Tolerance to potato cyst nematodes

There are two key genetic traits of relevance to growers in terms of management of potato cyst nematodes (PCN) – natural resistance and tolerance. These two properties are unrelated but there is frequently confusion between the two and what they mean.

Natural resistance acts to restrict or inhibit the multiplication of PCN on the plant and is mediated via host resistance genes. Natural resistance is well understood at a mechanistic level and a variety of potato resistance genes against PCN have been characterised, with some being deployed in cultivars via potato breeding. The most notable success in terms of PCN resistance is the widespread deployment of the H1 gene, which has provided resistance against the *Globodera rostochiensis* present in the UK for over 50 years. Two resistance sources (*H3* and *GpaV*, derived from *Solanum tuberosum* ssp *andigena* and *Solanum verneii* respectively) are currently being used in breeding programmes to provide resistance to *G. pallida* (*e.g.* Moloney *et al.,* 2010; Bryan *et al.,* 2002), although a more limited number of cultivars is currently available containing these genes. Although PCN multiplication is suppressed in resistant plants, **resistance does not necessarily mean that yield is protected when PCN is present**, particularly at high levels. This is, at least in part, because most resistance genes target the nematode after it has established a feeding site, meaning that root damage still occurs before this time point when the nematode migrates through the root.

Tolerance reflects the ability of the plant to withstand damage by PCN and thus to avoid the reduced growth and yield that is normally associated with PCN infection (*e.g.* Evans and Haydock 1990). It is critical to understand that **tolerance does not restrict the multiplication of PCN**. Although yield may be protected in a tolerant variety compared to an intolerant variety, PCN multiplication is frequently higher on tolerant varieties. **Use of tolerance in the absence of resistance may therefore allow build-up of very high (unmanageable) populations of PCN**.

Because tolerance and resistance are separate traits, potato cultivars vary on a spectrum for both, as summarised in the figure below.

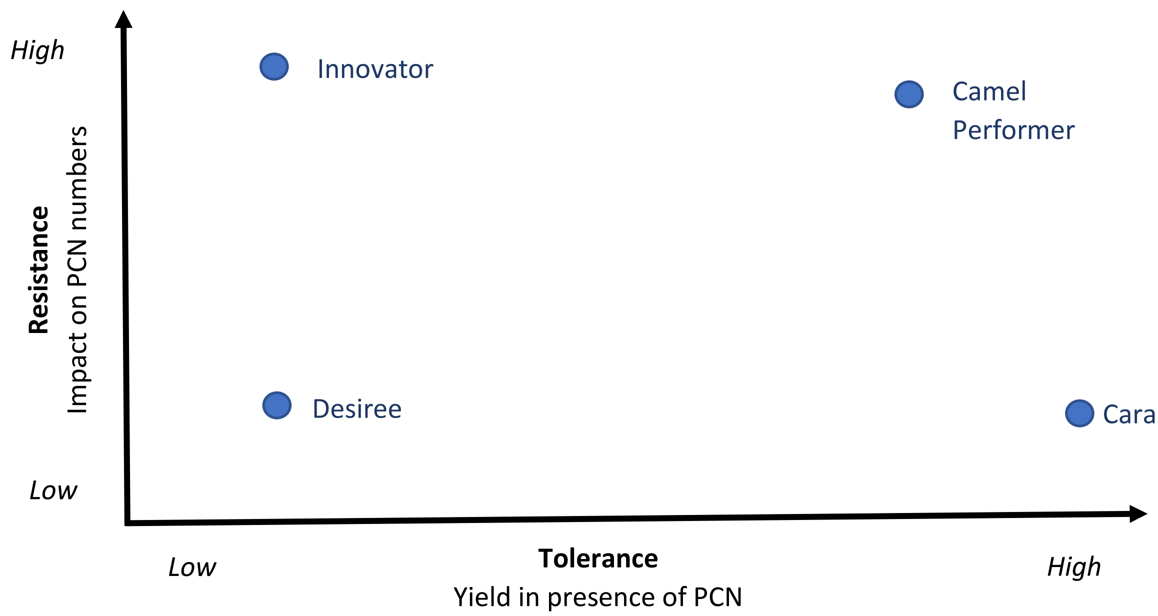

Figure 1: Tolerance and resistance are not correlated, as shown by plotting these properties for potato cultivars that display extremes of these traits. Resistance in this example relates to *G. pallida*.

Some of the more unexpected outcomes of this are that growing crops of potatoes that are both susceptible and tolerant in PCN infested land can lead to large increases in nematode populations, while still producing acceptable yields, whereas significant yield losses can occur using a resistant line if this is intolerant (Trudgill, 1991). **Clearly the ideal situation is for cultivars to be available that combine resistance and tolerance.**

Mechanisms underpinning tolerance to PCN

The damage caused by PCN, in addition to yield losses, may include a smaller root system, poor top growth, reduced ground cover and earlier haulm senescence (Evans 1982a). Infection and invasion of PCN causes damage to the root system that impairs moisture and nutrient uptake. Feeding of the nematodes also causes diversion of metabolites from plant growth to the nematode (Trudgill, 1991). One of the consequences of this reduction in nutrient availability is to reduce top growth of the plant and thus yield. Tolerant cultivars can recover from damage and achieve the expected level of top growth with a relatively minor delay.

The genetic basis of tolerance has not been elucidated, and tolerance is extremely unlikely to be a phenotype specific to PCN. Tolerance may relate to plant architecture (including canopy structure), enhanced root growth after the initial nematode attack and better water use efficiency (Evans and Franco, 1979; Evans 1982b). These properties may also confer the ability to tolerate other stresses, including drought (Trudgill, 1991).

Assessing tolerance for breeding

Although there has recently been increased emphasis on the importance of achieving tolerance to PCN in potato breeding programs, selection for this character is often compromised because tolerance assessments occur late in the breeding process. This reflects the fact that tolerance is notoriously difficult to assess, making it an unrealistic selection target in early breeding cycles due to the large numbers of clones that would have to be tested in very complex phenotyping experiments. Tolerance is also heavily influenced by environmental conditions, adding a further layer of complexity to the assessment of this trait (Evans and Haydock, 1990). Finally, because resistance and tolerance are independent characters, combining these traits is extremely challenging. Given these factors, current breeding is therefore primarily focused on resistance gene deployment for combating the threat posed by PCN. In addition to the problems in assessing tolerance for breeding purposes, the difficulty in accurately assessing this trait means that information on tolerance is not always available for established cultivars, making provision of advice to growers on this topic patchy.

Tolerance can be assessed by growing potatoes in a uniformly nematode infested field and comparing yields and plant growth to those in uninfested soil. Nematicides have been used to achieve different infestation rates at a single site. The details of how tolerance should be assessed have been debated in the literature. Assessments in the field, at several sites and over several growing seasons, are required for robust assessments of this trait. However, it has been suggested that assessments made in relatively highly infested untreated soils are sufficient to rank relative tolerance levels (Dale et al 1988). A correlation between top growth and yield under disease pressure has also been used to distinguish PCN tolerant and intolerant cultivars (Dale and Brown, 1989).

Pot tests, using multiple replicates of single plants in plots, have been developed so that tolerance assessments can be made earlier in the breeding process when tuber numbers are limited (Phillips, Trudgill and Evans, 1988, Evans and Russell, 1990). Tolerance tests from such pot trials have shown good agreement with assessments made in the field. For example, Trudgill and Coates (1983) found a good correlation between effects on root growth in 10 cm pots and tolerance in the field. Arntzen and Wouters (1994) used 325 ml pots and found a good correlation between dry weights of the plants grown in pots and tolerance assessed in the field. They also recommended using a high density of nematode infestation to assess tolerance ranking. They did not, however, find a relationship between tolerance and time to maturity with the 15 potato genotypes that were highly resistant to *G. pallida* (Arntzen and Wouters 1994, Arntzen, Visser and Hoogendoorn 1994).

The relationship between tolerance and determinacy

A further trait that may potentially be correlated with tolerance is determinacy. Stem determinacy relates to the growth habit of plants. A determinate plant variety will cease leaf production after it has initiated its first flower, whereas an indeterminate variety will continue to produce tiers of leaves and flowers until curtailed by decreasing day length or frost. A whole variety of pleiotropic effects is associated with stem determinacy, some of which have profound agronomic consequences. In tomato, for example, determinate varieties also have a short stature and show simultaneous fruit ripening. In tomato, a determinate growth habit is the result of loss of function mutations in the TFL1 gene SELF PRUNING (SP). Consequently, breeding the SP mutation into commercial tomato cultivars was critical for implementing mechanical harvesting for the processing industry.

The mechanisms controlling determinacy in tomato are well studied; loss of function mutations in the TFL1 gene SELF PRUNING (SP) result in a determinate growth habit (Pnueli *et al.,* 2001; Krylova *et al,* 2021). However, genetic studies on the mechanisms underpinning determinacy in potato are not as well advanced. SP is a member of a large family of genes encoding phosphatidylethanolamine-binding proteins. Work is currently in progress to identify the potato equivalent (orthologue) of SP and relate variation in this sequence to differences in stem determinacy (Mark Taylor & Glenn Bryan, JHI, *pers. comm.*). If such a relationship can be established, this would allow much easier screening for determinacy in potato on a high throughput basis.

In potato, stem determinacy and correlated traits are also important for productivity (Allison *et al.,* 2020). Determinate varieties senesce earlier and thus desiccation of haulm at harvest is not as problematic as for indeterminate varieties. Potato root architecture is also correlated with stem determinacy (Wishart *et al.,* 2013). Determinate varieties have a shallow rooting system, whereas indeterminate varieties are much more deeply rooting. The root structure has implications for water use efficiency and nitrogen fertilizer requirements. Determinate varieties have up to double the N requirement of indeterminate varieties and N rate application is based on the determinacy rating (Allison *et al.,* 2020). Despite the critical agronomic importance of how determinacy (and the associated pleiotropic traits) is controlled, the underlying genetic basis of this control is not clear in potato.

Determinacy has been assessed by a range of methods, for example measuring ground cover, where indeterminate varieties tend to have more persistent canopies than determinate ones. A more in-depth way of assessing determinacy is to count 'above-ground' stem/branch nodes on the main axis of the plant, and this method has been suggested as the preferred metric for assessing determinacy (AHDB report by Marc Allisson, Mark Stalham and David Firman 2020). Determinacy assessed by this method correlates well with canopy persistence (r^2 =0.46).

There is anecdotal evidence suggesting that determinacy status may also impact on a variety's tolerance to PCN. The concept that determinacy, and its associated pleiotropic effects, may be related to tolerance against PCN is intuitively appealing given the impact of this trait on root architecture. To further investigate this possibility, we have undertaken a preliminary analysis of the relationship between tolerance and determinacy for different potato cultivars, using data obtained from several sources. These analyses are summarised in Figures 2 and 3 below.

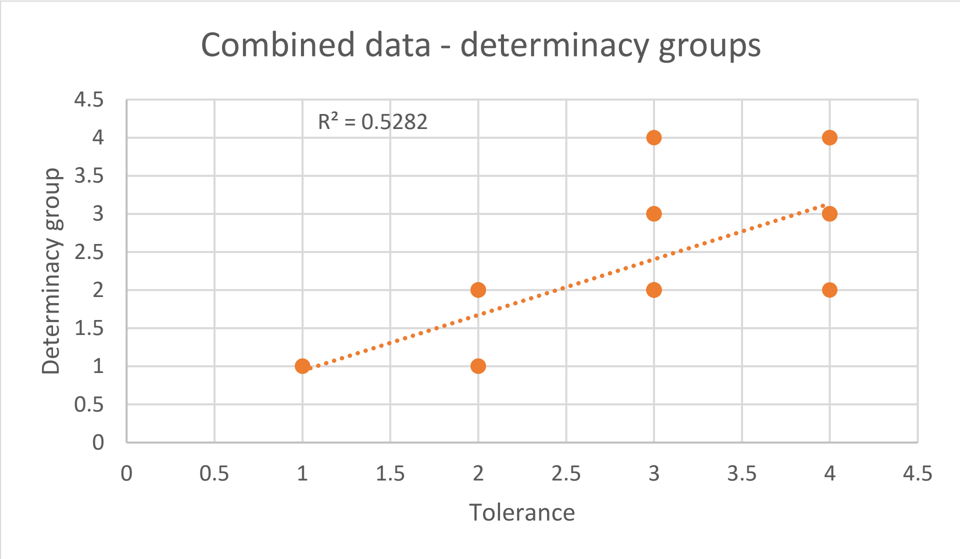

Figure 2: Relationship between tolerance ratings and determinacy groups (from Allison *et al* 2020).

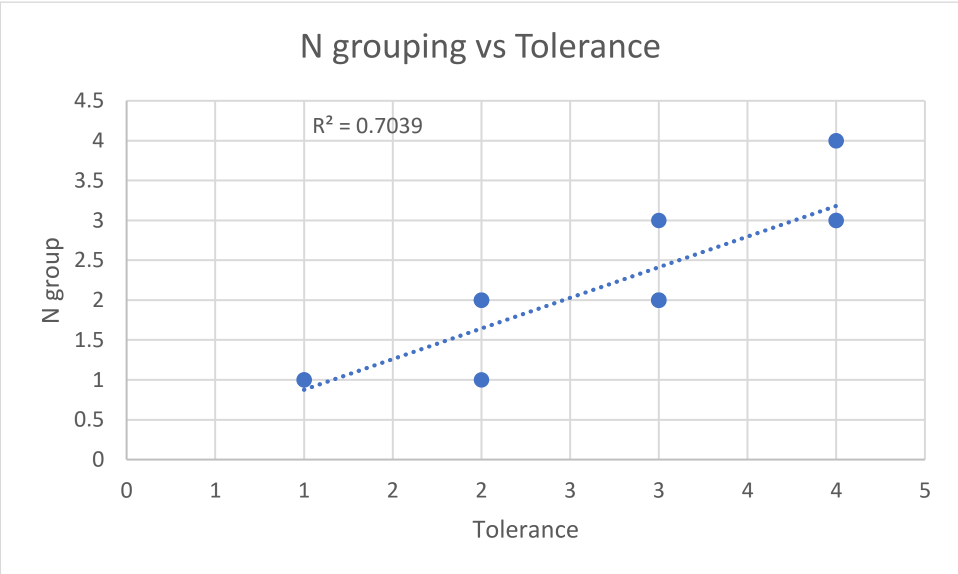

Figure 3. Relationship between tolerance and Nitrogen groupings (allocated by Allisson *et al.*, 2020).

Figure 2 shows the relationship between tolerance ratings, sourced from Tables 1-3 below (Appendix 1) and determinacy groups (allocated in Allison *et al.,* 2020), while Figure 3 shows the relationship between tolerance and nitrogen groupings, from the same report. In both cases a relationship is indicated, with data from the nitrogen groupings showing a compelling link. However, the different methods used to score tolerance in the different studies, and to place cultivars into determinacy groups, mean that these data need to be treated with some caution. In addition, both tolerance and determinacy can be challenging to score, particularly away from the extremes of each spectrum. This may explain why the link between the two traits is most clear at the extremes of the spectrum – cultivars in high determinacy groups are typically tolerant to PCN infection, while those in low determinacy groups are intolerant.

Conclusions and next steps

Few cultivars are available that combine tolerance and high levels of resistance. Reliable phenotyping of tolerance represents a major bottleneck that restricts the advice that can be given to growers on the tolerance properties of cultivars, and which also prevents incorporation of this trait into screening at the early stages of the breeding process. Work is therefore required to determine whether pot assays can be used for more rapid determination of tolerance levels. Field based assays of tolerance are also required to complement these pot trials.

Studies on the genetic control of determinacy are required, which examine whether the genes that control this trait in tomato play a similar role in this process in potato. This has the potential to provide a short cut to markers associated with determinacy and thus tolerance in potato, providing tools for very early incorporation of preferred determinacy/tolerance traits in potato breeding programmes.

Once these work areas are complete, we will know the best way to assess tolerance on a relatively large scale and can then reassess the link between tolerance and determinacy with more confidence. We will also then know whether assessments of tolerance can be included in breeding programmes and how best to assess tolerance of commercial varieties for growers.

Appendix 1: Properties of currently available cultivars

Resistance to *G. pallida,* scored on a scale from 1-9, is available for all commercially released cultivars. Tolerance ratings for cultivars are far less complete and are available from several sources (Tables 1 to 3).

Cultivar	Tolerance rating	*G. pallida* resistance rating
Cara	Very tolerant	2
Desiree	Intolerant	2
Estima	Intolerant	2
Hermes	Intolerant	2
Kerrs Pink	Tolerant	2
King Edward	Intolerant	2
Lady Rosetta	Intolerant	2
Marfona	Intolerant	2
Maris Peer	Very intolerant	2
Maris Piper	Intolerant	2
Nadine	Very Intolerant	3
Pentland Crown	Intolerant	2
Pentland Dell	Intolerant	2
Pentland Squire	Intolerant	2
Sante	Intolerant	4
Saturna	Very tolerant	2
Vales Everest	Tolerant	6
Vales Sovereign	Intolerant	2
Valor	Tolerant	3

Table 1: Tolerance data for potato cultivars gathered by the Agriculture and Horticulture Development Board (AHDB) for use in the PCN calculator: https://pcncalculator.ahdb.org.uk/

Other sources of information about tolerance of PCN cultivars can be found in trade articles. The tolerance rating and scales in such articles may be different from those above reflecting the variability in this trait and the difficulties in scoring it. Examples of these data are shown in Tables 2 and 3.

Cultivar	Tolerance rating	*G. pallida* resistance rating
Shepody	Moderate	2
Eurostar	Moderate	9
Performer	Good	9
Royal	Good	3
Innovator	Poor	9
Lanorma	Not known	5
Panther	Poor	8
Arsenal	Moderate	8-9
Cara	Good	2

Table 2: Tolerance scores for cultivars obtained from Bayer data:
https://cropscience.bayer.co.uk/blog/articles/2020/02/managing-pcn-6-key-actions-for-success/

Cultivar	Tolerance rating	*G. pallida* resistance rating
Camel	Very tolerant	9
Cara	Very tolerant	2
Performer	Very tolerant	8
Royal	Very tolerant	3
Arsenal	Tolerant	9
Brook	Tolerant	2
Eurostar	Tolerant	9
Lanorma	Tolerant	5
Markies	Tolerant	2
Marvel	Tolerant	5
Cabaret	Moderate	2
Divaa	Moderate	5
Harmony	Moderate	4
Maris Piper	Moderate	2
Rock	Moderate	9
Rooster	Moderate	2
Estima	Intolerant	8
Innovator	Intolerant	8
Maris Peer	Intolerant	2
Nadine	Intolerant	3
Panther	Intolerant	8
Pentland Dell	Intolerant	2
Ramos	Intolerant	4
Sante	Intolerant	4

Table 3: Tolerance data from Farmers Weekly article https://www.fwi.co.uk/arable/crop-management/pests/how-resistant-varieties-can-tackle-potato-cyst-nematode

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