# A CONTRIBUTION TO THE EXPERIMENTAL TAXONOMY OF POA ANNUA L.

# By T. G. TUTIN University of Leicester

#### INTRODUCTION

Poa annua is a grass which is all too familiar to most people. It is more abundant in the neighbourhood of habitations than anywhere else, being one of the commonest of garden weeds and forming the bulk of vegetation of suburban pavements. It also occurs in places less modified by man, though, as it is essentially a plant of open habitats, it is rather restricted and is practically absent from closed communities. Within these limitations it occupies a great variety of habitats, with the notable exception of saltmarshes. It can be found on stabilised dunes, in open turf on cliffs or near rock outcrops, at the margins of ponds and streams on bare mud or even in shallow water, and on the summits of mountains.

As is to be expected in a species capable of growing in such a diversity of habitats, a very considerable degree of variability is to be found and a number of varieties have been described (see, for example, Hegi, 1935, and Jansen, 1951). The nature of this variation has been investigated in four instances, and the first part of the present paper is concerned with this; in the second part the relationship between *P. annua* and two other species of *Poa* is considered.

#### INTRASPECIFIC VARIATION

The material used consisted of four stocks, three obtained from a garden in Leicester and the fourth from a somewhat moist depression in a sand-dune near Horsey in E. Norfolk. In the cultivation and hybridisation experiments all the plants of each stock used were grown from seed from a single parent plant.

The four stocks will be referred to as A, B, C and D and their chief distinguishing features are as follows :

A. Tufted, clear green. Leaves rather stiff, erect, 2-3 mm. wide. Stems erect or ascending, averaging about 15 cm. long. Longer panicle branches 2-3 cm. long; spikelets appressed to the rhachis, mostly with 4 florets, rarely with 3. Lowest lemma 2.7-3 mm. long with the mode at 3 mm. The most abundant form as a garden weed and in streets. This plant seems to correspond to var. *annua* (var. *typica* Beck). Plate 1 and Fig. 1, C.

B. Clear green. Stems creeping and rooting at the nodes then ascending, 20-30 cm. long. Leaves rather soft and drooping, 3-4 mm. wide. Panicle branches divaricate, longer ones 1.5-2.5 cm. long; spikelets spreading at a wide angle to the rhachis, with 4-5 florets. Lowest lemma 2.5-2.8 mm. long with the mode at 2.6 mm. Less common than A and found particularly on damp clayey soils and in wet places on mountains. ? var. *reptans* Hausskn. Plate 1.

C. Small tufts. Leaves dark green with purplish sheaths, rather stiff, 1.5-2 mm. wide. Stems spreading to ascending, about 5 cm., rarely up to 10 cm. long. Longer panicle branches 0.7-1 cm. long; spikelets purplish, slightly spreading, with 2-4 florets, Lowest lemma 2-2.4 mm. long with the mode at 2.3 mm. Rather uncommon, on firm dry soils. Plate 2.

D. Large very dwarf tufts. Leaves deep green, stiff, very short (1 cm. or less) and about 1 mm. wide. Stems geniculate, spreading to ascending, 3-7 cm. long, slender. Longer panicle branches 3-5 cm.; spikelets purplish, appressed to the rhachis, with 1-2, rarely 3 florets. Lowest lemma  $1\cdot8-2\cdot2$  mm. long with the mode at 2 mm. Moist places behind dunes. Plate 2 and Fig. 1, D.

The measurements given above are for average plants growing in good illumination on reasonably moist soils. There is, of course, considerable phenotypic variation which does not, however, obscure the differences between these 'races.' In shade the plants are taller with thinner leaves and long, often nodding panicles with few spikelets; the purplish colour of C is much reduced, sometimes the nodes alone showing it, but the leaves remain darker green than in A or B. In dry places or on poor soils A and C are both dwarfed, but the differences between them are, if anything, emphasised; B has not been found in such places.

A, B and C have been kept under observation for six years in the garden in which they grow as weeds. During this time they have remained distinct and no intermediates between them have been noticed. B and C are almost restricted to the same fairly small areas where they were first noticed six years ago, B in somewhat shady places with a very sticky always damp soil and C usually in full exposure on a heavy but well-drained soil. A is widespread and occurs, though not abundantly, in the habitats occupied by B and C; it can always be readily distinguished from them, and indeed the contrast between it and the dwarf purplish plants of C is very striking. These observations suggest that the differences between these ' races' are genotypic rather than phenotypic, and that cross-pollination rarely if ever occurs.

A study of anthesis in *P. annua* led Hackel (1904) to the conclusion that crosspollination as well as self-pollination occurred. Since this conclusion is not supported by the evidence given above it seemed advisable to re-examine the process of pollination. Hackel's observations were confirmed and somewhat extended but, as will be seen, another interpretation of what happens is possible and appears to be more likely.

In *P. annua*, anthesis starts from the top of the panicle and proceeds downwards, and the same order is followed in the individual spikelets. The uppermost floret or, in the larger spikelets, the two upper florets, are always female, the remainder being hermaphrodite. The female florets open in the early morning and, apparently regularly, remain partially open with protruding stigmas during the following day. On the succeeding morning they again open widely and, according to Hackel, this may in exceptional circumstances be repeated for three or four days.

The behaviour of the hermaphrodite florets varies a certain amount in detail with variations in humidity and temperature but the following example makes the main points clear.

Two plants were observed in detail, one (E) in a pot, which was brought indoors at 5.45 A.M., G.M.T. and the other (F) in the open ground. The morning was a misty one in late August when there was a heavy dew.

At 5.45 all the florets, except a few female ones, were tightly closed, but by 6.10 the lemmas and paleas of F had started to separate and one panicle was cut and brought indoors (G). Five minutes later the stamens of G had elongated so that they were slightly shorter than the lemmas and stiffly erect. (The anthers remain erect on the rigid filaments until the latter begin to wither.) The stigmas emerged, spreading nearly horizontally. At 6.25 the anthers of G started to dehisce from the top downwards and were then slightly above the top of the lemma. The rather sparse pollen fell on to the stigmas and lemmas, though some grains remained in the anthers. The anthers of the upper hermaphrodite florets were about on a level with the stigmas of the female florets which were pollinated

by them. At 6.28 dehiscence was complete, and by 6.40 the filaments were withering. Meanwhile, by 6.20, E had begun to open and five minutes later the filaments were elongating, dehiscence following at 7.9.

Out of doors things moved more slowly, though between 6.30 and 6.35 a large number of plants, mostly of race A but including some examples of races B and C were seen to have fully elongated stamens. Dehiscence of the anthers in F and other plants in the open ground did not occur until about 7.30, when the sun broke through the mist. This delay of  $1\frac{1}{4}$  hours between the extension of the filaments and the dehiscence of the anthers was unusually long, presumably because of the very high humidity. The hermaphrodite florets and the female ones, which had opened on the previous day, again closed gradually between 9.00 and 11.00. On wet days the anthers split but do not open wide; they, and the pollen, are beaten on to the top of the lemma, to which they stick, and pollen is washed in abundance on to the stigmas. In winter, cleistogamy is of frequent occurrence.

The features of anthesis in P. annua which would appear to favour self-pollination are :—

- 1. The flowers are homogamous (protandry appears to prevail in the majority of chasmogamous grasses).
- 2. The anthers are small (0.6-0.8 mm.) and are not versatile.
- 3. The filaments are rigid, until after most of the pollen is shed.
- 4. The amount of pollen is relatively small for a wind-pollinated plant (c. 800-1,000 grains per anther compared with something of the order of 10,000 per anther in *Brachypodium sylvaticum*) and the grains rather large (c. 32  $\mu$  in diameter).
- 5. The pollen is liberated not far from ground level and much of that which is not caught on the spikelets appears soon to reach the ground.
- 6. The pollen is shed very rapidly and almost simultaneously by all the plants in one area, so, even if some grains are carried about in the wind, the concentration of 'own' pollen must be very much greater than that of strange pollen.
- 7. In addition to the overlap between the anthers and stigmas of different florets in the same spikelet, neighbouring spikelets are often very close to each other at anthesis.

Even if self-pollination occasionally fails, the chance of true outbreeding, in the sense of crossing between different 'races', seems to be remote. This is because *P. annua* usually grows in patches, all the plants in which are most commonly the progeny of one parent plant which is likely to have been selfed.

As a further test for the view that selfing is the rule, the stigmas of 25 female florets from panicles in which no hermaphrodite florets had opened were examined. These florets were collected in the afternoon and were all ones which had already opened and from which the stigmas could be seen protruding. Not a single pollen grain was found on any of these stigmas, though a considerable amount of pollen must have been liberated the same morning from other panicles on the same plants and from other plants near at hand.

For comparison, stigmas from hermaphrodite florets, which had opened, were examined and on most of them 10–15 pollen grains were found, though, in one instance, there were as many as 38 grains. Thus, although the possibility of occasional crossing cannot be ruled out, it is evidently extremely rare.

One plant of each of races A, B and D was potted and put in a cold greenhouse. Panicles of each plant were covered before anthesis with bags of translucent paper which were folded round the culms and held securely in position by paper-clips until the seed was ripe.

A full set of good seed was obtained from all the covered panicles and samples were sown in sterilised soil on 12 June, 1952. A germinated in 10 days, B four days later and D seven days later. As soon as the seedlings were large enough to handle, 50 of each family, taken at random, were potted up in sterilised soil and the rest were discarded<sup>-</sup> The progeny of each plant was remarkably uniform and reproduced the characters of the parents, though there was a slight increase in size in 'race' D, presumably owing to the richness of the soil compared with that in the dune habitat of the parent.

This strongly supports the evidence from field observations that self-pollination is the rule and that the plants are therefore practically homozygous.

The differences between the rates of development of the 'races' were even greater than the differences between their speed of germination. By 30 August, i.e. 50 days after sowing, 92 per cent of the plants of race A were in full flower and were about 15 cm. high, while none of the plants of races B and D were showing any signs of flowering. The shoots of B were already spreading and rooting at the lower nodes and the plants were under 10 cm. high, while D was tufted and not more than 5 cm. high. Forty-five days later A had ripened one crop of seed but was still flowering sparsely. B was flowering, though the great majority of shoots was still in the vegetative state and most of the spikelets on the rather small, few-flowered panicles were viviparous. D was still entirely in the vegetative state and did not flower until early in the following summer, about eleven months after sowing. By this time the plants of A were dead. It is not possible to give an exact figure for the life-span of these different ' races,' since there is considerable variation between individuals in this respect, as well as variation with conditions. It is safe to say, however, that A and C only exceptionally live for as much as a year and normally have 2-3 generations in one year (Hackel, 1904), that B lives for at least 2 years and D for 3 years or more. There thus seems to be a correlation between the speed of germination, the time taken to arrive at reproductive maturity and the total length of life of the plant.

There are a number of other 'races' which almost certainly represent distinct genotypes, but which have not so far been investigated experimentally. Among these, two seem particularly well characterised by morphology and habitat; the shallow water form, var. *aquatica* Aschers., and the form found on the higher mountains.

The former grows up to 30 cm. or more high, with soft leaves, up to 4 mm. wide, which sometimes float on the water, when the whole plant rather resembles *Catabrosa aquatica*. The tufts are loose, with the stems spreading out at the base but not rooting at the nodes. The panicles are up to 7 cm. long and the longer branches up to 3 cm. The spikelets mostly have 4 florets and the lowest lemma is about 3 mm. long.

The mountain form occurs rather infrequently on stony slopes and damp rock ledges above 3,000 ft. in Scotland; along tracks and in the neighbourhood of cairns, dwarf specimens of var. *annua*, presumably introduced by man or sheep from lower levels, may also be found. The true mountain 'race' is tufted, with short broad leaves, rarely more than 1.5 cm. long but up to 3 mm. wide and often folded; the culms are stiffly erect and under 10 cm. high. One of the most characteristic features is the rather stout stem-bases with their covering of whitish, more or less coriaceous leaf-sheaths, somewhat reminiscent of *Poa alpina* on a small scale. The panicle is also characteristic, being short (usually 2 cm. long or less), dense, and having ascending or sometimes almost horizontal branches. The longest branches are 1 cm., or slightly more, with the rather broad brownish spikelets, each with 3–4 florets, densely clustered on them. The lemmas are broadly ovate with exceptionally prominent nerves, and the lowest is 2.6-2.9 mm. long. This race has the appearance of being perennial, but there is so far no certain information about this.

It has been suggested that perennation in P. annua is the result of a mycorrhizal



P. annua 'race' A.  $c. \times \frac{1}{2}$  (top). P. annua 'race' B.  $c. \times \frac{1}{2}$  (bottom).





P. supina. c.  $\times$  1 (top). P. annua  $\times$  supina. c.  $\times \frac{1}{2}$  (bottom).



PLATE 4.

infection. The breeding experiments with race B do not support this view, nor was Professor N. A. Burges able to find any fungus in the roots of this race.

It is thus evident that within Poa annua there are a number of infra-specific taxa differing both morphologically and in habitat and remaining distinct, probably owing to regular self-pollination. All the 'races' investigated are tetraploid with 2n = 28, and are interfertile if artificially crossed. The situation is thus rather similar to that found in other, mainly autogamous, species such as Senecio vulgaris, Capsella bursa-pastoris and the Bromus mollis aggregate. These species are, however, all essentially weeds of cultivated ground and have a far smaller range of habitats, though Senecio vulgaris, for instance, does occur among natural vegetation on stabilised dunes. In their diversity of habitat and degree of morphological differentiation, the 'races' of P. annua perhaps resemble more closely the microspecies of an apomictic aggregate and if, as appears likely, we are dealing with a number of homozygous entities there is, in fact, little practical difference between autogamy and apomixis. The rank of such entities in the taxonomic hierarchy is perhaps best left for future consideration. If, however, subspecies are defined as taxa which differ from one another in minor morphological characters, and in ecology or in distribution, but which are potentially, though not normally, completely interfertile, then subspecies would seem to be the appropriate category in which to place these taxa which have for convenience been referred to as 'races.'

In the classification of the experimental taxonomist they would seem to fall into the category of ecotypes.

#### The Relationships of Poa annua\*

P. annua belongs to the rather small section Ochlopoa Aschers. & Graebn. (Annuae Fr., Obsoletae Rouy, Vagantes Döll) with six known species in Europe and N. Africa, all of which are rather similar morphologically. The chromosome number of P. annua has been determined by a number of workers (Stählin, Avdulov, and Kattermann, quoted in Nannfeldt, 1937; Litardière, 1938); the remaining species have been counted by Nannfeldt and counts have also been made on the material used in the present investigation; no deviations from the numbers given have been found. There are two diploid species with 2n = 14, P. infirma Kunth (P. exilis (Tomm.) Murb.) and P. supina Schrader, the remaining four species, P. annua L., P. dimorphantha Murbeck, P. maroccana Nannfeldt and P. rivulorum Maire & Trabut, being tetraploids with 2n = 28. An account of these species and a key for distinguishing them is given by Nannfeldt (1938) The last three tetraploids appear to be confined to N.W. Africa where they are rather local. Morphologically, and apparently genetically, P. dimorphantha is an isolated species, while P. maroccana resembles the diploid P. infirma and P. rivulorum is similar to P. supina; P. maroccana gives a sterile hybrid with P. annua (Nannfeldt, 1938).

*P. annua* itself is as nearly cosmopolitan as any phanerogam is, occurring throughout the north and south temperate regions even on small and isolated islands such as the Azores, and in the tropics on mountains and in the neighbourhood of towns. It is also to be found near dwellings within the Arctic Circle, and, at the other extreme, in Tierra del Fuego.

*P. infirma* (Plate 2 and fig. 1 A) occurs throughout much of the Mediterranean region and extends up the west coast of Europe to the Channel Islands, Scilly Islands and the Lizard peninsula in S.W. Cornwall. It is also found in S. America, where it has no doubt been introduced from Spain.

P. supina (Plate 3 and fig. 1 B), in contrast to the other diploid, occurs in Central and

\* A brief summary of this section has already been published (Tutin, 1954).

Northern Europe and mainly in mountainous regions. It extends roughly from Spain to the Carpathians and north to Sweden, Poland and Siberia and is also reported from Abyssinia. Its exact distribution is somewhat uncertain as it has sometimes been confused with *P. annua* var. ? reptans.

As Nannfeldt (1937) has pointed out, *Poa annua*, though very variable, is in many respects intermediate between the two diploid species, though it has a far greater 'ecological amplitude' than either. The following table (modified from Nannfeldt) provides a comparison between the three species.



Fig. 1. Spikelets of *Poa* (from left to right) : A - P. *infirma* (Channel Is.); B - P. *supina* (Switzerland); C - P. *annua* var. *annua* (Leicester); D - P. *annua* var. (Horsey); E ? P. *infirma* × *supina* (4n); F - P. *annua* × *infirma* (3n); G - P. *annua* × *supina* (3n). All × 5.

Character	P. infirma	P. annua	P. supina
Colour of plant	Pale yellow-green	Variable	Dark green and purplish
Panicle	Rather narrowly oblong, 1.5-3 times as long as broad; spikelets along whole length of branches	Oblong-triangular, $1.2-$ 1.6 times as long as broad; spikelets $\pm$ uniformly spread along branches	Triangular, about as long as broad; spikelets clus- tered at end of branches
Panicle branches	Always ascending	Lower horizontal or de- flexed after flowering	All but uppermost hori- zontal or deflexed
Spikelets	Nearly always devoid of anthocyanin	Variable but usually with some anthocyanin	Nearly always dark purple
Florets	Widely separated; upper- most slightly longer than pedicel, hermaphrodite	Less distant; uppermost twice as long as pedicel, female	Close together; upper- most 5–6 times as long as pedicel, female
Nerves of lemma	All with dense appressed hairs	Hairiness variable, some- times glabrous	Glabrous, except for keel and margins
Anthers	0·22–0·4 mm. long	0.6–0.8 (–1.0) mm. long	1.6-2.0 (-2.5) mm. long
Dia. of pollen grains	c. 28.5 µ	c. $31.5 \mu$	c. 28.8 µ
Duration	Ephemeral	Ephemeral, annual or short- lived perennial	Perennial
Flowering times	March–April (in Britain)	January–December	Early summer

TABLE 1.

It therefore seems likely on morphological grounds that P. annua is an allotetraploid derived from the hybrid P. infirma  $\times$  supina.

That a relationship exists between P. annua and P. supina is shown by the occurrence of a hybrid between them, first recognised by Nannfeldt (1935), who showed it to be, as expected, a sterile triploid. In an attempt to obtain further evidence about the possible hybrid origin of P. annua, he investigated the idiograms of the hybrid and its parents, and of P. infirma, but found that analysis of somatic metaphase in the triploid and tetraploid was almost impossible. Attempts to obtain the hybrid P. infirma  $\times$  supina by open pollination of the former in early anthesis by the latter were also unsuccessful.

7

In April 1949, a supply of seed of P. infirma was collected from St. Brelade's Bay, Jersey, where the plant is abundant in short turf near the sea. Some of this seed was sown in the early summer of 1949, but did not germinate till autumn. A further sample was sown early in the spring of 1950 and germinated rapidly in a slightly warmed greenhouse. These two lots of *P. infirma* flowered in March-April and May-June respectively. The second lot was used for hybridising with P. annua. Two plants of this, taken from race A (see Plate 3) were used. On these approximately 60 florets were emasculated, using a binocular dissecting microscope and a magnification of  $\times 8.75$ ; the remaining spikelets were cut off, the plants repotted and the emasculated panicles covered. The plants were kept in a cold greenhouse, carefully weeded for other P. annua plants, and were pollinated daily for a fortnight with P. infirma pollen. Four seeds were obtained and these were sown in June, as soon as ripe, in sterilised soil; two germinated rapidly and reached maturity. One of these proved to be P. annua, presumably resulting from a failure to remove all the anthers completely, but the other was sterile with 2n = 21and was evidently the hybrid.

The following description of the hybrid was made on 1 August, when it had been flowering for about a fortnight.

*P. annua*  $\times$  *infirma* (Plate 4). Plant *c.* 15 cm. high. Leaves *c.* 2 mm. wide, tapering gradually to an acuminate apex, rather bluish green and firmer in texture than *P. infirma*, mostly smooth but a few with transverse wrinkles as in *P. annua*. Panicles up to 5 cm. long, lower branches spreading at about 70° in flower, later ascending at 20–30°. Uppermost floret about twice as long as its pedicel. Lemmas purplish at tip, silky on the nerves. Anthers 0.7 mm long, not dehiscing but remaining for some time projecting prominently from the florets, Pollen abortive. Spikelets (fig. 1 F) almost completely sterile, one inviable fruit being found, and therefore withering, but not breaking up, when old.

As previously reported briefly (Tutin, 1952), meiosis in the pollen mother cells of this hybrid showed seven bivalents and seven univalents. This indicated a high degree of homology between the chromosomes of P. infirma and one genome of the tetraploid P. annua.

In August 1951 a plant of *P. supina* was obtained, through the kindness of the late Dr. Walo Koch, from Alp Trida near Samaun, Graubünden, Switzerland. This, *P. annua* and *P. infirma* were all in flower in a greenhouse by 12 April 1952. On that date 100 florets of *P. supina* were emasculated, the large anthers making this a relatively easy operation. The panicles were covered and later pollinated from plants of *P. infirma* grown from seed sent by Mr. J. E. Raven from Porthloo, St. Mary's, Scilly Islands, in March 1950. The following day 78 florets of ' race ' A, *P. annua* were emasculated, covered and subsequently pollinated from the plant of *P. supina*. The seed from these 78 florets was sown in sterilised soil and 31 plants were obtained, one of which soon died. Of the remainder, 28 plants proved to be the hybrid described by Nannfeldt (Plate 3, and fig. 1 G), and two were *P. annua*, the result presumably of accidental selfing. Meiosis in the hybrids was examined and again seven bivalents and seven univalents were found.

From the cross, P. infirma  $\times$  supina, seven seeds were obtained. These were sown in sterilised soil in June and three germinated in a fortnight. The seedlings grew very slowly for a time, but after about six weeks the growth of two of them became more rapid and one of these flowered at the end of August and the other early in October. Both these plants were found to be tetraploid and were morphologically rather similar to P. annua, though they did not match exactly with any local 'race' of that species (Plate 4 and fig. 1 E).

Mr. C. E. Hubbard, to whom a specimen was submitted without any information about its possible origin, comments as follows : "The lemmas differ from those of

typical *Poa annua* L. in being perfectly glabrous; there is no sign of hairs – not even of minute outgrowths on the keel ( $\times$  50). The keels of the paleas are also only very slightly and obscurely ciliate about the middle third, the hairs being few and  $\pm$  appressed. The anthers are 0.8–1 mm. long. Your specimen is very similar indeed to material from England which I have included under *Poa annua* L. (sensu lato). It matches specimens from several places, including some from the allotments behind the Herbarium here."

The meiosis of the majority of pollen mother cells examined was normal, but in a few cases a single quadrivalent was observed. About 12% of the seed produced by these plants was obviously shrunken and bad. A hundred apparently sound seeds from one and 250 from the other were sown in sterilised soil and of these 35% and 43.2% respectively germinated. After two further generations no shrunken seed was produced and germination had risen to between 95% and 100%, being mostly 98-99%. The third seedling continued to grow slowly and eventually proved to be *P. supina*, the result of accidental selfing.

It is unfortunately not possible to be absolutely certain of the mode of origin of the tetraploid plants, as no determination of the chromosome number was made in the early stages. This was not done because it seemed undesirable to disturb the very small seedlings, and also because it was anticipated that if they were of hybrid origin they would prove to be diploid. If this had been so, it had been intended to try the effect of colchicine on some of the growing points.

The possibility of their origin from stray seed must be considered. This seems highly unlikely for a number of reasons. Sterilised soil and clean pots were used throughout, and the greenhouse was kept free from wild *P. annua*. If seed had blown in, the chances of a single seed arriving in each of two pots at about the time the supposed hybrid seed was sown, and then of no more chance seeds arriving during the next four months, are very small. Further, the plants obtained did not match exactly with wild *P. annua* in the neighbourhood, showed occasional abnormalities at meiosis, and the seed from them had less than half the normal germination-rate of *P. annua*.

The most likely hypothesis that can be put forward is that the seedlings were at first diploid and grew very slowly until chromosome doubling occurred, when the tetraploid cells displayed the vigour which often characterises polyploids, and started to grow at a more normal rate.

There are thus a number of different pieces of evidence, none absolutely conclusive in itself, which taken together make it practically certain that *Poa annua* is an allotetraploid derived from the hybrid between *P. infirma* and *P. supina*.

Litardière (1939) favours the view that P. annua "dérive d'une mutation du subsp. exilis (i.e. P. infirma) occasionée par une duplicature chromosomique." This hypothesis seems unlikely, since an autotetraploid would probably show quadrivalents at meiosis. The chromosome pairing in the hybrid, P. annua  $\times$  supina, and the intermediate morphology and increased variability of P. annua all favour an allotetraploid origin.

In support of the autotetraploid hypothesis, Litardière (l.c.) points out that the two diploid species do not at present appear to overlap in their distributions and also differ fairly widely in their habitat preferences. It is not, however, difficult to imagine conditions under which they might have come in contact. During the Quaternary glaciations, *P. supina* would presumably have been driven down to low altitudes on the northern shores of the Mediterranean, particularly in places where mountains occur not far from the coast. During one of the warmer interglacials, or perhaps at the end of the last glaciation, when the ice was melting rapidly and quite high temperatures were probably attained in summer not far from the ice edge, *P. infirma* might well have spread rapidly into freshly available habitats. Thus it would be likely to come in contact with *P. supina* which, being a perennial, would persist for some time in its glacial refuges. That *P. supina* can persist under fairly warm lowland conditions, is shown by the fact that the plant obtained from Switzerland is still alive after 5 years in a cool greenhouse.

It therefore seems possible that isolated colonies of *P. supina* surrounded by *P. infirma* occurred in one or more of the warmer periods in the Quaternary ice age. The more or less open plant communities, which appear to have been characteristic of the earlier parts of these periods, would provide a good opportunity for the survival of any hybrids which might have occurred between these two species. If spontaneous chromosome doubling then gave rise to *P. annua*, its vigour and versatility would ensure its establishment.

It therefore seems reasonable to suggest that *P. annua* is a species of recent origin and that it probably arose on the north side of the Mediterranean. Its recent origin is also suggested by the apparently perfect pairing of the seven bivalents in the two triploid hybrids. The chance of structural changes in the chromosomes or of mutations, which would prevent perfect pairing, is likely to increase with the age of the species.

If this hypothesis is correct, *P. annua* must have spread rapidly to have attained its present world-wide distribution. This rapid spread can be readily accounted for by its association with man; wherever it occurs in parts of the world far removed from its probable place of origin, *P. annua* appears to be always confined to tracks, gardens and the neighbourhood of habitations and to be an annual or ephemeral plant. It also seems to be always associated with man or with crop plants of European origin, and its occurrence in places uninfluenced by European man (if any still exist) has yet to be proved.

In Europe and Western Asia, the capacity of some of its 'races' for growing in a variety of natural habitats has given it a wider range; these 'races' not only lack the easy and rapid means of transport available to the weed varieties, but are also mostly perennial, and their occurrence in other countries has not been recorded.

Poa annua is, in fact, supreme among weeds for a number of reasons. It shows greater phenotypic and genotypic variability than most, if not all, others; it flowers and fruits throughout the year; it germinates rapidly, is small enough to escape notice and is not particularly easy to uproot; it also has great powers of survival when uprooted and thrown down. Its 'seeds' are readily dispersed in mud sticking to shoes, feet, implements or garden crops and its self-fertility and rapid life-cycle ensure that a single plant is enough to build up a large population in the course of a year or two.

The unusually great range of variation in duration and habit, as well as morphology, suggests that the present population of P. annua is not derived from one single hybrid, but from a number of different ones. The chances of hybridisation are obviously greatly increased when foreign pollen only is available, but the production of two plants, apparently of hybrid origin, from 100 emasculated florets of P. supina indicated that the fertility of this cross is high enough to make it possible for it to have occurred several times in nature. The fact, that the uppermost floret in each spikelet of P. supina is female and generally opens a day before the first hermaphrodite one, would also aid natural hybridisation.

Specimens of the material used in this investigation, and of the artificial hybrids, are in the Herbarium of the University of Leicester.

#### SUMMARY

- 1. A number of true-breeding ' races ' of Poa annua are described.
- 2. These differ in minor morphological characters, in speed of germination, rate of development and life-span.
- 3. It is shown that while crossing between these 'races' is possible, it is at most extremely rare in nature.
- 4. A description of anthesis in *P. annua* is given.

- 5. *P. annua* is a tetraploid intermediate in many ways between the diploids, *P. infirma* and *P. supina*. The distributions and chief characteristics of these three species are given.
- 6. Hybrids between the tetraploid and each of the diploids were obtained and were found to be triploid. Meiosis in the pollen mother cells of these hybrids showed, in each case, seven univalents and seven bivalents, indicating a close genetical relationship between the diploid and the tetraploid.
- 7. A hundred florets of *P. supina* were emasculated and pollinated with pollen from *P. infirma*. Three viable seeds were obtained, one of which produced a plant of the female parent, while the other two produced tetraploids resembling *P. annua*.
- 8. The two tetraploids had generally normal meiosis, but occasionally a single quadrivalent occurred. Nevertheless, over half the seed produced was inviable.
- 9. In the course of three generations, the germination-rate had risen to between 95% and 100%, the normal for *P. annua*.
- 10. The origin of these tetraploids is discussed and it is concluded that they most probably arose through spontaneous chromosome doubling in diploid hybrids.
- 11. The morphological evidence, the evidence from meiosis in the triploid hybrids and the probable production of P. annua-like tetraploids from the hybrid between the diploids make it practically certain that P. annua is an allotetraploid derived from the two diploids.
- 12. It is suggested that *P. annua* arose on the northern side of the Mediterranean in the Late Glacial or during an Interglacial, and owes its present distribution largely to human migrations and its own exceptional suitability for growth in disturbed habitats. It is also suggested that it may have arisen on a number of different occasions.

#### Acknowledgments

I am grateful to Mr. C. E. Hubbard for his comments on the probable artificial tetraploid, to Mr. J. E. Raven for material of *P. infirma*, to Professor N. A. Burges for examining perennial *P. annua* for mycorrhiza and to Dr. M. Borrill for assistance with the emasculation of *P. annua* spikelets. Dr. J. R. S. Fincham very kindly examined my cytological preparations and assisted with their interpretation; he has also given advice on several genetical points. My thanks are due to Miss S. J. Roles for the drawings of spikelets and to Mr. T. E. Bergstrom for the photographs.

It is a pleasure to acknowledge my indebtedness to the Research Board of the University of Leicester for grants in aid of field work.

#### REFERENCES

HACKEL, E., 1904, Zur Biologie der Poa annua L., Oesterreich. Bot. Zeitschrift, 54, 273-278.

HEGI, G., 1935, Flora von Mitteleuropa, ed. 2 (edited by K. Suessenguth), 1, 399-400. München.

LITARDIÈRE, R. de, 1938, Recherches sur les Poa annua subsp. exilis et subsp. typica. Relations taxonomiques, chorologiques et caryologiques, *Rev. Cytol. et Cytophysiol. végét.*, **3**, 134-141.

- —, 1939, Sur les caractères chromosomiques et la systématique des Poa du groupe du P. annua L., op. cit., 4, 82-85.
- JANSEN, P., 1951, Gramineae in Flora Neerlandica, 1 (2), 78. Amsterdam.
- NANNFELDT, J. A., 1935, Poa supina Schrad. i Sverige och dess hittills forbisedda hybrid med P. annua L., Bot. Notiser, 1935, 1-16.
- \_\_\_\_\_, 1937, The chromosome numbers of Poa sect. Ochlopoa A. & Gr. and their taxonomical significance, *Bot. Notiser*, **1937**, 238-254.
- ———, 1938, Poa maroccana Nannf. n.sp. and P. rivulorum Maire & Trabut, two more tetraploids of Sect. Ochlopoa A. & Gr., and some additional notes on Ochlopoa, Svensk Bot. Tidskr., 32, 295-321.

TUTIN, T. G., 1952, Origin of Poa annua L., Nature, 169, 160.

-, 1954, The Relationships of Poa annua L. Huitième Congrés international de Botanique -Rapports et Communications aux Sections 9 et 10, p. 88. Paris.