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Comparison of development of *Globodera rostochiensis* in four potato cultivars

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Abstract

Developmental stages of juveniles of *G. rostochiensis* Ro1 were studied in the susceptible cv. Marfona and in the resistant cvs Agria, Satina and Banba in glass-house conditions. The hatching response of the nematodes to root diffusates of these cvs was also investigated. Disinfected cysts of *G. rostochiensis* were placed in root diffusates and the numbers of hatched second stage juveniles (J_2) were counted weekly over a 6-week period. Pots were planted with a single sprout of each cv. and the soil was inoculated with a suspension of 400 freshly hatched J_2. There was a significant difference in the numbers of J_2 that had entered the roots as well as a delay of 1-2 weeks in the rate of development of juveniles in the resistant compared to the susceptible cvs. Overall, 44%, 23%, 10% and 4% of inoculated J_2 were found in the roots of susceptible Marfona, and resistant Satina, Agria and Banba cultivars, respectively. The first J_3 appeared in roots one week after J_2 entered the roots in Marfona and Satina, but after 2 weeks for the other cvs; the first J_4 was found 14 and 21 days after J_2 entry in the roots of susceptible and resistant cvs respectively. The numbers of white females found on the roots were fewer than 5 or none on roots of the potatoes resistant to pathotype Ro1. When cysts were exposed to root diffusates, 74% of J_2 hatched in Marfona diffusate as compared to 50% in Agria, 43% in Satina and 39% in Banba diffusates.

Keywords: *Globodera rostochiensis*, life cycle, resistant potatoes, root diffusate

Potato cyst nematodes (PCN), *Globodera pallida* and *G. rostochiensis* are major pests of seed and ware potatoes (*Solanum tuberosum* L.), occurring globally in many regions and pose considerable control problems (Mai, 1977; Turner & Evans, 1998; Whitehead & Turner, 1998; Fatemy & Aghazade, 2016). *Globodera rostochiensis* (Wollenweber, 1923) is the most economically important nematode pest of potatoes worldwide and occurs in both temperate and tropical zones (Brodie, 1984).

The life cycle of *G. rostochiensis* is generally influenced by accumulated temperature and different numbers of generations have been reported on potato in various geographical locations (Greco *et al*., 1988). In temperate regions, the nematode usually completes only one generation per year (Morris, 1971; Tiilikala, 1987; Stanton & Sartori, 1990), although a second generation may be initiated but not completed (Evans, 1969). However, Greco *et al.*, (1988) reported a complete second generation in some temperate regions with long potato growing seasons. A base of 10°C has been identified as the lower juvenile hatching threshold by Inagaki (1984), Magnusson (1986) and Greco *et al.*, (1988). In Finland, the first

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second stage juveniles (J_2) emerge in the soil at between 4 and 5°C according to Tiilikala (1987) whereas, 21°C is the optimum temperature for the hatch, which stops below 9 °C (Mulder, 1988). The second stage juvenile (J_2) of *G. rostochiensis* is stimulated to hatch from the egg by root diffusate of host plants, which are confined to a few members of the Solanaceae family (Franklin, 1940). In the absence of potato root diffusate (PRD), nearly 30% spontaneous hatch of J_2 may occur when compared with over 80% when a host plant is present (Jones, 1970). Byrne (1997) has demonstrated that the production of hatch inhibitors and hatching factor stimulants at different stages of the host plant`s maturity. Evans (1983) and Byrne (1997) showed that a series of dilutions of PRD resulted in a range of PCN hatch, and generally full strength PRD did not result in the maximum hatch. According to Byrne (1997), high concentrations of PRD may be indicative of reduced water content in the soil, thus so a reduced hatching response may act as a survival mechanism by limiting hatch into an unsuitable soil environment. In addition, it has been speculated that the co-evolution of potato species and *Globodera* would result in a reduced hatching response to leachates from hosts that have developed resistance to specific *Globodera* gene pools. The root damage caused by invasion of infective J_2 reduces crop yield (Evans & Rowe, 1998). Once inside roots, J_2 go through two more juvenile stages (J_3 and J_4) and become adult males or females. Vermiform motile males leave the roots to find and mate with the sedentary females, which have emerged through the root surface. Between 200 and 500 eggs (Evans *et al.*, 1993; Perry, 1998) are laid inside the females, which die and become cysts that protect the eggs while they remain dormant in the soil. Inside the egg, the first stage juvenile (J_1) develops and moults to J_2 (Stone, 1979). Juveniles can be stimulated to hatch by substances other than potato root leachate, including inorganic ions like Ca^{2+}, Mg^{2+}, K^+ and Na^+ as well as organic substances such as fumaric and citric acids (Clarke & Shepherd, 1966; Clarke & Hennessy, 1984). The stimulants change the permeability of the eggshell, allowing the sugar trehalose to diffuse out and so reducing its concentration in the vitelline fluid and the osmotic stress on the juvenile. Juveniles then absorb enough water to begin normal metabolism and movement (Clarke & Perry, 1977). They pierce the egg shell with their stylets, and emerge from the egg and then through the natural openings of the cyst if the conditions are suitable (Sharma & Sharma, 1998). Some potato cultivars are very susceptible to PCN but some are relatively little affected (Whitehead *et al.*, 1980). Since resistant cultivars are grown in infested soil it is ideal that they all be tolerant to damage from nematode attack (Evans, 1983). Features such as hatching, attraction to roots, degree of invasion, initiation and maintenance of transfer cells, maturation and egg production, to which tolerance has been attributed, are also important components of resistance to nematodes (Evans, 1983). Resistance is a measure of how the parasite is affected by the host, whereas tolerance is how the host is affected by the parasite (Evans, 1983). Initial damage to potato plants is caused by juveniles invading the roots of both susceptible and resistant plants (Trudgill, 1986). Arntzen & Wouters (1994) suggested that tolerance may be dependent on little damage being caused to the roots. When the J_2 enters the roots, initiation of a feeding site is a process involving physical probing and release of chemicals from the migrating nematode (Wyss, 2002). The host responses to these disturbances include localized cell necrosis and browning, followed by disorganization and lysis of the syncytial feeding site in incompatible hosts (Sheridan *et al.*, 2004). Robinson *et al.*, (1988) showed that in roots invaded by J_2 of PCN there is a correlation between a hypersensitive responses and the degree of compatibility of the host. Further work has revealed the role of Ca^{2+} channels in the signaling process of nematode invasion and the electrophysiological reactions of resistant and susceptible host plants to wounding and pathogen attack (Sheridan *et al.*, 2004). There is no information on the interaction of the Iranian population of *G. rostochiensis*

Pathotype Ro1 with its susceptible and resistant hosts. We studied the development of different juvenile stages of *G. rostochiensis* in one susceptible cv. (Marfona) and the resistant (to Ro1) cvs; Agria, Satina and Banba under glasshouse conditions. The hatching responses of the nematode to diffusates from these cvs were also investigated, and the numbers of juveniles hatched and time of hatching were compared.

Materials and Methods

For inoculums, infested soil from a field was used, cysts of *Globodera rostochiensis* pathotype Ro1 were extracted from 100 g soil samples by a flotation method, using a Fenwick can (Fenwick, 1940), and kept at 4°C for at least 4 months until used. Densities of eggs and J_2 were estimated as explained in Fatemy & Aghazade (2016). To obtain root diffusates sprouted tubers of each of the certified commercial susceptible Marfona, and resistant Agria, Satina and Banba were planted separately in pots containing one kg of sterile potting soil. The resulting plants were grown for 45 days, and the pots were not watered the day before the collection of leachates. Each pot was saturated with distilled water and then an additional 50 ml of distilled water was added to each pot and the solution draining from the pot was collected. This solution was returned to the pot twice and re-collected. The resulting 'root diffusates' were collected, filtered and kept in the dark at 4°C until used, half strength PRD was used for the hatching assay (Turner & Stone, 1981).

Hatch of *G. rostochiensis* in root diffusates: Cysts of *G. rostochiensis* were disinfected with 0.5% sodium hypochlorite for 1 min and rinsed with distilled water (DW). Three batches of 20 cysts pre-soaked for 1 week in distilled water were then placed in 4 ml of each of the PRDs from the various cvs; distilled water served as control. Dishes were covered and arranged randomly on a bench in the laboratory at room temperature (18-23°C) for 6 weeks. The numbers of hatched J_2 were recorded and cysts transferred to fresh PRD weekly. At the end of the sixth week, the cysts were crushed, the remaining unhatched eggs counted and the final percent J_2 that hatched were calculated for each treatment.

Pot experiment: Plastic pots of 6x6 inches were filled with one kg of sterile loamy soil (with 40% sand, pH 7.5). A single sprout attached to a small piece of tuber of Marfona, Agria, Satina or Banba was planted in each pot. When seedlings had developed three full leaves, each pot was inoculated with a 10 ml suspension of 400 freshly hatched J_2 poured into three holes made around the base of the plant stem. To obtain live J_2, egg-containing cysts were pre-soaked in distilled water for two days before they were transferred to a glass bottle containing PRD. Hatched J_2 were collected and used within 2-3 days. All treatments had three replicates, and the pots were arranged in a completely randomized block design in a glasshouse with a 16-h photoperiod and a 16.5-28°C temperature regime. One week after inoculation, three plants from each cv. were uprooted, roots were washed, carefully cut from the main stem, weighed and cut into 2 cm lengths. These root pieces were thoroughly mixed and a 1 g sub-sample taken. Roots were stained with a 0.05% (w/v) solution of acid fuchsine in lactophenol, homogenized by blending in distilled water and the numbers of juveniles counted in 2 ml sub-samples (Hooper, 1986). The sampling was repeated six times at weekly intervals.

Statistical analysis: Data analysis was performed using ANOVA, and the mean values were separated by Duncan's multiple range test.

Results

Hatching assay: Second stage juveniles (J_2) started to emerge from cysts during week 1 in PRD of all cultivars (Fig. 1). Hatching continued over a 6-week period, increasing at the beginning and decreasing later on. Significantly greater numbers of J_2 hatched in PRD from the susceptible Marfona than in PRD from the resistant cvs, and total percent hatch was poorer

in some resistant cvs than others (Fig. 2). When cumulative hatch figures were compared, it was seen that a considerable proportion of the total hatch occurred in the second and third weeks in PRD of resistant cvs.

Developmental stages in roots: The first J_2 were found in roots one week after inoculation of all cvs except Banba, which was first invaded during week 2. Invasion of roots by J_2 continued during the growth period but the numbers found decreased over time (Fig. 3). Peak infestation of roots by J_2 was observed in week 1 for Marfona and week 2 for the resistant cvs. The last J_2s were found 35 and 28 days after inoculation in roots of Marfona and the resistant cvs respectively. The greatest number of J_2 attracted to and entering roots, was with cv. Marfona, then Satina, Agria and Banba (Fig. 2).

The first J_3 (third stage juveniles) were observed during week 2 after inoculation in the roots of Marfona and Satina but in week 3 in Agria (Fig. 4a). J_3 continued to be present in roots of all cvs except Banba until the end of the experiment. Banba was slightly exceptional as the first J_3 were found in week 4 and then only in week 5. Fourth stage juveniles (J_4) were found in week 3 after inoculation in the susceptible cv. and week 4 in resistant cvs (Fig. 4b). This juvenile stage was present during the next harvests in all cvs except Banba. The first white females appeared from week 5 after inoculation on the roots of Marfona, Agria and Satina (Fig. 4c). The greatest numbers of nematodes that entered roots and developed to maturity were found in the susceptible cv. while very few to no white females were found on roots of the resistant cvs.

Discussion

In fields of Hamadan Province infested with *G. rostochiensis* Ro1, potatoes are grown from March to June, during which time the ambient temperature averages between 3.5 and 19.4°C. The average annual rainfall in this region is 384 mm. Use of the susceptible potato cv. Marfona has been very common until recently, when high infestation levels and poor yield resulted in incorporation of more resistant cvs into a rotation programme. Entry of J_2 into roots, stages of juvenile development and appearance of white females differed between susceptible and resistant potato cultivars in terms of time of appearance, duration and number of juveniles. Resistance to *G. rostochiensis* Ro1 in potato cvs is due to a single major dominant gene *H*1 (Howard, 1969). Cultivars having the *H*1 gene can decrease soil infestations of PCN by 80% in one season, and three consecutive years of growing it should therefore decrease soil infestation by 99% (Zawislak *et al.*, 1981). Alternating an *H*1 resistant potato with a susceptible cv. in a rotation may slow down the selection of species or pathotypes able to overcome the resistance (Jones, 1970). We found differences in the numbers of J_2 penetrating roots as well as a delay of 1 to 2 weeks in rate of development of juveniles to advanced stages in resistant compared to susceptible cvs. When potato plants were inoculated with a suspension of J_2 , they took 14 days to enter roots of Banba and only 7 days for the other cvs. Overall, 44%, 23%, 10% and 4% of inoculated J_2 entered roots of susceptible Marfona, resistant Satina, Agria and Banba, respectively. The entry of J_2 into the roots continued over the period of 4 to 5 weeks in resistant and Marfona potatoes respectively, although their numbers decreased as the experiment progressed. Similarly, in potato fields, J_2 invaded the roots of potato cultivars continuously over a period of nearly 25 days after first invasion (Renco, 2007), and J_2 were present in soil during the entire growing season (Greco *et al.*, 1988; Pilipenko & Sigar'eva, 1998; Renco, 2007). After J_2 entered the roots, it took a week for J3 to appear in Marfona and Satina, but 2 weeks for other cvs. And while J4 established 14 days after J_2 entry in the susceptible cv, it took 21 days after J_2 entry for them to appear in the resistant cvs. However, the numbers of white females that formed on the roots were fewer than 5 per g root of potatoes resistant to pathotype Ro1,

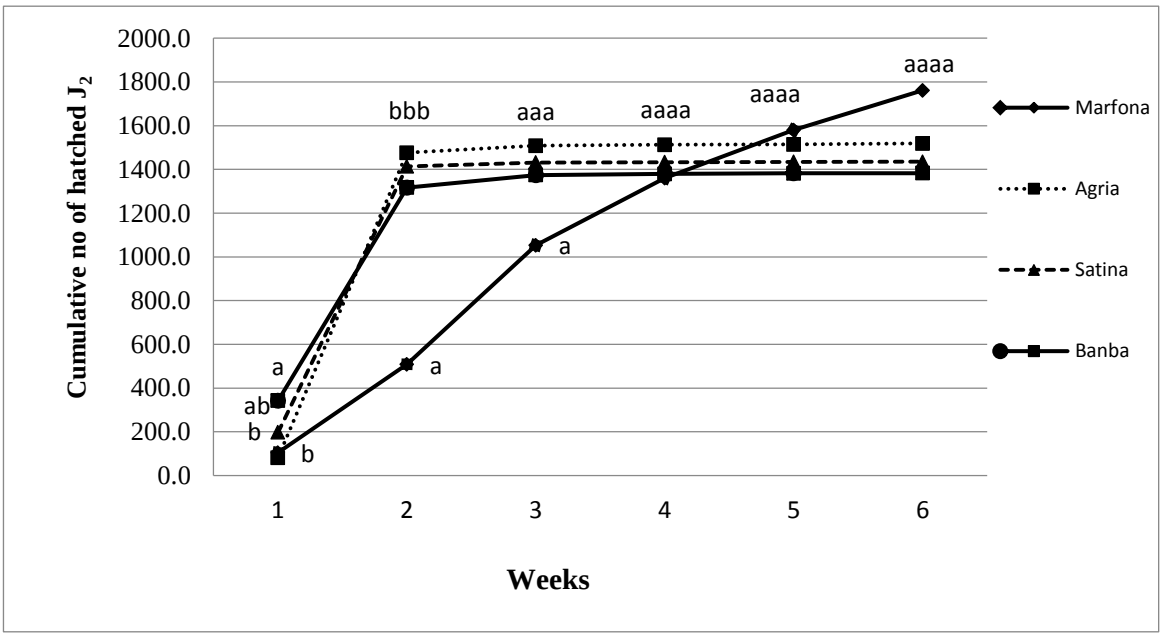

Fig. 1. Cumulative number of hatched second stage juveniles (J_2) of *G. rostochiensis* over time. (Similar letters are not different at 5% level according to Duncan`s test).

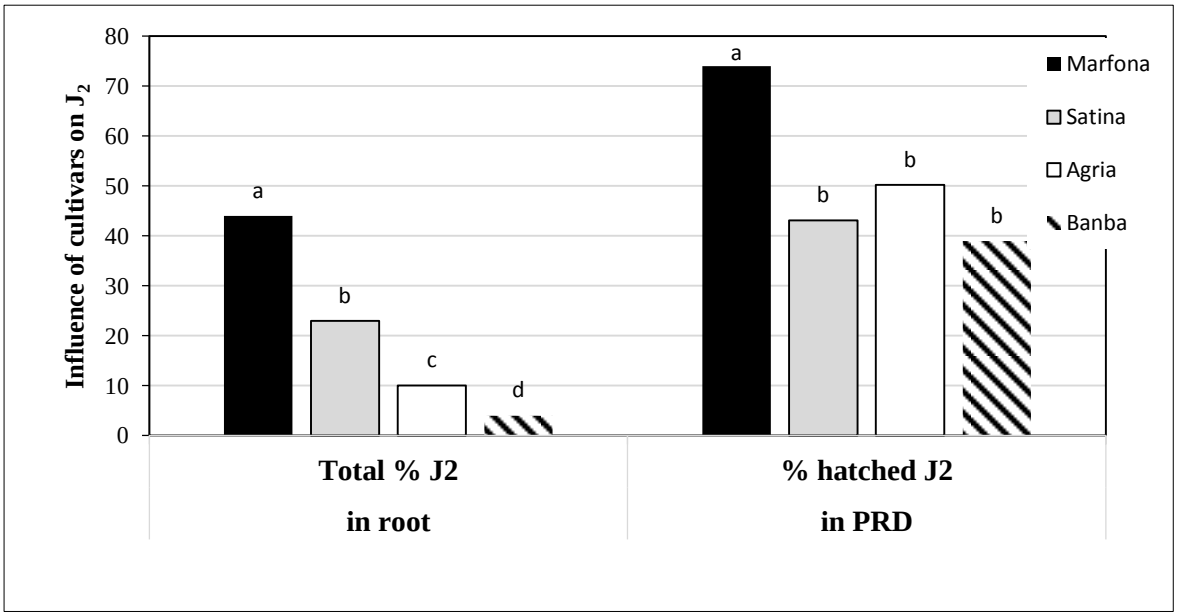

Fig. 2. Influence of potato cultivars on total % penetration and hatch of J_2 after 6 weeks. (Similar letters are not different at 5% level according to Duncan`s test.

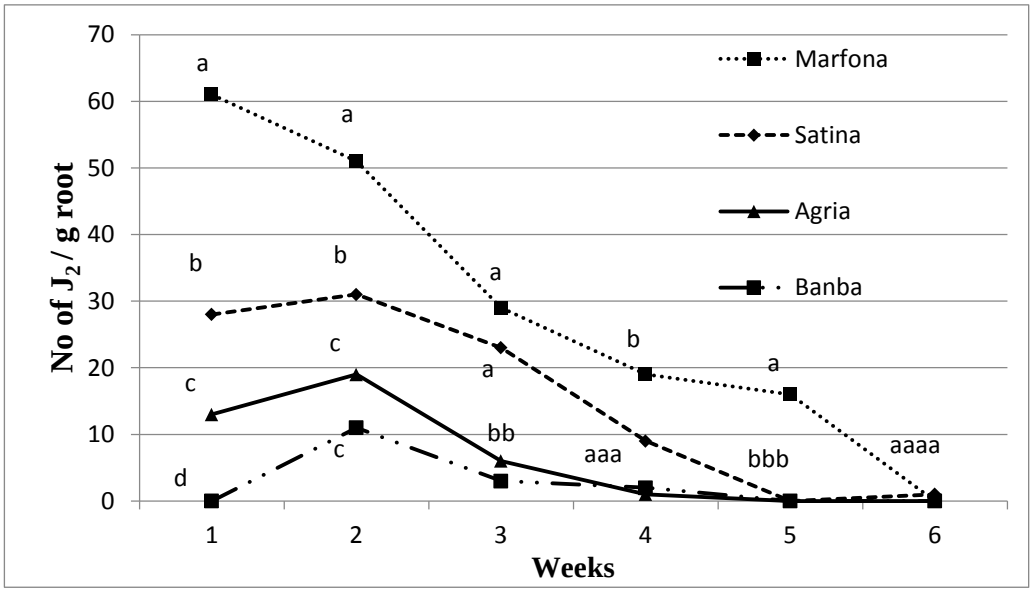

Fig. 3. Number of second stage juvenile (J_2) of *G. rostochiensis* in roots of potato cvs at weekly intervals. (Similar letters are not different at 5% level according to Duncan`s test).

as was expected. The duration of the experiment was not long enough to measure final number of cysts. In Italy, in a subtropical region with temperature above 10°C, J_3, J_4 and adult females were observed 14, 21 and 35 days after J_2 entry into roots respectively, and a second generations was completed (Greco *et al.*, 1988). Under field conditions, the adult females in England required 85 days to develop (Evans, 1969), whereas in Slovakia (Renco, 2007) and Japan (Inagaki, 1977) they required only 40 days to develop from the time of J_2 penetration into roots. In contrast, D`errico *et al.*, (1995) found the first J_3 and J_4 in roots of potato plants 66 and 79 days after planting and white females10 days later. Dissimilarity in results reported by some researchers could be related to several prevailing factors when the experiments took place, such as variation in climate, cultivar, and population of nematode. Our experiment took place in a glasshouse with an average temperature of 17 to 28 °C, and plants were inoculated with freshly hatched J_2s. Whitehead & Turner (1998) suggested that potato cvs differ in the extent to which they permit PCN to multiply on them; a fully susceptible cv. allows the nematodes to multiply on roots, stolons and tubers; and a fully resistant potato allows no multiplication. Phillips *et al.*, (1982) reported that the numbers of juveniles within the roots of a highly resistant genotype were significantly fewer than in roots of the susceptible Pentland Crown, and that the development of the juveniles was also largely retarded in the most resistant genotype. Williams (1958) indicated that potatoes with the *H*1 gene were still invaded by the juveniles but few females developed to maturity and that there were few giant cells associated with feeding juveniles. Their conclusion is supported by earlier work of Jones (1981) in that penetration of juveniles and syncytial initiation in potato with the *H*1 resistance gene occurs as in susceptible hosts but the syncytia are ultimately inactivated, destroyed or limited in their effectiveness, thereby slowing or halting the development of the juvenile nematodes. In addition, Rice *et al.*, (1985) found that, in *H*1 genotypes, root cells surrounding invading *G. rostochiensis* nematodes undergo a hypersensitive response and become necrotic. However, Rice *et al.*, (1987) reported no evidence of any limitation of syncytial

development by cell necrosis in *S. vernei*-derived material, implying a different resistance mechanism.

Significant differences between cultivars and in hatching behavior occurred in our experiment. Hatching tests were performed at room temperatures of 18-23 °C, which favors *G. rostochiensis* hatch requirements (Franco, 1979). 74% of J_2 hatched when exposed to root diffusate of the Marfona susceptible host, compared to 50% in Agria, 43% in Satina and 39% in Banba resistant potatoes. In addition, in PRD from the Marfona susceptible host, J_2 of *G. rostochiensis* Ro1 hatched more steadily than in PRD from resistant cvs over the 6-week period of the experiment; 50% of the total hatch occurred in the second and third weeks in Marfona, whereas 71 to 92% hatched in the first two weeks in PRD from resistant cvs.

It seems there still is some doubt on how the different sources of resistance to PCN work to reduce or prevent nematode increases. Hatch inhibition may be an important element in this respect (Turner, 1989). A reduction of hatch in leachates has been noted for *S. vernei*, and Williams (1958) have pointed to differences in hatching patterns in different *G. pallida* populations and variation in interaction between potato genotypes and nematode populations.

Turner *et al*., (2009) demonstrated that half-strength PRD stimulated the greatest levels of nematode hatch, and different population of PCN (*G. rostochiensis* and *G. pallida*) have shown differences in hatch in leachates from wild clones of resistant potato. The variation in hatch of PCN has been attributed partly to survival strategies acquired in the co-evolutionary process such that, as an insurance, a proportion of eggs do not hatch and thus serve as a reserve for the population. This might also be the case for a reduced hatching response of *Globodera* populations to leachates from resistant hosts (Turner *et al.*, 2009). Despite the finding of Rawsthorne & Brodie (1986), our finding of weaker hatching of the resistant cvs could not be related to their root weight (data not presented) since root weights were similar in all cvs. Arntzen *et al.*, (1993) have proposed variation in hatching may be caused by different amounts of hatching factors in diffusates of these cultivars.

Some tolerant genotypes/cultivars have induced poor hatch (Evans, 1983; Arntzen *et al.*, 1993). If some cvs induce hatch poorly in the field, they might be invaded less by *G. rostochiensis*, and thereby may suffer less damage and tolerate nematode attack better (Evans, 1983).

However, in Spain in the Balearic Islands, Alonso *et al.*, (2011) reported that Marfona has produced greater yields than Maris Peer at a given infestation level of *G. pallida*, despite both being susceptible to PCN (Halford *et al.*, 1999). In this respect, Marfona was more tolerant to *G. pallida* invasion in spite of the fact that its larger root system supported a large population of nematodes.

Since *G. rostochiensis* is a new pest in Iran, first detected in 2010 (Gitty & Tanha Maafi) in Hamadan Province, experimental data on many aspects as well as on interaction of nematode behavior with its new host and environment is few.

The results of this experiment have provided some basic fundamental insight regarding *G. rostochiensis* activity and used cvs. Similar features as well as the development of different densities of *G. rostochiensis*, number of generations and reproduction in relation to various hosts, need more verification under natural conditions in Hamadan Province.

The entrance and route by which the nematode has been spread to Iran is not clear. There is some speculation that unchecked infected tubers have been imported from Pakistan boundaries and planted by farmers at one time in Hamadan Province which still remains the only infected place. It would be interesting to evaluate this criterion using *G. rostochiensis* populations from both countries.

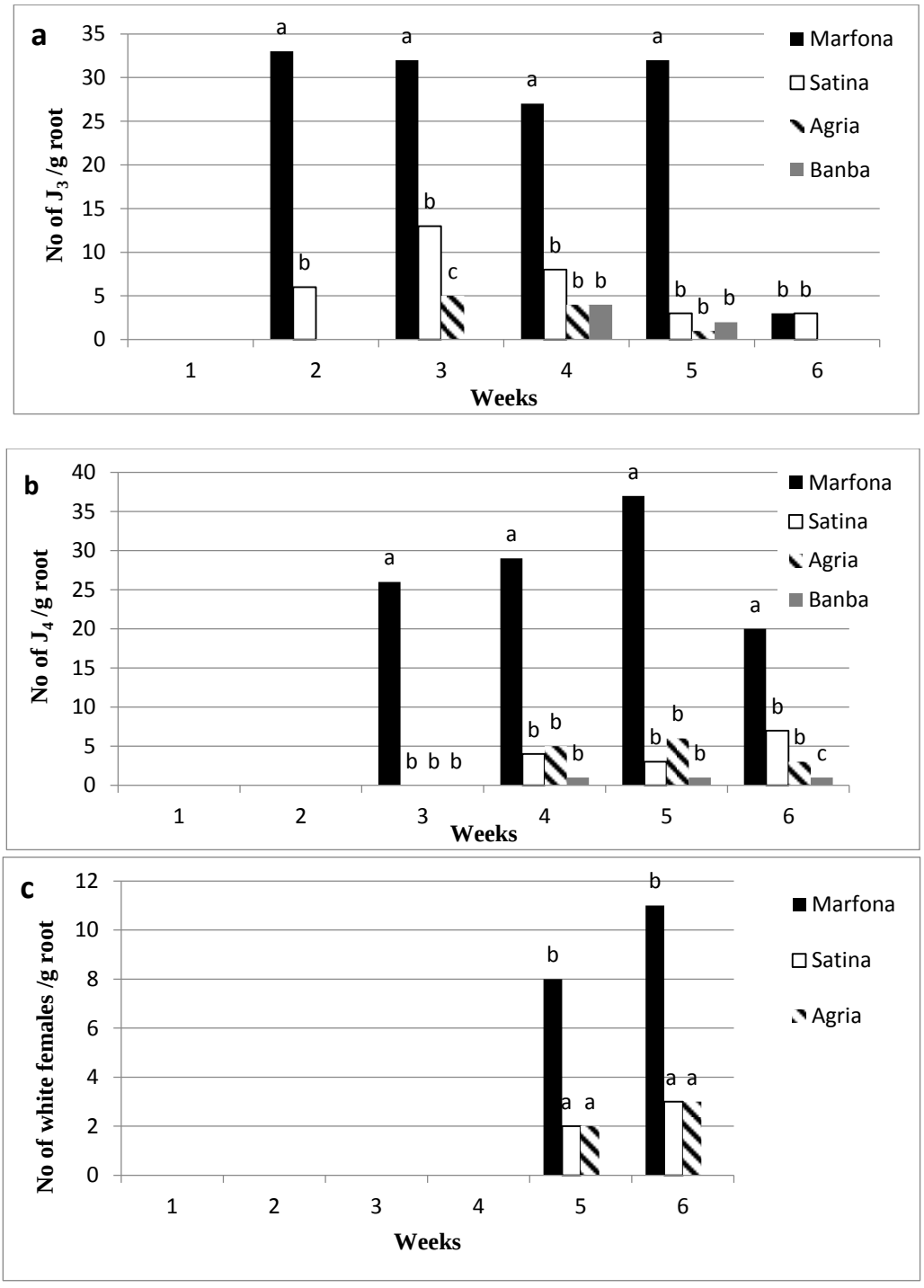

Fig. 4. Development of third (J_3), fourth stage juveniles (J_4) and white females (a, b, c) of *G. rostochiensis* in roots of susceptible Marfona, and resistant Agria, Banba and Satina potato cultivars. Columns with similar letters are not different at 5% level according to Duncan's test.

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