Literature Review

Potential trap crops for the control of Potato Cyst Nematode (PCN)

Author: Jessica Sparkes, ADAS UK Ltd.

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Contents

1. INTRODUCTION

This review forms part of a project entitled 'To investigate the potential of both native and non-native *Solanum* species as PCN trap crops' which is being jointly funded by AHDB Potatoes and Defra.

Potato cyst nematodes (PCN) are a major pest of potatoes. About 64% of the English and Welsh potato growing area is infested with PCN and this proportion is on the rise (Kerry *et al.*, 2009). There are two main species of PCN in the UK *Globodera pallida* (white PCN) and *G. rostochiensis* (yellow PCN). The white PCN remain white or cream-coloured before finally turning brown whereas the yellow PCN passes through a prolonged golden-yellow phase before it also turns brown. PCN can remain viable as cysts in the soil for over 20 years and emerge once stimulated by a root exudate released by a host crop. In the absence of a host crop, there is some degree of spontaneous hatch and therefore decline (20-40% per year for *G, rostochiensis* and 10-30% per year for *G. pallida*) but this varies considerably between populations (Kerry *et al.*, 2009). At least ten chemical compounds, referred to as hatching factors have been identified as playing a role in PCN hatch (Devine *et al.*, 1996). Once stimulated by a hatching factor, the juvenile nematodes are able to invade the host crop roots and feed in them. If the attack is severe the roots may be seriously damaged or sometimes killed. Impaired root function means that the ability of the potato crop to take up water and nutrients is reduced with the result that plants are stunted. Symptoms are worse during dry weather particularly if the crop is not irrigated. PCN infestation can result in a high level of economic loss for the farmer. Damages as a result of PCN infestation can range from slight yield loss to complete crop failure depending on a host of factors including the severity of the infestation.

Management of PCN typically relies on the use of resistant varieties, crop rotation and nematicides. One potential non-chemical control method is the use of trap crops. These are crops that trigger the hatch of PCN in soil but prevent the completion of the pest's lifecycle. The use of trap crops dates back to at least 1939 (Carroll & McMahon, 1939). Early research focused on the use of potatoes as trap crops and limiting the length of the growing season, so that PCN juveniles invaded the roots but failed to complete their life cycle. More recently, research on trap crops has also included other *Solanum* species. In the UK, *S. sisymbriifolium* is available commercially as a PCN trap crop as is sold as Foil-sis by Branston and DeCyst by Greenvale. However, commercial uptake has been very limited due mainly to the loss of a profitable crop in the year of the trap crop (Clayton *et al.*, 2008). Hatching agents have also been the subject of much research but their identification was never entirely successful.

This report reviews published literature to identify and critically appraise the potential trap crop species suitable for the UK climate.

2. POTENTIAL TRAP CROP SPECIES

2.1 *Solanum tuberosum* (Potato)

Potato (*S. tuberosum*) was the first species studied as a potential PCN trap crop. Early research found that removal and destruction of potato crops prior to nematode maturation reduced the population density of PCN in the soil (Carroll & McMahon, 1939; Lamondia & Brodie, 1986; Mugniery & Balandras, 1984; Whitehead, 1986). The length of time over which the trap crop is grown is critical for success. During May and June, Whitehead (1977) demonstrated that a six week growing period caused the greatest reduction in PCN numbers. Lane & Trudgill (1999) also considered that a growth period of six weeks is generally safe but the warmer the soil at planting the more rapidly the nematodes develop. In southern England, about 300 day-degrees above 4ºC accumulate by six weeks from a mid-April planting but six weeks after a June planting will allow nearer 600 day-degrees above 4ºC to accumulate. Trap crop destruction must be late enough for large numbers of juveniles to have invaded the roots but early enough to prevent multiplication. Experiments by Halford *et al*. (1999) showed that to achieve the greatest reduction in PCN, the potatoes should be sown later in the year and that the time the crop is left in the ground (5, 6 or 7 weeks) varies depending on cultivar . This research also showed that crop cultivar has an impact on the total PCN reduction; with cv. Santé being the most effective of those tested.

The level of reduction achieved at various sowing dates, crop growth periods and from different potato cultivars depends on the PCN species. The method by which the trap crop is destroyed may also have an effect on PCN decline (Lamondia & Brodie, 1986). In pot experiments, the degree to which levels of *G. rostochiensis* were reduced was greater when plants were hand pulled compared to when they were killed with glyphosate. The difference in PCN reduction between destruction methods is likely to be as a result of the additional time needed for the herbicide to kill the plants.

Experiments by Scholte (2000a) demonstrated that using potatoes as a trap crop could significantly reduce PCN numbers in the following potato crop. Lane & Trudgill (1999) demonstrated that trap cropping with potatoes can reduce PCN populations by between 73 to 87% and is effective on a commercial scale on a range of soil types (Lane & Trudgill, 1999). They considered that trap cropping should only be considered where PCN infestations are very large and need to be reduced quickly as the technique is costly and needs very careful management. The natural dormancy of PCN immediately after a potato crop is grown means that a trap crop is not very effective immediately after growing potatoes. A more suitable time would be after harvest of a winter cereal, providing the soil is moist enough and labour available. Scholte (2000a) also had reservations about the use of potatoes as a trap crop. This was primarily because of problems with timing the crop, increased incidence of potato diseases and the potential for tubers to remain in the soil and become problematic as volunteers the next year. Another researcher (Whitehead, 1977) also came to the same conclusion regarding the suitability of potatoes as trap crops.

It has also been suggested that double cropping of potatoes might be effective for trap cropping (Lane & Trudgill, 1999). Although this practice would appear to offer great potential for PCN multiplication observations suggested that there was little net multiplication on either of the crops. It was considered that both crops may function as a trap crop, although just a few days too long in the ground could make a large difference to PCN multiplication.

In the UK, it was originally suggested that it would be most sensible to grow trap crop potatoes as a set-aside crop, but this was not possible under the set-aside restrictions (Clayton *et al.*, 2008). As a result the trap crop potatoes would need to be grown as part of a crop rotation, effectively resulting in the loss of a cropping year. It is also possible that if wet weather delayed the harvest of the trap crop it would allow PCN to mature on the roots resulting in an increase rather than decrease in populations (Denis Bucley, Pers comm.)

In summary, potatoes as a trap crop can effectively reduce numbers of both white and yellow PCN. However the crop is not an ideal candidate as a control mechanism and non-tuber producing plants are preferrable.

2.2 *Solanum sisymbriifolium* (Sticky nightshade)

Solanum sisymbriifolium (sticky nightshade) is native to South America. However it is now found throughout many parts of the world. It is considered an invasive species in South Africa as it has the potential to outcompete the natural vegetation (Global Invasive Species Database, 2010). The plants are grown to approximately one metre tall with leaves highly dissected and covered with spines up to 15mm long. *Solanum sisymbriifolium* has been studied and commercially sold as a trap crop for PCN. When field sown, the seeds normally germinate in two to four weeks and then grow slowly for the next four to six weeks (PCN Control Group, 2004). After this time, the plants are typically quite vigorous.

After determining that potatoes were not the best choice for trap cropping (see Section 2.1), research began screening non-tuber bearing *Solanaceae* for their potential as trap crops in the Netherlands (Scholte, 2000b; Scholte, 2000c; Scholte & Vos, 2000). Early screening looked at the stimulatory effect on juveniles (i.e. hatching factors), resistance to PCN and growth under Dutch conditions (Scholte, 2000c) and narrowed the potential trap crops to three species: *S. sisymbriifolium* and two varieties of *S. nigrum* (black nightshade, see Section 2.3). *Solanum sisymbriifolium* displayed complete resistance to both PCN species (meaning roots could be invaded by juveniles yet no progeny were produced), a high hatching effect and performed well under Dutch field conditions. Further studies showed that a reduction of up to 80% of the soil population of PCN could be achieved using *S. sisymbriifolium* as a trap crop (Scholte, 2000b; Scholte & Vos, 2000) but that the severity of the initial PCN population affected the level of reduction achieved. In one year of study, the reduction by *S. sisymbriifolium* in moderately to severely infested soils (2-19 juveniles/ml soil) was 77% whilst the reduction in very severely infested soils (110-242 juveniles/ml soil) was only 52%.

As *S. sisymbriifolium* is considered an invasive species in some parts of the world and largely considered a weed the risk of its commercial application were evaluated. In the Netherlands, the risk of becoming an invasive weed was considered to be low as was the risk of inclusion in cropping rotations because the species will not act as a host for problematic pests or diseases (Scholte & Vos, 2000) such as Northern root knot nematode (*Meloidogyne hapla*). Other studies by Flier *et al.* (2003) show that *S. sisymbriifolium* was an alternative host plant for *Phytophthora infestans* and that infection occurred at a reasonably high rate. However, two experiments carried out by Timmermans *et al.* (2005) show that although *S. sisymbriifolium* is susceptible to *P. infestans,* its susceptibility is very low (infection efficiency on leaves of *S. sisymbriifolium* was 20-36.% compared to 100% on potatoes) and the lesion size, was significantly smaller than that on potato. Therefore, the risk of *P. infestans* is low and can be mitigated through thorough crop destruction. *Solanum sisymbriifolium* has also been shown to be susceptible to Verticillium wilt (Bletsos *et al.*, 1998) which can potentially damage the potato crop.

To further explore the potential of *S. sisymbriifolium* as a trap crop, a PhD project was done by Timmermans (2005). This project evaluated the ecology, agronomy and ability of *S. sisymbriifolium* to reduce levels of PCN. Emergence of *S. sisymbriifolium* is linked to temperature and at ambient temperatures below 8°C emergence is almost non-existent. To achieve full ground cover with the recommended sowing density the crop should be sown between May and July under Dutch conditions. Seeds should be sown within 1-2 cm of the soil surface, pressed into the soil and then covered with a thin layer of loose soil. Sowing densities of 200-400 seeds/m^2 as well as 50-100 seeds/m^2 have been shown to be sufficient however to encourage high root density (and thus great PCN reduction) the higher sowing density is preferred. It is recommended that the seed is sown in 12.5cm rows. The number of PCN juveniles hatching from cysts increased from 47% to 75% after 6 and 21 weeks of crop growth, respectively (Timmermans *et al.*, 2006).

Further work *(*Timmermans, 2005; Timmermans *et al.,* 2006*)* also found that PCN reduction was positively correlated to root length density (the length of roots per volume of soil), which could be assessed with reasonable accuracy from the aerial crop characteristics (Timmermans *et al.*, 2007a; Timmermans *et al.*, 2007b). PCN reduction ranged from 42.6% at 0.26 cm cm^3 root length density to 85.3% at 5.8 cm cm^3 root length density (Timmermans *et al.*, 2006).

To achieve significant PCN reduction *S. sisymbriifolium* needs to accumulate at least 700g/m^2 dry matter (Timmermans *et al.*, 2007b). As the growth of this plant is dependant on temperature, a model was developed to predict the European area which would be suitable for this species as a trap crop (Timmermans *et al.*, 2009). Using weather data collected between 1996 and 1999, simulations were run on the model for 64 sites across Europe. In all regions tested, the crop could reach the minimum required size for adequate PCN reduction. The southern part of the UK was deemed an area where the weather was adequate for the crop if allowed to grow for an entire growing season. However, in the northern regions of the UK conditions were more marginal.

Solanum sisymbriifolium has also been assessed in the UK for suitability for our climatic conditions (PCN Control Group, 2004). For field applications, the trap crop can be sown in rows or broadcast over the soil at a rate of 100seeds/m^2. This should yield a plant density of 20-30 plants/m^2. Due to the slow initial development of *S. sisymbriifolium*, weed competition may be problematic and additional control measures such as stale seedbed preparations should be employed. Promising results of the use of this species resulted in commercial production of *S. sisymbriifolium* as Foil-sis (Branston, 2013) and DeCyst (Greenvale).

Clayton *et al*., (2008) discussed the use of S. sisymbriifolium as a trap crop in the UK. The price of seed is £285/ha and establishment costs are £70-100 /ha, making it more expensive than a conventional nematicide application. Use of *S. sisymbriifolium* can be very successful in the right circumstances, reducing PCN populations by 65 – 75% in sandy loam soils. However, efficacy declines with increasing soil organic matter. The main issue is finding a suitable place in the rotation to grow the trap crop. Current varieties are more suited to a Mediterranean climate, and need to be sown in May/June to give three months of good growing weather. Attempts have been made to drill crops after winter barley and peas, but this is restricted if cereal or pea harvest is delayed. In the future, varieties more suited to UK conditions may become available.

2.3 *Solanum nigrum* (Black nightshade)

Solanum nigrum (black nightshade) is a common annual plant native to the UK. It is considered a weed to both arable and horticultural crops as well as in gardens. In the natural soil seedbank, seeds typically germinate in spring-summer. When sowing stored seeds, populations tested would not germinate at constant temperatures of 10 or 15°C and even at constant temperatures of 20 and 25°C germination was low depending of how the seed was collected (Bithell *et al.*, 2002). Germination was much greater when seeds were chilled for 14 days and then subjected to alternating temperatures of 20:30°C (16:8 hours). This study indicates a level of dormancy which may be present in stored seeds. For use as a trap crop this dormancy will need to be understood and overcome as it is likely to differ considerably between seed populations. *Solanum nigrum* is not frost-tolerant so any late-germinating seedlings rarely reach maturity (Bond *et al.*, 2007). The plants flower from July to September

(Clapham *et al.*, 1987) depending on emergence date with individual plants producing approximately 400 berries, each containing approximately 40 seeds. Buried seeds can remain dormant but viable for over 50 years (Ødum, 1974). Control of *S. nigrum* is possible through the use of herbicides and non-chemical techniques such as hoeing.

This species is very morphologically and genetically complex and several sub-species have been identified. Over 50 genetic classifications have been assigned to *S. nigrum* (Dehmer & Hammer, 2004). Differences have been detected in how the various accessions respond to PCN. Although most of the *S. nigrum* accessions tested were host to two isolates of *G. rostochiensis*, two accessions were only host to one of the two isolates (Rott *et al.*, 2011). This work not only emphasises the complex genetics of *S. nigrum* but also that of PCN and how the compatibility of individual populations is so important in developing potential trap crop species.

Solanum nigrum has long been known as a potential PCN trap crop. Like *S. sisymbriifolium,* this species was also identified in a screen of non-tuber bearing *Solanaceae* as a potential PCN trap crop species (Scholte, 2000c). In this screen, two separate populations of *S. nigrum* showed complete resistance to *G. rostochiensis* and high resistance to *G. pallida* and also performed well under Dutch growing conditions. Compared to potato and *S. sisymbriifolium*, two separate populations of *S. nigrum* were not as effective in reducing PCN populations in the soil (Scholte, 2000b; Scholte & Vos, 2000) however, all still resulted in a greater PCN reduction than non-host crop control. Unlike *S. sisymbriifolium,* the risk of *P. infestans* on *S. nigrum* was low although it was also considered to be an alternative host for the disease (Flier *et al.*, 2003).

In pot experiments carried out in the UK in 2011 (unpublished, Highfield Lodge Agronomy) two locally collected strains of *S. nigrum* were at least as good as *S. sisymbriifolium* in reducing *G. pallida* populations. The results are summarised in Table 1 below.

Table 1: The impact of a range of potential trap crop species (spring barley was included as a control) on PCN populations (eggs/g soil).

	PCN egg numbers/g soil		**Pf/Pi %**	**% reduction**
Crop	**Initial**	**Final**		
Spring barley	396	178 cd	61.4 bc	38.6
S. sisymbriifolium	349	77 abc	30.0 abc	70.0
Datura stramonium	353	159 bcd	47.8 abc	52.2
True Potato Seed	418	235 d	70.8 c	29.2
S. nigrum - Bratton	494	50 a	9.4 a	90.6
S. nigrum - Weston	343	64 ab	19.9 ab	80.1
S. laciniatum (kangaroo apple)	400	51 a	20.4 ab	79.6
S. nigrum - Bratton double crop	300	32 a	10.3 a	89.7
SED (df)	91.8 (28)	46.2 (27)	20.6 (27)	

a, b and c are Duncan's Multiple Range Test indices. Numbers followed by the same letter are not statistically different (P >0.05).

In summary, research indicates that *S. nigrum* is a complex species with a variety of populations, each with a potentially different effect on PCN populations. Although the populations included in previous Dutch studies show that the reduction in PCN is less than that for other candidate trap crop species UK pot experiments suggest that *S nigrum* has significant potential. Furthermore, this species' ability to grow very well in UK conditions makes it a desirable candidate for further experimentation.

2.4 *Solanum dulcamara* (Bittersweet or woody nightshade)

Solanum dulcamara (woody nightshade) is a widespread plant native throughout Europe and considered a common weed. *Solanum dulcamara* grows to over 1 m tall, contains leaves of variable shape and purple flowers. The plant fruits are bright red.

Solanum dulcamara was found to be not resistant to a Canadian isolate of *G. roshochiensis* (Rott *et al*., 2011) meaning that after hatching, juveniles would be able to reproduce if not first destroyed.

Little other work has been done specifically on this species as a potential PCN trap crop but it has been included in the current study as it is widespread plant in the UK and therefore likely to be adapted to UK growing conditions. In addition, it is useful to evaluate its efficacy against UK populations of the PCN.

2.5 *Datura stramonium* (Thornapple)

Datura stramonium (thornapple) is an annual weed belonging to the Solanaceae family. It is common in warm counties around the world but has also become well established throughout the UK, especially in wasteland and cultivated areas. Plants grow to up to 1 m tall and consist of an extensively branched hollow stem (Royal Horticultural Society, 2013). Leaves are varied in shape but typically broad and toothed. Flowers are about 5-10 cm long, white or purple and trumpet-shaped (Weaver & Warwick, 1984). Germination requirements vary considerably but optimal temperatures are between 20-35°C, with alternating temperatures better for germination than constant temperatures (Weaver & Warwick, 1984). Flowering typically occurs from July to October (Royal Horticultural Society, 2013).

All parts of *D. stramonium* plants, in particular the seeds, are poisonous if consumed. If cut prior to seed set, the toxins in the plant will naturally break down in the soil (Royal Horticultural Society, 2013).

No literature could be located on the use of *D. stramonium* as a PCN trap crop but as it has become well established in the UK it is clearly well adapted to growing in our climate. As a member of the Solanaceae it may have potential as a PCN trap crop and therefore has been included in this study.

3. SUMMARY

In summary, there are a range of potential candidates for PCN trap crops suitable for use in the UK. *Solanum sisymbriifolium* has been identified previously as a very strong candidate due to its potential to substantially reduce PCN populations. However it is a non-native species in the UK and growth may not be optimal in UK conditions. *Solanum nigrum* is a native species which grows very well in the UK but genetic variation within the species means that different populations may have a variable effect on PCN populations. Little work has been done with *S. dulcamara* or *D. stramonium* to date so their potential as trap crop species is largely unknown. However these species should grow well in UK conditions.

The ideal timing to establish a trap crop species is following winter cereals. The aim would be to grow the crop for as long as possible before removing it to establish a potato crop the following spring. This will be the optimum timing to fit with the majority of current commercial rotations and has the additional advantage that it does not result in the loss of a cropping year.

4. REFERENCES

Bithell, S. L., McKenzie, B. A., Bourdôt, G. W., Hill, G. D., and Wratten, S. D. (2002). Germination Requirements of Laboratory Stored Seeds of *Solanum nigrum* and *Solanum physalifolium* . *New Zealand Plant Protection* **55**, 222-227.

Bletsos, F. A., Thanassoulopoulos, C. C., and Roupakias, D. G. (1998). Sensitivity of Two Greek Eggplant Varieties and the Wild Species *Solanum sisymbriifolium* Lam. to Verticillium Wilt. *Journal of Genetics and Breeding* **52**, 99-102.

Bond, W., Davies, G., and Turner, R. (2007). The biology and non-chemical control of black nightshade (*Solanum nigrum* L.). Accessed 14-6-2013 from http://www.gardenorganic.org.uk/organicweeds/.

Branston. (2013). PCN trap crop. Accessed 27-6-2013 from http://www.branston.com/fresh_potatoes/products_for_suppliers/pcn_trap_crop/.

Carroll, J. and McMahon, E. (1939). Experiments on Trap Cropping With Potatoes As a Control Measure Against Potato Eelworm (*Heterodera schachtii*). *Journal of Helminthology* **17**, 101-112.

Clapham, A. R., Tutin, T. G, and Moore, D. M. 1-1-1987. Flora of the British Isles, Cambridge University Press, Cambridge, UK.

Clayton, R., Storey, M., Parker, B., Ballingall, M., and Davies, K. (2008). Impact of reduced pesticide availability on control of potato cyst nematodes and weeds in potato crops. Potato Council

Dehmer, K. J. and Hammer, K. (2004). Taxonomic Status and Geographical Provenance of Germplasm Accessions in the *Solanum nigrum* L. Complex: AFLP Data. *Genetic Resources and Crop Evolution* **51**, 551-558.

Devine, K. J., Byrne, J., Maher, N., and Jones, P. W. (1996). Resolution of Natural Hatching Factors for Golden Potato Cyst Nematode, *Globodera rostochiensis*. *Annals of Applied Biology* **129**, 323-334.

Flier, W. G., Van Den Bosch, G. B. M., and Turkensteen, L. J. (2003). Epidemiological Importance of *Solanum sisymbriifolium*, *S. Nigrum* and *S. Dulcamara* As Alternative Hosts for Phytophthora Infestans. *Plant Pathology* **52**, 595-603.

Global Invasive Species Database. (2010). *Solanum sisymbriifolium* (herb). Accessed 14-6-2013 from http://www.issg.org/database/species/ecology.asp?si=1216.

Halford, P. D., Russell, M. D., and Evans, K. (1999). Use of Resistant and Susceptible Potato Cultivars in the Trap Cropping of Potato Cyst Nematodes, *Globodera pallida* and *G. Rostochiensis*. *Annals of Applied Biology* **134**, 321-327.

Kerry, B., Davies, K., and Esteves, I. (2009). Managing potato cyst nematode through maximising natural decline and population suppression. Potato Council, R269.

Lamondia, J. A. and Brodie, B. B. (1986). The Effect of Potato Trap Crops and Fallow on Decline of *Globodera rostochiensis*. *Annals of Applied Biology* **108**, 347-352.

Lane, A., and Trudgill, D. (1999). Potato Cyst Nematode: A management guide. MAFF publications, London. 31pp.

Mugniery, D. and Balandras, C. (1984). Examen Des Possibilités D'Eradication Du Nematode a Kystes, *Globodera Pallida* Stone. *Agronomie* **4**, 773-778.

Ødum, S. (1974). Seeds in Ruderal Soils, Their Longevity and Contribution to the Flora of Disturbed Ground in Denmark. *Proceedings of the 12th British Weed Control Conference, Brighton, UK*, 1131-1144.

PCN Control Group (2004). Introducing *Solanum sisymbriifolium* as a trap crop for potato cyst nematodes in the UK, SA-LINK 112.

Rott, M., Lawrence, T., and Belton, M. (2011). Nightshade Hosts for Canadian Isolates of *Globodera rostochiensis* Pathotype Ro1. *Canadian Journal of Plant Pathology* **33**, 410-415.

Royal Horticultural Society. (2013). *Datura stramonium* (thorn apple). Accessed 10-7-2013 from http://apps.rhs.org.uk/advicesearch/profile.aspx?pid=536

Scholte, K. (2000a). Effect of Potato Used As a Trap Crop on Potato Cyst Nematodes and Other Soil Pathogens and on the Growth of a Subsequent Main Potato Crop. *Annals of Applied Biology* **136**, 229-238.

Scholte, K. (2000b). Growth and Development of Plants With Potential for Use As Trap Crops for Potato Cyst Nematodes and Their Effects on the Numbers of Juveniles in Cysts. *Annals of Applied Biology* **137**, 031-042.

Scholte, K. (2000c). Screening of Non-Tuber Bearing Solanaceae for Resistance to and Induction of Juvenile Hatch of Potato Cyst Nematodes and Their Potential for Trap Cropping. *Annals of Applied Biology* **136**, 239-246.

Scholte, K. and Vos, J. (2000). Effects of Potential Trap Crops and Planting Date on Soil Infestation With Potato Cyst Nematodes and Root-Knot Nematodes. *Annals of Applied Biology* **137**, 153-164.

Timmermans, B. G. H. (2005). *Solanum sisymbriifolium* (Lam.): A trap crop for potato cyst nematode. PhD Thesis, Wageningen University, the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC), Wageningen, The Netherlands.

Timmermans, B. G. H., Vos, J., and Stomph, T. J. (2009). The Development, Validation and Application of a Crop Growth Model to Assess the Potential of *Solanum sisymbriifolium* As a Trap Crop for Potato Cyst Nematodes in Europe. *Field Crops Research* **111**, 22-31.

Timmermans, B. G. H., Vos, J., Stomph, T. J., Van Nieuwburg, J., and Van Der Putten, P. E. L. (2006). Growth Duration and Root Length Density of *Solanum sisymbriifolium* (Lam.) As Determinants of Hatching of *Globodera pallida* (Stone). *Annals of Applied Biology* **148**, 213-222.

Timmermans, B. G. H., Vos, J., Stomph, T. J., Van Nieuwburg, J., and Van Der Putten, P. E. L. (2007a). Field Performance of *Solanum sisymbriifolium*, a Trap Crop for Potato

Cyst Nematodes. II. Root Characteristics: Research Article. *Annals of Applied Biology* **150**, 99-106.

Timmermans, B. G. H., Vos, J., Van Nieuwburg, J., Stomph, T. J., Van Der Putten, P. E. L., and Molendijk, P. G. (2007b). Field Performance of *Solanum sisymbriifolium*, a Trap Crop for Potato Cyst Nematodes. I. Dry Matter Accumulation in Relation to Sowing Time, Location, Season and Plant Density: Research Article. *Annals of Applied Biology* **150**, 89-97.

Weaver, S. and Warwick, S. (1984). The Biology of Canadian Weeds. 64. *Datura stramonium* L. *Canadian Journal of Plant Sciences* **64**, 979-991.

Whitehead, A. G. (1977). Control of Potato Cyst-Nematode, *Globodera rostochinsis* Rol, by Picrolonic Acid and Potato Trap Crops. *Annals of Applied Biology* **87**, 225-227.

Whitehead, A. G. (1986). Problems in the Integrated Control of Potato Cyst Nematodes, *Globodera rostochiensis* and *G. pallida*, and Their Solution. *Aspects of Applied Biology* **4**, 363-371.

APPENDIX

Plate1. Sticky nightshade (*Solanum sisymbriifolium*). Spines are clearly visible on the stems

Plate 2. Sticky nightshade (*S. symbriifolium*) from seed supplied by Chiltern.

Plate 3. Sticky nightshade (*S. sisymbriifolium*) from seed supplied by GVAP.

Plate 4. Black nightshade (*Solanum nigrum*) 15 July.

Plate 5. Black nightshade (*S. nigrum*) from seed collected from the field in Shropshire.

Plate 6. Black nightshade (*S. nigrum*) from seed collected from the field in Wiltshire.

Plate 7. Bittersweet or woody nightshade (*Solanum dulcamara*)

Plate 8. Thornapple (*Datura stramonium*).

Plate 9. Thornapple seed pod splitting open to reveal black seeds inside.