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Flower-colour polymorphism in *Impatiens glandulifera* Royle

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Impatiens glandulifera Royle (= *I. roylei* Walp.), a Himalayan species, was introduced into Europe in 1838 as a horticultural plant. According to COOMBE (1956), seed from three plants of *I. glandulifera* with magenta flowers and one of var. *candida* with white flowers was sent to Kew at this time and then distributed; this seed probably came from the W. Himalayas. Later, in 1898, Hooker refers to a var. *pallidiflora*, a plant which he had previously seen in the Sikkim Himalayas, and which had become a weed in his London garden. It seems probable that all three varieties are involved in the present European populations of *I. glandulifera*.

According to BRITTEN (1900), the earliest records of the species as a naturalised plant in Britain are in 1855 in Hertfordshire and in 1859 near Manchester. Although it was introduced into Continental Europe at almost the same time, the species appears to have become naturalised later, since it was apparently first recorded as a naturalised plant in Germany in 1895. It has now become widely naturalised; and it is recorded from 21 European territories in Flora Europaea.

I first became acquainted with the species in 1930, when it was common along the banks of the River Irwell in Manchester. This is a polluted river and at that time the atmosphere was highly polluted too; but this did not seem to inhibit the growth of the plant. It is an annual, producing large quantities of seeds which lie dormant in the winter and germinate in large quantities the following spring. It grows rapidly and in good situations may reach a height of 1.5 or 2 metres. Little is known of its ecology in the W. Himalaya, where according to KHOSHOO (1957) it occurs at 1800-3000 m, sometimes along stream banks or on the margins of fields. These are very much its habitats in Europe. In Britain it is found mainly along the banks of rivers and streams, where it is sometimes partially submerged at times of flood; it also occurs in disturbed, damp woodland. It is found in similar habitats in Poland, Czechoslovakia, Austria and Holland; LHOTSKA & KOPECKÝ (1966) mention some of the river-bank communities in which it occurs in Czechoslovakia. In these habitats, it is often very successful, forming extensive communities of many thousands of individuals; and it has clearly found ecological niches for itself which appear to correspond to those of its native home. According to DAUMANN (1967), *I. glandulifera* has in some places in southern Bohemia suppressed and eliminated the native *I. noli-tangere* L.

The cytology of the species is also of interest. KHOSHOO (1957) studied wild specimens from localities in Kashmir and Dalhousie, and found both $2n = 20$ in root-tips and $n = 10$ at meiosis and in pollen grains. JONES & SMITH (1966) have counted both $n = 9$ and $n = 10$ in naturalised plants at Kew; while our counts on plants near Manchester have given $2n = 18$ in root-tips and $n = 9$ in pollen-grain mitoses. Counts of both $2n = 18$ and $2n = 20$ are also cited by DARLINGTON & WYLIE (1955) from various authors. There seems here to be a genuine variation, which may also be associated with differences in chromosome morphology, and further investigation is required.

My main interest in *I. glandulifera* at present is the great variation in flower colour which can be seen in many populations. Near Manchester, most populations are polymorphic, the colour of the petals varying from deep magenta or purple to pink and almost white; individual petals vary, somewhat, independently of one another. We are just beginning experiments on the genetics of flower-colour. The variation in colour is similar to that in a related species, *I. balsamina*, which has been studied by DAVIS & al. (1957) and in which it is known that at least three genes are involved.

Variation in colour has been noted and recorded from many parts of Europe though there are, so far as I know, no quantitative data. Professor J. KORNAŚ has informed me, for instance, that in S. Poland naturalised populations are purple or dark pink, while in gardens pale pink and white forms are grown; and in Bielsko a few of these pale individuals have escaped and become naturalised. This appears to be the case in most European countries; the predominant colour is magenta, with few or no pale flowers. However, Dr. J. MENNEMA has informed me that in N. Holland, one population in Bussum has a dominant colour of pale pink, with very few purple-flowered plants; and in one locality near Manchester there is a population which is composed of very pale or white flowered plants, with no darker colours at all.

But a mixture of colours is much more typical of the Manchester populations. Some of these have been scored, in a rather crude way, and the results are given in Table 1. It will be noted there is little difference between the same population scored in two successive years. Population 2 is about 400 metres from population 1, in a different type of habitat, but the colour spectrum is much the same.

This variation raises a number of problems. The first is that of its origin. It seems most likely that the present polymorphism is derived from a mixture of intro-

| Population | No. of plants scored | Flower colour (as percentages) | | | | |
|-------------------------------|----------------------------|--------------------------------|------|-------|-------|------|
| | | Purple | Pink | Lilac | White | Blue |
| 1 (1969), hedgebank | 298 | 13 | 42 | 32 | 8 | 5 |
| 1 (1968), hedgebank | 153 | 19 | 38 | 25 | 13 | 5 |
| 2, river-bank | 130 | 13 | 41 | 32 | 9 | 5 |

Table 1. — Flower colour in 2 populations of *I. glandulifera* in S. Manchester.

duced genotypes, and it is possible that new introductions are constantly taking place. In this context it is interesting that although the first record of naturalised *I. glandulifera* was in 1855, naturalised specimens of the white form were not recorded in Britain (Cornwall) until 1921 (THURSTON & VIGURS 1922). It is my impression, though unfortunately I have no data, that white- and pale-flowered plants are commoner around Manchester now than they were in 1930; it is possible that the polymorphism is not stable.

If this is so, then one needs to ask, what are the external factors which influence the proportion of flowers of different colours in the populations, and how does natural selection operate? For example, there is great competition between seedlings every spring; are there factors which affect seedling growth and which are linked with flower colour? Again, are flowers of different colours visited selectively by insect pollinators, and if so, is this a factor which determines the frequency of the different colour varieties?

Knowledge of the breeding system of the species is essential here. The flower is so constructed that self-pollination does not normally occur. However, pollination of one flower by flowers on the same plant may well occur. DAUMANN (1967) has found that *I. glandulifera* is self-compatible and this is borne out by the few experiments we have made. The species is insect-pollinated and it is common to see an insect visiting several flowers on the same plant before moving to an adjacent plant. However, the amount of self-pollination, as compared with cross-pollination, will be low, since it can only occur when the insect flies from a flower in the male stage to a flower in the female stage on the same plant, and the female stage only lasts for a few hours. As regards the insect pollinators, DAUMANN reports that in Czechoslovakia bumble bees and hive bees predominate. Our own observations near Manchester have shown that bumble bees and wasps (*Bombus lucorum* and *Vespa vulgaris*) are the most frequent pollinators and are clearly very effective. It is interesting to see how well an Asiatic plant is able to make use of European pollinators; this is a kind of pre-adaptation. Presumably in the Himalayas the plant has pollinators of the same, or closely related, genera. According to DAUMANN, pale-coloured flowers produce less nectar and are less frequently visited by honey bees than magenta flowers, in a proportion of 2 to 3. If this were the case (and we have not yet confirmed it) the proportion of pale flowers in the population should gradually decrease.

At the moment we have no quantitative data as to the relative frequency with which flowers of different colours are visited by the various pollinators; but on several occasions it has been noted that an insect may visit flowers of different colours during a single flight.

Experiments on these and other aspects of the polymorphism of *I. glandulifera* have been started in Manchester; and one of the purpose of this paper is to stimulate observations on populations in different parts of Europe. Another purpose is to draw attention to some of the questions of evolutionary interest which are raised by a consideration of naturalised aliens in a flora. Aliens are perhaps most commonly found as weeds, and as such are very definitely associated with man's activities. Man performs two functions here; he introduces the plant, either deliberately, as into a

garden, or by accident, as in ballast, and he provides habitats in which the plant is able to grow. These habitats are commonly in artificial communities, such as roadsides or cultivated fields, in which competition from native species is modified or eliminated. Alien species, which by definition are growing in an area and a climate different from their own, must also be adaptable. ANDERSON (1949) many years ago suggested that weeds owed a part of their variability and adaptability to a genotype which had been modified by contact with allied species, and that hybridization was sometimes an important factor in successful colonisation of a new habitat.

All these considerations apply to some extent to *I. glandulifera*; as was pointed out earlier, seeds from four different plants, one of which had white flowers, were introduced into Britain, so that the possibility of hybridization of different genotypes was there from the start; and the species often grows in disturbed habitats. But this is not necessarily the whole story. It is at least possible that an alien species, if it can find some means of transport, can establish itself in natural, undisturbed vegetation. With aliens, man is usually the obvious transporting agent, although long-distance dispersal by natural means undoubtedly occurs. To give only one example, the close resemblances between certain species of the Californian flora and of the flora of Chile, in S. America (CONSTANCE 1963), are most probably explained by long-distance dispersal.

In the case of *I. glandulifera*, dispersal has undoubtedly been by man; but it would appear that the species has been able to establish itself in some river-bank habitats which are quite natural. These are habitats which are not normally fully colonised by native plants because of riverflow, crumbling of the banks and so on. The *Impatiens* could thus be pre-adapted to a natural habitat, which is probably similar to its native habitat.

If this hypothesis is correct, then either this ecological niche along the river-bank was completely unoccupied before *I. glandulifera* arrived, which is rather unlikely, or competition in this habitat is not very intense. There was thus a vacancy for a rapidly-growing tall annual with high seed production which is adapted to moist habitats. The conclusion could also be drawn that a plant of this kind had, for one reason or another, failed to evolve in Europe; *Impatiens noli-tangere* is a much smaller plant, and, as has been mentioned earlier, may actually be overwhelmed by competition from *I. glandulifera* in some C. European habitats. It would obviously be very interesting to know more about *I. glandulifera* and its native habitats in the Himalayas, to see to what extent they are comparable with the European. It would also be of interest to survey the alien flora of Europe to look for parallel examples. One which comes to mind is *Epilobium nerterioides* A. Cunn., from New Zealand, which has become completely naturalised in the British Isles, often in apparently quite natural habitats.

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