato crop in the early stages of growth. In the Netherlands, however, drought spells usually occur later in the growing season, after the crop's canopy has closed. Until now, no indication has been found that a *drought x PCN* interaction plays an important role in tuber yield during these later periods of drought (Chapters V and VI). At present, a cultivar-specific interaction factor for drought and initial PCN density is not included in the equation, but can be easily incorporated if conditions so require.

Interaction between pH and PCN.

At similar nematode densities with increasing soil pH values, increasing damage by PCN was demonstrated (Fig. 1, Chapter VIII). To quantify how much the slope of the Yield/PCN density curve increases with increasing soil pH, an interaction factor (F_{pHxPCN}) is calculated, by which the cultivar tolerance value for PCN (TV_{PCN}) must be multiplied, correcting it for the soil pH value. Although a significant *Cv · pH · PCN* interaction was also found, and therefore the *pH · PCN* interaction seems cultivar-specific, this interaction is not included here only because the cultivar specific data are not yet available.The three cultivars, of which data are available for two years, seem to respond slightly more to pH than average (Chapter VIII, Table 1). The relationship between this interaction factor and pH_{KCl} is depicted in Fig. 3 and is best described by a third order equation (11).

$$F_{pHxPCN} = 15.70 - 9.95 \cdot pH + 2.239 \cdot pH^2 - 0.1675 \cdot pH^3 \qquad (11)$$

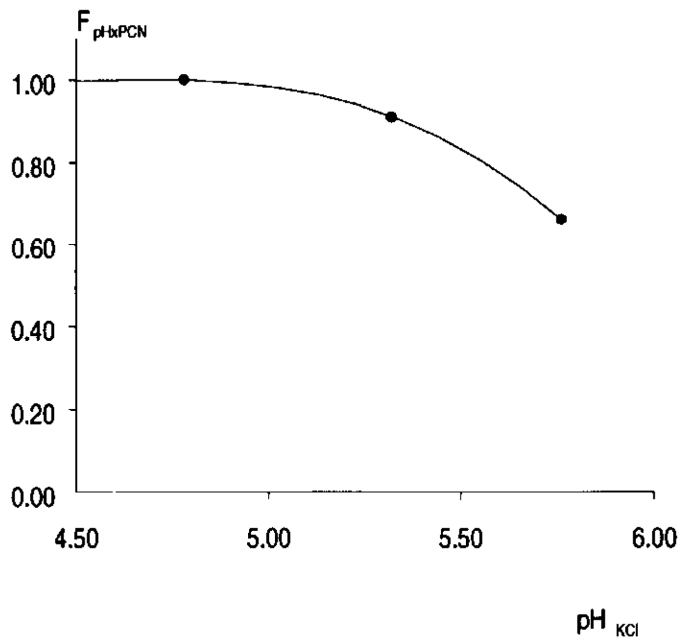


Fig. 3 The interaction factor F_{pHxPCN} for different pH_{KCl} values of the soil.

Parameter "b" can now be expressed as:

$$\mathbf{b} = -\,\mathbf{a} \cdot (1 - TV_{PCN} \cdot F_{pHxPCN}) \qquad (12)$$

where: a = value of intercept,
TV_{PCN} = cultivar's tolerance value to PCN,
F_{pHxPCN} = pH · PCN interaction factor.

In Chapter III it was demonstrated that, averaged over the cultivars, the slope of the yield/PCN density equations became less steep at lower yield levels, coinciding with less precipitation. The effects of drought tolerance of the cultivars and water retention of the soils are already incorporated in parameter "a". Since the amount of precipitation expected during the growing season can not be predicted at the time of planting, it is pointless to incorporate precipitation as an additional factor determining the slope of the Y/P_i curve.

The model

Combining all obtained yield/PCN density regulating factors gives the equation:

$$E(Y) = a_1 + b_1 \cdot \log(P_i+1)$$

where:

$$a_1 = Y_{pot} \cdot Y_{rel} \cdot F_{WR} \cdot F_{pH}$$

and

$$b_1 = - a_1 \cdot (1 - TV_{PCN} \cdot F_{pHxPCN})$$

with:
- $E(y)$ = expected yield,
- Y_{pot} = yield potential of a cultivar with a Y_{rel} = 100 % under stress-free conditions (estimated at 1650 g tuber dry matter per m²),
- Y_{rel} = relative yield, given as a percentage (Anonymous, 1991a), and used as proportion,
- F_{WR} = Soil water retention factor,
- F_{pH} = the pH tolerance factor,
- TV_{PCN} = PCN tolerance value,
- F_{pHxPCN} = pH · PCN interaction factor, and
- P_i = initial PCN density.

For the above mentioned parameters the following input parameters, which can be used directly to calculate the required corresponding parameter, are available:

- Y_{pot} = yield potential of a cultivar with a Y_{rel} = 100 % under stress-free conditions (estimated at 1650 g tuber dry matter per m²),
- Y_{rel} = relative yield, given as a percentage (Anonymous, 1991a), and used as proportion,
- WR = water retention of the top and subsoil in mm between pF 2 and pF 3,
- TV_{dr} = drought tolerance value of a cultivar,
- TV_{PCN} = PCN tolerance value,
- TV_{pH} = pH tolerance value,
- P_i = initial PCN density, and
- pH_{KCl} = soil pH.

Once a cultivar is selected and planted, the actual yield will depend on the weather. For the Netherlands this means mainly the amount and distribution of rainfall and solar radiation. Irrigation is then the only way of influencing yield in cases of drought stress, that can be influenced by man.

Chapter X

Importance of pH and tolerance to PCN and drought to crop husbandry, breeding and potato processing industry

Introduction

In Chapter IX, a model is described which relates the effects of the stress factors PCN, drought and pH to the growth, development and yield of potato crops. This model helps farmers to select the best yielding cultivars to be grown in any particular field, provided they are well informed about soil properties, PCN infestation level and cultivar characteristics, such as potential yield and tolerances to PCN infection, drought and soil pH.

Dutch farmers have easy access to information about soil condition and cultivar characteristics. Soil and crop analysis can be performed on request and for an acceptable price, and the well known Dutch list of cultivars for arable crops summarizes a range of important cultivar characteristics. The experimental data presented in Chapters V and VI indicate that tuber number and tuber yield can be assessed by estimation of intercepted radiation through periodical infra-red reflection measurements. In this chapter, possible further applications are considered.

Cultivar choice based on expected yield

When preparing a cropping plan for the coming season, the farmer uses the available information about his fields and the cultivars of the crops to be grown. In addition to important soil borne pests and diseases, soil pH and water-retention of top and subsoil are of prime importance. In the north-eastern parts of the Netherlands, where mainly starch potatoes are grown, the texture of the sandy and peaty soils constitutes a good biotope for many species of (plant-parasitic) nematodes. Currently, *Globodera pallida* is a major threat to starch potato production. The nature of the PCN population in the field should contribute substantially to the choice of the cultivars used, based on their resistance spectra and tolerance levels.

With proper information on the soil (PCN infestation level, pH and water-retention) and the cultivar (tolerance to PCN, drought and pH), the farmer is able to maximize tuber yield. Tolerance values of the various stress factors, PCN, drought and pH (Table 1) have been developed for a number of cultivars. Such figures can be used directly to calculate the cultivars expected performance on a specific field in an average year.

Table 1. Tolerance values of 18 cultivars for PCN, drought (dr) and pH, (TV_{PCN}, TV_{dr} and TV_{pH}). Cultivars with an * were bred in the last fifteen years and selected for tolerance to PCN. - = unknown. Data from field experiments of the Hilbrands Laboratory for Soil-borne Pests and Diseases.

cultivar	TV_{pcn}	TV_{dr}	TV_{pH}
Appassionato	0.45	0.70	-
Astarte	0.72	0.59	0.83
Astol	0.92	0.68	-
Belita	0.54	0.82	-
Darwina	0.49	0.74	0.70
Ehud	0.57	0.71	-
Elkana	0.64	0.72	0.90
Element	0.49	0.63	-
Elles *	0.81	0.76	0.73
Karida *	0.81	0.69	-
Kardal	0.56	0.67	-
Karnico *	0.79	0.72	1.00
Krostar	0.55	0.61	-
Mentor	0.55	0.93	0.74
Producent *	0.84	0.60	0.95
Prominent	0.58	0.66	-
Prevalent	0.47	0.56	-
Vebeca	0.67	0.70	-
mean	0.64	0.69	0.83

However, these stress factors do not always act independently. Some interactions have proved to be important, therefore these should also be considered (this thesis).

The field stress factors - yield model developed in Chapter IX provides a tool to combine the various soil and cultivar characteristics and their interactions. Examples are given in Tables 2 and 3.
In Table 2, the expected tuber yield of four cultivars is given for a heavily infested field soil (12 eggs per g of soil), with pH_{KCl} = 5.2 and a water-retention of 35 mm.

Table 2. Values of the intercept a (potential yield), the slope b (yield reduction per log unit PCN infestation) and E(Y), the expected yield potential at the given set of values for the various soil and cultivar characteristics (cf. equations 1, 12a and 12b of Chapter IX). Y_{rel} = relative yield, F_{WR} = soil water-retention factor, F_{pH} = soil pH factor, F_{pHxPCN} = interaction factor for soil pH and PCN, and TV_{PCN} = the PCN tolerance-value of the cultivars.

cultivar	Y_{rel}	F_{WR}	F_{pH}	a	F_{pHxPCN}	TV_{PCN}	b	E(Y)
Astarte	115	0.82	1.00	1685	0.95	0.72	-553	1090
Darwina	95	0.82	1.00	1390	0.95	0.49	-799	560
Elles	110	0.82	1.00	1615	0.95	0.81	-404	1195
Mentor	100	0.84	1.00	1520	0.95	0.55	-775	710

The effect of pH and water-retention of the soil at a PCN infestation level of 12 eggs per g of soil is presented in Table 3. It is shown that, irrespective of water-retention, increasing pH_{KCl} level of 5.2 to 5.7 on this heavily infested soil results in approximately 30% yield loss. When pH_{KCl} equals 5.7 and water-retention equals 25 mm, the expected yields become too low to grow starch potatoes economically.

Table 3. Expected tuber yield in g dry matter per m² on a soil with P_i = 12 eggs per g and differing in pH_{KCl} and water-retention (WR) in an average year.

pH_{KCl}	5.2	5.7	5.2	5.7
WR (mm)	35	35	25	25
Astarte	1090	740	600	400
Darwina	560	360	310	200
Elles	1200	800	650	320
Mentor	710	460	450	290

PCN Tolerance

Restricted use of pesticides will lead to higher levels of PCN infestation. PCN-tolerance is a prerequisite in all farming systems; the use of non-tolerant cultivars will become very limited in the near future.

As a result of the increasing interest by breeders in tolerance in recent years, more attention has been given to the PCN-tolerance of new cultivars. The cultivars which have been recently developed are, on average, considerably more tolerant than those of some 20 years ago (Table 1).

The inheritance of tolerance to PCN (Arntzen, 1993) appeared not to be based on a single factor, but to be rather a quantitative characteristic. Such characteristics are not easy to handle in breeding programmes and often require large numbers of plants to screen. In order to reduce the number of plants as early as possible, it is necessary to perform screening for tolerance of PCN as a routine in the early stages of the programme.

No indication was found that tolerance of a cultivar to massive invasion of the juveniles by maintaining root growth was associated with maturity class. A simple pot screening method for root growth at a high infestation level was found to correlate well with yield ($r = 0.87$). Late-maturing cultivars did apparently recover better from initial root growth retardation than early ones, as clearly indicated by ground cover patterns. For 52 cultivars, 76% of the variation of tolerance was explained by the initial root growth response to infection (Chapter IV). The remaining 24% might well be attributed to the effect of maturity class on yield of PCN infected plants. These findings were confirmed by Arntzen (1993).

Screening for tolerance to PCN is therefore relatively simple.The root test described in Chapter IV made use of 1 litre containers. Recent experiments with transparent closed polystyrene containers with a volume of only 150 cc, showed that an initial screening for tolerance, based on root growth, might well be possible, at least for a negative selection, identifying the intolerant genotypes.

Resistance to PCN and tolerance are not genetically linked, but these characteristics can be combined in one genotype (Van der Wal, 1978; Arntzen 1993). When a tolerant cultivar is also resistant, yield loss is not only reduced, but the increase of PCN populations is checked at the same time. It appears to be a matter of planning the breeding programme to combine tolerance and resistance in single cultivars.

Drought- and pH-tolerance
As indicated above, a first step with respect to tolerance to drought and pH is the screening of existing cultivars for these characteristics, and to list the tolerance values for both characteristics, preferably in the list of cultivars for arable crops. Also, screening of breeding material seems feasible, and one should consider the further development of tests for tolerance to drought and pH.

Estimating tuber number and tuber yield

Tuber number
In a search for factors which determine yield and yield loss to PCN, and which can be measured in the field, ground cover was measured and related to tuber number and tuber yield (Chapter V and VI). Field experiments with four cultivars during three successive years indicated that the tuber number was related to intercepted radiation in the first 12 weeks after planting, and was described (r=0.98) by the equation:

$$N_t = 0.000137 \cdot IR_1^2 - 0.0281 \cdot IR_1 + 30.3 \qquad (1)$$

in which: N_t is the number of tubers per m^2 and IR_1 is the intercepted radiation (MJ per m^2) during the first twelve weeks after planting. Tuber number increases with increasing intercepted radiation, and, as a consequence, the average tuber weight usually decreases. This shift in grade is of importance to seed growers and potato processing industries.

Tuber dry matter yield
All data on intercepted radiation and yield, collected with the use of the infra-red reflection meter for ground cover, fitted (r=0.995) the equation:

$$Y = 1.08 \cdot IR_{tot} - 52.6 \qquad (2)$$

in which: Y is tuber dry matter in g per m^2 and IR_{tot} is the total intercepted radiation in MJ per m^2 from planting to harvest.

The situation 12 weeks after planting might not only be used to estimate tuber number using equation (1), but also provides an opportunity to make a first estimate of the final yield. Crops under stress, whether induced by PCN or by drought, always produced less ground cover in the first 12 weeks, and they always matured earlier than non-stressed crops (Chapter VI), and the yields concerned appeared to be reduced proportionally. Thus, the intercepted radiation in the first twelve weeks after planting forms the basis for a first assessment of final yield.

The second part of the growing season has increasing effects on yield the later the cultivars mature. Due to weather variation yield concordingly differs with time. Hence, the longer the second part of the growing period the larger the modifying effect of weather conditions will be. Therefore, the estimate of final yield, based on the intercepted radiation during the first part of the growing season will be more precise for early cultivars than for later maturing ones.
Continuing assessment of intercepted radiation in the course of the second part of the growing season will increase the accuracy of the estimate of final tuber yield, especially so the later the cultivar.
Measuring ground cover in the second part of the growing season (e.g. after the 1st of July) at weekly or 10 day intervals to calculate the intercepted radiation will serve this purpose. Such yield estimates are useful for those involved in the logistics of transport, stock control, planning processing capacities in the various industrial plants, and allocation of storage capacities.

Other nematodes than PCN

In the last 25 years, the chemical control measures aimed at controlling PCN also have helped to control a number of other nematode pests at the same time. Crop rotation (potatoes, sugar-beet and cereals) combined with soil fumigation has kept populations at low and sometimes undetectable infestation levels. This does not mean, however, that the nematodes have disappeared. With the expected reduction in the use of nematicides in the Netherlands, the average level of PCN infestation will increase in areas where quarantine regulations do not require the absence of PCN. Recently, field observations indicate a comeback of "old" nematode problems, such as *Meloidogyne hapla*, *Pratylenchus penetrans* and *Paratrichodorus pachydermus/Trichodorus similis* (Mulder *et al.*, 1990b). Unfortunately, potato cultivars tolerant to PCN are not equally tolerant to *Meloidogyne hapla* (Mulder and Veninga, 1988b).
The potato breeders are well aware of these developments and associated risks (Van der Haar, 1991).
Other biotic stress factors, such as the fungi *Rhizoctonia solani* and *Verticillium dahliae* also influence crop development and yield. It should be investigated whether similar eco-physiological approaches might be applied.

Conclusion

With the information presented in the previous chapters of this thesis, there is a good scope for implementation of yield prediction models to aid the farmer with cultivar choice, and for breeding strategies to obtain potato cultivars which combine resistance and tolerance to PCN. They also seem a useful tool for those involved in logistics, transport and stock control.

Summary

Potato cyst nematodes (*Globodera rostochiensis* and *G. pallida*) are a serious threat to potato production in many countries. Since these nematodes became established in Western Europe, literature on them has become extensive, certainly with respect to their biology and ecology. Chapter I presents an overview of tolerance, which is the capacity of a cultivar to suffer less yield loss, compared with other cultivars under the same conditions.

Tolerance is discussed in relation to resistance, which is the capacity of a potato plant to check PCN multiplication. Tolerance seems to depend mainly on the way the cultivar is able to respond with minimal growth delay to the massive invasion of second stage juveniles. However, the yield loss in PCN infested fields appears to be influenced by many more factors, such as maturity class of the cultivars, soil factors, drought, and other diseases and pests.

Various authors have given different equations to describe the yield/PCN-density relationship. The equations given by Brown, Oostenbrink, Seinhorst and Elston *et al.* have been discussed, and their properties analyzed (Chapter II). In field experiments with PCN densities (Pi) ranging from 1 to 100 viable eggs per g soil, Oostenbrink's equation: Yield = a + b LogPi proved to fit as well as, or even better than, other more complicated models (Chapter III). Precipitation in a crucial part of the growing season affected the yield/PCN density relation significantly. In years with a reduced precipitation and lower yield levels, the absolute yield loss per unit increase of LogPi was less than in years with ample rainfall and high potato production.

In three greenhouse tests, 52 cultivars were screened for growth response to a PCN infestation level of 300 eggs per g soil. Twenty out of these 52 cultivars were then tested in the field and the data of three years of field experiments were compared with those obtained in the greenhouse tests. The tolerance differences between cultivars, based on yield data, appeared to be largely correlated with the differences in initial growth response determined ten weeks after planting in the greenhouse on heavily infested soil, based on root and shoot growth (R^2 = 0.76; Chapter IV).

This phenomenon was the motive to study the growth performance of various cultivars in the field over a number of years and under varying conditions of PCN infestation,

soil type and weather. When necessary, overhead irrigation supplemented precipitation to avoid drought stress. The large scale experiments with four cultivars conducted over three successive years, are described in Chapter V. They all resulted in a simple equation relating yield and intercepted radiation. It was consistent over the years for the cultivars and treatments. Tuber number and, consequently, the grade were closely correlated with the intercepted radiation in the first twelve weeks of the growing season, irrespective of treatment. A quantitative basis of this relationship is given.

In a following field experiment, 18 cultivars were planted to obtain more information on the specific responses of cultivars and to detect possible interactions. Ground cover patterns of all cultivars belonging to the five maturity classes were determined. It was found that the initial response of a delay in growth to massive invasion of juveniles, measured as a reduction in ground cover, was not related to maturity class of the cultivars. However, when the ground cover curves of cultivars grown on heavily infested soil were compared with those on non or lightly infested soil, the late- and very late-maturing cultivars showed, on average, a recovery from the initial delay, resulting in a two peaked difference curve. In contrast, the early-maturing cultivars, having a much shorter growing period, could not make use of their recovery from initial growth delay, resulting in a single peaked difference curve (Chapter VI). Yield figures were in accordance.

In the same way, differences in growth were determined for crops grown on irrigated and non-irrigated plots. It was conspicuous that on lightly infested soil drought had the same impact on potato crops in all maturity classes, in this case resulting in double peaked difference curves, as a result of an early dry period. On heavily infested soil however, early and mid early-maturing cultivars again showed single peaked difference curves, while double peaked curves were evident only for late-maturing and very late-maturing cultivars, indicating a recovery from PCN infection.

Plotting tuber dry matter yield against the amount of intercepted radiation, a constant relationship was found between yield and intercepted radiation, for all cultivars and treatments. Although the growth patterns of cultivars may differ as a consequence of maturity class and stresses caused by drought or PCN infection, the conversion factor (the increase of tuber dry matter yield per additional intercepted MJ) does not change. It is estimated at 1.08 g tuber dry matter per MJ intercepted radiation. Well established plants under stress, either through PCN or drought, intercept different amounts of light, as do cultivars of different maturity classes. But per MJ, they appear equally efficient in producing tuber dry matter.

Cultivars differed largely in their tolerance to PCN and to drought; these characteristics were not related (Chapter V and VI).

Soil type influenced the yield/PCN density relationship significantly. At non-damaging pH_{KCl} values of circa 5.0, water retention, measured in the topsoil, affected both yield level at logPi = 0, and amount of yield loss with increasing nematode density. The availability of water from the subsoil appeared also to contribute to the yield level at logPi = 0 and the amount of yield loss induced by PCN (Chapter VII).

Soil pH induced yield loss for most cultivars when it was over 5.5, but again cultivars appeared to differ in tolerance to pH, some of them showing no yield reduction even at $pH_{KCl} = 6.3$.
The interaction between pH and PCN was highly significant, as was the three way interaction between Cultivar, pH, and PCN. In the presence of PCN, yield reduction started at a lower pH than it did without PCN. Apparently, under non-stress conditions, although the root system is already affected in size and rooting depth by increasing soil pH, it is not reflected as yield loss. But, when PCN is present in the soil, the injurious effect of pH becomes clearly visible (Chapter VIII).

Oostenbrink's equation was used as a framework for a model to make optimal use of cultivars, based on their tolerance to various factors in relation to soil properties (Chapter IX). Input parameters are: 1) the soil characteristics: initial PCN infestation (P_i), the water retention of top- and subsoil and soil pH_{KCl}, and 2) the cultivar tolerances to PCN, to drought and to soil pH. They are expressed as Tolerance Values (TV), relative figures, indicating the yield loss per unit stress factor.
When $\log(P_i) = 0$, the yield level, the intercept ("a") in Oostenbrink's equation, is calculated through combining the corresponding soil and cultivar characteristics: soil pH and pH tolerance of the cultivar, water retention of the soil and the cultivar's drought tolerance, and the relative yield, which is a cultivar characteristic, in which the average yield level of the cultivar is expressed.
The slope ("b") of the curve, generated by Oostenbrink's equation is calculated from the "Tolerance Values" of the cultivars to PCN, modified by the *pH x PCN* interaction. So far, an interaction *PCN x Irrigation* (drought) has not been found for tuber yield and therefore, is not included in the model. However, the structure of the model allows for additions and improvements of estimates of the parameters. Since weather conditions during the growing season cannot be predicted at the time of planting, the assessment of the expected yield reduction due to drought has the character of a risk analysis.

Using infra-red crop scanning, it appeared feasible to monitor crop growth and, combined with measurements of solar radiation, to calculate the intercepted radiation.

The number of tubers formed have been found to be closely related to the intercepted radiation in the first twelve weeks after planting. This information is useful for seed potato growers. The correlation between the intercepted radiation in the first twelve weeks and the final yield can be used to estimate production figures relatively early. This estimate can be made more accurate through (week by week) monitoring of changes in ground cover. These estimates might be useful in improving the planning of transport, storage and processing capacities.

Knowledge about cultivars can be improved by proper screening for tolerance to PCN, pH and drought. A system of assigning "Tolerance Values" to individual cultivars has been developed. They are meaningful in themselves, but their values can be used directly in the model mentioned above, and thus directly and quantitatively help the farmer to optimize his production. It is recommended that these "Tolerance Values" are included in a List of Cultivars.
In addition, improving the cultivars, with respect to these tolerances, is possible when screening is done at an early stage of the breeding programme. Tolerance to PCN can also be screened in the greenhouse by taking a measure of root growth at one high PCN density. A relative simple screening for tolerances to pH and drought also seems feasible.

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Appendix I

Solar radiation (MJ per m²) in May, June, July, August and September of 1988 until 1992 at the nearby airport of Eelde (Anonymous, 1988b, 1989b, 1990b, 1991b and 1992d).

Month	Solar radiation					
	1988	1989	1990	1991	1992	normal
May	578	674	597	444	647	529
June	410	662	429	421	618	539
July	422	502	551	605	570	517
M+J+J	*1410*	*1838*	*1577*	*1470*	*1835*	*1585*
August	456	437	473	511	427	467
Sept.	273	325	245	297	321	306
A+S	*729*	*762*	*718*	*808*	*748*	*773*
Total	2139	2600	2295	2278	2583	2358

Appendix II

Summary of temperature conditions during the growing seasons of 1988, 1989, 1990, 1991 and 1992 at the nearby airport of Eelde. M = mean monthly value, h/l = Highest day temperature / lowest night temperature (derived from Anonymous, 1988b, 1989b, 1990b, 1991b and 1992d).

Month	10 d period	1988			1989			1990			1991			1992		
		Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min
May	I	13.7	19.2	8.7	10.6	16.8	3.7	16.1	23.7	8.3	7.3	11.0	3.1	10.6	13.3	4.8
	II	13.8	20.4	6.9	13.0	19.1	6.1	11.4	15.8	7.3	9.4	13.6	4.2	14.4	20.3	9.2
	III	14.0	20.5	8.2	14.6	21.1	7.1	10.8	17.3	3.4	10.4	13.9	7.0	19.7	26.4	12.9
	M	13.8	20.0	8.0	12.8	19.1	5.7	12.7	18.9	6.2	9.1	12.9	4.8	14.7	20.2	9.1
	h/l	--	*30.2*	*0.0*	--	*29.1*	*0.7*	--	*28.8*	*0.4*	--	*18.0*	*-0.4*	--	*28.6*	*-0.3*
June	I	13.5	17.3	9.7	11.2	16.3	5.5	13.4	17.9	8.4	10.4	143.8	5.3	17.5	22.8	12.4
	II	14.1	18.2	10.3	18.4	24.6	10.7	13.9	17.4	10.3	11.9	15.4	9.1	16.0	21.4	10.1
	III	15.2	19.6	11.0	16.3	21.5	10.5	16.6	21.4	11.7	14.1	17.6	10.0	17.7	24.0	10.8
	M	14.3	18.4	10.4	15.3	20.8	8.9	14.6	18.9	10.1	12.1	15.9	8.1	17.1	22.7	11.1
	h/l	--	*24.9*	*6.2*	--	*26.4*	*1.5*	--	*25.3*	*3.6*	--	*20.4*	*1.0*	--	*31.4*	*5.1*
July	I	15.4	19.9	11.5	18.2	22.9	13.2	13.8	17.3	9.7	20.6	25.8	14.9	17.3	23.1	11.2
	II	14.7	18.7	10.9	14.4	19.6	8.8	15.7	21.3	9.6	16.8	20.7	12.4	17.5	22.4	13.1
	III	16.0	20.1	11.5	17.4	23.4	11.6	17.4	22.7	11.6	17.8	23.2	12.0	17.7	23.8	11.3
	M	15.7	19.5	11.3	16.7	22.0	11.2	15.7	20.5	10.3	18.4	23.2	13.1	17.5	23.1	11.8
	h/l	--	*26.1*	*8.3*	--	*30.7*	*6.7*	--	*28.1*	*4.4*	--	*32.4*	*7.8*	--	*28.4*	*6.7*
Aug	I	16.5	22.5	10.6	15.6	21.1	10.2	18.2	25.2	10.9	18.6	24.1	13.3	19.0	25.4	12.6
	II	16.1	21.0	10.7	17.9	23.4	12.2	16.7	22.9	10.3	16.1	21.4	10.6	15.9	20.6	11.7
	III	14.5	18.9	10.3	14.7	19.7	9.5	17.2	22.8	10.9	16.6	23.6	9.2	16.3	20.8	12.2
	M	15.7	20.7	10.5	16.0	21.3	10.6	17.3	23.6	10.7	17.1	23.0	11.0	17.0	22.2	12.1
	h/l	--	*25.8*	*6.6*	--	*30.0*	*4.4*	--	*34.1*	*5.1*	--	*31.1*	*5.5*	--	*32.5*	*6.4*
Sept	I	14.0	19.3	8.8	14.3	20.0	9.2	13.5	17.2	9.8	16.5	22.6	10.7	12.9	17.3	8.7
	II	13.1	16.2	10.2	15.8	20.5	11.2	12.1	16.7	7.0	13.1	19.7	5.7	13.5	18.4	8.3
	III	12.6	16.5	8.9	14.3	18.8	9.9	11.0	14.9	7.5	13.5	17.0	9.9	15.1	20.2	11.0
	M	13.3	17.4	9.3	14.8	19.8	10.1	12.2	16.3	8.1	14.4	19.8	8.8	13.8	18.6	9.3
	h/l	--	*24.0*	*2.7*	--	*26.9*	*5.5*	--	*19.7*	*4.3*	--	*30.0*	*2.9*	--	*24.7*	*4.1*

Appendix III

Number of days per month with highest day and night temperature values during the growing seasons of 1988 till 1992, as indicated above the columns; [e.g. May 1988, with 16 days with highest day temperatures ≥ 20 °C, of which on 3 days temperatures reached 25 °C or higher, including one day when 30 °C or higher was reached. Highest day temperature measured during May 1988 was 30.2 °C, highest night temperature 14.4 °C (see value between brackets)]. (Anonymous 1988b; 1989b; 1990b; 1991b; 1992d).

Year and month	highest day temperature			highest night temperature		
	≥ 20 °C	≥ 25 °C	≥ 30 °C	≥ 10 °C	≥ 15 °C	≥ 20 °C
1988						
May	16	3	1 (30.2)	9 (14.4)	-	-
June	6 (24.9)	-	-	18 (13.5)	-	-
July	9	1 (26.1)	-	26	1 (16.5)	-
Aug.	16	3 (25.8)	-	19	1 (15.4)	-
Sept.	3 (24.0)	-	-	12 (14.4)	-	-
1989						
May	12	3 (29.1)	-	5 (11.0)	-	-
June	18	7 (26.4)	-	-	1 (15.5)	-
July	21	6	1 (30.7)	19	2 (16.6)	-
Aug.	21	5	1 (30.1)	19	-	-
Sept.	12	2 (26.9)	-	41	1 (16.5)	-
1990						
May	10	4 (28.8)	-	3 (11.0)	-	-
June	12	1 (25.3)	-	17	1 (15.9)	-
July	14	6 (28.1)	-	17	3 (15.6)	-
Aug.	24	11	3 (34.1)	21 (14.4)	-	-
Sept.	-	-	-	5 (12.8)	-	-
1991						
May	-	-	-	2 (11.6)	-	-
June	1 (20.4)	-	-	10 (13.0)	-	-
July	29	12	2 (32.4)	27	8 (18.2)	-
Aug.	29	8	1 (31.1)	19	4 (17.3)	-
Sept.	10	3	1 (30.0)	13 (13.9)	-	-
1992						
May	17	12 (28.6)	-	16	1 (16.4)	-
June	22	7	2 (31.4)	22 (14.1)	-	-
July	27	7 (28.4)	-	21	4 (17.3)	-
Aug.	22	4	2 (32.5)	27	6 (17.7)	-
Sept.	8 (24.7)	-	-	12 (12.6)	-	-

Appendix IV

Differences in ground cover between cultivars

Ground cover curves of eighteen individual cultivars, grouped in five maturity classes, on lightly and heavily infested soil are shown in Figs 1 to 5. The ground cover of the crops on lightly infested soil as well as the ground cover on heavily infested soil are given for each cultivar, both under irrigation (graphs A) and drought stress (graphs B).

Early cultivars: The ground cover curves of these three cultivars (Fig. 1) were very similar under light infestation, but on the heavily infested soil were very different. Ground cover of cv Appassionato was strongly reduced by nematode attack. Cv Ehud was comparatively little affected, whereas cv Krostar showed an intermediate response. A similar pattern was found for lightly and heavily infected crops under drought stress, although the initial growth of the cultivars at light infestation differed clearly, indicating a different response to drought. Cv Krostar seemed to suffer more from drought than cvs Appassionato and Ehud.

Mid-early cultivars: The curves of the cvs Element and Belita (Fig. 2) at light PCN infestation with irrigation were almost identical during the first part of the growing season, but differed for the second half. The haulm of cv Belita died rapidly, whereas cv Element senesced later and more gradually. On the heavily infested irrigated plots, cv Element was not much retarded in the first weeks, but then the curve deviated from the control. Hardly 70% ground cover was reached, and ground cover rapidly declined 10 weeks after planting. Cv Belita was retarded from the time of emergence, reached a little over 60% ground cover, which started to decrease one week later than cv Element's (Fig. 2A).
Under drought stress, the curves of cvs Element and Belita at the light infestation were almost identical, while those on the heavily infested soil differed markedly. In contrast to high nematode infection under irrigation, cv Element was severely affected, reaching a lower maximum (40%) two weeks earlier than cv Belita. Cv Belita performed better than cv Element under the combination of PCN attack and drought, with a maximum ground cover of 55% (Fig. 2B).

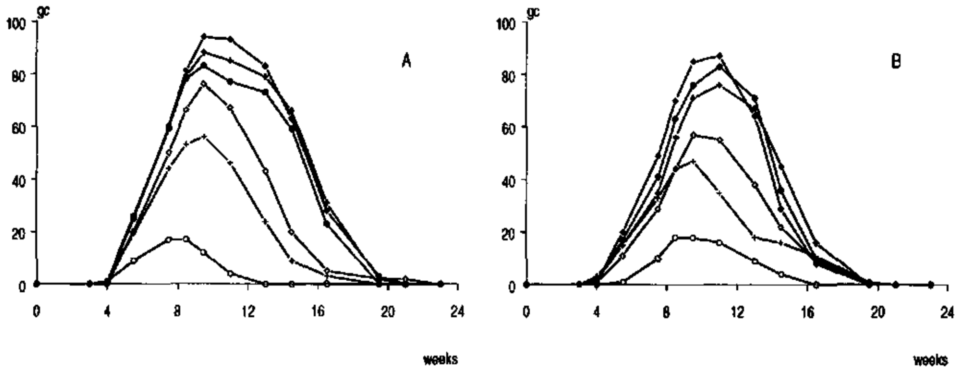

Fig. 1 Ground cover curves of the early-maturing cultivars Appassionato (-•-), Krostar (-+-) and Ehud (-♦-) on lightly infested soil (solid symbols) and on heavily infested soil (open symbols). A: irrigated , B: non-irrigated.

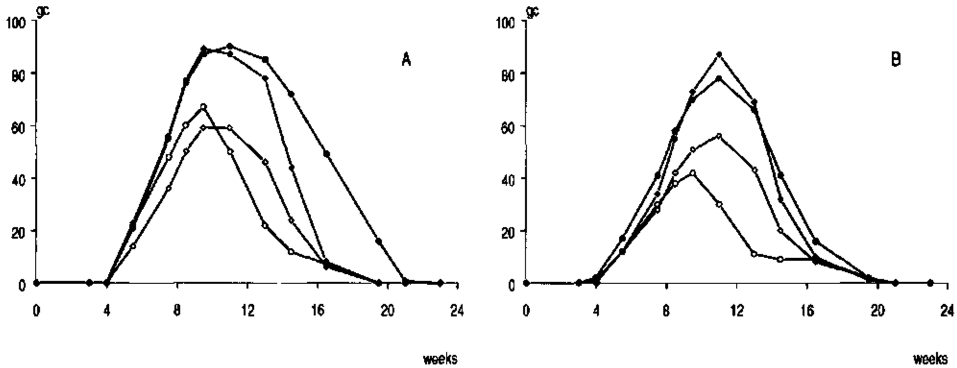

Fig. 2 Ground cover curves of the mid-early-maturing cultivars Element (-•-) and Belita (-♦-) on lightly infested soil (solid symbols) and on heavily infested soil (open symbols). A: irrigated , B: non-irrigated.

Mid-late cultivars: Under irrigation, the curves for the cvs Mentor and Karida were identical at the light infestation level, but those on the heavily infested soil differed considerably. Both cultivars showed almost the same retardation in response to infection up to the 9th week after planting. Then the ground cover of cv Mentor, with its maximum just over 60%, declined sharply, so that after 16 weeks only 5% ground cover remained, whereas 60% was left on the lightly infested soil. Cv Karida, however, maintained a ground cover of over 70% in heavily infested soil for about four weeks, but then showed the same rate of decline as the control, two weeks earlier (Fig. 3A).

Under drought stress, the curves of these cultivars at the light infestation level were identical, but those on the heavily infested soil differed considerably. Under these conditions, cv Karida showed hardly any retardation in response to infection, and senescence was hardly accelerated either, whereas cv Mentor showed a marked retardation in ground cover combined with an early senescence (Fig. 3B).

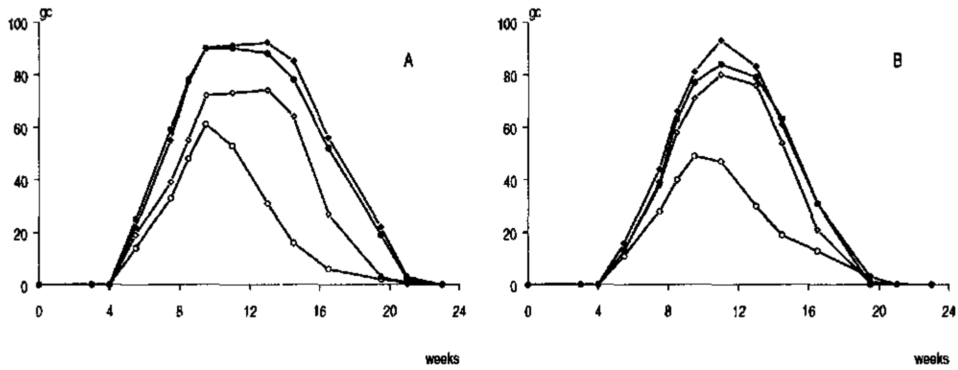

Fig. 3 Ground cover curves of the mid-late-maturing cultivars Mentor (-•-) and Karida (-♦-) on lightly infested soil (solid symbols) and on heavily infested soil (open symbols), under irrigated (A) and non-irrigated (B) conditions.

Late cultivars: Under irrigation, cvs Darwina and Prevalent had almost identical curves for the lightly infested soil, although cv Prevalent had a slightly higher maximum ground cover. The curves of both cultivars for the heavily infested soil were almost identical too, with a somewhat longer maintenance of maximum ground cover (60%) by cv Prevalent (Fig. 4.1A). Cvs Prominent and Elkana showed almost identical ground cover curves at both infestation levels. Compared to cvs Darwina and Prevalent, these two cultivars seemed less affected by PCN at high infestation levels (Fig. 4.2A).
The curve of cv Vebeca for the light infestation level was not much different from those of the four other cultivars in this group, but the curve on heavily infested soil differed greatly from the others (Fig. 4.3A). There was a certain retardation in ground cover

up to 13 weeks after planting, when it reached its maximum ground cover of over 80%, but then the decline did not differ much from the control.

Under drought stress, cvs Darwina and Prevalent did not have identical curves for the lightly infested soil, as they had under irrigation. Although they reached the same maximum of 85% ground cover, cv Darwina died sooner than cv Prevalent (Fig. 4.1B). On heavily infested soil, cv Darwina was more retarded in ground cover than Prevalent. Both cultivars reached maximum ground cover 11 weeks after planting, and their rate of senescence was almost the same. Cvs Prominent and Elkana showed almost identical ground cover curves on lightly infested soil (Fig. 4.2B). Compared with the cvs Darwina and Prevalent, these two cultivars seemed less affected by PCN at the high infestation level, even though cv Elkana showed a marked retardation in ground cover establishment, and reached a lower maximum two weeks later than cv Prominent. Thereafter, the rates of senescence were almost the same for both cultivars.

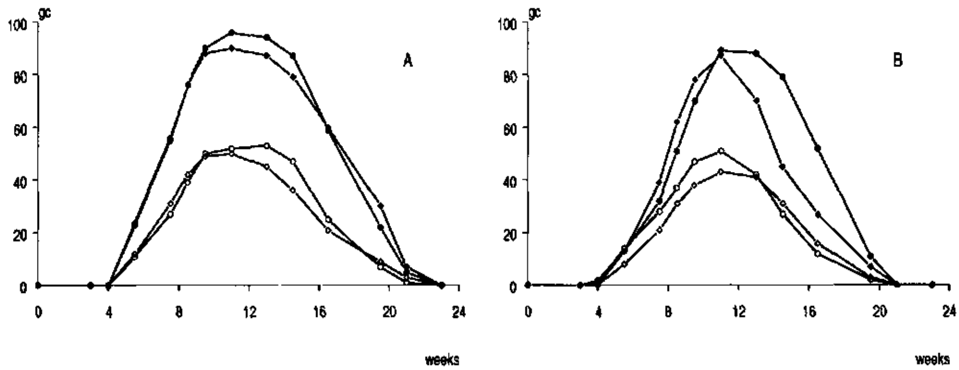

Fig. 4.1 Ground cover curves of the late-maturing cultivars Prevalent (-•-) and Darwina (-♦-) on lightly infested soil (solid symbols) and on heavily infested soil (open symbols), under irrigated (A) and non-irrigated (B) conditions.

The curve of cv Vebeca under light infestation was not much different from those of the four other cultivars in the first part of the growing season (Fig. 4.3B), but senescence was similar to that of cv Prevalent after maximum (92%) ground cover was reached 11 weeks after planting.

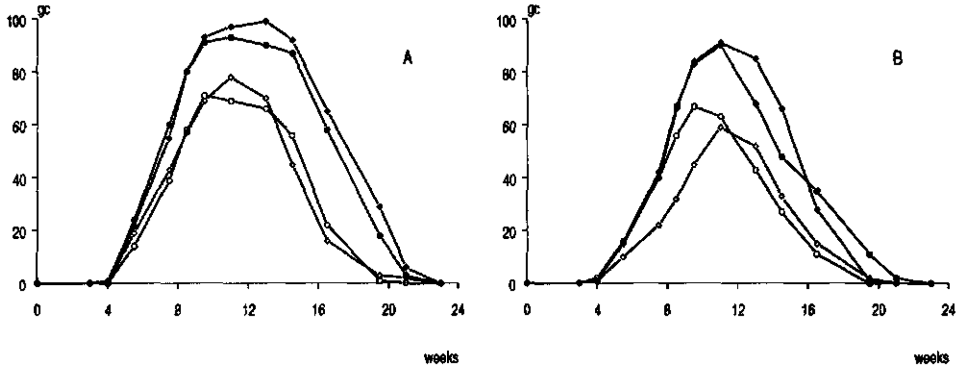

Fig. 4.2 Ground cover curves of the late-maturing cultivars Prominent (-•-) and Elkana (-♦-) on lightly infested soil (solid symbols) and on heavily infested soil (open symbols), under irrigated (A) and non-irrigated (B) conditions.

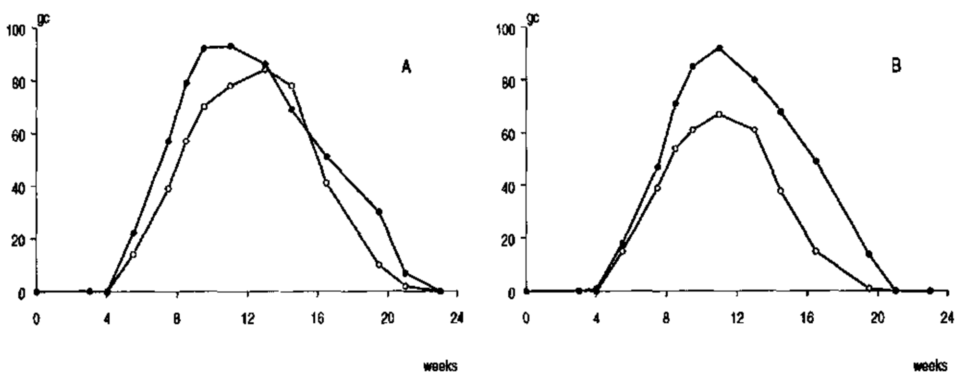

Fig. 4.3 Ground cover curves of the late-maturing cultivar Vebeca (-•-) on lightly infested soil (solid symbols) and on heavily infested soil (open symbols), under irrigated (A) and non-irrigated (B) conditions.

On heavily infested soil, the ground cover of cv Vebeca showed only a little retardation. It reached its maximum of over 60% eleven weeks after planting, and decline was slower compared to that of the other cultivars in this group.

Very late cultivars: The ground cover curves of these very late cultivars were identical up to 12 weeks after planting, but in the second half of the growing season they differed more than the cultivars in the other maturity classes.

When irrigated and on lightly infested soil, cv Karnico reached maximum ground cover about 10 days later than cv Astarte, and matured one week later as well (Fig. 5.1A). On heavily infested soil, both cultivars showed initially little difference in ground cover, but cv Karnico obtained a 10% higher ground cover maximum, and maintained this difference almost to the end of the growing season. Cvs Kardal and Producent initially showed identical ground cover curves for the lightly infested soils and reached the same maximum 12 weeks after planting (Fig. 5.2A). Cv Producent matured earlier than cv Kardal. On heavily infested soil cv Kardal showed a curve identical to its control up to 8 weeks after planting, but then deviated rapidly, reaching a maximum of only 80% and declining rapidly from 13 weeks after planting onwards. Cv Producent showed retarded ground cover from emergence to 13 weeks after planting, but eventually reached 90% ground cover. Hereafter, it maintained the same ground cover as the control on lightly infested soil. Cvs Elles and Astol showed almost identical ground cover on lightly infested soil (Fig. 5.3A). On heavily infested soil they responded differently to infection. Cv Elles showed some retardation from emergence to 13 weeks after planting, at which time it reached a maximum ground cover similar to that on lightly infested soil. From 14 weeks after planting, the decline of ground cover was faster than on lightly infested soil. Cv Astol, on the other hand, showed a severe retardation from emergence to maximum ground cover (75%), reached 14 weeks after planting, followed by a sharp decline.

Under drought stress, the ground cover curves of these very late cultivars, grown on lightly infested soil, were almost identical up to 11 weeks after planting, but cv Karnico yielded a lower ground cover maximum than the other cultivars (Fig. 5.1B). In contrast to all cultivars tested, both cvs Karnico and Astarte showed a slightly faster establishment of ground cover in the first 5 weeks after emergence in the heavily infested plots than on lightly infested soil. Both reached maximum ground cover about 11 weeks after planting at both infestation levels. On heavily infested soil, ground cover of cv Astarte declined earlier than that of cv Karnico (Fig. 5.1B). The unexpected deviation from the smooth senescence curve of Karnico between 17 and 20 weeks after planting might well have been caused by large amounts of rainfall in the first ten days of September (Anonymous, 1990), to which cv Karnico was still able to respond in growth, being the latest cultivar of all.

Cvs Kardal and Producent showed identical ground cover curves on the lightly infested soil and reached their maxima 11 weeks after planting (Fig. 5.2B).

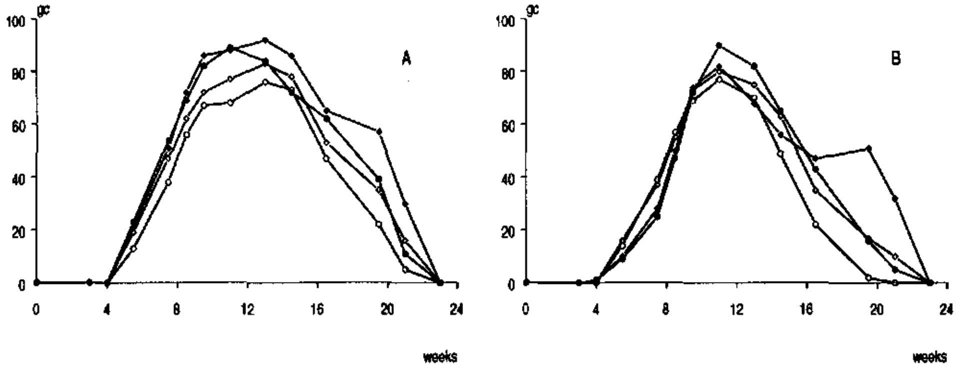

Fig. 5.1 Ground cover curves of the very late-maturing cultivars Astarte (-•-) and Karnico (-♦-) on lightly infested soil (solid symbols) and on heavily infested soil (open symbols) under irrigated (A) and non-irrigated (B) conditions.

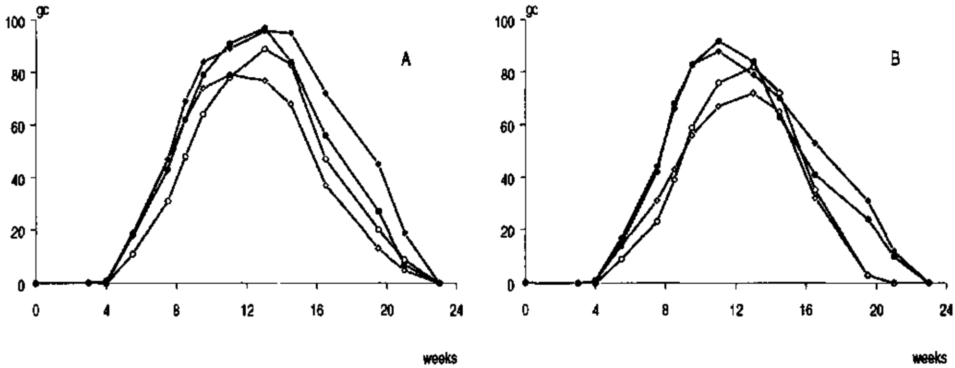

Fig. 5.2 Ground cover curves of the very late-maturing cultivars Producent (-•-) and Kardal (-♦-) on lightly infested soil (solid symbols) and on heavily infested soil (open symbols), under irrigated (A) and non-irrigated (B) conditions.

On heavily infested soil, the ground cover establishment by both cultivars was retarded, maxima being reached 13 weeks after planting, two weeks later than on the lightly infested soil. Cv Producent obtained a 10% higher maximum than cv Kardal. From fourteen weeks after planting, their rates of senescence were identical.

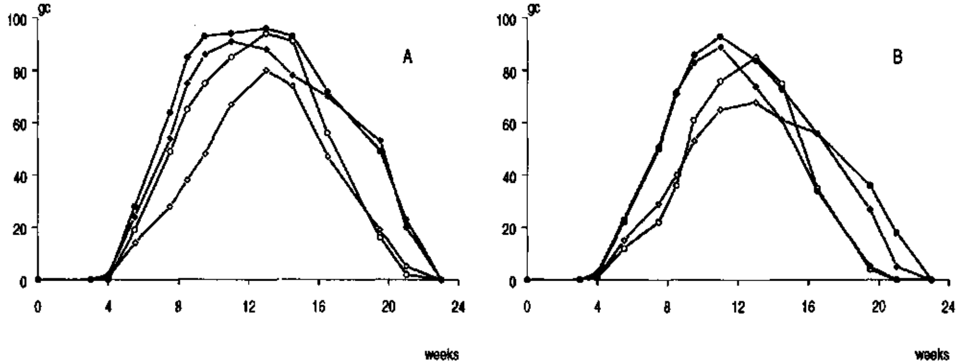

Fig. 5.3 Ground cover curves of the very late-maturing cultivars Elles (-•-) and Astol (-♦-) on lightly infested soil (solid symbols) and on heavily infested soil (open symbols), under irrigated (A) and non-irrigated (B) conditions.

Cvs Elles and Astol showed almost identical patterns of ground cover on lightly infested soil, maxima (90%) being reached 11 weeks after planting (Fig. 5.3B). On heavily infested soil, they responded differently to infection. Both showed a clear retardation from emergence to 13 weeks after planting, when maximum ground cover was reached, for cv Elles 85% and for cv Astol 70%. From 16 weeks after planting the decline of ground cover was identical.

Curriculum Vitae

Persoonsgegevens:

naam:	Arnold Mulder
geboortedatum:	7 februari 1933

Opleiding:

1947 - 1951	3-jarige HBS te Assen
1951 - 1952	praktijkjaar
1952 - 1955	Rijks Middelbare Landbouwschool (thans Agrarische Hogeschool het van Hall Instituut) te Groningen
1955 - 1957	Canada
1957 - 1958	Landbouw Hogeschool, Wageningen - propadeuse
1958 - 1960	Vervulling van de militaire dienstplicht
1960 - 1965	Landbouw Hogeschool, Wageningen Ingenieursvakken: Landbouwplantenteelt (verzwaard), Entomologie en Nematologie. Officiële datum van afstuderen: 17 april 1970.
1 maart 1965	Aangesteld als wetenschappelijk onderzoeker bij de "Werkcommissie Aardappelmoeheid van het Provinciaal Onderzoekcentrum voor de Landbouw in Drenthe". De opdracht luidde: in goede samenwerking met de in 1963 aangestelde wetenschappelijk onderzoeker ir H.M. Nollen te zoeken naar een voor de praktijk bruikbare oplossing van het aardappelmoeheidsprobleem. Door verkregen onderzoekresultaten te combineren met die van onderzoeken van IPO, SVP en PD werd een op vruchtwisseling, afwisselend gebruik van vatbare en resistente aardappelrassen en grondontsmetting gebaseerd geïntegreerd bestrijdingssysteem ontwikkeld waarvan het gebruik in 1968 officieel werd toegestaan en dat ook in 1992 in het fabrieksaardappelgebied nog algemeen wordt toegepast.
1973 - heden	Directeur "Stichting Bodemziekten". (m.i.v. 1984 "H.L.Hilbrands Laboratorium voor Bodemziekten" (HLB) te Assen.

In 1973 werd de Stichting P.O.C. Drenthe opgeheven. Haar werkzaamheden werden voortgezet door de "Stichting Onderzoek Bestrijding Aardappelmoeheid en andere Bodemziekten op de zand- en dalgronden van Middenoost en Noordoost Nederland".
De onderzoekopdracht luidde: het veiligstellen van de fabrieksaardappelteelt, voor zover deze wordt bedreigd door ziekten en plagen vanuit de bodem. Daartoe wordt ondermeer in vruchtwisselingsverband onderzoek verricht naar beheersing van belangrijke bodemgebonden ziekten en plagen van aardappels, suikerbieten en granen en hun interacties, en sinds kort ook van akkerbouwmatig geteelde (grove) groenten. Het werkgebied omvat het noordoostelijke zand- en dalgrondgebied.