

Observations on the morphology and fertility of *Juncus* × *surrejanus* Druce ex Stace & Lambinon in north-western Wales

T. H. BLACKSTOCK

Nature Conservancy Council, Penrhos Road, Bangor, Gwynedd, LL57 2LQ

and

R. H. ROBERTS

51 Belmont Road, Bangor, Gwynedd

ABSTRACT

The range of morphological variation of hybrid plants from a number of different populations of *Juncus* × *surrejanus* Druce ex Stace & Lambinon (Juncaceae) in north-western Wales is described. The variability of the hybrid is compared with that of its parent species, *J. acutiflorus* Ehrh. ex Hoffm. and *J. articulatus* L., growing in the same localities. The production of viable (i.e. germinable) seed by this hybrid, as found in many of the *J. × surrejanus* populations investigated, is reported for the first time from British plants, which had previously been described as seed-sterile.

INTRODUCTION

The hybrid *Juncus acutiflorus* Ehrh. ex Hoffm. × *J. articulatus* L. was first found by W. H. Beeby in Surrey in 1882 (Beeby 1884). Specimens sent to F. Buchenau for his opinion were tentatively identified as "*J. lamprocarpus*, Ehrh., var. *macrocephalo affinis*", but with the further comment that they were "more likely a hybrid between *lamprocarpus* and *acutiflorus*." Beeby, however, having observed the plant during a second season, was impressed by its complete failure to produce seed and its intermediacy in some respects between the two species. Consequently, in the following year, he sent a further gathering of specimens to Buchenau (Beeby 1885) and at the same time drew his attention to the constant sterility of the plant. To this Buchenau replied that "from the form of the perianth, and from your observations, probably = *J. acutiflorus* × *lamprocarpus*." This hybrid was listed as "× *Juncus Surrejana* Dr." by Druce (1929) but the name *Juncus* × *surrejanus* Druce ex Stace & Lambinon has only recently been validated (Lambinon & Stace 1983).

Cytological evidence was obtained by Timm & Clapham (1940), who showed that while *J. acutiflorus* had a chromosome number of $2n = 40$ and *J. articulatus* $2n = 80$, the plants they had identified as the hybrid had $2n = 60$ and a study of meiosis in these plants confirmed their hybrid origin. Further chromosome counts of $2n = 60$ for this hybrid have been obtained by Zandee (1981) from various localities in western Europe.

Although Timm & Clapham found that *J. × surrejanus* was very common in the Oxford area, subsequent records of it in the British Isles have been very uneven. A recent map of its distribution in Wales (Ellis 1983), for example, shows a preponderance of records in Merioneth, v.c. 48, where it has been recognized in many places by Benoit & Richards (1961), but only a very thin sprinkling of records elsewhere. This is possibly because identification of the hybrid is not always as straightforward as the published descriptions suggest. Whilst Timm & Clapham, like Beeby, emphasized the complete sterility of the hybrid plants they had studied, Chapple (1948) found that though, in general, capsules are not formed, when they are, "an occasional unformed seed will be found". Chapple's use of the word "unformed" was unfortunate: no doubt what he meant was "poorly-developed".

Subsequent descriptions of *J. × surrejanus* have either overlooked or ignored Chapple's observations and most of them follow Timm & Clapham (1940) in emphasizing the complete absence of seed production (Richards 1962; Stace 1975). Nilsson & Snogerup (1972), on the other hand, state that, rarely, one or a few seeds are formed in some capsules, and their illustration of the hybrid shows a moderately well-developed capsule.

Our own interest in this hybrid arose from our independent observations that plants collected from a number of localities in north-western Wales, which appeared from their morphology to be this hybrid, occasionally produced plump, normal-looking seeds. Furthermore, the extreme variation found amongst the hybrid plants was much greater than one is led to expect from published descriptions. Consequently, in 1983 a more extended search was made for this hybrid to enable its morphological variability to be investigated more thoroughly, and sufficient material was gathered late in the year in order to estimate the frequency with which seeds occur and to test their viability. It was also possible to locate plants in two localities in Anglesey and Caernarvonshire where Zandee (1981) had previously reported hybrid material confirmed by him cytologically.

TABLE 1. COMPARATIVE CHARACTERS FOR *J. × SURREJANUS* AND ITS PARENT SPECIES**

	<i>J. articulatus</i>	<i>J. acutiflorus</i>	<i>J. × surrejanus</i>
Rhizome system	Subcaespitose or shortly creeping	Far creeping	1
Flowering stem	Decumbent, flexible	Erect, stiff	1
*Length of flowering stem, cm	35.8 (s.d. 15.4), 14–58	71.7 (s.d. 16.4), 27–110	(
*Number of leaves per stem	3.7 (s.d. 1.2), 2–8	2.7 (s.d. 0.6), 2–4	3
Appearance of leaves	Ribbed, dull, soft and curved	Smooth, shining, stiff and straight	Smooth, somewhat shining, moderately flexible and often curved
*Length of second leaf from stem apex, cm	8.8 (s.d. 3.4), 3.0–15.3	28.7 (s.d. 6.2), 18.0–41.2	14.0 (s.d. 4.7), 6.2–27.8
Flattening of leaves	Strongly compressed	Subterete	Subterete or somewhat compressed
Inflorescence branches	Generally few; ascending at a narrow angle to the vertical	Many; basal long, ascending almost vertically; shorter branches widely spreading	Variable in number; long branches ascending almost vertically; shorter branches widely spreading
Peduncles of flower heads	Long	Short	Variable; mostly intermediate
*Number of heads of flowers per inflorescence	18.2 (s.d. 11.9), 3–55	50.1 (s.d. 24.9), 11–102	24.9 (s.d. 15.9), 3–65
*Number of flowers per head	6.4 (s.d. 2.6), 2–15	8.3 (s.d. 3.3), 2–20	11.7 (s.d. 5.6), 2–34
*Length of perianth segments, mm	2.6 (s.d. 0.2), 2.3–3.3	2.1 (s.d. 0.2), 1.5–2.5	2.7 (s.d. 0.3), 2.0–3.4
Length of inner perianth segment relative to outer	Equal	Greater	Generally equal, occasionally slightly longer
Tips of outer perianth segments	Straight	Curved outwards	Often straight, sometimes slightly curved outwards
Length of ripe capsule relative to perianth	Longer (up to 3.5 mm) and protruding	Longer (up to 3.0 mm) and protruding	Very little longer and scarcely protruding
Colour of ripe capsule	Black and shining	Brown	Greenish-brown

* Figures given represent sample mean (standard deviation), range.

** Data for all characters are based on plants collected from populations in north-western Wales

MATERIAL AND METHODS

Altogether, material was gathered from 22 plants of the hybrid from 15 separate localities in north-western Wales; material of the parent species was also collected from each locality when available. The hybrid was found in a variety of different habitats, including a range of lowland mire types which had generally been partially drained and where *J. × surrejanus* at times occurred in considerable abundance.

The search for seeds was made by opening undehisced capsules, and all the seeds obtained, regardless of their quality, were placed immediately on damp blotting-paper in Petri dishes.

At the same time a count was made of the number of flowers per head and data were later collected for culm stature, number of leaves per stem, length of the second leaf from the stem apex and number of heads per inflorescence. A sample of five or more perianth segments from dissected flowers was measured under the low power of the microscope, inner and outer segments being measured separately. Capsules were also measured when present. Similar morphological data were collected from material of the parent species for comparison.

Living material of one hybrid plant from Cors Geirch was brought into cultivation and actively-growing root-tips were used to obtain a somatic chromosome count. Root-tips were fixed in acetic alcohol and subsequently hydrolyzed in 0.1M HCl prior to being stained and squashed in aceto-orcein.

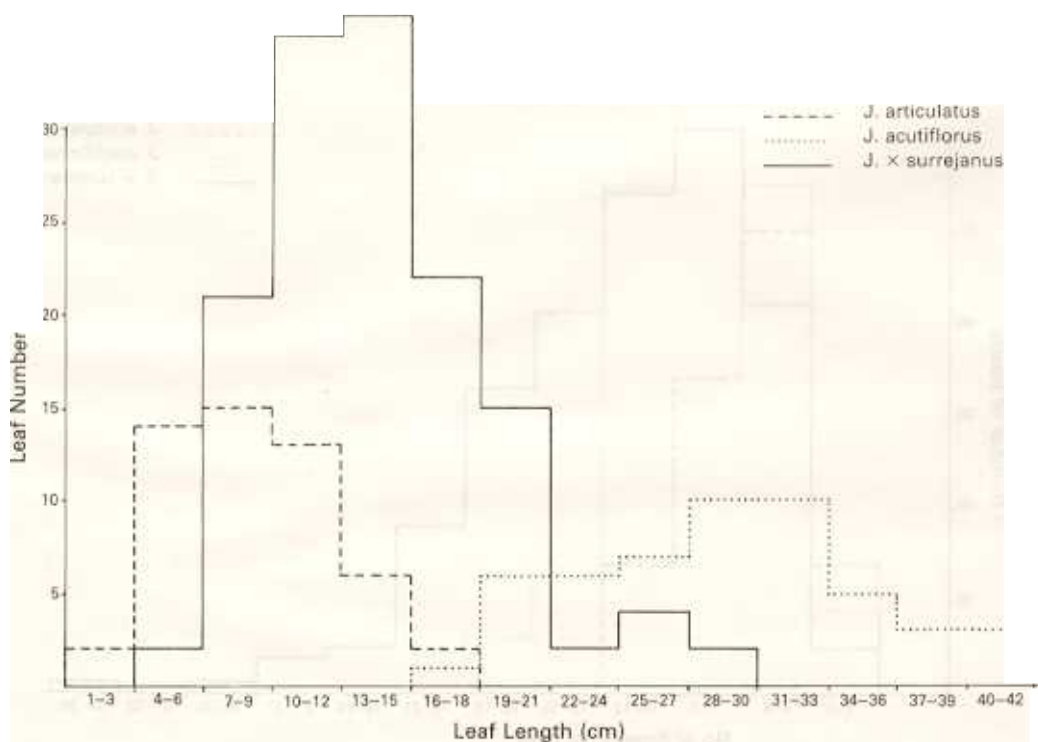


FIGURE 1. Histograms of leaf lengths of *J. × surrejanus* and its parent species for samples from populations in north-western Wales. In all cases measurements were made on the second leaf from the stem apex.

RESULTS

MORPHOLOGY

Morphologically the hybrid shows a very wide range of variation in almost all characters; data for the hybrid and both parent species are summarized in Table 1. The mean stature (69 cm) is similar to that of *J. acutiflorus* (72 cm) but the range of variation (20–126 cm) is greater than in that species (27–110 cm). The flowering stems are stouter than those of *J. articulatus*, but are usually flexible and never as stiffly erect as those of *J. acutiflorus*. The habit of the hybrid plants is generally intermediate between that of the parents, most of those observed being partly decumbent and only rarely prostrate.

The leaves of the hybrid are mostly intermediate in appearance between those of the parents, often somewhat curved, smooth and shining and never as straight and stiff as those of *J. acutiflorus*, nor as dull and strongly compressed as those of *J. articulatus*. The number of leaves per stem varies from 2 to 6, compared with 2 to 4 in *J. acutiflorus* and 2 to 8 in *J. articulatus*. Although there is overlap with its parent species in leaf length (Fig. 1), the leaves of the hybrid tend to be intermediate (mean 14.0 cm) between the much shorter leaves of *J. articulatus* (mean 8.8 cm) and the much longer leaves of *J. acutiflorus* (mean 28.7 cm). These mean values agree remarkably closely with those given by Timm & Clapham (1940) for plants from the Oxford district: *J. articulatus*, 9.3 cm; *J. × surrejanus*, 13.8 cm; and *J. acutiflorus*, 28.0 cm.

The inflorescence in general resembles more closely that of *J. articulatus*, both in its longer (but more spreading) branches and in the number of heads per inflorescence (range 3–65). The number of flowers per head is often much greater (range 2–34) than that reported by Timm & Clapham (1940) (range 3–6), and the heads themselves are often enlarged by continuous flowering, so that there can be a larger number of flowers per head than in either *J. acutiflorus* or *J. articulatus* (Fig. 2). This was also remarked on by Timm & Clapham (1940) and by Nilsson & Snogerup (1972).

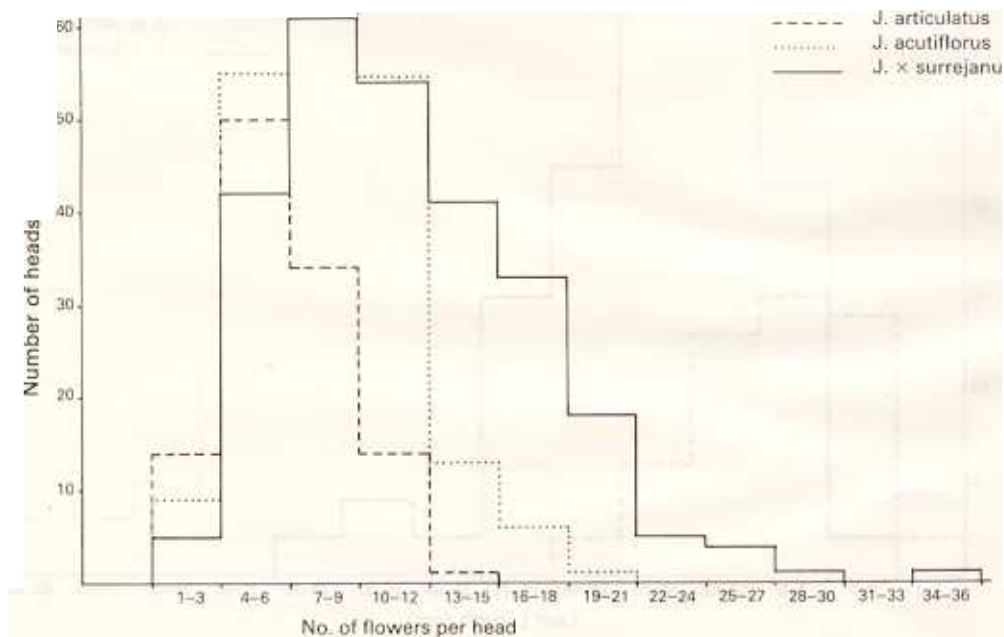


FIGURE 2. Histograms of number of flowers per head in inflorescences of *J. × surrejanus* and its parent species for samples from populations in north-western Wales.

MORPHOLOGY AND FERTILITY OF *JUNCUS* × *SURREJANUS*

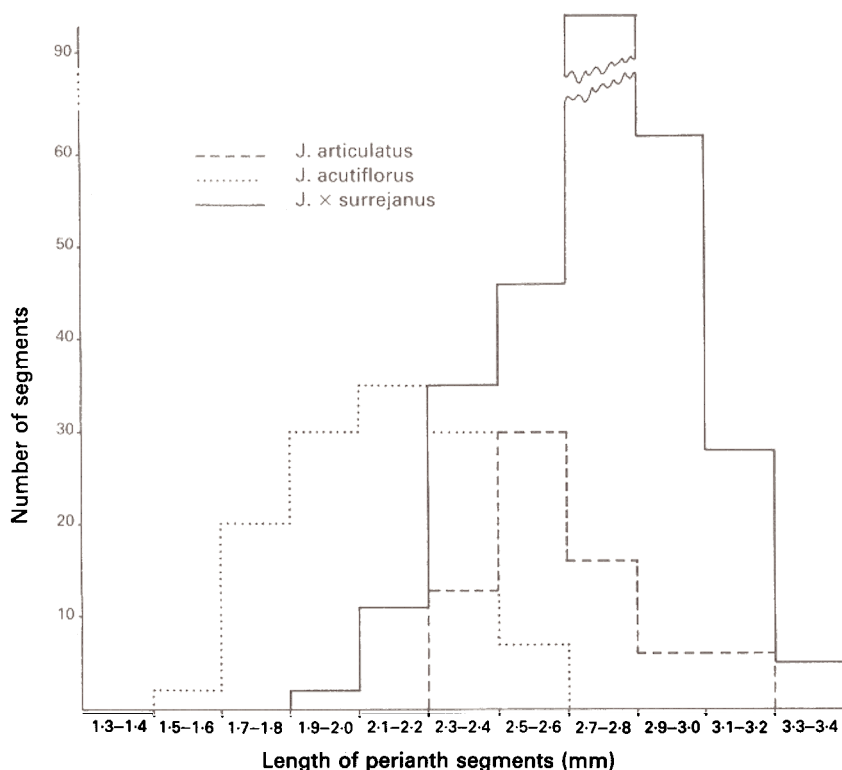


FIGURE 3. Histograms of perianth segment lengths of *J. x surrejanus* and its parent species for samples from populations in north-western Wales. Measurements of both inner and outer perianth segments are included.

A feature of the hybrid plants which becomes more noticeable later in the season (mid-October to November), and which can give some of them a striking and attractive appearance, is the ability to proliferate both from the nodes of the stem and from the axes of the flower heads. Such plants were also noticed by Timm & Clapham (1940) who were undoubtedly correct in suggesting that plantlets arising from proliferation constitute an effective method of vegetative reproduction.

Flower size in the hybrid and its parent species is very variable, as can be seen in Fig. 3. The mean length of perianth segments in different hybrid plants ranged from 2.2 mm – similar to that in many plants of *J. acutiflorus* – to 3.3 mm, which is larger than that in any of the plants of *J. articulatus* studied. The size of the flowers varies a good deal even among those of a single head, e.g. 2.4 mm–3.4 mm in the Plas Bog hybrid, and the mean for the aggregate of all samples of perianth segment length in the hybrid (2.7 mm) is greater than the mean in either *J. acutiflorus* (2.1 mm) or *J. articulatus* (2.6 mm). The inner perianth segments are longer than the outer in *J. acutiflorus*, whereas in the hybrid they are equal in length, or the inner may be very slightly longer.

The frequency with which capsules are developed in different plants of the hybrid varies from 20% to almost 100% of the flowers. The capsules are more or less intermediate in shape between those of the parents and their colour is greenish-brown in contrast to the shining black capsules of *J. articulatus* and the brown capsules of *J. acutiflorus*; they are also shorter in relation to the perianth so that only the beaks of the capsules protrude beyond the perianths at maturity. This is also true of capsules in which seeds have developed, and only rarely do these show a better development than the empty ones. It is possible that the capsules swell in response to pollination even though fertilization does not take place.

Timm & Clapham (1940) found that examination of pollen in aceto-carmin was not helpful in distinguishing the hybrid as about 80% of the tetrads appeared normal. Lambinon & Stace (1983), on the other hand, state that the pollen of the hybrid is largely sterile. The pollen of hybrid plants in north-western Wales was found to be highly variable in both quantity and quality. Anthers and pollen from freshly-gathered material of *J. × surrejanus* as well as its parent species were stained in lignin pink. In contrast to *J. acutiflorus* and *J. articulatus*, where abundant and evenly-formed pollen tetrads are produced, the anthers of many hybrid plants were either empty or contained only very few grains. In others there was a full complement of pollen, but closer examination showed that often a high proportion of the grains had malformed tetrads with one or more of the units either small and misshapen or completely lacking. Most anthers also contained some completely empty grains, and in a few instances a small supernumerary unit was observed amongst the other four parts of the tetrad. Only occasional plants had a relatively high proportion (up to c. 60%) of normal-looking pollen.

SEED PRODUCTION

Out of 22 plants of the hybrid examined only two failed to yield any seed at all. In the other 20 the proportion of flowers which produced seed varied from 0.3% to 20%. The quality of the seed varied from completely empty testae through thin, partly-developed seeds to some which were plump and normal-looking; these last were as large as the seeds of *J. articulatus* and occasionally larger (up to 0.75 mm long). The quality of the seed also varied from one flower to another on the same plant and even within the same capsule, when more than 1 seed was present. In the great majority of plants (16), seeds were found to occur singly within the capsules, only rarely were two or three found together and only in one plant were there more, as can be seen from Table 2, which also shows the number of flowers examined, the number of seeds found and the number of these which germinated.

TABLE 2. SEED PRODUCTION AND GERMINATION IN *J. × SURREJANUS*

Plant no.	Locality (v.c.)	No. flowers examined	No. seeds found	Max. no. seeds capsule ⁻¹	No. seeds germinated
1	(48)	85	1	1	0
2	(49)	92	6	1	2
3	(49)	44	3	1	2
4	(49)	10	2	2	0
5	(49)	530	24	1	9
6	(49)	380	36	1	7
7	(49)	84	28	8	3
8	(49)	59	3	1	0
9	(49)	85	0	—	
10	(52)	63	0		
11	(52)	127	1	1	0
12	(52)	45	7	3	0
13	(52)	38	3	1	0
14	(52)	390	1	1	1
15	(52)	82	10	3	3
16	(52)	32	6		0
17	(52)	51	1	1	0
18	(52)	67	4		3
19	(52)	88			
20	(52)	270	5		3
21	(52)	170	14		5
22	(52)	90			0
		2882	157		39

SEED GERMINATION

The first seed germinated five weeks after sowing; others germinated at intervals from 25th November 1983 to 12th April 1984. As soon as they had germinated the seedlings were placed on sterilized compost. In a few instances the seedlings failed to develop chlorophyll or showed some other abnormality, made no further growth and eventually died. Out of 39 seeds which germinated, eight have failed, but the other 31, from eleven separate plants, are growing (some of them quite vigorously) and it is worth noting that, of these, two are from the Cors Geirch plant whose identity was confirmed cytologically ($2n = 60$).

DISCUSSION

Observations on the plants from different populations of *J. × surrejanus* have revealed that this hybrid exhibits considerable morphological variation in north-western Wales. Although there is generally a broad overlap with its parent species, the hybrid shows a degree of intermediacy in some characters, e.g. growth habit, mean number of leaves per stem, mean leaf length and inflorescence branch angles. In other respects, however, *J. × surrejanus* tends more closely to approach one or other of its parents, especially *J. articulatus*, which it resembles, for instance, in the inner and outer perianth segments of each flower being more or less equal in length and in the frequent occurrence of vegetative proliferation. This wide morphological overlap can result in considerable difficulties in the recognition of *J. × surrejanus* in the field. In our experience, identification can only be tentative until mature inflorescences of all three taxa are available for comparison in a particular locality. At that stage the ripe capsules of both *J. acutiflorus* and *J. articulatus* protrude well beyond the perianth segments whereas, when capsules are formed in the hybrid, they hardly exceed the perianths. The length of the perianth segments in at least some flowers is generally greater than in either of the parent species and, late in the year, when continued flowering has often taken place, the combination of large flowers with non-protruding or undeveloped capsules and large number of flowers per head gives the hybrid a particularly distinctive appearance, as may be seen from the silhouettes in Fig. 4.

The morphological variability of *J. × surrejanus* may be in part due to the range of environmental conditions in which it and its parent species grow. The plants included in this investigation came from a variety of lowland habitats, including damp depressions in fixed-dune grassland, partially drained valley mires and flood-plain alluvial marshes, amongst which there is a considerable range of soil conditions, water-table behaviour and vegetation structure. Although the majority of localities reported for *J. × surrejanus* are in the lowlands, there is a specimen of this hybrid in UCNW collected at c. 1200 feet [370 m] on Snowdon by S. M. Walters in 1950. The extreme variability of *J. articulatus* is well known, and some of the characteristics of different variants of this species are associated with certain ecological conditions (Clapham 1949), so that the morphology of hybrid progeny in a particular locality may be influenced by an interaction of environmental and genetical factors.

All the previously published descriptions of *J. × surrejanus* in the British literature emphasize the feature of complete seed-sterility for this hybrid. In marked contrast, many of the hybrid plants examined from populations in north-western Wales have been found to be partially fertile and produce germinable seed, albeit in usually very small quantity. Although there is no conclusive evidence that either backcrosses or F_2 hybrids have become established in the wild, the possibility that hybrid complexes might occur should be borne in mind in future population studies of these jointed rushes. It is also not inconceivable that some of the morphological variation of *J. × surrejanus* described here and elsewhere could be accounted for by the inclusion of individuals of subsequent generations, derived at least partly from F_1 plants. Nilsson & Snogerup (1972) have suggested that the plants referred to by Timm & Clapham (1940) as "large 80" might have resulted from backcrossing of *J. × surrejanus* to *J. articulatus*. These "large 80" plants had a mixture of characters of both *J. acutiflorus* and *J. articulatus*, but were seed-fertile with a chromosome number of $2n = 80$, which led Timm & Clapham (1940) to postulate a number of other possibilities regarding their taxonomic status, and the situation clearly requires further cytological and experimental investigation.

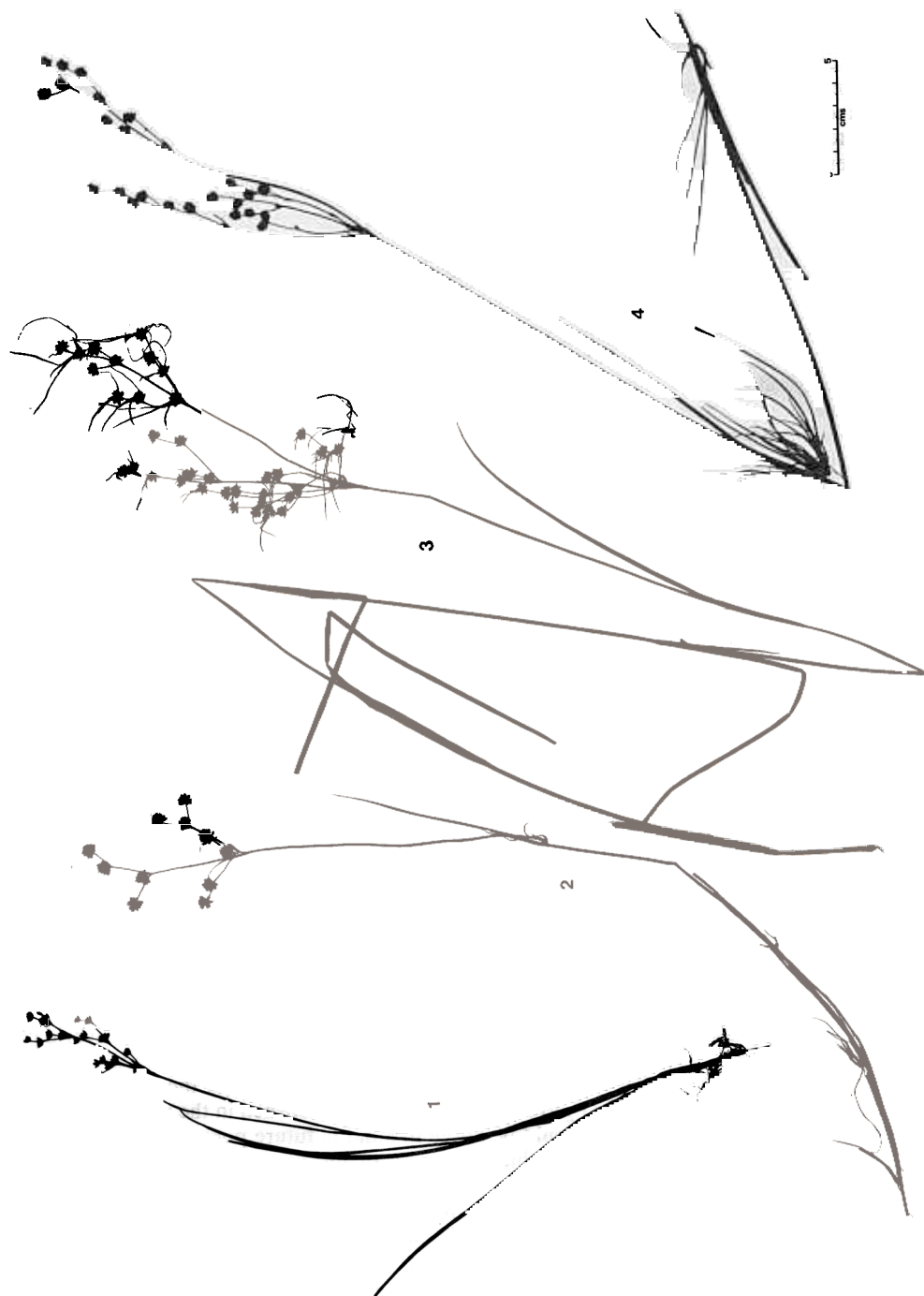


Figure 4. Silhouettes of flowering stems of *J. x surrejanus* from four localities in north-western Wales: 1. Newborough Warren, 2. Nant Ffrancon, 3. Cors Geirch, 4. Malltraeth Marsh.

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