

THE INTERSPECIFIC RELATIONSHIPS OF *JUNCUS EFFUSUS* AND *J. CONGLOMERATUS* IN BRITAIN

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ABSTRACT

Juncus effusus and *J. conglomeratus* appear to be specifically distinct in the British Isles; *J. conglomeratus* is the rarer species. Their principal diagnostic features are given.

Evidence is presented to show that the two species hybridize at higher altitudes in Britain, probably because the overlap of their flowering periods is longer in these regions than at low altitudes.

Evidence is also found for gene flow within *J. effusus* populations from *J. conglomeratus* and the reasons for the continuing specific distinctness of these two species is discussed.

INTRODUCTION

Juncus effusus has long been known as an extremely variable species. This is reflected at once both in its wide range of ecological tolerance (Agnew 1961) and in its morphological variability, and it is clear that, since both these features are simultaneous expressions of the inherent variability, no full appreciation of the species can be made without considering its variation with respect to its taxonomy.

From the start the species in its relation to *J. conglomeratus* has been a puzzle to taxonomists. Thus, although the species is known under its Linnaean name, Linnaeus himself seems to have had no clear idea of the differences delimiting it from *J. conglomeratus* or *J. inflexus*, two closely related species, although he evinced some interest in them, as his annotated copy of the *Species Plantarum* (1753) shows. The position may be summarized thus: in the Linnaean Herbarium (LINN) the specimens annotated by Linnaeus as *J. conglomeratus* (Savage 1945, no. 449.2) are in fact *J. effusus* var. *compactus* as we know it, while those annotated as *J. effusus* (Nos. 449.4 and 449.5) are *J. inflexus* as we know it. Due to the extraction of some parts of the original description of *J. effusus* for inclusion in other later species (this has been summarized by Tweed and Woodhead 1947) and subsequent further doubt concerning the delimitations of the two species, they were both included under the one specific name *J. communis* by Meyer (1819).

Krisa (1962) has drawn attention to this confusion in Czechoslovakia, and has concluded that the two species are only recognizable as end points in a continuously variable series of forms, which are regarded as introgressive hybrid populations. The whole series of forms including both species is regarded by Krisa as a 'conspecies'. It will be noted that the conclusions of the present author, who upholds the complete validity of the two species, based on examination of material from the British Isles, differ from those of Krisa. It is due to this discrepancy in views that the following account of work undertaken between 1952 and 1955 is presented. The present author has examined some stands of the two species in Czechoslovakia and feels that the situation there may not be very different from that in Britain, once the restricted nature of the much rarer *J. conglomeratus* is recognized.

Table 1 is a list of the specific differences which have been found most constant in Britain.

CHARACTERS FOR BIOMETRIC ANALYSIS

Work on the variation of both species was done at Edinburgh (Scotland) in 1952 and in 1953-55 at Bangor (North Wales).

To make comparisons between *J. effusus* and *J. conglomeratus*, characters must be used which show a difference between the two species; the form of the inflorescence is such

TABLE 1. Diagnostic features of *J. effusus* and *J. conglomeratus*.

Character	<i>J. effusus</i> L.	<i>J. conglomeratus</i> L.
Stem sheathing scales	Black to red-brown at base	Red-brown to olive at base
Stem-ridges at inflorescence	30-60	15-24
Spathe-length	Usually 15-30 cm	Usually 5-15 cm
Bract of second cyme	Not as long or as long as split in spathe	Longer than split in spathe
Inflorescence	Diffuse or compact	Almost invariably compacted into globose head
Perianth	Outer whorl of three segments about 0.5 mm longer than inner whorl Perianth segments olive with green or light brown centres	Outer whorl as long as inner whorl Perianth segments with dark red-brown edges, lighter centres
Stamens	Anthers oval, shorter than filaments	Anthers strap-shaped, longer than filaments
Style	Very short or absent	One third as long as ovary
Fruit	Retuse or truncate, not apiculate	Truncate, apiculate

a character. The other two chosen were ridge-number and the length of the spathe above the inflorescence. These will be dealt with in turn.

Since the varietal classification of both *J. effusus* and *J. conglomeratus* depends on the condensed or diffuse nature of the inflorescence, this is an obvious character to choose; however there are some difficulties in its measurement. The method chosen has been to measure three axes of the inflorescence at right angles to one another, taking the first measurement parallel to the stem and spathe. The product of the three lengths is then calculated and from this and a count of the total number of flowers in the inflorescence a figure is obtained of the number of flowers per unit volume (ml) of inflorescence ('condensation'). It will be seen that this is in many ways an arbitrary figure since the product of the axes does not give the true volume of inflorescence. However, sufficiently comparable figures can be obtained in this way.

The axes were measured to the nearest millimetre and commonly were less than 10 mm in length. Clearly, this introduces an error in the figure obtained for 'condensation' which increases as length decreases; thus the variance of figures obtained for condensation should increase as the mean condensation increases. This has proved a drawback to the treatment of *J. conglomeratus* by this character, and it has been necessary to transform all figures of condensation logarithmically before statistical treatment.

Spathe length is short (5-15 cm) in *J. conglomeratus* and long (15-25 cm) in *J. effusus*. However it is not a very good character since there are many intermediates. It is very quick to measure and does give a separation of the two species on the scatter diagrams mentioned below.

Ridge-number on the stem below the inflorescence has been found to be very useful indeed. Not only is it easy to observe, especially when the stems have been left to dry for a period, but it gives effective separation between *J. effusus* and *J. conglomeratus* with no overlap and takes an intermediate value for hybrids.

An experiment was carried out to test the plasticity of these characters. Two adjacent populations of *J. effusus* differed in their growth form, i.e. clumped and unclumped (diffusely growing), and occupied distal ends of a soil and vegetation catena from very wet conditions (the unclumped form) to drier grassland (the clumped form). Twenty individuals of each population were transplanted and grown under similar conditions; the results are summarized in Table 2. The previously significant difference in the spathe-length disappeared

TABLE 2. Transplant experiment of *J. effusus* plants from Braint, Anglesey.

	Mean spathe-length	Significance of difference	Mean ridge no.	Significance of difference	Mean no. 'flowers per ml'	Significance of difference
Before cultivation:						
Clumped population	15.48	++	43.9	N.S.	43.05	+++
Unclumped population	19.90		42.9		20.28	
After cultivation:						
Clumped population	16.12	N.S.	34.60	N.S.	72.53	++
Unclumped population	14.13		36.20		44.88	

't' test probabilities given as: + = 5 per cent. $\geq p > 1$ per cent., ++ = 1 per cent. $\geq p > 0.1$ per cent., +++ = $p \leq 0.1$ per cent.

under cultivation, but the difference in inflorescence condensation remained, indicating that this character at least is genotypically controlled.

The value of this experiment is enhanced by the seed-size measurements. The mean seed-size of these two populations was almost identical so that it was not expected that a significant difference in any other character would remain after cultivation. At the same time these results do not invalidate the continued use of ridge-number and spathe-length as population parameters when comparing *J. effusus* and *J. conglomeratus*, although spathe-length is of doubtful use when *J. effusus* alone is dealt with.

POPULATION ANALYSES

The population analyses initially carried out were those of mixed *J. effusus* and *J. conglomeratus* populations. A scatter diagram of such an analysis is shown in Fig. 1. It can be seen that there is a good separation of the two species on ridge-number, spathe-length,

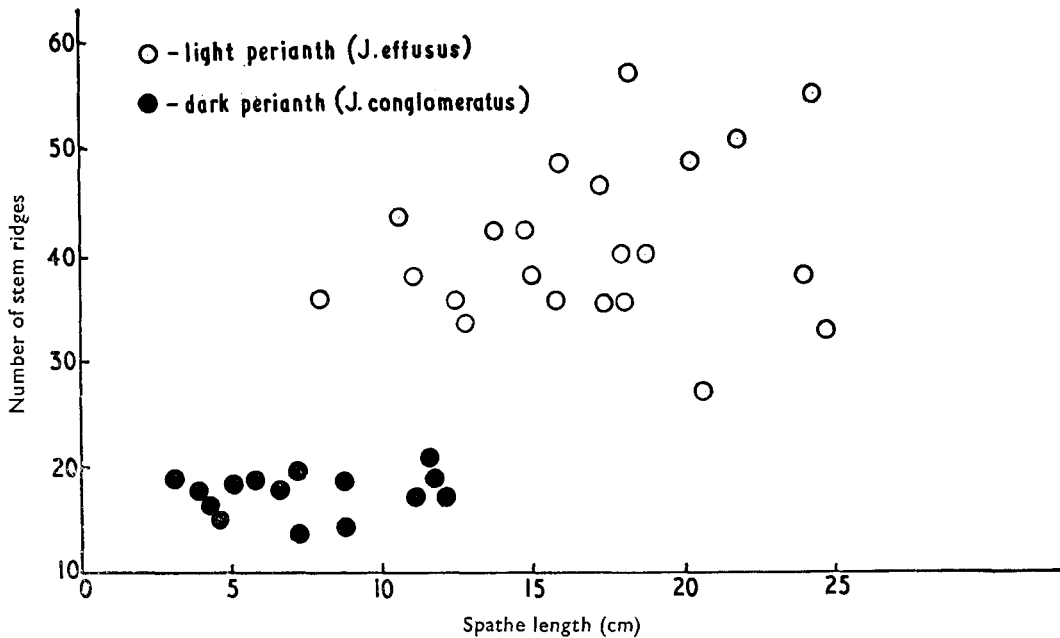


Fig. 1. Scatter diagram of a community containing *J. effusus* and *J. conglomeratus*. The scatters of the two species are easily separated.

and a qualitative character, that of perianth-colour. There are no complications in this diagram.

Two populations have been found, one near Edinburgh (Fig. 2) and one near Glasgow, which do not show such a clear separation of the two species. Here there are individuals which have some characteristics of each species. These plants have been found to be easily separable from both *J. effusus* and *J. conglomeratus* by their intermediate number of stem ridges, the dark perianth segments (the latter typical of *J. conglomeratus*) and the intermediate character of the inflorescence.

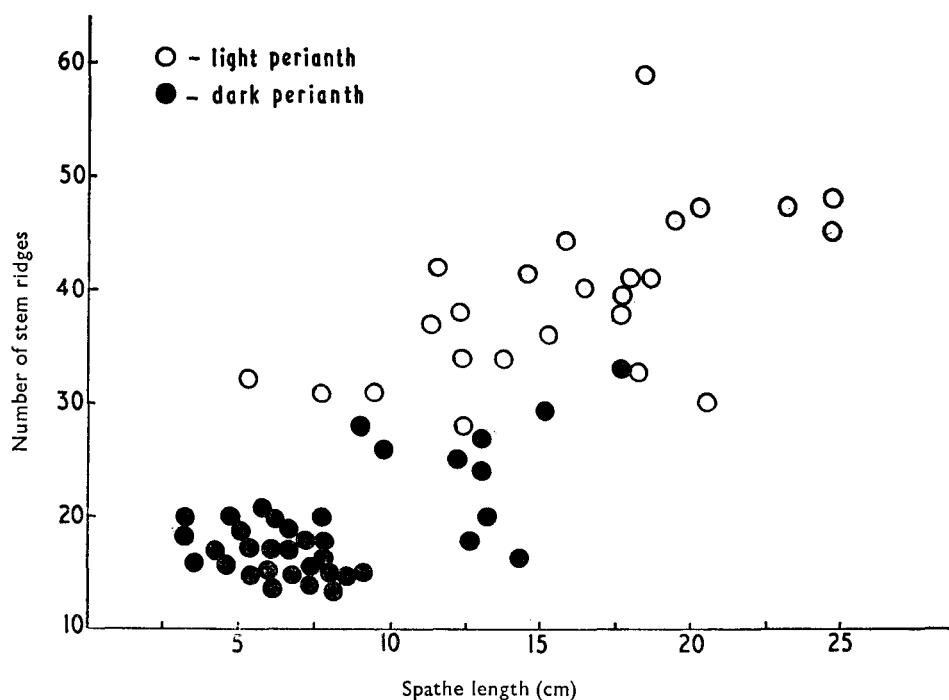


Fig. 2. Scatter diagram showing an intermediate between *J. effusus* and *J. conglomeratus*, from a population at Penicuik, Midlothian.

In North Wales this type of complex has been found on two occasions. The analysis of one of these populations (Fig. 3) shows as before a group of plants intermediate between *J. effusus* and *J. conglomeratus*. In this case there were enough plants of all groups to attempt a statistical analysis, when a positive correlation was found between ridge-number and spathe-length only in the intermediate group. This shows, in my opinion, that the intermediate type is a hybrid, since one would expect a hybrid to show correlations between the characters which distinguish its parents. It has been supposed in this case that these intermediates are groups of F_1 or subsequent generation hybrids, with a little back-crossing.

Populations showing introgression have however been found at Edinburgh and on the Snowdon massif. Scatter diagrams of the former are shown in Figs. 4 and 5. They can be seen to include characters of both species in a complex which shows recombinations of many types. These populations show also introgression only with *J. effusus*, the scatter being between the position of the supposed hybrid and that of *J. effusus*. The correlation of these two characters, ridge-number and spathe-length, is significantly positive in both cases.

That hybrids can occur between the two species has been recognized for some time (Buchenau 1906; Richards & Clapham 1941). The two species were artificially crossed in the garden in 1955. Seeds set in normal numbers in all the flowers crossed and germinated

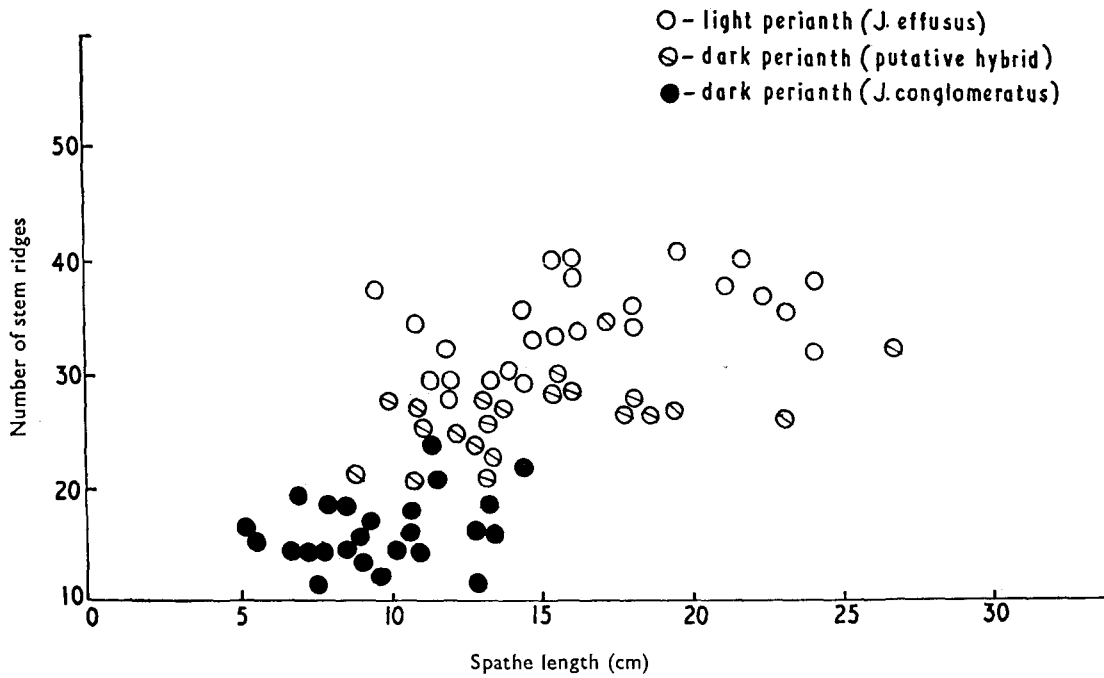


Fig. 3. Combined scatter diagram of three populations, distinguished on this diagram by the use of three symbols. The intermediate grew spatially between the others and in an intermediate habitat. All were from within 100 m of each other at Llyn Idwal, Caernarvonshire.

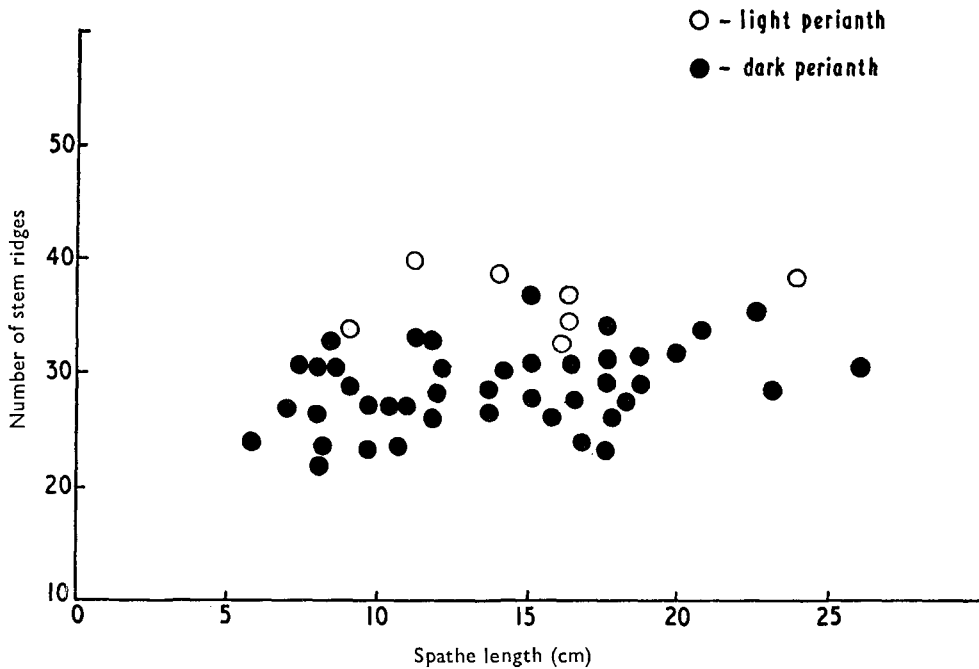


Fig. 4. Scatter diagram of a population from West Linton, Midlothian. The intermediate introgressive nature of the population can be seen by comparison with Fig. 1.

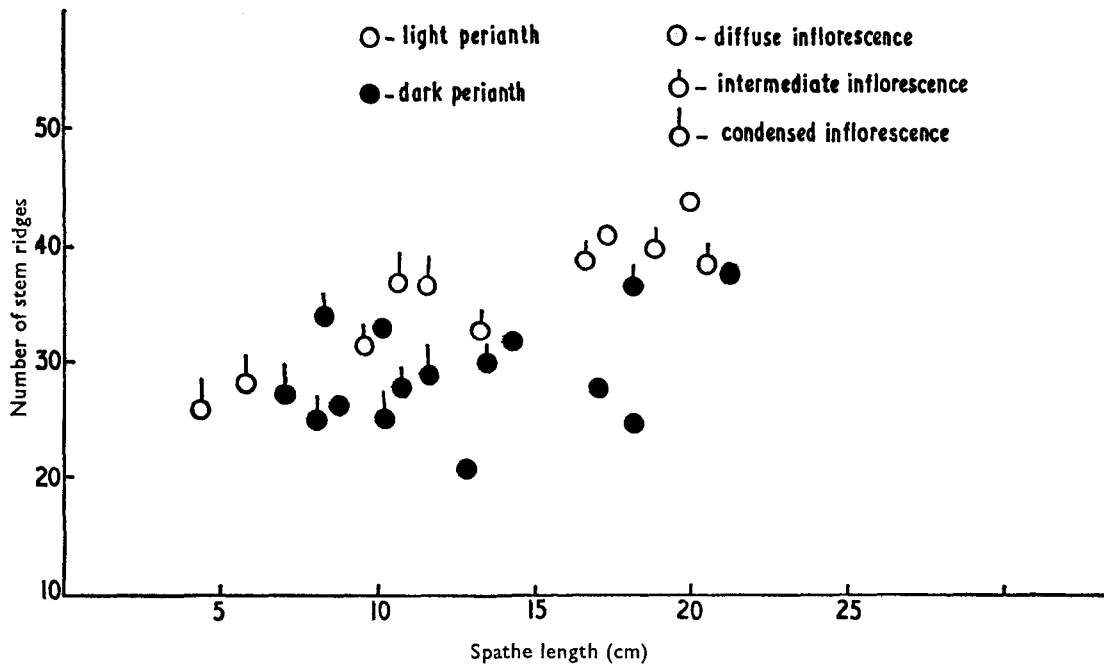


Fig. 5. A further population from West Linton, Midlothian, where inflorescence condensation is also represented.

normally, the seedlings unfortunately being killed by damping off before reaching the 4-leaf stage. There seems no reason to suppose that they could not have developed into mature plants. The hybrids observed in the field moreover appeared fully fertile. This is in contrast to the statements made by Buchenau (1906, p. 137) that he considers the hybrids to be highly sterile and rare. Richards & Clapham (1941, p. 378) state that the presence of hybrids needs confirmation in Britain.

It seems, then, that hybrids exist both as populations of hybrids and as populations introgressing with *J. effusus*. No signs of introgression with *J. conglomeratus* have been found in any population. This may be due to the type of crossing available to the species. As has been repeatedly noted (Richards & Clapham 1941; Buchenau 1906; Krisa 1962) the flowering times of the two species differ and are perhaps responsible for the lack of hybrids. *J. conglomeratus* flowers before *J. effusus* and the flowers of both are protogynous. This means that most crossing between species will be between the pollen of the earlier and the ovules of the later flowering species and this should hold true for hybrids as well. Thus all crossing, introgressive or otherwise, would be in the direction of *J. effusus* as seed parent. This will lead to the seeds being deposited around the plant genetically nearest to *J. effusus* giving an increased likelihood of the progeny being themselves crossed with *J. effusus*. Since the two species usually grow in slightly different habitats, *J. conglomeratus* preferring the drier areas, it can be seen that this effect could have great significance.

Having shown the evidence for hybridization, I propose now to deal with the analyses of the variation within *J. effusus* itself.

VARIATION OF *J. EFFUSUS*

The figures for the variation of populations of *J. effusus* were obtained at Edinburgh with the exception of those analysed for the experimental investigation into the amount of phenotypic variation to be expected. A scatter diagram, made up of four populations, of condensation of inflorescence against ridge-number is shown in Fig. 6. The means of the

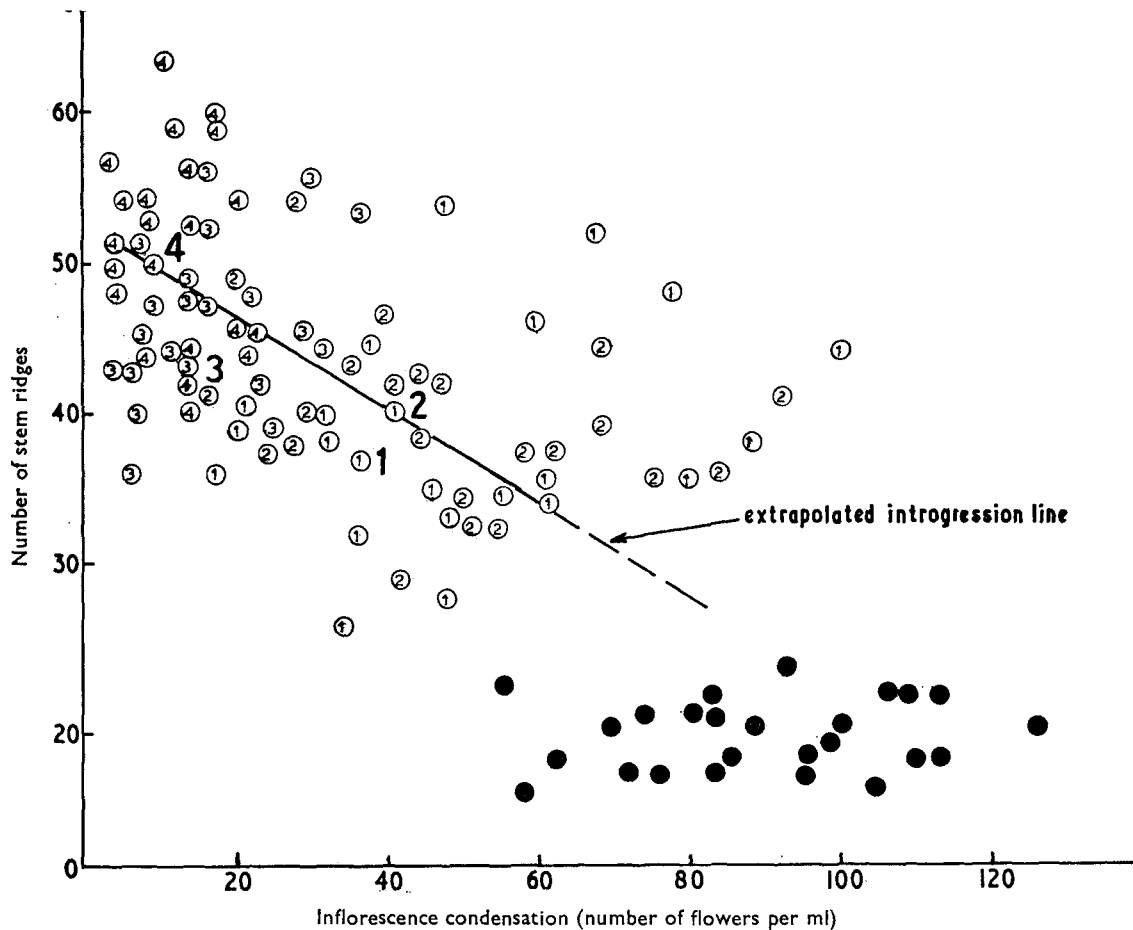


Fig. 6. Scatter diagram of four populations of *J. effusus* where the individuals are numbered according to their population and the mean for each population is plotted as a large, uncircled figure. A population of *J. conglomeratus* (solid dots) is given so that it can be seen to lie on the extrapolated regression line of the four *J. effusus* populations.

populations are shown within the diagram. It is evident that there is some correlation between these two characters, and that the correlation is in the general direction of the position that *J. conglomeratus* occupies in this diagram.

With this in mind the four populations were analysed for correlations between the three parameters measured. The significance of any correlation observed is shown in Table 3. It can be seen that only one population shows significant correlations within

TABLE 3. Correlations between and within four populations of *J. effusus*. Correlations determined between spathe length (A), number of ridges (B), condensation of inflorescence (C). Significance of correlation coefficient gives as: N.S., not significant; + = 5 per cent. $\geq p > 2$ per cent.; ++ = 2 per cent. $\geq p \geq 1$ per cent.; +++ = $p < 0.1$ per cent.

Analysis of each population:	A/B	A/C	C/B
1	N.S.	N.S.	N.S.
2	N.S.	N.S.	N.S.
3	++	+	N.S.
4	N.S.	N.S.	N.S.
Combined analysis of all populations:	++	N.S.	+++

itself and that both of these are positive correlations. The populations taken together show two significant correlations—between spathe-length and ridge-number (positive) and between ridge-number and condensation (negative).

Anderson (1953, p. 287) has suggested that when a scatter diagram shows a correlation of characters there is evidence for gene flow from some other species, and that the characters of the species responsible for this may be found roughly by extrapolation—that is, by producing the line of the correlation until it enters the region in the diagram which would be occupied by a known species were it present. That species is suggested as the one responsible, by hybridization and subsequent backcrossing, for the gene-flow responsible for the correlation. In the present instance, it can be seen from Fig. 6 that the correlation line would in fact produce through the area representing *J. conglomeratus* on the diagram; that is, the area of high inflorescence-condensation and low ridge-number. In the same way the correlation of spathe-length against ridge-number also is in the direction of *J. conglomeratus*.

The lack of correlations within populations shows that the correlation between these characters is not due to genetic linkage. The correlation between spathe-length and ridge-number is possibly not very important; as noted above spathe length is very plastic, and there is a correlation within one of the populations of the group. The correlation between ridge-number and condensation however appears to be very important. Not only are no correlations between these two characters shown within the population, but also these two characters seem to be the most environmentally stable of those used.

The explanation, in the author's opinion, is that gene flow is occurring from *J. conglomeratus* into *J. effusus* populations. This would fit all the facts of variation within and between populations and explain why the correlations between populations are in the direction of the *J. effusus*—*J. conglomeratus* regression.

Another line of evidence, from the mean seed-size of populations of *J. effusus*, confirms this hypothesis. Seed-size was taken as the product of length and breadth. Fifty seeds were taken from each population by taking at random 50 stems from each, shaking these over paper, and taking a small sample of the seeds so gathered. The size of samples was checked several times by measuring a further 50 seeds when it was invariably found that the means approached each other very closely. The means observed differed significantly from population to population and this was found to correlate with the altitude at which the sample was taken, the mean seed-size increasing with altitude. The means of seed-size are shown in Fig. 7. Analysis gives the regression as highly significant ($p < 0.1$ per cent).

Now *J. conglomeratus* has a larger mean seed size than *J. effusus* (0.13–0.15 sq. mm in the scale given in Fig. 7). Gene flow from hybridization at high altitudes could give a series of this sort with the genes of *J. conglomeratus* becoming progressively diluted with those of *J. effusus* as lower altitudes are reached. This hypothesis implies greater hybridization at high altitudes; there is evidence for this and for its cause.

The hybrids and introgressive hybrid swarms so far found in Scotland and North Wales have been at altitudes exceeding 150 m although both species occur, in non-hybridizing populations, down to sea level. There follows a list of the hybrids found, with their altitudes.

Type of hybrid	Place	Altitude
Probable F ₁	Penicuik, Midlothian (Scotland)	183 m
Probable F ₁	Rutherglen Park, Glasgow	152 m
Probable F ₁	Llyn Idwal, Caerns. (Wales)	366 m
Probable F ₁	Cwm Glas, Caerns. (Wales)	381 m
Introgressive hybrid	West Linton, Midlothian (Scotland)	305 m
Introgressive hybrid	West Linton, Midlothian (Scotland)	305 m
Introgressive hybrid	Llyn Llydau, Caerns. (Wales)	457 m

Taking the latitude into account, it can be seen that the hybrids so far found have been at the higher altitudes. This was realized some time ago and a search has been made in

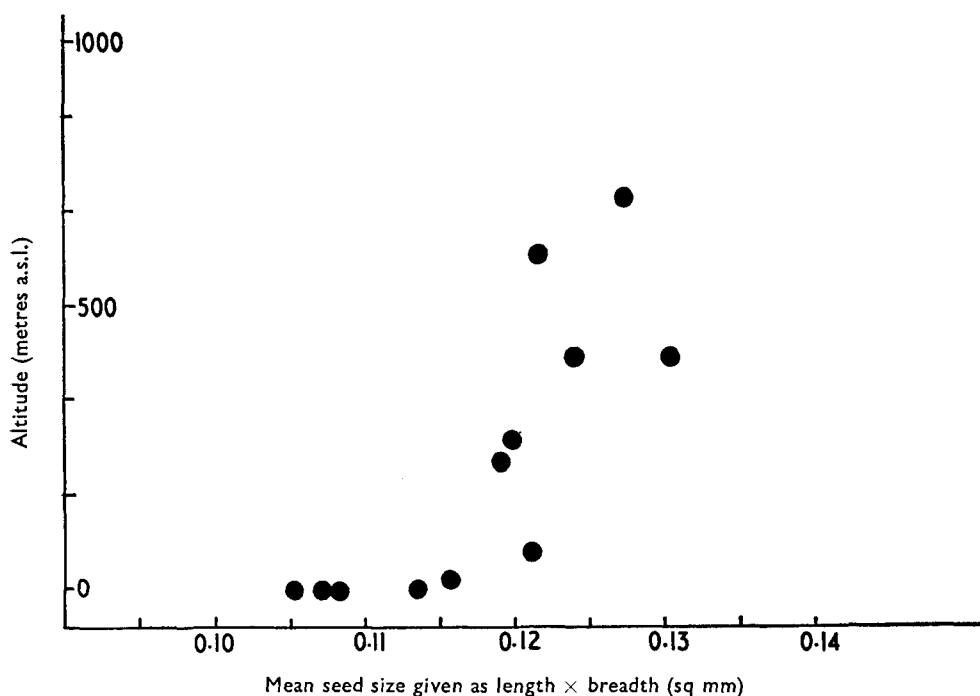


Fig. 7. Mean seed size of twelve *J. effusus* populations from North Wales plotted against altitude of occurrence.

lowland *Junceta* for the hybrids, as yet with no result. It is not intended to show that there are no hybrids at low altitudes, but that they are much more frequent on high ground. Since *J. effusus* is tolerant of the acid conditions so prevalent on British mountains of high rainfall, whereas *J. conglomeratus* is not, it follows that the number of habitats available to *J. conglomeratus* in the mountains are few. *J. conglomeratus* does however occur to 450 m on the Pentland Hills, Midlothian, and to 630 m on the Tarmachan crags above Killin (Scotland). It can be seen therefore that altitude is no barrier to this species in Britain.

In view of the sympatry of the species it is surprising that hybrids do not occur more often. Anderson (1948) has postulated the existence of 'hybrid habitats' as accounting for many of the hybrids observed between sympatric but not concomitant species. In the present case, of course, the species are almost always concomitant. Possible 'hybridity' of the habitat occurs often through human interference, but although search has been made for hybrids in those types of community with agricultural disturbance, none has been found. The hybrids observed were only in one case found to occupy an intermediate type of habitat which was recognizable as such. This was at Llyn Idwal (Wales).

FLOWERING PHENOLOGY

One difficulty attendant on a comparative study of flowering times is that a large distance must be covered during the flowering season to observe sample localities. It has thus been found possible to sample only four localities, ranging from sea level to 381 m. It is unfortunate that the information provided by the analysis of seed size was obtained, initially, somewhat fortuitously and no effort was made in previous years to study the phenology of the two species. Thus a record of flowering times has been made for only one year in North Wales.

Difficulties have also been experienced in the measurement of flowering. The method finally employed was to take five random stems from the stand under consideration and dissect flowers from them. If both dehisced and undehisced anthers were present on any stem the stand was considered to be in flower.

The data obtained are represented in Fig. 8. The altitude has been placed on a logarithmic scale for convenience only. With the few samples taken it cannot be said to be significant

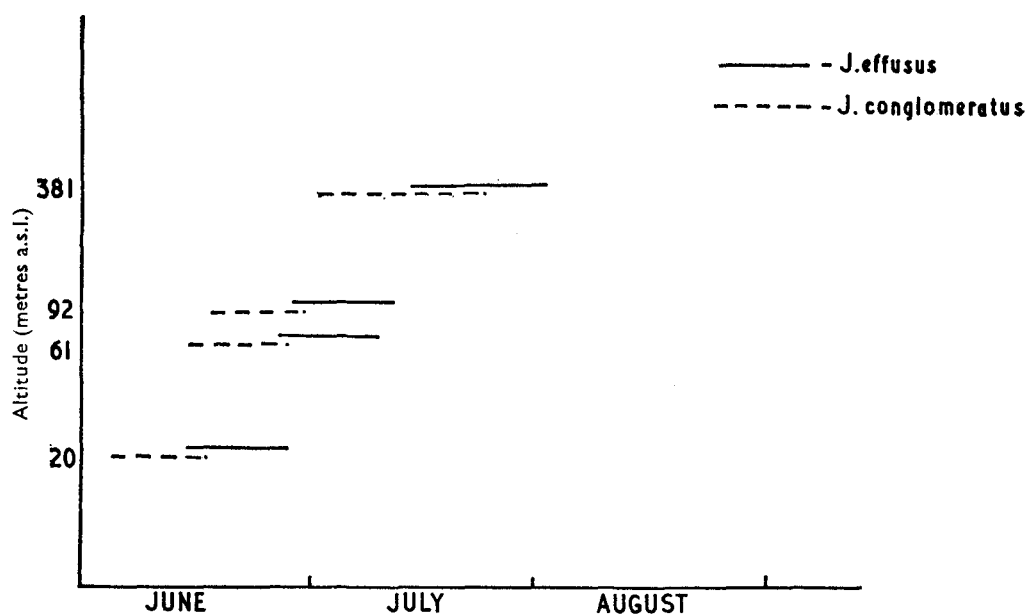


Fig. 8. Variation in flowering periods of *J. effusus* and *J. conglomeratus* with altitude in North Wales, in 1956.

that this allows a straight line to join the starting points of flowering for each species. Due to the preference of *J. conglomeratus* for the more base-rich habitats there are no intermediate stations between 121 and 366 m at which both species may be found close enough together to be influenced by the same environmental conditions. Thus in this area of North Wales, at least, it is unavoidable that there should be a gap here. For reasons of transport and time it was impossible to visit continuously more than one site above 366 m.

Fig. 8 shows that there is some overlap in flowering times at all altitudes. This has also been found in Midlothian. The high altitude population however shows the same difference in the start of flowering times between the two species but a much greater overlap between them. These few results are somewhat inadequate, but indicate that flowering times of the two species may show greater overlap and thus allow a greater chance of hybridization at high altitudes.

No cause, phenological or otherwise, has been found for the apparent lack of hybrids over part of the range of the two species in Britain.

DISCUSSION

It has been shown that hybrids and particularly introgressive hybrids do occur between *J. effusus* and *J. conglomeratus*. Back-crossing does appear to take place, but only with *J. effusus*, and there is thus a possibility of gene flow from *J. conglomeratus* into *J. effusus*. That this occurs is shown by two lines of evidence: (i) correlations between characters which separate the two species in four populations of *J. effusus* taken together, but not within each population, and (ii) increasing seed-size with altitude. The latter corresponds

to the increased hybridization at high altitudes, allowing, so to speak, *J. conglomeratus* genes into the populations there, from whence they 'percolate' in increasing dilution to sea level. The greater overlap of flowering times observed at high altitudes is responsible for greater frequency of hybrids there.

From the foregoing some tentative conclusions may be drawn as to the nature of *J. effusus* variation.

It has already been stated that the species is extremely variable both ecologically and morphologically. This variation may be due in part to the possible genetic amplitude available to the species due to gene flow with *J. conglomeratus*. Thus *J. conglomeratus* has the more condensed inflorescence of the two species. If gene flow is occurring predominantly in the direction of high to low altitude, one would expect the more compact forms of *J. effusus* at higher altitudes. This is found to be generally the case in the writer's experience, and in that of Tweed and Woodhead (1946) who state that the variety (*J. effusus* var. *compactus*) is the dominant one on high ground. In fact no truly effuse forms have been found by the writer in high or exposed habitats.

However, this does not altogether fit the pattern of the ecological variation of *J. effusus* (Agnew 1961). *J. conglomeratus* is associated with the more basic type of habitat. Thus in North Wales at least it is associated with the basic rock outcrops of the mountains, and with the boulder clay and limestone regions of Caernarvonshire and Anglesey. The only site in my experience where it is dominant to the exclusion of *J. effusus* is on the Carboniferous Limestone at Penmon Point, Anglesey. No pH values of lower than 4.3 have been recorded for it by the present author, and Pearsall is quoted by Richards & Clapham (1941) as considering it more basicole than *J. effusus*. The flow of *J. conglomeratus* genes through *J. effusus* should confer a basicole tendency and, since the compact form of *J. effusus* presumably contains more of these genes than the effuse form, one would expect the latter to be the more acidicole variety. In fact the reverse is the case in North Wales at least. This is one of the problems that might be solved by further transplant experiments.

There is also the problem of interspecific barriers between *J. effusus* and *J. conglomeratus*. A hypothesis has been put forward in this paper to explain the apparent lack of introgression and gene-flow into *J. conglomeratus*, the latter species acting as a 'gene reservoir' to *J. effusus*. It is curious that *J. effusus* has remained distinct from *J. conglomeratus*, since it cannot be envisaged that this gene flow is a recent process; the factors acting in favour of *J. effusus* cannot include a sterility barrier, and the effect of phenology has been discussed. There remains therefore selection pressure.

Only one possible example of this has been found. It has been noted that the *J. effusus* plants of North Wales are prone to a fungal infection of the capsules. This was first investigated during the comparatively wet summer of 1954 when many samples taken from a marsh area showed no uninfected capsules at all. The infection allows the carpel wall to reach maturity but it contains no seed, only a mass of fungal hyphae. This fungus was not identified. It was noted that the compact variety of *J. effusus* was very much more heavily attacked than the effuse form, probably owing to contagion between capsules. In one pair of populations, one compact, the other effuse, of 5,000 capsules examined from each, 2,560 in the former and 606 in the latter were infected.

This is the only quantitative evidence obtained for selection against *J. conglomeratus* characters in *J. effusus*. It is interesting to note that this fungal infection was never observed by the present author on *J. conglomeratus*. In any case it seems likely that this is one of the factors operating in favour of the effuse *J. effusus* form, thus preventing the species from drifting wholly towards *J. conglomeratus*.

ACKNOWLEDGMENTS

Dr. P. H. Davis initiated and guided this study while I was an undergraduate, and it gives me pleasure to acknowledge my debt to him. I am also grateful to Professor P. W. Richards under whose supervision this work was continued in North Wales.

APPENDIX

Locations and habitats of populations of *J. effusus* and *J. conglomeratus* cited in text figures.

	Population	Location and Habitat
Fig. 1	All	Marshy grassland at edge of Threipmuir reservoir, Balerno, Midlothian, with <i>Deschampsia caespitosa</i> and <i>Molinia caerulea</i> .
Fig. 2	All	Flush area on hillside, with <i>Agrostis</i> spp. at Penicuik, Midlothian.
Fig. 3	All	Flush area and adjacent hillside, with consequently varying associated species, at Llyn Idwal, Caernarvonshire.
Fig. 4	All	Grassland (rough pasture) with <i>Nardus stricta</i> and <i>Deschampsia flexuosa</i> adjacent to streamsides with <i>Agrostis tenuis</i> and <i>Holcus lanatus</i> $\frac{3}{4}$ km west of West Linton, Midlothian.
Fig. 5	All	As for Fig. 4.
Fig. 6	1	Threipmuir reservoir, Balerno, Midlothian, as in Fig. 1.
	2	Penicuik, Midlothian, as in Fig. 2.
	3	Wet open woodland with <i>Holcus lanatus</i> at Penicuik, Midlothian.
	4	In <i>Salix</i> carr bordering Threipmuir reservoir, Balerno, Midlothian.
Fig. 7	All	These were spot samples and no record remains of their detailed provenance.
Fig. 8	Lowest	<i>Agrostis tenuis</i> grassland at Bangor, Caernarvonshire.
	next	<i>Agrostis tenuis</i> grassland 1 km south-west of Bangor.
	next	Coarse wet grassland with <i>Deschampsia caespitosa</i> at Llandegfan, Anglesey.
	highest	As for Fig. 3 at Llyn Idwal, Caernarvonshire.

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