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The invasion and spread of Lepidoptera in Britain

D. AGASSIZ

Abstract

A short history is given of the study of invasions of Lepidoptera into Britain with the associated ecological theory. The rate of spread was calculated for each of 29 spp. which showed a range from near zero to 10.3 km/year. Data from the USA show a marked contrast, with a rate of spread greater by an order of magnitude. The reasons for this are discussed, and it is suggested that invasions from another continent are much less predictable and have the potential to spread at greater speed, reaching higher density. Invaders from other continents are mentioned, and the likelihood of these reaching Belgium is discussed.

Keywords: invasions, Lepidoptera, ecology.

Introduction

In 1990 the British Government realised that it was likely that Genetically Modified Organisms (GMOs) would be introduced into the country within the foreseeable future. They were anxious that ecological theory about the spread of such organisms should be tested so that their spread could be predicted.

There had been a recent symposium on this subject in Britain arranged by the Royal Society and the papers had been published (KORNBERG & WILLIAMS 1986). Much of the theory was also included in a book by Rob HENGEVELD (1989) of the Netherlands. Such works took examples from many different organisms, from mammals and birds to diseases and human practices. For this reason an insect was considered as suitable an organism as any other.

The UK programme

It happened that at this time a small leaf-mining moth *Phyllonorycter leucographella* (ZELL.) had been found newly established in Britain and its distribution at that time had been carefully mapped by amateurs including myself. It was an ideal model to monitor since it was harmless, established naturally of its own accord and could easily be seen in the larval stage. A three-year programme was begun which involved monitoring the spread of the moth nationally, studying the dynamics of its spread at a smaller scale and analysing the response of its natural enemies. Shortly into the programme another moth was found belonging to the same genus: *Phyllonorycter platani* (STDGR), which was discovered newly resident in London. Equivalent sampling of this species was also undertaken.

Ecological theory predicted that the insects should spread radially outwards with uniform speed from the point of introduction, given a homogeneous environment. The food plant used by the first species is *Pyracantha* which is widely planted in gardens and urban environments, enough to approach a uniform distribution. The food plant of the second species is *Platanus*, also introduced into Britain but much less widely planted outside London and major towns.

The presence (and density) or absence of both species were carefully monitored in each 10 km square of the National Grid throughout their known range for three years and for at least 10 km beyond so that the boundary of the range could be known exactly. The area was then

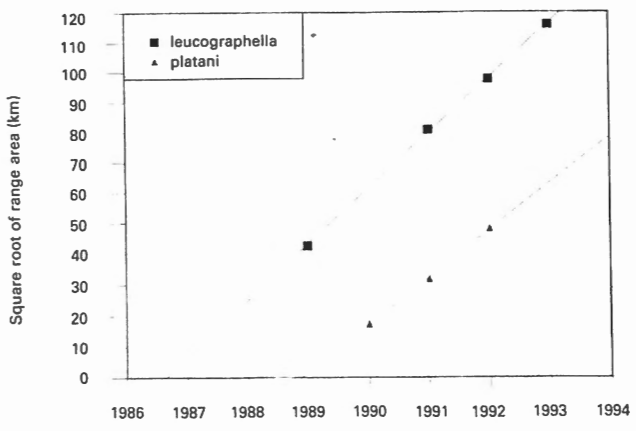

Fig. 1 — The square root of area colonized by *P. leucographella* (squares) and *P. platani* (diamonds). Range area was calculated as the number of 1010 km squares within which the moth was recorded. The lines are fitted regressions.

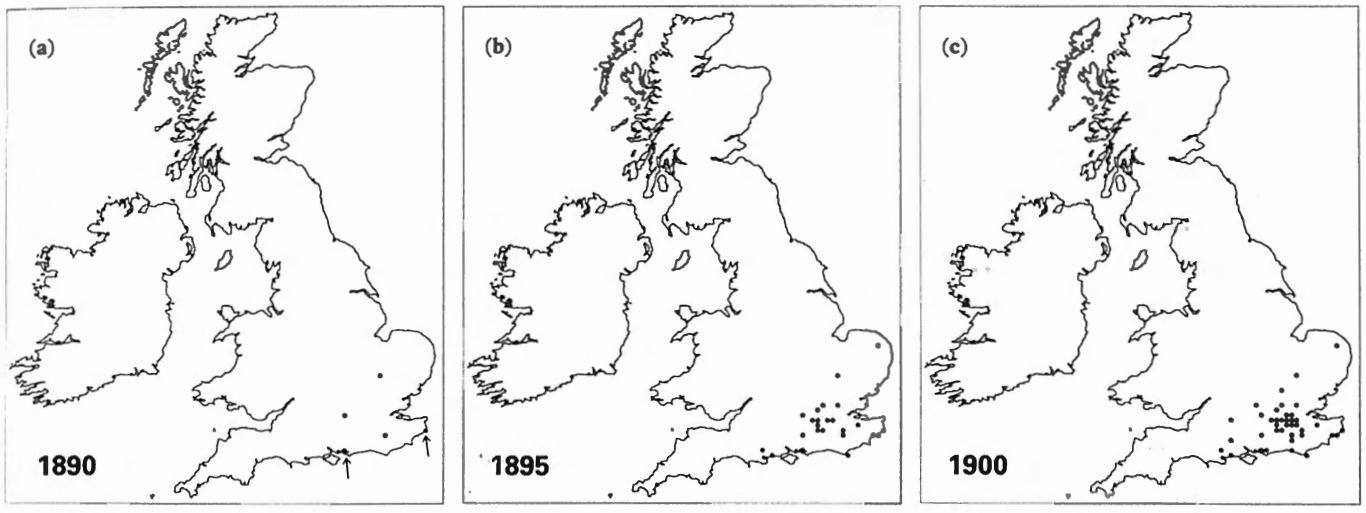

Fig. 2 — Records of *Polychrysia moneta* in Britain 1890-1900.

calculated as the number of squares occupied. The results have been published (NASH *et al.* 1995) and show a remarkable fit to the theory, *P. leucographella* advancing at a uniform 10.3 km/year and *P. platani* at 8.6 km/year, measured by the simplest method of plotting the square root of area [$(\text{area})^{1/2}$] against time (fig. 1).

Other research

The British Isles have a remarkable history of biological recording, chiefly by amateurs. On account of this I was able to extract data for a further 27 species of Lepidoptera which had successfully established and spread during the previous 100 years up until 1991. I hope soon to extend this data set for a further 10 years. Most of the records of species were made by amateurs, often from moth traps or other observations in their own gardens.

An example of this are maps (fig. 2) showing the records of the noctuid moth *Polychrysia moneta* (FABR.) for the ten years from its first record until 1900, there were sufficient records to draw a line around them on the map to define the range area of the species at that time. Data regarding the absence of species could not be obtained with the same rigour as was possible with leaf mining species, but it could often be implied where someone was recording on a regular basis.

Some of these data have also been published (AGASSIZ 1996) so I will confine myself to a single example: the noctuid moth *Lithophane leautieri* was first found in Britain in 1951. It is a European species whose larva feeds on cypress trees *Chamaecyparis* spp. etc. which have been widely planted. The moth extended its range with the availability of food, moving northwards up the west coast of France before becoming established in the south of Britain. From there it spread northwards with the front of its range advancing at a rate of 6 km/year (fig. 3).

Of the 27 species investigated, a linear relationship between the square root of range area and time was statistically significant in 22 cases, which is further strong evidence that invading species will normally advance with constant speed. What is of interest is that the range of speed with which the front advanced was small, ranging from close to zero to 10.3 km/year (table 1). Individual moths can fly much further than that in the course of their lives, or even in one night or day, and one wonders why such a slow rate of progress is achieved. Although this was a large data set, the shared characteristics of the species may be quite strong. An analysis of the origin of the invading species showed that the majority came from elsewhere in Europe, none from the Americas (although there is one more recent arrival, *Argyresthia cupressella*, it is too early to say how it will spread) and only two or three from Australasia.

Some research has been undertaken in North America, notably by Doug FERGUSON who collected data on the spread of moths introduced chiefly from Europe. Of these there were quite a number. The same detail of recording is not available in North America, but even so he calculated the rate of spread which was of an order of magnitude greater than my studies in Britain had revealed. One can joke that everything in the USA is bigger, better and faster, but are there other factors to be considered?

The British Isles are by definition islands and instead of being able to expand in all directions, many species, beginning in the south east of England, have only a sector of a circle to the north west into which they can move. Some attempts at dispersal will end up in the sea, but this can only have a partial reduction on the rate of progress. It was not a factor in the spread of the *Phyllonorycter* species mentioned above, which began their establishment inland, not near the coast.

Of more significance, surely, is the fact that the invaders of North America came from another continent,

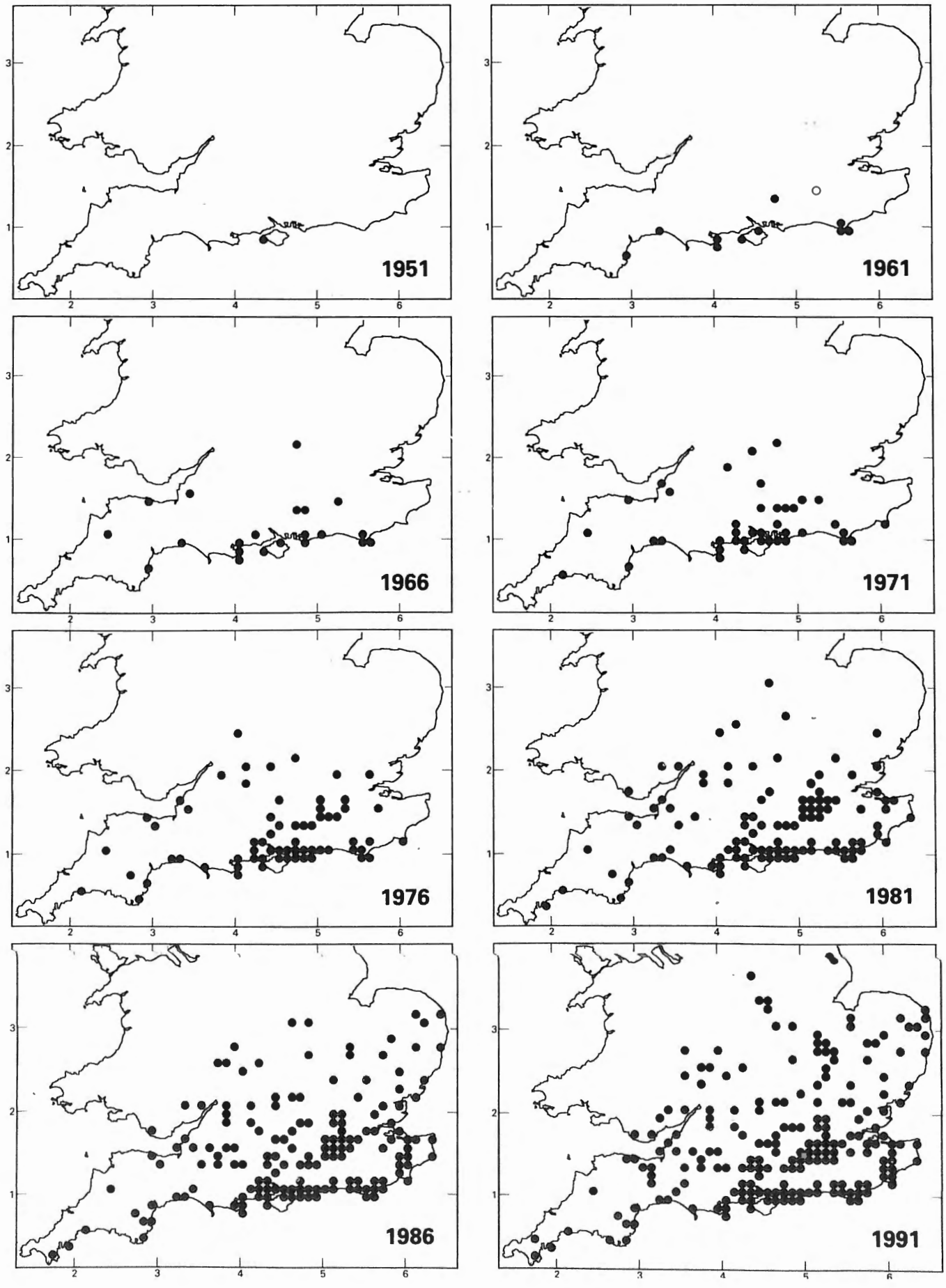

Fig. 3 — The spread of *Lithophane leautieri*.

Table 1 — Rate of spread of Lepidoptera invading Britain.

Species	rate of spread (km/year)
Etainia decentella	3.05
Stigmella suberivora	2.20
Psychoides filicivora	1.69
Caloptilia rufipennella	7.33
Phyllonorycter platani	8.63
P. leucographella	10.30
Tachystola acroxantha	0.06
Argolamprotes micella	3.89
Carpatolechia alburnella	3.72
Blastobasis decolorella	2.20
Cacoecimorpha pronubana	2.26
Ptycholomoides aeriferanus	2.31
Epiphyas postvittana	2.54
Adoxophyes orana	1.07
Lozotaeniodes formosanus	2.65
Acleris abietana	4.12
Pammene aurita	2.43
Phlyctaenia perlucidalis	4.68
Dioryctria shuetzeella	5.36
Xanthorhoe biriviata	1.81
Spargania luctuata	1.24
Eupithecia phoeniceata	2.14
Peribatodes secundaria	3.46
Hadena compta	2.54
Lithophane leautieri	3.78
Polychrysia moneta	2.99
Mean value	3.40

and the natural enemies of related species were not so prepared to react as to species with which a balance had been achieved over evolutionary time. There are species from North America which have become established in Europe in recent decades. In particular two leaf-mining moths feeding on *Robinia*, a tree introduced from the Americas. One was reported by VIDANO (1970) from northern Italy which by 1990 had reached as far as Hungary and Yugoslavia. The second was found near Basle in 1983 (WHITEBREAD 1990) and had spread into Austria, Switzerland, France, and Germany by 1990. I am not aware of any study to calculate the rate of spread, but taking the furthest points of each and their distance from the starting points, gives a rate of the order of 50 km/year. SIMBERLOFF (1989) observed that more successful invasions had originated in Europe and had happened to the New World and Australia, and he argued that the bulk of trade had been in that direction. It would be hard to argue that this is still true, and one should consider the hypothesis that evolution over the larger area of Eurasia had better equipped European species to make or resist invasion. Certainly Australia has suffered the worst catastrophes from exotic invasions and this seems likely because of its isolation from so much competition before the modern era.

Asian species are also known to be spreading across Europe. Again leaf miners are represented with *Phyllonorycter issikii* (KUMATA) being a noted example. I am not aware of any data regarding this species but anecdotal accounts suggest that it is also advancing at a speed more like those from America. In southern Europe the leaf miner *Phyllocnistis citrella* appeared in 1994 and rapidly spread to all countries from Portugal to Yugoslavia. Perhaps *Cameraria ohridella* is also in this category but since it will be dealt with by other speakers I will do no more than mention it.

Species introduced from the Southern Hemisphere tend to be used to warmer climates than we experience in Northern Europe, and their spread may be limited by minimum temperatures. It may also be that their natural food plants do not occur here. There were two species definitely originating from Australia among those I studied. *Epiphyas postvittana* (WALK.) is well known as a pest of apple orchards in Australia and New Zealand. When first discovered in Britain there was great alarm that it would become a pest there, but it remains an insect of gardens where it is polyphagous. *Tachystola acroxantha* (MEYR.) is the other species which feeds as a larva on decaying leaves. Both these species were slow to spread at first, but in the last ten years have done so much more rapidly as shown by the successive distribution maps of *T. acroxantha* (fig. 4). This could be because milder winters have facilitated their survival, or else they took generations to adapt to European conditions and are now ready to make their presence felt. *E. postvittana* is now the commonest moth in many urban and coastal parts of Britain, as far north as North Wales and northern England. It is abundant in the Channel Isles and although not yet reported from France must surely have invaded

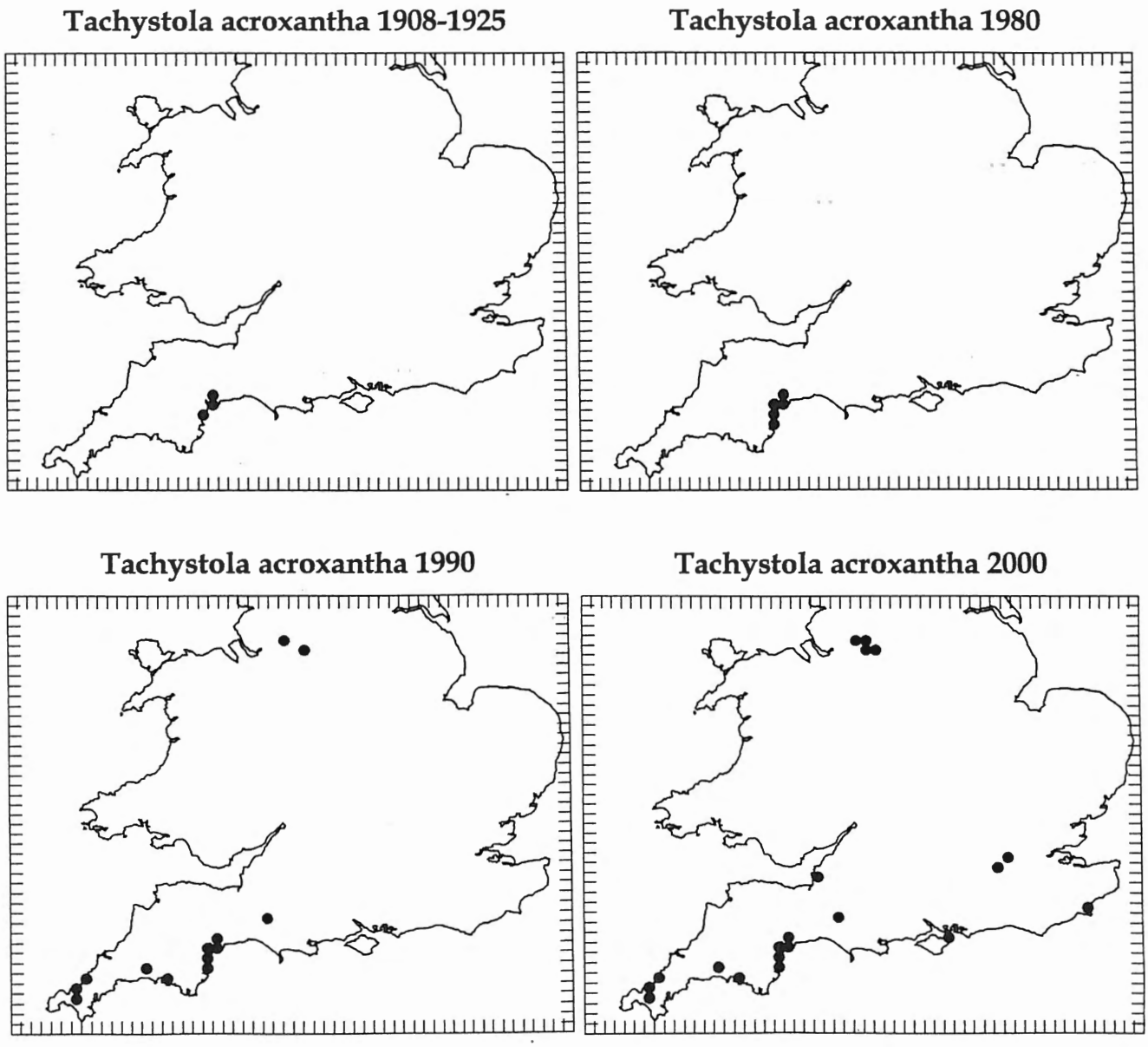

Fig. 4 — The spread of *Tachystola acroxantha* in Britain.

Normandy. If mild winters persist it is probable that this species will extend its range throughout the southern coasts of the English Channel.

In more southern parts of Europe this situation is very different as has been demonstrated by the invasion of the South African butterfly *Cacyreus marshalli* BUTLER which is devouring *Pelargoniums* in Spain and along the nearby Mediterranean coast (see SARTO 1992).

Means of introduction

An analysis of the food plants used by Lepidoptera invading Britain showed that of 29 species, 13 fed on non native plants, especially sycamore *Acer pseudoplatanus*, conifers and cypress. In the last ten years since my data were assembled, a further three species have become established and are spreading: *Argyresthia trifasciata* STDGR, *A. cupressella* WALS. and *Gelechia senticetella* (STDGR) all of which feed on cypress, although the first and last have transferred from juniper.

There is a huge amount of international trade in plants, especially that serving the Garden Centre Industry, based chiefly in the Netherlands. Undoubtedly this has been the means by which many species have been introduced. There is less of such trade between continents, but specimens can be transported in different stages and in packaging in ways that are not easily detected. Those responsible for phytosanitary control, such as EPPO, the European Plant Protection Organisation, have long lists

of potential pests. They are well aware of the risks and do much to reduce them, but no system is perfect. There is also the question of whether every spreading insect should be regarded as a pest!

Relevance to Belgium

Since Belgium is part of continental Europe any invaders originating from within Europe are not likely to progress at great speed, nor reach epidemic proportions, but can be expected to behave in a similar way to those studied in Britain. Those from other continents present a much greater challenge, provided they can use a food plant which is widespread in Belgium. Of those mentioned above *Epiphyas postvittana* is a likely colonist, at least of coastal and urban areas. *Argyresthia cupressella* is also likely to find its way into gardens and plantations of cypress and possibly may cause more damage than species of European origin. *Phyllonorycter issikii* is spreading from the east and likely to reach Belgium within the foreseeable future.

Conclusion

Lepidoptera invading Britain have behaved in a way which support ecological theory, which means that their rate of spread can be predicted with reasonable confidence provided their origin is known and their food plant is widespread. Species from different continents are much less easy to predict, both in terms of their likely appearance, how quickly they will spread, and what density will be reached.

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David AGASSIZ
Department of Entomology
The Natural History Museum
Cromwell Road
London SW7 5BD
United Kingdom