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CLIMATE CHANGES AND NEMATODES: EXPECTED EFFECTS AND PERSPECTIVES FOR PLANT PROTECTION

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Some factors interfering with plant protection from phytoparasitic nematodes are reviewed in the light of changes brought about by the global warming in action. The mechanisms mainly concern changes in temperature and water regimes. The effects of climate changes on the epidemiology and management of the main phytoparasitic species occurring in Mediterranean environments include the alteration of the reproductive cycles due to plants productivity, the geographic dispersion by more northern or higher altitude shifts, the spread of vectors. Other related indirect mechanisms are feedback effects due to the reactions of cultivated species or weeds, and those related to natural enemies. The potential management of some operational tools are briefly discussed, including the development and application of models and monitoring. An exemple of modeling changes induced by increasing temperatures on the carrot cyst nematode *Heterodera carotae* is briefly discussed.

KEY WORDS: climate change, crop production, nematodes, phytoparasites.

INTRODUCTION

Significant changes induced by variations in climate extremes (mainly, but not uniquely, related to temperature and moisture regimes) are expected within the next decades. Among other environments and natural systems, they will also affect crops as well as plant parasites and biological control agents, with different outcomes, depending on geographic regions and agricultural systems (OLFERT & WEISS, 2006). Nematodes, either parasitic on plants, predatory or free living in soil, will be affected by climate changes in a complex way. Beneficial or negative effects are expected, depending on species, regional situations, crops, climate and geography. In this review we briefly examine some of the possible outcomes expected on a global scale, and the actions eventually required to sustain actual levels of crop production. An exemple of modeling changes induced by increasing temperatures on the carrot cyst nematode *Heterodera carotae* is illustrated and briefly discussed.

CHANGES IN WATER REGIMES AND TEMPERATURES

Increasing temperatures and changes in water regimes are expected to interact with other human factors such as land use, urbanization and water management, affecting crops productivity and sustainability, in many ecosystems. Also, changes interacting constructively, balancing other negative factors (increased rainfalls in semi-desert areas or natural re-forestation) cannot be excluded. However, it is worth to take into account adverse events, especially extreme rainfalls, with direct consequences as the loss of irrigated areas or of agricultural land, due to higher intensities or frequencies of floods, droughts or erosion. Changes in the water regime will influence the water availability for plants and will affect yields, increasing densities and levels of nematode parasitism, due to positive effects on total plant biomass.

Increased flood rates are expected to raise the frequencies of several water-borne (aquatic fungi) or moisture dependent (powdery mildew) diseases, indirectly affecting plants productivity and nematode densities. Availability of water affects soil nematodes, whereas changes in plants communities are known to indirectly affect their abundance and community structure (KARDOL *et al.*, 2010). Changes in water regimes may also influence the duration of a nematode parasitic event, i.e. the infection phase or the progeny produced in a season, with final outcomes on total numbers. Similarly, higher/lower incidence of droughts will affect either the survival of field inocula, the frequency of parasitism by endemic aquatic or nematophagous fungi, or the time spent in soil by juveniles seeking for an available root penetration sites.

Factors affecting a function's response (i. e. crop productivity, pest or disease prevalence) to a given climatic change are key elements and must be correctly identified, in order to yield reliable information for modelling or preventive measures. They include also physical properties of soil, i.e. texture or water retention capacity which may affect, at different extents, soil nematodes responses to changes of the hydrologic cycle (WESSOLEK & ASSENG, 2006).

The effect of increasing rainfall regimes may vary: in arid climates higher water availability may yield positive consequences on agricultural practices, increasing crops productivity or cultivated surfaces. Increasing rainfalls may also induce changes in the selection of varieties or cultivated species that may increase the incidence of nematodes, switching either their species composition (replacement) or even increasing natural antagonists and prevalence levels, due to higher moisture, affecting i.e. the spreading of antagonists or predators (i.e. *Pasteuria* spp. parasites). On the opposite, in an already moist climate, an increasing rainfall regime of the same magnitude may yield floods, with soil losses due to erosion, forcing the adoption of other plants/cultivars or sowing periods. Higher amounts of water in soil will either increase the incidence of nematodes dispersion and the probability of a local extinction. Catastrophic rainfalls may also affect some management practices, like soil labour, solarization, sowing and fertilization, or vanish the effects of chemicals.

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Increasing temperatures are expected to enhance plant growth rates and yields, providing a greater food source for nematode pests but also increasing the whole ecosystem complexity. Temperatures will also affect plants phenology, (earlier germination of seeds, plant flowering or ripening). Both factors will be responsible for a higher carrying capacity of plants, an earlier emergence of pests/diseases/vectors and crop attacks, longer life-cycles and reduced pest/disease generation times.

As GOUDRIAAN & ZADOKS (1995) pointed out for plant diseases, also nematodes will thrive where host plants grow best. However, the range of genetic variability and adaptability is still unknown thus far, for several nematode species. The identification of these adaptive boundaries is important, since they represent the basis for future expansions and colonization of new areas, following isothermal shifts. The reduction or elimination of natural barriers confining a species in a particular geographic or climatic area should always represent a source of concern: for example, changes are expected in the distribution of insects, due to movements towards higher altitudes or latitudes, as a response to higher temperatures (WALTHER *et al.*, 2002). Reaching a higher altitude may allow a species to overcome a natural barrier, thus colonizing new geographic regions from which it was previously excluded. Although this factor is a major concern for insect pests, nematode phoresis or vectoring capacity by insects, i.e. *Monochamus* sp., provide a link to the potential spread of nematode pests (i.e. *Bursaphelenchus* spp., pine wilt nematodes).

Combined changes in temperature and moisture regimes will also affect biological control agents (BCA). As for nematodes, increased numbers due to higher yields and plants carrying capacities will affect BCA densities, an effect also expected to produce earlier emergence times and outbreaks due to a corresponding earlier host nematode emergence. Other effects will be the longer life cycle and/or the reduced generation time, an increased spatial spread to newly colonized areas following nematodes spreading, or the increased spread of water related parasites (i.e. *Catenaria*).

Other indirect mechanisms will favour nematodes insurgence or spreading of invasive species (GOUDRIAAN & ZADOKS, 1995; FUHRER, 2003). Among them, the increased (reduced) leaf moisture in wet (dry) conditions (affecting i.e. foliar nematode species), the changes in the survival of BCA or endophytes propagules (spores, bacterial cells, mycorrhizae), in soil or other host tissues, the reduced (increased) plants resistance due to physiological adaptations to temperature changes (i.e. prolonged vegetation, lignification, longer lasting resistance-breaking temperatures, insurgence of virulent nematode populations), changes in the nutritive value of host plant tissues, higher densities of alternated or secondary hosts (weeds).

CHANGES IN ATMOSPHERE COMPOSITION

Positive effects of increased CO_2 levels alone are expected on plants productivity (OLSZYK & INGRAM, 1993; GOUDRIAAN & ZADOKS, 1995; MANNING & THEDEMANN, 1995; CHAKRABORTY *et al.*, 2000). They will also increase the numbers of herbivores or efficiency in water, N use and conversion of radiation (OLESEN & BINDI, 2002). However, nematodes reaction to rising CO_2 levels is complex, depending on trophic groups: no effect was reported on nematodes from prairie soil (FRECKMAN *et al.*, 1991), but numbers decreased in cotton rhizosphere (RUNION *et al.*, 1994), or increased in forest (HOEKSEMA *et al.*, 2000), grassland (HUNGATE *et al.*, 2000) and pasture soils (YEATES & ORCHARD, 1993; YEATES *et al.*, 1997; 2003). Higher CO_2 levels lowered the numbers of bacterial feeders, increasing fungal feeders and predators in forest (NEHER *et al.*, 2004) or prairie soils (YEATES *et al.*, 2003).

Air pollutants affect phytoparasitic nematodes through changes in the physiology of the host plant. Synergistic interactions between ozone or SO_2 and *Meloidogyne incognita* were observed on tomato, as higher levels of foliar damage were found on nematode infested plants. Galls on roots were higher in nematodes infested plants exposed to 100 ppb ozone at 5 hours intervals every third day. Ozone, however, reduced the reproduction performance of *M. incognita*, with lower numbers of eggs and masses at 50 and 100 ppb (KHAN & KHAN, 1997).

ADAPTIVE STRATEGIES, MODELLING AND MANAGEMENT

Any research programme aiming at introducing new varieties or improving the long-term application of biological, genetic or agronomic tools (i.e. irrigation programmes, soil labour techniques, forest management or land use) should take into account the effects of climate and environment changes. Particular attention must be paid in the management of nematodes through the introduction of resistance genes in commonly used varieties, since an evaluation is needed about the persistence of the genetic pool introduced, on a scale of decades or years. Protection of biodiversity of plant genetic pools have hence a practical and immediate justification. The term "adaptive strategy" reflects, in this sense, the need for a quick and flexible response, since some climate changes are expected to occur on a short temporal scale. Some changes are already in action and newly introduced varieties may display in a few years unsuitable agronomic traits, i.e. higher susceptibility due to increased air moisture or rainfall, or may become susceptible to newly colonizing or substitution pests, thus vanishing long term research investments.

Models may help in evaluating a number of different outcomes and situations, i.e. providing a basis to identify the best among different options, to select in case of invasive species (eradication, suppression, no action) (FRASER *et al.*, 2006). In general, an insight on the possible outcomes of climate changes may be facilitated by the application of simulation models. Their sensitivity should be checked, however, with real scenarios, to verify the level of uncertainty and affordability, as well as their effectiveness as informative tools (KICKERT *et al.*, 1999).

One key issue in modelling is the level of resolution achieved and the forecasting precision. The asymmetric increase of temperatures (with different shifts for minima and maxima), as well as the non-linearity in growth or development responses, require sub-daily resolutions when modelling climate changes effects on fungal plant pathogens, due to a bias introduced when only mean temperatures are used, without considering the amplitude of the fluctuations (SCHERM & VAN BRUGGEN, 1994). Nematodes, however, due to a longer time required for completion of the different life-stages (eggs, juveniles, adults), may be modelled with different scenarios of daily mean temperature changes, aiming at providing a first rough insight about possible field situations and outcomes.

A difference model for the carrot cyst nematode, *Heterodera carotae* (fig. I), was constructed and applied using the daily mean temperatures registered at Manfredonia, a typical carrot growing area in Apulia, during

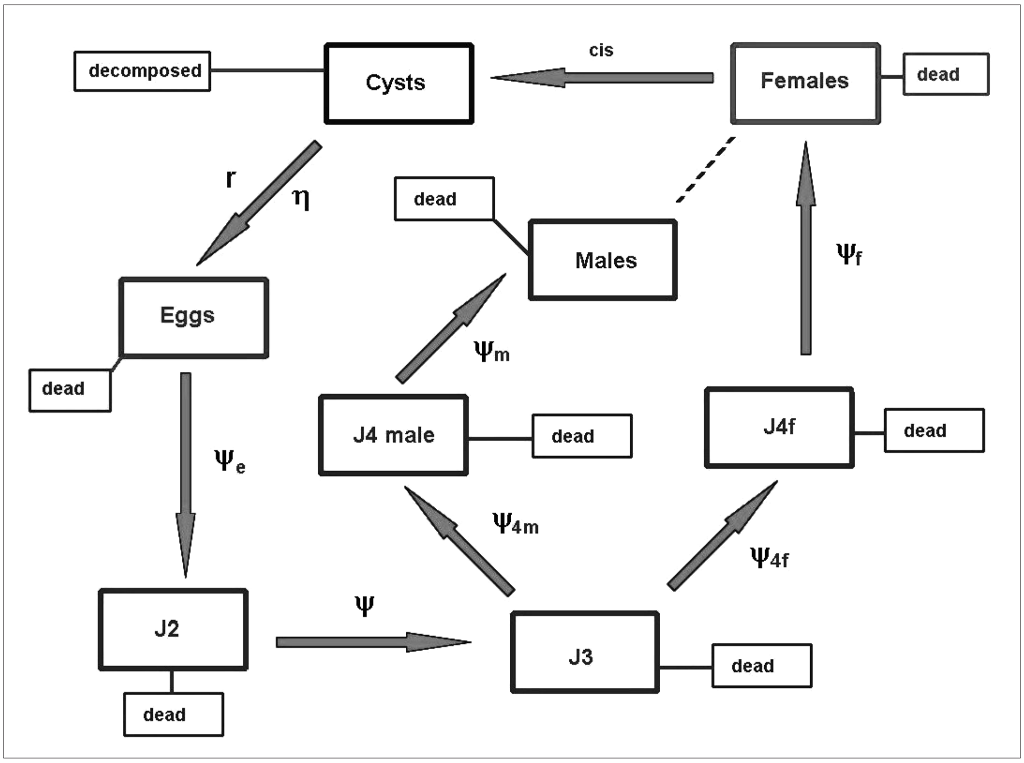

Fig. I – Components of the model applied to simulate the density changes of the carrot cyst nematode, *Heterodera carotae* in function of temperature shifts. Parameters show the maturing rates of life-stages, or the rates of eggs development and release.

two years (2006-2007) (fig. II). The life stages considered eggs, second stage juveniles (J2), third stage juveniles (J3), fourth stage females (J4f) and males (J4male), together with adult females, males and cysts. The model was constructed using published data to derive the daily rates of eggs release and of development, for the other stages of *H. carotae* (GRECO & BRANDONISIO, 1986; MUGNIERY & BOSSIS, 1988; BARNEY & BIRD, 1992). The relationship of the daily egg production rate with temperature was provided by a gaussian function, considering the difference between the daily mean value and the optimal temperature for eggs release (20°C) (fig. III, 1). Similarly, the rate of eggs development was calculated using a higher corresponding optimal temperature (24.5°C), whereas the rates of maturation from J2 to J3 and J4 were calculated using the relationship between temperature and length of stage, provided by MUGNIERY and BOSSIS (1988). Due to the dependency of *H. carotae* on host plant roots for eggs hatching, the model included also a parameter K, accounting for the presence (K=1) or absence (K=0) of roots, and hence for the production or hatching of eggs during a simulated, two years cropping cycle (August to February). A further parameter was also used to account for a daily minimal egg hatching probability (0.005), in

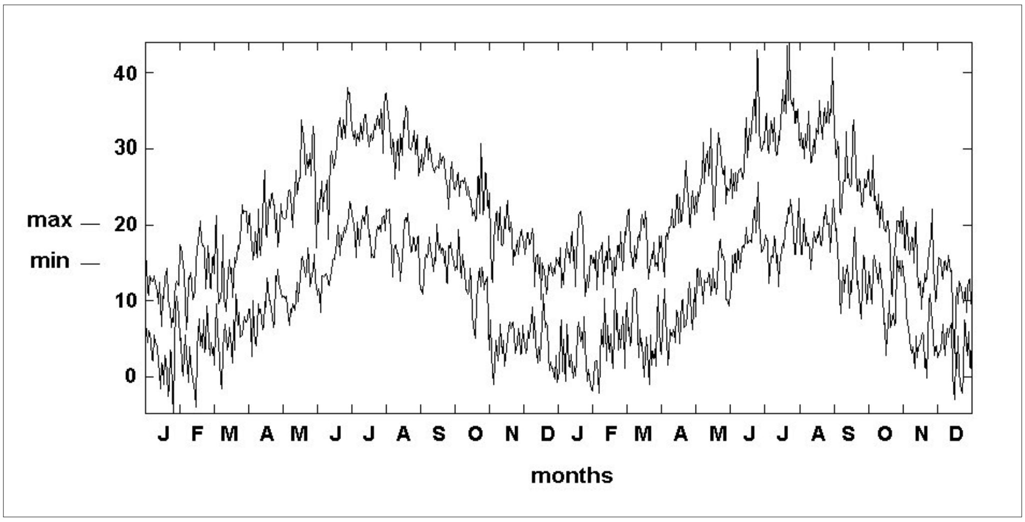

Fig. II – Minimum and maximum temperatures registered at Manfredonia (Foggia, Italy), in the years 2006-2007 (source: Protezione Civile).

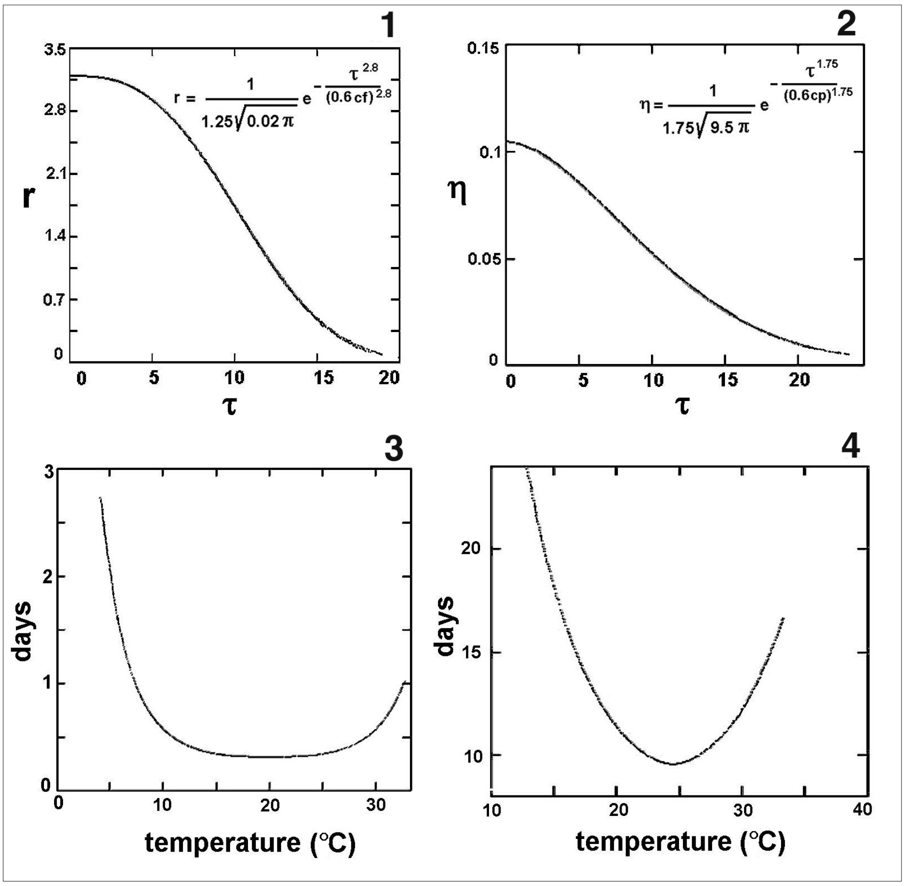

Fig. III – Daily rates of eggs production r (1) and development η (2), estimated in function of the absolute difference τ between mean daily temperature and optimal stage values (cf and cp, respectively), used for modelling *H. carotae*. Inverse values (3 and 4, respectively) show the corresponding stage lengths, in days.

absence of roots. All stages were subjected to natural mortality rates, estimated as the inverse of the corresponding stage average life-length.

Simulations of an *H. carotae* population dynamics, started from 50 initial eggs, 40 J2-J4f stages, 3 females and cysts and one male per ml of soil, showed the expected numbers of 2-3 nematode generations, observed during the autumn-spring periods (fig. IV, 1). A progressive 0.25°C shift in temperatures, equally applied at each daily mean value to simulate a uniform increase of temperatures, affected the maximum numbers reached by eggs, J2 or cysts in a non linear way, with highest rates of increase observed at highest (1.5-2°C) increments (Table 1, figs. IV and V). At these temperature shifts, simulations showed further juvenile and eggs generations in winter (fig. IV, 4 and 5).

Although modelling necessarily represents a simplification of the more complex, non-linear relationships occurring in soil among different organisms, it provides an insight on dynamics otherwise difficult to trace, due to the amount of experimental data and time required to investigate these relationships. At small scales, generic dynamic crop modelling may result informative about the effects of weather, variety, pests, soil and management practices on crop growth and yield, as well as on soil N and organic carbon dynamics in aerobic as well as anaerobic conditions. Data generated include pest induced yield losses, allowing a comparative analysis with i.e. different greenhouse gas emission situations (AGGARWAL *et al.*, 2006). Weather variables introduced in modelling result fundamental to explore the different outcomes of climate changes and hence estimate the spatial and seasonal dynamics of pests, in the mid-term (YONOW *et al.*, 2004).

A further tool is given by probability distribution maps (PDM). Their use allows the identification of potential risks related to the distribution of pests, vectors or plant diseases. PDMs are calculated on the basis of the combined use of local records of pest occurrence, climate data and subsequent statistical analysis. They show the areas susceptible of colonization or of endemism, for a given organism (MORALES & JONES, 2004). This tool has several practical advantages, including the possibility of early identification of invasion areas by a pest or the possibility to anticipate the insurgence of epidemics for secondary pests, already present in areas with sub-optimal conditions for life-cycle. PDMs require the monitoring of different climatic variables at the regional scale and a given resolution level, as well as the implementation of an early monitoring and detection support system.

CONCLUSIONS

Adaptive strategies will be required for integrated or biological monitoring in high altitude areas of insect nematode vectors as a preventive action against "biological surprises". At the same time, probability maps distribution

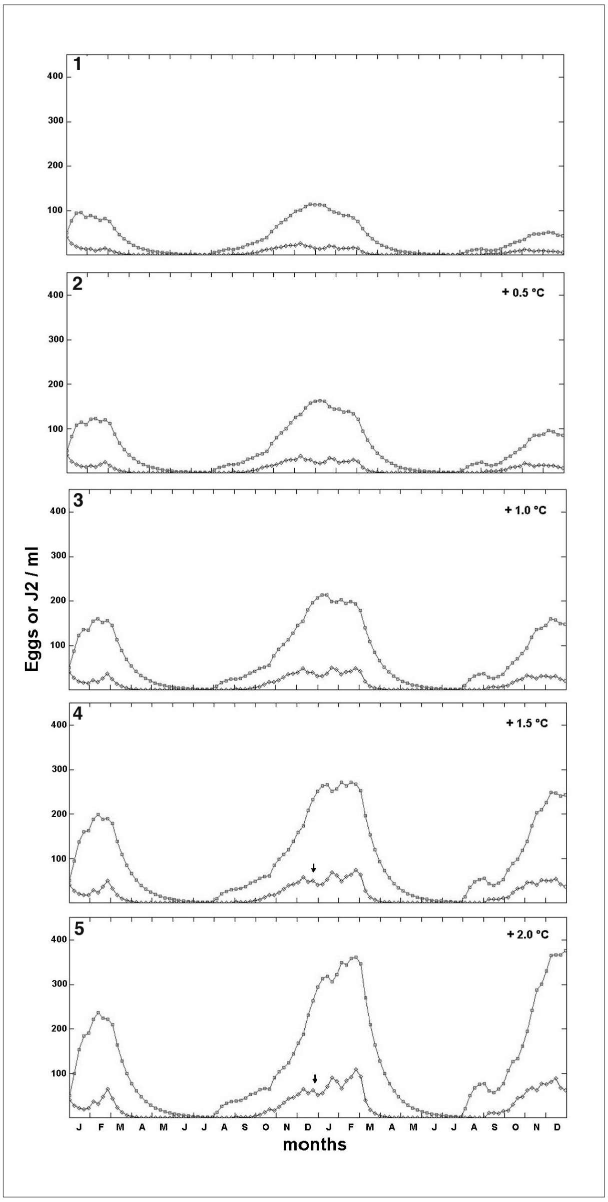

Fig. IV – Two years (2006-2007) modelled population dynamics of eggs (squares) and J2 of *H. carotae*, and changes observed with uniform mean daily temperature increases ranging from 0.5 to 2°C. Arrows show an additional J2 generation, at highest temperature shifts.

Table 1 – Simulated effects of daily temperature increases (D) on maximum densities reached in soil by *Heterodera carotae*, expressed as ratio with densities at D = 0.

D (°C)	Eggs ml^{-1}	J2 ml^{-1}	Cysts ml^{-1}
0.25	1.19	1.0	1.28
0.5	1.41	1.0	1.60
0.75	1.64	1.14	1.97
1.0	1.88	1.38	2.39
1.25	2.12	1.66	2.90
1.5	2.40	2.05	3.48
1.75	2.81	2.50	4.16
2.0	3.29	3.02	4.97

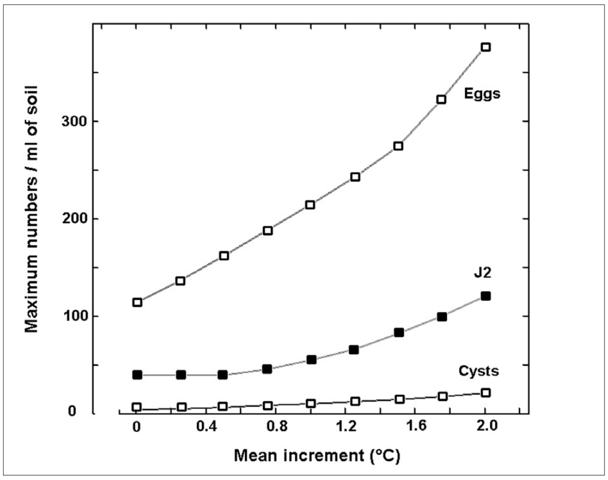

Fig. V – Relationship between mean temperature increments and maximum simulated numbers per ml^{-1} of soil reached by eggs, J2 and cysts of *H. carotae*.

will allow the identification of potential risks related to distribution of main nematode species. Programs on the introduction of resistance genes in plant varieties should consider their durability in a changing environment, and how much they will remain useful.

The protection of natural biodiversity represent an "adaptive strategy" with a rapid and flexible response. Models for invasive species, for possible effects of climatic changes and the integration of a global climate model with local, specific sub-models, also represent useful tools, but require a continuous check for their fitness and reliability.

Finally, it is possible that not all of the changes expected for the next decades will produce negative consequences. Knowledge base prevention plays an important role, including consideration of minor species that may become insurgent, as novel pests.

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RIASSUNTO

CAMBIAMENTI CLIMATICI E NEMATODI: EFFETTI PREVISTI E PROSPETTIVE PER LA PROTEZIONE DELLE PIANTE

Alcuni fattori che interferiscono con la protezione delle piante da nematodi fitoparassiti vengono esaminati, alla luce dei cambiamenti indotti dal riscaldamento globale in atto. I meccanismi riguardano principalmente i cambiamenti nei regimi di temperatura e idrologici. Gli effetti dei cambiamenti climatici sull'epidemiologia e gestione delle principali specie fitoparassite che si verificano in ambienti mediterranei comprendono l'alterazione dei cicli riproduttivi dovuti alla produttività delle piante, la dispersione geografica verso livelli più settentrionali o a maggior altitudine, la diffusione di vettori. Altri meccanismi indiretti sono effetti di retroazione causati dalle reazioni di specie coltivate o di erbe infestanti e quelli relativi ai nemici naturali. Le potenzialità gestionali di alcuni strumenti operativi sono brevemente discusse, compreso lo sviluppo e applicazione di modelli ed il monitoraggio. Viene brevemente discusso un esempio di modello dei cambiamenti indotti da temperature più alte sul nematode cisticolo della carota *Heterodera carotae*.

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