

NATURAL HYBRIDIZATION IN BRITAIN BETWEEN *PRIMULA VULGARIS* HUDS. (THE PRIMROSE) AND *P. ELATIOR* (L.) HILL (THE OXLIP)

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ABSTRACT

In Britain *Primula vulgaris* and *P. elatior* meet in woodlands on the fringes of the restricted area of distribution of the latter species. Where they meet a limited amount of hybridization occurs, aided by frequent and regular disturbance. There is evidence that gene flow occurs in both directions. Despite high inter-fertility the extent of hybridization is limited, and it is suggested that ecological differentiation, probably partly the result of differential drought tolerance, is responsible. The hypothesis that *P. vulgaris* is 'hybridizing *P. elatior* out of existence' is examined, and is regarded as being without foundation. Indications are that these populations are changing little at the present time.

INTRODUCTION

It has been known for many years that *Primula vulgaris*, the primrose, and *P. elatior*, the oxlip, hybridize in Britain (Christy 1897, Valentine 1948). Christy (1922a) suggested that *P. elatior* was being 'hybridized out of existence' in Britain by the 'aggressive' *P. vulgaris*; this possibility will be discussed later, but it was based partly on the incorrect assumption that the F_1 hybrid was sterile. Valentine (1948) believed that most hybrids were of the F_1 generation, but he has more recently (1961) modified this view. Clifford (1958) on the basis of a brief visit to some of the localities where these species occur together, suggested that introgression was taking place. The present investigation was undertaken to determine whether introgression is occurring between these two species in Britain, and to assess Christy's hypothesis of replacement. Some preliminary ecological investigations have also been carried out, in relation to the mutual exclusiveness of the two species in Britain.

Artificial crossing between the species has yielded much information on their inter-fertility. Reciprocal crosses produce different results (Valentine 1947, 1956). The highest germination recorded from the cross using *P. vulgaris* as female parent is 64 per cent., and from the reciprocal cross 39 per cent. These are results produced under good greenhouse conditions; most crosses even under such conditions give much lower germination. The differences in seed germination are reflected in hybrid seed development (Woodell 1960a). When *P. vulgaris* is the female parent the seeds are small and well filled with endosperm and contain a well developed embryo. The reciprocal cross results in two types of seed, both large. One contains well developed endosperm and embryo, the other, more frequent, has aborted endosperm and embryo.

Valentine (1947) demonstrated that F_1 hybrids produce a high yield of viable seed, and have a pollen fertility of about 75 per cent. Using the hybrids as female parents he was able to obtain good seed set and vigorous and fertile backcross plants.

Primula elatior is distributed over western and central Europe, ranging from southern Russia in the east to England in the west, and from the Carpathians in the south to southern Sweden in the north. In Europe it occurs in meadows and open woodlands, with a preference for moist places. *P. vulgaris* is a species of 'Atlantic' distribution, having its northern limit in southern Sweden and extending from Spain to Syria in the south. It is generally a lowland species, and in Britain is a plant of woodland except in the far west, where in company with several other woodland herbs it emerges into less shaded habitats such as hedgebanks, meadows and cliff ledges.

Primula elatior in Britain is almost confined to oak-ash woodland on the chalky boulder clay of East Anglia, where it grows in great abundance to the almost total exclusion of *P. vulgaris*, except on the margins of its range. In one or two outlying localities it can be found outside woodland (Woodell 1965b). On the fringes of the area of *P. elatior* hybridization is frequent.

MATERIALS AND METHODS

A number of woodlands, containing either 'characteristic' species populations or hybrid populations, were sampled. In the 'characteristic' populations a random sample of thirty long-styled (pin) and thirty short-styled (thrum) plants were collected; from each the largest flower and leaf was taken. In hybrid populations a small area was selected and every plant within it sampled.

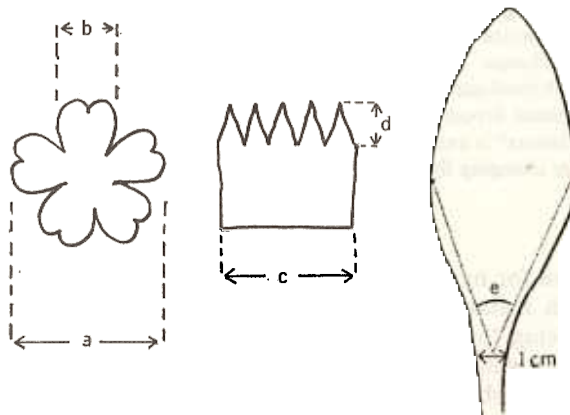


Fig. Measurements made on flowers and leaves of sample plants. *a*, Corolla diameter. *b*, Petal width. *c*, calyx circumference. *d*, Calyx tooth length. *e*, leaf angle.

On each plant the following measurements were made (Fig. 1)

1. Corolla diameter (mm)
2. Petal width (mm)
3. Circumference of calyx (mm)
4. Length of calyx teeth (mm)
5. Leaf angle.
6. Throat pattern, scored in three classes:
 - O. Flower pale yellow with diffuse orange marks in throat, not distinguishable from 'characteristic' *P. elatior*.
 - OP. Intermediate between O and P.
 - P. Flower sulphur yellow, with greenish stellate throat markings; not distinguishable from 'characteristic' *P. vulgaris*.

After measurement each flower was kept in 80 per cent. alcohol, and pollen fertility was estimated later by teasing out anthers in acetocarmine and counting the proportion of round, stainable pollen grains. In order to minimize seasonal differences in dimensions of floral parts (Woodell 1965a) all populations were sampled within a few days.

One character that has been shown by Valentine (*in litt.*) to be important is the pedunculate nature of the inflorescence. In cultivation F_1 hybrids can show both non-pedunculate and pedunculate inflorescences, and backcrosses to primrose likewise. However I regard this as an unreliable *field* character since I have collected plants in the field which have only pedunculate inflorescences, and in cultivation they have produced non-pedunculate flowers.

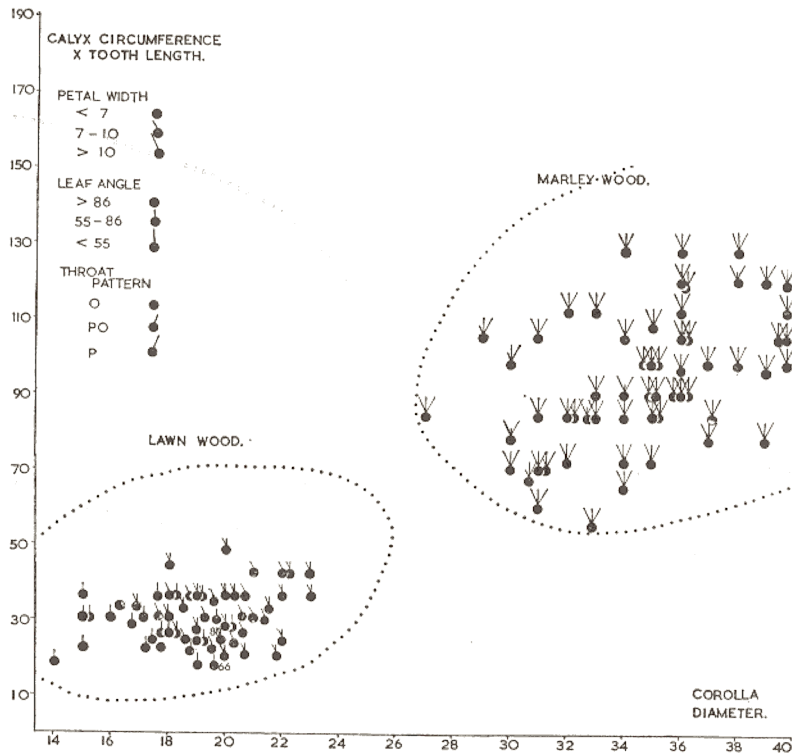


Fig. 2. Pictorialized scatter diagram of populations of 'characteristic' *P. elatior* from Lawn Wood, Suffolk, and *P. vulgaris* from Marley Wood, Berkshire.

While some characters, e.g. corolla diameter, clearly distinguish these two species, others e.g. petal width and leaf angle, show some overlap. However they show sufficient differences to make them valuable in displaying the overall variation within and between the species. Other characters which have been assessed, e.g. flower colour, show environmental fluctuation or change with age, and so cannot be used.

RESULTS

Before presenting the results of this investigation it should be pointed out that these are species that show considerable plasticity in response to environmental changes (Woodell 1965a) and that some of the measurements may therefore show these effects. For instance, individuals in some mixed populations fall outside the range of either species in 'characteristic' populations. This may be a plastic response. However, although such responses will be involved, they are unlikely to be large enough to invalidate the conclusions, and they have been avoided as far as possible by confining sampling to a short period.

The scatter diagrams in Figs. 2-7 depict samples from several populations, representative of the whole range of populations studied. Two 'characteristic' populations are shown in Fig. 2, one of *Primula vulgaris* from Marley Wood, Berks. about 85 Km from the nearest population of *P. elatior*, and one of *P. elatior* from Lawn Wood, Suffolk. Lawn Wood is well within the larger of the two areas of distribution of *P. elatior* in Britain and 4 Km from the nearest known populations of *P. vulgaris*. Other populations of both species were sampled, and they fell within the ranges indicated by the dotted lines on the diagrams. These lines, showing the total range of variation found in the pure species populations, are on all the scatter diagrams. In addition all the individuals with pollen fertilities of less than 90 per cent. are indicated on the diagrams by numbers giving the percentage fertility.

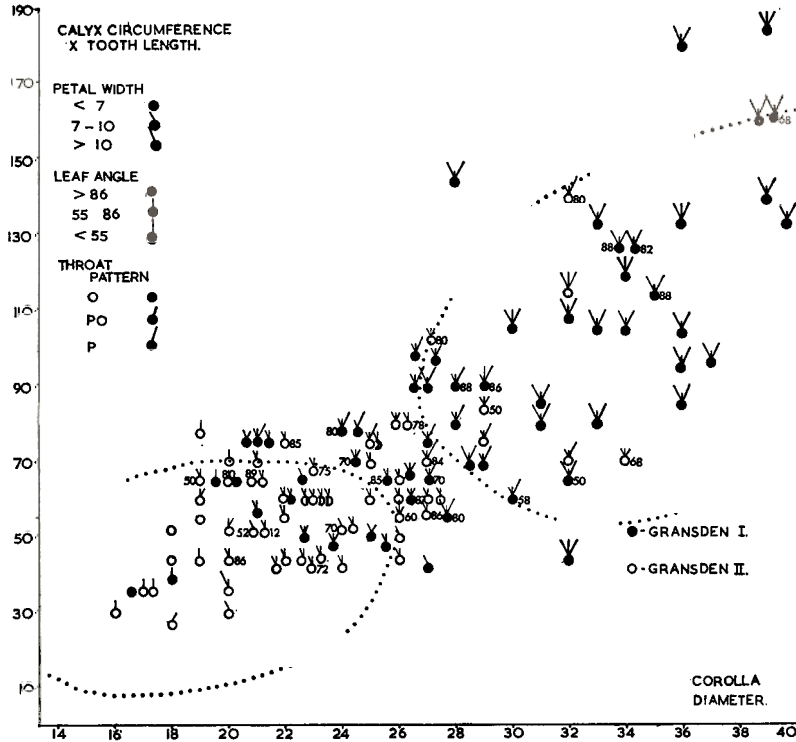


Fig. 4. Scatter diagram depicting two populations from Gransden Wood, Cambridgeshire.

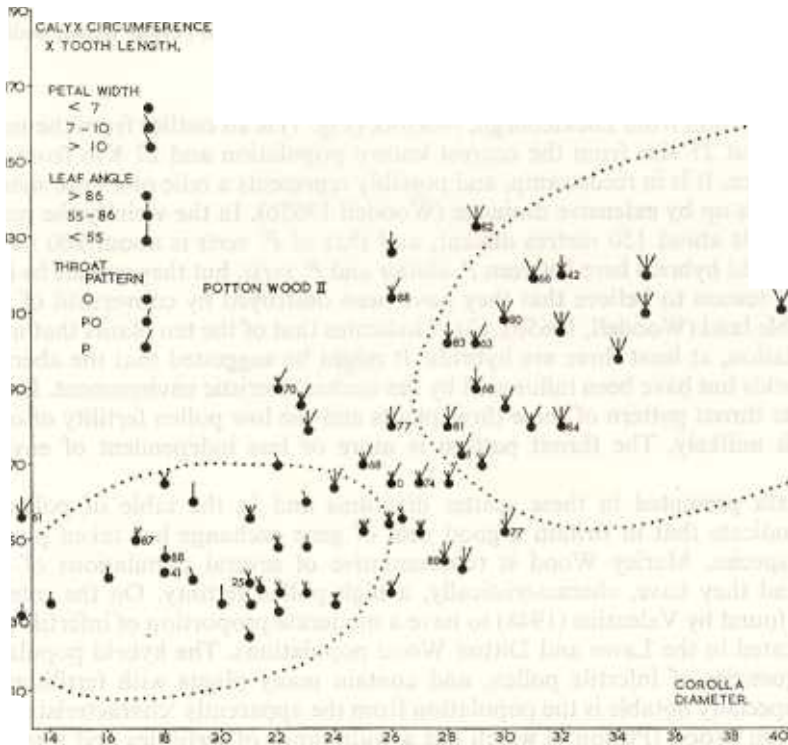


Fig. 5. Scatter diagram of mixed population from Potton Wood, Bedfordshire.

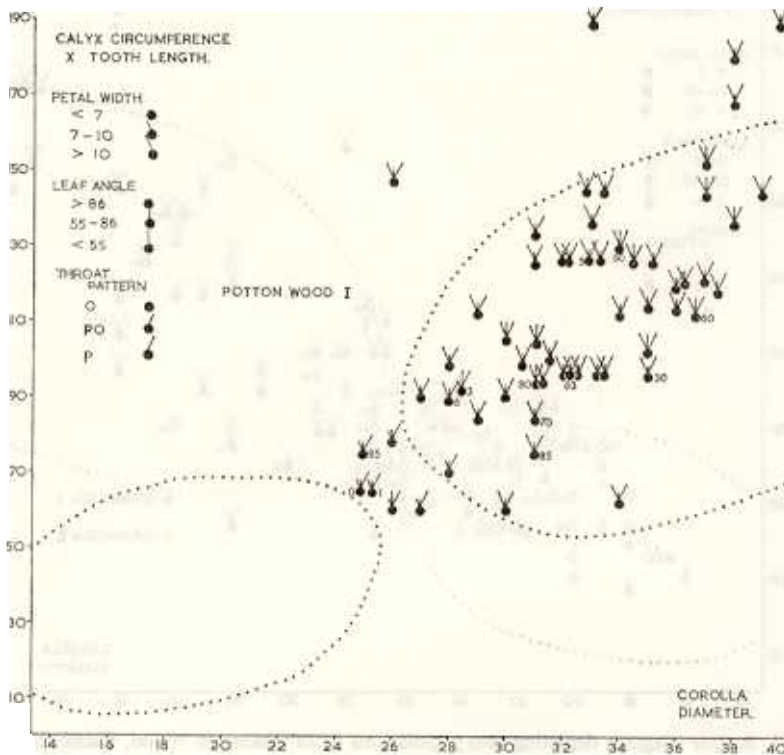


Fig. 6. Scatter diagram of apparently 'characteristic' *P. vulgaris* from Potton Wood, Bedfordshire.

The population from Dickleburgh, Norfolk (Fig. 7) is an outlier from the main area of *P. elatior*, about 21 Km from the nearest known population and 27 Km from the border of the main area. It is in reedswamp, and possibly represents a relic of a once more continuous range, split up by extensive drainage (Woodell 1965b). In the vicinity the nearest plant of *P. vulgaris* is about 150 metres distant, and that of *P. veris* is about 200 metres away. Christy reported hybrids here between *P. elatior* and *P. veris*, but they cannot be found now, and there is reason to believe that they have been destroyed by conversion of part of the area to arable land (Woodell, 1965b). Fig. 7 indicates that of the ten plants that make up the total population, at least three are hybrids. It might be suggested that the aberrant plants are not hybrids but have been influenced by the uncharacteristic environment. In view of the intermediate throat pattern of these three plants and the low pollen fertility of one of them I think this unlikely. The throat pattern is more or less independent of environmental fluctuation.

The data presented in these scatter diagrams and in the table of pollen fertilities (Table 1) indicate that in Britain a good deal of gene exchange has taken place between these two species. Marley Wood is representative of several populations of *P. vulgaris* sampled, and they have, characteristically, a high pollen fertility. On the other hand *P. elatior* was found by Valentine (1948) to have a moderate proportion of infertile pollen, and this is indicated in the Lawn and Ditton Wood populations. The hybrid populations have higher frequencies of infertile pollen, and contain many plants with fertilities below 60 per cent. Especially notable is the population from the apparently 'characteristic' *P. vulgaris* area in Potton Wood (Potton I) which has a wide range of fertilities and a relatively low mean fertility.

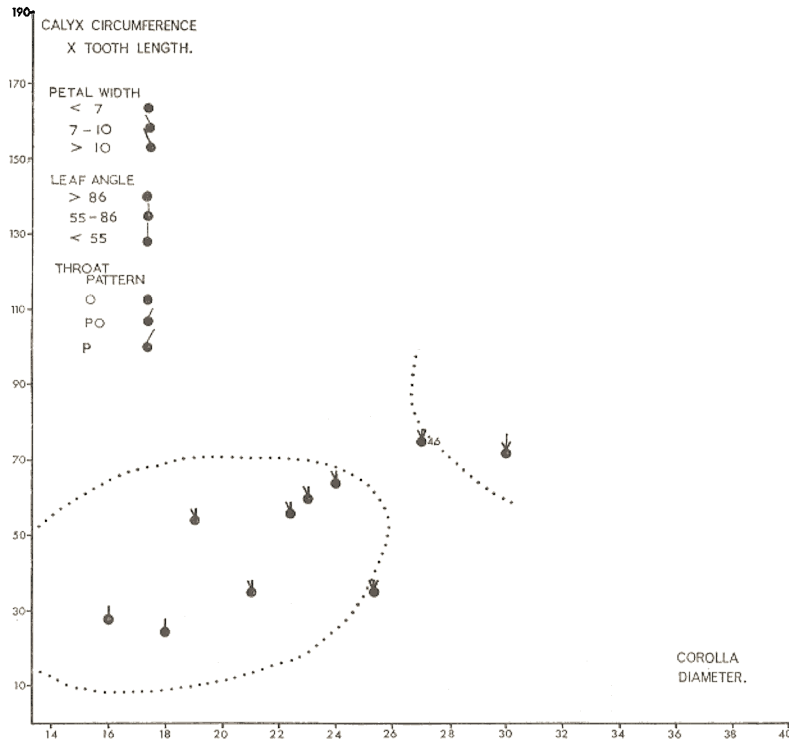


Fig. 7. Scatter diagram of population from Dickleburgh, Norfolk.

DISCUSSION

1. The background to hybridization

Primula elatior and *P. vulgaris* are largely allopatric, and this fact alone is responsible for maintaining them as separate species over most of their ranges. They meet often on the western fringes of the range of *P. elatior*, where they hybridize frequently. Hybrids occur in Austria, and further east in Europe populations of the species are close to each other. In Britain *P. elatior* is a woodland species and in woodland is in direct contact with *P. vulgaris*. In the woods on the margins of its British range it occurs together with *P. vulgaris*, often occupying the damper portions of the woods. However the habitat requirements of the species are so similar that they overlap considerably in many woods.

It is agreed (*e.g.* Anderson 1953, Baker 1951) that hybridization is often a consequence of human disturbance of the habitat. These woodlands are subject to disturbance that is both sustained and regular. In many examples of introgression that have been described, the causal disturbance has ceased, and the return to more 'normal' conditions has resulted in the elimination of most hybrids and the establishment of a variable parent population; the only evidence of past introgression. Dansereau (1941) cites *Cistus ladaniferus* and *C. laurifolius* as an example of this. Disturbance maintained over a long period in the same place is uncommon. One natural situation in which this occurs, so that hybridization between *Aquilegia formosa* and *A. pubescens* is aided by a permanent intermediate natural habitat, is discussed by Grant (1952).

The British woodlands containing *P. elatior* are often managed as reserves for pheasant raising, or as fox coverts. The timber has frequently been exploited by the declining practice of coppicing. Under this régime there are widely spaced 'standard' trees, usually oaks, giving an open canopy. Beneath them is a luxuriant growth of understory shrubs, the most

| Site | Pollen Fertility (per cent.) | | | | | | | | | | N | Mean | S.E.M. | |
|-------------|------------------------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|----|------|--------|--------|
| | 0-10 | 11-20 | 21-30 | 31-40 | 41-50 | 51-60 | 61-70 | 71-80 | 81-90 | 91-95 | | | | 96-100 |
| Marley | | | | | | | | | | | 60 | 60 | 99.9 | 0.01 |
| Lawn | | | | | | | 1 | 1 | | 1 | 57 | 60 | 98.9 | 0.66 |
| Ditton | | | | | | 1 | 3 | 3 | 4 | 5 | 43 | 59 | 93.9 | 1.35 |
| Dickleburgh | | | | | | | | | | 1 | 7 | 10 | 91.9 | 1.64 |
| Gransden II | | | | | | 1 | 2 | 2 | 11 | 17 | 25 | 59 | 91.5 | 1.32 |
| Potton I | 2 | | | | | 2 | 2 | | 3 | 3 | 42 | 56 | 90.1 | 3.68 |
| Hardwick II | | | | | 2 | 2 | 2 | 1 | 11 | 1 | 38 | 59 | 88.8 | 2.62 |
| Rockells | | | 1 | | 2 | 1 | 3 | 5 | 7 | 9 | 30 | 58 | 88.0 | 2.45 |
| Hardwick I | | | | 1 | 3 | 4 | | 5 | 8 | 6 | 31 | 58 | 87.7 | 2.21 |
| Gransden I | | 1 | | | | 2 | | 2 | 6 | 12 | 24 | 58 | 87.6 | 2.13 |
| Potton II | | | 1 | | 2 | | 6 | 4 | 12 | 4 | 27 | 56 | 87.5 | 5.56 |

TABLE 1. Pollen fertility: Numbers in different percentage classes from samples of 'characteristic' and hybrid populations. (Marley Wood: *P. vulgaris*. Lawn and Ditton Woods: *P. elatior*. Remaining sites: Hybrid).

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commonly used being hazel (*Corylus avellana*). The shrubs are allowed to grow for some years (usually between eight and fourteen) and then cut, leaving the stumps or 'stools' to regenerate. The timber is used for such purposes as fencing. Regeneration is rapid and the cycle is regularly repeated. Every century or so the standard trees are felled and replaced. This régime results in moderate disturbance every decade and major disturbance every century. When the canopy is opened up, encouraging profuse growth and flowering of the herbaceous vegetation, the soil is churned up by the foresters. In these circumstances it is hardly surprising that where partly inter-fertile species grow together hybridization occurs. Hybrids produced by one coppicing disturbance can live through at least one cycle, and probably through more. There is unpublished evidence that individual plants of both species may live for several decades, and I know of one hybrid between *Primula veris* and *P. elatior* that has almost certainly survived in the wild for over sixty years. Each coppicing provides the opportunity for new F₁ hybrids to be produced and for existing hybrids to interbreed and to backcross with the parent species. A very similar situation in a Buckinghamshire wood has led to limited introgression between two species (*Primula veris* and *P. vulgaris*) which normally remain distinct throughout Britain (Woodell 1965a).

Thus conditions in these woods would seem to be ideal for almost unrestricted hybridization. Yet the amount of hybridization is restricted. The possible reasons for this must now be considered.

2. The restriction of hybridization

The area occupied by *P. elatior* in Britain is one of cold winters and warm summers; a relatively 'continental' climate. Little is known of the vegetational history of the region, or of the history of the *Primula* species there. Though the area was poorly drained, and may have had large areas of swamp before drainage, it seems unlikely that it was distinct from the rest of southern Britain in being unforested. Similarly it seems likely that *P. elatior* has been here for a long time, and is not a recent immigrant. If the trends of recent decades, with the increase in land drainage, are any indication, then *P. elatior* was probably more continuous throughout this part of Britain, not split into a number of relatively small isolated populations as it is now. Valentine (1948) has suggested that the surrounding areas were completely forested prior to clearance and that *P. vulgaris* has been similarly split into discrete populations by man's activities. He pointed out that there is no evidence that *P. vulgaris* has ever migrated in any quantity across the intervening open land since clearance. If *P. elatior* was restricted to the chalky boulder clay before clearance and *P. vulgaris* was excluded from it then the conditions controlling their distributions were presumably maintained until forest clearance. It is not possible to say whether conditions have altered in favour of either species, but *P. vulgaris* cannot now successfully invade the area of *P. elatior*.

It is probable that in the wild germination is much lower than that obtained under greenhouse conditions by Valentine (1947) in the absence of competition. A significant establishment of hybrids is probably restricted to each coppicing disturbance. The quantity of hybrid offspring must be measured in terms of viability, opportunity (which includes flowering overlap and common insect pollen vectors) and competition, and also in terms of the ecological differentiation between the species.

Viability is high, as we have seen, and none of the other factors classed as internal restrictive factors by Baker (1951) is known to operate. Flowering overlap is complete; *P. elatior* flowers almost exclusively in April, within the longer flowering period (February to May) of *P. vulgaris*. What is known of the pollen vectors indicates that the two species share at least some of them (Christy 1922b, Woodell 1960b). We have seen that disturbance is frequent and regular, yet relatively few hybrids become established, and their rate of spread is such that in the few thousand years since forest clearance began they do not appear to have materially altered the balance between the two species.

Valentine (1948) presented arguments for the view that these mixed populations have remained stable for a very long time, and that if any change in the balance occurs it will be

as a result of a shift in climatic or edaphic conditions. He states: 'hybridization is symptomatic of the mixture of the species, but it is not fundamentally concerned with the replacement of one species by the other.' This statement was made in the belief that most of the hybrids were F_1 plants, and in spite of the fact that my data show that there are many backcrosses there is no reason to disagree with it.

Since coppicing is now declining, many of these woods may revert to a more 'natural' condition, and I would expect that in the long term the number of hybrids will decrease and the boundaries between parent species become sharper. The factors restricting hybridization under the present régime are still not clear, but in the light of the evidence discussed above internal restrictive factors are unlikely to be involved. Ecological differentiation may be very important, however, and this will be discussed later. Before this is done it is necessary to examine briefly the hypothesis, put forward by Christy (1922a) that *Primula elatior* is being 'hybridized out of existence' in Britain.

3. Christy's hypothesis

Christy's argument, briefly, is as follows: Woodlands containing *P. elatior* are frequently cleared. Such clearance results in profuse flowering, and at the same time pollen vectors have freer access to the flowers and pollen transfer is likely to take place from the *P. vulgaris* plants outside (*sic*) the woods to *P. elatior* within them. A good deal of hybridization takes place, and then when the wood grows up again both the plants of *P. elatior* and the hybrids cease to flower. The next time the wood is cleared, both hybrids and *P. elatior* will flower, but many of the latter will have died, and hybridization will again occur between the remaining plants of *P. elatior* and *P. vulgaris*. Frequent repetition of this process will result in complete elimination of *P. elatior* and the possession of the ground by hybrids. These in turn will die because they are likely to be shorter lived. This would mean that when the hybrids had died the ground would be unoccupied by any species of *Primula*. Christy had never seen *P. elatior* extending its boundaries, and he considered *P. vulgaris* to be an 'aggressive' species which would ultimately occupy the ground vacated by *P. elatior*.

There is much evidence which indicates that this hypothesis is unlikely to be correct, but it is unnecessary to detail all of it. The points enumerated here are sufficient to indicate the unsoundness of Christy's view:

- (i) Christy was of the opinion that F_1 hybrids between these species are sterile. This is incorrect.
- (ii) Christy stated that hybrids are shorter-lived than parents. Present indications are that they are longer-lived.
- (iii) He transplanted several plants of *P. vulgaris* to a pure *P. elatior* wood in Essex. After seventeen years they had declined in numbers, and there were a few hybrids. This wood was carefully searched in 1967 but no primroses or hybrids could be found. Similarly, attempts to establish *P. vulgaris* in woods containing *P. elatior* in continental Europe were unsuccessful.
- (iv) Valentine (1948) found that the numbers of *P. vulgaris* plants on the margins of the predominantly *P. elatior* Knapwell Wood, Cambs., declined markedly during the period 1937-1947.
- (v) *P. elatior* has been isolated and has survived at Dickleburgh, Norfolk, possibly for centuries, surrounded by *P. vulgaris*.
- (vi) Buff Wood, Cambs., has been under observation by Valentine for thirty years, and Gransden and Hardwick Woods have been visited for ten years. In none of these is there any obvious change in the proportions of hybrids and parents.*

None of this evidence supports Christy, and I have no evidence that does support his hypothesis. In the present state of our knowledge it must be regarded as unproven.

* Dr. S. M. Walters and Mr. D. J. Ockenden conducted a field class in Buff Wood in April 1968, in which they resurveyed Valentine's transect of 30 years ago. Their results suggest that there has been no major change in this population in the last 30 years.

One fact that may have influenced Christy's interpretation of the situation is that in several woods more hybrids occur in association with *P. elatior* than with *P. vulgaris*. Hardwick Wood (Fig. 3) and Gransden Wood (Fig. 4) illustrate this. In woods which have both species *P. elatior* often occupies areas with more bare soil than *P. vulgaris*, and it is possible that reduced competition may favour the establishment of hybrids in these areas.

4. Ecological differentiation of the two species

Baker (1951) has mentioned several examples of the fact that, where two species hybridize, knowledge of the ecological factors distinguishing the species' ranges often help to indicate factors restricting gene flow. In the case of *Primula vulgaris* and *P. elatior*, the ecological differentiation of their areas of occurrence is not immediately apparent. In the British Isles *P. elatior* is almost exclusively confined to the chalky boulder-clay, and *P. vulgaris* is found on the margins of this soil type. Valentine (1948) investigated associated species and soil moisture in Buff Wood. The areas occupied by the two species are floristically similar, but *P. vulgaris* is abundant in areas dominated by *Mercurialis perennis* and *Endymion non-scriptus* whereas *P. elatior* is found in association with *Anemone nemorosa*, *Ranunculus ficaria* and *Filipendula ulmaria*, the last being a common species of moist places. Valentine concluded that soil moisture was a controlling factor. However, his measurements of soil moisture were inconclusive.

If soil moisture *per se* was responsible for the distribution of these species the extensive drainage of recent years would favour *P. vulgaris*, and we have seen that this is apparently not so. Furthermore, Good (1944) showed that in Dorset *P. vulgaris* is limited, on light soils, to areas of high precipitation, indicating a high water requirement. This clearly needs further investigation.

A number of woods has been sampled in the study area, 20 with populations of *P. elatior*, 9 with *P. vulgaris* and the remainder with both species and hybrids. Using thrown quadrats, percentage frequencies of associated species were determined. Most of the species showed little differences in frequency between *P. elatior* and *P. vulgaris* woods. Five species merit comment, and the results for these are in Table 2.

TABLE 2. Mean percentage frequencies of five species in 20 woods containing *P. elatior* and 9 with *P. vulgaris*.

| Species | Mean per cent. frequency in woods containing: | |
|------------------------------|---|--------------------|
| | <i>P. elatior</i> | <i>P. vulgaris</i> |
| <i>Filipendula ulmaria</i> | 30 | 9 |
| <i>Endymion non-scriptus</i> | 15 | 41 |
| <i>Poa trivialis</i> | 44 | 19 |
| <i>Ranunculus ficaria</i> | 24 | 47 |
| <i>Mercurialis perennis</i> | 40 | 43 |

These data agree with Valentine's in showing the association of *Filipendula ulmaria* with *P. elatior*. Of the other species, *Endymion non-scriptus* has a preference for well drained soils, and little is known of *Ranunculus ficaria* and *Poa trivialis* with respect to soil preferences. The apparent indifference of *Mercurialis* is interesting in view of Valentine's data. However, in woods where the two *Primula* species occur together the differences in associated species are accentuated; for instance in Rockell's Wood, Essex, in populations about 100 metres apart, *P. vulgaris* is associated with *Brachypodium sylvaticum*, *Deschampsia cespitosa*, *Endymion non-scriptus* and *Mercurialis perennis*, the last named being dominant. With *P. elatior*, *Filipendula ulmaria* is abundant, *Poa trivialis* and *Arum maculatum* are frequent, and *Mercurialis* is rare. This is comparable with Valentine's account of Buff

Wood, and would suggest that where the two species grow together competition forces them into more distinct habitats than those they occupy when apart.

Martin (1965) investigated soil waterlogging and aeration in relation to nutrient availability in Cambridgeshire boulder clay woods, with special reference to *Mercurialis perennis*, which is excluded from the more waterlogged soils. He found that soil acidity and the distribution of major plant nutrients could not account for the distribution of this species. Low oxygen concentration, and especially the presence of toxic quantities of ferrous iron exclude *Mercurialis* from the wetter soils. *Deschampsia cespitosa* is tolerant of wet soils, possibly because it has an effective intercellular air space system and can protect itself by a zone of oxidation round the roots. *Primula elatior* can tolerate these waterlogged soils but as yet the mechanism of tolerance is unknown.

In these woods the association of *Primula vulgaris* with *Mercurialis* suggests that it is unable to tolerate waterlogging as well as *P. elatior*. Some experiments have been carried out to test this view.

Seeds and young plants were planted in John Innes potting compost under three different water régimes; free drained, water table 4 cm below soil surface and waterlogged. Germination was so poor that no conclusions could be drawn from this part of the experiment. (Abeywickrama (1949) stated that seeds of both species will germinate under water.) The young plants of both species performed best in the soil with a 4 cm water table. In waterlogged soils both species performed very poorly, and in free drained soils *P. vulgaris* was superior. Table 3 summarises the results. I have included the results for *P. veris*, a plant of much drier habitats in Britain, and it will be seen that it performed very well in free-drained pots, and disliked waterlogging.

TABLE 3. The mean number of leaves, and mean dry weights of plants of *Primula vulgaris*, *P. elatior* and *P. veris* after 25 weeks under three different drainage régimes. Six plants used for each treatment.

| Species | Free drained | | Water table at 4 cm | | Waterlogged | |
|--------------------|-----------------|--------------|---------------------|--------------|-----------------|--------------|
| | Mean no. leaves | Mean dry wt. | Mean no. leaves | Mean dry wt. | Mean no. leaves | Mean dry wt. |
| <i>P. vulgaris</i> | 11 ± 3.3 | 2.86 ± 0.77 | 12 ± 2.6 | 6.44 ± 1.4 | 6 ± 2.4 | 0.64 ± 0.23 |
| <i>P. elatior</i> | 2 ± 0.6 | 0.87 ± 0.02 | 4 ± 0.9 | 2.5 ± 0.62 | 0.5 ± 0.3 | 0.45 ± 0.01 |
| <i>P. veris</i> | 26 ± 5.21 | 6.76 ± 0.78 | 13 ± 3.03 | 3.76 ± 0.59 | All dead | |

Clearly neither species is tolerant of waterlogging, and this result agrees with those of Abeywickrama (1949) who found little difference in their tolerance to drowning. He suggested that *P. elatior* is less tolerant of low soil moisture than *P. vulgaris* and my results agree with this. I think it very likely that the controlling factor of these species' distribution in these woods is drought tolerance; *P. vulgaris* may resist dry spells more successfully. One indication of this is the poor flowering of *P. elatior* in the spring following a dry summer.

5. Conclusion

Despite a high interfertility, and the provision by regular disturbance of ample opportunity for hybridization, the amount of hybridization between these species is restricted. Internal restricting factors are probably less important than external ones, especially ecological differentiation, the nature of which is not yet clear, but which probably involves drought tolerance. In woods where the species co-exist they are more clearly differentiated ecologically than when they grow apart, and the hybrids occupy mainly the intermediate zone between them. There is little evidence of extensive infiltration of the genes of either of these species into the other, or of replacement of one by the other.

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