

The status of *Puccinellia pseudodistans* (Crép.) Jansen & Wachter in Great Britain

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ABSTRACT

Puccinellia pseudodistans is described in literature as intermediate between *P. distans* and *P. fasciculata*. It was found to be cytologically and morphologically distinct from *P. distans*, but in most characters is similar to *P. fasciculata*. Experimental work suggests that it is conspecific with *P. fasciculata*, the two taxa representing environmentally induced phenotypes with no genetic distinction. *P. fasciculata* is the earlier name for the species.

INTRODUCTION

Puccinellia pseudodistans was first described in 1865 by the Belgian botanist François Crépin. Crépin's material was from the western Mediterranean and was published as *Glyceria pseudodistans* Jansen and Wachter, who found the plant in Spain and in Holland, transferred the species to Parlature's genus *Puccinellia* in 1935. The first published record of its occurrence in Britain was in 1936, in a paper by Lousley, who had collected specimens at Seasalter, Kent in 1930 and at Grain, Kent in 1935. In the British Herbarium at the British Museum (Natural History) (BM) there is a specimen collected at Grain, Kent in 1893 as *Glyceria borveri* (= *Puccinellia fasciculata*) and which is annotated by Lousley 'earliest British specimen seen' (i.e. of *P. pseudodistans*).

Tutin (1962) lists five species of *Puccinellia* in the British flora. Whilst the other species are described fully, *P. pseudodistans*, which is described as 'more or less intermediate between *P. distans* and *P. fasciculata*', is dismissed rather briefly. Tutin also reports that 'Sterile plants intermediate between *P. distans* and *P. fasciculata* and probably hybrids between the two, occur occasionally where these species grow together'. Hubbard (1954) also treats *P. pseudodistans* with brevity in a work which is of value generally for its detailed accounts of British grasses. These scant references seem to imply that the authors do not consider *P. pseudodistans* to have the same taxonomic status as the other species, and Tutin has said elsewhere (Tutin 1955) that he regards it as an 'uncertain entity'.

In published descriptions of the three species *P. pseudodistans*, *P. distans* and *P. fasciculata* the principal differences are as shown in Table 1 & Plate 1. These differences were examined critically by investigations on wild populations and by cultivation experiments. Material was collected from various localities in South-East England, mostly from Essex and Kent (Newton 1965).

INFLORESCENCE FORM

Four of the characters given in Table 1 concern the form of the inflorescence. In the field it was found that these characters were quite distinctive, and with a few exceptions there was no difficulty in determining collected material.

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Plants of *P. fasciculata* were always found in very dry habitats, whereas the other two species always occurred in wet situations. In cultivation, *P. fasciculata* responded to a rich soil and abundant water by growing much more vigorously.

TABLE 1. DIAGNOSTIC CHARACTERS REPORTED IN PUBLISHED DESCRIPTIONS.

<i>P. distans</i>	<i>P. pseudodistans</i>	<i>P. fasciculata</i>
Panicles symmetrical.	Panicles symmetrical.	Panicles unilateral.
Panicle branches all bare at base.	Only longer panicle branches bare at base.	Only longer panicle branches bare at base.
Panicle branches fully deflexed at maturity.	Panicle branches spreading but not deflexed.	Panicle branches obliquely erect.
Panicle branches swollen at base.	Panicle branches not swollen at base.	Panicle branches not swollen at base.
Nerves of lemma not reaching the tips	Middle nerve of lemma minutely projecting at tip.	Middle nerve of lemma usually minutely projecting at tip.
Anther length: 0.5-1.0 mm	Anther length: 0.4-0.5 mm	Anther length: 0.6-1.0 mm

When this species flowered for the first time in cultivation, the inflorescences were observed to be different in general form from those remaining from the last flowering season in the wild. The characters of the new inflorescences were similar to those of *P. pseudodistans*. One of these plants was then transferred to a soil-filled earthenware pipe in order to simulate the dry conditions of the habitat, which was usually a dry bank. The base of the pipe was set in a pan of soil and apart from an occasional overhead spray, water was given only through the pan. The panicles produced after transfer to these conditions, especially the later ones, were similar to those on the original collected plant (Fig. 1).

Further cultivation experiments were then prepared to investigate the plasticity of the inflorescence characters. Three clones of each of the three species were used. Three sets of material were planted in four-inch clay pots, and a fourth set was planted in pipes as described above. All were kept in a greenhouse. One pot of each clone was kept in a mist unit; a second was placed on a tray of sand which was permanently moist; a third was placed on an open staging of wooden slats and watered only once a week. The pipes were placed on the open staging; they were watered from above once a week, and the soil in the pans was watered every day. The experiment was set up in March so that the plants would have a full growing season before flowering in late summer.

Plants in the mist unit produced similar results to those which were on the trays of damp sand. The plants which were in pots and watered only once a week showed poor growth, and several died in hotter weather. Plants in the pipes were healthy, though less vigorous than the well-watered plants.



FIGURE 1. The effect of returning a plant of *P. fasciculata* to drought cultivation. The inflorescence on the left was developed when water supply was abundant; the inflorescences in the centre and on the right were formed when water supply was limited. (Drawn from a photograph in Newton 1965).

Differences of cultivation conditions produced little variation in the inflorescence characters of *P. distans*. The four panicle characters given for this species in Table 1 were manifest in all conditions of cultivation. *P. pseudodistans* and *P. fasciculata* were similar to one another in their different response to the different conditions. In drought cultivation all plants of both 'species' produced short unilateral panicles with all branches bearing spikelets down to the base. In wet cultivation they all produced long symmetrical panicles, the longer branches of which were bare at the base. None had branches with swollen bases or becoming deflexed.

MORPHOLOGY OF LEMMAS

Fresh flowers from living plants were dissected and examined under a low power binocular microscope. Floral bracts were flattened for observation by spreading them with needles on strips of transparent cellulose tape. No appreciable difference was observed between flowers at different positions in a spikelet.

Lemmas have rounded apices in *P. distans* and are subacute in the other two

species. The hyaline margin, which is characteristic of all floral bracts in this genus, was much more prominent at the lemma tips in *P. distans* than in the other species (Fig. 2). In *P. distans* the nerves all stopped well short of the tip

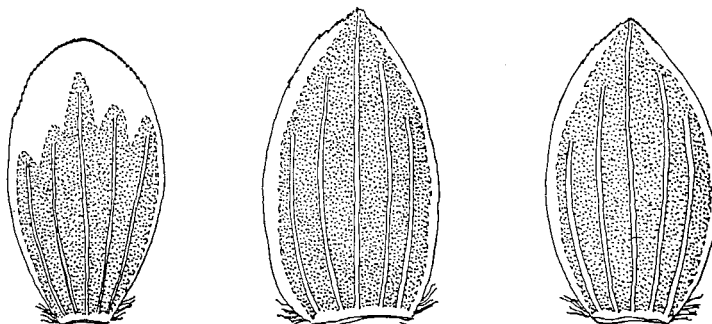


FIGURE 2. Lemmas of *P. distans* (left), and *P. fasciculata* (right) compared with a lemma of *P. pseudodistans* (centre). (The stippled areas are green, the clear areas membranous; all $\times 20$).

of the lemmas, never extending into the hyaline region. In the other species the central nerve always extended to the apex, as did the region of chlorenchyma, but was never observed to be excurrent. In all three species, as also in the other two British species of *Puccinellia*, the tips of all floral bracts were found to be finely denticulate (Fig. 3). This is easily visible with the $\times 40$ power of the binocular microscope but is scarcely visible with a $\times 10$ hand lens. This character appears not to have been reported before. When an unflattened lemma is examined with a hand lens the curled denticulate apex can easily give the impression of being finely mucronate.

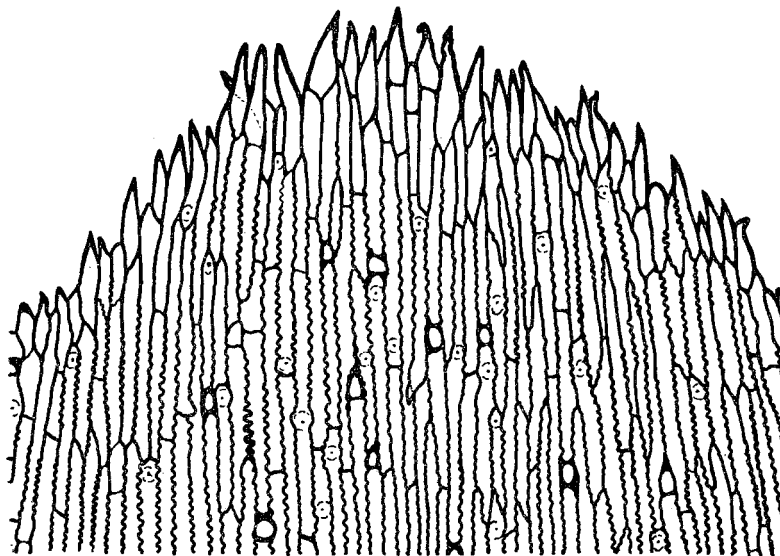


FIGURE 3. Apex of lemma in *P. distans* ($\times 120$). (Drawn from a photograph in Newton, 1965.)

ANTHER SIZE

Lousley's (1936) measurements for *P. pseudodistans* are quoted by Tutin (1962), but he and Hubbard (1954) give different ranges for *P. distans*:

	<i>P. distans</i>	<i>P. pseudodistans</i>	<i>P. fasciculata</i>
Tutin	0.5–0.75 mm	0.4–0.5 mm	0.75–1.0 mm
Hubbard	0.8–1.0 mm	—	0.6–1.0 mm

Anther length was determined from flowers collected in the field and also from flowers produced by plants in the cultivation experiment. In all cases the measurements were made on exerted but undehisced anthers, and were obtained with a low power microscope and camera lucida. The results (Newton 1965) reveal so much overlapping of ranges for the three species as to indicate that anther length is not a reliable diagnostic character for individual plants. Observations upon anthers from plants used in the cultivation experiments indicate that water supply has some effect on anther length (Fig. 4).

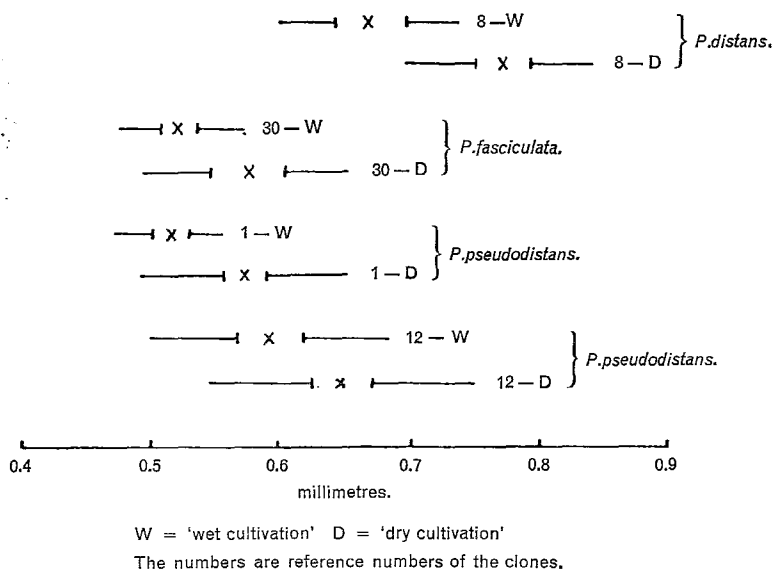


FIGURE 4. Anther length of *P. distans*, *P. fasciculata* and *P. pseudodistans* at the conclusion of the cultivation experiment. (Means, twice SE and ranges are shown).

LEAF EPIDERMIS

In his work on the Greenland species of *Puccinellia*, Sørensen (1953) found that characters of the leaf epidermis were of taxonomic value. He found that if the examination was made at a similar position on each plant, the variability of the characters observed was no greater than that of the floral parts, and he was able to prepare an identification key for the Greenland species based entirely upon the structure of the leaf epidermis. None of the three British species under discussion here occurs in Greenland.

Metcalf (1960) examined only *P. fasciculata* and *P. maritima* in his anatomical survey of the Gramineae. His descriptions for these two species differ in only one character, *viz.* the presence of 'macro-hairs' on *P. fasciculata* and their absence from *P. maritima*.

In a paper concerning the use of epidermal characters in taxonomy, Tutin (1955) compared the leaf epidermis of *P. distans* with that of *P. pseudodistans*, which he had previously regarded as an uncertain taxon. No conclusion is stated in the paper, but differences between the two are described and the text implies that the author regarded these two taxa as distinct species. The principal differences given by Tutin are shown below.

	<i>P. distans</i>	<i>P. pseudodistans</i>
Epidermal cells	Relatively short and broad	Long and narrow
Stoma length	30–35 μm	30–35 μm
Stomatal pit	Somewhat cruciform Broader than long	Oval About twice as broad as long
Stomatal flap	Overlaps guard cells obliquely	Overlaps guard cells symmetrically Longer than in <i>P. distans</i>

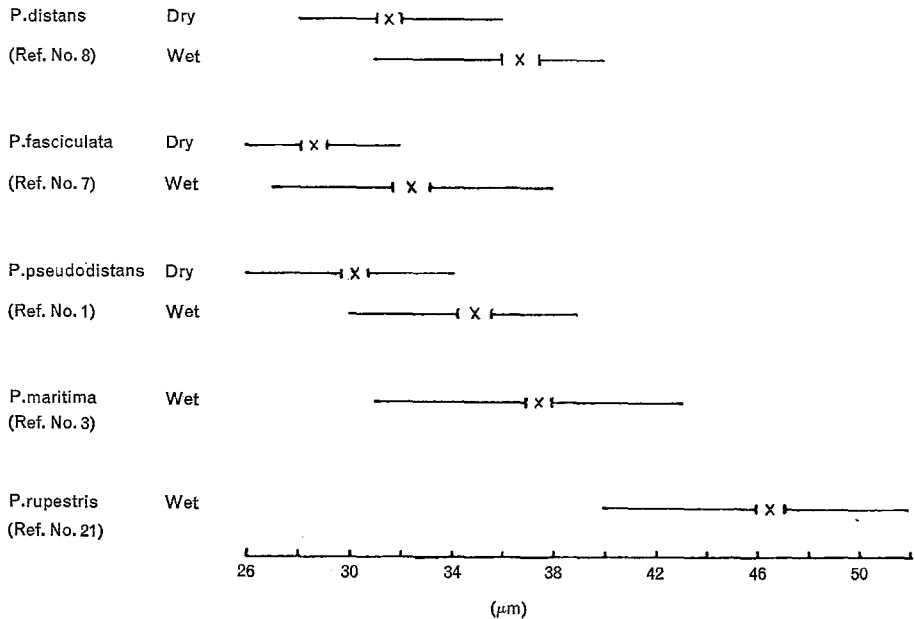


FIGURE 5. Guard cell lengths from culm leaves of *Puccinellia* species in cultivation experiments. (Means, twice SE and ranges are shown).

Observations were made on the uppermost mature culm leaves of plants in the cultivation experiment at least six months after the experiment was set up. The leaves were boiled in ethyl alcohol for a few minutes and then in water. Small portions from the middle of the leaf were mounted in lactophenol for examination.

The size of the 'long-cells' was not found to be a useful diagnostic feature, and it is clear from the literature that it is not reliable. Tutin described the cells of *P. distans* as 'relatively short and broad', whilst Sørensen describes the pidermis of this species as 'narrow-celled'. The ranges of stoma length were found to be

somewhat wider than those given by Tutin, and were of no diagnostic value (Fig. 5). The shape of the stomatal pit varies considerably on any one leaf according to the nature and position of adjacent cells, and it is not always easy to apply the terms 'cruciform' and 'oval' as used by Tutin. The way in which the stomatal flap overlaps the guard cells was not a consistent character. Some distinct differences were observed, however. Papillae were fewer on *P. distans* than on the other two. The cell walls were markedly sinuous on *P. distans*, whereas those of the other two species were only slightly rippled. The cell walls in *P. fasciculata* and *P. pseudodistans* had a conspicuous pitted appearance which was not seen in *P. distans*. These observations support the apparent view of Tutin that *P. pseudodistans* and *P. distans* are morphologically distinct, but go further in showing a similarity between *P. pseudodistans* and *P. fasciculata*.

TABLE 2. NEW CHROMOSOME COUNTS ON NATIVE BRITISH
PUCCINELLIA SPECIES.

Species	Origin	Somatic chromosome number
<i>P. distans</i>	N. of Leysdown, Kent	$2n = 42$
	Swalecliffe, Kent	$2n = 42$
	Reculver, Kent	$2n = 42$
	Jaywick, Essex	$2n = 42$
<i>P. fasciculata</i>	Allhallows, Kent	$2n = 28$
	Grain, Kent	$2n = 28$
	Shellness, Kent	$2n = 28$
	Wakering Stairs, Essex	$2n = 28$
	Jaywick, Essex	$2n = 28$
<i>P. pseudodistans</i>	Erith Marshes, Kent	$2n = 28$
	Shellness, Kent	$2n = 28$
	Wakering Stairs, Essex	$2n = 28$
	Jaywick, Essex	$2n = 28$
	Between Burnham-on-Crouch and Creeksea, Essex	$2n = 28$
<i>P. rupestris</i>	Swalecliffe, Kent	$2n = 42$
	Reculver, Kent	$2n = 42$

CYTOLOGY

Previous chromosome counts for British material of these species are as follows:

<i>P. distans</i>	$2n = 42$	Lovis, in Tutin, 1955.
<i>P. fasciculata</i>	$2n = 28$	Rutland, 1941.
<i>P. pseudodistans</i>	$2n = 28$	Lovis, in Tutin, 1955.

Root tips from plants used in the present study were given a pretreatment in a 0.002 M solution of 8-hydroxyquinoline for three hours at 10°C, fixed for one hour in 45 per cent. acetic acid, hydrolysed for 8 minutes in N/1 HCl at 60°C., stained in leucobasic fuchsin, and squashed in acetic carmine. The results are given in Table 2. In all cases the counts obtained confirmed the earlier counts quoted above.

FLORAL BIOLOGY AND HYBRIDISATION

Most Puccinellias begin to flower in June, but the main flowering period is July–August. Flowers on the plants in cultivation began to open at about 5.30 a.m. Anthers and stigmas started to emerge within an hour, and dehiscence of the anthers was completed in most cases by about 8 a.m.

In *P. distans* the anthers protrude prominently in the manner expected of an anemophilous plant. In the other two species, however, the anthers were hardly clear of the lemma and palea when dehiscence occurred. Stigmas protrude at the same time as the anthers and it seems most likely that self-pollination occurs in these cases, with the pollen dropping on to the stigmas of the same floret or other florets in the same spikelet. Bagged inflorescences on each species produced abundant seeds which germinated freely soon afterwards. Several flowers on each species were emasculated immediately before anthesis and bagged; none of these set seed.

Several plants were collected from wild populations as possible interspecific hybrids because they were not easily determined on inflorescence characters. At one locality (Jaywick, Essex), plants answering the descriptions of all three species were found growing together in a small area, with some plants whose characters were somewhat intermediate. All these plants were found to have a pollen fertility of over 80 per cent. Those readily determined as *P. distans* had a chromosome number of $2n = 42$; all other plants in this collection were $2n = 28$.

ECOLOGY AND DISTRIBUTION

The Puccinellias are generally referred to in British literature as salt-marsh plants, and they are listed under 'Salt-marshes and Coastal mud flats' in Hubbard's habitat lists (1954). Early field excursions in search of material soon showed that this habitat description is misleading. Only *P. maritima* was found on inter-tidal salt-marshes; the other species were always found well above high water level.

P. distans and *P. pseudodistans* occur mostly in wet, muddy situations. In contrast, *P. fasciculata* is found in dry places, as also is *P. rupestris* (Jones & Newton 1965). Analysis of soil and mud samples from some localities showed that *P. distans* and *P. pseudodistans* occur in poorly drained soils and *P. fasciculata* grows in well drained soils. All are salt tolerant, but none is an obligate halophyte as all survived with fresh water cultivation for up to three years. Seeds germinated readily when supplied only with fresh water. It is interesting to note that at the locality where all three species were found together, referred to in the previous section, *P. distans* and *P. pseudodistans* were in silty soils in the drip-zone of rain water from the top of a wall against which they grew, whilst the *P. fasciculata* plants were growing in sandy shingle in a drier situation further from the wall.

These plants were never found to be dominant in a mixed community, and usually there was little or no competition from other plants. Results of a competition experiment with the eminently successful weed *Poa annua*, in which plants were grown together in pans, suggest that these species cannot withstand competition. Field observations on collecting excursions suggest that they appear mainly as pioneer plants on disturbed ground, succumbing later when other plants invade the area. Coastal erosion, common in

south-east England where these species are mostly found, and human activity would provide the temporary habitats in which these relatively uncommon species are able to grow.

DISCUSSION

Although *P. pseudodistans* is described in literature as intermediate between *P. distans* and *P. fasciculata*, when they are encountered in the field all three taxa normally present no difficulties in identification. They are readily determined on the basis of inflorescence form alone, and all the character differences for the panicle given in Table 1 were found to be reliably diagnostic.

P. distans and *P. pseudodistans* are similar in their habitat preference, and the panicle differences were still evident on plants in varying conditions of the cultivation experiment, in spite of the greater plasticity of *P. pseudodistans*. A detailed comparison (Newton 1965) showed that the two taxa are cytologically and morphologically distinct.

As well as having distinctive panicle forms, *P. fasciculata* and *P. pseudodistans* normally occur in different habitat conditions. In morphological characters other than the panicle form, however, they were found to be remarkably similar. In the cultivation experiments the two panicle forms were shown to be extremes of a phenotypic plasticity which was parallel in the two taxa. The plasticity was induced by variation in water supply, and characters appearing in the cultivation experiment corresponded to those found in similar water supply conditions in habitat. When grown in similar cultivation conditions the two taxa could not be distinguished. This leads to the conclusion that the two taxa as found in the field represent environmentally induced phenotypes of one species.

Continental material has not been investigated extensively, but some plants collected by one of us (L.E.N.) as *P. pseudodistans* on the Mediterranean coast showed a similar response to the cultivation experiment as that described for the British material. It seems likely, therefore, that Continental plants corresponding to Crépin's original material will be found to have the same status as the British material.

The small size of the anthers in *P. fasciculata* and *P. pseudodistans* might account for reports of sterile plants being found. There are two main reasons why a particular plant may have smaller anthers than in related species, *viz.* pollen abortion, often an indication of hybridity, and the occurrence of regular self-pollination. Both in cultivated plants and in plants sampled in the field there was no indication that small anthers were associated with reduction in fertility. Whilst both Hubbard (1954) and Tutin (1962) say that sterile plants occur in the wild, neither states how it was determined that the plants were sterile. Herbarium specimens in BM labelled as hybrids and having small anthers were found to have no indication of pollen sterility. Use of small anther size as an index of pollen sterility is clearly misleading.

That self-pollination may account for the small anthers is suggested by other observations. It was noted earlier that at anthesis the anthers protrude very little from between the bracts and are not well exposed for wind-pollination. Both taxa are described in literature as perennial, and they lived for three years in cultivation. In the wild, however, they often behave as annuals; dead plants were frequently found at the end of the flowering season, mainly in places where the substrate had dried out. It is known that annual plants in north temperate

regions are almost exclusively self-pollinated (Stebbins, 1960). It was found that the *Puccinellias* (except *P. maritima*) are confined to situations where disturbance creates a fresh substrate whose salinity inhibits rapid colonisation by other plants. Self-pollination is probably a selective adaptation for survival in this unstable ecological niche.

TAXONOMIC CONCLUSIONS

It is concluded that *P. pseudodistans* and *P. fasciculata* are ecads of one species. However, as they appear in the field and herbarium as strikingly different phenotypes with few intermediates, it seems useful to distinguish between them at the level of *forma*. The nomenclature of the taxa investigated is as follows:

PUCCELINELLIA DISTANS (L.) Parl., Fl. Ital., **1**: 367 (1848).

Poa distans L., Mant., **1**: 32 (1767).

Glyceria distans (L.) Wahlenb., Fl. Upsal: 36 (1820).

Sclerochloa distans (L.) Bab., Man. Brit.: **1**, 370 (1843).

PUCCELINELLIA FASCICULATA (Torr.) Bickn., Bull. Torr. Bot. Club, **35**: 197 (1908).

forma FASCICULATA

Poa fasciculata Torr., Fl. N. Am.: 107 (1824).

Glyceria borreri Bab., Suppl. Engl. Bot., t.: 2797 (1837).

forma pseudodistans (Crép.) Newton & Jones, **comb. nov.**

Glyceria pseudodistans Crép., Nouv. Rem. Glyceria Gr. Heleochloa, **15** (1865).

Puccinellia pseudodistans (Crép.) Jans. et Wacht., Nedl. Kruidk. Archief.: **14**: 10 (1935).

Voucher specimens of material used in this investigation have been lodged with the British Museum (Natural History) (**BM**).

This work forms part of the material submitted by L. E. Newton for the degree of M.Sc. in the University of London.

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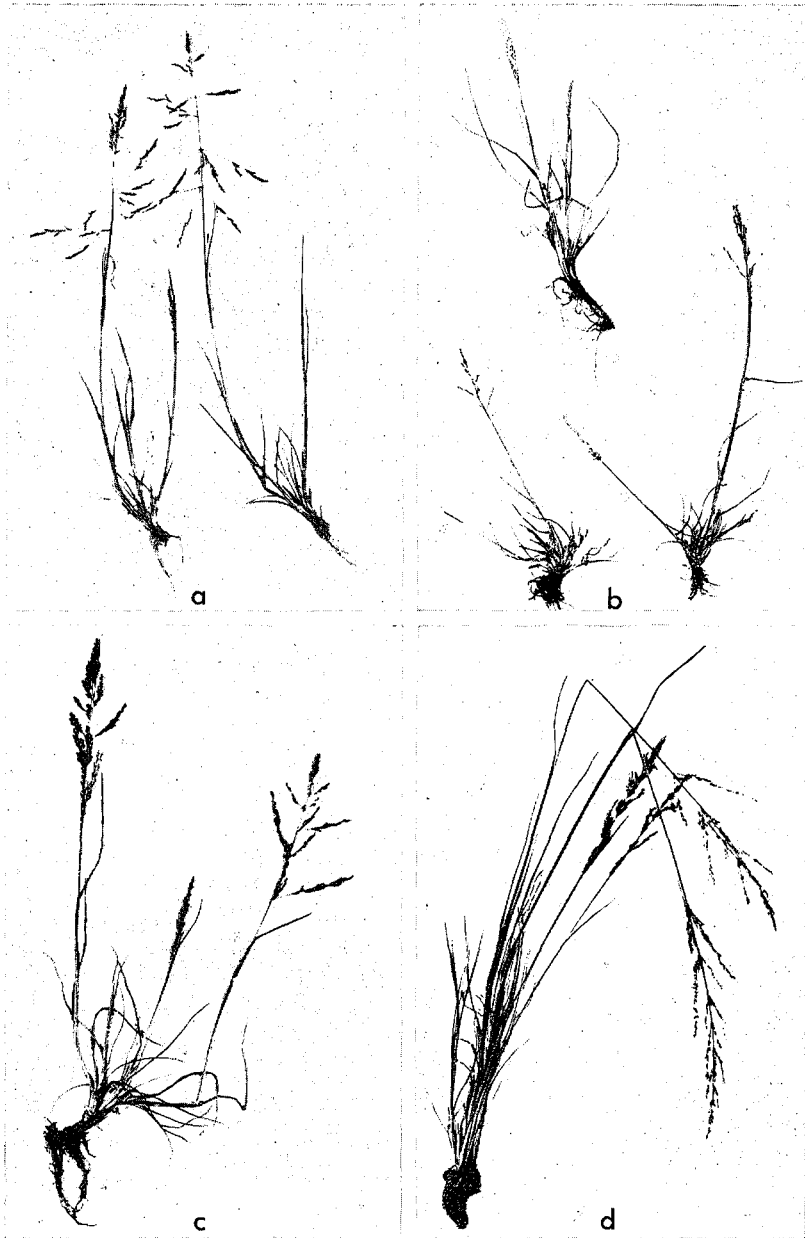


PLATE 1. Herbarium specimens of *Puccinellia*

- a. *P. distans*: Swalecliffe, Kent. Wet flush on the side of the sea-wall. $2n = 42$ (L. E. Newton No. 53).
- b. *P. fasciculata*: Grain, Kent. Dry ground on sea-wall. $2n = 28$ (L. E. Newton No. 43).
- c. *P. pseudodistans*: Erith marshes, Kent. Muddy waste-heaps by roadside. $2n = 28$ (L. E. Newton No. 36).
- d. *P. pseudodistans*: Jaywick, Essex. Mud at side of lane behind sea-wall. (L. E. Newton No. 58)