The predicted impact of possible climatic change on virus-vector nematodes in Great Britain

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Abstract

Data extracted from surveys of plant-parasitic nematodes in Great Britain allowed relatively detailed maps of the geographical distribution of various longidorid and trichodorid virus-vector nematode species to be produced. These distributions are related to long-term monthly mean temperature. Recently published figures for climate change were applied to the distribution data. A potential increase in nematode associated problems due to climate change using examples of existing published data are examined and discussed.

Introduction

Estimating the extent to which the United Kingdom climate will change is problematical [MacKerron *et al.*, 1993]. Some models have suggested global temperature increases of up to 2.5 °C [Hansen *et al.*, 1988; Wigley and Rapier, 1992] which is substantially less than proposed by Houghton *et al.* [1990].

MacKerron *et al.* [1993] presented 'best estimates' of changes in mean values of several weather elements over 40 years for the United Kingdom. They suggested that the rise in temperature would be in the order of 0.5 °C to 1.1 °C and that rainfall would increase by between 5 to 15%.

The potential effect of global climate change on pests and considerations of the implications on agricultural production have been discussed for the United Kingdom [Crawford *et al.*, 1989; Sutherst, 1991; MacKerron *et al.*, 1993]. Although virus-vector nematodes are important soil-borne plant parasites which occur in most terrestrial biotopes they have so far received less attention compared with airborne pests, e.g. aphids, with respect to potential climatic changes [Collier *et al.*, 1991].

Taylor *et al.* [1978] commented that studying single factors e.g. temperature did not take into account the complex interactions between many of the abiotic and biotic components of the ecosystem. However, it is generally agreed that nematode survival and reproduction are dependent upon the following important factors: soil type, presence of a suitable host, temperature and soil moisture [Taylor *et al.*, 1978; Brown and Coiro, 1983]. Plant-parasitic nematode species are known to have different optimum temperatures for feeding [Boag, 1980], hatching [Shepherd and Clark, 1971], reproduction [Malek, 1980] and survival [Bergeson, 1959]. The majority of longidorid and trichodorid species, with a few exceptions, do not have a restricted host range [Taylor, 1967; Alphey and Boag, 1976] or soil type [Alphey and Boag, 1976]. In contrast to Jones [1975], Boag [1982] reported that in Great Britain soil moisture rarely restricted nematode movement in soil and subsequently Boag *et al.* [1991] agreed with the previous findings of Topham and Alphey [1985] who concluded that in Europe, soil moisture was unlikely to affect the geographic distribution of virus-vector nematodes in most agricultural soils. Consequently, Boag *et al.* [1991] considered soil temperature to be the main factor limiting the geographic distribution of virus-vector nematodes. This assumes that temperature, specifically summer temperatures, are solely limiting the present distribution of nematodes. Lahtinen *et al.* [1988] noted that the relative rate of nematode development could alter as the threshold extremes were approached. Temperature can operate in two ways. Firstly by presenting

an absolute barrier where certain species would not survive (e.g. certain *Meloidogyne* spp. cannot withstand winter freezing in temperate regions). Secondly, as mean summer temperatures decrease with increasing latitude, so generation times are increased with a subsequent decrease in reproduction and competitive ability. Thus, establishment of viable communities at the northern range of their distribution becomes marginal. It is evident that the means by which temperature operates to limit the current geographical distribution of nematodes is complex.

Since virus-vector nematodes are incapable of rapid and independent migration, it should be possible to forecast changes in their geographical distribution due to long-term climatic change with more certainty that most other pests. Baseline geographical distribution maps of virus-vector nematodes have been published on a 10 km grid for Great Britain [Taylor and Brown, 1976; Alphey and Taylor, 1986; Brown and Taylor, 1987]. However, detailed prediction of such changes are impeded by the lack of published information concerning threshold temperatures for embryogenesis and life-cycles of most species of plant nematode.

The aims of this paper are to anticipate the possible effect of climatic change on the distributions of some common virus-transmitting longidorid and trichodorid nematode species within Great Britain, assuming that temperature is currently the major limiting factor to species distribution. The probable impact on agricultural production, the potential for an increased incidence of nematode-transmitted virus, introduction of novel crops to Great Britain, e.g. Lucerne, potential selection pressures on viruses to evolve and produce new serological variants, and thus the possibility of either new virus-vector associations or new plant hosts for existing vectors will also be discussed.

Materials and methods

Data recording the distribution of Longidoridae and Trichodoridae in Great Britain were initially obtained from the following sources: a North Atlantic Treaty Organisation (NATO) – financed survey of the distribution of Longidoridae [Taylor and Brown, 1976]; a survey financed by the Natural Environment Research Council (NERC) of nematodes associated with forest and woodlands in Scotland [Boag, 1974]; sampling records from the Scottish Crop Research Institute (SCRI); records received from advisors from the Scottish Agricultural College, the Agricultural

Development and Advisory centres in Scotland, England and Wales respectively and also those extracted from published papers and research reports and on occasions unpublished data from nematologists within the United Kingdom.

The NATO, NERC and SCRI surveys were all sampled on the Ordnance Survey 10 km-square grid basis. At each 10 km grid square, samples, where possible, were taken from five vegetative habitats, arable land, coniferous forest, deciduous woodland, permanent pasture and scrub/heathland. Nematodes were extracted from a 200 to 400 g sub-sample taken from a *c*. 1 kg composite soil sample using a modification of a sieving and decanting technique [Boag, 1974], heat killed at 60 °C and fixed in triethanolamine formalin (TAF) [Courtney *et al.*, 1955].

The long-term monthly mean air temperature was obtained from the Monthly Weather Report (The Meteorological Office, HMSO, London). Although soil temperature influences nematode survival and multiplication, it was not available for many of the meteorological stations used. However, a linear relationship between soil and air temperature has been shown to exist [Toy *et al.*, 1978] and air temperature has previously been used to study the biology of nematodes [Boag, 1982]. Maximum and minimum development temperatures were obtained from a plot of nematode density versus temperature by interpolation of the data using Lagrange polynomials [Ortega and Poole, 1981]. Nematode density for a particular temperature band was calculated by counting the number of 10 km grid squares with positive detections and dividing by the total area of land covered by the band. No corrections were attempted to account for possible differences in soil type, topography or the sampling density within a 10 km grid square, which could affect the statistical weight of a particular square. Since there is unlikely to be a strong correlation of sampling density with temperature, or topography with latitude and thus the large-scale variation of temperature, the omissions of the latter two would only contribute statistical noise to the analysis.

The optimal developmental temperature was calculated by setting to zero the first derivative with respect to temperature of the corresponding polynomial, and solving for temperature. Polynomial regression was not performed in the interpolation procedure because there was judged to be insufficient data.

Results and discussion

Figure 1 shows the distribution of 10 km squares from which samples were collected. Whilst sampling did not encompass all 10 km squares nor was it regular, sufficient squares were sampled to determine the different geographic distribution patterns for the virus-vector nematode species that were studied. *Longidorus elongatus* was distributed throughout Great Britain [Taylor and Brown, 1976], whereas, both *L. attenuatus* and *L. macrosoma* were restricted to an area south of the Midlands. *L. attenuatus* was mainly confined to East Anglia (Fig. 2a), while *L. macrosoma* was present in Wales, the Midlands and southern England [Taylor and Brown, 1976]. *Xiphinema diversicaudatum* was restricted to southern Scotland, England and Wales (Fig. 2b). Of the two trichodorid species studied, *Trichodorus primitivus* was widely distributed although it was not recorded in the far north of Scotland, whereas, *T. viruliferus* was only recorded in East Anglia, Kent and the Lothians [Alphey and Boag, 1976].

The long-term monthly mean air temperature (Table 1) at meteorological stations located at the northern most ranges for the species studied, suggests that their different patterns of distribution coincide well with published nematode developmental temperatures and July summer isotherms [Phillips' Universal Atlas, 1983; Boag *et al.*, 1991]. Lagrange polynomial interpolation of the data (Table 2) indicated that the minimum developmental temperature required for *L. macrosoma* and *X. diversicaudatum* was 13.0 °C and 12.8 °C respectively; therefore, data from Table 1 suggests that these two species could be present as far north as the north east of Scotland. However, their distribution seems to be restricted to an area south of the Midlands and southern Scotland respectively. This may be due to the fact that populations of these two species do exist in more northern areas but below detectable levels. It may also be possible that there is insufficient accumulated temperature in any one year in northern areas for these two species to complete a life-cycle. For example, only two months in Grampian region have mean monthly temperatures above the minimum developmental temperature of 12.8 °C for *X. diversicaudatum* [Boag *et al.*, 1991] whereas Tayside region has four months (Table 1).

Taylor *et al.* [1994] demonstrated that under stable conditions over a 30 year period the horizontal distribution of *X. diversicaudatum* remained virtually unchanged. It is difficult to ascertain whether under
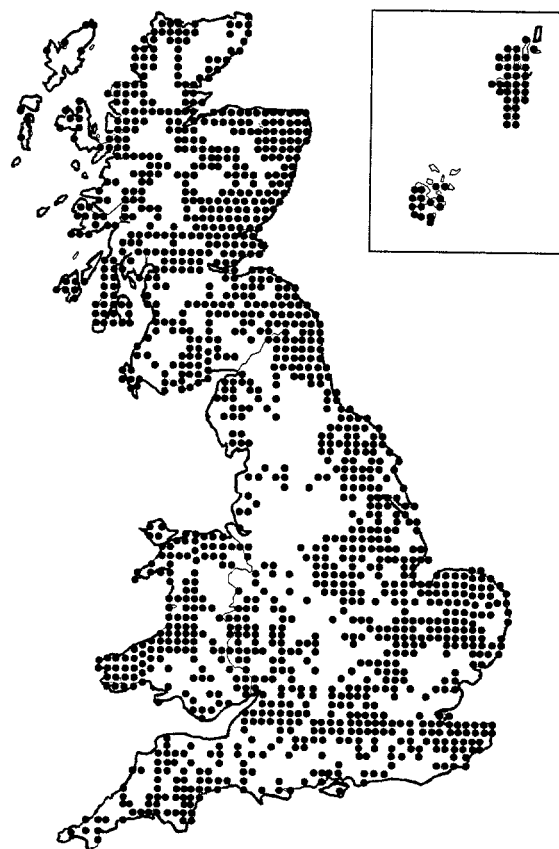

Fig. 1. Distribution of 10 km grid squares from which samples were collected in Great Britain.

a modified climate such distributions would remain static. Assuming that current nematode distributions are limited by temperature, theoretically an increase of *c.* 1 °C in mean temperature [MacKerron *et al.*, 1993] would allow the northward extension of the virus-vector nematode species under study by approximately 160–200 km depending upon the starting location (Table 1). Nevertheless, the rate of nematode migration through soil is too slow for them to have any impact on their distribution in the short to medium term [Thomas, 1981]. However, Boag [1985] showed that man can efficiently disseminate nematodes, and Brown and Taylor [1987] also considered that man was probably the most important influence on the dissemination of nematode species. Therefore, although further nematode dispersal can potentially be controlled by phytosanitary regulations, spread could continue by birds and other animals [McNamara and Flegg, 1981].

Table 1. Long-term (30-year) monthly mean air temperature for selected meteorological sites* in Great Britain

Region	Shetland	Grampian	Lothians	Tayside	N. Yorks	W. Yorks	Kent	Worcester
Weather Station	Lerwick	Craibstone	Turnhouse	Mylnefield	Harrogate	Bradford	East Malling	Ross-on-Wye
	Mean Air Temp C	Mean Air Temp C	Mean Air Temp C	Mean Air Temp C	Mean Air Temp C	Mean Air Temp C	Mean Air Temp C	Mean Air Temp C
Month								
May	7.5	8.7	10.0	9.7	10.1	10.5	11.5	11.5
June	10.0	11.8	13.0	12.9	13.2	13.5	14.6	14.5
July	11.4	13.2	14.4	14.5	14.9	15.0	16.5	16.2
August	11.7	13.1	14.2	14.3	14.6	14.9	16.2	15.9
September	10.3	11.5	12.4	12.1	12.6	12.9	14.1	13.7
October	8.3	9.1	9.6	9.4	9.5	9.7	10.8	10.6
Altitude (m)	82	102	35	30	63	134	33	57
Latitude (°N)	60°08	57°11	55°57	56°57	54°01	53°49	51°17	51°55

* Meteorological sites were chosen on the ability to provide long-term monthly means.

Fig. 2. Distribution of 10 km grid squares in which the following longidorids were recorded: A, *Longidorus attenuatus*; B, *Xiphinema diversicaudatum*.

Table 2. Minimum, maximum and optimal developmental temperatures for virus-vector nematode species derived from Lagrange polynomial interpolation of nematode density and temperature using data from United Kingdom maps

Species	Minimum	Optimum	Maximum
Longidorus elongatus	12.0	12.6	16.0
L. macrosoma	13.0*	15.7*	16.6
Trichodorus primitivus	12.0	13.6	16.2
T. viruliferus	14.0	15.0	16.0
Xiphinema diversicaudatum	12.8	14.5*	24.1*

* Data from European maps [Alphey and Taylor, 1986].

Soil moisture is not currently considered to be a limiting factor for the geographical distribution of virus-vector nematodes in Great Britain [Topham and Alphey, 1985] and it is difficult to predict whether the estimated 5–15% increase in rainfall [MacKerron et al., 1993] will alter nematode distribution on a large scale.

Colonisation of new areas by virus-vector nematodes has implications for agriculture. Applying the previously suggested figure of 160–200 km increase in nematode range, a 1 °C rise in temperature would permit populations of X. diversicaudatum, a vector of both arabis mosaic (AMV) and strawberry latent ringspot (SLRV) viruses; L. macrosoma, a vector of raspberry ringspot virus (RRV) and L. attenuatus, a vector of tomato black ring virus (TBRV) to extend northwards into north-east Scotland and southern Scotland respectively. These four viruses can infect a wide range of plants including raspberry and strawberry [Brown and Trudgill, 1989; Brown et al., 1989]. Depending upon many factors such as nematode abundance, level of virus infection, virus strain present and cultivar grown, yield losses for raspberry and strawberry crops can on occasions be up to 100% (D. J. F. Brown, pers. comm.).

Additionally, the introduction of new or novel crops into Great Britain could also result in new nematode problems. Lucerne, currently an important fodder crop in near continental Europe [Anon, 1991] is one such crop that could realistically be introduced and commercially grown as far north as north-east Scotland (Scottish Agricultural College, pers. comm.). Lucerne is a suitable host for an existing nematode transmitted virus, Pea early-browning virus (PEBV) [Harrison, 1973] which is transmitted by T. viruliferus [Brown et al., 1989]. Initially this may result in only localised outbreaks as T. viruliferus and PEBV have restricted

distributions [Gibbs and Harrison, 1964; Alphey and Boag, 1976]. As suggested by Brown and Trudgill [1989] such novel crops may exert selection pressure on viruses leading to the evolution of new serological and/or symptomatological variants. Furthermore, virus variants may be efficiently transmitted by their associated vectors to a greater or lesser extent and could even exploit alternative nematode species as their vectors. Ploeg [1992] found such a recombinant virus variant vectored by T. cylindricus which serologically resembled PEBV but contained RNA-1 sequences homologous to tobacco rattle virus (TRV). Although rare in Great Britain, similar recombinant tobraviruses are common in the Netherlands (A. T. Ploeg, pers. comm.). It can be speculated that increased problems could occur if a recombinant tobravirus evolved which was transmitted by the widely distributed T. primitvus.

Further nematode problems could manifest themselves with the introduction of new crop cultivars. For example, the 1 °C increase in temperature under consideration suggests that, depending on extreme events such as drought and late frosts, commercial viticulture could extend northwards to the north Midlands of England (Table 1). New cultivars would likely be introduced to take advantage of the differing biotopes. Potential new or introduced cultivars may be more severely affected by existing viruses than former cultivars e.g. 'Kerner' disease in Germany that is caused by X. diversicaudatum transmitting AMV leading to a graft union necrosis between the rootstock and recently introduced Kerner fruiting scions [Rüdel, 1985; Gärtel, 1985].

Furthermore, new crops may also lead to the introduction of new nematode species. New nematode species may also be viruliferous and introduce new viruses, e.g. Xiphinema index with grapevine fanleaf virus (GFLV) which has been spread throughout areas of viticulture on infected rootstocks. Although present in almost every European and Mediterranean country with a viticulture industry, reducing yields up to 60%, GFLV and X. index have yet to be identified in Great Britain [Taylor and Brown, 1976; Brown and Trudgill, 1989]. Cotten et al. [1970] demonstrated that the X. index can presently survive outdoors only in southern England, thus, if imported on infected rootstocks, populations of X. index have the potential to become ubiquitous in areas of extended viticulture under modified conditions.

However, as Boag et al. [1991] and Hillier [1993] note, predicting the effect of climate change on nematodes and plants is difficult and speculative because

the magnitude and range of that change is so uncertain. Furthermore, depending on the extent to which spread by man can be controlled, any alterations to the distribution of virus-vector nematodes and proliferation of their associated problems under a modified climate would probably occur over an extended time scale. Nevertheless, although speculative, this paper using published data has suggested potential problems that may exist under a modified climate. With the recent easing of restrictions on the movement of plant material within the European Community such importations may become frequent. As Mackerron *et al.* [1993] note, a fundamental aspect of limiting these problems would be to increase the importance of vigilance against accidental introductions.

Acknowledgements

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