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The spread of *Epilobium ciliatum* Raf. in the British Isles

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ABSTRACT

Epilobium ciliatum Raf. (*E. adenocaulon* Hausskn.) was first collected in Britain at Cropston Reservoir, Leicester, in 1891, and by 1894 it was well-established there. It was gathered in a further five vice-counties before 1930, but not correctly identified until the 1930s when G. M. Ash realized that it was naturalized in Surrey. Thereafter it spread rapidly, reaching Wales by 1942, Scotland by 1957 and Ireland by 1958. This spread is illustrated by a series of distribution maps; some of the problems it poses are discussed, and the possible reasons for the success of *E. ciliatum* as a weed are briefly reviewed.

INTRODUCTION

Of the many thousands of plant species which have been deliberately or accidentally introduced into the British Isles, relatively few have become widely naturalized. Some of these, notably certain arable weeds, were introduced in prehistoric times, so long ago that they are difficult to distinguish from native species. *Silene alba*, probably introduced with crops in the Neolithic (Baker 1947; Godwin 1976), provides one such example. Other species spread in historic times. These include plants, such as *Acer pseudoplatanus*, which were so widespread before systematic recording began that their spread cannot be reconstructed from botanical records. Such records have, however, been used to study the spread of those naturalized aliens which were introduced more recently. These include *Cardaria draba* (Scurfield 1962), *Elodea* spp. (Simpson 1984), *Polygonum* and *Reynoutria* spp. (Conolly 1977), *Senecio squalidus* (Kent 1956 *et seq.*) and *Veronica filiformis* (Bangerter & Kent 1957, 1962). This paper documents the spread in the British Isles of *Epilobium ciliatum* Raf. (*E. adenocaulon* Hausskn.), American Willow-herb, which is now one of the more widespread weeds of alien origin.

Epilobium ciliatum is native to North America, from Newfoundland and Alaska south to Baja California, Sonora, New Mexico and Virginia. In this area the name *E. ciliatum* covers a complex which "is far from resolved taxonomically" (Raven & Raven 1976). It is an established alien on the European mainland and in Australasia: the early records from these areas are reviewed by Lawalrée & Reichling (1961) and Raven & Raven (1976) respectively.

The biology of *E. ciliatum* has been studied by Myerscough & Whitehead (1966, 1967). The seeds can retain viability for several years. Seeds which germinate in autumn give rise to plants which overwinter as rosettes and produce flowering shoots in spring in response to increasing day length. Seeds germinating in early summer can flower within 5·5 weeks. The flowers are automatically self-pollinated, and the fruit capsules dehisce about 4 weeks after pollination. The seeds possess a tuft of silky hairs, and are wind-dispersed. Plants perennate by means of leafy rosettes, which develop at the base of the stem and produce their own adventitious root systems independent of the parent plant. Despite this ability to perennate, Raven & Raven (1976) have noted that *E. ciliatum* often behaves as an annual, relying on its abundant seed production for survival.

SOURCE OF RECORDS

This study is based on records held by the Biological Records Centre, Monks Wood Experimental Station. In order to ensure that these are as complete as possible I have extracted records from the

following herbaria: **ABRN**, **BM**, **CGE**, **E**, **GL**, **K**, **LIV**, **LTR**, **NMW**, **RNG**, **OXF**. I have also searched appropriate literature sources, including the *Proceedings of the Botanical Society and Exchange Club of the British Isles* (from 1935), the *B.S.B.I. Year Book*, the *Proceedings of the B.S.B.I.*, *Watsonia* and many county and local Floras published up to the end of 1986.

THE SPREAD OF *EPILOBIUM CILIATUM*

In describing the spread of *Epilobium ciliatum* it is convenient to consider four arbitrarily chosen time spans: 1891–1929, 1930–1949, 1950–1969 and 1970–1986.

1891–1929

The presence of *Epilobium ciliatum* in Britain was not announced until 1934, but subsequent investigation has unearthed a number of earlier herbarium specimens which were not correctly identified at the time of their collection. All the specimens cited below have been determined by G. M. Ash.

The species was first collected by the Rev. T. A. Preston on 20 July 1891 at Cropston Reservoir, Leics., v.c. 55 (**BM**). Preston collected the plant again in 1894 (**BM**, **CGE**, **NMW**). Both gatherings were named as the hybrid *E. obscurum* × *E. roseum*, an identification "confirmed" by the Rev. E. S. Marshall, then the British expert on the genus. Fortunately a detailed description of the habitat of *E. ciliatum* at Cropston in 1894 is available (Mott 1895): "On the muddy shores left dry by the receding water of Cropstone Reservoir . . . sprang up vast beds of plants, sometimes a belt of one genus followed lower down by a belt of a quite different genus. One of these was an *Epilobium* belt. The species were *hirsutum*, *parviflorum*, *montanum*, *obscurum* and *roseum*, but hybrid forms occupied by far the largest area, the individuals of the pure type being comparatively rare. Among the hybrids, what appears to be *obscurum* × *roseum* [i.e. *E. ciliatum*] was perhaps most conspicuous. This belt being rather high on the sloping banks has probably been exposed for at least two summers, so that it is possible the hybridizing may have taken place on the spot." A. R. Horwood collected *E. ciliatum* at Cropston in 1905 (**CGE**, **NMW**), noting that it "continues to flourish on the silty ground . . . growing in great profusion, and reaching a height of 3–4 feet".

S. H. Bickham and R. F. Towndrow collected *E. ciliatum* at a second locality on 31 July 1905, a timber yard at Malvern Link, Worcs., v.c. 37 (**CGE**). This collection was again named *E. obscurum* × *E. roseum*, with the assent of E. S. Marshall. The next record was also from a timber yard, at Woodchester, W. Gloucs., v.c. 34, where H. J. Riddelsdell found it in 1920 (**NMW**, **OXF**). In 1921 J. Fraser gathered it on heaths north of Woking (**K**) and in 1927 E. C. Wallace found it at Ballards Plantation near Croydon (**RNG**); both localities are in Surrey, v.c. 17. Two more collections were made in 1928, from Coleman's Moor, Berks., v.c. 22 (*G. C. Druce*, **OXF**) and from a wood near Meopham Green, Kent, v.c. 16 (*A. R. Horwood*, **K**). This wood may have been Ryarsh Wood, as in 1929 Horwood collected *E. ciliatum* there. It seems to have been well-established, as there are 15 plants on the seven sheets at **K** gathered by Horwood in 1929.

Records of *E. ciliatum* made up to 1929 are plotted in Fig. 1.

1930–1949

G. M. Ash first collected *Epilobium ciliatum* in 1931. By the time that the plant was identified and its discovery published, it was clear that the species was well-established in Surrey. During the period 1930–1934 there are records of *E. ciliatum* from seven 10-km squares in that county; it was also recorded from five of the six neighbouring vice-counties, v. cc. 12, 13, 14, 16 and 22. Ash (1934) described it as abundant in south-western Surrey, and "as common as any other *Epilobium* about Witley, Godalming and Eashing". It grew in a range of habitats: "damp woods, copses and along stream-sides far from houses, as well as on railway-banks and in gardens, timber yards and waste places" (Ash & Sandwith 1935).

During the next five years, 1935–1939, *E. ciliatum* was recorded from a further six vice-counties in south-eastern England, v. cc. 11, 15, 18, 20, 23 and 24. In addition it was found further west, in v. cc. 6, 33 and 34, and further north, in v. cc. 31 and 39. G. M. Ash and J. F. G. Chapple also revisited the original British locality, Cropston Reservoir, and found that *E. ciliatum* still persisted there and also occurred at the nearby Swithland Reservoir.

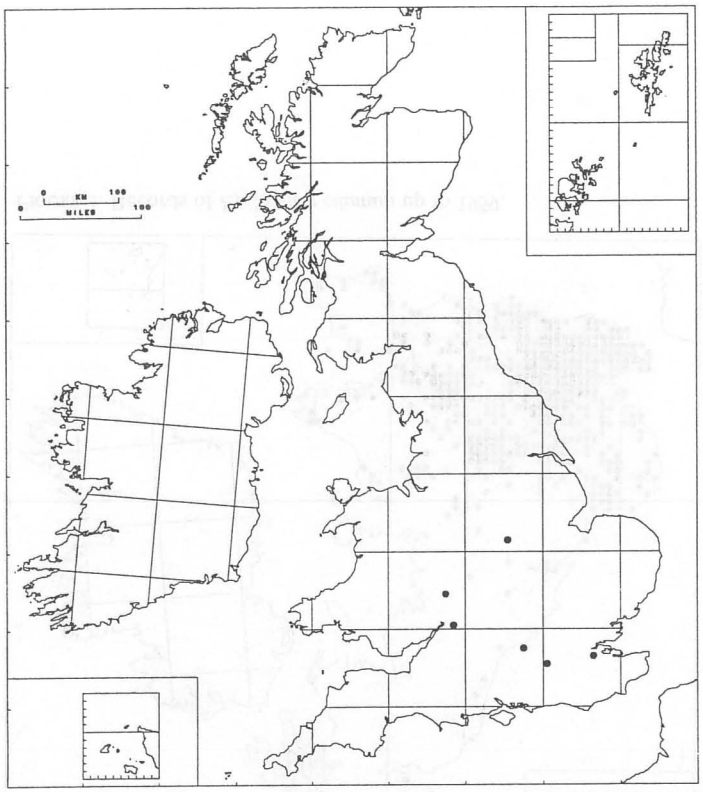

FIGURE 1. Records of *Epilobium ciliatum* up to 1929. Records are plotted in 10-km squares of the British and Irish national grids.

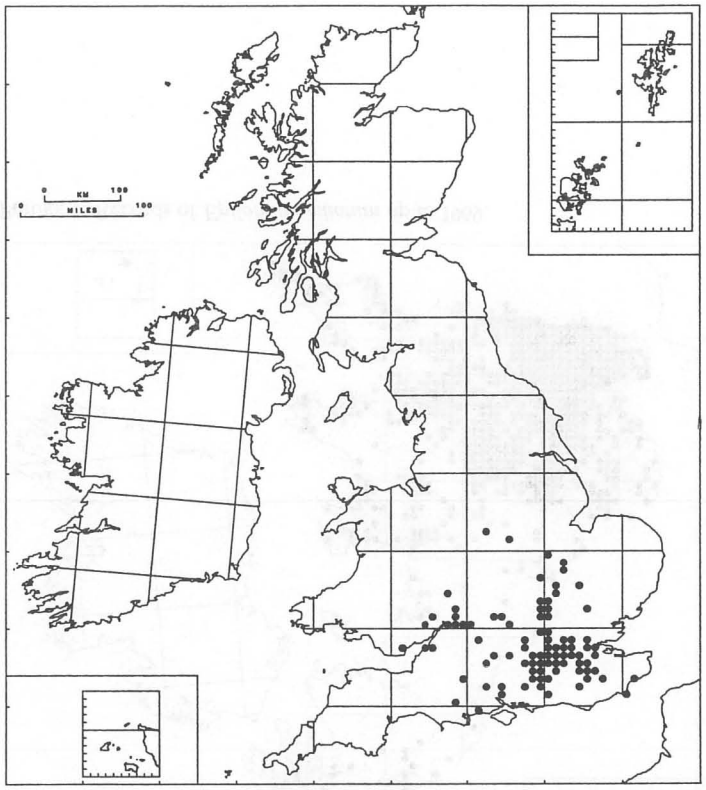

FIGURE 2. Records of *Epilobium ciliatum* up to 1949.

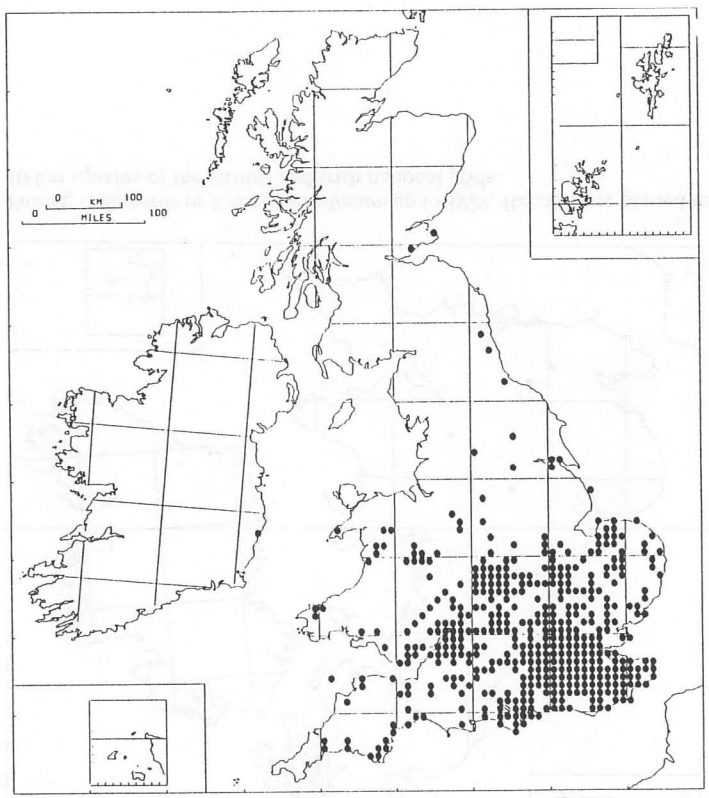

FIGURE 3. Records of *Epilobium ciliatum* up to 1959.

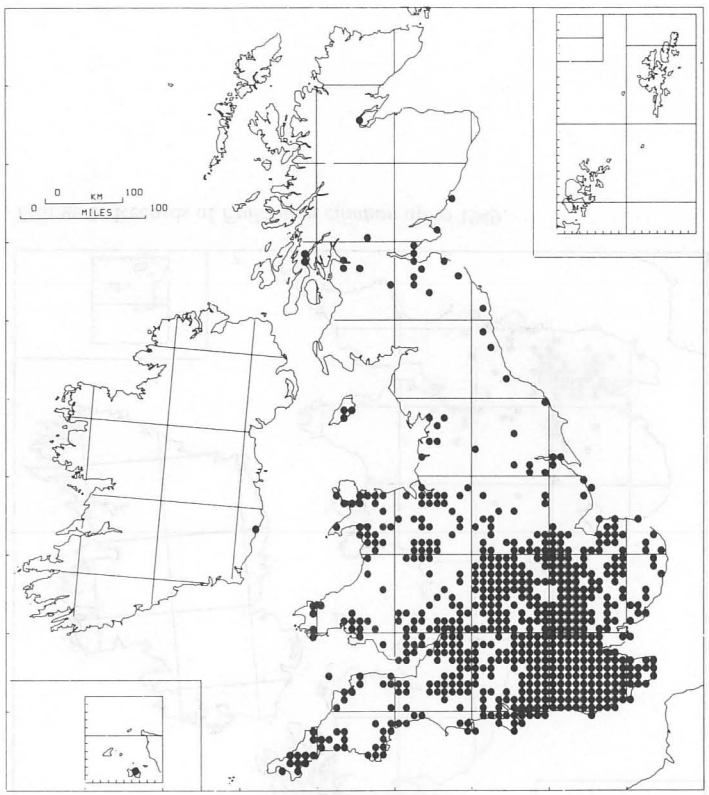

FIGURE 4. Records of *Epilobium ciliatum* up to 1969.

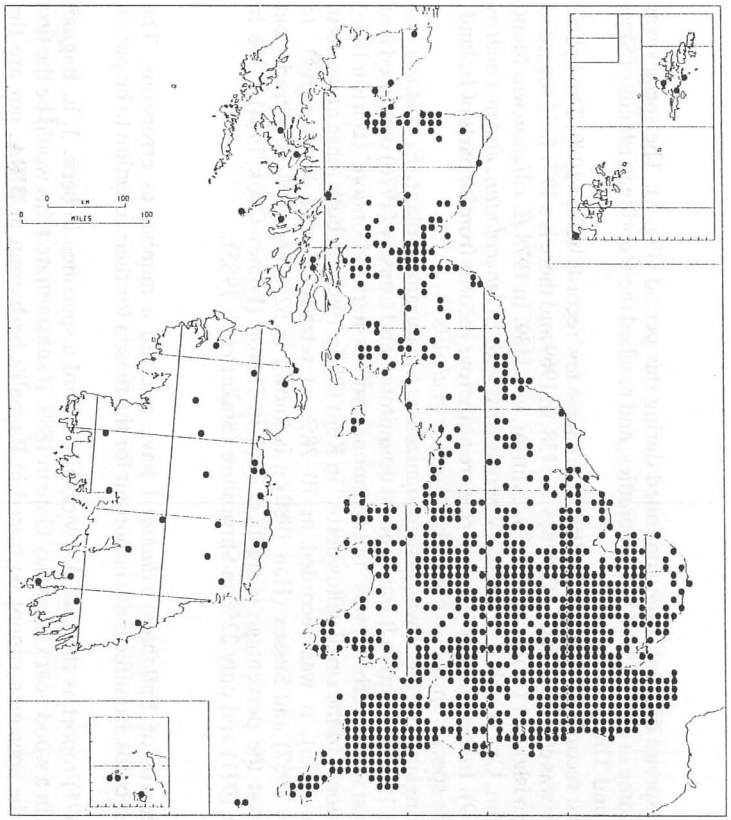

FIGURE 5. Records of *Epilobium ciliatum* up to 1986.

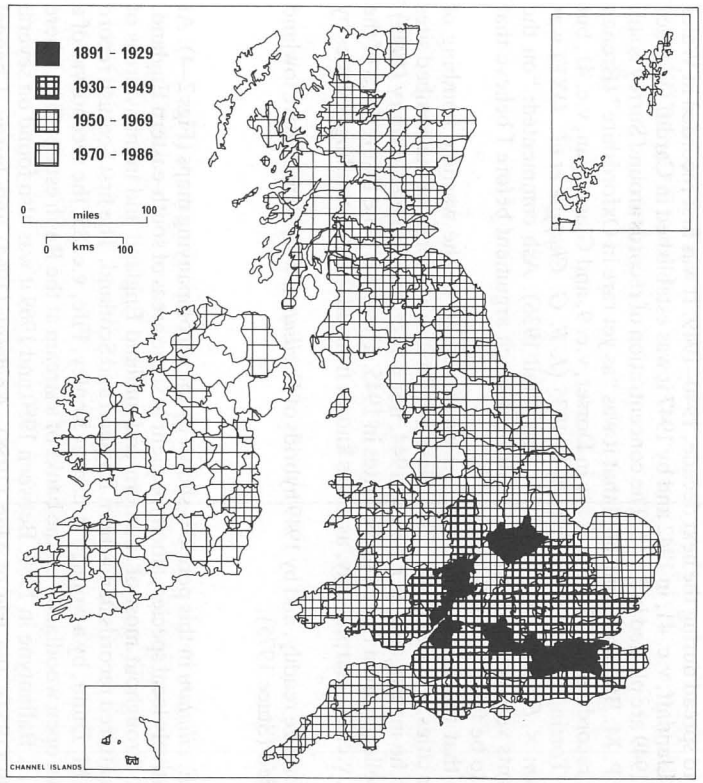

FIGURE 6. The date of the first record of *Epilobium ciliatum* in the vice-counties from which it has been recorded. Unshaded vice-counties are those in which the species has not yet been found.

E. ciliatum continued to spread during the next decade, 1940–1949. It was first recorded in Wales at Rookwood Hospital, Llandaff, v.c. 41, in 1942 and by 1947 it was established in Cardiff (Wallace 1949). All records up to 1949 are plotted in Fig. 2. The concentration of records around Surrey is still apparent, and in 1946 J. P. M. Brenan commented that it was "as yet rare in Oxfordshire" (Brenan 1948). The westernmost records mapped in Fig. 2 are in Dorset, v.c. 9, and Glamorgan, v.c. 41, but a specimen collected at Torrington in Devon, v.c. 4, in 1935 (*J. F. G. Chapple et al.*, **OXF**) was determined as *E. ciliatum* × *E. obscurum* by G. M. Ash (Hall 1936). Ash commented: "on the whole I consider the plants very convincing and I shall want much argument before I believe that *Ep. adenocaulon* is not to be found near Torrington".

There is no evidence that the spread of *E. ciliatum* was favoured by the wartime bombing of London and other major cities. Lousley (1944, 1946) does not list it as a colonist of the bombed sites in central London which he investigated in 1942 and 1944, nor is it referred to by Salisbury (1945). Lousley did, however, collect it from three bombed sites in 1945. These were the first records of the species from Middlesex, v.c. 21 – surprisingly, as it was known from all the surrounding counties by 1937.

Epilobium species hybridize readily, and by 1949 hybrids of *E. ciliatum* with all the native lowland species had been recorded (Stace 1975).

1950–1969

The dramatic spread of *E. ciliatum* in this period is shown by the accompanying maps (Figs 2–4). At the start it was still a relatively local species, albeit frequent in some areas of south-eastern England. By 1969 it was frequent throughout most of southern and midland England and in many areas of Wales, and there were scattered records in northern England and Scotland. The first Scottish record was made in 1957 by Dr M. Dunn, by a wooded stream at Kenley, Fife, v.c. 85; the second was of a population in "overgrown open woodland" on the banks of a stream at the Raith estate, Fife, where it was discovered by G. H. Ballantyne in 1959. Between 1950 and 1969 it was also found on several islands, including Lundy (1952), the Isle of Man (1958), Anglesey (1964) and Jersey, Channel Islands (1968). In 1958 it was collected by J. G. and C. M. Dony at Arklow, Co. Wicklow, v.c. H20, the first Irish record.

1970–1986

In Great Britain the spread of *E. ciliatum* continued during this period (Fig. 5). The species was recorded for the first time in many Scottish vice-counties, and reached the Hebridean islands of Skye (1976), Ulva (1982) and Tiree (1982).

Although it was first recorded in Ireland in 1958, there were few records before 1980. The hybrid *E. ciliatum* × *palustre* was collected in Co. Down, v.c. H38, in 1969 and there is a 1971 field record of *E. ciliatum* itself on an island in Lough Neagh, Co. Antrim, v.c. H39. In 1978 *E. ciliatum* was found in a garden at Aughrim, Co. Wicklow, v.c. H20, where it grew with *E. lanceolatum*, and in a nearby nursery (Walters 1979). In the next few years there were numerous records from all parts of Ireland, and in some areas the species spread explosively (Doogue *et al.* 1985).

In south-eastern England, where it was first recognized as a naturalized plant, *E. ciliatum* was very abundant by the 1970s. In Surrey it was "almost ubiquitous" and Lousley (1976) described it as "by far our commonest willowherb". It was "the commonest willow-herb in London" (Burton 1983) and "much the commoner of the small willowherbs" in Kent (Philp 1982); in both these areas, as in Bedfordshire (Dony 1976), it was recorded in 70–78% of tetrads (2 × 2 km squares). In Hertfordshire (Dony 1967) and Sussex (Hall 1980) it is known in 62% and 64% of tetrads, but further north and west the percentage is smaller: 47% in Devon (Ivimey-Cook 1984), 43% in Rutland (Messenger 1971) and only 22% in Shropshire (Sinker *et al.* 1985).

ERRONEOUS RECORDS

In compiling the records of *Epilobium ciliatum* I have rejected a number as erroneous. The following published records are sufficiently important for the reason for their rejection to be put on record.

Cadbury *et al.* (1971) report as the first Warwickshire record a specimen in **herb. J. E. Bagnall** collected by Bagnall in a wood near Gannaway Gate in 1889. If substantiated this would be the first British record, but the specimen cannot be traced in Bagnall's herbarium at **BIRA**, nor are the

details known to Mrs P. Copson, the vice-county recorder. It seems likely that the reference is an error introduced in the compilation of the Flora. The earliest acceptable record from Warwickshire known to me is dated 1952.

The first Sussex record is given by Wolley-Dod (1937) as Lurgashall, 1930, det. G. M. Ash, but Ash & Sandwith (1935) cite "Lurgashall, 1934" as the only Sussex record. There are no Lurgashall specimens in **BM**, where both herb. Wolley-Dod and herb. Ash are lodged. I prefer to follow Ash & Sandwith, and to regard Wolley-Dod's date as a misprint.

Epilobium ciliatum was reported from the dried up bed of a loch at Gallanach Dunes, Coll, v.c. 103 (Harrison *et al.* 1941) and from the Bornish-Stoneybridge area, South Uist, v.c. 110 (Harrison 1941). Harrison's (1941) comment that *E. ciliatum* "is an American species and may not be a colonist in the Hebrides" suggested that it might be native at these sites. However these records have not been accepted by other botanists (e.g. Perring & Walters 1962).

DISCUSSION

HISTORY OF SPREAD IN THE BRITISH ISLES

The records of *Epilobium ciliatum* in Britain and Ireland are summarized above. The first question that needs to be considered is whether or not these accurately reflect its spread in the British Isles. The genus *Epilobium* is somewhat difficult and is sometimes ignored by field botanists. The smaller species cannot be distinguished without close scrutiny, and unusual plants can be explained away as hybrids. If *E. ciliatum* was overlooked for a considerable period or recognized by only a few botanists, the picture of its spread presented above might be misleading.

Until the early 1930s botanists were unaware that *E. ciliatum* occurred in Britain. A few specimens collected before then have been found, but it would be unwise to deduce too much from this fragmentary evidence. *E. ciliatum* was well-established at Cropston Reservoir by 1894. It is difficult to say whether it was established or casual at the other localities where it was collected before 1930, and the date when it became established in Surrey is not known. As Ash & Sandwith (1935) pointed out, the Rev. E. S. Marshall lived in the very area of Surrey in which *E. ciliatum* was well-established by the 1930s. Marshall was successively curate at Witley (1885–1890) and Vicar of Milford (1890–1900), and it was in this period that he carried out most of his work on *Epilobium* (Britten 1920). Although Marshall failed to recognize the pressed specimens of *E. ciliatum* that were submitted to him, it seems rather less likely that he would have overlooked the living plant and highly probable that he would have at least collected it in mistake for some other species or hybrid. It is tolerably certain, therefore, that *E. ciliatum* became established in Surrey between 1900 and 1930.

The first detailed account of *E. ciliatum* in Britain was published in 1935. Even after this there must have been some delay between the appearance of the plant in an area and its recognition by botanists, and no doubt this delay was greater in some regions than in others. Even the map of the current distribution (Fig. 5) shows some areas where the scarcity of records probably reflects a lack of recorders rather than any real scarcity of the plant. With these qualifications, it seems likely that the records available do provide a reasonably accurate picture of the spread in Great Britain of *E. ciliatum* after 1935. The extent to which Irish records reflect its spread there is discussed by Doogue *et al.* (1985).

A number of other questions can be asked about the origin of *E. ciliatum* in Britain. Did it arrive directly from North America? Were the scattered early records the results of separate introductions? Is the fact that two of its first three localities were timber yards significant, indicating that it may have been introduced or spread with timber?

Raven & Raven (1976) pointed out that *E. ciliatum* in Britain and New Zealand appears to be identical, despite the fact that they are drawn from a highly variable complex in N. America, and suggest that the New Zealand plant might have been introduced from Britain. *E. ciliatum* was first recorded in New Zealand in 1896. By 1905 it seems to have been widespread in North Island, and it was first recorded in South Island in 1912. Thus the species was found in Great Britain five years before it was collected in New Zealand, but appears to have spread more rapidly in New Zealand. The possibility that it was introduced from New Zealand to Britain, rather than vice versa, cannot be ruled out.

This raises perhaps the most mysterious question about the spread of *E. ciliatum* in Britain, first posed by Ash (1953) who wrote "Why has it made such rapid progress in recent years whilst remaining more or less static near Leicester for 50 years?" Although *E. ciliatum* was well-established and persistent at Cropston Reservoir there is no evidence to suggest that it spread beyond the immediate neighbourhood. It did not become a weed in T. G. Tutin's Leicester garden until 1965 (Tutin 1973). The distribution maps suggest that the populations near Cropston were engulfed by the advancing front of *E. ciliatum* from further south. It is tempting to suggest that the plants at Cropston had a different genotype from those which spread so rapidly, but this is only speculation.

After the initial scattered records, the spread of *E. ciliatum* in Britain appears to have been continuous rather than discontinuous. This is suggested by Fig. 6, which illustrates the date of the first record from each vice-county. This continuous spread presumably reflects a natural expansion of an established population, rather than introduction by man at different sites which then acted as foci for secondary expansion. The spread of *E. ciliatum* contrasts with that of *Senecio squalidus*, described by Salisbury (1961) as "markedly discontinuous with respect to the more remote infections, whilst at the same time spreading locally around each new station".

POSSIBLE REASONS FOR THE SUCCESS OF *E. CILIATUM* AS A WEED

Myerscough & Whitehead (1966, 1967) compared the germination behaviour and subsequent growth of *Epilobium ciliatum* with that of the native species *E. montanum*. Both species possess many of the attributes of successful weeds: considerable phenotypic plasticity which enables them to grow in a range of environmental conditions, efficient vegetative and sexual reproduction and seeds with the capacity to survive in a dormant state. However, the minimum period from germination to flowering is shorter in *E. ciliatum*, 5·5 weeks compared to 7, and its relative growth rate is greater. The overwintering rosettes of *E. ciliatum* are larger than those of *E. montanum*, which probably allows it to make more growth during the winter although it renders the plant more susceptible to adverse weather conditions. Flowering and fruiting plants of *E. ciliatum* are less leafy than those of *E. montanum*, and the green stems and capsules make a greater contribution to photosynthetic assimilation. Raven & Raven (1976) stress the "enormous seed production" of *E. ciliatum* as a factor in its spread in Europe and Australasia, but quantitative comparisons with other species have not been made.

It has recently been suggested that the evolution of resistance to the widely used persistent triazine herbicides such as simazine might be one factor responsible for the predominance of *E. ciliatum* in urban areas. S. M. Walters (pers. comm.) found that it was the only species which flourished on soil in an area of Grantchester churchyard, Cambs., which had been subjected to excessive applications of simazine, and resistance to pre-emergence treatments has been demonstrated experimentally (Bailey *et al.* 1982).

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