VARIABILITY OF *ELYTRIGIA REPENS* (L.) DESV. (SYN. *AGROPYRON REPENS* (L.) P.B.) ON DUTCH AGRICULTURAL SOILS

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CONTENTS

1. INTRODUCTION

In the Netherlands three species of the genus *Elytrigia* Desv. occur: *E. juncea* (L.) Nevski, *E. pungens* (Pers.) Tutin and *E. repens* (L.) Desv. (syn. *Agropyron repens* (L.) P.B.) (HEUKELS-VAN OOSTSTROOM, 1973). They are all species of the temperate climates. The first two are found almost exclusively along the sea coast and consequently have a restricted area of distribution. *Elytrigia repens* is a very common species in the Netherlands, which does not occur on acid peat soils and on the poorest sand soils. The species is considered to be one of the most serious weeds on cultivated soils, which is probably due to its ability to form rhizomes. These rhizomes can remain alive in the soil for two or three years (SAGAR, 1960) and are hard to eradicate. *Elytrigia repens*

can also reproduce by seeds. Seed production can be considerable and seeds are capable of germinating immediately after shedding. Yet few seedlings are found in the field and it is therefore assumed that seeds are mainly important in establishing the species in new areas.

Elytrigia repens is particularly a weed of arable land, but can also show an undesirable expansion in grassland (KREIL and KALTOFEN, 1966; BLATTMANN, 1966; WETZEL, 1966; HOOGERKAMP, 1970). In horticulture and in forestry *Elytrigia repens* can be a problem as well (VAN GOOR and JAGER, 1962).

The species is highly variable. In Floras different forms of *Elytrigia repens* are even described as varieties (JANSEN, 1951; HEGI, 1935)*; In the Flora Neerlandica JANSEN (1951) described five varieties of the species which differ mainly in morphological characters such as awn length of the lemmas, plant colour, leaf size and ear length. HOLLY and PARKER (quoted by PALMER and SAGAR, 1963) compared *Elytrigia repens* samples from the British Isles and Norway and noted differences in characters such as commencement of growth in spring, time of flowering and resistance to mildew infection. Within the species HADDAD and SAGAR (1968) reported genetic differences in shoot and rhizome production.

The ability of *Elytrigia repens* to propagate on different soils and under divergent cultivation systems indicates a remarkable adaptability of the species and might be connected with its genetic variability.

To get an idea of the variability of *Elytrigia repens* on Dutch agricultural soils and particularly of its variability within and between fields, groups of *Elytrigia repens* plants were collected from various arable lands and grasslands in the Netherlands and compared on an experimental field at Wageningen. In experiments with smaller numbers of plants the heredity of certain characters was further investigated. The results will be discussed in this paper.

2. MATERIAL AND METHODS

Data of the variability of *Elytrigia repens* were obtained from the following experiments:

Experiment 1

In 1965 groups of *Elytrigia repens* plants were collected from 3 arable lands, 5 leys and 13 permanent grasslands (11 of which were at least 50 years old). The fields were scattered all over the Netherlands (fig. 1). The soil consisted of sand (15 fields), clay (1 field river clay, 3 fields marine clay), peat soil (1 field) and reclaimed peat soil (1 field). The size of the fields varied from a half to over 1 hectare.

In the sampled arable lands and leys large quantities of *Elytrigia repens* were

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* Furtheron in this paper the varietal names and the names of forms are based on JANSEN (1951) and HEGI (1935), who used the generic name *Agropyron* instead of *Elytrigia* for couch.

FIG. 1. Origin of the plant groups (experiment 1) indicated by dots. Sampled routes in studying the awn length indicated by dotted lines.

found, as in one permanent grassland. In a second permanent grassland a moderate quantity of the species was found (estimated coverage 10%) and in the remaining permanent grasslands small quantities of the species (one or more small plants per 10 m²). In each field 24 or 48 shoots of *Elytrigia repens* were collected along diagonals.

Of the 21 fields 13 were sampled in September and 8 in October. The September material was planted outdoors before winter, the October material was kept during the winter in a frost free glasshouse in jiffy pots. In both cases the developed plants were divided into individual shoots in the second week of March, after which of each plant one rooted shoot of a uniform size and with two fully developed leaves was planted in an experimental field. The distance between the plants was 1.25 m. The reason for dividing the plants anew was the still considerable variation in size of the originally collected shoots which might have been due to characteristics of the fields from which they were collected.

The experiment was laid out on a sandy soil of a homogeneous structure. Therefore the shoots were planted together according to their original habitat, which facilitated the observations. Later on, indeed, regarding the plant characters observed, no indications were found of systematic effects of this way of planting on the variability within or between the plant groups. In March the shoots of the September plants were somewhat smaller than those of the October plants. Therefore the plants which developed from the September- and October-material will be indicated henceforth as plants of the *A collection*, and plants of the *B collection*, respectively. The A collection consisted of 360–, the B collection of 304 plants.

The experimental field was fertilized with P and K in February. In the third week of March a nitrogen dressing was given of 60 kg/hectare. This dressing was repeated on 20 July, when the plants were cut for the first time. The plants were cut for a second and a third time in the third week of August and in the fourth week of September.

Experiment 2a

In the autumn of 1964 shoots of *Elytrigia repens* were collected from 24 grasslands, leys and arable lands in the Netherlands, always 4 shoots out of 1 dm². During the winter (1964–1965) these shoots were grown in pots in a glasshouse, one shoot per pot. The climate conditions in the glasshouse were: temperature 20°C, HPL-supplementary light with 840 J. $cm^{-2}day^{-2}$, photoperiod 16 hours.

Experiment 2b

In the spring of 1965, plants from individual shoots of 20 clones of experiment 2a were grown outdoors in pots, 10 plants per clone. As far as possible shoots of comparable sizes were selected. In this experiment the persistency of characters of the clones was studied after propagation.

Experiment 3

In an outdoor experiment in the spring of 1966, plants from 3 clones of experiment 2a were grown from one-noded rhizome pieces under various photoperiods, viz. of 12, 14, 16 and 18 hours. The plants were grown in flower pots, one plant (rhizome piece) per pot. The day lengths were realized by giving

the plants 12 hours of daylight and 0, 2, 4 and 6 hours of supplementary incandescent light in cabinets. The experiment was started on 22 April and ended on 1 August. The starting material for the experiment was directly obtained from outdoors and had consequently received a normal winter treatment.

Experiment 4a

In the growing season of 1967 individual shoots of comparable sizes from 6 clones (K) out of experiment 1 were grown on a sandy soil and were subjected to various clipping treatments. The shoots were planted on an experimental field before the winter (November 1966), at distances of 1.50 × 1.50 m. The clipping treatments varied with regard to the first clipping date (T), June 6 and July 20, and with regard to the frequency of clipping (F), 3- and 6-weekly clippings. All treatments were cut for the last time on 31 August. The clipping height was 0.5 cm. The experiment was laid out as a randomized block design with 4 replicates (R). The total number of plants amounted to 6 (K) × 2 (T) × 2 (F) × 4 (R) = 96. The experimental field received a moderate NPK-dressing.

Experiment 4b

In 1968 sods were grown in Mitscherlich-pots from four clones of the six in experiment 4a; 30 sods per clone. These sods were cut in June and October 1968 and were planted in a 3-years old grassland in April 1969 at distances of 4 × 4 m. The grassland mainly consisted of *Lolium perenne* and *Phleum pratense* and was moderately fertilized with NPK, and cut in the beginning of June and in September.

Experiment 5

In 1969 monocultures of two *Elytrigia repens* clones and of the *Lolium perenne* variety *Cropper* (Nederlandse Rassenlijst voor Landbouwgewassen, 1974) were laid out in plots of 1.50 × 1.50 m². In 1970 these monocultures were cut every six weeks, the first cut taking place at a different date, viz. May 14 and June 3. The experiment was set out as a randomized block experiment with 4 replicates. Each plot received a total yearly dressing of 300 kg N/ha, and P- and K-fertilizer adjusted to the N-application.

The observations concerned in the first place those plant characters used in the Floras mentioned to distinguish the varieties of *Elytrigia repens*; characters such as awn length, plant colour, growth habit, shoot height, leaf size and ear length (experiments 1 and 2). In this way also an impression was gained of the possible ecological relevance of these varieties to Dutch agricultural soils. Measurements of the rhizome thickness of plants (experiments 1 and 4) were also performed. Furthermore characters with regard to growth and development of the *Elytrigia* plant were observed. In the experiments 1, 3 and 5 the heading date of the plants was recorded. Since *Elytrigia repens* manifests itself in grassland as a species with a considerable tendency to elongate, attention was also paid to the behaviour of the *Elytrigia* plants with respect to stem elongation (experiments 1 and 4).

With regard to their characters the plants in experiment 1 were sometimes grouped into classes. The classifications will be given with the interpretation of the results. Differences in characters as a result of the various populations were tested on significance by an analysis of variance; only differences with a probability of over or equal to 95% were indicated as significant. The differences between pairs of populations were submitted to a student-test, in which the same interval of confidence was used. In experiment 4a also an analysis of variance was carried out. In experiment 1 simple correlations between characters were calculated.

3. RESULTS

From now on the notional words 'plant', 'clone' and 'population' will be used. By 'plant' any plant-individual is meant, by 'clone' plants are indicated which were obtained by vegetative reproduction from a similar plant-individual, whereas 'populations' are the groups of *Elytrigia* plants collected from the various fields in experiment 1.

A distinction will be made between 'parent plants' and 'daughter plants'. 'Parent plants' are those parts of the plant developed by tillering of the single shoots that were planted in experiment 1 and experiment 4. 'Daughter plants' are those plant-individuals in experiment 1 and experiment 4 developed from rhizome tips (also from the tips of rhizome branches) or from lateral nodes on the rhizomes. Due to tillering daughter plants can have more than one shoot.

3.1. MORPHOLOGY

Growth habit: ASCHERSON and GRAEBNER (1898–1902) and HEGI (1935) described *Elytrigia repens* forms with upright-growing and geniculated stems, the varieties *majus* Parl. and *caesium* Bolle, respectively (footnote on page 2). Similar differences were found with respect to the habit of the parent plants in experiment 1, in the first year of the experiment. The growth habit was described after almost all parent plants had fully developed ear-bearing culms. The extreme forms found were called prostrate and erect. The prostrate types for the major part had stems with bases bent towards the ground, the last internode only growing vertically upwards. The erect types showed almost exclusively fully upright growing stems. As an intermediate form between prostrate and erect, a type of plant with an U-shaped habit occurred. Of this type several, but not all internodes of the shoots were growing vertically upwards. The growth habit was eventually classified according to a quinque-partite scale, in which the evaluation numbers 1, 3, 5 were attributed to the prostrate, the U-shaped and the erect types, respectively. In the collections A and B (experiment1) plants with an intermediate prostrate to U-shaped habit and plants of the U-shaped type were most frequently found (fig. 2). These two plant collections did not show a systematic difference in growth habit, but between the popula-
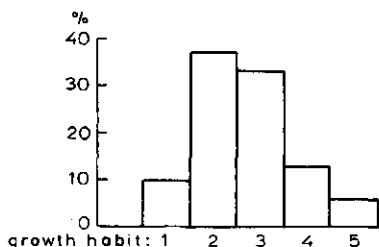
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FIG. 2. Histogram of growth habits in experiment 1. Plants of the A and B collection together, 660 plants.

tions significant differences in this character were observed. In two populations only plants of one type occurred (means for the growth habit 2 and 3, respectively), while within most other populations the habit varied considerably.

The prostrate habit is due to a tendency of the shoots to grow out horizontally in early development. For that reason differences in growth habit can already be distinguished roughly before culms are formed and were also observed in experiment 1 among the daughter plants which developed from rhizomes after the cutting treatment on 20 July. In general these daughter plants showed the same habid as their parent plants.

Of 76% of the prostrate parent plants the daughterplants were prostrate (9% erect) and the 'daughters' of 68% of the erect parent plants erect (7% prostrate). The growth habit was positively correlated with the degree of tillering and to characters concerning the shoot size of the parent plants (shoot length, leaf length, leaf width, stem thickness and ear length); in other words prostrate types were found more often among the plants with small shoots and less tillering, whereas the erect types occurred more among the plants with robust shoots and more tillering. The correlations, however, were low, varying from 0.16 to 0.28.

Differences in growth habit have also been described for other grass species, i.a. by HESSING (1922) for species of the genus *Lolium*. According to 'T HART (1947) the growth habit of *Lolium perenne* in old grassland is correlated with the grassland use. Prostrate types of this species occur frequently in grasslands which are continually grazed, more erect types particularly in those which are always cut late for hay in spring. One of the reasons for a better adaptation of prostrate ryegrass types to grazing conditions could be the decumbent shoots escaping from grazing which might also apply to *Elytrigia repens* in grassland. In experiment 1, however, no indications were found of a relation between the growth habit and the grassland use.

Typical specimens from experiment 1 kept their habit fairly well when they were reproduced from individual leafy shoots in the next year, which points to heredity of the character. On the other hand, environmental factors may appreciably affect the habit of the couch plant. WILLIAMS (1971) found that plants of the species growing under a short photoperiod are more prostrate than growing under a long photoperiod. PALMER (1956) who worked with some tropical grass species showed that shoots of these species tend to grow more horizontally when grown under high light intensity. This could also apply to *Elytrigia repens*, since in a high and dense crop clearly prostrate forms will seldom occur.

Plant colour: In the Flora Neerlandica JANSEN (1951) described a variety *glaucum* (Döll) Volkart with a typical blue-green or grey-green colour. The colour is caused by a wax layer on the stems, leaves and ears. In experiment 1 10% of the plants showed this colour. In one group 44 plants out of 47 showed a pronounced blue-green colour, blue-green plants in other groups being completely absent.

Hair characters of the leaves: JANSEN (1951) mentioned that the upper side of the leaves of *Elytrigia repens* bears scattered long hairs. According to HEGI (1935) the upper sides of couch leaves are rough, because of the presence of short hairs and HUBBARD (1968) considers them loosely to sparsely hairy or hairless. In experiment 1, the extremes were: practically hairless plants (30% of the individuals) and plants with relative dense and long hairs on the upper side. Leaves with the latter characteristic were somewhat velvety to the touch. Intermediate types showed various combinations with regard to hair length and hair density. In general hair density and hair length of the individual plants seemed to be positively correlated.

Hair characters of couch leaves were also studied in the experiment 2a en 2b. Hair length as well as hair density were observed on the basal part of the first three fully developed leaves of the main shoot of each of the 86 plants (plants collected from different locations). Only hair density was determined in the middle and the tip of the same leaves. Countings and measurements of hairs were performed with the aid of a microscope. In fig. 3a the means of hair density and hair length at the leaf base of the plants have been plotted against each other. The two characters were found to be positively correlated. For neither of the two characters a frequency distribution of the plants showed a clear two – or more – peaked curve. Almost 50% of the plants had relatively short and sparsely haired leaf bases (10 or less hairs per 15.5 mm^2 average hair length <0.5 mm), whereas the frequency of plants decreased at increasing hair length and hair density. Hair density generally increased from the base of the leaf (averaging 12 hairs per 15.5 mm^2) to the tip (50 hairs per 15.5 mm^2). On an average the upper leaves had a somewhat higher hair density than the lower leaves. The longest hair length was 1 mm. Although leaves without hairs were found, absolutely hairless plants did not occur in the collection. Typical specimens proved to keep their hair characters fairly well, as illustrated in fig. 3b showing the hair density on the middle of the upper side of the leaf.

The hair density on the leaves of the plants in experiment 1 was evaluated with values from 1 (practically hairless) to 3 (with a high hair density). The means per plant per population varied from 1.2 to 2.9. Although the variation of the two means was relatively small and populations differed significantly, practically hairless plants as well as plants with densely hairy leaves were found in each population. Especially in early spring the leaves of a good many plants showed densely haired leaf sheaths and in some of these cases hairs were also found on the under side of the leaf bases. This character (densely hairy leaf sheaths) seemed to be heriditary. Forms with this character are indicated by JANSEN (1951) as f. *hirsutum*.
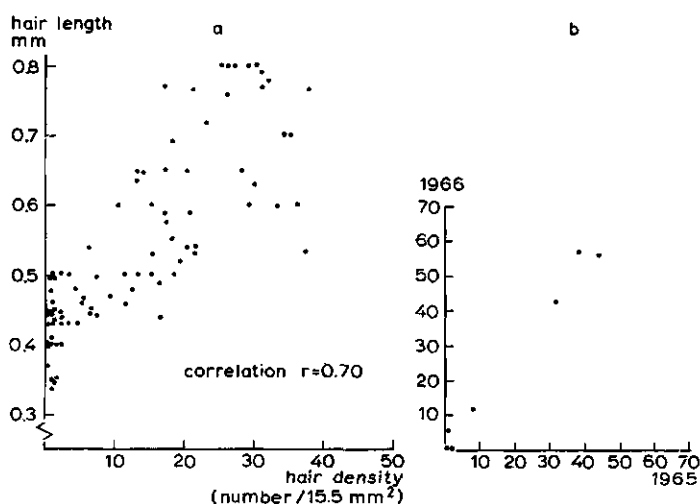
Fɪɢ. 3a. Relation between hair density and hair length at the leaf base of 86 plants of *Elytrigia repens*.
b Relation between hair density (number of hairs per 15.5 mm²) in the middle of the upper side of the leaf for 7 *Elytrigia repens* clones in 1965 and 1966.

Awn length: In the Flora Neerlandica (Jansen, 1951) all forms of *Elytrigia repens* with normal colour and normal size are subdivided into the varieties *vulgare* (Döll) Volkart and *aristatum* (Döll) Volkart on the basis of awn length of the lemmas. The variety *vulgare* has no awns and its lemmas are blunt or pointed, whereas the variety *aristatum* has awns varying from very short to as long as the length of the lemma. The variety *vulgare* is supposed to be a very common variety as well as the short-awned forms of the variety *aristatum* (awns to 0.25 of the length of the lemma). Couch forms with awns to 2/3 of the length of the lemma are called fairly common in this Flora and those with longer awns (from 2/3 to as long as the lemma) rare.

The awn length of couch ears was also studied in 1969. In that year couch ears were collected along secondary roads of five different routes in the Netherlands. Always three ears were collected at distances of 1 km, whereas the distance between the three ears was always 10 m. Altogether 512 ears were collected along roads with a total length of well over 150 km. Of each ear the length of the longest awn was measured together with the length of the lemma belonging to it. The lengths of the two organs varied from 0 to 9.5 mm and from 4 to 14 mm, respectively. The two lengths were not correlated. To facilitate a comparison with the Flora Neerlandica, the ears were grouped into five classes according to the ratio between the awn and lemma lengths, this ratio being indicated as 'the relative awn length'. The following classes were distinguished: relative awn length $\leqslant \frac{1}{8}$ (class 1), $> \frac{1}{8}$ and $\leqslant \frac{1}{4}$ (2), $> \frac{1}{4}$ and $\leqslant \frac{1}{2}$ (3), $> \frac{1}{2}$ and $\leqslant 1$ (4) and > 1 (5). In accordance with the Flora Neerlandica ears
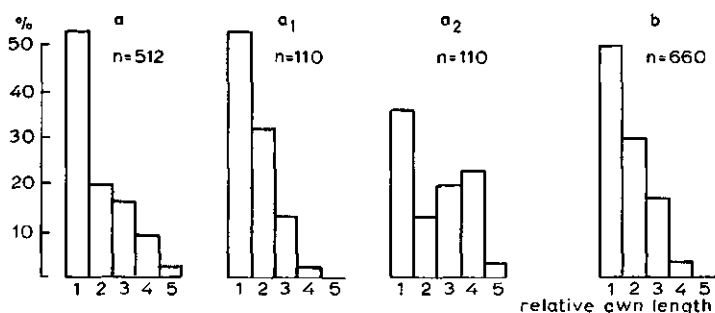
FIG. 4. Histogram of rel. awn lengths of couch ears a: Netherlands, 150 km (5 routes); a_1: Friesland, 37 km; a_2: South Limburg, 37 km; b: Experiment 1; n: number of ears.

with short to very short awns were most frequently found (fig. 4a, class 1, over 50% of the ears), although there were clear differences between the sampled routes. Along a route in the loess area, e.g. along the brook 'De Geul' in South Limburg, a comparatively great number of long-awned forms was found (fig. 4a2), whereas in the Friesian marine clay area a relatively great number of very short-awned forms occurred (fig. 4a1).

Also in experiment 1 (1966, fig. 4b) most frequently plants with short to very short-awned lemmas were found. In that experiment the relative awn length of the longest lemma of the longest ear was determined. Populations differed significantly with respect to the relative awn length. The means per plant per population for this character (5 classes) varied from 1.2 to 3.1. The coefficient of variation (CV) with the highest mean was small (19%), but varied from 30 to 50% with the remaining population means.

According to JANSEN (1951) and HEGI (1935) the variety *vulgare* is found especially on arable land. This is not confirmed by the data from experiment 1. The plants of the three arable populations were indeed on an average short awned (population means for the relative awn length varying from 1.4 to 1.6), but the same applied to 9 grassland populations out of 11 (population means varying from 1.2 to 1.8). Only in two ley populations and in one grassland population longer awns were found (population means 3.1, 2.1 and 2.3, respectively). According to KRAUS (1912) the variety *aristatum* flowers earlier than the variety *vulgare*. Awn length and heading date, however, did not appear to be correlated significantly, either in the A or in the B collection (correlation coefficients ⩽0.08, number of plants 300 and 250, respectively). Awn length is a character easy to observe, but was not significantly correlated with any of the other characters studied.

Size of leaves, stems and ears: JANSEN (1951) recorded that stems of *Elytrigia repens* may attain a length of more than 1 m and leaves generally a width of 6 mm, ear length amounting to 10 to 15 cm. However, he also described a robust variety *majus* (Döll) J. et W., with shoots up to 2 m in length and leaves up to 15 mm wide. Couch plants of a comparable size and even larger with leaves up to 22 mm wide were found by the present author along dunghills near

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farms on the northern border of the Veluwe (Nunspeet). In an investigation of root-tip cells of three of these plants (Feulgen staining) chromosome numbers were found varying from 38 to 41. This may have been 2n = 42, corresponding to the chromosome number of couch most frequently mentioned (PALMER and SAGAR, 1963). The chromosomes were small and difficult to count.
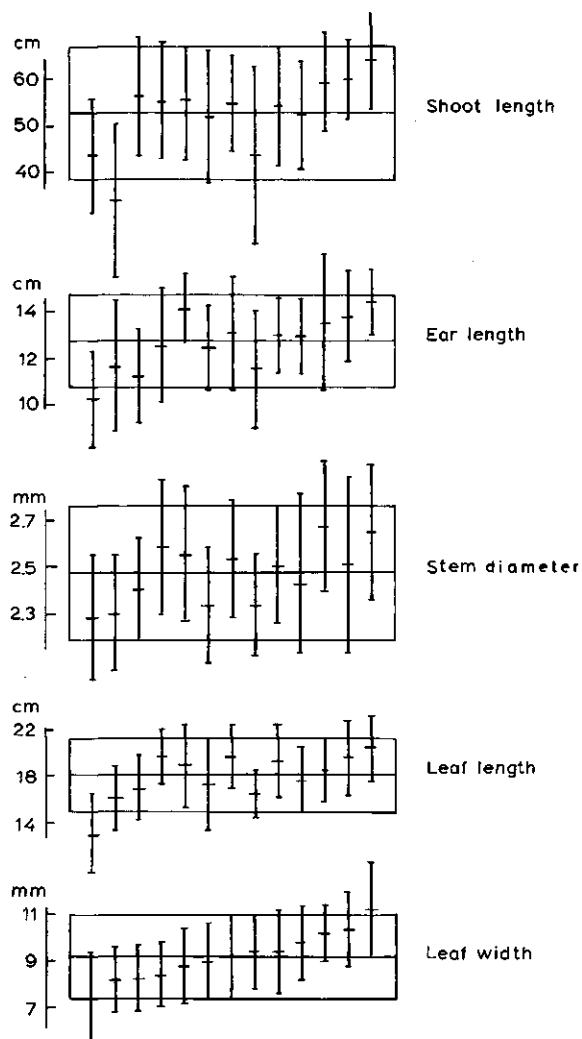

FIG. 5. Means per plant and standard deviations of some characters concerning shoot size in the A collection, experiment 1. Means per plant of 13 populations (horizontal dashes) and means per plant for the whole collection (long horizontal lines in the middle of the blocks). The total length of a vertical line represents twice the standard deviation of a population, the total height of a block corresponds with twice the standard deviation of the whole collection of plants.

The size of leaves, stems and ears of the plants in experiment 1 were measured in the second week of July in the first year of the experiment (1966). At that date practically all plants had developed one or more fully developed ear culms. Of each plant the total length of the longest shoot was determined and also the length of the ear, the length and width of the largest leaf and the diameter of the thickest internode. In fig. 5 the means per plant per population are represented with regard to these characters. Only data of the A collection are given, because the A and B collection differed slightly, among other things, with respect to ear length. In the figure the populations are arranged from left to right in order of increasing leaf width; within the group of five characters this was the character for which the highest correlations were found. Populations within the A as well as within the B collection differed significantly with respect to each character. The characters of the individual plants were significantly correlated, but the correlations were relatively low, correlation coefficients (r) varying from 0.26 to 0.50 (plants of the A collection, over 300 plants). For the same characters also the means per plant per population were slightly positively correlated (fig. 5).

After uninterrupted spring development the smallest and most robust clones in experiment 2b differed in shoot length, leaf length, leaf width, stem diameter and ear length by a factor 1.6, 1.7, 1.8, 1.7 and 2.0, respectively. Also with respect to these characters the clones showed a regular distribution. Otherwise, clone differences e.g. leaf dimensions are not always constant during the growing season as is illustrated in table 1. The table represents the data of leaf dimensions in the six-weekly mown monocultures of two couch clones in experiment 5. The data refer to two cutting dates of the treatment with the late first cut in that experiment. On the first cutting date in the first week of June the clones differed slightly in leaf dimensions, but later on (3rd cutting date) the one clone (KA) produced significantly longer leaves than the other clone (KB), which then produced significant wider leaves. The modified differences in leaf dimensions between the clones were possibly related to the behaviour with regard to stem elongation. An illustration of this could be that on the first cutting date clone KA was found to be more elongated than clone KB, whereas on the second and later cutting dates the reverse was seen (fig. 7).

In the spring of the second year the populations in experiment 1 showed

TABLE 1. Means and standard errors of length and width of the largest leaf of shoots of two *Elytrigia repens* clones in monocultures mown every six weeks (1970). Means of observations of 40 leaves per clone per harvest date.

Harvest date	Clone	Leaf length (cm)	Leaf width (mm)
June 3, 1970	KA	19.8 ± 0.4	6.1 ± 0.1
(first cut)	KB	20.5 ± 0.6	6.4 ± 0.2
August 26, 1970	KA	39.1 ± 0.8	4.8 ± 0.15
(third cut)	KB	24.1 ± 0.5	5.9 ± 0.14

roughly the same differences in shoot dimensions as in the first year, but one population behaved completely different. The plants of this population had produced relatively large-leaved and thick-stemmed shoots in the first year, but now produced shoots with strikingly small leaves and thin stems. Also in the spring of the third year shoots with relatively small leaves were found in this population.

Weight of rhizome pieces in borings, rhizome thickness: In the autumn of the first year 16 soil samples (borings) in experiment 1 were taken around each of 10 parent plants in each of the populations to collect data on the rhizome production. The borings were always taken around the parent plant, within a radius of 25 cm. The boring had a diameter of 7 cm, the boring depth was 20 cm. The rhizome pieces in the borings were rinsed and collected per plant in one sample. The roots on the nodes of the pieces were removed after which the number and the dry weight of the pieces were determined per sample. The amount of rhizome material (dry matter) in the borings was only slightly correlated with the total rhizome production of the plants and therefore not fit for measuring this rhizome production ($r = 0.50$ determined in a number of 30 plants). Individual plants as well as populations of plants, however, differed considerably in the mean weight per rhizome piece in the borings. With regard to this character systematic differences between the plants of the A and the B collection were not found. The mean weight per rhizome piece per plant in 16 borings, independent of the number of pieces in the borings, varied from 24 to 170 mg, the means per plant per population from 70 to 132 mg for this character. Light pieces were found especially in the grassland populations, relatively heavy pieces especially in the three populations from arable land. The grassland populations and the populations from arable land differed significantly in the mean weight per rhizome piece per plant (t-test, $p < 0.01$). In the ley populations rhizome pieces were found of an intermediate mean weight, but these populations did not differ significantly in this regard from the grassland populations. For the mean weight per rhizome piece per plant in the arable, ley and grassland populations values of 114.2, 89.0 and 82,4 mg were found, respectively. The standard errors of these means were 5.0, 2.0 and 3.6 mg, respectively. The plant and population differences in the character seemed to be clearly related with differences in rhizome thickness and in so far as the distinction between arable and grassland populations is concerned, were not caused by differences in the number of rhizome branches per boring. In the arable and grassland populations these branches accounted for 14 and 16% of the total number of pieces, respectively. In later clone experiments the mean weight per unit of rhizome length and the rhizome thickness seemed distinctly determined by hereditary factors (experiment 2a). It was striking that on clone level the two characters were not correlated with the stem thickness or the leaf size of the aerial shoots, although rhizomes are stems as well. In experiment 1 a correlation of only 0.08 (200 plants) was found between the mean weight per rhizome piece and the greatest internode diameter of the main shoot of the plants.

Heading: In 1966 every 3 or 4 days it was recorded in experiment 1 when the first head emerged from the leaf sheaths of the plants. Observations on ear emergence (heading) were also performed in 1967. In 1966 the first plants headed on 27 May. The average heading date (50% of the plants headed) was 11 June, in 1967 it was 4 June. In addition to other factors, the later heading in 1966 may have been caused by a slower development that year due to the plants being grown from individual leafy shoots. In fig. 6 the course of heading is represented by plotting the total percentage of headed plants before successive dates against time (1967). The earliest and latest populations (both from grassland) showed a difference of 18 days in average heading date. In the same year JONKER (1966–1967, not published) observed much greater differences in heading dates between *Lolium perenne* populations, the greatest difference being 33 days. The *Lolium perenne* populations were collected from more than 100 old permanent grassland sites in the Netherlands and planted on the same farm as the couch populations (experiment 1). As the date of heading of the plants JONKER noted the date on which three heads were visible. In a similar investigation by SONNE-VELD and JONKER (SONNEVELD, 1966) *Lolium perenne* populations showed a difference in average heading date of more than one and a half months. The heading date of these populations was found to be correlated, among other things, with the grassland use, especially in the first part of the growing season. Early heading populations were mainly found in grasslands of which the first cut was mown late for hay every year, late-heading populations in grasslands which were always intensively grazed in spring. In the couch collection (experiment 1) grasslands used in these ways were represented by five and one popula-
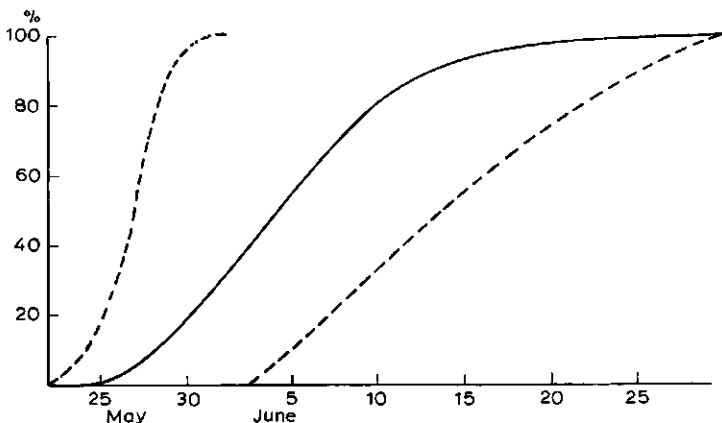

FIG. 6. Cumulative curves of the percentages of *Elytrigia repens* plants heading before successive dates, experiment 1, 1967. Curve for the whole collection of plants and curves (interrupted lines) for the earliest and the latest population.

tion, respectively. These populations also headed early (average heading dates between 27 May and 5 June) and late (heading date 13 June), respectively. On the other hand, the heading dates varied considerably between four populations from grasslands which were intensively grazed and mown late in spring every other year (average heading dates 28 and 30 May, and 5 and 10 June, respectively). Of the remaining couch populations collected from grasslands the use was not precisely known. Regarding the heading date the arable land and ley populations of couch belonged to the middle groups.

The couch plants opened their flowers in 1966 on an average 23 days after emergence of the first ear. The earliest plants did so on 22 June, in 1967 on 16 June. In 1972 already 10 days after emergence of the stamens viable seeds were found (seeds germinated in Petri dishes with moist filter paper at alternating temperatures, 25°C by day, 15°C at night). All this means that under Dutch conditions early clones in early-heading years may have produced viable seeds on about 26 June. In 1966 on an average the couch plants (experiment 1) opened their flowers on 15 July. This corresponds with the results found for *Elytrigia repens* by WILLIAMS (1971) in England (Rothamsted); average flowering date: 19 July (1968), 12 July (1969) and 27 June (1970). According to WILLIAMS more than half of the final number of viable seeds can germinate within 10 days of flowering.

According to ROBERTS and STRUCKMEYER (1938) *Elytrigia repens* needs long day for ear formation. From experiment 3 too, it was evident that ear formation of this species is accelerated by long photoperiods. In this experiment plants of three clones were grown from one-noded rhizome pieces under different photoperiods in the spring of 1966; photoperiods of 12, 14, 16 and 18 hours. Heads were only formed under photoperiods of 16 and 18 hours, although under these photoperiods too, some plants remained without ears. The stage at which 50 % of the plants had formed visible ears was reached 8 days earlier in the 18-hour treatment (4 July) than in the 16-hour treatment (12 July, experiment starting on 22 April). In both treatments the clones showed slight differences with regard to the moment the first plants showed ear emergence. The number of plants with ultimate heading varied from 5 to 6 between clones (6 plants per clone per treatment). It is true that in the 14-hour treatment, at the end of the experiment some main shoots with growing points were found which had entered the reproductive phase, but these growing points had scarcely developed in length. Some stem elongation had occurred in these plants. The 12-hour plants only showed leafy shoots with vegetative growing points. In 1968 already on 19 April outdoors under a daylength of 14 hours a good number of couch tillers had entered the reproductive phase, the first tillers in that phase were found that year on 10 April (photoperiod 13.5 hours).

The plant material for experiment 3 (one-noded rhizome pieces) came directly from the field and thus had received a normal winter treatment. In the 18-hour treatment, however, also rhizome pieces were set out which were grown in a heated glasshouse under a long photoperiod for one year (glasshouse temperature 18–20°C, photoperiod 16 hours). Within the same period of this

material as many plants headed as plants of the outdoor material. Couch therefore seems to require no or little low-temperature or short-day induction for flowering. In any case, low spring temperatures seem to meet a need, if any, for low-temperature induction in the species. In spring only a limited number of shoots developing heads and, generally speaking, no new heads of *Elytrigia repens* being produced after mowing in early June may also be due to other phenomena than a need for low-temperature induction or particular photoperiods. Later in the growing season the temperature is possibly too high for ear formation as was found by COOPER (1958) for strains of timothy (*Phleum* ssp.). In an experiment done in 1968 (not published) indications were found that a similar phenomenon occurs in couch. The tendency of couch to form few heads in spring, however, would still require another explanation then.

Stem elongation: Lolium perenne like *Elytrigia repens* is a long-day species, with evident need, however, for low temperature induction. Shoots of this species apart from the phenomenon of 'shoot-raising' (KRUIJNE, 1958), only elongate appreciably when the growing points have attained the reproductive phase. In *Lolium perenne* stem elongation can therefore only occur in the relatively short period of ear formation and even then in only a limited number of shoots. *Elytrigia repens* also produces a limited number of ears, but during, and even after the period of ear formation, vegetative shoots of this species can also show considerable internode elongation (SHARMAN, 1947). Therefore with *Elytrigia repens* stem formation generally occurs more extensively and also during a longer period in the growing season. This is illustrated in table 2. In this table the stem elongation of *Elytrigia repens* is compared with that of a late heading type of *Lolium perenne* at 5 to 6 weekly mowings and at two dates of the first cut in spring (15 May and 9 June). The observations were done in a supplementary experiment with monocultures of both species, which received an NPK dressing on the basis of 200 kg N/ha. *Lolium perenne* shoots with growing points at a height of 5 cm or more had nearly always entered the reproductive phase, wheras comparable shoots of *Elytrigia repens* were in the

TABLE 2. Stem elongation of *Elytrigia repens* (mixed population of clones) and of a late heading type of *Lolium perenne* in monocultures mown every 5 or 6 weeks, the first cut being on two different dates (1969). Represented are percentages of shoots with a growing-point height of more than 3 cm and, in brackets, of more than 5 cm, for successive harvest dates. The figures are always the result of measurements of more than 600 shoots of both species.

Harvest date	15/5	23/6	1/8	9/9
Ely	43 (26)	86 (78)	15 (7)	+
Lp	–	13 (10)	–	–

Harvest date	9/6	18/7	24/8
Ely	93 (91)	39 (22)	5 (2)
Lp	7 (3)	2 (+)	+

reproductive as well as in the vegetative phase (the two first cutting dates) or almost only in the vegetative phase (later cutting dates).

Characteristics of stem elongation were described by BRANSON (1953), for e.g. *Poa pratensis* and *Agropyron smithii*, in elongation behaviour corresponding with *Lolium perenne* and *Elytrigia repens*, respectively. According to BRANSON species with a type of elongation of *Poa pratensis* are better adapted to intensive grazing than species that elongate like *Agropyron smithii*. This corresponds with the idea in agricultural practice that in grassland *Elytrigia repens* is susceptible to frequent cutting or frequent grazing (MINDERHOUD et al., 1974) This susceptibility probably depends on the large number of growing points that is cut off or damaged during these treatments.

Especially in the second year of experiment 1 (1967) the couch populations showed considerable differences in the date on which the plants started elongating in spring. In that year already in the first week of May in one population all plants had formed short stems of 3 to 10 cm, whereas the plants of some other populations did not start elongating until the third week of May.

Fig. 7 clearly seems to demonstrate that *Elytrigia repens* is genetically variable with regard to stem elongation. The data in this figure are obtained from experiment 5, in which the behaviour of couch clones was studied in monocultures at six-weekly cuttings and a first cut on 14 May. In the experiment also monocultures of an early heading variety of *Lolium perenne* were included (variety *Cropper*, Rassenlijst voor Landbouwgewassen, 1975). The experiment was performed at a high fertilizer level. The monocultures were cut at a height of 3.5 cm. The figure shows data on the height of growing points. The two couch
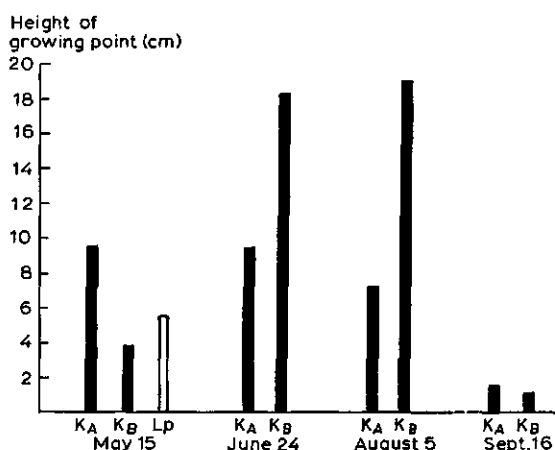

FIG. 7. Mean height of the growing point of shoots on successive harvest dates (1970) in monocultures of two clones of *Elytrigia repens* and in monocultures of an early heading variety of *Lolium perenne* (first harvest date only). The mean was always calculated from data of 40 shoots. The standard errors of the means varied from 0.2 to 0.7 cm.

clones in the figure differed in stem elongation on the first as well as on the following cutting dates. After the first cut advanced stem elongation occurred in the clone (KB) which had started elongation later in spring. Even on the first mowing date the stem elongation of the clones was mainly vegetative, as only 5% (KA) and 34% (KB) of the growing points above mowing level were in the reproductive phase. The two clones were obtained from experiment 1, in which they had been fairly characteristic of the original populations.

Of the *Lolium perenne* variety, only data on the first mowing date are given. With regard to the extent of stem elongation the variety then behaved as an intermediate between the two clones. Also the most fully developed shoots of the variety were clearly shorter than those of the most elongated couch clone. With that variety shoots with elongated stems were all in the reproductive phase.

Generally speaking the populations with early stem elongation in experiment 1 also headed earliest. On the other hand the two clones in experiment 5 hardly differed in heading date. Both clones headed in unmown monocultures between 2 and 4 June. For that reason the heading date within the species does not seem to be strictly correlated to the beginning of stem elongation. An interesting point is that the *Lolium perenne* variety, in spite of its moderately early stem elongation, formed heads two weeks earlier than the two couch clones; between 18 and 20 May (heading in monocultures which had neither been cut). It seems therefore that also on a species' level early heading cannot always be associated with early stem elongation.

Vegetative stem elongation is also observed with *Arrhenatherum elatius*, but according to BOMMER (1964) long day is necessary for this elongation. A glass-house experiment in 1968 showed that this also applies to *Elytrigia repens*. Couch plants were collected from an experimental field in mid August 1968 and grown in a heated glasshouse under 12 hours HPL-light $(750 \text{ J.cm}^{-2}\text{day}^{-1})$ and 12 hours HPL-light supplemented to 18 hours with incandescent light. No ears were formed in either treatment. After 4 months the growing points of the highest shoots were 6 cm in the short-day and 48 cm in the long-day treatment. The slight stem elongation which occurred during the short-day treatment was a result of elongation of several internodes with individual lengths varying from 1 to 2.5 cm. During the long-day treatment individual internodes with lengths to 19 cm were formed. The requirement of long day for stem elongation could possibly explain the decreasing tendency of couch to elongate after July (table 2, fig. 7).

3.3. TILLERING AND VEGETATIVE PROPAGATION

In the first year (1966) the populations in experiment 1 were found to differ considerably in the degree of tillering and in the number of daughter plants produced from rhizomes. The number of tillers on the parent plants were counted on 20 July. The daughter plants were counted in the fourth week of
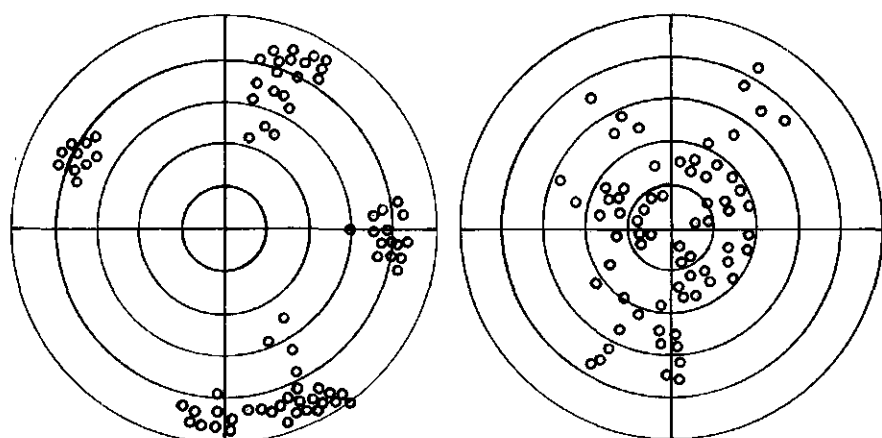
Fɪɢ. 8. Distribution of daughter plants of two parent plants in experiment 1. For the plants the distribution is given of the daughter plants within a set of concentric iron wires placed on the ground with the parent plant in the centre. The radius of the innermost ring was 10 cm, the radius of the following rings was always increased by 10 cm.

September. The plants (parents and daughter plants) had been clipped before that time on 20 July and in the third week of August (clipping height 0.5 cm). Also maps were drawn of the plants, on these the distances of the daughter plants to the parent plants could be measured later (fig. 8). The A and the B collection did not show reliable differences, but populations differed significantly in the tiller number as well as in the number of daughter plants per parent plant. With regard to these two characteristics the most extreme populations differed by a factor 2.1 and a factor 2.7, respectively (table 3). With regard to both characters the populations showed a gradual variation. Yet the number of daughter plants does not exactly reflect the population differences in shoot production around the parent plants, because populations also differed visibly in the degree of tillering of the daughter plants. However, in the total number of shoots from daughter plants the extreme populations likewise differed by a

TABLE 3. Means and standard errors of the shoot number and number of daughter plants per parent plant in experiment 1, 1966 (n = number of plants).

	Number of shoots parent plant – July 20	Number of daughter plants per plant – September
Whole collection of A and B plants	28.5 ± 0.5 (n = 620)	34.8 ± 1.2 (n = 594)
Population with the lowest mean	20.4 ± 0.9 (n = 46)	21.1 ± 1.0 (n = 45)
Population with the highest mean	42.8 ± 4.0 (n = 23)	57.2 ± 5.1 (n = 43)

factor 2 to 3, roughly estimated. The daughter plants had developed e.g. at a considerable distance from the parent plants. The average distance per plant for the remotest daughter plant was 47 cm for the whole collection of A and B plants. The means per plant per population varied from 42 to 49 cm for this distance.

The tiller number and the number of 'daughters' per plant were significantly correlated within the whole collection of plants, but the correlation was low ($r = +0.26$, more than 500 plants). Within the A as well as the B collection both characters were only slightly correlated with shoot length, leaf length, leaf width, stem thickness and ear length of the plants; correlation coefficients varied from 0.11 to 0.29. These results correspond with the field observation, that not only robust plants, but also plants with small shoots had sometimes developed a strikingly great number of daughter plants. Among other things, the number of daughters per plant was not correlated with the weight per rhizome piece in 16 borings of the plants ($r = +0.05$, examined on 200 plants). There was no relation between tillering and the number of daughters of the parent plants, on the one hand, and characteristics of the original habitats, on the other hand. Thus the populations from arable lands, leys and permanent grasslands did not differ significantly with regard to the number of daughters per plant and likewise did not seem to differ with respect to the total number of shoots of daughter plants.

Fig. 9 with data on experiment 4a points to the variability of couch with regard to tillering and vegetative propagation. The experiment was set up in the same way as experiment 1 (plant development from individual leafy shoots), but was carried out with plants of a restricted number of clones (K) (6 clones, 96 plants). Moreover, the plants in the experiment were subjected to different clipping regimes; these regimes differed in the date of the first clipping (T), 9 June and 20 July and the frequency of clipping (F), 3- and 6-weekly clippings. In general no significant interactions between the main factors K, T and F were found in the experiment with respect to the plant characters studied. Therefore the clones may be compared on the basis of their means for the whole experiment (fig. 9) with regard to these characters. Clones differed significantly at $P = 0.001$ with regard to each of the characters.

The clones differed considerably in tillering of the parent plants (fig. 9, characters 1a and 1b). In June they varied from 0.65 to 1.35 with respect to the general mean (A) of the experiment, in August from 0.21 to 2.39. The sequence of the clones was the same in both cases. The great difference between the two observations was caused by the fact that in two clones the shoot number of the parent plants continued to increase up to the last clipping date, whereas that of the remaining clones after an initial increase, remained the same or decreased. Thus the period in which the shoot number increased differed widely between the clones. The effect of the clipping treatments on the tillering of the parent plant was significant (fewer shoots per plant as the frequency of clipping increased), but small compared with the clonal effect. Thus on the last clipping date 62 % of the total variation in the character could be attributed to the
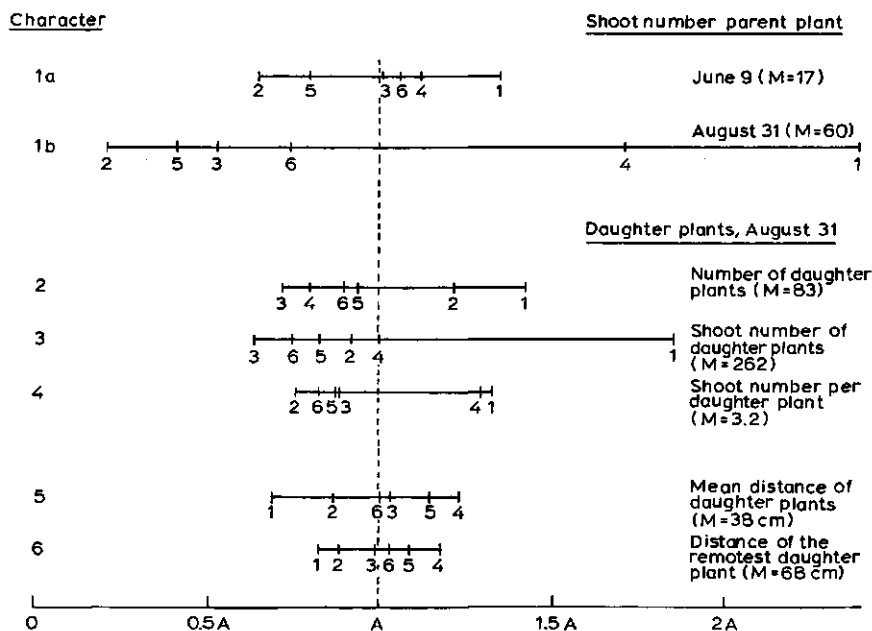
FIG. 9. Number of shoots of parent plants and daughter plants, number of daughter plants, mean distance of the daughter plants and the distance of the remotest daughter plant of 6 clones in experiment 4. The means of all clones are put at A, the means per clone are represented as relative values of A. In brackets are the real means of the clonal characters (M). The clones in the figure are indicated by a number.

clonal factor and only 7.5% to the factors T and F and the interaction of T × F. Later in the growing season the clones showed about the same sequence with regard to tillering of the daughter plants (character 4).

The most extreme clones differed by a factor 2 in the number of daughter plants, but a greater number of daughter plants was not always accompanied by a greater distance, as shown in fig. 9 by comparing the sequence of the clones with regard to character 2 and characters 5 and 6. On an average, the clones did not show great differences in tiller size during the growing season; however, they differed considerably in rhizome thickness. A relationship between the latter character and the degree and distance of daughter plant production, however, could not be demonstrated.

Of course the number of daughter plants and the distance of daughter plants were also determined by the date of the first clipping (T) as well as by the frequency of clipping (F). In general the plants produced more daughter plants and daughter plants at a greater distance as they were cut less frequently. The T and F effect on the two characters were of the same order as the clonal effect (K).

Of the clones 1, 2, 3 and 4 the vegetative propagation was also studied in a

3-years old grassland, around couch sods with a diameter of 20 cm, which were planted at distances of 4 m (experiment 4b). The grassland was cut twice a year and received a moderate NPK dressing. The vegetative propagation from the sods in the surrounding grass vegetation progressed very slowly in the first year (1969), but by 1972 had taken place to the same extent as in experiment 4a in 1967. With regard to the degree of propagation the clones now differed to a less extent, but as in 1967 considerably more daughter plants were again produced by the clones 1 and 2 than by the clones 3 and 4. Still, clone differences are not constant under all conditions with regard to vegetative propagation, as was found in 1970, when a final observation was carried out in the above-mentioned experiment 4a. The individual plants in this experiment had then changed into one homogeneous couch vegetation, but the largest areas with the most daughter plants were ultimately formed by clone 4 (fig. 9). Thus the clone with the remotest daughter plants and with good tillering stood out now, and not clone 1 which had indeed produced the greatest number of daughter plants in the first year, but at a relatively short distance. Since 1968 the experimental field was treated in the same way as the grassland in experiment 4b, i.e. cut twice a year and moderately dressed with N, P and K.

4. DISCUSSION

In the Flora Neerlandica (JANSEN, 1951) a number of varieties and various forms of *Elytrigia repens* are described, which reflect the variation within the species with regard to a number of morphological characters. A highly variable character is awn length, on the basis of which the varieties *vulgare* (Döll) Volkart (lemmas unawned, blunt or pointed) and *aristatum* (Döll) Volkart (lemmas short- to long-awned) are distinguished in the Flora. In accordance with the Flora we found that in the Netherlands forms of *Elytrigia repens* with short awns or with hardly any awns were the most frequent. Over 50% of the ears collected along roads in different parts of the Netherlands showed a relative awn length varying from 0 to $\frac{1}{8}$, whereas the frequency of ears decreased at increasing awn length. The same was found in experiment 1. The material as a whole did not show a two- or more-peaked frequency distribution, but those collected along one route in South Limburg did show a tendency towards a two-peaked frequency. The highest frequency was found at a relative awn length of 0 to $\frac{1}{8}$ and subsequently a high frequency at a relative awn length of $\frac{1}{2}$ to 1. In this case a non or short-awned and a relatively long-awned variety might have occurred. JANSEN also described another variety *glaucum* (Döll) Volkart with a bluish or grey-green colour. The variety is supposed to occur particularly along the Dutch main rivers and has non-keeled lemmas. In experiment 1 10% of the plants were entirely bluish-green (wax layers on leaves, stems and ears), but these plants mainly belonged to two populations. Fewer than 30% of the bluish-green plants were distinctly short-awned (relative awn length < $\frac{1}{8}$) or unawned.

Robust plants with a shoot length of 2 m, which are described by JANSEN as variety *majus* (Döll) J. et W. and which are occasionally found on fertile soils, did not occur in the plant collections in experiment 1. They were found outside this collection, however, and then sometimes had leaves of over 2 cm wide. When grown at Wageningen, the forms proved to keep their characters with regard to the shoot size. In root tip cells of some robust forms of *Elytrigia repens* chromosome numbers were found which agreed more or less with 2n = 42, a number in literature considered to be normal for the species (PALMER and SAGAR, 1963) In the Flora Neerlandica another variety *stenophyllum* (A. et G.) J. et W. is described with very narrow, often folded leaves and with a short ear. Plants of this type often show a slightly red colour. They were not found in experiment 1, but occurred in a pot experiment (1970) with plants grown in poor woodland soil. According to JANSEN the form is found along the North Sea behind the dunes and perhaps should be considered as a phenotypical modification.

In an experiment in which plants of 24 couch clones were grown under equal conditions (experiment 2) the genetic variability of the species with regard to a great number of morphological characters seemed obvious, among other things, hair length and hair density on the upperside of the leaves. Also with regard to these two characters a gradual variation of couch forms could be taken into consideration. In the same experiment the species seemed variable with regard to characters not mentioned yet, such as length of the auricles on the leaf base, the number of spikelets per ear (means per plant per clone varying from 16 to 24) and the number of flowers per spikelet (means per plant per clone varying from 4 to 8).

In experiment 1 both within the A and the B collection simple correlations were calculated between the plant characters observed. For the A collection these correlations are represented in table 4, but only those correlations which proved to be significantly positive or significantly negative in both plant col-

TABLE 4. Correlations between characters of the plants in the A collection (over 300 plants); n.s.: not significant within the A and/or B collection.

	Growth habit	Shoot length	Leaf length	Leaf width	Stem diameter	Ear length	Number of shoots parent plant	Number of daughter plants
Shoot length	0.27							
Leaf length	0.28	0.28						
Leaf width	0.16	0.30	0.50					
Stem diameter	0.16	0.34	0.38	0.47				
Ear length	0.25	0.28	0.26	0.31	0.34			
Number of shoots parent plant	0.20	0.29	n.s.	0.20	0.22	0.26		
Number of daughter plants	n.s.	0.19	0.13	0.19	n.s.	n.s.	0.15	
Heading date	n.s.	−0.34	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

lections (A and B). Significant correlations were found between the characters concerning the shoot size of the parent plants: shoot length, leaf length, leaf width, stem thickness and ear length, between each of these characters, on the one hand, and the plant form, tiller number of the parent plant and number of daughter plants per plant, on the other hand, and also between the plant form and the number of tillers of the parent plant, the number of daughter plants and the tiller number of the parent plant, and between the heading date and the shoot length of the plants. The latter correlation was negative, which may have been due to not all plants having fully developed shoots, when shoot length was measured. The characters 'awn length', 'hair density of the leaves' and 'mean weight per rhizome in 16 borings' have not been mentioned in the table, because they did not show a significantly negative or positive correlation in both plant collections.

In experiment 1 the possibility was investigated on a limited scale of a classification of the plants in types on the basis of more than two characters. For this purpose the plants were classified according to the various possible combinations of plant-form classes, awn-length classes and the classes of hair density of the leaves. A few combinations occurred more frequently than might be expected at a random combination of characters, but this was caused by two populations a and b (table 5). In population a a plant type dominated (74.5%) in which an intermediate prostrate U-formed habit was related to rather long awns and densely haired leaves. In the collection as a whole (A and B plants together) 7.2% of the plants belonged to this type, whereas only 3.5% was to be expected at a random combination of characters. In population b a plant type dominated (73.3%) in which another habit (U-formed) was related to rather long awns and densely haired leaves. In the collections as a whole 6.9% of the plants belonged to this type, whereas only 4.6% was to be expected at a random combination of these characters. After excluding these two populations, the two plant types within the collections were represented by only 0.9%

TABLE 5. Frequency percentages of two plant types in two populations a and b and in the whole collection of plants in experiment 1, including and excluding the two populations. The plant types are distinguished on the basis of the various possibilities of combining the classes of growth habit, of hair density and of relative awn length. Represented are frequency percentages observed in the experiment and expected frequency percentages of the plant types at a random combination of characters.

Plant type			% Plants in:					
Class growth habit	Class relative awn length	Class hair density leaves	Whole collection		Collection minus populations a and b		Populations a	b
			observed	at random	observed	at random		
2	3 + 4	3	7.2	3.5	0.9	1.0	74.5	
3	3	2 + 3	6.9	4.6	1.1	1.6		73.3

and 1.1 % of the plants. Especially the former percentage (0.9%) was in agreement with the expected percentage for independent characters (1.0%). Both populations were collected from leys and had possibly developed after tillage from a limited number of patches of genetically related couch plants. Generally speaking a considerable variation was found within populations with regard to characters, but concerning many characters populations differed significantly. This has been illustrated for a number of shoot characters in fig. 5.

The populations were collected from fields on various soil types (sand, clay, peat soil, reclaimed peat soil) and with different uses (arable land, leys and grasslands differing with regard to cutting or grazing). The shoot characters studied (fig. 5), the degree of tillering and the number of 'daughters' of the parent plant did not show any relationship with these characteristics of the fields. This may have been due partly to the fact that precise data on all these characters were only collected once in experiment 1 in the first year. For, the clone study showed that during the growing season clone differences with regard to leaf dimensions are not always constant (table 1). With regard to the vegetative propagation the data further suggested effects other than seasonal ones on the expression of probable genetic differences within the species.

Indications for correlations between growth habit, hair density of the leaves and awn length, on the one hand, and characters of the original locations of the plants, on the other hand, were neither found. Taking a character like awn length this was self-evident, because on agricultural soils no important ecological function can be attributed to awn length and also because the character was not significantly correlated with any of the other characters studied. The varieties *vulgare* and *aristatum* described in the Flora Neerlandica therefore seem to have no particular relevance on agricultural soils.

The data on the average weight per rhizome piece in the borings of the plants in experiment 1 suggest that particularly forms of *Elytrigia repens* with thick rhizomes can propagate on arable land. This seems to be contradictory to the rhizome thickness in experiment 1 being correlated neither with the shoot size nor with the measure of daughter plant production from rhizomes. However, thick rhizomes may contain more food reserves per unit of length which could accelerate the regeneration of the species. Indications of such a relation between rhizome thickness as well as rhizome length and the rate of first shoot growth, can be obtained from data of HÅKANSSON (1968). However, a greater rhizome thickness should then be a positive character not only in arable land but also in grassland. Here, it is remarkable that the data on the 13 permanent grasslands seem to contradict this. It is also possible that in arable land thicker rhizomes are less susceptible to drying out when brought to the surface by cultivation. Indications for this were found by GRÜMMER (1963). Anyhow, the significance of the rhizome thickness in arable land and grassland seems to require a closer investigation. The relationship found could possibly be tested anew in a comparative investigation of populations.

Experiment 1 does not clearly show in how far the heading date of *Elytrigia repens* in grassland is correlated with the use in spring (always a late first cut or

intensive grazing in spring) as was found by SONNEVELD (1966) for *Lolium perenne*. Anyway, with couch the population differences in heading date found were relatively small. Moreover, with this species such a correlation cannot be directly expected. For, in *Lolium perenne* this correlation is in fact one between the period of stem elongation and the mentioned use, in which the stem elongation can be easily described by stages of the ear formation. So, with *Lolium perenne* stem elongation and ear formation are more or less synchronized processes. With *Elytrigia repens* the time of the first stem elongation and heading date show more divergence, with clear differences between clones in this regard (experiment 5). Moreover, shoots of the species can also elongate considerably after the period of heading (vegetative stem elongation). In general the strong tendency of the species to elongate seems to be a weak point in grasslands with intensive use, particularly when *Lolium perenne* has been sown. As a result of its good tillering and of the fact that before and after the period of heading mainly leafy shoots are formed, the latter species is pre-eminently fit for intensive grazing or frequent cutting. The clonal differences in elongation behaviour with *Elytrigia repens* (fig. 8) could also be interesting with regard to the production pattern of this species in grassland.

Elytrigia repens is a long-day plant in the sense that heading is promoted by long day. The species seems to need little or no low temperature or short-day induction for flowering. However, the differences in heading date between the populations (experiment 1) need not be necessarily caused by differences in day length requirements. They might also be connected with differences in the date of first leaf development and consequently with the trend of temperature in spring. Owing to its relatively late heading in the Netherlands, *Elytrigia repens* also produces viable seeds relatively late; even in early years viable seeds of early clones cannot be expected before mid-June. This implies that in grassland even in cases of a late first cut the chance of seed production and consequently reproduction of the species is small.

With regard to the variability in the dry-matter production by the various organs of the couch plant some remarks can be made. Clones can differ in shoot production as well as in rhizome production (HADDAD and SAGAR, 1968), but also these two characters are not simply correlated. In fact, the shoot and rhizome production have to be considered in relation to the total dry matter production of the plant. Root production is also important, the species being very variable in this respect. In a pot experiment with two clones from experiment 4 (clones 1 and 2) the proportional distribution of the dry matter of shoots, rhizomes and roots, amounted to 35, 32, 33 and 31, 61, 8, respectively, at a more or less equal dry-matter production. The high root production of the first clone was partly due to significantly more root development of the individual rhizome internodes. The roots of couch plants are not mentioned usually in papers on the control of the species, because especially the rhizomes are considered to be the cause of couch problems in cultivated soils. Otherwise, also the root system of the defoliated couch plants could be important in the rate of shoot formation from new rhizomes, for example, in grassland after

cutting. Indications were found in support of this. This regrowth might be of another type than that in arable land after tillage, where no root system remains for the regrowth of *Elytrigia repens*. This should be taken into consideration in further studying the importance of genetic differences in rhizome thickness with regard to the occurrence of *Elytrigia repens* in arable land and in grassland.

The species probably showing considerable variability with regard to various ecologically important characters as well as these characters being weakly correlated, indicate the possibility of a great ecotypical variation within the species.

5. SUMMARY

Groups of *Elytrigia repens* plants of various grasslands, arable lands and leys in the Netherlands, were grown together in one experimental field. The plant groups differed in morphological characters, as growth habit, awn length, hairiness, size of stems, leaves and ears and in rhizome thickness, as well as in more physiological characters, as time of ear formation, time of stem elongation, tillering and rate and distance of daughter plant production from rhizomes. Generally, however, variability with regard to these characters was also considerable within the plant groups. The differences seemed to be due to heritable variation within the species. The data suggest a relation between rhizome thickness and use of the field as arable land or as grassland. The plant characters observed in general were not or only slightly correlated and so the plants could not be subdivided into distinct types, as is usual in keys.

A few experiments are discussed in which a further study is made of the variability within the species with respect to characters as, e.g. stem formation, ear formation, tillering and vegetative reproduction.

SAMENVATTING

Variabiliteit van Elytrigia repens *(L.)* DESV. *(Syn.* Agropyron repens *(L.) P.B.) op Nederlandse landbouwgronden.*

Groepen van *Elytrigia repens*-planten van verschillende graslanden, bouwlanden en kunstweiden in Nederland, werden op eenzelfde proefveld opgekweekt. De groepen van planten verschilden zowel in morfologische eigenschappen als plantvorm, kafnaaldlengte, beharing, afmetingen van stengels, bladeren en aren en in rizoomdikte, als in meer fysiologische eigenschappen als tijdstip van aarvorming, tijdstip van eerste stengelstrekking, uitstoeling en mate en afstand van nakomelingen-vorming via rizomen. In het algemeen was echter de variatie t.a.v. deze eigenschappen ook binnen de groepen aanzienlijk. De verschillen leken te moeten toegeschreven aan erfelijke verschillen binnen

de soort. De gegevens suggereren een verband tussen de rizoomdikte van de planten en de gebruikswijze van de percelen van herkomst als bouwland of als grasland. De waargenomen eigenschappen van de planten waren in het algemeen niet of slechts zwak gecorreleerd, waardoor de planten niet, zoals in flora's, in duidelijke typen konden worden onderverdeeld.

Enkele proeven worden besproken waarin is getracht nadere informatie te verkrijgen over de variabiliteit binnen de soort ten aanzien van eigenschappen als stengelvorming, aarvorming, uitstoeling en vegetatieve vermeerdering.

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