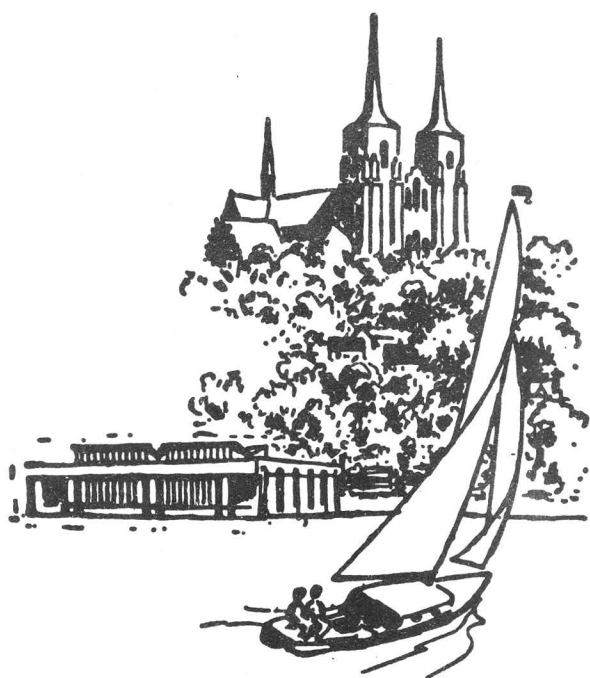# Breeding Methods and Variety Testing in Forage Plants

EUCARPIA

Report of Meeting of Fodder Crops Section

Roskilde 7-9 September 1976

Breeding Methods and Variety Testing in Forage Plants

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Report of Meeting of Fodder Crops Section
held at Lyngby Landbrugsskole
Roskilde 7–9 September 1976

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Organizing Committee

K. J. Frandsen

G. Julén

Hj. Møller Nielsen

Chr. Skov Larsen

B. A. Dennis

Frontispiece: Roskilde Cathedral and Viking Ship Museum
from the Fjord.

CONTENTS

PREFACE

Following a kind invitation forwarded by Dr. K. J. Frandsen, a meeting of the Fodder Crops Section of Eucarpia was held in Denmark on 7th-9th September followed by a one-day excursion to Sweden.

The subjects dealt with during the meeting were:

1) Selection criteria and methods
2) Adaptability and competitive ability
3) Adaptability and uniformity

During the two first sessions series of papers were presented followed by discussions. The third session was organized as a panel discussion. All papers presented are included in this report together with discussions.

The organizing committee under the chairmanship of Dr. K. J. Frandsen and with Dr. B. Dennis as secretary arranged the meeting in a very efficient way. The meeting was held at the Lyngby School of Agriculture which offered excellent accomodation and meeting facilities. The kind support received from the Department of Crop Husbandry and Plant Breeding, the Royal Veterinary and Agricultural University, during the planning phase is gratefully acknowledged, as well as the willing and efficient help offered by the secretariat staff.

During the meeting excursions were arranged to Danish Plant Breeding A/S at Boelshøjgård, to the Royal Veterinary and Agricultural University research station Højbakkegård, to the Carlsberg Breweries and to the town of Roskilde. On 10th September visits were made to the Weibullsholm Plant Breeding Institute, Landskrona, and to the Swedish Seed Association, Svalöv.

The generous hospitality offered by the Carlsberg Breweries, the Tourist Association of Roskilde, W. Weibull Ltd. and the General Swedish Seed Co. was highly appreciated.

Svalöv, Sweden, November 1976
G. Julén
President of the Eucarpia Fodder Crops Section

Session I

SELECTION CRITERIA AND METHODS

Chairman: Dr. J. Norrington-Davies

PHYSIOLOGICAL AND MORPHOLOGICAL SELECTION CRITERIA IN GRASSES

David Wilson

Welsh Plant Breeding Station, Aberystwyth, Wales.

SUMMARY

Some of the difficulties in identifying superior phenotypes at an early or even late, stage of plant development are discussed. Recent progress in the development of physiological and morphological selection criteria which can be used to distinguish potential parents from populations of otherwise similar young spaced plants is described. Examples are given from work on, i) biological potential, ii) water-use efficiency, and iii) nutritive value. The studies described have shown that, i) selection for a slow rate of dark respiration of mature, healthy, ryegrass leaves produces populations with more rapid crop growth rates in simulated swards than selections for fast respiration, with the original variety intermediate. This is thought to affect the 'maintenance' component of respiratory losses, ii) selection for leaf morphological adaptations affecting stomatal responses in ryegrass and cocksfoot has produced types with improved ability to conserve soil moisture and improved water-use efficiency, iii) selecting for leaf quality components also improves quality of other plant parts and, in tall fescue and cocksfoot in particular, low leaf cellulose and weak leaves (high quality) is associated with more profuse tillering, rapid leaf appearance and slightly shorter leaves than high cellulose.

INTRODUCTION

The selection of suitable parents for new grass varieties usually has to be based on assessment of productivity of individual plants in the field. Data is obtained from plants grown at different locations, in successive seasons and years and may use varying plant densities to simulate sward conditions. Highly sophisticated biometrical techniques have been developed to handle information obtained in this way and many excellent herbage varieties have been produced using mother plants selected on this basis. However, the process is very time consuming, the repeatability af field environments is often poor and there are some important aspects of yield in swards which would be difficult or impossible to detect by simply observing dry matter production of either isolated plants in a competitive situation.

We would of course be able to circumvent many of these difficulties if we knew which plant characteristics contributed most to high yield of digestible dry matter under the range of climatic and management conditions encountered during the life of the sward. Although far from complete, knowledge of the consequences to productivity of contrasting physiological behaviour and plant structure has progressed to the stage where we can expect to improve particular aspects of yield by selecting for specific quantifiable criteria (Rhodes 1973, Cooper 1974). These criteria can often be used to distinguish potential parents from populations of otherwise similar young spaced plants whose growth rates at the time of assessment may be identical. I will illustrate these points with recent results from physiological and selection studies on yield components contributing to, i) biological potential, ii) water-use efficiency and iii) nutritive value.

BIOLOGICAL POTENTIAL

The biological potential of a crop is reached when the assimilation of carbon by photosynthesis is maximised and the losses through respiration are minimised. All plant production ultimately depends on photosynthesis, which is determined by the size and distribution of the photosynthetic apparatus and by the rates of the process in the individual units. However, there is no reason why photosynthetic rate *per se* need bear a close relationship with productivity since processes such as respiration or translocation, or other limitations on the capacity of plants to grow and utilise photosynthate can be major determinants of production.

In temperate grasses, attempts to increase biological potential by increasing the maximum photosynthetic efficiency of individual leaves have so far been disappointing because of relationships between photosynthesis and leaf morphology. Genetic variations in rate of photosynthesis of unit leaf area or leaf volume are usually associated with variations in the size and number of mesophyll cells so that leaves with rapid rates tend to be relatively small (Wilson and Cooper 1969) and this leaf morphology is not in itself well suited to high rates of production under infrequent cutting systems (Rhodes 1973). On the other hand, selection for canopy characteristics, mainly long leaves, which improve light penetration and consequently whole crop assimilation, has resulted in increased yields in those conditions. However, the notion that it may be possible to improve the carbon economy of plants independently of morphology is still an attractive one, since this would open up the possibility of constructing a much wider range of ideotypes than would be possible on the basis of morphological type alone.

We have examined the genetic relationships of growth attributes of mature plants and swards with the gas exchange activities of individual leaves (Wilson 1975a). By screening and selection from within a population of perennial ryegrass of highly diverse origins we isolated a number of genotypes which, between them, exhibited a wide range in vigour of regrowth, net photosynthesis per unit leaf weight and leaf area, dark respiration, CO_2 compensation concentration, daily leaf starch accumulation and water soluble carbohydrate level. Assessments of these characteristics made on clonal replicates of mature plants showed that the only characteristic which was consistently associated with growth was the rate of dark respiration (Table 1). The more rapidly growing genotypes seemed to have inherently slower rates of respiration of their mature leaves. This respiratory activity was measured as oxygen uptake after a dark period. Leaves with faster photosynthetic rates tended to accumulate more starch during the light periods but, perhaps not surprisingly, did not necessarily grow faster.

Table 1. Significant correlation coefficients between leaf and growth characteristics of contrasting *Lolium* genotypes.

Correlated characters		r
Net photosynthesis	: daily starch increment	+0.89[***]
Dark respiration	: starch after 1 h light	−0.64[*]
Dark respiration	: rate of leaf expansion	−0.78[**]
Dark respiration	: regrowth dry matter yield	−0.89[***]
Rate of leaf expansion	: regrowth dry matter yield	+0.79[**]

(From Wilson 1975a)

This relationship is now being studied more closely by asking two questions: firstly, "are plants whose mature leaves exhibit relatively slow rates of dark respiration more productive in sward conditions?", and if so, "under what conditions and at what developmental stage does this become evident?". To do this, we initially screened two different S23 perennial ryegrass populations for dark respiration. Briefly, the technique used was to grow pop-

ulations of replicated genotypes in a controlled environment and measure
dark respiration of segments from several mature healthy leaves of each
ramet removed from plants immediately after the dark period. A 'steady
rate' respiration was then recorded over several hours. Mature roots exhib-
it similar rates to those of leaves, but the rates of actively growing tis-
sue are much faster and reflect different biochemical processes within the
leaf.

Using this technique we now have a number of independently selected groups
of ryegrass genotypes with either slow or fast respiration. From a cross-
ing programme we also have first and second generation families. Table 2
shows the range in respiration rates in two of the original populations.
Realised heritabilities from four different selection programmes were 0.65,
0.40, 0.53 and 0.90 respectively in the first generation.

Table 2. Initial screening: mean dark respiration rates (μl min^{-1} mg^{-1}
x 10^{-3}) of groups of genotypes selected for either fast (FR)
or slow (SR) respiration rate and of the original populations.

Selection	Population	Respiration rate	S.D.
1	FR	33.0	3.2
	S23	25.7	5.6
	SR	21.6	2.6
2	FR	32.3	5.9
	S23	24.9	4.9
	SR	18.0	1.9

Our growth data on this material so far confirms the earlier findings. Sim-
ulated swards made up of mixtures of clonally replicated genotypes with slow
respiration rates have consistently shown more rapid crop growth rates than
those with fast respiration, both in warm growth room conditions (25°C)
(Table 3) and at temperatures above 10°C in a glasshouse from August through
to April (Table 4) (Wilson 1975a).

Table 3. Mean Crop Growth Rates (CGR) (g dry wt m^{-2} day^{-1}) at two
successive harvest intervals in the growth room at 25°C of
simulated swards of plants with slow (SR) or fast (FR) dark
respiration rate. Each value is the mean of 8 replicates.

| Harvest interval | Selection group | | |
	FR	SR	5% LSD
1(4 wk)	5.78	9.14	2.03
2(5 wk)	4.97	8.19	1.80
(From Wilson 1975a)			

Table 4. Mean Crop Growth Rates (CGR) (g dry wt m^{-2} day^{-1}) in the
glasshouse of simulated swards of slow (SR) and fast (FR)
respiration selections. Each value is the mean CGR of
12 swards - 4 replicates of each of 3 independently se-
lected groups of genotypes.

Growth period (mean $^{\circ}$C)		FR	S23	SR	5% LSD
Sept	(18.3)	5.5	–	7.9	0.8
Oct	(13.8)	1.5	–	3.2	0.9
Nov-Dec-Jan	(10.0)	0.9	–	1.4	NS
Feb-March	(12.5)	2.5	3.0	3.4	0.5
Apr	(16.0)	8.6	10.2	15.5	1.6
(Data from Wilson 1975a)					

One explanation of this association is that our measurements of respiration of mature leaves might reflect relative differences between genotypes in the so-called 'maintenance' component of respiration, which, unlike the 'synthesis' component, is considered to be temperature dependent and can differ between species. Certainly loss of photosynthate by dark respiration of mature plants can be substantial (Robson 1973, Biscoe, Scott and Monteith 1975) and although it is not altogether clear what we mean biochemically by maintenance, as against synthesis, respiration, the proportion of respiration which represents the cost of growth does decline to relatively low levels in the mature crop. At the same time, the total respiratory cost of maintaining the integrity of leaves, stems and roots increases.

Under this hypothesis, it might be expected that if two populations differed only in the respiratory cost of maintaining mature tissues then any effect of this difference on growth rates would only be apparent at later stages of development of the crop. In our comparisons of growth of first generation families selected for either slow or fast respiration, these expectations were largely realised. During early seedling growth of young primary swards and up to an LAI of about 7, there was no distinct advantage in having a slow respiration rate, although the slow respiration families had developed a significantly greater LAI by about 9 weeks from emergence, (Table 5).

Table 5. Mean Leaf Area Index (LAI) and plant dry wt (dw) of slow (SR) and fast (FR) respiration families growing as simulated swards in day/night temperatures of $25^{\circ}/20^{\circ}C$. Each value is the mean of 4 families.

Days from 3 leaf stage	LAI$(cm^{-2} cm^{-2})$			dw(g)		
	FR	SR	5%LSD	FR	SR	5%LSD
7	0.09	0.08	NS	0.21	0.19	NS
14	0.53	0.55	NS	0.23	0.21	NS
21	1.53	1.45	NS	0.37	0.34	NS
32	3.95	3.96	NS	0.92	0.91	NS
39	5.07	5.40	NS	1.64	1.76	NS
46	6.63	7.91	1.23	2.25	2.92	NS(0.80)

However, the mature sequentially harvested swards of the slow respiration families had consistently greater crop growth rates over six consecutive monthly harvests than the fast respiration families (Table 6).

Table 6. Crop Growth Rates (CGR) (g dry wt m^{-2} day^{-1}) of sequentially harvested simulated swards of slow (SR) and fast (FR) respiration families growing in day/night temperatures of $25^{\circ}/20^{\circ}C$. Each value is the mean of 4 families.

Monthly harvest interval	CGR		
	FR	SR	5%LSD
1	7.7	8.8	NS
2	7.5	10.0	2.0
3	6.3	9.1	2.2
4	5.7	9.5	2.0
5	4.7	7.4	1.8
6	4.6	7.7	2.1

Using the same experimental material we are now recording similar differences in the field and we are turning our attention to determining the extent of variation in this character in our more common agricultural grasses and to combining it with other plant characteristics associated with dry matter production and quality.

WATER-USE EFFICIENCY

The rate of plant water-use either in the absence or presence of stress can be modified by variations in leaf epidermal structure. These sort of adaptations seem to lead to better conservation of water and may improve yield at times when growth may otherwise be restricted by lack of available soil moisture. The characteristics that we have so far studied in this way are those involved in stomatal control of water loss. In temperate (C_3) grasses we seem to be in the fortunate position of being able to reduce stomatal conductance, by selection or breeding, without apparently affecting potential rates of CO_2 uptake.

In the ryegrass/fescue group there appears to be at least two separate leaf anatomical mechanisms controlling water loss through stomata (Wilson 1975b, c). In these plants, stomata occur mainly on the adaxial (upper) surface where they are found in rows on the sides of the epidermal ridges. Abaxial stomata are usually few or may be absent altogether. Most of these species are outbreeding and there is a lot of genetic variability, both between and within species, in numbers and length of stomata and in the severity of the epidermal ridging. This makes it possible to produce populations with particular stomatal and structural characteristics to use in physiological studies. A reduction in theoretical stomatal conductance at any assumed pore opening can be achieved by having relatively few or short stomata (Wilson 1972). Operationally, this has the effect of reducing transpiration in the absence of stress and apparently delaying the onset of drought (Wilson 1975b). However, once stress becomes sufficient to affect leaf expansion and stomatal opening, stomatal numbers appear to make no difference to rate of water loss. The extent of stomatal opening is then critical. Stomatal response to changes in leaf water status or to changes in humidity of the external air is greatly affected by the severity of the epidermal ridges (Plate 1). Where ridges are not very large, stomata are very responsive to changes in water status and are capable of acting to conserve moisture quickly. The effect of more severe ridging seems to be to provide a humid microenvironment which buffers the stomata from environmental changes which might otherwise cause them to close. These differences in stomatal action are reflected in differences in growth responses at low soil moisture levels. Plants with more severe ridging seem to use all available soil moisture rapidly and become wilted much faster than plants with flatter leaf surfaces, which tend to be 'water-savers' (Wilson 1975c).

Trials in small ($1m^2$) field plots in which we monitored soil moisture with a neutron probe over a 6 week natural drought, showed that populations with either few stomata or less severe epidermal ridges continually maintained higher soil moisture levels in the main rooting zone, than plots of the variety from which they were selected (Table 7). This difference was accompanied by a 20-25% difference in dry matter yield. Interpretation of these sort of field results is often difficult but they are certainly promising enough for us to go ahead on the genetical side with producing populations combining different leaf characters. It is not difficult to see why such variation exists in ryegrass populations. Both of these strategies could be of advantage in different ecological situations. Sites with adequate soil moisture but low humidity and heavy radiation loads would be more favourable to plants with severe ridging, whereas soil moisture conservation would be better achieved with the 'water-saver' type.

We are also investigating a leaf structural adaptive mechanism which exists in *Dactylis*, another common agricultural genus. In this case the leaf surface is flat but individual stoma are surrounded on all sides by epidermal papillae cells. In the subspecies *marina*, which is found in coastal Portugal and the Canary Islands, these cells are large and seem to reduce wa-

ter loss (Plate 1). Unstressed leaves with this characteristic have rel-
atively low stomatal conductance but similar rates of CO_2 uptake to leaves

Table 7. Growth and soil moisture use of plots of *Lolium perenne*
experimental lines selected for either low theoretical
stomatal conductance (LC) or flatter leaf surface (WR)
compared with unselected base variety (GR).

Date (1975)	Soil moisture at 12 cm depth (arbitrary units)			
	LC	WR	GR	5%LSD
July 2	198	228	174	
4	239	258	194	50
7	177	185	155	
14	240	263	200	51
18	208	195	183	10
25	222	206	190	15
31	175	171	161	10
Aug 8	175	171	146	20
Crop Growth Rate(gm^{-2})	129	123	103	20

of the *glomerata* type with small epidermal cells (Wilson and Abdullah 1975).
The two types behave as 'water-spenders' and 'water-savers'. Breeding and
selection between *glomerata* and *marina* produces a whole range of leaf types
with consequent variability in water use patterns. In the field of course
the full advantage of a plant with water conserving characters would only
be apparent if it was grown in a sward composed of plants of a similar type.
This implies the need to breed varieties of a range of herbage species with
similar water use efficiency.

NUTRITIVE VALUE

More research effort has been put into developing reliable selection crite-
ria for nutritive value than possibly any other aspect of herbage yield.
Consequently, a range of chemical and physical methods of evaluation are
now available to the breeder. These generally provide, with varying degrees
of accuracy, direct or indirect assessments of either i) the proportion of
the feed which is indigestible, is not broken down by ruminal micro-organ-
isms, and generally passes straight through the gut, or ii) among tissues
which are digested, the relative proportions of more or less rapidly di-
gested materials (associated with intake). The relative merits of the
more recent techniques have already been discussed by Jones (1975) who
suggests that the general aims of improving firstly digestibility and
then intake characteristics are not inhibited by lack of appropriate cri-
teria. What are less clear, and just as important for varietal production,
are the sampling and screening techniques used and the effects of the selec-
tion on the physiology and agronomy of the plant.

Logic suggests that, for screening, assessment of nutritive quality should
be made on all plant parts above defoliation height. However, because of
differences in digestibility, and in characteristics affecting intake,
between leaves and vegetative and reproductive tillers this sampling proce-
dure may simply produce contrasting morphological types which have improved
nutritive value as a result of a change in the relative proportions of plant
parts. Such types may not only exhibit less variability in the sward than
as spaced plants, because of competitive effects on morphology, but may also
be of less value agronomically than the original variety (Davies 1974).
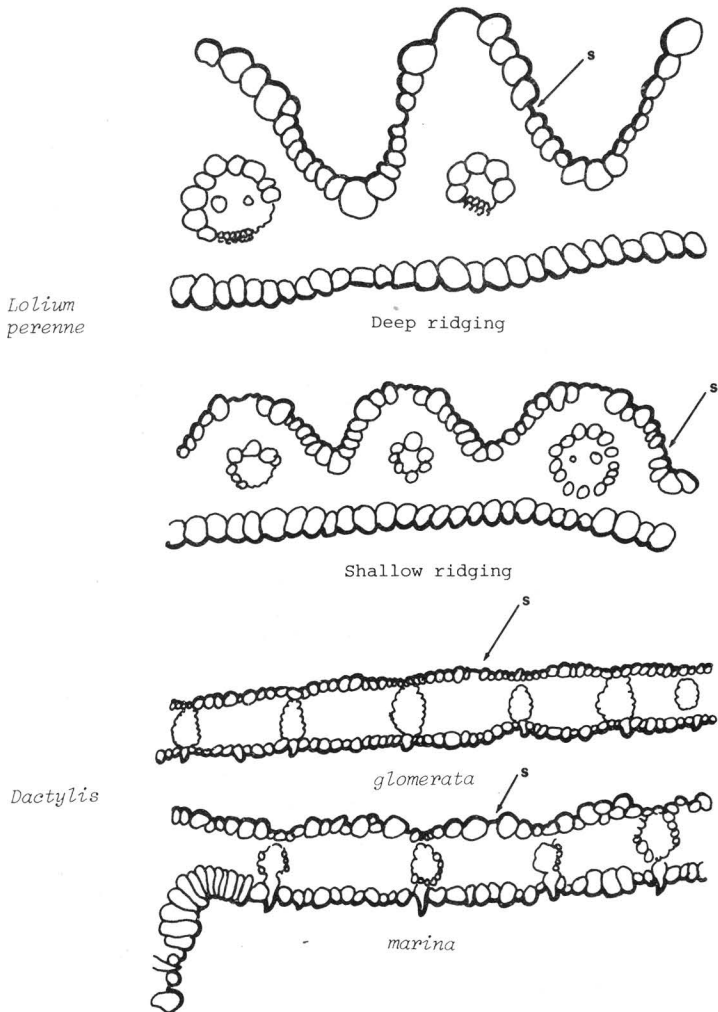Therefore while it is clearly possible to improve digestibility by, say,

Plate 1. Sections of *Lolium perenne* and *Dactylis* leaves with contrasting leaf surfaces and stomatal (S) sites.

having fewer reproductive tillers at any given time, or producing types with thicker vegetative stems, a more desirable objective would be to reduce the total amount of indigestible, or slowly digested, materials in all plant parts. Results from current selection experiments in tall fescue indicate that this can be done by screening for leaf quality (Table 8).

Table 8. Leaf tensile strength, Percentage cellulose and *in vitro* dry matter digestibility (IVDMD) of leaves and vegetative stems of four tall fescue families selected for contrasting leaf cellulase, and growing in simulated swards.

Family	Leaf strength (g mg^{-1})	% Cellulose		IVDMD	
		Leaves	Stems	Leaves	Stems
14	122	28.7	29.8	68.5	72.0
86	103	27.7	29.2	68.7	72.0
22	84	25.7	26.8	71.3	74.1
23	83	24.0	26.6	72.4	74.3
5% LSD	15	1.2	1.4	1.2	1.3

The specific anatomical fractions involved in genotypic differences in leaf or stem quality can be microscopically identified by digesting leaf sections in rumen fluid (Hanna, Monson and Burton 1973) or in solutions of cellulo-lytic enzymes (Selim, Wilson and Jones 1975). The first tissue to breakdown is the mesophyll followed by phloem, parts of epidermis and schlerenchymatous cells around the vascular bundles. Much epidermis, cuticle, xylem and lig-nified cells adjoining vascular bundles remain undigested even after rela-tively long experimental periods. Among tissues which are digested, differ-ences in their rates of breakdown can be associated with age, temperature during growth or inherent differences in cell wall structure (Table 9). The most readily soluble materials are of course contained within cells.

Table 9. Effect of genotype and temperature during growth on rate of digestion by cellulase, after 18 h in pepsin, of tall fescue leaf sections.

Source of variation		Time taken for mesophyll to disappear (min)	Leaf tensile strength (g mg^{-1})
Genotype	A	60-75	60
	B	60-75	65
	C	60-75	88
	D	75-90	147
	E	75-90	146
	F	75-90	157
Temperature	15°/10°C	45-60	−
	"	45-60	−
	"	60-75	−
	"	60-75	−
	25°/20°C	75-90	−
	"	75-90	−
	"	75-90	−
	"	75-90	−

It is the more complex cell wall polysaccharides, cellulose and hemicellu-lose which take longer to breakdown. Cellulose, in particular shows a strong negative correlation with intake (Jones 1975) and exhibits marked genetic variation, both between and within species. Leaves with relatively low levels of cellulose have low leaf tensile strength (Wilson 1965), tend to have thin primary cell walls, and are usually found in populations di-gested fastest by animals (Jones 1975).

It is clearly important that both digestibility and intake characteristics be considered as separate important aims in selection. Although these two can be correlated, wide variations in, for example, cellulose can occur at the same digestibility, even under sward conditions.

Table 10. Mean leaf and tiller characteristics, at the 6th leaf stage of first generation tall fescue families selected for either weak or strong leaves, together with the variety they were selected from (S170).

Character	Weak leaf	Selection S170	Strong leaf	5%
Rate of leaf appearance (days/leaf)	7.58	80.2	8.22	0.24
Tiller numbers	14.7	10.8	10.6	1.0
Leaf length (cm)	20.2	23.0	24.4	2.4
Leaf tensile strength (g mg^{-1})	54	89	110	10.1

Part of our programme concerns an evaluation of the relationships between quality and other characteristics which might affect plant growth responses. Initial results now show that in tall fescue and cocksfoot selecting for low leaf cellulose (or low leaf strength) produces types with relatively lax, smooth, leaves, a capacity for profuse tillering, and, at least as seedlings, slightly faster rates of leaf appearance and shorter leaves than the original variety (Table 10). These morphological changes have been less obvious in ryegrass. However, a low cellulose selection from a hybrid ryegrass has exhibited much better productivity in dry summer conditions in New Zealand than the original variety (Lancashire, Wilson, Bailey, Ulyatt and Singh 1976). Although we do no yet fully understand the physiological basis of this particular difference, I think it is clear from this and from our work on water-use efficiency and respiration that there seems to be no reason why we can't combine high quality with high productivity and ability to withstand at least some field stresses. In time the breeder should have available to him a range of criteria which he can use to assess the likely responses of his genetic material when it is in a sward situation.

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OPTIMAL NUMBERS OF PLANTS PER PLOT AND REPLICATIONS
FOR FAMILY SELECTION

F. England

Scottish Plant Breeding Station
Pentlandfield, Roslin, Midlothian, Scotland.

SUMMARY

The usual formulae for calculating the expected response to family selection compared to that for mass selection are modified for use where a family consists of Rn plants, where R is the number of replications and n is the number of plants per plot. Two methods of selection are considered, Method I where the plants comprising the selected families contribute to the family average, that is, are drawn from those actually tested, and Method II where the plants selected are collateral relatives of those actually tested. Two different assumptions are made, (a) in which the magnitude of R has no effect on the proportion of families selected and (b) where the proportion selected is itself proportional to R.

It is shown that:-

1. Under Method I there is, from the genetic viewpoint, no point in using more than one plant per plot. In practice n should be kept as small as practical considerations permit. Under Method II there is little point in increasing n beyond about twenty.

2. If single plant plots are acceptable there is rarely, under Method I, any advantage in using more than one replication, i.e., mass selection is the best system although there are exceptions when individual heritability is low and members of the same family are closely related. Under Method II the situation for clones, highly inbred lines and F_1 hybrid families is the same as under Method I but for full- and half- sib families there is some advantage in increasing replication of single plant plots.

3. When n is large the effect of increasing R is the same for both methods. There is always some advantage in increasing R if this does not reduce the intensity of selection (assumption a). Under assumption b optimal R lies between one and eight depending on the value of individual heritability and the degree of relationship within the families.

In this paper the term family is taken to mean any set of individuals, from one to infinity in number, within which set there is some known and constant degree of relationship. Besides the usual full- and half- sib families we also consider families consisting of clonal propagules of the same individual (e.g. potato varieties), of highly inbred lines (e.g. most small grain cereal cultivars) or of F_1 hybrids between inbred lines.

When discussing family selection it is convenient to consider two distinct methods which we will call Method I and Method II.

In Method I, the selected individuals contribute to the family average; that

is they are taken from the plants actually assessed, usually in some form of field trial. In Method II the selected individuals are the collateral relatives of those actually tested. With some modifications Method II also applies to progeny testing schemes.

The usual formulae for calculating the response to family selection compared to that for mass selection are given by Falconer (1960), Lerner (1958) and Lush (1937). They are, for Method I:

$$\text{Relative response} = \frac{1 + (N - 1)r}{\sqrt{N(1 + (N - 1)t)}} \qquad (1)$$

and for Method II

$$\text{Relative response} = \frac{Nr}{\sqrt{N(1 + (N - 1)t)}} \qquad (2)$$

Where:

N = the number of individuals in a family

r = the correlation between additive breeding values of members of the same family (1/2 for full- sibs, 1/4 for half- sibs and 1 for families of clonal propagules, for highly inbred lines or for families of F_1 hybrids between inbred lines)

t = the phenotypic correlation between members of the same family. If there are no phenotypic similarities between members of the same family which are due to common environment, then:

$$t = \frac{rA + \text{other common variance due to genetic causes}}{\text{total genetic variance} + E}$$

where $A = \sigma_A^2$ = additive genetic variance

E = variance due to environmental causes. In plant work, in the simplest cases, this will be due to plot effects and will in this paper be replaced by:

P = variance due to plot effects (it is assumed that the environment within a plot is uniform and that there are no competition effects).

It is also convenient at this stage to define

$D = \sigma_D^2$ = variance due to dominance

If we ignore more complex types of genetic variance, we may write:

$$t = \frac{rA + cD}{A + D + P}$$

Where c is a coefficient which varies with the type of family (1/4 for full-sibs, 0 for half- sibs and 1 for clonal families).

If all members of the same family share the same environment, different from the environment of other families, as may often happen in full- sib animal families, then:

$$t = \frac{rA + cD + P}{A + D + P}$$

This formula is given by Lush (1937).

In plant breeding we have a rather different situation in that our plants are commonly grown in replicated trials so that any individual may share the same environment with some of its relatives but not with all.

If we let

R = number of replications

n = number of plants per plot

we may rewrite (1) and (2)

$$\text{Relative response} = \frac{1 + (Rn - 1)r}{\sqrt{Rn(1 + (Rn - 1)t}} \qquad (3)$$

for Method I and

$$\text{Relative response} = \frac{Rnr}{\sqrt{Rn(1 + (Rn - 1)t}} \qquad (4)$$

for Method II. It remains to find an appropriate value for t and it can be shown that this is:

$$t = \frac{rA + cD + (n - 1)P/(Rn - 1)}{A + D + P} \qquad (5)$$

The coefficient, $(n - 1)/(Rn - 1)$, of P in (5) is the *a priori* chance that two plants taken at random from the trial will come from the same plot. In passing, we may note that if we grow our plants at l locations we could calculate

$$t = \frac{rA + cD + (Rn - 1)L/(Rnl - 1) + (n - 1)P/(Rnl - 1)}{A + D + L + P}$$

where L is the variance due to locations.

Before we can use (3), (4) and (5) to examine the expected relative response for various combinations of R and n we need estimates, or at least reasonable guesses, of the relative magnitudes of A, D and P. For purposes of illustration I have set A at 1 and then chosen values of D and P to give individual narrow sense heritabilities of 0.2, 0.5 and 0.8 where

$$h^2_{\text{individual}} = \frac{A}{A + D + P}$$

For simplicity's sake, we first consider examples with no dominance, that is

$$h^2_{\text{individual}} = \frac{A}{A + P}$$

or, since we have fixed A = 1

$$P = \frac{1}{h^2_{individual}} - 1$$

Figure 1 shows the effect of varying n while keeping R constant at four. We need only consider the full- sib curves in detail. The curves occur in pairs, the members of each pair merging into a single horizontal line to give the appearance of a 'Y' on its side. The upper line of each pair is for Method I. Increasing n always reduces the response until some lower limiting value is reached. This reduction is essentially due to the fact that we are selecting a more "diffuse" genotype and also that we are increasing the contribution of P to the magnitude of t. The lower line of each pair is for Method II and the response increases as n increases because, despite the increase in t we are also taking a more adequate sample of the family gene pool.

The story for the half-sib families is similar although at lower levels of relative response. The fact that all three pairs of lines converge to the same limiting value is an artefact due to, in the example chosen, r = 1/R.

The important conclusion from Figure 1 is that any increase in n, beyond about 20, has only trivial effect on relative response. If I had included the curves for clones, each pair of lines would appear as a single horizontal line because increasing n does not involve any increase in the number of genotypes per family.

All the remaining figures show the effect of varying R while holding n constant at one of two values, n = 1 or n = 128. The latter number is of no special importance, any value of n > 20 would have done.

Figure 2 shows the effect of varying R with n = 1 for Method 1. With clonal families increasing R always increases response and since t cannot exceed 1 and r = 1, this kind of "family" selection can never be less effective than mass selection. The lower the value of t, which in effect means the lower the individual heritability, the greater the benefit from increased replication.

The curves for full-sibs show two opposing tendencies, one in the "diffusion" effect already mentioned causing a reduction in response; but if we have a low value of t there is still some advantage from increasing replication. In the case of half-sibs, over the range of heritabilities chosen, family selection can never be better than mass selection. This is because the degree of relationship within the families is low (r = 1/4); the "diffusion" effect swamps any benefit from increased family size.

The column of figures at the right side of the graph shows the limiting values of relative response:

$$\text{Relative response} \xrightarrow[\lim]{} \frac{r}{\sqrt{t}}$$

which, in the absence of non-additive genetic effects, amounts to:

$$\text{Relative response} \xrightarrow[\lim]{} \frac{r}{\sqrt{rh^2_{individual}}}$$

Figure 3 shows the effect of increasing R when n = 128. The curves are applicable to either Method I or Method II. The curves for 'clonal' families

are as before and the limiting values for all types of family are also as before but until these values are reached the response under Method I is always less than when n = 1. The reason is that the value of t is now augmented by a proportion of the plot variance, P. The limiting values of response are unaffected because by indefinitely increasing R we can reduce this fraction of P to insignificance.

One point worth noting is that if we are using a polycross test, assessing half sib families, we may expect up to twice the response that we obtain from the half sib families, themselves.

Figure 4 is for n = 1, Method II, a rather unlikely situation in plant breeding, probably only of relevance when we have to destructively test our plants and therefore have to practise selection upon their relatives. The curves for clones are as in Figures 2 and 3; those for full- and half-sibs are similar to those in Figure 3, starting at slightly lower levels but reaching the same limiting values.

In Figures 2, 3 and 4 I have made one rather unrealistic assumption, that is that we can increase R without affecting our intensity of selection (assumption a). At some stage, increasing R must reduce the number of families which we can test and if we wish to retain some pre-determined number of families we have to retain an increasing proportion of those we test, thus decreasing the value of i, the standardized selection differential. The same arguments must apply with rather less force to increasing n. Under Method I, the lower the value of n, subject to practical considerations, the better and under Method II there is little point in increasing n beyond about 20.

Figures 5, 6 and 7 correspond to Figures 2, 3 and 4 respectively except that allowance has now to be made for the maximum effect that increasing R can have on the proportion of families retained (that is, that the proportion retained is itself proportional to R). The similarities between the two sets of figures are, I hope, obvious. Essentially, all the curves have been "bent" downwards, limiting values are all zero because, on the assumption made, we eventually reach the situation of growing the same number of families that we wish to retain and therefore not being able to make any selection at all.

In figure 5 (n = 1, Method I) we see that maximum response is usually obtained when R = 1, that is, mass selection offers our best chance. The two clonal families of lower heritability are the exceptions. In Figure 6 with n = 128 the clonal curve is, of course, the same as in Figure 5. Increasing R beyond 1 usually has some beneficial effect because it reduces the value of t. Figure 7 is very similar to Figure 6.

There remains one aspect that we have not so far considered, that is the effect of the inclusion of dominance in the model. Figure 8 shows the effect of including various magnitudes of dominance variance, D, for n = 128 for Methods I and II and assuming that the proportion selected is proportional to R. The curves for clones (and inbred lines and F_1 hybrids) are unchanged because we are selecting the whole genotype and it doesn't matter what kind of genetic effects are contributing to the differences between families. The main effect of increasing levels of dominance in full- and half- sib families is to decrease the optimum values of R; this, however, is somewhat artificial and is a result of the way I have chosen to illustrate the effects. If we hold A and $h^2_{individual}$ constant, any increase in D "creates" a more than compensatory decrease in P.

CONCLUSIONS

1. Under Method I there is, statistically speaking, no point in using more than one plant per plot. In practice, n should be kept as small as practical considerations permit. Under Method II there is little point in increasing n beyond about 20.

2. If single plant plots are acceptable there is rarely, under Method I, any advantage in using more than one replication, i.e. mass selection is the best method although there are exceptions when individual heritability is low and members of the family are closely related. Under Method II the situation for clones and highly inbred lines is the same as under Method I but for full- and half-sib families there is some advantage in increasing replication of single plant plots.

3. When n is large the effect of increasing R is the same for both methods. There is always some advantage in increasing R if this does not reduce the intensity of selection (i). If increasing R reduces the value of i, then optimal R probably lies between one and eight.

4. For any given individual heritability the inclusion of dominance reduces the optimal number of replications (because if $h^2_{individual}$ and A are assumed constant, then any increase in P "creates" a decrease of D).

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EXPLANATION OF FIGURES

KEY   CL = "clonal families", FS = full-sib families, HS = half sib families.

Value of $h^2_{individual}$ ..... = 0.2, ----- = 0.5, ——— = 0.8

I = Method I   II = Method II.

Figure 1. Relative response (%), assuming no dominance (D = 0), using four replications (R = 4) and varying the numbers of plants per plot from 1 to 128 (n = 1 ——→ 128) Methods I and II as indicated.

Figure 2. Relative response for Method I when D = 0, n = 1 and R varies between 1 and 16.

Figure 3. Relative response when D = 0, n = 128 and R varies between 1 and 16. The graphs are applicable to either Method I or Method II.

Figure 4. Relative response for Method II when D = 0, n = 1 and R varies between 1 and 16.

Figures 5, 6 and 7. As Figures 2, 3 and 4 respectively but assuming that the proportion of families selected, (p) is proportional to R.

Figure 8. Relative response in the presence of dominance n = 128, R varies between 1 and 16. The graphs are appplicable to either Method I or Method II.
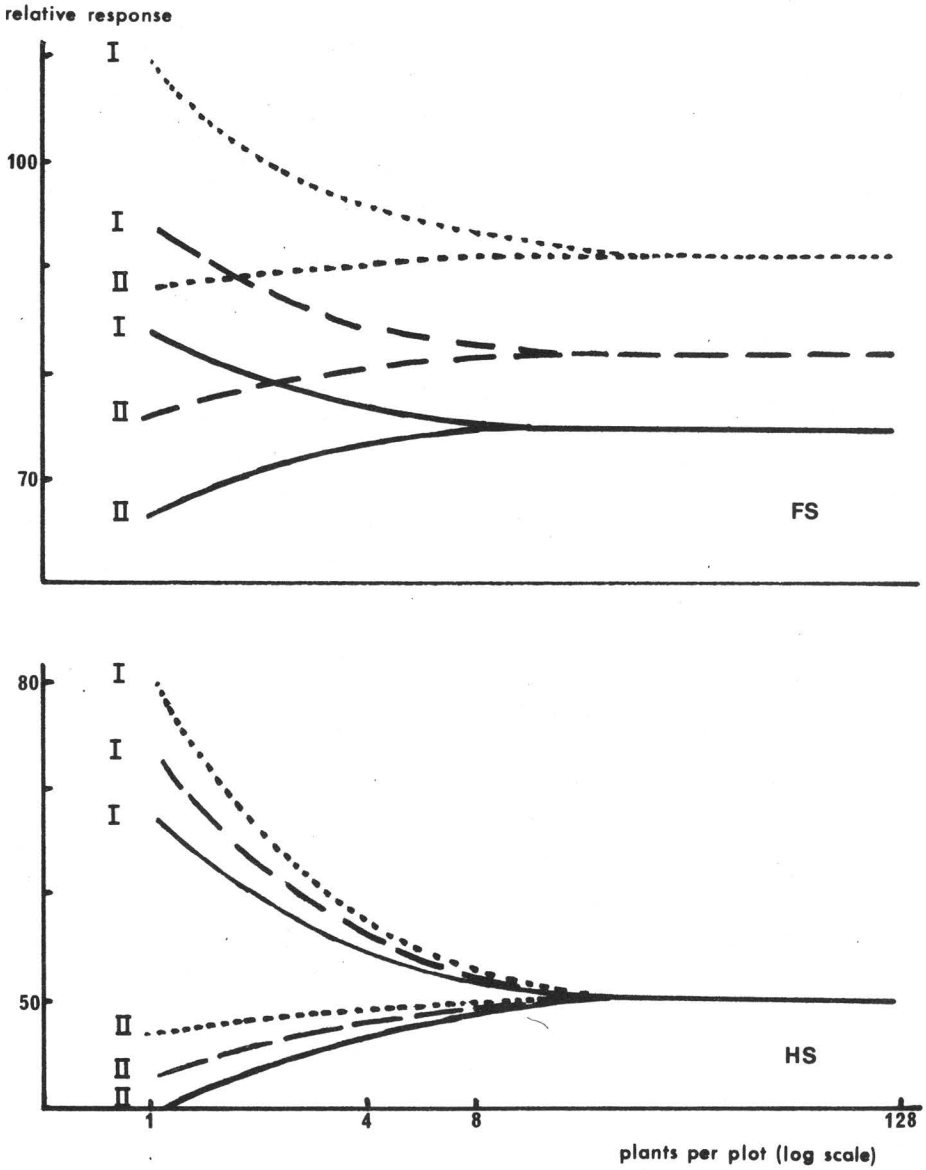
Figure 1. D = 0, n = 1→128, R = 4.

224
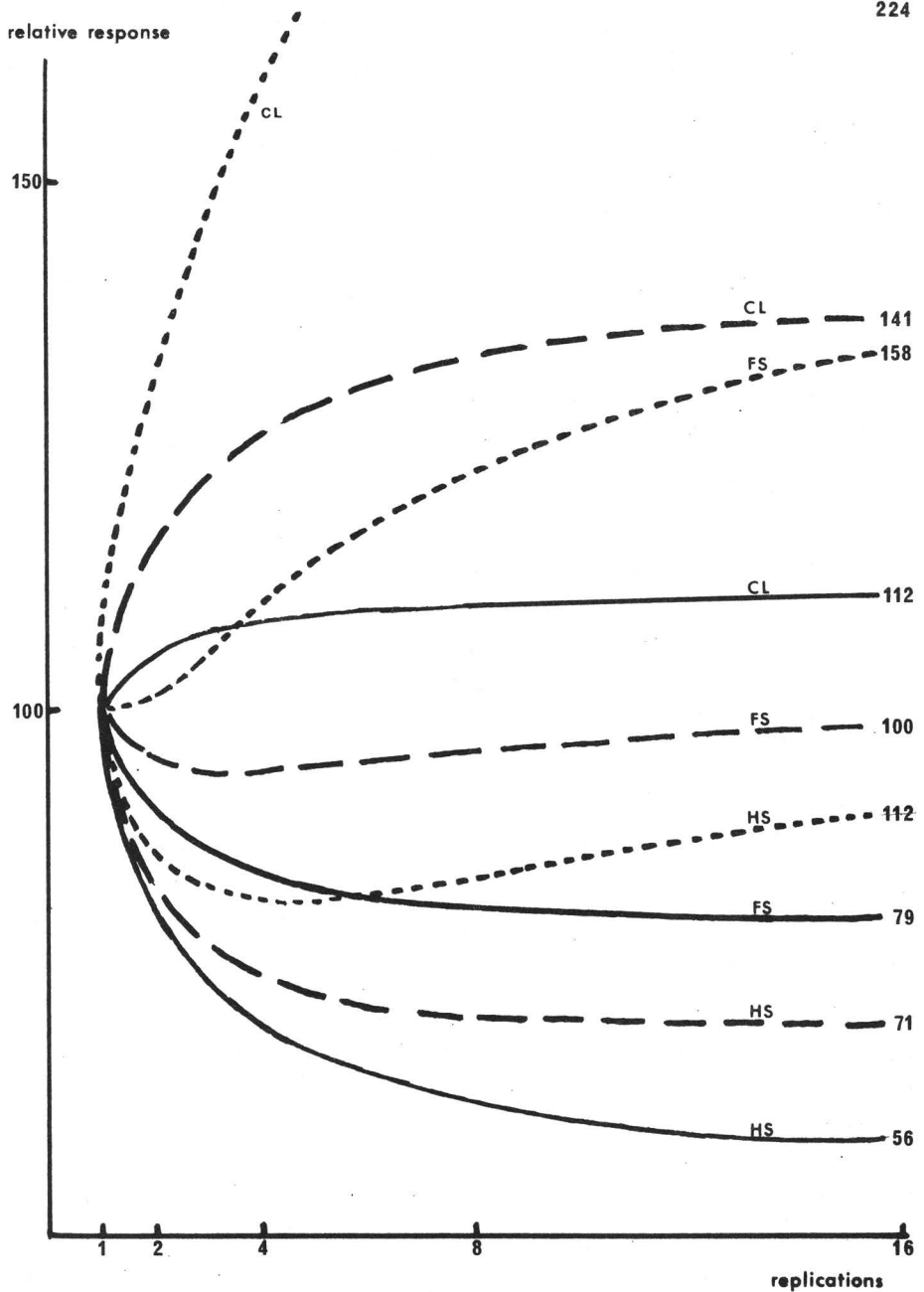
Figure 2.   D = 0,   n = 1,   R = 1→16.   Method I.

relative response

28

100

50

1 2 4 8 16

replications
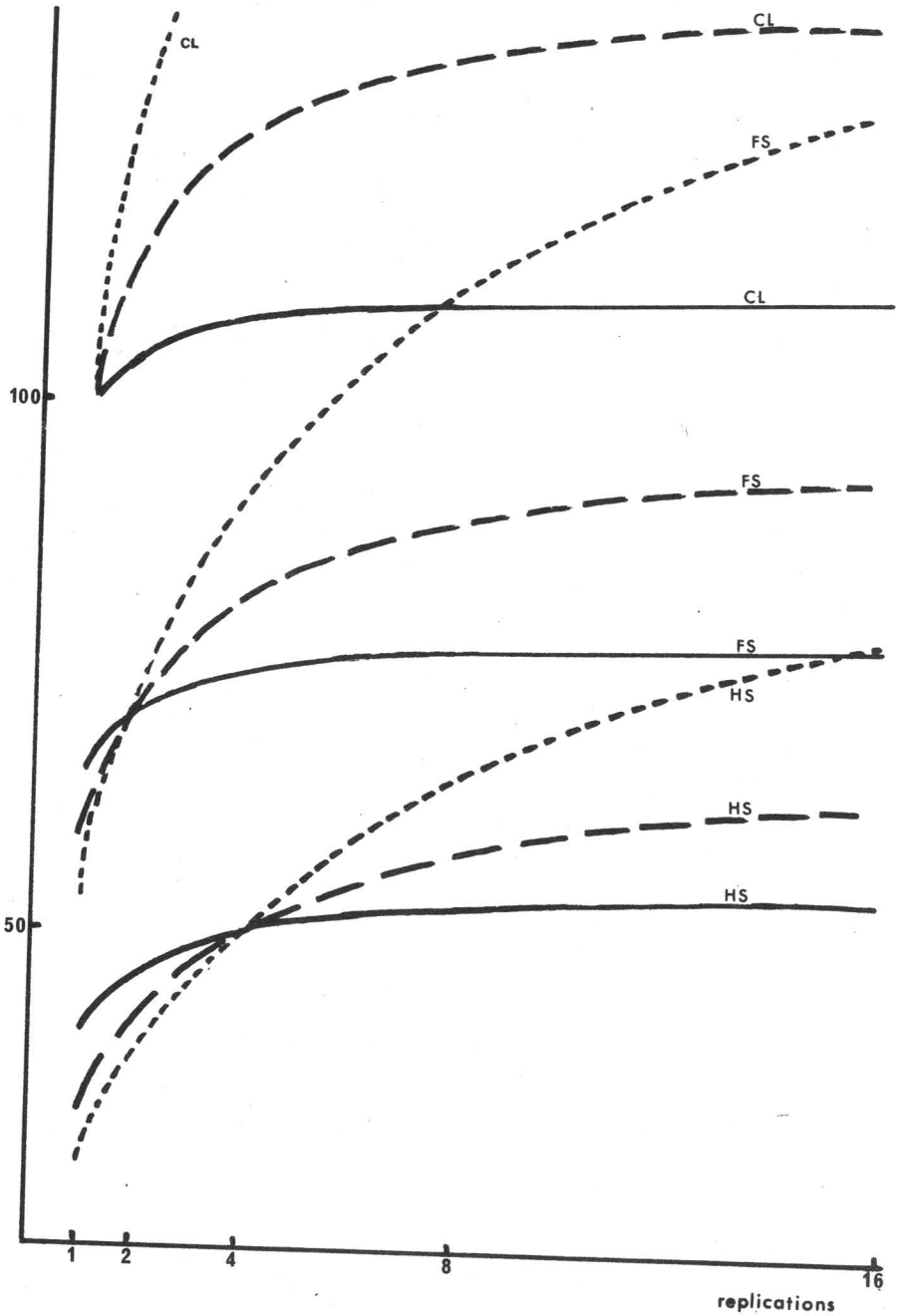
Figure 3. D = 0, n = 128, R = 1→16. Methods I and II.
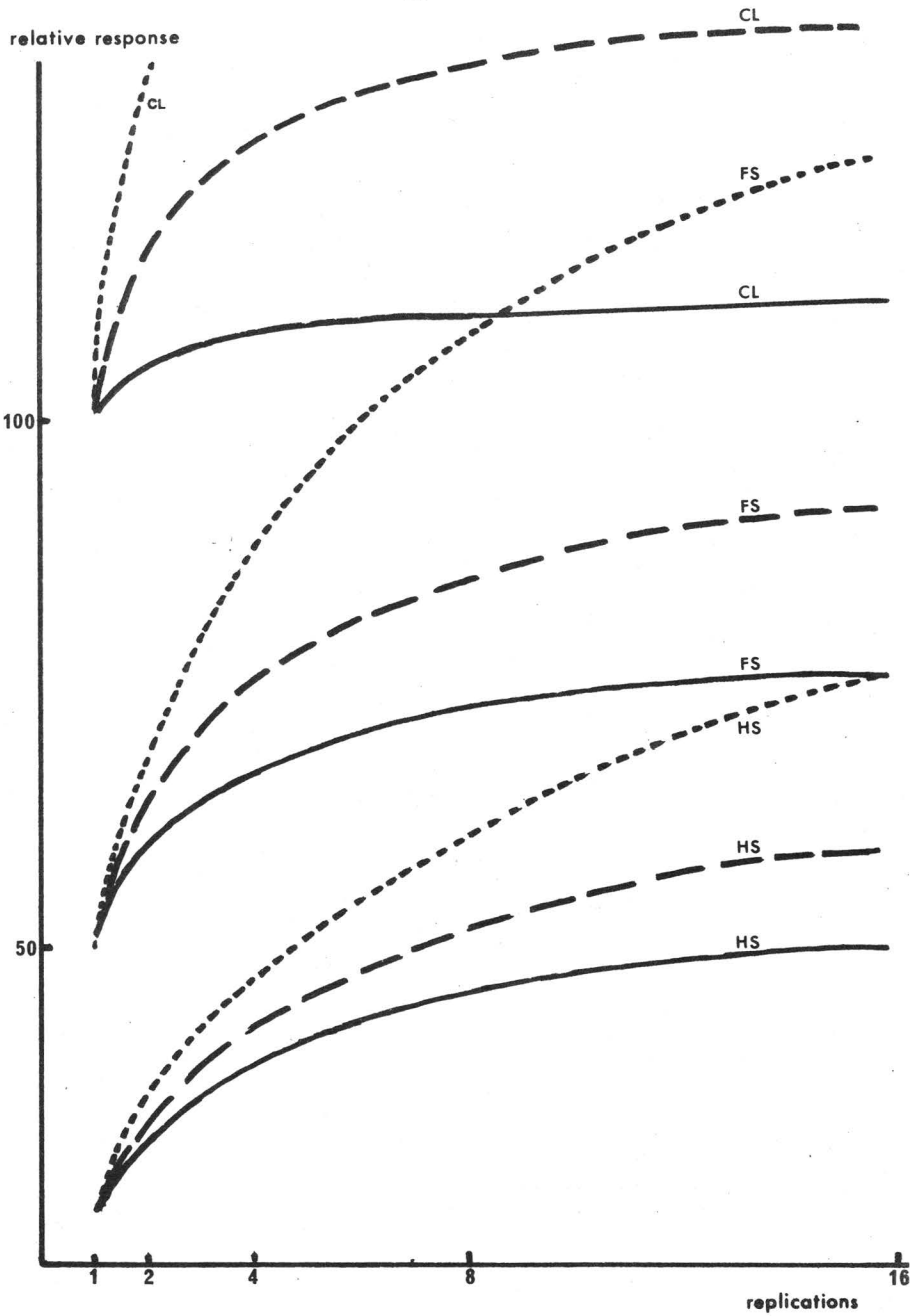
Figure 4. D = 0, n = 1, R = 1→16. Method II.
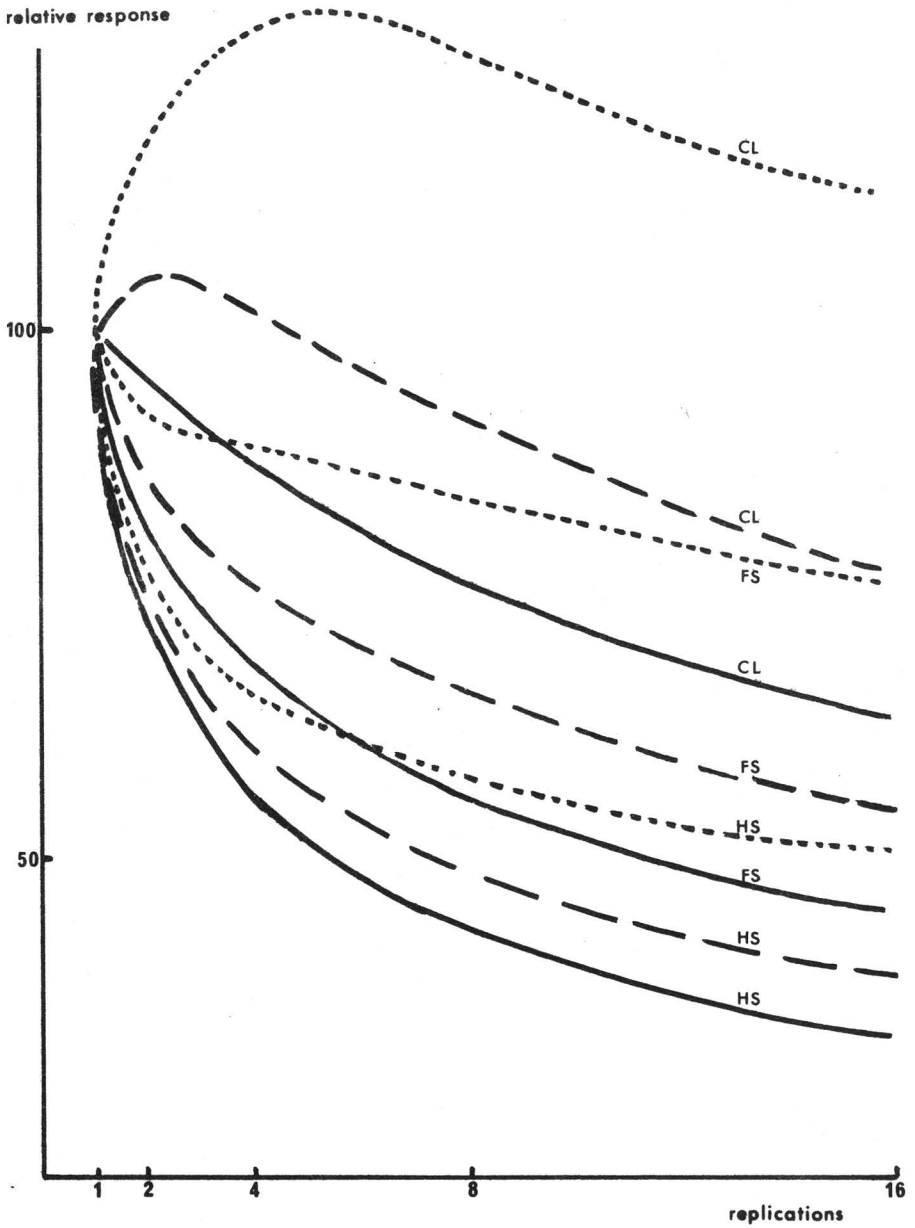
Figure 5. D = 0, n = 1, R 1→16. Method I, p ∝ R.
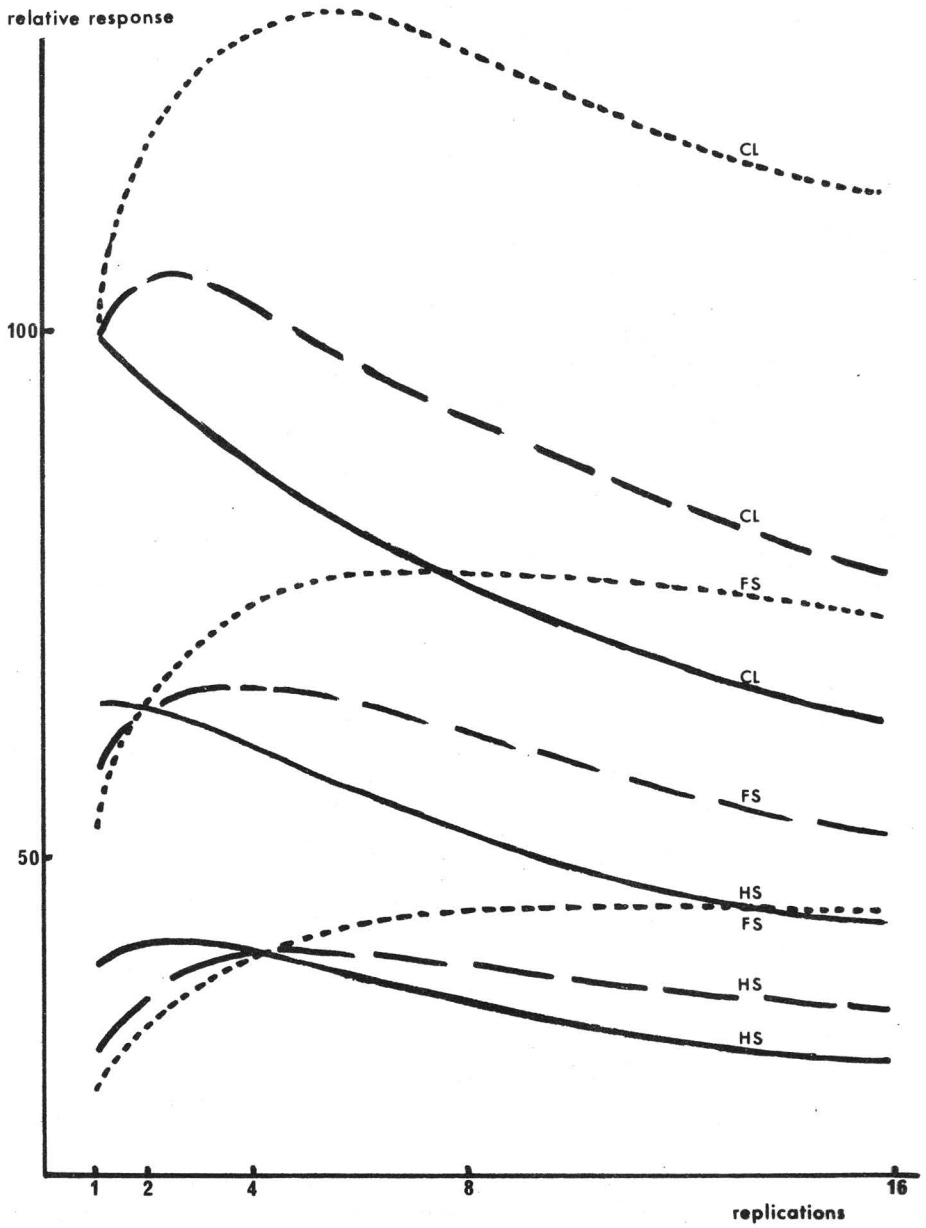
Figure 6. D = 0, n = 128, R = 1→16. Methods I and II, p ∝ R.

Figure 7.   D = 0,   n = 1,   R = 1→16.   Method II,   p ∝ R.
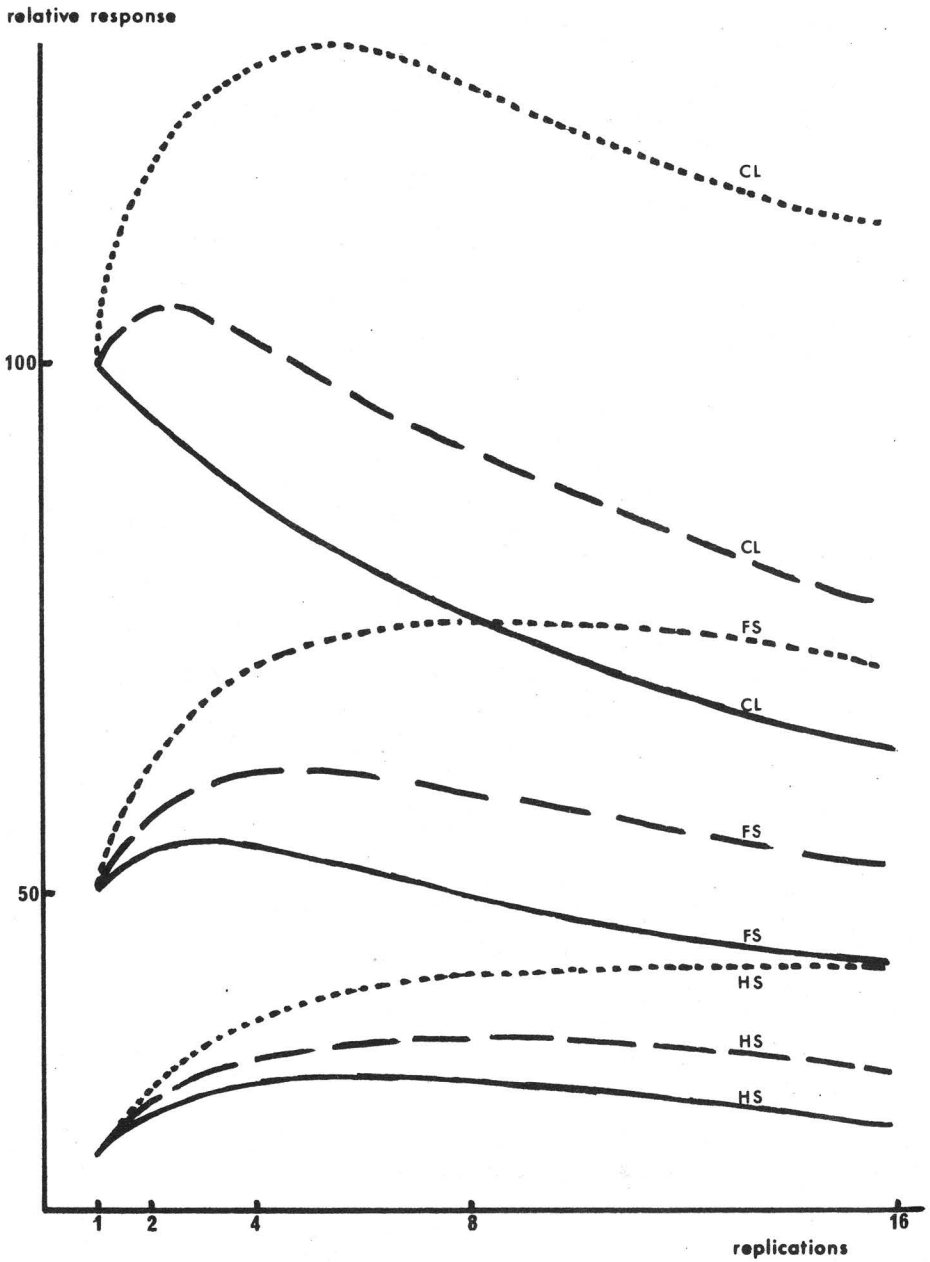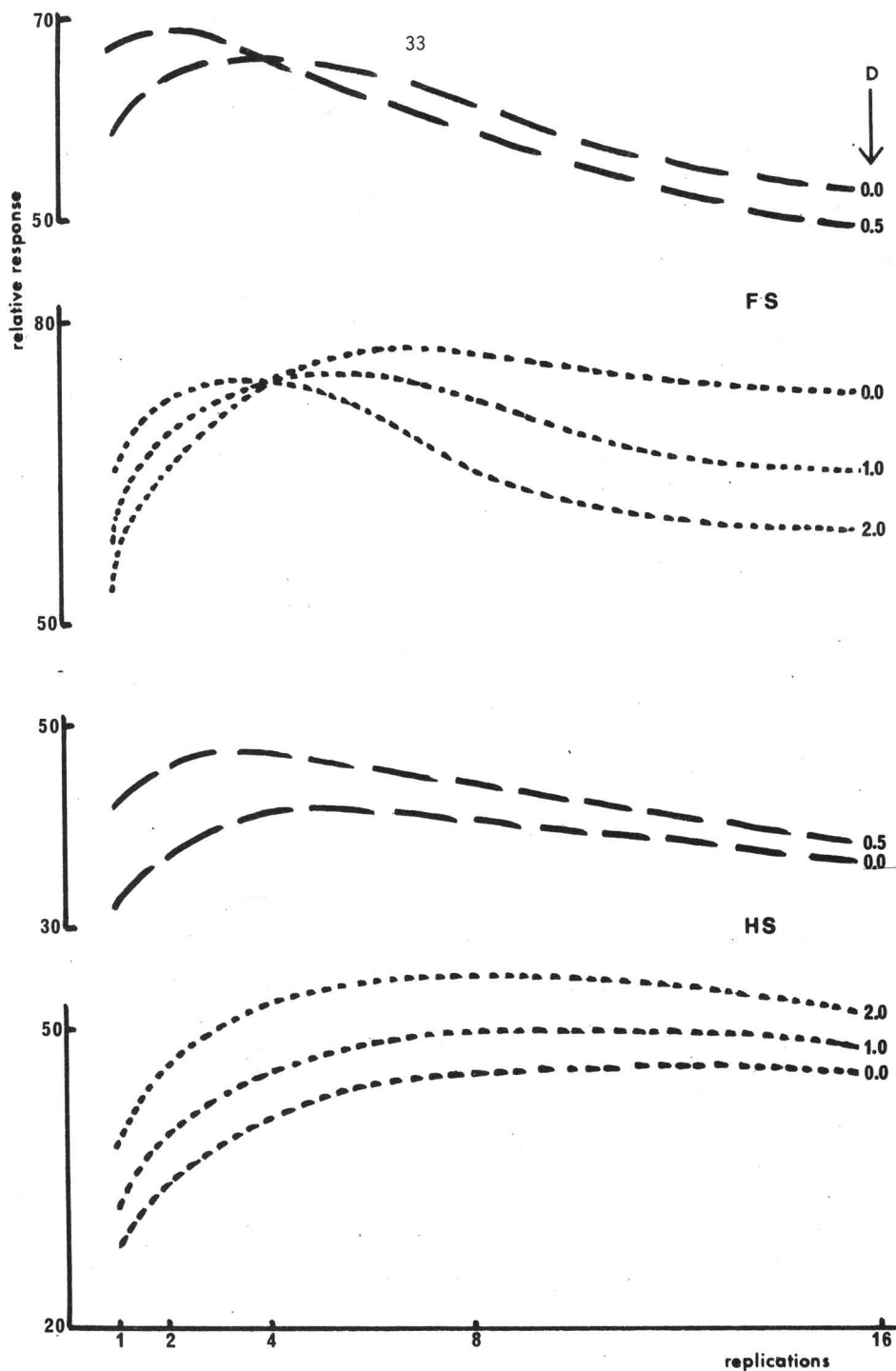
Figure 8. D varies, n = 128, R = 1→16. Methods I and II, p ∝ R.

MULTIPLE TRAITS SELECTION IN BRACHYPODIUM PINNATUM (*)

S. Ceccarelli

Plant Breeding Institute, University of Perugia, Italy.

SUMMARY

Tandem selection, independent culling levels and two types of index selection have been used for the choice of the best plants in a population of *Brachypodium pinnatum* P.B. The characters used were summer and autumn regrowth, green matter yield and winter regrowth. The paper illustrates the application of the different methods and the results so far obtained; the plants chosen by the indexes are 15% better than those chosen by direct selection for green matter yield; the total genetic gain expected with both indexes is about 35% greater than that expected by direct selection for green matter yield. The results are discussed in relation to the usefulness of selection indexes in plant breeding.

INTRODUCTION

Brachypodium pinnatum is a cross-pollinated, wild grass species, widespread in Central Italy mainly on the marginal lands abandoned by farmers during the last 20 years. The species is characterized by an high resistance to drought and by a very strong competitive ability; it can be utilized to protect the soil against the erosion and to ensure some green yield during the summer, which in Central Italy is usually very dry.

Breeding a variety from a wild species needs certainly a modification of more than one trait. The three standard methods available for selecting on more than one trait are tandem selection, independent culling levels and index of selection. The relative efficiency of these three methods has been discussed by Hazel and Lush (1942) for uncorrelated traits and by Young (1961) for two correlated traits. With few exceptions (Manning 1956, Caldwell and Weber 1965, Elgin et al. 1970, Pesek and Baker 1970, Subandi et al. 1973), these methods have been largely disregarded in plant breeding work. The purpose of this paper is to illustrate the application of the different methods of multi-trait selection in the breeding of *Brachypodium pinnatum*.

MATERIAL AND METHODS

In order to obtain the necessary information to develop the selection indexes, 160 genotypes and their open-pollinated progenies have been evaluated in a randomized block design with four replicates. Each mother genotype was represented in each replicate by a clone of 10 individuals and each open-pollinated progeny by 10 plants. In 1972 the following characters were recorded in this material:

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1. Spring growth, evaluated on 15th February 1972 (1 = min, 9 = max)
2. Heading time (days from 20th March 1972)
3. Green matter yield (g) at heading time
4. Summer regrowth (cm) after cutting on 2nd August 1972
5. Autumn regrowth (cm) after cutting on 16th November 1972
6. Leaf coarseness (1 = min, 9 = max)

Under the assumption of random mating, the variance between the open-polli-
nated progenies is equal to 1/4 of the additive variance between the mother
plants, and the covariance between a trait of the mother plants and a sec-
ond trait of the progenies is equal to

$$1/2 \ \sigma_{AxAy} + 1/4 \ \sigma_{(AA)x(AA)y}$$

where σ_{AxAy} is the additive covariance between traits x and y,

and $\sigma_{(AA)x(AA)y}$ is the epistatic covariance additive by
additive (Kempthorne 1957).

The composition of variance and covariance shows a very small amount of ge-
netic variability for leaf coarseness and an high phenotypic correlation
(-0.5752**) between heading time and spring growth. On the basis on this
information heading time and leaf coarseness were not included in the in-
dexes.

The first index of selection (index A) is that developed by Smith (1936) and
Hazel (1943): they defined the aggregate economic breeding value as

$$H = a_1 A_1 + a_2 A_2 + \ldots\ldots\ldots + a_j A_j$$

where a_j is the economic weight and A_j is the breeding value for trait j.
The selection index is

$$I = b_1 P_1 + b_2 P_2 + \ldots\ldots\ldots + b_j P_j$$

where b_j is the least square partial regression coefficient and P_j is the
phenotypic value of trait j. The regression coefficients of the index are
computed to maximize the regression of the aggregate economic breeding value
(H) on the selection index (I) and then the response to selection.

The second index of selection (index B) is that proposed by Pesek and Baker
(1969) in which the desired genetic gains take the place of the economic
weights.

In the development of the index A we used an economic weight of 1 for all
the four traits; for the index B we specified the following desired genetic
gains: rank 4 for spring growth, 35 g for green matter yield, 1 cm for both
summer and autumn regrowth.

The two selection indexes resulted as follows:

Index A = 1.5068 (spring growth) + 0.3607 (green matter yield) + 0.4692 (sum-
mer regrowth) + 1.6301 (autumn regrowth)

Index B = 1.6138 (spring growth) + 0.0238 (green matter yield) + 3.6387 (sum-
mer regrowth) + 2.3043 (autumn regrowth).

The two indexes have been used to select two groups of 12 genotypes each,
using as selection criterion the value of the index (A or B); a third group
of 12 genotypes was selected using the independent culling levels method.
The phenotypic values of the four characters entered in the indexes were
used to select four groups of 12 genotypes, and each group can be considered
as the selected parents for the first cycle of tandem selection. The selec-

Table 1. Selection differentials applied in seven selected groups of genotypes of *Brachypodium pinnatum* using different methods of selection.

Character	Means of the base population	Selection criterion						
						Direct selection for:		
		Index A	Index B	Ind. Cull. levels	Spring growth	Green matter yield	Summer regrowth	Autumn regrowth
Spring growth (1= min, 9 = max)	3.1	3.7	3.3	3.6	4.6	1.4	0.3	2.6
Green matter yield (g)	56.3	27.6	15.4	24.2	16.3	31.0	7.9	11.1
Summer regrowth (cm)	4.2	0.7	1.3	0.8	0.3	0.6	1.8	0.7
Autumn regrowth (cm)	3.1	0.9	1.4	0.8	1.0	0.7	0.7	1.6

tion pressure was always equal to 7.5%. The expected genetic gains with
the different methods have been computed using the formulae of Finney (1962)
and Subandi et al. (1973).

RESULTS AND DISCUSSION

In table 1 the different methods of selection are compared by means of the
selection differentials applied on the base population. The data show that
the selection differentials applied by the use of index A for spring growth
and green matter yield are greater than those applied by index B and by the
independent culling levels method; whereas with index B more emphasis is
given to summer and autumn regrowth. Compared to the methods of multitrait
selection, the direct selection applies greater selection differentials only
on the selected trait.

In table 2 heading time and leaf coarseness (the two traits excluded from the
indexes) of the genotypes selected with the indexes and with the independent
culling levels are presented. It can be seen that all the selected geno-
types are earlier than the base population, while leaf coarseness changes
significantly only in the group selected by index B. These results justify
the exclusion of heading time from the indexes, indicating that the observed
phenotypic correlation with the spring growth allows simultaneous improve-
ment of these two traits.

Table 2. Heading time and leaf coarseness of the 12 genotypes
selected by two types of selection index and by inde-
pendent culling levels.

Character	Average of 12 genotypes selected by:		
	Index of selection A	Index of selection B	Independent culling levels
Heading time $\bar{x}$ base population = 15.7	6.9	7.8	6.1
Leaf coarseness $\bar{x}$ base population = 5.7	5.5	5.3	5.6

$S_{\bar{d}}$ heading time $\quad = 0.9$

$S_{\bar{d}}$ leaf coarseness $= 0.11$

In order to compare the efficiency of the different methods two criteria
can be used: the phenotypic superiority of the selected materials and expect-
ed genetic gains. The results of the comparison between methods using the
first criterion are presented in table 3; while in table 4 the same compar-
ison is made on the basis of the expected genetic gains. In both tables
the efficiency of the direct selection for green matter yield has been as-
sumed as reference because the improvement of this trait is undoubtly the
ultimate goal of a breeding programme.

The data in table 3 show that the individuals with the better combination
of the four traits are those selected with the two indexes, the independent
culling levels and the direct selection for spring growth. The greater
efficiency of the indexes is evident in all traits with the exception of
green matter yield; for this trait however the individuals selected with
the index A are only below those selected directly for green matter yield.
Table 4 gives the expected genetic gains in each character (as percent of
the base population means) and in the last column the total expected gains

Table 3.   Phenotypic superiority of the materials selected with different methods compared
with the efficiency of the direct selection for green matter yield (=100).

Method of selection	Spring growth	Green matter yield	Summer regrowth	Autumn regrowth	Average
Index of selection A	1.45	0.99	1.04	1.08	1.14
Index of selection B	1.36	0.85	1.17	1.22	1.15
Independent culling levels	1.43	0.95	1.06	1.05	1.12
Direct selection for:					
Green matter yield	1.00	1.00	1.00	1.00	1.00
Spring growth	1.62	0.83	0.96	1.08	1.12
Summer regrowth	0.72	0.73	1.23	0.95	0.91
Autumn regrowth	1.09	0.76	0.98	1.16	0.99

Table 4. Expected genetic gains in the single traits (as % of the base population means) and total expected genetic gains (direct selection for green matter yield = 1.00).

Method of selection	Spring growth	Green matter yield	Summer regrowth	Autumn regrowth	Total
Index of selection A	0.95	0.65	0.37	0.40	1.36
Index of selection B	1.00	0.78	0.19	0.36	1.35
Independent culling levels	0.12	0.27	0.08	0.09	0.97
Direct selection for:					
Green matter yield	0.03	0.63	0.01	0.01	1.00
Spring growth	0.75	0.08	0.03	0.09	1.06
Summer regrowth	0.08	0.04	0.15	0.01	0.91
Autumn regrowth	0.16	0.08	0.01	0.21	0.95

have been obtained, giving the same weight to the four characters.

These data show that the total genetic gains expected with the indexes are 36% greater (index A) and 35% greater (index B) than those expected with the direct selection for green matter yield. The two indexes have, however, a different effect on the single traits, as the index A is expected to produce greater genetic gains in summer and autumn regrowth, while index B is expected to produce greater genetic gains in spring growth and green matter yield. It is of interest to note that, because of the correlations between traits, the direct selection methods are expected to give different responses; the greater genetic gains are expected by selection for spring growth.

CONCLUSIONS

The results presented in this paper indicate that two types of index of selection, one proposed by Smith (1936) and Hazel (1943) and the other described by Pesek and Baker (1969), have been the most effective methods of multitrait selection. They permit the identification of the best phenotypes and are expected to give greater genetic gains when compared with independent culling levels and tandem selection. It should be remarked, however, that these conclusions strictly apply only to this case; the choice of the economic weights in the index A, and the specification of the desired genetic gains in the index B, largely affect the results. Furthermore, the evaluation of the relative efficiency of independent culling levels depends on the selection intensity applied to each character. With more than two traits the choice of the selection intensity which maximizes the expected genetic gain is very complex (Finney 1962). As we have maintained a constant selection intensity for all traits the relative efficiency of the independent culling levels may have been underestimated.

The results show the importance of the phenotypic correlations between traits in the development of the indexes. When two or more traits are phenotypically correlated, only one may be incorporated in the index, avoiding a great deal of complexities in the computations. In our case the indexes were developed to include only four traits, but their use permitted an improvement of a fifth character, heading time, which was phenotypically correlated with spring growth. The problems, that discourage many breeders, particularly those who "just close their eyes and their ears as soon as they see a mathematical formula" (Julén 1973), form the use of selection indexes, may be greatly simplified.

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PROBLEMS OF F_1-BREEDING IN LOLIUM MULTIFLORUM L.

G. Kobabe

Institut für Pflanzenbau und Pflanzenzüchtung,
Georg-August-Universität, Göttingen, Germany.

SUMMARY

There are several possibilities for producing pure F_1-hybrids in *Lolium multiflorum*. The simplest method is the crossing of male sterile genotypes with fertile inbreds. By using such male steriles (1975 and 1976) a large number of F_1-seeds were harvested, and replicated trials could be carried out. Preliminary observations from these field trials are presented in this paper.

If there are heterotic effects with respect to certain important characters, further investigations are necessary in order to develop new breeding methods. These methods should aid the use of heterotic effects and guarantee economic seed production.

There are several possibilities for producing F_1-hybrid seed. In addition to emasculation by hand followed by crossing, self-incompatibility and male sterility may also be successfully utilized. If there are two plants which are absolutely self-sterile these genotypes may be vegetatively propagated and the clones planted as a mixed population. All the seed harvested from these plants are pure hybrid seeds. If two lines which are intrasterile can be selected and if their propagation does not present any difficulty, a mixed population would also produce pure F_1 seed. However, these methods can only be applied in an experimental field. They are not applicable to the propagation of hybrid seed on a larger scale.

A 1:1 mixture of two lines with self-incompatible plants will produce 50% hybrids only. Of course, the same result will be obtained when the lines are not absolutely self-sterile. Foster (1971) and Wright (1972) have discussed this problem in detail.

The utilization of male sterility in grasses opens the possibility of producing pure hybrid seed very easily. The method is similar to hybrid breeding in corn, onions, and other crops. Growing the crop in alternate rows and harvesting the seeds from the male sterile genotypes only guarantees pure hybrid seed production.

In grasses, however, it is not economical to grow and harvest different genotypes in different rows. Instead of this a mixture of, for example, 75% male steriles and 25% normal types could be grown. The seeds harvested from this population may consist of 75% hybrids and 25% normal seeds. Presumably the proportion of male steriles can be increased up to 90%. However it is not yet clear whether under these circumstances pollination will be satisfactory.

Synthetic varieties in most cases consist of more than two lines. If there are, for example, four lines the first generation after Syn_0 will consist of 75% hybrids of all possible combinations. If all these lines are intra-

observations can be made here. The trial included 150 different F_1 combinations sown in 1 m^2 plots with two replications. In this way it was possible to obtain data from swards which is of greater value in practice than the data which can be obtained from spaced F_1 plants.

Compared with the German cultivar Lema, eight F_1 hybrid combinations were found to have a significantly higher dry matter yield. The best of these eight combinations outyielded Lema by 27%. This indicates that heterozygosity in *Lolium* may be utilized to increase yield.

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TESTING OF LOLIUM PERENNE CULTIVARS FOR VIRUS TOLERANCE
UNDER NATURAL CONDITIONS

Gerta Ziegenbein

*Hessische Lehr- und Forschungsanstalt für Grünlandwirtschaft
und Futterbau, Eichhof, Bad Hersfeld, Germany.*

SUMMARY

In the course of a breeding programme for persistence in *Lolium perenne*,
the virus diseases BYDV and RMV were found to have increased in both breed-
ing material and in swards surrounding the nurseries. This infection reser-
voir was utilised to test the response of cultivars and strains to both vi-
rus diseases. Since 1970 single plants of a total of 272 seed samples have
been tested for virus symptoms, vigour and yield in four trials. It was
concluded that the short duration of life and the decline in production of
many *Lolium perenne* cultivars and strains is mostly caused by their suscep-
tibility to virus diseases. Most of the varieties were heterozygous for
their response to virus diseases, and showed a wide variation in virus tol-
erance between individual plants. It should be possible to improve the per-
sistence of varieties by cultivating them under conditions of high natural
infection, and by selecting and propagating single plants found to be tol-
erant to virus diseases. Moreover it can be recommended for practical
breeding purposes that the testing and selection of new breeding strains is
performed under such severe conditions in order to obtain new virus-tolerant,
persistent and high yielding cultivars.

Lolium perenne is a very important grass species in our permanent pastures.
At the beginning of our breeding work, 18 years ago, the varieties of *L.
perenne* in our country were less perennial. Our most important breeding
aim was thus to improve the persistence of this species, and to achieve this
aim each breeding unit was grown under field conditions for several years.
Single plants, derived from ecotypes or from artificial populations, were
grown for at least three years in the nursery, and clones produced from the
best single plants were again grown for at least three years in the field
before the best of them were given to private breeders who continued selec-
tion and finally produced new cultivars.

In 1964 an abnormal growth habit was observed for the first time in parts of
certain clones. Most showed dwarfism, and in some cases all plants within
a clone were stunted. Reports in 1969 of severe infections of barley yellow
dwarf disease on barley and oats growing near old permanent pastures (Buhl
1969, Huth 1969), prompted us to study other reports of virus diseases in
L. perenne, especially the investigations of Catherall (1966). W. Huth, a
virus specialist of the Biologische Bundesanstalt Braunschweig, identified
both BYDV and RMV in our breeding material. Up to 1975 only these two virus
diseases were found in our fields, but in 1975 a new virus causing enations,
detected by Huth (1975) in several parts of Germany, was found in ecotypes in
our material.

As the result of the long period over which our breeding material had been

grown, the virus diseases were maintained and multiplied, and the breeders engaged with this material have been trained to recognize the natural infections. The response of the *Lolium* plants to virus diseases was very different. Some of them died, others had a more or less stunted growth, but survived. Certain plants were also found to be infected, as shown by colour deviations, but were not affected in terms of vigour or economic features. Such plants also survived severe winter conditions. During the course of our breeding work we have subsequently selected virus-tolerant and persistent clones of this type.

It was supposed that the low persistence of many *L. perenne* cultivars might be due to a high susceptibility to virus diseases. To check this hypothesis a variety test was set up in 1970 under the natural virus infection conditions described above. This trial comprised 37 varieties, some of which were well known with regard to yield and persistence attributes.

One hundred single plants of each variety, raised in a glasshouse, were planted in the field, treated with insecticides until they were established, and subsequently abandoned to natural virus infection. No morbid changes in the plants were observed in the first year. Only few plants of several varieties died during the winter, but mortality was high in the following growing season, especially in varieties known to be short-lived. Clear indications of virus diseases such as growth stunting and the typical yellow-orange discoloration by BYDV were first observed in the regrowth. The frequency of plants with definite symptoms varied in different varieties from 51 to 99%. By the end of the year 0-35% of the plants in different varieties had died. In terms of productivity the following overall frequencies of plants were found:

Reduced productivity	15-80%
Intermediate productivity	7-56%
Good or excellent productivity	0-51%

Plants with good or excellent productivity can be regarded as virus-tolerant. Plants of this type were cloned and used as parents for hybridization, and the resultant progenies appear to show greater virus tolerance. Several breeders also received tolerant plants of their varieties for improvement purposes.

This test of *L. perenne* varieties for tolerance to BYDV and RMV under natural conditions led to the following conclusions:

1. 100 single plants of a cultivar or strain are enough to demonstrate the dependence of its yield capacity on virus tolerance.

2. Already at the end of the second year of cultivation it is possible to assess the degree to which the yield and the persistence of a cultivar or strain is influenced by virus infection, although this assessment will be reliable only in highly susceptible varieties. An additional trial year is necessary to find the most virus-tolerant varieties.

Based on this experience, variety testing was continued. The 100 single plants of a cultivar were planted in two plots of 50 plants in different parts of the trial field. We found this division to be not absolutely necessary as the plants have the same chances of infection by BYDV and RMV in all parts of our experimental field. The possibilities for virus infections have now been increased such that a number of plants show infection symptoms already in the first year.

In 1973 the trial included 18 cultivars, in 1974 106 cultivars, and in 1975 111 cultivars and strains. A certain number of the seed samples were supplied by the Genebank in Braunschweig. Details of these trials cannot be given in this report and only the most striking results are summarized here.

In the 1970 test several cultivars from the Netherlands and Belgium were most virus tolerant, as the cvs. Mommersteegs pasture type, Mommersteegs Weidauer, R.v.P. pasture type and Terpas. Virus-tolerant single plants of these cultivars gave high yielding and persistent clones. But clones with good persistency were also obtained from sporadically occurring virus-tolerant plants from cultivars which on average showed medium tolerance to virus diseases. The most virus-tolerant varieties in the 1973 trial were Perma, Splendor and Manhattan. One of seven Russian cultivars also contained a high frequency of virus-tolerant plants. In the 1974 test the best variety was Mombassa, and the varieties Chantal, Marathon, Melino and Pablo were also fairly tolerant, together with the two cvs. Splendor and Lamore (= Mommersteegs Weidauer) which had been found tolerant in earlier tests. The trial established in 1975 will be evaluated next year.

Our future work will be concerned with the new virus on *L. perenne*, and it seems probable that we will also find tolerant types to this disease.

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RELATIONSHIP BETWEEN WILT-RESISTANCE AND TOLERANCE TO FREQUENT CUTTING IN LUCERNE

I. Bócsa, J. Buglos and S. Manninger

Agricultural Research Institute, Kompolt, Hungary.

SUMMARY

Seven varieties with known agronomical characteristic were grown in spaced plantings and cut three times in the first and seven times in the second year. Intervals between cuts averaged 23 days.

Our objective was to establish possible intervarietal differences in reaction to frequent cutting.

Results indicate that cultivars Vertibenda and Furez (both tolerant to wilt) have essentially better tolerance to frequent cutting than the other entries; their overwintering also shows marked superiority, suggesting a close interrelationship between wilt tolerance and frequent cutting.

INTRODUCTION

The idea of breeding lucerne to withstand frequent cutting originates from Demarly (Guy 1970, pers. comm.). The notion of tolerance to "frequent cutting" was first published by Guy et al. (1971) and Mansat (1971). Such a variety might be cut more frequently at an early stage of maturity and it could yield more protein and carotin with less cellulose without the duration of its stand being impaired. Since the express drying of lucerne came into general use, cutting has become more frequent and has resulted in an early thinning out of the stands. The need for a variety, which with intensive use could yield a crop of full value for at least 3 years, is now quite obvious, but to meet this demand the breeding of new varieties also appears indispensible.

Researchers who first suggested the possibility of relationship between pathogens and management were Kehr et al. (1972). Twamley (1960), however, demonstrated much earlier in Canada that varieties combining resistance to bacterial wilt (caused by *Corinebacterium insidiosus*) with winter hardiness could endure mismanagement with less damage. In the opinion of Smith (1972) varieties with good persistence can only be found among those resistant to bacterial wilt. Contrary to Twamley, he does not denote frequent cutting as mismanagement. Publications so far have referred to the correlation between persistence and resistance, and a relationship between bacterial wilt and frequent cutting has also been pointed out. However, the interdependence between *Verticillium* and *Fusarium* resistance on the one hand and frequent cutting on the other has not yet been demonstrated. *Verticillium albo-atrum* has according to Graham et al. (1972) not yet been found in USA. Furthermore the term "frequent cutting" as used by American authors does not cover Demarly's and our notion as used in this paper.

MATERIAL AND METHOD

In looking for the best ways and means of breeding a variety capable of

withstanding frequent cutting, our first step has been to investigate differences in this character between the best known varieties and resistant strains. In Hungary we are most interested in the reaction of our resistent strains to two very widespead pathogens of lucerne, namely *Verticillium albo-atrum* (Szőkő 1968) and *Fusarium* sp. (Mesterházy-Manninger 1972). We have therefore included the following varieties in our experiments:

1) Europe (F), international standard variety.
2) Orca (F), variety with good standing power.
3) Everest (F), variety with good standing power.
4) Magali (F), variety tolerating frequent cutting under south-European conditions, type of Provence.
5) Vertibenda (H-DDR), *Verticillium*-resistant variety with resistance similar to that of Vertus.
6) "Furez" (H), new *Fusarium*-tolerant variety intended for registration (the only European cultivar with this character).
7) S-66 (F), inbred line, selected for frequent cutting tolerance.

The varieties were planted at the seedling stage at a spacing of 70 x 70 cm in spring 1974 with 4 replications of 200 plants. Cutting was performed at the early primordium stage, with an average of 23 days intervals between cuttings. This meant a very strong stress on the plants by defoliation.

As our only aim in this experiment was to test the survival and persistency of the plants, we have merely noted plant numbers in the autumn and spring. We have also noted the individual variability in tolerance to frequent cutting, but this will not be included in our present paper. The experiment was evaluated in the 3rd year after planting, following a hard and long winter.

RESULTS AND DISCUSSION

The degree of tolerance of varieties to frequent cutting is given by the number of regrown plants at the end of the second year, after seven cuts, compared to the plant number in spring. Degree of persistency or of reduced viability is shown by the proportion of over-wintering plants after the seventh cut, or by the number killed during winter, respectively.

In this case the comparison was effected with the autumnal plant number.

Far the most outstanding and significantly best values were shown by the *Verticillium*-resistent Vertibenda and the *Fusarium*-resistent "Furez" in terms of tolerance to frequent cutting as well as winter survival. The other varieties were much inferior. In consequence, we may conclude that a close relationship exists between wilt resistance and tolerance to frequent cutting. The data obtained also showed that the variety Magali, which tolerates frequent cutting in its Mediterranean native country, was not tolerant in our country, propably because of lack of resistance. This also applies for the line S-66 selected for frequent cutting. It is also worth noting that the proportion of winterkilling in Magali is less than or practically identical with that in Flanders-type varieties.

The closest connection exists without doubt between wilt-resistance and tolerance to frequent cutting. The relationship between lack of resistance and state of reduced viability caused by frequent cutting is an indirect consequence of infection by *Verticillium albo-atrum* or *Fusarium* species. These infectants are so-called weak parasites which cause speedy and extensive thinning out of the crop.

It also appears that winter survival in frequent cutting is something else or involves more than just the heritable character of mere winter hardiness

of frost resistance. The behaviour of the variety Magali provides indirect proof of this.

Proportion of killed plants of different varieties after frequent cutting and after the following winter.

Variety	% of plants killed after frequent cutting	in following winter after frequent cutting
1. Vertibenda	3.9	12.4
2. "Furez"	6.1	7.4
3. S-66	34.0	35.3
4. Magali	34.9	50.2
5. Orca	51.1	42.1
6. Everest	65.3	67.4
7. Europe	68.5	76.4
LSD (5%)	4.78	3.00

The degree of winter killing is connected with the difference in speed to which nutrients are restored in rhizomes, i.e., a difference in capability of regeneration, which is a heritable character. A more favourable scale and speed of regeneration on the other hand is made possible by a greater resistance.

The process can probably be represented as follows:

Resistance
↓
Tolerance to frequent cutting
↓
Indirectly greater winter hardiness)
↓
Better persistence.
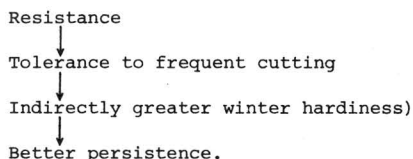
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PERFORMANCE OF DIALLEL CROSSES AMONG SINGLE CROSSES OF ALFALFA AND COMPARISON OF DOUBLE CROSSES AND SYNTHETICS DERIVED FROM THE SAME PARENTAL CLONES (*)

P. Rotili and L. Zannone

Istituto Sperimentale per le Colture Foraggere, Lodi, Italy.

SUMMARY

In an alfalfa (*Medicago sativa* L.) breeding study conducted under conditions of high competition between plants, combining ability for forage yield was evaluated from diallel crosses among single crosses derived from selected parents which had been partly inbred. The performance of 4-clone Syn 2 gen- eration synthetics was also studied in comparison with that of double crosses derived from the same parents. General combining ability (GCA) was consid- erably larger than specific combining ability (SCA) for all generations of parental inbreeding (S_0, S_2, S_3 and S_4). GCA increased with inbreeding of parental clones. A good correspondence exists between the observed and expected breeding values of single crosses at every level of inbreeding. A good association is also evident between the observed and the expected values of double crosses. The best double crosses derived from the clones showing the highest values of general combining ability. At every level of inbreed- ing, the double crosses surpassed the synthetics; both the best double cross and the best synthetic variety were found at the S_2 level of parental inbreeding. Double crosses, by natural crossing in the field (semi-hybrid varieties), might well be the most efficient varietal model for alfalfa.

INTRODUCTION

The aim of the breeding program carried out at the Institute for Forage Crops in Lodi was to determine the effectiveness of selfing, followed by intentional selection in competitive conditions, in improving the genetic value of parents for alfalfa varieties. This program was divided into three phases: 1) self-pollination for four generations; 2) diallel crosses and second generation synthetics from partly inbred clones; 3) diallel crosses among single crosses and comparison of double crosses and synthetics derived from the same parental clones.

Data concerning the first and second phases have been published (Rotili 1970a, 1970b, 1976a, 1976b; Rotili and Zannone 1974). This paper presents a part of the third phase results.

MATERIAL AND METHODS

The material used in this study derived from the populations Florida and Friulana (Table 1). Within each of these varieties, selection was practised for plant vigour at both ends of their distribution curves. Plants with dry matter weight less than the mean were designated as group A and plants

Table 1. Clones used in diallel crosses.

Clones	Diallel crosses				
	S_0xS_0	S_2xS_2-I	S_2xS_2-II	S_3xS_3	S_4xS_4
127 A	*	*	*	*	*
633 B	*	*	*	*	*
1171 C	*	*	*	*	*
1497 D		*	*	*	*
649 E	*	*	*	*	*
652 F		*	*	*	*
940 G		*	*	*	*
1836 H	*	*	*	*	*
719 P	*				
1678 Q	*	*	*	*	*
259 R	*				
301 S	*	*	*	*	
453 T					*
1169 U	*				

A, B, C, D, P, Q   = FLORIDA
E, F, G, H, R, S, T, U = FRIULANA

exceeding the mean by two standard deviations were designated as group B. Selection was practised in competitive conditions (150 plants/m^2). The selected S_0 plants were inbred by selfing for four generations. A complete description of the selection procedures was given previously (Rotili 1970a, 1976a, Rotili and Zannone 1974).

Within group B the following diallel crosses were made:

Level of inbreeding	Description
S_0 x S_0	Diallel cross among 5 single crosses derived from noninbred plants
S_2 x S_2 - I	Diallel cross among 5 single crosses derived from S_2 plants
S_2 x S_2 - II	Diallel cross among 5 additional single crosses derived from the same S_2 plants
S_3 x S_3	Diallel cross among 5 single crosses derived from S_3 plants
S_4 x S_4	Diallel cross among 5 single crosses derived from S_4 plants

Each single cross was represented by 5 plants selected at random in a population of 40 plants. Pollen was collected on all of the 5 plants (two flowers per plant) of the first parental single cross and transferred to one flower of the first plant of the second parental single cross; again, pollen collected on all of the 5 plants (two flowers per plant) was transferred to one flower of the second plant of the partner and so on. The diallel cross scheme included the reciprocals.

To produce seed of double cross F_2, 40 plants were selected at random in a population of 100 plants within each double cross F_1. Pollen was collected on 10 plants at random (one flower per plant) and transferred to one flower of one plant taken at random. Again, pollen collected on 10 random plants (one flower per plant) was transferred to one flower of another plant. Such a procedure was repeated several times to obtain 5 pods per each of the 40 plants. F_2 generation was made for all the double crosses, except for those of the diallel cross S_2 x S_2 - II.

Each 4-clone Syn 2 was produced by mating 60 random F_1 plants, 10 from each of the six single crosses among the four plants. These plants were grouped in 10 crossing blocks of six plants. Pollen was collected on all of the six plants within each crossing block (two flowers per plant) and transferred to one flower of the first plant. Again, pollen collected on all of the six plants (two flowers per plant) was transferred to one flower of the second plant and so on. Two 4-clone Syn 2 were made at each of the following generations of inbreeding: S_0 x S_0, S_2 x S_2 - I, S_3 x S_3 and S_4 x S_4.

All crosses in this study were made by hand in the greenhouse without emasculation.

The seeds were planted in April 1975 in Rome. The plantings were made in boxes with removable bottoms. Each box was 40 cm long, 20 cm wide and 10 cm high. Twenty six seeds of an entry were planted in a single row in the box, providing 1.5 cm between the plants. To avoid missing plants due to poor germination, the seeds were germinated in Petri dishes and seedlings with roots about 1 cm long and cotyledons well opened were transplanted into the boxes. To avoid the selective effect of seed hardness and to obtain homogeneous and complete germination, the seeds were pierced by a needle after soaking 12 hours in Petri dishes. In this way, all of the plants which produced seeds were represented in the boxes. Concerning F_1 double

crosses, all the 10 plants of both parental single crosses were equally represented in each entry. After about ten days, abnormal seedlings that had stopped development at the unifoliate leaf stage were replaced by healthy seedlings. After 30 days the bottoms were removed from the boxes which were then buried in the field in a randomized block design with six replications. The boxes were placed against each other in rows. A border of 40 plants was added on each side of each row. The final plant density was 330 plants/m^2. One irrigation was made during the first week after every cutting. All the material was harvested at the same time, when most of the entries were about 20% bloom stage. Dry matter weight, earliness, mortality, saponin and protein content were determined. Five cuts were taken during the first year and till now three cuts have been taken in the second year. The green forage was dried in an oven at 100°C for 40 hours. In the present paper only data concerning forage yield are given (for four cuts in the first year and three cuts in the second year).

The data were analyzed according to Griffing's method IV, model I.

RESULTS

Table 2 presents the single cross and double cross values for each diallel cross. From this table the following observations can be made:

1) The difference between the mean value of parental single crosses and the mean value of double crosses increases with the level of inbreeding. Such increase reaches 20% in the diallel crosses S_2 x S_2 - II, S_3 x S_3 and S_4 x S_4. This result underlines the importance of the degree of heterozygosity in the expression of hybrid vigour in autotetraploid plants (Busbice and Wilsie 1966, Demarly 1963, 1970).

2) At the levels of inbreeding S_2, S_3 and S_4 the best double crosses are better than the best single crosses. These results are in agreement with those presented by Gallais and Guy (1970).

General combining ability (GCA) is highly significant in both years and at all levels of parental inbreeding (Table 3). Specific combining ability (SCA) is significant only in the S_2 level (in the diallel cross S_2 x S_2 - II it is significant only in the first year). The GCA mean square increases at the levels of inbreeding S_2, S_3 and S_4. From results of diallel crosses among parental clones (Rotili 1976a), the conclusion was drawn that the greatest progress will result from working with general combining ability estimates. This conclusion is much more valid when referred to the results presented here for diallel crosses among single crosses.

Table 4 shows a very good correspondence between the ranking of the observed and breeding values of single crosses at every level of selfing. Such correspondence is maintained also when variations occur between the two years (see A x E). As a consequence, it is possible to foresee the performance of a double cross on the basis of the single cross performance. In fact, the double crosses show a good association with the average of the two parental single crosses (Table 5). In addition, the best double crosses derive from the clones which in the previous experiment showed the highest values of general combining ability (Rotili 1976a, Rotili and Zannone 1974). Thus, it seems possible to obtain a good prediction of the double cross performance on the basis of the clone value measured by polycross progeny test. This fact might be very important in the practical breeding.

Data concerning the inbreeding depression are given in Table 6. Only little differences are observed between the levels of selfing in both years. In the second year the inbreeding depression increases at every level of selfing. A statement should be made: the double crosses were obtained by

Table 2. Forage yield (g/plot) of single and double crosses, average of 7 cuts.
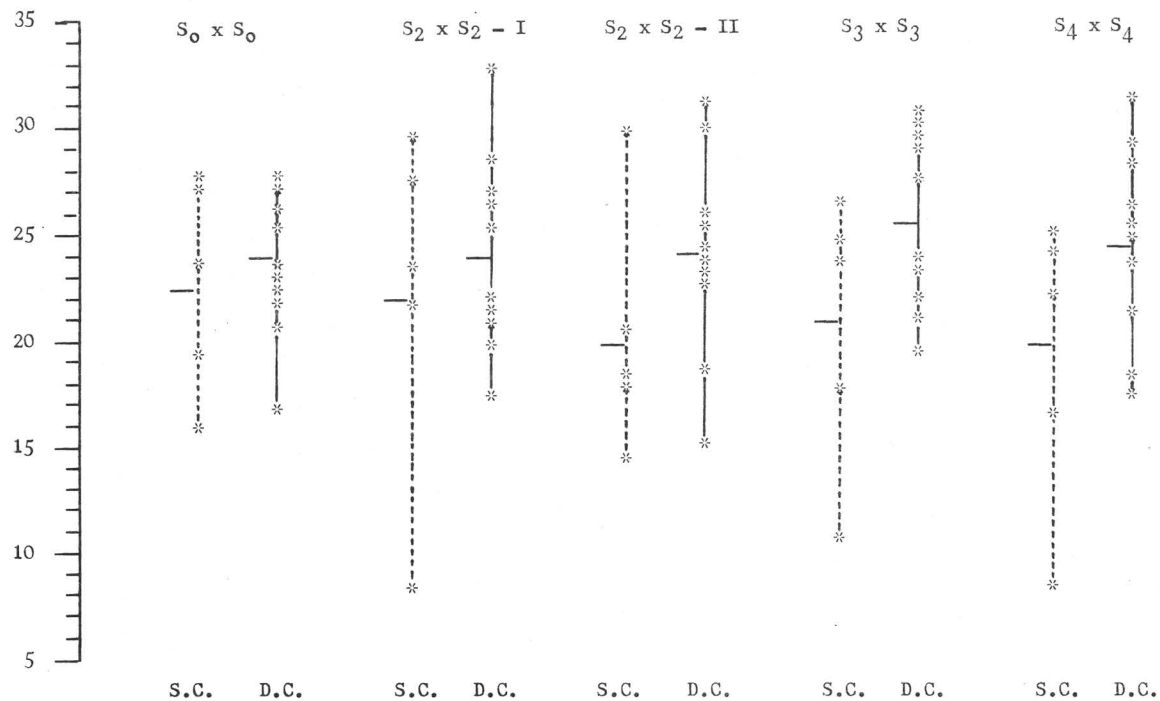
Table 3.   General (GCA) and Specific (SCA) combining ability mean squares for yield in diallel crosses

	Generation of inbreeding				
	$S_o \times S_o$	$S_2 \times S_2 - I$	$S_2 \times S_2 - II$	$S_3 \times S_3$	$S_4 \times S_4$
1975 — Average of 4 cuts					
GCA	4.59**	8.62**	8.58**	26.15**	20.84**
SCA	1.89	4.70**	2.91**	1.15	1.65
Error	0.98	1.34	0.78	1.49	1.21
1976 — Average of 3 cuts					
GCA	63.84**	115.23**	163.83**	59.50**	99.13**
SCA	15.33	28.56*	6.60	13.57	18.65
Error	9.72	9.41	7.91	10.47	13.84

*, ** Significant at the 5% and 1% level, respectively

Table 4. Observed (1) and expected breeding (2) values for single crosses. Forage yield (g/plot).

$S_0 \times S_0$			$S_2 \times S_2 - I$			$S_2 \times S_2 - II$			$S_3 \times S_3$			$S_4 \times S_4$		
Single crosses	(1)	(2)	Single crosses	(1)	(2)	Single crosses	(1)	(2)	Single crosses	(1)	(2)	Single crosses	(1)	(2)
1975 (4 cuts)														
A x P	20.5	19.1	A x E	26.8	20.6	A x C	18.3	20.5	A x E	24.3	22.9	A x E	20.8	20.9
Q x S	19.3	17.1	B x F	18.8	19.5	B x D	17.6	20.3	D x H	17.3	19.3	Q x T	18.2	20.0
B x E	18.4	18.2	Q x S	17.4	18.7	Q x S	15.3	19.3	B x F	15.2	19.1	D x H	15.7	17.0
C x R	16.7	17.9	D x G	15.2	18.9	E x G	15.1	18.0	Q x S	14.6	21.5	B x G	12.2	17.7
H x U	14.0	16.7	C x H	10.6	17.1	F x H	13.7	17.8	C x G	10.9	17.2	C x F	8.6	16.4
1976 (3 cuts)														
Q x S	38.0	32.2	B x F	42.6	34.8	B x D	45.5	38.2	D x H	39.4	35.3	D x H	37.9	35.1
A x P	36.9	32.5	Q x S	30.8	31.3	Q x S	27.9	33.7	B x F	35.2	34.8	Q x T	31.7	36.4
B x E	30.2	32.5	D x G	30.1	34.7	E x G	21.1	27.5	A x E	25.8	34.4	A x E	24.3	33.6
C x R	22.6	27.2	A x E	28.4	29.9	A x C	18.5	28.8	Q x S	22.4	34.9	B x G	22.7	35.1
H x U	17.7	25.2	C x H	8.0	23.5	F x H	15.7	24.1	C x G	10.8	27.4	C x F	7.7	25.6

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Table 5. Correlation between observed and expected value of double
          crosses (n = 10)

Year	Generation of inbreeding				
	$S_0 x S_0$	$S_2 x S_2-I$	$S_2 x S_2-II$	$S_3 x S_3$	$S_4 x S_4$
1975 (4 cuts)	0.565	0.736*	0.770**	0.794**	0.844**
1976 (3 cuts)	0.820**	0.804**	0.925**	0.730*	0.788**

*, ** significant at the 5% and 1% level, respectively

Table 6 — Relative performance of the double cross F_2 ($F_1 = 100$)

		Generation of inbreeding			
		$S_0 \times S_0$	$S_2 \times S_2 - I$	$S_3 \times S_3$	$S_4 \times S_4$
1975 (4 cuts)					
	MEAN	92	89	86	91
	MIN.	80	66	72	82
	MAX.	105	105	110	103
1976 (3 cuts)					
	MEAN	85	81	78	81
	MIN.	64	53	66	60
	MAX.	104	96	102	104

Table 7. Correlation between F_1 and F_2 double crosses (n = 10)

Year	Generation of inbreeding			
	S_0 x S_0	S_2 x S_2 - I	S_3 x S_3	S_4 x S_4
1975 (4 cuts)	0.427	0.732*	0.748*	0.929**
1976 (3 cuts)	0.509	0.861**	0.649*	0.665*

*, ** significant at the 5% and 1% level, respectively

Table 8. Forage yield (g/plot) of the best 4-clone Syn 2 and their
correspondent F_1 double crosses. Average of 7 cuts.

	Generation of inbreeding			
	S_0 x S_0	S_2 x S_2 - I	S_3 x S_3	S_4 x S_4
4-clone Syn 2	21.81	29.52	28.70	20.83
Double crosses	27.49	32.74	29.56	25.34
$100 \cdot \dfrac{\text{Double cross}}{\text{Syn 2}}$	126	111	103	122

interpollination of random selected single cross plants which were grown in spaced plantings. If the choice of single cross plants had been realized in swards, the inbreeding depression would be lower because of the interplant competition effect (Gallais 1975, Rotili 1976c). A good correlation exists between F_1 and F_2 generations at the levels of inbreeding S_2, S_3 and S_4 (Table 7).

The comparison between the best 4-clone synthetics and the double crosses derived from the same parental clones is made in Table 8. At every level of inbreeding, the double crosses overcome the synthetics. Both the best sunthetic variety and the best double cross are found at the $S_2 \times S_2$ level: here the gain of double cross is 11%.

CONCLUSIONS

From these results and the others previously published, the following conclusions can be drawn:

1) The double cross model in uncontrolled pollination seems to be the best solution, because it combines the maximum yield with a good homogeneity for flowering, which allows a better longevity (Rotili 1976b). The constitution of a double cross hybrid by natural crossing in the field (semi-hybrid variety) will give positive results, because in dense stand the individuals resulting from consanguineous crossing will be dominated and eliminated by the more vigorous individuals. The success is warranted also by phenomena of pollen competition in favour of the allopollen (Demarly 1963). Nevertheless, if we consider all the difficulties in the seed production (climatic effects, presence of pollinators, etc.), it is questionable whether the advantage of the semi-hybrid varieties over the 4-clone-synthetics would be sufficient to justify the increased cost involved in producing semi-hybrid seed.

2) The use of selfing in the breeding of alfalfa is very advantageous. But how many generations of selfing have to be employed? Concerning the forage yield, the selection of vigorous clones could continue positively also after the second generation, if suitable solutions are employed. On the contrary, concerning the seed production, the limit of profitable use of selfing is related to the variety model employed. For instance, for a 4-clone synthetic variety there are no difficulties; on the other side, if a semihybrid variety is created by natural crossing of two 2-clone synthetics, the use of mother plants with a level of inbreeding over S_2 does not seem to be economically convenient. In fact, if S_3 parental plants are employed, a sharp decrease in fertility will be reached during the multiplication phase, and the production of commercial seed of first generation will no longer be economically practicable. This is demonstrated by our still unpublished data.

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USING SELF-FERTILITY IN BREEDING OF PERSIAN CLOVER

F. Morgner

Hessische Lehr- und Forschungsanstalt für Grünlandwirtschaft und Futterbau, Eichhof, Bad Hersfeld, Germany.

SUMMARY

To improve seed set in breeding material of Persian Clover, crosses were made between the self-fertile, low yielding "Common Variety" from Louisiana and cross-pollinating material with high dry matter yield. In the resulting progenies self-fertile plants were selected. After four generations, including one backcross to the high yielding parent (DM) seed yield was efficiently increased. The average seed yield of single plants in the best lines exceeded 10 g. By inbreeding a wide range of genetic variability in the lines was revealed. Uniformity for several characters within the strains was rapidly attained.

Persian clover is a new forage crop in Germany, but no German varieties are at present available. Each year about 2000 tons of seed are imported, mainly from Iran and Portugal, but the genetical quality of this seed differs very much from year to year, which was one of the reasons for starting our own breeding work. In recent years we have developed a large number of strains of Persian clover. This species is basically cross-pollinating, but during our breeding work one source of self-fertility was found, the so-called "Common Variety" from Louisiana, USA. As this variety has a low forage yield, we attempted to combine self-fertility with the high forage yield of material from Iran and from Portugal. By this means we hoped to achieve a more stable seed production in breeding material under our climatic conditions.

After crossing, the resulting F_1-plants were selected for self-fertility. For this purpose single plants were planted in pots and isolated with a very close meshed Trevira net, which could not be penetrated by insects. Plants, which produced seed under such conditions, must be not only self-fertile, but must possess true self-compatibility, because they could not be pollinated by insects. About 50% of the F_1-plants produced seed, and yields ranged between 0 and 16 g per single plant.

Isolation of single plants was continued for a further two generations, by which time all plants produced seed under isolation. The average seed yield was about 10 g per single plant.

Both the progeny from the initial cross and the plants of the following inbred generations had relatively low forage yields. Backcrosses were therefore made to the high-yielding parents from Iran or Portugal. In order to maintain self-fertilization the single plants of the backcross progeny were isolated as described above. They were sown in December in the greenhouse and cut two or three times prior to isolation. Only plants with good regrowth were propagated. By this means the forage yield after two backcrosses reached or exceeded the yield of the high-yielding parent. Some of the strains showed inbreeding depressions such as chlorophyll defects and dwarfness, but by selection these depressions were eliminated during the breeding

programme. A second effect of inbreeding was a rapid increase in uniformity of characters which are suitable for the identification of new varieties, such as leaf and flower colour, leaf form and time of flowering. Furthermore strains were also found with higher dry matter and protein content. Several strains produced in three or four cuts up to 150 dt dry matter per ha. This increase in performance can be explained by the elimination during inbreeding of genes which have a negative effect on yield. Other strains were able to produce up to 60 dt/ha dry matter within ten weeks after sowing, and such strains would be well suited for intercropping.

By finding self-fertility in Persian clover it was possible to analyse the variability in this species within a short time, but the most important effect was the increase of seed and forage yields by the elimination of sublethal genes during inbreeding.

The method described demonstrates the possibility of rapidly improving new crop species.

BREEDING METHODS AND VARIETY TESTING IN SWEDES

S. Gowers

Scottish Plant Breeding Station
Pentlandfield, Roslin, Midlothian, Scotland.

SUMMARY

The methods available for use in swede breeding are described, taking into account that what is now a basically inbreeding crop could be converted into an outbreeder by the introduction of self-incompatibility. The range of variation within the species could be increased considerably by inter-specific crossing, and the characters which at present are being introgressed into swedes from *B. campestris* and *B. oleracea* are described. Some preliminary results of an analysis to show the optimum plot size for swede trials are given.

Swedes (*Brassica napus* ssp. *rapifera*) are a very interesting crop and appear to have tremendous breeding potential. *B. napus* is a natural amphidiploid originating from *B. oleracea* and *B. campestris*, both of which have a sporo-phytically controlled incompatibility system. Swedes, however, are basically self-compatible. A sporophytic system should function at the tetraploid level, and it has, in fact, been found to do so in *B. napus* (Olsson 1960, Gowers 1974). It would, however, be a considerable problem for a naturally occurring amphidiploid to be self-sterile. It is assumed that the original *B. napus* was derived from parents with weak S alleles, which, when acting in competition at the tetraploid level, produced a self-compatible plant. The species we are dealing with at present is, therefore, mainly self-fertile, but has the possibility of being developed into an outbreeding species.

At the moment, swede breeding at Pentlandfield is concerned with two main programmes. Treating swedes as inbreeders, a line breeding programme is being developed whereby crosses between two cultivars are selfed for several generations, under selection, to produce nearly true breeding lines. The first set of lines to be produced by this method is now at F5, and is under-going evaluation as pre-varietal material.

The other main programme being developed is the production of F1 hybrid swedes, and is largely due to results obtained from the initial crosses made for the inbreeding programme. Yield data from some of the F1 hybrids (McNaughton and Munro 1972) showed increases in dry matter yield of up to 25% over that of the higher parent.

The initial problem was to develop a means of utilising this degree of het-erosis. Self-incompatibility appeared to be the most likely means of enforc-ing crossing and, although it was expected that specific crosses would be required to bring S-alleles into swedes from kale and turnips, it was found that sufficient alleles were already present within the existing range of *B. napus*. At least eight different S-alleles have now been obtained, of which six appear to be strong enough for the crossing sequence proposed. This sequence (Gowers 1975) involves the use of self-compatible lines as pollinators for isogenic S-allele lines in the single crosses. If the S-

alleles used are strong enough when heterozygous, sowing the single crosses
together should produce Fl hybrid swedes. It appears that this method may
also be used to advantage in producing Fl hybrid oil-seed rape.

With the means of producing Fl hybrids in *B. napus* being available, the
main problem now is to identify the crosses producing the highest yielding
hybrids. The best hybrid swede found so far was 17% higher yielding than
the best control variety, but this was not significant at p = 0.05. For
the time being, work will concentrate on producing hybrids from the highest
yielding crosses, on the assumption that they would prove to be higher
yielding if sufficient trials could be sown to show significant differences.
It is hoped that the seed set from the pollinations made this year will al-
low a 10 x 10 half-diallel to be sown next year, and that this may show
higher yielding hybrids than those previously obtained.

Another aspect being examined has important applications to swede breeding
as a whole. Davey (1938) and Rives (1957) have shown that inbreeding prod-
uced lines of swede and rape, respectively, which outyielded their parent
varieties. Last year 33 lines derived by selfing from the variety Scotia
were examined, and their yields were found to vary from 22% less to 23%
more than the parent variety. Scotia is an old mass selected variety, and
these results may not apply to more recent varieties. However, it does
suggest that improvements in yield and uniformity could be made in existing
varieties.

The implications to the two main programmes are also of great importance.
Any programme based on pair crosses depends on the plants used, and if, by
chance, they happened to be 20% lower yielding than expected, it would not
be a very good start to a breeding programme.

Consideration of the degree of self-pollination in the field shows that the
results from the inbred lines could, theoretically, be expected. Data on
outcrossing from swedes with a genetic marker shows the degree of selfing
to be about 80%. The inbreeding coefficient expected from this is 0.67,
giving a 67% loss of any yield advantage shown by the mean of the F2 over
the mid-parent value. It should not be surprising, therefore, that select-
ed inbred lines can be obtained showing yield superiority over their paren-
tal variety.

It is also seen that this loss of yield with inbreeding could be avoided by
converting a variety to an outbreeder by introducing self-incompatibility.
If, however, an outbreeding variety were to be produced, it would be as
easy to make a synthethic variety, if the data was available to show which
lines to incorporate into the synthetic. It is hoped that the results of
the Fl trial to be sown next year will give an indication of the possible
performance of a synthetic variety as well as showing which parents to use
for Fl hybrid production.

The previous comments have related to breeding methods in general. When
individual characters are considered, it becomes apparent that the varia-
tion within swedes is somewhat restricted in comparison to that available
in *B. napus* as a whole, and very restricted in comparison to that available
in the ancestral species, which possess a vast range of variation.

Swede breeding at Pentlandfield is involved with the introgression of sev-
eral characters into *B. napus* from *B. oleracea* and *B. campestris*. Self-in-
compatibility has already been transferred from turnips, and possibly club-
root (*Plasmodiophora brassicae*) resistance also. Better clubroot resist-
ance, involving at least 3 major genes, is now being transferred and better
mildew (*Erysiphe cruciferarum*) resistance is being introduced from a cross
between Chinese cabbage and kohl rabi made by Dr. Harberd of Leeds Univer-
sity. High growth rate, to produce an early variety, and high dry matter

content, to produce a late hardy variety, are also being introduced from appropriate parents.

There are several other interesting possibilities for swede breeding, and it is seen that there is an enormous amount of work which could be attempted. It could take several years before the best approach to swede breeding is defined, and at the present the range of variation in swedes and turnips seems to be decreasing rapidly as old varieties are taken off the market. Another aspect that needs immediate attention, therefore, is the setting up of a gene-bank for swedes and, in particular, for turnips. If anyone knows of an old seed stock which has, or will become unavailable on the market, could they please send a small sample of seed so that we can try to maintain as much variation as possible within these species for future use.

PLOT SIZES AND VARIETY TESTING

In each of the last two years, a plot of commercial swedes has been harvested to provide information on optimum plot sizes. The total size was 60 m by 30 drills (21 m) wide, and this was harvested in 5 m lengths. The results for the relevant plot sizes for use in trials are shown in Figure 1. It was found that with increasing length and width, the coefficient of variation drops sharply at first and then levels out. These figures, however, would appear to give a poor comparison between the plot sizes, because the number of plots varies. For instance, with a 30 m x 8 drill plot size there were only six plots in the analysis whereas for 5 m x 1 drill plots there were 360.

Keeping the number of plots constant and increasing the area could give a better comparison. For a plot number of six, the results from one trial are shown in Figure 2. In all cases it was found that the coefficient of variation rose when the plot width was increased above 4 drills. This number of plots is too small for most practical purposes, and further analyses are needed for higher numbers of plots.

Table 1. Coefficients of variation and relative block sizes to show the effect of using guard rows for each plot.

No. of plots	Plot Size length x no. drills	C.O.V.	Relative block size
42	10m x 2	6.5	0.5
	20m x 1	6.6	0.5
	10m x 4	4.4	1.0
	20m x 2	4.3	1.0
	10m x 2	6.7	1.0
	+ 2 guard rows		
28	15m x 2	5.0	0.5
	30m x 1	6.0	0.5
	15m x 4	3.7	1.0
	30m x 2	3.4	1.0
	15m x 2	5.3	1.0
	+ 2 guard rows		

Two comparisons using plot numbers of the order likely to be found in variety trials are shown in Table 1. A further consideration taken into account here is the use of guard rows for each plot. From the examples shown, it is seen that using guard rows either doubles the size of the trial to give an equivalent C.O.V., or that there is a 50% increase in the C.O.V. in comparison to harvesting the whole plot. It would appear that strong evidence of large competition effects between cultivars would be needed before the use of guard rows was considered.
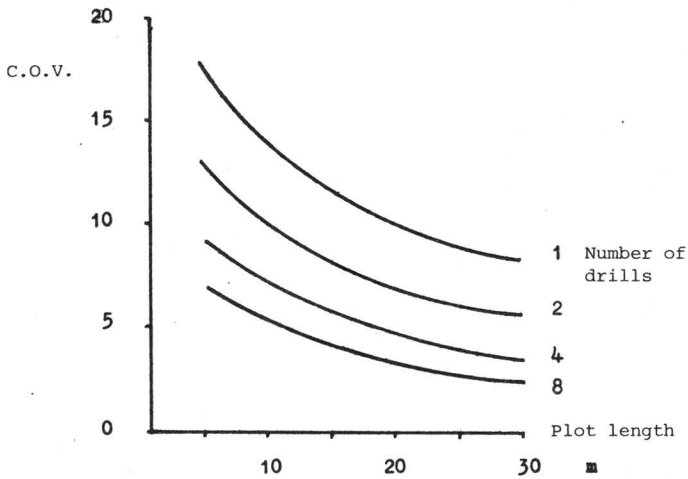
Figure 1.   Graph of coefficients of variation for various
plot sizes from the full block analysis.
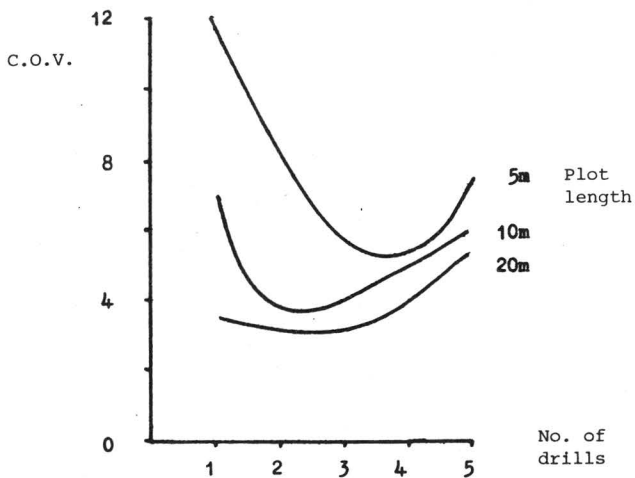
Figure 2.   Graph of coefficients of variation for various plot
sizes with six plots of each size being analysed.

There are several factors to be taken into account when evaluating these figures, and deciding which plot size to use. Taking into account trial size and ease of management, these results suggest that 20 m x 2 drill plots would be the most practical choice.

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SESSION I: DISCUSSION

G. Julén: Dr. Wilson indicated in his first example that a lower respiration rate gave a greater yield. His graphs also showed this to be the case during the winter, although the difference was not as pronounced as in summer. How does a low respiration rate influence hardiness and persistency during the winter? Winter-hardiness is mainly dependent on direct cold resistance and the ability to survive during long periods with no assimilation. The latter factor is important in northern countries where we have very low temperatures and prolonged snow cover. Is there any relationship between low respiration rate and winter-hardiness, and is it possible to have a high yield during the summer and a low respiration rate in winter?

D. Wilson: A low respiration rate of mature tissues goes with high crop growth rates. I would imagine that if there is an effect of respiration on winter survival, then it will be the low respiration material which will survive best. We have not had severe winters in Aberystwyth to test this in the field, and we have not as yet been able to set up an experiment under controlled environments specifically to look at this. We have, however, had this material in the cold rooms for other purposes, and there are some indications that it may be slightly more cold hardy. This is not necessarily the same thing as your winter-hardiness.

B. S. Ahloowahlia: Under long daylengths when most of the growth takes place, would you not think that photorespiration rather than dark respiration might be more important in determining the net photosynthesis. Would you expect a similar kind of variation in photorespiration as you have found in dark respiration?

D. Wilson: The significance of variation in photorespiration and CO_2 compensation points in C_3 plants is something I started to look at some years ago. The particular genotypes in Table 1 were isolated specifically from a wide gene pool because they differed in CO_2 compensation concentration which is a differentiating character when comparing C_3 and C_4 species. We also measured their apparent photorespiration as well as we could at the time, and were able to isolate individual ryegrass genotypes which differed very markedly in these characters. Our hypothesis was that low photorespiration might possibly give an advantage, but the curious thing was that the genotypes with apparently low photorespiration and low CO_2 compensation points were among the most miserable plants in the summer. I think this underlines simply that we do not know the biochemical role of photorespiration in C_3 plants. There is some indication that it is a necessary characteristic for C_3 plants in the winter, but for some reason it was certainly not related to growth in our experiment, whereas dark respiration has shown a consistent negative relationship.

P. Dickie: Dr. Wilson was talking about silica levels in grass plants, suggesting that they have some effect on the amount of material digested. Could I ask at what water levels he was working? Work done by myself and Parry at North Wales suggests that in saturated soils silica uptake is increased, and in drier soils it tends to drop.

D. Wilson: I don't believe I said anything about silica in relation to the animal. What I said was that by selecting for low cellulose or weak leaves,

we obtained plants which, growing under the same conditions as the popula-
tion we selected from, had less observable silica on the leaf surface than
plants from a population selected for high cellulose. There was an
apparent correlation between the amount of leaf cellulose or leaf strength
and the amount of observable silica. This was when grown under the same
conditions; I do not know what would happen if we grew them under wet or
dry conditions and looked at the interactions.

G. E. van Dijk: I would like to ask Dr. Wilson about leaf tensile strength.
Twenty years ago results were published from New Zealand on this method.
After twenty years experience are the New Zealanders still enthusiatic a-
bout this technique? Is there any time of year best suited for measuring
leaf tensile strength, and how many leaves per plant are required for meas-
urement?

D. Wilson: The New Zealanders are still interested in leaf strength. The
reported work was done on a selection from hybrid long-rotation ryegrasses
(Evans 1964). One of the main things that emerged from animal production
trials with low leaf strength selections from hybrid ryegrass material was
a dramatic difference in growth in the summer (Lancashire et al. 1976).
Consistent differences in liveweight gain at other times of the year were
also observed on the low leaf strength material compared with the original
variety. The overall difference was about 7%, but the correlated effects
on summer growth were more dramatic. We find in other species that the
effect of selection for leaf strength or leaf cellulose tends to be more
visually obvious than in ryegrass. In tall fescue and cocksfoot partic-
ularly, one tends to get very different types of plants, possibly because
of the association with other structural features. As cocksfoot, for exam-
ple, tends to have a lower digestibility than ryegrass, improving this in-
take characteristic (cellulose) also seems to improve digestibility, some-
thing that is less likely to happen in ryegrass. The same is true of tall
fescue.

As far as sampling procedure is concerned, our experience in ryegrass is
that with vegetative plants 3 young, fully expanded leaves per plant are
sufficient to give a repeatable difference on a selection basis. However,
one flag leaf at heading time is sufficient to differentiate one genotype
from another. Screening at this latter stage is obviously better in terms
of economy of effort, provided that flowering times are more or less the
same and the leaves are formed under the same conditions of temperature
and light intensity.

E. L. Breese: Can you enlarge on why selection for leaf characteristics of
this sort should also affect the stem, whereas selection for whole-plant
digestibility affected stem rather than leaf?

D. Wilson: One of the most important characteristics affecting digestibil-
ity is the relative proportions of different tissues, i.e., the amount of
leaf, the amount of reproductive tillers. If you simply cut plants at a
given height above the soil surface and measure the total digestibility of
the cut material, one of the effects may well be that you select for diff-

Evans, P. S. 1964: A study of leaf strength in four ryegrass varieties. -
    N.Z. J. agric. Res. 7: 508-513.

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    in press.

erent leaf/stem ratios which also affects digestibility. If you select on the basis of some common part of the plant like a leaf you will then hopefully affect only the inherent anatomy of the plant, and if it is possible to change the quality components without changing the proportions of different tissues, I think that this is theoretically the only way we can do it. We have found that if we select for low leaf lignin anatomically, we also get reduced levels of lignin in reproductive tillers. One of the side effects in tall fescue and cocksfoot of selecting for low leaf cellulose is that we also get more tillers, but this does not seem to affect the leaf/stem balance.

K. Aastveit: I would like to ask a question of a more general nature. I believe you mentioned that the main concern in grass breeding is to increase dry matter yield, nutritive value and stability. You then went on to discuss photosynthetic efficiency, respiration rate, stomatal density, etc. I also think you mentioned that these characters or sub-characters could be used in the search for potential parents. Do you think that these sub-characters can be used in practical plant breeding work for the final selection of families, varieties or even clones? In other words, would you recommend practical plant breeders to use these sub-characters in their selection work?

D. Wilson: I would say yes. For some of the characteristics I have been talking about I do not think there is any other way that a plant breeder can choose the right plants. Taking the control of water use by transpiration as an example, there is no way in which, without actually looking at the adaptive character that affects transpiration, you could decide whether plant A is going to be better than plant B, because as an isolated individual in the field with access to a large pool of moisture it is not going to show to any advantage. Furthermore, in a competitive situation, one individual with better water conservation is not going to show any advantage because its competitors around it are going to use all the soil moisture. It is only when you have a plant individual surrounded by like individuals in terms of water use efficiency that you get any benefit. This also implies that if we breed a variety with improved water use efficiency, the farmer sowing this variety in a mixture should also have access to varieties of the other species with improved water use efficiency, otherwise the better efficiency of his new variety will be of less advantage.

D. Aldrich: Are the ryegrass varieties that are resistant to barley yellow dwarf the same that are resistant to ryegrass mosaic?

G. Ziegenbein: I do not think it is resistance, but rather tolerance. We do not know whether the stunting in our material was due to barley yellow dwarf or to ryegrass mosaic. We do know that both were present, and most infections were probably mixed.

G. Julén: I would like to put a question to Dr. Bócsa concerning the relationship between cutting frequency and *Verticillium* resistance. Is there a direct relationship between resistance to frequent cutting and to the disease, or do you in your material have such a general *Verticillium* attack that all plants are more or less affected and thus subjected to a double stress? In the latter case you would have better survival from resistant plants than from non-resistant, i.e. an indirect relationship.

I. Bócsa: I think the relationship must be indirect. *Verticillium albo-atrum* and *Fusarium* sp. are so-called weak parasites, i.e., half-saprophytes and half-parasites, and due to the frequent cutting the susceptible plants

are not able to regenerate, i.e., their weakened state provides conditions whereby the harmless semi-parasites become severely parasitic. In the absence of frequent cutting persistence will not be revealed, and without wilt resistance the plants are intolerant of frequent cutting.

J. Norrington-Davies: I wonder if Dr. Ceccarelli could tell us a little more about his selection index, because the key thing appeared to the selection of the index itself, and as soon as you have done this you have decided a lot of other results. How sure can you be when you are making a selection of this index?

S. Ceccarelli: This is the weakest point of the index, because the way in which you weight the single traits very much affects the results. This is probably the reason why animal breeders use these indices much more than plant breeders. Many of the animal traits can be expressed in terms of market prices which can be used to weight each trait. It is much more difficult to establish the economic value of dry matter yield, heading date, and similar characters. However, I believe that these methods can be very useful, and that work should be done to improve their efficiency and to establish a fair way to weight single traits such that the methods are less affected by subjective choice.

J. Norrington-Davies: I think also that the idea of creating a model concentrates your attention on those features that are really important, and that by improving or trying to get a better index you are going to produce a better end product.

E. L. Breese: Could I ask Dr. Kobabe about his investigations with heterosis in *Lolium multiflorum*? You said that you were able to demonstrate up to 27% superiority of the F_1 hybrids relative to Lema. Was this estimated in plots or spaced plants?

G. Kobabe: With our technique of using male steriles we were able to harvest considerable quantities of seed, which permitted the use of 1 m^2 plots with 2 replications.

E. L. Breese: I recall that Foster in the literature you referred to was able to demonstrate quite strong heterosis under spaced plant conditions when he was using a 50 : 50 mixture of F_1 and the parents, but was unable to demonstrate this under competitive conditions in swards.

G. Julén: May I ask Mr. Morgner for what purpose you are using Persian clover?

F. Morgner: Persian clover is a true annual, and we badly need annual forage crops in our rotations which are characterized by increasing cereal areas. It is a very stable crop with high protein yields. We also have no problems with *Sclerotinia* in Persian clover, and to date we have had no problems with nematodes.

J. Hill: Is Persian clover resistant to *Sclerotinia* or have you not observed infection?

G. Ziegenbein: There is no possibility for infection by *Sclerotinia*. Infection by this pathogen takes place in November by which time Persian clover has been harvested.

Session II

ADAPTABILITY AND COMPETITIVE ABILITY

Chairman: Dr. O. Bosemark

BREEDING FOR ADAPTABILITY IN GRASSES

E. L. Breese

Welsh Plant Breeding Station, Aberystwyth, Wales.

SUMMARY

Grassland crops have to be adapted to survive and yield over a range of climatic conditions in which cold temperature and/or water stress may feature prominently. Regional differences will involve variations in these stresses as well as in soil factors. Diseases are becoming increasingly important under intensive farming systems. The type of plant which can yield and persist under these conditions is largely determined by the mode of utilization, whether for conservation or for grazing; but there is increasing insistence on management flexibility and a call for a versatile sward which can be used in alternate grazing/cutting situations. Three approaches to breeding for widely adapted, versatile swards will be briefly discussed: (i) breeding genetically heterogenous varieties with a high degree of 'population buffering', (ii) breeding co-adapted varieties which are complementary in balanced mixtures and (iii) breeding for an improved 'individual buffering capacity' of genotypes, particularly through hybrid varieties. The problems associated with each approach in relation to distinctiveness, uniformity and stability as required for variety registration are mentioned.

INTRODUCTION

Herbage crops will long continue to be used as a source of ruminant food, and the emphasis will be on reducing production costs. The requirements are for a crop which can be repeatedly harvested by cutting or grazing throughout the seasons and over a varying number of years depending on the crop rotation. Matching the requirements of different animal systems to sward production calls for considerable skill on the part of the grassland manager. Generally, the requirements are for a high annual yield and a good seasonal spread of dry matter, good nutritive value and persistency, including tolerance of winter cold and summer drought. The management inputs are generally restricted to soil amelioration (fertilizer application, etc.) and control of the frequency and intensity of defoliation by cutting or grazing. Artificial buffering of the crop is thus minimal and genetic buffering has to be provided against disease, pests and competition from weeds.

In defining adaptability I am going to take a very broad view and consider it to include high productivity of the sward throughout the year, over different locations and years, and over different managements. Indeed, let us consider the truly versatile sward and then the limits to, as well as the means of, achieving this.

PAST AND PRESENT APPROACHES

Ecological studies have shown that material from natural grasslands is precisely adapted to specific environmental conditions. The yielding capacity of these adaptations thus interact strongly with climatic, edaphic and management factors. Nevertheless, a number of present day varieties, founded

on ecotypes which had become adapted to specific management systems, have been exploited by appropriate management well beyond their regions of max-imum adaptations with regard to soil type and, to some extent, climate. This, perhaps, provides good evidence of the over-riding role of manage-ment in determining and maintaining plant type. Indeed, National List Trials in the United Kingdom have chiefly drawn attention to regional interactions between grass or clover varieties that are associated with major stress factors, e.g., winter hardiness, drought tolerance, or dis-ease resistance, although we may question whether the evaluation technique employed or the analysis of data is designed to show other interactions with soil type, fertility levels, etc., which might be important at the farm level.

However, there is a marked reluctance by farmers to adopt the rigidity of a one-field to one-variety system and, frequently, a greater flexibility of management is sought through the use of mixtures. These are designed variously to ensure long season growth, nutritional complementation, or to provide for grazing and conservation potentialities. Even on intensive all-grass dairy farms, a two block system designed to cater independently for grazing and conservation managements is often regarded as too inflex-ible. Clearly, there is a high demand for a versatile sward. To what ex-tent can we cater for this?

We may recognize two approaches to breeding at present. The first may be termed *physiological*, which focuses on the efficiency of the sward in con-verting solar energy and soil nutrients into high quality herbage and then considers the management which best exploits this (e.g., Cooper 1972). Here it is likely that the management will have to be increasingly precise for optimum expression. We may cite the experience of Rhodes (1973) in this connection, where selection for an efficient sward canopy arrangement involving long, erect leaves, results in yield increase which can only be realized under an infrequent cutting system. The second approach may be termed *agronomic*; here the inadequacies of existing varieties in relation to farm systems are considered, and emphasis is placed on management flex-ibility as a first requirement. We are thus led to consider sward versatil-ity. To label the first approach as inevitably leading to specifically adapted varieties as opposed to the second leading to general adaptability would clearly be too great a distinction. These are complementary approach-es, but we have to consider their inter-relationships in achieving fully integrated and efficient farming patterns with a prime regard for manage-ment flexibility.

POPULATION STRUCTURE IN RELATION TO VERSATILITY

Studies in ecological genetics have clearly shown us that the versatility of a population of organisms is determined by two aspects (i) genetic heteroge-neity and (ii) genotypic flexibility (Mather 1973). These are the equiv-alent of 'population buffering' and 'individual buffering' as defined by Bradshaw (1965). The first situation is potentially unstable and is usually only maintained by complex interdependencies between the constituent geno-types which are often affected by density and frequency (e.g., balanced polymorphisms). The second situation is potentially stable within limits. These principles apply to the sward.

SWARD VERSATILITY THROUGH GENETIC HETEROGENEITY (POPULATION BUFFERING)

(a) Varieties with a wide genetic base

The outbreeding system of grasses and clovers naturally maintains a high

level of heterozygosity and genetic heterogeneity and the synthetic variety is designed to perpetuate this. It was mentioned earlier that some of these varieties have wide adaptability in relation to climate and soil if properly managed. The late flowering perennial ryegrass pasture variety S23 is one of these. Its breeding history indicates that the basic plants of the variety, although of similar morphological type, derived from a number of typical, but widely scattered, old grazed pastures under moderate levels of fertility. We may expect therefore that it would show a fair range of adaptation, and this has been demonstrated by joint regression analysis (Samuel et al. 1970). Valentine and Charles (1975) show that this is due in part to individual (genotype) buffering and in part to genetic heterogeneity (population buffering).

The potentialities of these widely based populations are also mentioned by B. Nüesch in a later paper to this meeting. The populations are potentially unstable, however, since selective changes of genotype frequencies in response to particular environments may occur rapidly during the establishment phases of the sward and may be irreversible (Charles 1966). Indeed, survivors from S23 swards under different management intensities have been used as the basis of new, specially adapted varieties by A. H. Charles (e.g., better recovery growth and survival under high stock densities with heavy N applications). Again S23 has responded to selection for a large number of physiological characters and factors affecting nutritive value (see contribution by D. Wilson). To what extent these changes are irreversible (i.e., non plastic) under sward conditions is not precisely known and requires further research. It depends on the capacity of the sward to maintain genetic heterogeneity, and initial studies by Hayward (unpublished) indicate that this can be considerable with a consequent continuing capacity for flexible response. The wide genetic base does, however, provide problems with regard to the distinctiveness, uniformity and stability requirements for variety registration.

(b) Co-adapted varieties for use in mixtures

If it is too much to expect that we can incorporate all the requirements of particular swards into one variety, to what extent can we breed complementary varieties which will form an integrated, stable and versatile sward? In practise, mixtures of grasses, with and without legumes, are widely grown in farm systems. Recommendations for specific mixtures are arbitrarily based on the performance of the components as individual swards in plot trials and from farm experience of their use in mixtures. Can we produce varieties which can be more determinately labelled than this?

Clearly, there are many problems associated with breeding co-adapted lines for use in mixtures. This includes competition and co-operation effects which might be density and/or frequency dependent, and thus difficult to maintain under sward conditions. The need is perhaps for a large degree of individual buffering, because the components have to be adapted not only to changing environmental conditions, but also to each other. These aspects are considered in subsequent contributions. In these studies grass/legume interactions have a special significance, since such mixtures will be of paramount importance under extensive grazing systems with low levels of applied N until such time as we can conjoin nitrogen fixing organisms with, or incorporate the faculty into, grasses.

It is worth emphasizing that in seeking sward versatility through mixtures we are attempting a special balanced form of population buffering, but the achievement of this requires components with wide genotypic flexibility (individual buffering).

SWARD VERSATILITY THROUGH GENOTYPIC PLASTICITY (INDIVIDUAL BUFFERING)

(a) Improving the versatility of synthetic varieties by breeding and/or selection for specific characteristics

Where identifiable features of the environment limit crop production and utilization (e.g., winter temperature, summer drought or disease) we have the opportunity to increase the adaptability of the crop by incorporating genetic factors for tolerance or resistance. In the complex sward situation the physiologists and chemists can help here by identifying plant characteristics which are important in sward production and animal nutrition (see contribution by D. Wilson). The extent to which these characteristics can be built into varieties as a means of extending general adaptability, as distinct from forming the basis of more precisely adapted varieties, depends on their association with other characters, and whether this is due to un-breakable pleiotropic gene action or breakable gene linkage. For example, the critical and complex relationship between spring growth and cold tolerance is discussed in a later paper (A. Panella et al.). Again, in this context the most efficient canopy structure of infrequently cut swards for conservation regimes, i.e., long, erect leaves, is the inverse of the best canopy arrangement for intensively grazed pastures, i.e., prostrate and smaller leaves (Rhodes 1973).

(b) Hybrids and allopolyploids

As noted earlier, the wide distribution of the grasses has ensured that during the course of evolution races and species have developed with markedly different spectra of characteristics. Many of our breeding processes have perpetuated these differences. Cytogenetic investigations have now shown us that we have the opportunity to combine in individual genotypes attributes which hitherto could only be introduced into a sward as mixtures of varieties or species.

Early successes included a tetraploid hybrid cocksfoot (*Dactylis glomerata* x *D. lusitanica*) which incorporated a capacity for early spring growth with an acceptable mid season yield and winter hardiness (Rep. Welsh. Pl. Breed. Stn for 1966, pp. 51-56). The ryegrass/fescue complex of races and species offers particularly large scope for exchange of genetic material and thus of producing potentially widely adapted material through race and species hybrids and their derivatives. Thus stable allotetraploids between Italian and perennial ryegrass combine a greater tillering capacity and persistency under cutting and grazing treatments with the otherwise excellent growth and nutritive characteristics of Italian ryegrass (Breese et al. 1975). By judicious choice of parents, enhanced tolerances of cold temperature and water stress, together with improved resistance to disease, has been achieved. Relatively stable allotetraploids between both ryegrass species and meadow fescue have also been obtained (Lewis 1974) and are now under advanced testing.

The success of particular hybrids depends on the dominance relationships of the genes controlling the various characters. It has been shown that dominance and epistasis are environmentally dependent and are much more overt in extreme environments (e.g., Breese 1969). Thus the hybrid state can be particularly effective in buffering individuals against environmental vicissitudes. Much more genetic information on gene action in the hybrids is required before we are able to predict the full potential of this approach in extending the adaptability and increasing the versatility of grass varieties. So far we have concerned ourselves with the production of stable allopolyploids, though other approaches are possible (Breese et al. 1971). In cytologically stable allotetraploids the heterozygous conditions of homoeologous chromosomes is permanent, but the tetraploid state allows a second level of heterozygosity between homologous chromosomes to be achieved.

The extent to which this multiple heterozygosity allows a further combination of characters leading to an even greater versatility in performance is being investigated.

CONCLUSIONS

Widely adapted, versatile swards may be achieved through genetically heterogenous varieties (population buffering), through the use of mixtures or through plastic genotypes (individual buffering). Success requires a high level of organization in the action of constituent genotypes or genes. Also important is the distinctiveness, uniformity and stability of the variety for identification and registration purposes. Electrophoretic techniques have revealed a range of isozyme markers which are being used at the Welsh Plant Breeding Station for identification purposes and for monitoring stability aspects (Rep. Welsh. Pl. Breed. Stn for 1975, in press).

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ADAPTABILITY THROUGH MIXED SWARD COMPONENTS

J. Hill

Welsh Plant Breeding Station, Aberystwyth, Wales.

SUMMARY

Herbage breeding programmes have hitherto paid scant attention to the performance of cultivars in mixtures. The development of high performance, stable mixtures requires the production of agronomically compatible cultivars. Before this can happen more information is needed about the competitive and co-operative interactions which occur between individuals under sward conditions. Because of the wide range of environmental conditions under which herbage crops are expected to thrive it is clear that potential mixture components must possess a wide adaptability not only to changes in the environment but to the other components of the mixture. Adaptability can be attained by different mechanisms and experimental evidence for the operation of these mechanisms in perennial ryegrass (*Lolium perenne*) and white clover (*Trifolium repens*) is discussed in relation to the formulation and management of co-adapted mixtures.

INTRODUCTION

Adaptability may be defined as the capacity of individuals, genotypes, varieties, etc., to respond to changing environmental conditions. In relation to herbage mixtures interest centres upon those which can sustain their superiority over single cultivar swards despite environmental changes.

Traditionally British grassland farming was founded upon complex mixtures consisting of several different grasses, legumes and even herbs. Such mixtures were regarded as an insurance both against mismanagement and the more natural hazards of pests, diseases and drought. Moreover, largely as a result of the work of Elliot at Clifton Park and Gilchrist at Cockle Park, mixtures of grasses and legumes, known as leys, played a prominent part in rotational farming systems, where they were used to improve the physical and manurial status of the soil for succeeding crops in the rotation.

In any examination of the role of herbage mixtures in farming systems one fact emerges very clearly, namely that no serious attempt has been made to select and breed herbage cultivars for their performance in mixtures. At present breeding programmes are designed to select only cultivars which are highly productive in their own right. Clearly we need to re-think our whole approach to the breeding of suitable components for herbage mixtures. Our present piecemeal approach of bringing together high performance cultivars in the hope that they will, *ipso facto*, produce a high yielding mixture must be abandoned. We must try to develop varieties which are agronomically compatible and to do this we need to know more about the competitive and co-operative interactions which occur between genotypes, cultivars and species under sward conditions. Hopefully we shall then be able to breed co-adapted varieties for use in mixtures suitable for a range of managements and purposes.

That is in the future, however: for the present the all-important question is how productive are mixtures compared to single variety swards. Here the

experimental evidence strongly suggests that binary mixtures generally yield less than monocultures of their better component (Trenbath, 1974). Only in specific instances has a yield advantage been recorded for a binary mixture over its better monoculture (Rhodes, 1970; Hall, 1974; Hill, 1974; Wells and Haggar, 1974). Why should the performance of binary mixtures regularly fall below that of their better monocultures? Although there is no simple answer to this question, it probably depends upon a combination of factors, including the appropriate balance between the components of the mixture and their response to changing environmental conditions. To counter these factors demands a wide adaptability on the part of the components, not only to changes in the environment but to each other.

ADAPTABILITY IN HERBAGE CROPS IN RELATION TO THE FORMULATION AND MANAGEMENT OF MIXTURES

As the main herbage crops are outbreeders there are essentially two methods by which mixture components can adapt themselves. First, different genotypes may be adapted to a different spectrum of environments (population buffering); secondly, individual genotypes may be adapted to a range of environments (individual buffering).

Dealing first with population buffering, survivor material of S.23 perennial ryegrass (*Lolium perenne*) extracted from several different leys differed significantly for such characters as coldhardiness, rust resistance, persistency under high nitrogen, heading time, etc., when tested in trials at the Welsh Plant Breeding Station (Charles, 1973). Each of these populations had clearly undergone a shift in the expression of these characters which may be genetic in origin. Such shifts would of course then be irreversible if certain sectors of the original population had been eliminated.

Work by Hill (1973 and unpublished) with a small number of selected perennial ryegrass and white clover (*Trifolium repens*) genotypes, which had been propagated asexually, has demonstrated the existence of individual buffering in both these herbage species. In one experiment, in which five perennial ryegrass genotypes were grown as monocultures and all possible 50:50 mixtures, analysis disclosed that the yield of these five competitors depended upon its associate competitor background. The extent of this dependence may be gauged from Fig. 1, in which the dry matter yield of each competitor is regressed against an index based primarily, but not exclusively, upon the mean dry weight of all competitors growing with a common associate competitor. It should be pointed out that if, amongst a particular set of individuals, competition is a purely physical process whereby the strongest competitors secure for themselves a disproportionate share of the limited resources available, then these strong competitors will supply a poor associate environment and *vice versa*. A linear model provided a satisfactory fit to the data, with the stronger genotypes, A, C and E, having a significantly higher response to changes in the associate environment than genotypes B and D. Being more responsive genotypes A, C and E were consequently better able to capitalize upon any improvements in the associate environment. By contrast genotype B was such a poor competitor that its dry matter production was virtually independent of its associate background. Although the environmental index was based mainly upon associate effects it also embraced different cutting regimes as well as successive harvests throughout the growing season. The fact that a single line adequately fitted the data for each competitor despite the inclusion of such disparate factors in the index suggests that the stress imposed by neighbours was no different in kind from those imposed by other environmental agencies.

Initially mixture advantage was recorded within several of these binary combinations of ryegrass genotypes. There was little evidence to suggest, how-
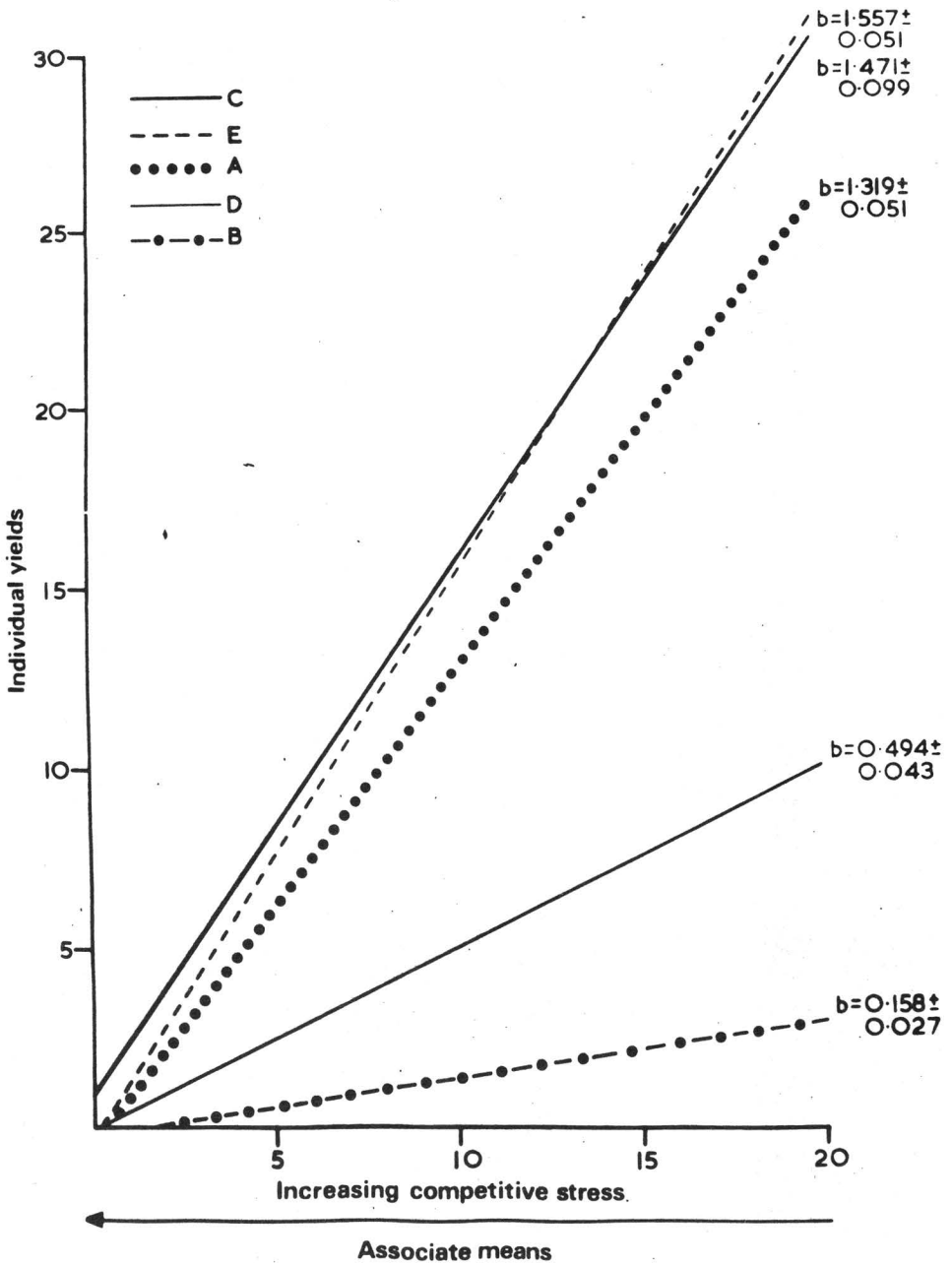
Figure 1.   Regression of dry matter yields (g) of five perennial
            ryegrass genotypes against environment (associate) means.

ever, that this advantage stemmed from co-operation between the components concerned. Rather was it due to over complementation on the part of the stronger component. Indeed such an advantage proved to be transitory, whilst its size was found to depend upon the magnitude of the competitive interactions in relation to the difference between the appropriate mono-cultures and also upon the proportions of the two components in the mixture (i.e. it was frequency dependent). Clearly these results highlight some of the problems of maintaining a stable mixture performance.

On a farm scale how are mixtures based solely on grasses to be used? In general grass cultivars currently used in agriculture have been selected for high performance in pure sward. To achieve this level of performance requires large inputs of fertilizer, particularly nitrogen, and as a consequence the sward will probably be intensively managed for a specific purpose throughout its productive lifetime. Though management will tend to be consistent from year to year, the sward as a whole has to be versatile because it must be capable of responding to the inputs applied during its lifetime. The consequent homogenizing effect which a consistent management regime will have upon the niches available for supporting the components argues that such mixtures should be based upon similar components. For binary mixtures there is evidence to suggest that a 1:1 proportion may give the highest yields (van den Bergh, 1968; Rhodes, 1970; Hill, 1974).

Studies on the co-adaptability of perennial ryegrass/white clover genotypes show how some white clover genotypes are able to modify their phenotype. In the presence of applied mineral nitrogen the white clover was repressed. Where reliance was placed solely on rhizobial nitrogen the degree of clover dominance depended upon the aggressiveness of the companion grass. However, some of the white clover genotypes not only performed well under a rhizobial nitrogen regime, they also tolerated ryegrass competition in the presence of applied nitrogen. Clearly, the behaviour of the white clover genotypes in this experiment was determined jointly by the grass associate and the nitrogen source, a fact which is illustrated in the analysis of petiole length data presented in Table 1. Here also the level of individual buffering (phenotypic plasticity) varied from genotype to genotype.

Table 1. Analysis of petiole length data for 3 recordings in 1975

Item	d.f.	Mean Square
Nitrogen source (N)	1	0.01
Recordings (R)	2	427.37
Clover genotypes (Cl)	4	1814.24***
Associate competitor (ass)	5	238.83
Cl x Ass	20	127.61
N x R	2	29.19
N x Cl	4	2o4.17
N x Ass	5	146.43
R x Cl	8	80.95
R x Ass	10	96.74
N x R x Cl	8	26.55
N x R x Ass	10	55.35
N x Cl x Ass	20	116.53***
Cl x R x Ass	40	71.98**
N x R x Cl x Ass	40	29.62***
Differences within boxes	4320	4.40

** P = 0.01 - 0.001; *** P < 0.001.

Farming systems which place greater reliance upon the legume component of the sward for nitrogen are usually less intensive than those referred to

earlier. The need to retain the legume in the sward, coupled with the pur-
pose-oriented nature of the mixture, again allows no room for management
flexibility. Indeed, because it is necessary to take advantage of the dif-
ferent growth rhythms and spatial relationships of the components in the
mixture, a very precise management regime is demanded. But, in addition,
it is important in such mixtures that the components can adapt to each other.
Thus individual buffering (phenotypic plasticity) is likely to figure prom-
inently in such mixtures. Evidence suggests that for maximum yields the
proportions of the components in binary mixtures based upon dissimilar compo-
nents should be approximately 3:1 in favour of the higher yielding component
(Wells and Haggar, 1974; Hill, 1974).

Although the experiments described here have been conducted on a very limited
and selected sample of genotypes, the results do at least demonstrate the
existence of individual buffering within perennial ryegrass and white clover,
two of the major components of herbage mixtures used in British agriculture.
This is a step in the right direction as far as the development of co-adapted
cultivars suitable for use in mixtures is concerned. The deliberate incorpo-
ration of this property of individual buffering into perennial ryegrass and
white clover cultivars could well become a breeding objective in the future.

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CONSIDERATION OF ADAPTABILITY IN SWISS FODDER PLANT BREEDING

B. Nüesch

*Swiss Federal Research Station for Agronomy,
Zürich-Reckenholz, Switzerland.*

SUMMARY

Although in Swiss ley farming we observe comparatively uniform ecological conditions, we notice in the official tests with fodder plant varieties a remarkable environmental interaction. In order to obtain a good adaptability in our varieties we have pooled many different ecotypes with similar morphological characters. Unfortunately, it is not possible to test our breeding material to an ideal extent. This lack can be partly compensated by a longer duration of the observations. Thus, we are able to calculate very useful indices of adaptability. By undersowing meadow-grass in the nursery we hope to select for a good competitive ability, especially in cocksfoot and perennial ryegrass. Seedling infections with stem nematodes in red clover and crown rust in the ryegrasses allow a selection for resistance and contribute furthermore to a better adaptability of the varieties.

INTRODUCTION

In Switzerland leys are included in the rotation of arable crops. They are therefore cultivated under limited ecological conditions; i.e., precipitation between 90 and 120 cm, fairly well distributed over the growing season, mean temperature 8.4°C, with a mean of -0.9°C in January and a mean of 17.7°C in July. In this region we find mainly cambisols or luvisols of high fertility with a pH of 6 or 7.

The leys are generally sown with mixtures of one or two legumes and two to five grasses. These mixtures are bought as so-called "standard mixtures" which are tested, recommended and controlled by the Swiss Research Stations for Agronomy. Most leys are sown for three years (sowing year included).

As breeders we have to build up varieties suitable for the whole ley-growing area. Therefore, we have to know the adaptive qualities of the species to be bred and to select for good competitive ability in order to meet the requirements of mixed sowing.

INTERACTIONS OF THE ENVIRONMENT

A good insight into the interactions of the environment was obtained by the analysis of variance over varieties, cuts, sites and years. Unfortunately, the fodder plant trials are very unsuitable for this analysis because firstly the harvest dates of the varieties vary and are not easy to define, secondly in the last days of the cutting stage they develop very rapidly and a delay of a few days causes considerable differences in yield, and thirdly they are highly dependent on local weather conditions because of the short period between two cuts. For these reasons such analyses of variance are often questionable. Furthermore one often observes that some cuts have not been recorded and that some varieties are not included in all trials. We have therefore used the results of the official variety trials to calculate only the correlations between two sites, as given in table 1. Since good correlations are obtained more easily in trials with large yield differences

Table 1 Investigations on the results of Swiss official trials with varieties of some fodder plants. Summary of differences in yield between varieties within trials and coefficents of correlation between the yields of the same varieties at two different sites (basic values from Mitteilungen für die Schweizerische Landwirtschaft, 1967 - 1975)

Species	Number of		Differences between varieties in % of the means per trial			Coefficients of correlation (r) significance (number of cor- relations)				
	varieties	trial-sites	minimum	mean	maximum	mean	n.s.	0.05	0.01	total
Red clover	41	12	10.4	22.7	65.8	0.57	9	2	8	19
Italian ryegrass	12	4	5.9	11.3	17.6	0.20	6	0	0	6
Westerw. ryegrass	14	3	16.2	20.4	22.9	0.50	2	1	0	3
Perenn. ryegrass	14	5	15.6	20.7	24.4	0.36	9	1	0	10
Meadow fescue	13	4	8.5	14.4	23.9	0.36	5	0	1	6
Cocksfoot	56	17	6.4	21.1	64.5	0.30	33	5	2	40

between varieties than with varieties of similar yields, we have also listed in table 1 the differences between the varieties, relative to the mean. From high correlation coefficients combined with large differences between varieties we conclude that the varieties perform very similarly at the two places concerned. There are both well adapted and badly adapted varieties. Small correlation coefficients together with small differences between varieties signify that there are no differences between varieties and sites. Good correlations and small differences between varieties are the results of small environmental interactions.

In our official trials we include only varieties which have successfully undergone a preliminary test. If differences are observed as large as those shown in table 1, we have to assume little adaptation of certain varieties. With respect to the species concerned we conclude:

Red clover: We observed the largest differences between varieties of all species tested. In 10 out of 19 comparisons significant correlations resulted and the mean correlation value is larger than in any other species. The interactions of the sites are considered to be of secondary importance.

Italian ryegrass: Differences between varieties and correlations are comparatively small. There seems to exist a large site x variety interaction.

Westerwold's ryegrass: Here we observe relatively large differences between varieties and correlations of only moderate expression. Probably due to the short duration of only one year, the environmental interactions were less effective than in Italian ryegrass.

Perennial ryegrass: According to the enormous variation of types, the differences between varieties are very large. The same is true for the differences between sites. There exist interactions of high expression between sites and varieties.

Meadow fescue: Here interactions sites x varieties are very pronounced, the differences between varieties and sites are fairly low.

Cocksfoot: There are in some instances very high differences between varieties, and the interactions sites x variety are also large.

All these trials include a representative and modern spectrum of varieties. We especially note that neither sites of comparable altitude nor precipitation have narrower correlations. This reveals the importance of other factors. The results emphasize the great economic importance of the actual choice of varieties.

Table 2 shows the results of individual harvests and sums of harvests obtained from breeding material. Compared with the variety trials the correlations are lower for red clover. In Italian ryegrass, however, the results are very different. Here we notice partly very high correlations. This is due to foreign varieties used as standards which performed in all sites very differently from our material. Comparing the correlations of single cuts with those of the sum of two or three years, we observe no relevant difference in red clover but undoubtedly so in Italian ryegrass. With this species the selection becomes the more accurate the more harvests we consider. In red clover we note a distinctly stronger interaction between genotype and harvests. Observations on the spot show that mainly differences in weather, soil fertility, attacks by diseases (*Sclerotinia trifolium*, fusarioses, bacterioses) as well as damage by nematodes and mice are responsible for the manifold interactions.

In this connection it may be of interest to look at the investigations of Bieri (1967) who studied the genotype-environment interactions in Swiss breeding material of several cereals. In cereals the conditions seem more simple, because there is only one harvest at a very well fixed term. Never-

Table 2 Coefficients of correlation (r) between the yields of breeding material of red clover and Italian ryegrass at two sites. A = Year of sowing; H_1 = second year; H_2 = third year. I, II, III etc. for 1st, 2nd, 3rd cut. S = sum of ...

Cut	Red clover					Italian ryegrass				
	Number of trials		Coeff. of correlation			Number of trials		Coeff. of correlation		
	Total	with sign. r	r mean	r max.	r min.	Total	with sign. r	r mean	r max.	r min.
A II	8	1	0.062	0.454	-0.755	3	0	0.321	0.493	0.162
A III	7	2	0.285	0.827	0.039	3	1	0.361	0.816	-0.101
H_1 I	19	6	0.268	0.766	-0.338	3	1	0.463	0.802	0.009
H_1 II	20	6	0.243	0.881	-0.328	3	2	0.588	0.797	0.397
H_1 III	19	5	0.191	0.730	-0.276	3	2	0.616	0.710	0.554
H_1 IV	12	1	0.145	0.434	-0.435	3	1	0.302	0.659	-0.071
H_2 I	3	0	0.269	0.459	0.145	1	0	-0.054		
H_2 II						1	0	0.431		
S A	13	3	0.204	0.686	-0.265	3	0	0.570	0.683	0.402
S H_1	16	2	0.182	0.606	-0.116	3	2	0.757	0.846	0.648
S A + H_1	15	5	0.293	0.798	-0.138	5	5	0.792	0.953	0.729
S A+H_1+H_2	3	0	0.061	0.490	-0.307	3	2	0.767	0.892	0.645

theless, this study shows a high error component of variance. In most cases the interactions between genotypes and surroundings were significant. The author concludes that the breeder must enlarge the genetical variation and test his material by choosing more representative trial sites in order to minimize interactions between genotypes and the different locations.

Thus the situation seems to be similar to that of herbage genotypes and, therefore, the conclusions for breeding are the same.

REQUIREMENTS ON THE BREEDING PROCEDURES AND THEIR ACCOMPLISHMENT

For breeding adaptable and high-yielding varieties of fodder plants the following requirements must be considered:

a) Wider genetic variation

It is easy to answer this requirement for the allofertile fodder plants used in Swiss leys. Firstly, we have immense resources of genotypes in local races and ecotypes and secondly we have the possibility of pooling plants of the same type, but of different origin and adaptive potential. In the varieties of our Station we have a broad genetic base obtained by combining components of many different ecotypes, mainly of Swiss origin.

(In red clover, for example, we tested more than 200 local races and wild ecotypes. To build up the variety "Renova" we chose components from more than 20 different local forms and 4 wild ecotypes. For the tetraploid red clover "Temara" we selected material within the variety "Renova" and some Swiss landraces for colchicine treatment and used more than 2100 successfully induced C_0-plants as a basis. The C_2 and C_3 generations were sown at 14 different sites in the Swiss Plateau and put under practical management. In the third year we harvested seed heads and selected at the same time for a high seed set per head. The following generations were observed in the nursery again. A similar procedure was followed for Italian ryegrass.)

b) Tests at representative sites

We think that testing at four or five representative sites would be suitable. These localities should primarily differ in climatic conditions and in soil quality (e.g., 1) dry summer, little snow in winter; 2) average precipitation and snow cover; a) light soil, b) medium soil, c) heavy soil; 3) high precipitations, 4-8 weeks of snow cover). Among these four or five sites there should be one or two with conditions favourable for attack by fungal diseases. Due to lack of manpower we are not able to manage more than two or three trial sites. In fodder plants we have, however, the possibility of extending our observations and to consider up to eight or ten harvests per trial. This may partly compensate for the lack of sites. Very useful observations can also be obtained by row sowings, which are a little expensive but give good estimates of growth rhythms, resistance to diseases and endurance.

c) Exact registration of the environment interaction

We try to state the adaptability of our breeding material by calculations based on the harvest results. We use the analysis of variance for single sites to test the significance of the performance of our material. In addition the regression technique of Breese (1969) and/or the value of ecovalence of Wricke (1962) with the results from all trial sites give an estimate of the adaptability of the individual strains. As there are at least 10 to 12 yields at our disposal, valuable indices may be obtained. In table 3 we give an example for the estimation of breeding lines by the methods of Breese and Wricke. The strains in this table are listed according to their distribution about the regression line. The correlation of this value with

Table 3 Equations of regression of some red clover lines on mean yield for each harvest, distribution about the regression line and WRICKE's indices of ecovalence (results of 15 harvests 1973 - 1975, Reckenholz and Rütti)

Line No.	Equation of regression	Distribution about regression line	WRICKE's indices of ecovalence	Total yield green matter q/ha
15	1.01 x + 1.57	0.041	574	4060
2	1.00 x + 7.91	0.042	590	4120
5	0.96 x + 4.37	0.043	1164	3909
8	0.99 x + 0.74	0.052	1483	3977
10	1.07 x - 16.54	0.059	1628	4014
4	1.03 x - 0.27	0.064	1425	4092
7	1.01 x - 4.77	0.066	1480	3970
3	0.97 x - 11.24	0.069	1637	4047
1	1.00 x - 0.50	0.070	1608	3982
11	0.97 x + 8.17	0.075	1990	3979
12	0.97 x + 1.98	0.080	2696	3892
14	1.08 x - 23.55	0.090	3453	3969
6	1.05 x - 8.94	0.094	3211	4064
9	1.01 x - 7.76	0.102	3373	3898
13	0.88 x - 20.91	0.132	7483	3815

that of Wricke can easily be detected. For the selection we choose lines with high yield and narrow variation about the regression or with low Wricke-index. These are the lines with a high and constant yielding potential. The regression equation gives us the possibility to estimate the circumstances for the optimal expression of a certain line.

d) Selection for competitive adaptability

This selection seems to be of great importance due to the fact that throughout mixtures of different species are used. Originally, mainly for practical reasons, we started to undersow our nursery with meadow-grass. In this way, we subject our plants to a natural competitive stress. Although we cannot prove it yet, we think that we get a good selection for competition. This seems to be true especially for cocksfoot and perennial ryegrass.

In order to improve resistance against the most common diseases, certainly another contribution to good adaptability and competition, we infect our red clover seedlings with stem nematodes and the *Lolium* species in the young plant stage with crown rust. Though our pre-selection for rust resistance is only weak, we induce at least an even and rather constant infection in the nursery, so that the selection is more effective than with natural infection.

Finally it is to be mentioned that selecting very long living plants (4 to 5 years) is in itself a selection for good adaptability and competition. This was proved several times with our red clover and Italian ryegrass.

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ESTIMATION OF YIELD STABILITY PARAMETERS FOR ALFALFA IN THE HIGHLANDS OF PERU

Oscar R. De Cordova D.

Universidad Nacional Agraria La Molina, Departamento de Fitotecnia, Programa de Farrajes, Lima, Peru.

SUMMARY

Replicated yield trials were conducted during three years in the Highlands of Peru to compare the responsiveness of Peruvian ecotypes and introduced cultivars of alfalfa to a range of environmental conditions over four locations ranging from 2,300 to 3,900 m above sea level.

Yield data was analyzed by previously described techniques to obtain estimates of genotype x environment variance components and parameters describing yield stability over environments. Variance component estimate for entries x locations interaction was more than four times greater than entries x years interaction and four times greater than entries x locations x years interaction. The three factor, entries x locations x season within years interaction, was of considerable magnitude but smaller than entries x locations interaction.

The combined analysis of variance when stability parameters were estimated showed that the major part of entries x environment variance was explained by differences in slopes of linear regressions between Peruvian ecotypes vs introduced cultivars and entries within each group. Ranger, Buffalo and Caliverde are the most desirable cultivars for the Highlands of Peru as far as yield performance, regression coefficients and deviations from regression are concerned.

INTRODUCTION

Alfalfa (*Medicago sativa* L.) is the most important and widely distributed forage crop in both coastal and highland ecological-geographical regions in which it is grown in Peru. Variety trials conducted by government research stations and University research programmes have shown that coastal Peruvian ecotypes, typically hairy Peruvian alfalfas, perform much better in total fresh matter in the coastal region than any introduced cultivars. However, when they were tested at different altitudes above sea level in the highland region, most of the introduced cultivars performed better than almost all of the Peruvian ecotypes, although location responses among introduced cultivars were different (De Cordova and Florez 1973, De Cordova et al. 1969). A portion of the variability expressed by changes in cultivar rankings in locations, seasons within years and over years can be attributed to experimental error and the remainder to interaction of genotypes with environment. As stated by many authors, these interactions are of major practical importance as well as of theoretical interest (see reviews by Freeman (1973) and Moll and Stuber (1974)). Stratification of environments has been suggested in order to reduce genotype x environment interaction (Moll and Stuber 1974), but even with this technique, in geographical areas such as the Highlands of Peru, the interaction of genotypes with locations in a subregion and with environments encountered at the same location in different seasons within each year and over years, probably would remain too large. Performance tests over a series of en-

vironments have been used and are still being used to obtain information on genotype x environment interactions when analyzed in the conventional manner to identify those environmental factors which interact most strongly with genotypes as used in the first part of the present study. But this approach does not give a measurement of the stability of individual entries. Finlay and Wilkinson (1963) proposed the average yield of all cultivars grown at a particular location in a particular season as a measure of that environment and Eberhart and Russell (1966) suggested the use of an environmental index to measure environments, instead of the actual mean yield. Both apply the regression analysis technique, suggested originally by Yates and Cochran (1938), in which the cultivar means are regressed against the average yield of all cultivars in each location or against the environmental index. In addition to the regression coefficient, the mean square deviation from the regression has been suggested by Eberhart and Russell (1966) as a measure of estimating another stability parameter.

During the last ten years, many authors have found that the relationship between the performance of different genotypes in various environments is often linear, or nearly so (Finlay and Wilkinson 1963, Eberhart and Russell 1966, Breese 1969, Hill and Samuel 1971, Jappa et al. 1971, Jowet 1972, Taliaferro et al. 1973, Patanothi and Atkins 1974, Varela and Franco 1974, De Cordova 1975, Shen Li and Thompson 1975). Therefore there is a strong evidence to indicate that the response of individual genotypes can be expressed as a simple linear function of the environmental measures to which they have been collectively exposed. Although the regression analysis approach has frequently been subjected to controversy mainly because of the choice of measurement of environmental effects upon which the regression is made (Freeman and Perkins 1971), it is still more widely used than any other suggested approach, such as multivariate techniques (Freeman 1973) and the unweighted pair-group cluster analysis (Shen Li and Thompson 1975), to provide measures of phenotypic stability.

The investigation reported in this paper was undertaken in order to identify those environmental factors which interact most strongly with alfalfa genotypes when grown at different altitudes in the Highlands of Peru, and also to select an alfalfa cultivar with appropiate phenotypic stability for national certified seed production.

MATERIALS AND METHODS

Yield data and some agronomic characteristics were collected from a national alfalfa trial in which Peruvian ecotypes and introduced cultivars, mostly from the U.S.A., were included. Peruvian ecotypes represent genetic populations upon which long term natural selection has acted to produce locally adapted strains. San Pedro and Monsefu are the best yield performers in the north central part of the coastal region, in which alfalfa is grown under irrigation throughout the year. Eleven cuts can easily be obtained, and are mainly utilized for hay production. The ecotypes are named according to place of seed production and are almost indistinguishable on the basis of morphological and agronomic characteristics (De Cordova 1968). They are of erect growth type, non-grazing and non-winter resistant, and should be considered as typical "hairy Peruvian" alfalfas as they are known abroad. Tambo is the best ecotype for the southern coastal region as it is very well adapted to the new sandy irrigation areas. It is less hairy, shorter, with underground crowns, but with a higher leaf area and greener leaves than San Pedro and Monsefu (De Cordova 1968). Tambo can be harvested throughout the year every 45 days and is mostly utilized for grazing and for hay production in winter and summer, respectively.

The winter ecotypes are grown in the highlands but mostly in the warm Andean

valleys. Yaragua is grown in the southern and Macate and Alta Sierra in
the central and northern parts of the highlands. The latter two ecotypes
are morphologically indistinguisable, but differ from Yaragua in yield ca-
pacity and other genetic and agronomic characteristics (De Cordova 1968).
All of them are grazing and winter tolerant, with bigger crowns, less hairy
leaves, and shorter than the coastal types (De Cordova and Florez 1973).

The Highlands of Peru are formed by the "Cordillera de los Andes" crossing
the country from South to North. Most of the utilizable land (24,000,000 ha)
is grassland but many of the Andean valleys are suitable for agricultural
and fodder crops. The altitude of the four locations used in the present
experiment ranges from 2,300 to 3,900 meters above sea level. Arequipa and
Puno are located in the southern highlands at 2,600 and 3,900 m, respective-
ly, and Huancayo and Cajamarca in the central and northern part at 3,300
and 2,300 m. The highlands are characterized by rainy summers from October
to March with 450 - 650 mm precipitation and dry winters from April to Sep-
tember with 100 - 150 mm annually. The temperature of the Andean valleys
ranges from $5^{o}C$ - $24^{o}C$ in summer, to $-5^{o}C$ - $12^{o}C$ in winter. The average
monthly temperatures are $12^{o}C$ and $9^{o}C$, respectively.

The field plot design at each location was a randomized complete block with
four replications. Each plot consisted of ten 8 m long rows spaced 30 cm
apart. Yields were obtained by harvesting and weighing 6 centre rows of
each ten row plot. Plots were harvested from four to nine times per year
depending upon entries and growing conditions at particular locations. Yield
data were summed over cuts in each of the two seasons within a year to give
seasonal (summer and winter) production figures on which the analyses were
conducted. In all locations growing fields were irrigated at least once
every two weeks during winter seasons.

The combined analysis of variance for estimating the variance components was
conducted in the manner described by Cochran (1962). All effects were as-
sumed to be random and uncorrelated with variances, here denoted by

$$\sigma^2_L, \ \sigma^2_Y, \ \sigma^2_{LY}, \ \sigma^2_{RwL}, \ \sigma^2_{SwY} \text{ and } \sigma^2_e$$

where L, Y, R, S and e signify locations, years, replicates, seasons and
error, respectively.

The combined analysis of variance over all 24 environments (two seasons
within a year, four locations and three years) was computed by using the
method of Eberhart and Russell (1966), with slight modifications as suggested
by Freemann and Perkins (1971). The sum of squares attributable to entries
was partitioned into orthogonal comparisons between groups (Peruvian ecotypes
vs introduced cultivars) and among entries within groups. The entries x
environment sum of squares was partitioned similarly into interactions of
environments with individual comparisons.

Responses of the entries to different environments were analyzed by using
an environmental index calculated for each of the 24 environments subtract-
ing the grand mean of all experiments from the mean of all entries in each
environment. By regressing the mean of each entry in each environment upon
the environmental index, a regression coefficient (b) and the deviation from
regression (S^2d) were obtained for evaluating the stability of yield over
environments. The regression coefficient measures the increase in average
yield of an entry per unit increase in the environmental index. The mean
square for deviations from regression measures how well the predicted re-
sponse agrees with the observed response and includes entry x environment
interactions.

Table 1. Combined analysis of variance and estimates of variance components, based on fresh weight data, of cultivar x environment interaction.

Sources of variation	d.f.	M.S.	$\hat{\sigma}^2$
Environments (E)	23	803.45**	
Locations (L)	3	3519.4**	
Years (Y)	2	272.3	
L x Y	6	346.2**	
Seasons within Y (SwY)	3	992.2*	
L x SwY	9	258.3**	
Ecotypes and cultivars (V)	12	617.08**	11.35
V x E	276	60.48**	
V x L	36	158.4**	6.53
V x Y	24	54.2*	1.40
V x L x Y	72	31.8*	2.75
V x SwY	36	78.4**	3.83
V x L x SwY	108	42.3**	
Replicates within L	12	100.39**	
Residual (Error)	924	20.81	

*), **) Indicate significance at the 5 and 1% levels of probability, respectively.

$\hat{\sigma}^2$ Indicates the estimates of variance components assuming all effects to be random and uncorrelated with variances.

Table 2. Combined analysis of variance with estimation of stability parameters.

Sources of variation	d.f.	M.S.
Environments	23	803.45**
Replicates within locations	12	100.39**
Ecotype (E) and Cultivars (C)	12	617.08**
E vs C	1	800.9**
Among E	5	680.0**
Among C	6	533.3**
E + C x Environments	276	60.48**
E + C x Env. (1)	12	772.4**
E vs C (1)	1	846.0**
Among E (1)	5	616.2**
Among C (1)	6	890.3**
Pooled deviation	264	28.1
Residual	924	20.81

**) Indicates significance at 1% level of probability

(1) Indicates linear effects

RESULTS AND DISCUSSION

Mean squares and estimates of variance components pertinent to entries x environment interactions are presented in table 1. Significance (P > 0.01) was indicated for environments, entries and entries x environments. Partitioning of the entries sum of squares into orthogonal comparisons between groups and among entries within groups (Table 2) showed highly significant differences in fresh matter yield in all cases. The conventional analysis of variance of entries x environment interaction showed significant mean squares for VY and VLY (P > 0.05) and for VL, VSwY and VLSwY (P > 0.01). The variance component estimate for VL was more than four times greater than VY and double that of VLY. The estimate of the component for the three factor VLSwY is rather large although smaller than VL. Statistically highly significant mean squares and respectively large variance components for VL and VSwY interactions suggest maximum effects of locations (altitudes) and seasons within years on the comparative yielding ability of alfalfa. The relatively large VLSwY variance component indicates that testing in different altitudes (locations) is necessary in order to reliably estimate relative yield performance in alfalfa in the Highlands of Peru. Location mean yields over seasons and years, shown in table 3, indicated that yield reduction with increasing altitude was considerable in the Peruvian ecotypes compared with the introduced cultivars in which no reduction was observed up to 3300 m above sea level. The smaller average yield observed in Cajamarca (2300 m) compared to Arequipa (2600 m) was mainly due to an attack of leaf diseases at the former location, probably caused by higher relative humidity than in Arequipa.

Table 3. Mean performance in tns/ha of Peruvian ecotypes and introduced cultivars of alfalfa.

Entries	Locations				
	Coastal[*] 200-500	Cajamarca[**] 2300	Arequipa[**] 2600	Hvancayo[**] 3300	Puno[**] 3900
	Peruvian ecotypes				
San Pedro	116.33	75.06	74.00	63.86	55.73
Monsefu	114.66	71.56	68.50	61.93	49.26
Tambo	89.40	67.60	97.50	62.06	47.20
Yaragua	81.06	76.46	95.66	71.10	59.46
Macate	70.93	76.86	72.73	73.96	58.20
Alta Sierra	63.46	77.43	76.66	75.50	60.30
Average	89.31	74.16	80.84	68.07	55.02
	Introduced cultivars				
Moapa	85.60	93.90	97.80	83.26	57.93
Du Puits	68.73	92.23	91.56	88.26	60.30
Ranger	58.76	89.00	90.53	90.03	89.20
Buffalo	55.66	84.23	83.03	87.63	74.56
Caliverde	62.53	91.40	90.00	86.66	79.30
Atlantic	--	52.10	49.36	61.13	61.63
Lahontan	--	48.36	47.76	57.23	60.00
Average	66.26	78.74	78.57	79.17	67.98

[*] Average of three locations: Lambayeque, La Molina and Ensenada in the northern, central and southern part of the coastal region, respectively. Altitudes ranging from 200 - 500 m above sea level.

[**] Altitude in meters above sea level. Yield average over two seasons per year and over three years (Highlands of Peru).

Table 4. Mean performance in tns/ha, regression coefficients and deviations from regression for alfalfa entries tested at four locations in the Highlands over three years.

Entries	Stability parameters		
	Green matter	Regression coefficients	Deviation from regression
	Mean[a)	b	S^2d
Peruvian ecotypes			
San Pedro	67.16 (30)	0.88	39.7
Monsefu	62.81 (32)	0.82*)	45.2
Tambo	68.57 (33)	1.36*)	62.2
Yaragua	75.67 (38)	1.39*)	54.2
Macate	70.44 (40)	0.91	9.8
Alta Sierra	72.47 (41)	0.89	8.2
Average	69.52 (36)		
Introduced cultivars			
Moapa	83.22 (35)	1.30*)	69.5
Du Puits	83.09 (36)	1.28*)	67.3
Ranger	87.94 (45)	0.92	39.8
Buffalo	82.35 (42)	0.88	31.6
Caliverde	86.84 (43)	1.05	26.4
Atlantic	56.05 (44)	0.76*)	18.3
Lahontan	53.34 (42)	0.72*)	15.4
Average	76.12 (41)		

a) Annual fresh matter yield in tns/ha. Figures in parenthesis indicate winter production in per cent of total annual production.

*) Indicates significance at the 5% level of probability.

The combined analysis of variance when stability parameters are estimated shows that the major part of entries x environment variance is explained by differences between groups and within group slopes of linear regressions. As stated by Breese (1969), Hill and Samuel (1971), Jowet (1972) and Moll and Stuber (1974), the regression technique has transformed the complex of genotype x environment interaction into an orderly series of linear and therefore predictable responses. Mean yields over environments, regression coefficients and individual deviations from regression are given in table 4. For this evaluation of response to different environmental conditions, a stable entry is defined as one that has a regression coefficient approaching 1.0 and small deviations from regression. In addition, a high mean yield is also a desirable attribute, although not necessarily an indicator of yield stability. The introduced cultivars as a group performed much better in 18 out of the 24 environments with an average yield over environments of 76.12 tns/ha/year in comparison with 69.52 tns/ha/year for the Peruvian ecotypes. In addition, most of them gave a better yield distribution during the winter season than the Peruvian ecotypes, as shown in table 4. Entries regression coefficients (b) ranged from 0.82 - 1.39 and 0.72 - 1.30, and deviation from regression (S^2d) from 9.8 - 62.2 and 15.4 - 69.5 for Peruvian ecotypes and introduced cultivars, respectively. Figure 1 illustrates the differences in stability of certain entries within groups and their performance in relation to the average of the test. Figure 2 gives a graphic summary of the entries average yield and regression coefficients that may be useful in selecting stable entries. Introduced cultivars such as Ranger, Buffalo and Caliverde are very desirable because their performances are better than average in all
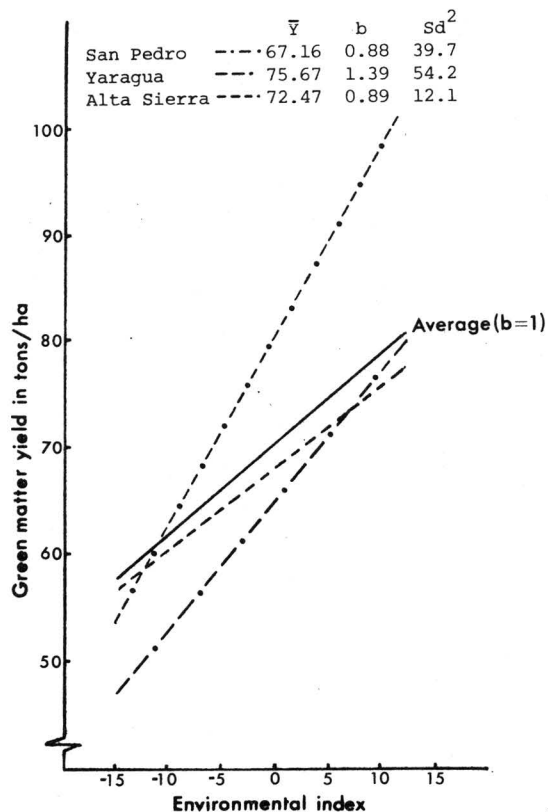
Figure 1a: Regression lines of individual
            Peruvian ecotypes on the envi-
            ronmental index.
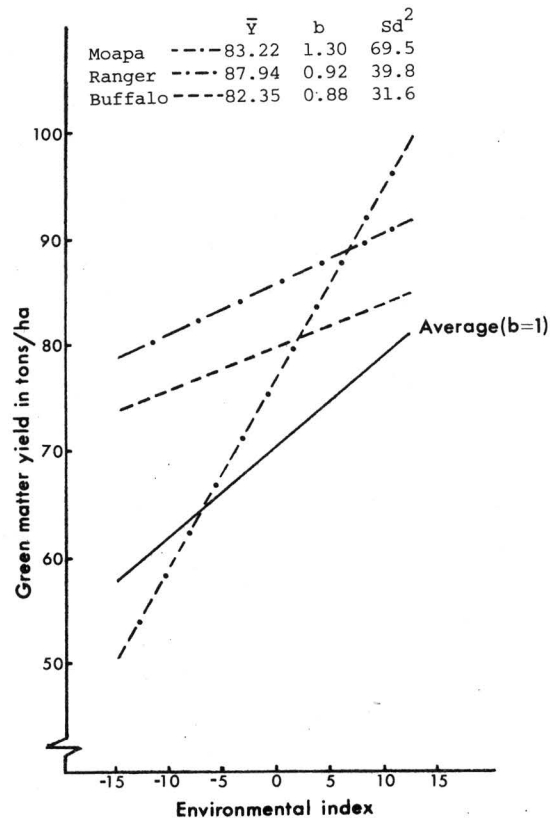
Figure 1b: Regression lines of individual
            introduced cultivars on environ-
            mental index.
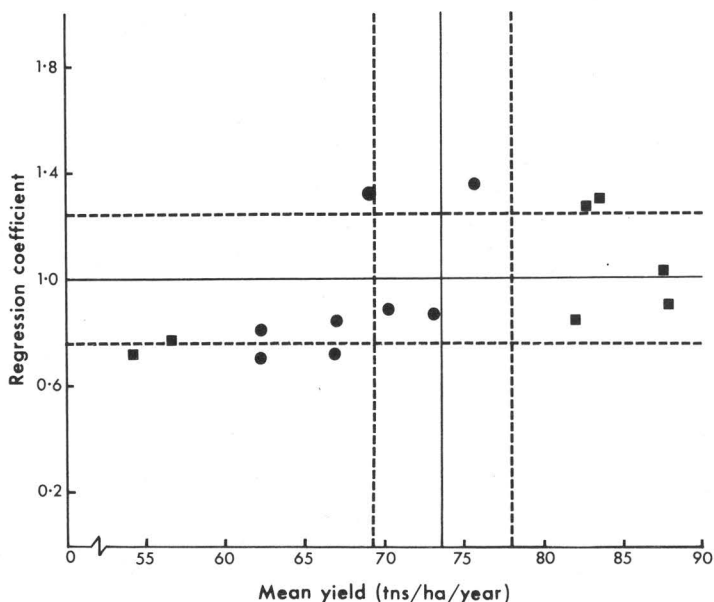
Figure 2. Relationships among mean yields and regression
coefficients for alfalfa Peruvian ecotypes (●)
and introduced cultivars (■).

environments, the regression coefficients do not differ from b = 1.0, and
deviations from regression values are intermediate between the highest and
lowest deviations shown by Peruvian ecotypes. In contrast, Tambo, Yaragua,
Moapa and Du Puits exceed average performance only under very favorable con-
ditions. Yaragua is a typical, mildly winter resistant type, widely distrib-
uted in the southern highlands up to an altitude of 2600 m where Moapa has
become very popular. Although the latter ecotype is less persistant than
Yaragua, it is well accepted by southern alfalfa growers due to its earliness
and fairly good quality (higher protein content and leaf-stem ratio than
Yaragua). The regression analysis technique has also showed that Alta Sierra
and Macate, widely distributed in the central and northern highlands, showed
quite good stability; the b and S^2d values (b = 0.91 and 0.89, S^2d = 9.8
and 8.2, respectively) did not differ statistically from b = 1.0 and S^2d =
0.0, respectively. However, their yield performances are expected to be
slightly lower than the test average, but very much lower than Ranger, Bufalo
and Caliverde.

It is concluded that alfalfa trials can probably be adequately evaluated in
the Highlands of Peru by testing for three years at a selected number of
locations varying mainly in altitude. Analyses of yield stability by the
regression technique as proposed by Eberhart and Russell (1966), appears
valuable and justified by the additional information made available to the
variety trials as well as the plant breeders.

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GROWTH RHYTHM AND PRODUCTIVITY OF DIFFERENTLY ADAPTED TYPES OF FORAGE SPECIES (*)

A. Panella, F. Lorenzetti and S. Ceccarelli

Plant Breeding Institute, University of Perugia, Italy.

SUMMARY

Results are presented of two experiments with different species and varieties of forage grasses designed to gain information on dry matter yield and its distribution throughout the year.

The first experiment conducted at Perugia with 42 varieties of 11 grass species, utilized with simulated grazing in the period 1972/1974, has shown, along with the expected differences in dry matter yield among species, significant differences among varieties within species.

The relative importance of varieties within species has not been uniform; it has reached the maximum in *Lolium perenne* L., while in *Festuca arundinacea* Schreb. it was irrelevant.

The dry matter yield of all the tested species has been characterized by a striking seasonality.

In a second experiment the dry matter yield of two contrasting types of *Lolium perenne*, a continental and a maritime type, was determined in a pasture utilized by sheep. Also this experiment demonstrates that seasonality is a prominent feature of *Lolium perenne* yield in Central Italy; in the winter less than 5 kg/ha DM per day are obtained, while in April and May DM yield exceeds 40 kg/ha per day; in July/August DM yield is almost nil but after the rainfalls of September it again reaches 5-6 kg/ha per day.

The continental type of *Lolium perenne* when grown in Umbria, which is its region of adaptation, is less productive than the maritime type from the Marches; the latter type also has a longer growth season, perhaps as a consequence of the milder climate of the area of origin.

It is concluded that the basic material for new varieties to be employed in the area where the experiment has been carried out (Umbria) should be selected among types from an area slightly milder, in order to realise a useful compromise between ability to grow from autumn to spring and cold tolerance. In Central Italy seasonality cannot be overcome simply by breeding *Lolium* or other cool-season grasses.

INTRODUCTION

The two main problems of grassland utilization and management in Central Italy are the distribution of yield during the year and the persistence of the sward over a relatively long period. These problems largely depend on

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the climate of Central Italy and on the type of materials usually grown. The climate of Central Italy, which is mostly hilly and suited for pasture use, is characterized by low temperatures during winter and severe drought stresses during summer; these conditions give rise to two growth gaps which the joint efforts of breeders and farmers are trying to overcome. The grass varieties grown at present in this area are usually those bred in foreign countries where grasses grow under very different climatic conditions.

The present paper presents the results of two experiments with different species and varieties of forage grasses designed to gain information on persistence and dry matter yield and its distribution during the year.

MATERIALS AND METHODS

In the first experiment the material consisted of 42 varieties of 11 grass species: *Agrostis alba* (1 variety), *Agrostis tenuis* (1), *Brachypodium pinnatum* (1), *Dactylis glomerata* (10), *Festuca arundinacea* (9), *Festuca pratensis* (4), *Festuca rubra* (4), *Lolium perenne* (5), *Phalaris truncata* (1), *Phleum pratense* (2), *Poa pratensis* (4). The varieties were sown broadcast in autumn 1971 in 6 m^2 plots arranged in a randomized block design with four replicates. The trial included some unidentified types because the Italian National List of varieties had not come into force in 1971; in these cases only the country of origin is specified. Furthermore, some species were soon found to be of no value for our environment, while others were represented by only one type. Only the data relating to species represented by many types of contrasting origin and therefore differently adapted will be considered here. The species chosen by these criteria were *Dactylis glomerata*, *Festuca arundinacea* and *Lolium perenne*, which are also the species that have been found in many trials to be of interest in Central Italy. The characters which received consideration were: persistence, evaluated by visual estimate of ground cover at each cutting time; dry matter yield, and seasonal productivity. The dry matter yield of the sward was determined on forage harvested by simulated grazing when the height of the sward reached 10-12 cm and is expressed as grams/m^2.

In a second experiment the dry matter yield of two contrasting types of *Lolium perenne* L., one of continental origin (Umbria) and the other of maritime origin (Marches), was determined in a pasture utilized by sheep; in this case there were 8 replicates of 100 m^2 plots sown broadcast in autumn 1968.

RESULTS AND DISCUSSION

The results of ground cover evaluation are reported in Fig. 1 where, for each species, the data of foreign and Italian varieties have been pooled because no significant differences were observed within groups. In tall fescue the differences between the Italian ecotypes and the foreign group of varieties were not significant and the ground cover values were almost constantly over 80%. In cocksfoot the pattern was quite different because at the end of summer 1973 the two groups began to diverge progressively. In 1975 the ground cover of the Italian group was 93% while that of the foreign group was only 36%. In perennial ryegrass the divergence between groups began at the same time as in *Dactylis glomerata* but at the end of 1974 ground cover in the foreign group continued to fall sharply to a negligible value (1%) while the Italian variety (Vejo) still had a ground cover of 74%.

The dry matter yield data, reported in table 1, reflect the pattern observed
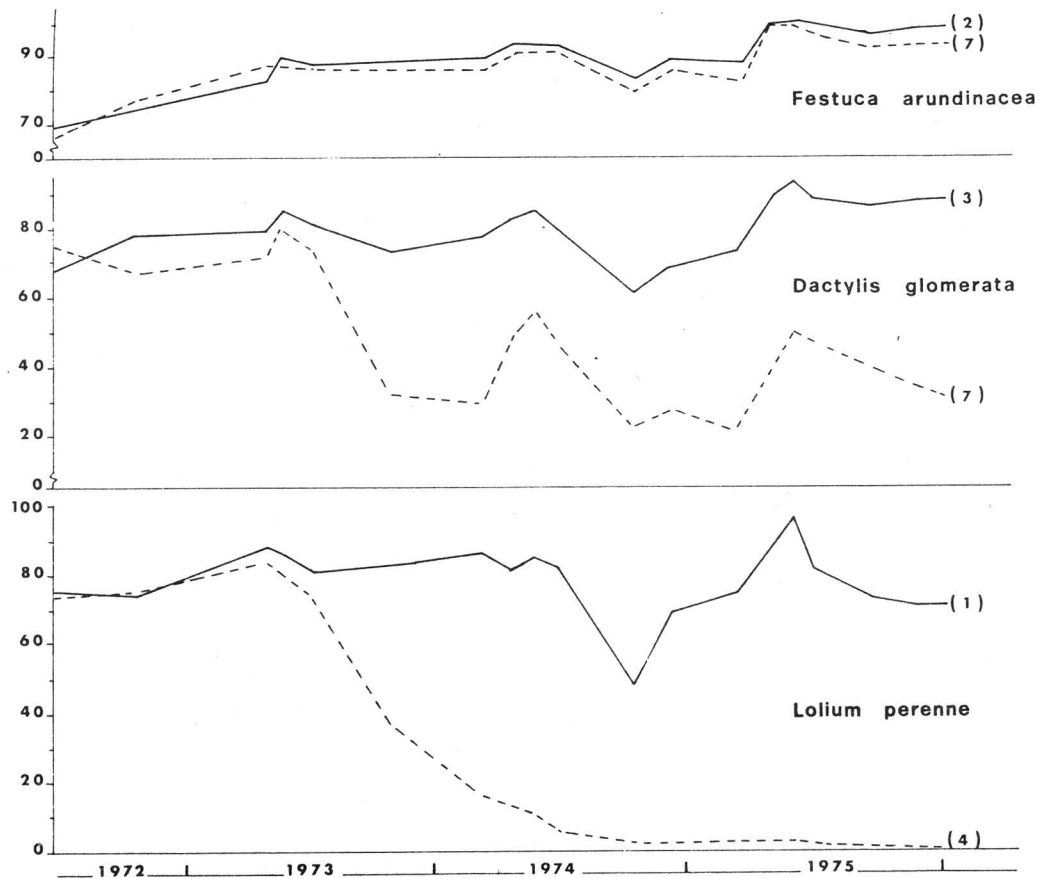
Figure 1. Ground cover (%) of Italian (——) and foreign (- - -) varieties or ecotypes of three species of forage grasses (in brackets the number of varieties and ecotypes in each group)

Table 1. Dry matter yields (g/m^2) of varieties of three grass species grown at Perugia, Italy (1972/1974). Figures relating to Italian types are underlined.

Varieties or ecotypes and country of origin		1972	1973	1974	Total
Dactylis glomerata					
Cesarina	(I)	553	257	344	1154
Ecotype from Tuscany	(I)	416	228	257	901
Germinal	(F)	476	250	257	989
Floreal	(F)	465	241	157	863
Lucifer	(F)	387	204	187	778
Marta	(I)	319	224	236	779
Nika	(PL)	426	204	135	765
Prairial	(F)	373	222	143	738
—	(DK)	504	217	114	835
—	(PL)	400	233	114	747
Festuca arundinacea					
Alta	(USA)	579	314	393	1286
Ecotype from Umbria	(I)	397	268	305	970
Ecotype from Marches	(I)	649	285	387	1321
Ludelle	(F)	526	321	302	1149
Ludion	(F)	579	299	315	1193
Manade	(F)	620	395	400	1415
—	(USA)	560	324	435	1319
—	(Can)	417	262	269	948
—	(USA)	564	334	408	1306
Lolium perenne					
Pacey	(NL)	1034	214	6	1254
Verna Pajbjerg	(DK)	763	189	1	953
Vejo	(I)	720	216	236	1172
—	(DK)	853	212	53	1118
—	(USA)	895	224	19	1138
LSD ($P < 0.05$)		219	78	92	

for ground cover. All species gave the highest yield in the first harvest year (1972); a strong decline of productivity was observed in all the varieties from the first to the second harvest year; the greatest differences were observed in *Lolium perénne*. In the third harvest year (1974) the behaviour of the three species was very different. In *Festuca arundinacea* there was an average yield increase of 15% relative to 1973 for all varieties with the exception of Ludelle, with no important differences between Italian and foreign varieties. In *Dactylis glomerata* there was an average increase of productivity of 18% for the Italian types whereas a decrease of 29% was observed for the foreign group. In *Lolium perenne* there was a 9% increase for the Italian variety, whereas the stand of the four imported varieties was so poor in 1974 (see Fig. 1) that their yield was negligible.

The pattern of seasonal productivity, which is a striking feature of the behaviour of forage grasses in the Mediterranean ares, is shown in table 2; it is clear that in winter and in summer the yield of all the varieties of the three species is very poor: the winter contributions to annual yield are 2.8%, 3.5% and 6.9% for cocksfoot, tall fescue and perennial ryegrass, respectively; the corresponding figures for summer yield are 5.7%, 7.9% and 6.2%. The highest contribution is given by the spring yield with 76.0%, 66.6% and 75.1% for the three species, respectively. The data in table 2 also indicate that the Italian types in comparison with the foreign varieties seem to give a relatively higher yield in autumn; this can be due to the joint effects of mortality in foreign types after summer stresses (Fig. 1) with a longer growing season of the Italian types.

The results insofar illustrated strongly support the view that the most obvious sources of adapted types lies in the indigenous materials. On the other hand it is well known that adaptation of local types depends largely on their ability to survive the extreme climatic events of their own area, but this does not necessarily mean that they have the highest agronomic value. In particular, when the breeder is mainly concerned with productivity, the best types can be found in regions with fertile soils and mild climate, in any case the first step of a breeding programme must be the collection and the evaluation of many, not just one, adapted types.

In Central Italy, in a relatively small area it is possible to identify two contrasting environments: 1) Umbria, characterized by low soil fertility and continental climate with cold winters and dry summers and 2) the maritime region of the Marches, where soils are richer and the climate is milder.

Two ecotypes of *Lolium perenne* from these two contrasting regions were grown at Perugia in the period 1969-73 and the results are shown in fig. 2. The Umbrian ecotype is less productive than the maritime one (the average DM yield over three years was 11.2 and 13.0 kg/ha/day respectively); the latter is more productive in autumn, winter and spring while no differences have been detected for summer yield. This is due to the longer growing season of the maritime type and to its ability to give some growth in winter.

The figures obtained for *Lolium* in this trial are of the same magnitude of those obtained from Vejo under simulated grazing conditions (Table 1). Vejo is a new variety of *Lolium perenne* obtained by mass selection from an Umbrian type; it is clear from fig. 3 that it behaved in the same way as its basic population did under simulated grazing.

Figure 3 also shows the patterns of seasonal yield for two types of *Festuca arundinacea* and *Dactylis glomerata* from the same contrasting areas (Table 1). It is evident that for all three species the maritime type is more productive than the continental one.
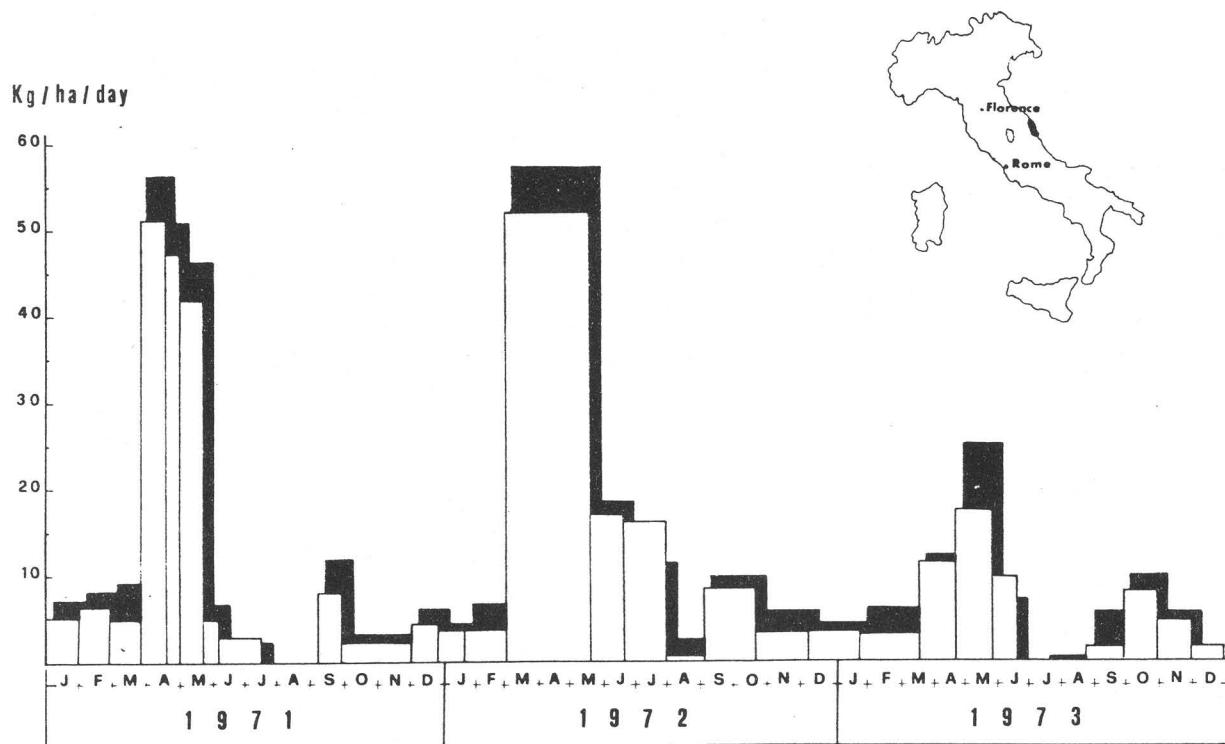
Figure 2. DM yield of two contrasting ecotypes of *Lolium perenne* L. from Marches (■) and Umbria (□). Perugia 1971-1973.

Table 2. Seasonal yield (g DM/m^2) of varieties of three grass species grown at Perugia, Italy (1972-1974). Figures relating to Italian types are underlined.

Varieties or ecotypes and country of origin		Winter	Spring	Summer	Autumn	Year
Dactylis glomerata		2.8%	76.0%	5.7%	15.5%	100
Cesarina	(I)	15	258	22	90	385
Ecotype from Tuscany	(I)	7	226	17	51	301
Germinal	(F)	9	252	18	51	330
Floreal	(F)	8	231	14	35	288
Lucifer	(F)	8	189	16	46	259
Marta	(I)	7	191	13	49	260
Nika	(PL)	5	203	17	30	255
Prairial	(F)	8	196	15	27	246
–	(DK)	7	216	17	38	278
–	(PL)	5	205	15	24	249
Festuca arundinacea		3.5%	66.6%	7.9%	22.0%	100
Alta	(USA)	16	279	35	99	429
Ecotype from Umbria	(I)	10	209	26	78	323
Ecotype from Marches	(I)	14	283	40	103	440
Ludelle	(F)	12	261	28	82	383
Ludion	(F)	14	258	31	95	398
Manade	(F)	22	302	38	110	472
–	(USA)	21	303	30	86	440
–	(Can)	6	226	25	59	316
–	(USA)	12	301	34	89	436
Lolium perenne		6.9%	75.1%	6.2%	11.8%	100
Pacey	(NL)	32	329	24	33	418
Verna Pajbjerg	(DK)	19	238	22	38	317
Vejo	(I)	28	271	29	62	390
–	(DK)	23	287	24	39	373
–	(USA)	28	285	18	48	379
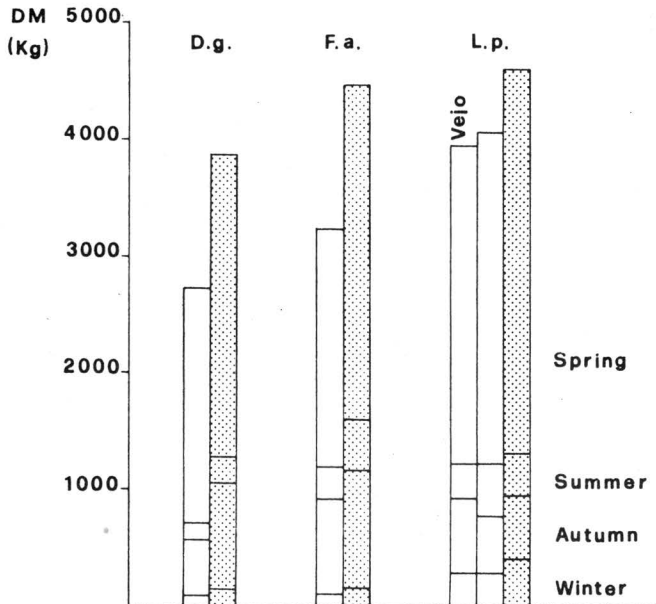
Figure 3. Seasonal yield of ecotypes of *Dactylis glomerata* (D.g.),
Festuca arundinacea (F.a.) and *Lolium perenne* (L.p.)
from Umbria ▢ and the Marches ▨

CONCLUSIONS

The data for ground cover (Fig. 1) clearly show that the local types of
grasses tend to be, as expected, more persistent than foreign types. An
important feature of the data is that the impact of the choice of variety
within species is not always the same: it is very important in *Lolium
perenne*, it is also of some importance in *Dactylis glomerata*, but it seems
irrelevant in *Festuca arundinacea*.

Another consideration is suggested by the seasonal pattern of productivity
of the three species which is characterized by an approximate 70% contribu-
tion by spring and a 17% contribution by autumn yields.

The behaviour of types from contrasting environments suggests that varieties
to be employed in the area where the trials have been carried out (Umbria)
should be obtained by selection among types from an area slightly milder, in
order to realize a useful compromise between ability to grow from autumn to
spring and winter-hardiness. Types from milder areas are also characterized
by a longer growing season, but the winter and summer gaps are so impressive
for all the tested types that they cannot be overcome simply by breeding
cool season grasses. It is evident that careful attention must be extended
to other forage plants and to all the management practices that farmers can
follow in such situations.

ADAPTATION AND COMPETITIVE INTERACTIONS
BETWEEN RYEGRASS PLANTS OF DIFFERENT CHROMOSOME NUMBER

J. Norrington-Davies

Department of Agricultural Botany, U.C.W., Aberystwyth, Wales.

SUMMARY

Information obtained from experiments concerned with the interactions of
the diploid Hora and the tetraploid Terhoy during early growth show that:

(1) When a 50:50 mixture of the two varieties was sown in boxes, it was
found that there were 22% fewer tetraploids than diploids after 15 months
had elapsed. There were even fewer tetraploids (44%) under conditions of
high fertility.

(2) The relative uptake of P, when the two varieties were grown together
in the field, differed to the uptake of either when grown alone. In mix-
tures the uptake of the tetraploid increased at the expense of the diploid
in the 10 cm zone whilst the diploid compensated for this by an increased
uptake in the 20 cm zone.

(3) In germination tests the diploid has a higher final germination value
than the tetraploids when the varieties were sown as pure stands, but in
mixtures the converse was true. An elute could be produced from each vari-
ety which had an inhibitory effect upon germination.

INTRODUCTION

Tetraploid grasses have been in common use for a number of years, and many
of their production and quality characteristics have been well documented.
There is still much that has not been recorded of their behaviour during
the establishment phase and their interactions when used in mixtures.

A series of experiments have been undertaken at Aberystwyth using the tetra-
ploid Terhoy and the diploid Hora from which it has been derived. Informa-
tion from several of these experiments are used here to illustrate certain
features of the two varieties during the establishment phase when grown in
mixtures together.

1. THE RELATIVE SURVIVAL OF THE DIPLOID AND TETRAPLOID COMPONENTS
OF A BINARY MIXTURE.

Equal numbers of seeds of the diploid Hora and the tetraploid Terhoy were
mixed. This seed mixture was sown in wooden seed boxes measuring
41 x 41 x 6 cm at two densities, a high density equivalent to 44 kg/ha and a
low density equivalent to 22 kg/ha. Two different levels of soil fertility
were used, the first, representing high fertility, was made up with a John
Innes No. 2 potting compost, and the second utilized the same potting com-
post but without the nutrients.

The relative abundance of diploids and tetraploids was determined at 2, 6
and 15 months after sowing. Plants were removed at each time interval from
a central area measuring 25 x 25 cm and split up into tillers. A sample of
tillers was taken at random, and each tiller was grown on in separate pots
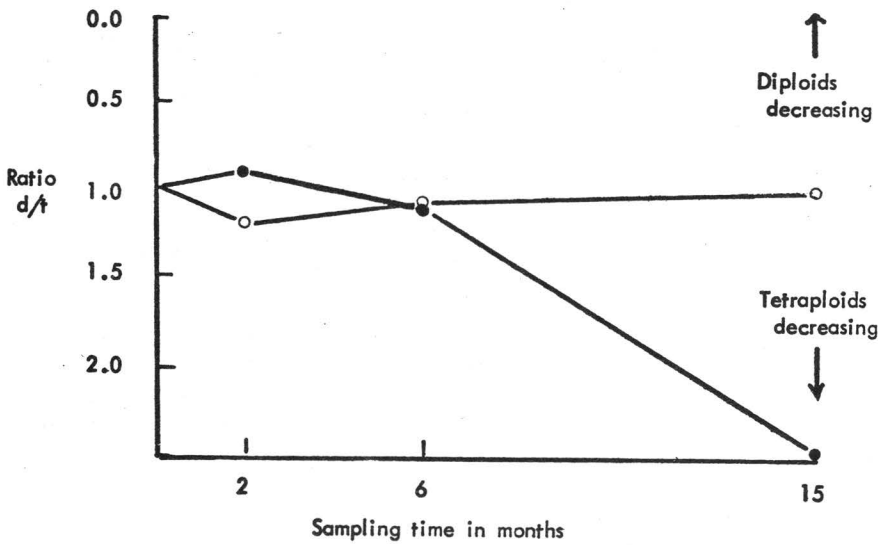
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Fig. 1(a). Changes in the relative proportion of diploid
and tetraploid plants with time at high and low fertility.
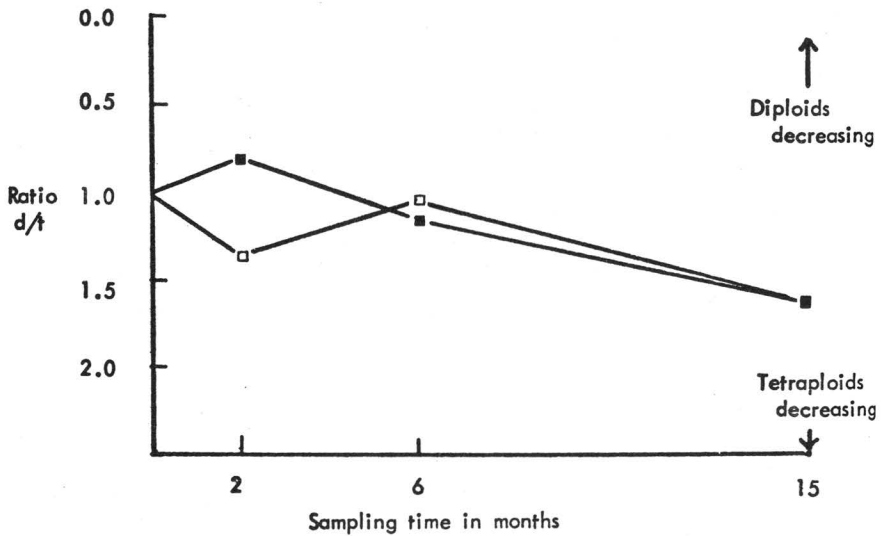● = High Fertility   O = Low fertility

Fig. 1(b). Changes in the relative proportion of diploid and
tetraploid plants with time at high and low density.
■ = High density   □ = Low density

for 2-3 months. Root tips were then taken for chromosome counts. A total of 2,400 slides were scored (Blijenburg and Norrington-Davies, 1976 unpublished).

RESULTS

The results expressed as the ratio of diploid to tetraploid tillers are shown in Table 1. Any ratio less than 1 means that the tetraploid is in the majority, whereas a ratio greater than 1 shows the diploid to be more abundant.

Table 1. Ratio of diploid and tetraploid tillers.

Treatment	Sampling Time (months)		
	2	6	15
High Fertility - High Density	0.80	1.24	2.02
High Fertility - Low Density	1.06	0.98	2.29
Low Fertility - High Density	0.79	1.04	1.13
Low Fertility - Low Density	1.61	1.12	0.86

Overall there was a significant decline ($P = < 0.05$) in the proportion of tetraploids present in the population between months 6 and 15.

Whilst there was no effect of fertility on the relative proportions of diploid and tetraploid plants over the first 6 months (Fig. 1a), by the 15 month there were considerably fewer tetraploids surviving under high fertility. At this time the diploid and tetraploid under the low fertility regime were in equilibrium. The difference between month 2 and months 6-15 with respect to fertility was highly significant ($P = < 0.01$).

Differences in survival between the two varieties with respect to density are shown in (Fig. 1b). There were significant differences due to density between the 2 and 6-15 month ($P = < 0.05$). The tetraploid was favoured at high density and the diploid at low density during the first 2 months, but by month 6 the effect of density was no longer evident. The situation may be summarized as follows:

Table 2. The effect of treatment on the survival of the diploid and the tetraploid.

	Months from sowing		
Treatment	2	6	15
1. Overall	-	-	22% fewer tetraploids
2. Density	21% more tetraploids under high density	-	-
	21% more diploids under low density		
3. Fertility	-	-	44% fewer tetraploids under high fertility

To test whether these observations are relevant on a field scale, a trial using the same two varieties sown at 22 kg/ha and 66 kg/ha with two levels of fertility has been laid down.

Two systems of defoliation, the first based on sheep grazing and the second on cutting for silage, have been imposed. Results obtained so far show that at 2 months the tetraploid was in the ascendency under both the high and the low density treatments. The respective d/t ratios were 0.67 and 0.62.

2. THE RELATIVE UPTAKE OF PHOSPHATE BY THE DIPLOID AND THE TETRA-PLOID IN PURE STANDS AND IN MIXTURES.

The two varieties Hora and Terhoy were sown both as pure stands and as

50:50 mixtures in the field. Labelled phosphate was injected into the soil at placement depths of 2.5 - 12.5 cm, 12.5 - 22.5 cm, 22.5 - 32.5 cm and 32.5 - 42.5 cm. To facilitate both the sowing of seed and the placement of ^{32}P a wooden template based on four concentric circles (A, B, C and D) each divided by radii into 12 equal segments was constructed (Fig. 2). Each point for injecting ^{32}P was equidistant from the four planting positions, which surrounded it.
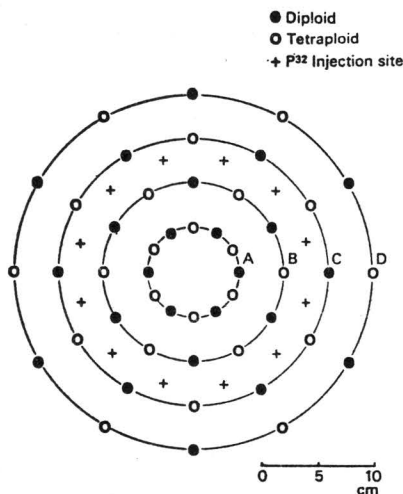
Fig. 2. Diagram of template, labelled for sowing a 50:50 mixture.

Plants occupying sites on the circles A and D acted as guard rows, whilst those planted on the available sites of B and C represented the high and low density treatments respectively. When sowing pure stands all sites were occupied by a single variety, whereas for 50:50 mixtures seed of each variety was alternated within the circles and along the radii (Harries, Norrington-Davies and Howse, 1974).

RESULTS

The results expressed as the relative uptake of P are given i Table 3 below.

Table 3. The relative uptake[x] of P by Hora and Terhoy.

| Depth (cm) | High Density | | | | Low Density | | | |
| | Pure Stand | | Mixture | | Pure Stand | | Mixture | |
	Dip.	Tet.	Dip.	Tet.	Dip.	Tet.	Dip.	Tet.
10	95	82	85	114	66	49	58	63
20	80	67	99	68	46	43	81	38
30	54	65	43	61	33	35	25	24
40	23	30	11	56	15	11	21	14

[x] Means of four replicates.
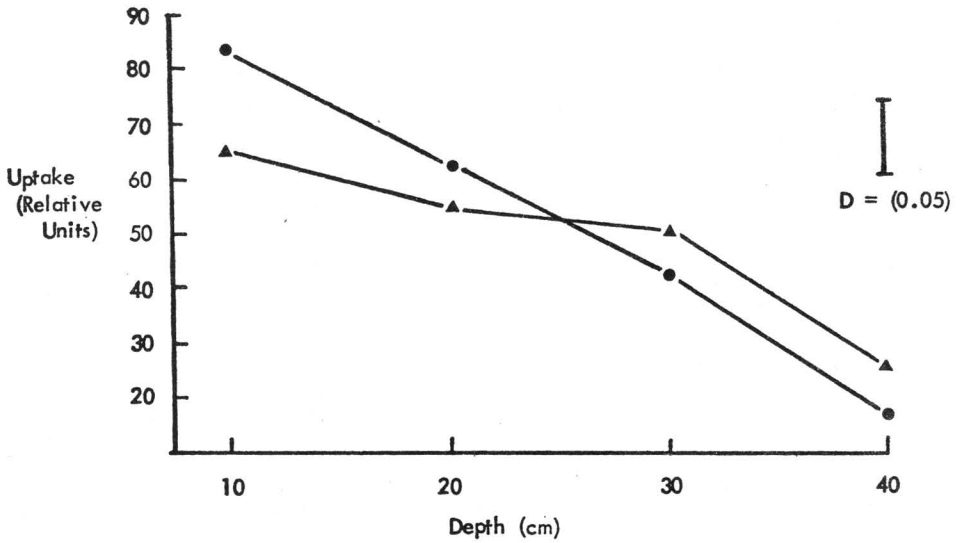
Fig. 3(a). Relative uptake of P by the two varieties grown in pure stands (means of values for densities and replicates combined). ● = Diploid, ▲ = Tetraploid.
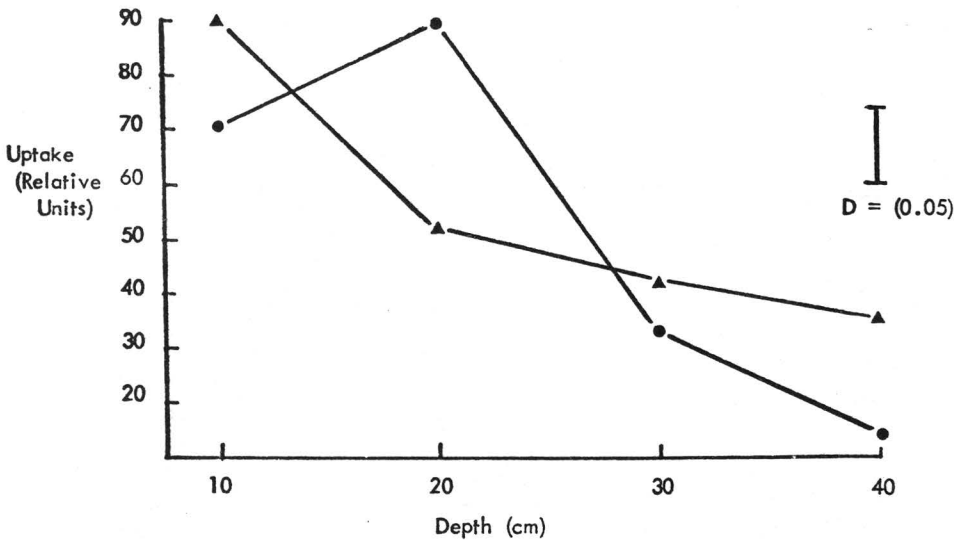
Fig. 3(b). Relative uptake of P by the two varieties grown in a 50:50 mixture (means of values for densities and replicates combined). ● = Diploid, ▲ = Tetraploid.

In general, the uptake of P occurred predominantly in the upper 10 cm zone of the soil, and there was a marked decrease in uptake with increasing depth (P = < 0.001). The diploid when grown as a pure stand absorbed more P than the tetraploid from the upper, 10 cm zone, but with increasing depth each variety had a similar uptake of P (Fig. 3a).

In mixtures it is the contrasting pattern of behaviour of the two varieties that is of particular interest (Fig. 3b). The tetraploid increases its relative uptake of P in the 10 cm zone by 37% of its pure stand value, whilst the uptake of the diploid is depressed relative to its pure stand value. The diploid, in compensation, shows a considerable increase in absorption of P in the 20 cm zone. Although there was no overall difference in uptake between pure stands and mixtures, significantly more P was taken up by the mixtures at a depth of 20 cm (P = < 0.05).

As well as reacting differently to depth the two varieties also differ in their reaction to density. Whilst the tetraploid absorbs more P at high density than the diploid, the diploid absorbs more P than the tetraploid at low density (P = < 0.01).

3. THE RELATIVE GERMINATION VALUES OF THE DIPLOID AND THE TETRAPLOID WHEN SOWN AS MIXTURES OF VARYING PROPORTION.

To test the relative germination of the two varieties their seed was surface sown on a John Innes compost contained in plastic multipots of 6.6 cm diameter. Each variety was sown either as a pure stand or as a binary mixture of varying proportion, but constant density, as follows:

Hora	Terhoy
100	0
75	25
50	50
25	75
0	100

The multipots were kept in a warm glasshouse at a temperature of approximately 20°C. The compost was kept constantly moist by means of capillary action from water trays placed beneath the multipots and by regular daily watering from above. Identification of the components of each mixture was made by marking the seed of one variety at its distal end with black waterproof ink, earlier tests having shown that this procedure had no effect upon germination. Daily counts of germinated seed were made for a period of 14 days after sowing (Norrington-Davies & Harries, 1976).

RESULTS

The final germination values of the two varieties are shown in Fig. 4. All the differences in germination, with the exception of the mixture of 75 diploid with 25 tetraploid seed (points 2 and 8 in Fig. 4) were highly significant.
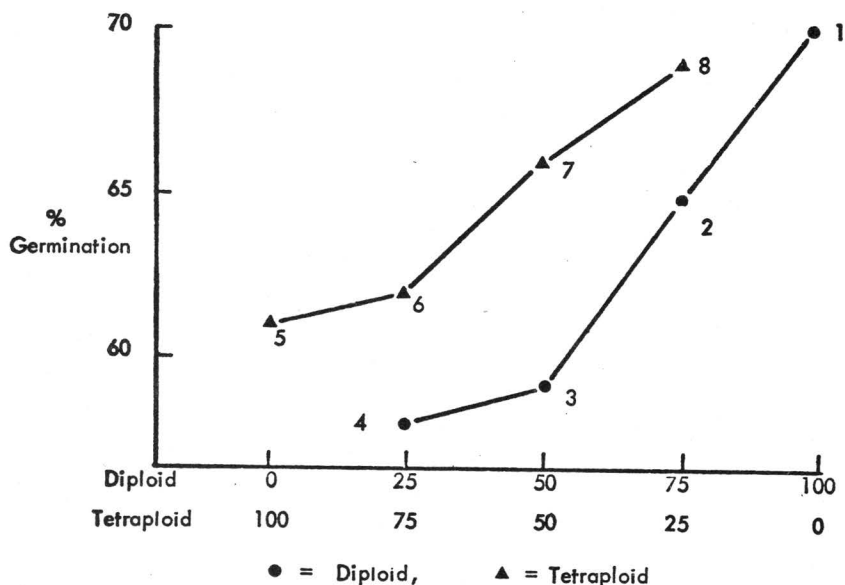
Fig. 4. Final germination (angular transformation) of diploid and tetraploid seed sown in varying proportion.

The diploid and tetraploid are seen to behave in marked contrast to one another. In pure stands the diploid has a considerably higher final germination value than the tetraploid (points 1 and 5 in Fig. 4). In mixtures the converse is true, the tetraploid has considerably higher values than the diploid.

The percentage germination of the tetraploid increases, when it is the minority component of the mixture, whilst the percentage germination of the diploid increases, when it is the majority component of the mixture.

It was later found that an elute could be produced from each variety, which had an inhibitory effect upon germination, (Harries & Norrington-Davies, 1976).

The final reduction (Day 10) in the germination of diploid seed was 16% in the presence of its own elute and 27% in the presence of elute prepared from the tetraploid. A final reduction of 14% in the germination of the tetraploid was found in the presence of either extract. Each elute also had the effect of delaying germination.

DISCUSSION

The three experiments described here illustrate the principal reactions of a plant to the presence of neighbouring plants - Mortality, Plasticity and Germination failure.

The high degree of plant mortality that occurs during the establishment of

grassland may be readily demonstrated, but it is the differential survival of the mixture components that is of particular interest in this instance. One of the underlying assumptions in compounding mixtures of diploids with tetraploids is that because of the more open habit of the tetraploid the likelihood of productive interactions with other components of the sward is high. This in turn assumes that the established sward is made up of a random distribution of the mixture components. These assumptions will be nullified, if the environmental pressures affect the sward components differentially.

Clearly, the environmental conditions in the box experiment were such that a mixture of equal proportions was not achieved by the end of the establishment phase. Considered overall, the tetraploid component had been reduced to just over one third of the mixture, whilst under conditions of high fertility it made up less than one quarter of the mixture.

It is implicit to the acceptance of a forage mixture that each component will make its full contribution to the sward. The first attribute of any mechanical mixture must therefore be the survival of the component parts in the proportions intended. The work of Charles (1961) on the differential survival of grass cultivars shows not only how dramatic the changes may be during the establishment phase, but also how laborious are the methods necessary to determine the relative survival of the cultivars.

The technique used here whilst tedious, is not technically difficult to apply. It affords a method whereby mixtures comprising a diploid and a tetraploid could readily be screened for their adaptability.

Adaptation, in terms of the adjustment of an organism to its environment, is shown by the plastic response of the two varieties in their uptake of P when grown together in a mixture. In this example, where one component of the mixture has its uptake of P reduced in the 10 cm zone, it is able to compensate for this by an increased level of absorption in the 20 cm zone. As the uptake of the tetraploid is reduced less than the uptake of the diploid is increased, the consequence is a significantly increased uptake in the 20 cm zone by the mixture compared to the pure stand means.

The techniques of Newbould et al. (1971) used here for indicating root activity, combined with those of Caldwell & Camp (1974) for investigating root morphology, might usefully be employed in the screening of varieties for their co-adaptability. Legislation governing the sale of ryegrass seed to farmers requires a minimum germination of 80%. Again, the assumption will be that the number of seedling plants to be derived from a given weight of seed may be predicted and the seeds mixture compounded accordingly. It is seen that under laboratory conditions the tetraploid can reduce the percentage germination of the diploid by as much as 27%. If similar results were to be obtained under field conditions then the event would be of some consequence. It would become necessary to re-consider the proportion of sowing in relation to the anticipated establishment of the mixture components. An alternative application based on the behaviour of the tetraploid when sown with the diploid would be the deliberate incorporation of a second component to encourage the germination of the first without reducing the overall density of the establishing sward. It could be argued that the experimental density used here is not relevant to agronomic practice; nevertheless, it is possible that the overlying of an individual of one variety by that of another could produce an inhibitory effect under certain environmental conditions. It is one thing to recognize some of the biological interactions that are possible in the establishing sward, but quite another to take account of them in a breeding programme. The difficulties inherent in selecting characters one by one

for the production of co-adapted varieties for growing together in mixtures are such that other approaches based upon population buffering are likely to be more rewarding.

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COMPETITION IN LOLIUM PERENNE L.   AS MEASURED BY YIELD AND PERSISTENCY

H. Larsen Petersen

Department of Crop Husbandry and Plant Breeding
Royal Veterinary and Agricultural University, Copenhagen, Denmark

SUMMARY

Four genotypes of *Lolium perenne* were selected for high and four for inter-
mediate or low dry matter yields under sward conditions. Clone plants of
these genotypes were established in spaced plantings and swards under field
conditions to give four sets of competition conditions, viz. between high
yielding genotypes, between intermediate and low yielding genotypes, between
high, intermediate and low yielding genotypes, and between spaced plants (no
competition). Persistency after the first harvest year was generally greater
in the absence of competition. Pronounced differences were found between
genotypes in response in terms of yield and persistency to different inten-
sities of competition, and even the strongest competitor was found to respond
to differences in competitive stress. Neither yield nor persistency, however,
were related to the performance or survival of genotypes under spaced condi-
tions. Differences were also noted in the ability of genotypes to exploit
the improved spatial conditions resulting from plant mortality in the second
year. Each of the competitive environments was dominated by one genotype
after two years. It is concluded that selection for yield and persistency
characteristics must be performed under competitive conditions.

INTRODUCTION

Competition can be defined as that condition in which one plant obtains an
advantage at the expense of another. For any individual plant competition
starts when the immediate availability of one or more necessary growth fac-
tors is insufficient due to the requirements of adjacent plants (Clements et
al. 1929, Mather 1969, Jacquard 1973). Mutual influence and thus competitive
ability can be estimated by seed set and/or vegetative development, although
these two criteria do not always give the same result. Persistency can also
be used as a measure of competitive ability.

The high seed rates and irregular plant spacings common in densely sown crops
result in a competitive stress such that a large number of plants die during
the first few months after sowing. The productivity of all genotypes will
be affected by the prevailing competition conditions. In the experiments
described below the behaviour of *L. perenne* genotypes under different com-
petition environments is examined in terms of both dry matter yield and per-
sistency.

MATERIALS AND METHODS

Plots of each of the perennial ryegrass varieties Øtofte Dux, Pajbjerg Verna
and Aberystwyth S23 were drilled with 15 cm between rows at a seed rate
of 15 kg per ha. Dry matter yields were determined the following year in
two cuts on approx. 200 plants of each of the three varieties. Only plants
separated from adjacent plants by a distance of 1 cm and thereby exposed to

'normal' competitive conditions were included in these three samples.
The average yield for all 600 plants was 6.8 g per plant, ranging from
0.1 to 42.7 g. Eight plants were subsequently selected for dry matter
yield, viz. four for high, one for intermediate, and three for low dry
matter yield:

Clone	Variety	Dry matter g	Date of ear emergence
1	Verna Pajbjerg	42.7	June 7
2	Verna Pajbjerg	32.3	10
3	Dux Øtofte	24.8	12
4	Verna Pajbjerg	23.5	1
A	Dux Øtofte	0.9	14
B	Verna Pajbjerg	0.8	9
C	Dux Øtofte	0.3	16
D	Dux Øtofte	14.0	16

In subsequent spaced plantings these eight genotypes were found to be of an
intermediate growth type, i.e., the basal shoots of the plants formed an
angle of approx. 45° with the soil surface.

The eight plants were cloned repeatedly to give a total of 220 individuals
which were used to establish the following four competitive environments:

1. Four high yielding clones - 117 plants per clone
2. Four intermediate or low yielding clones - 117 plants per clone
3. All eight clones - approx. 60 plants per clone
4. All eight clones planted without competition at 55 x 55 cm
   with 13 plants per clone.

This design enabled a study of the behaviour of the selected genotypes under
supposedly different degrees of competitive stress, ranging from severe com-
petition between highly productive plants in environment 1, through less
severe competition in environments 3 and 2, to non-competitive conditions
in environment 4.

Three replications of environments 1-3 were established as microplots with
52 cm rows, 11 cm between rows and 1 cm between plants. The microplots were
planted in September 1967 in boxes with homogeneous soil and were given op-
timum conditions in a greenhouse for about 1 month, before being transferred
to the field and planted intact such that the surface of the soil in the
boxes levelled with that of the field. By this time the root system of the
plants was so well developed that the boxes could be removed. The guard
plots were made up of randomly mixed plants of the same material. After
transfer to the field, both microplots and guard plots were supplemented up
to the full plant number. The guard plots were again supplemented in April
1968 after the first winter.

Within each microplot plants of the eight clones were arranged systematically
as listed below:

Plot no.	Clone no. and order	
1	1 2 3 4	High yielding
2	2 1 3 4	(competition environment 1)
3	1 4 2 3	
4	A B C D	Intermediate or low yielding
5	B A C D	(competition environment 2)
6	A D B C	

```
Plot no.        Clone no.
                and order
   7            1 A 2 B 3 C 4 D⎤  Mixture of clones with
   8            2 C 1 B 3 D 4 A⎬  different yielding ability.
   9            1 B 4 D 2 A 3 C⎦  (competition environment 3)
```

In each plot the order of the plants was changed within the row, viz.:

```
                ⎧1st row: 1 2 3 4
     Plot 1     ⎨2nd  "  : 2 3 4 1
                ⎩3rd  "  : 3 4 1 2
```

Thin plastic strips 14 x 80 mm were used to separate plants within rows, pushed into the soil with 1-4 mm above and 10-13 mm below the soil surface. This method ensured normal competitive conditions in both above and below ground parts of the plant, but enabled the separate harvest of each plant.

The plots were cut 3 times in the first harvest year and twice in the second at a stubble height of 4 cm. In both years the first cut was taken when the majority of the plants were between half and full ear emergence, and subsequent cuts were taken at intervals of 4-5 weeks. Approx. 90 kg N per ha was applied early in the spring and after each cut.

In autumn 1968, after the first harvest year, all 8 clones were planted out in 13 replications with a plant and row spacing of 55 cm (competition environment 4). During the following year, i.e., in the second harvest year for the microplots, these spaced plantings were cut 5 times. Cutting height and fertilizer rates were the same as for microplots.

RESULTS

a) Yields in swards and spaced plantings

The average dry matter yield of selected genotypes under competitive and non-competitive conditions is given in Table 1. A comparison of the values for cloned plants shows that the rank of the eight genotypes was greatly influenced by the competitive environment. This demonstrates the difficulty often encountered in predicting yielding ability in swards on the basis of yield in spaced plantings.

Differences can also be seen between the rank of dry matter yields of cloned plants in microswards compared to the yield of the same genotypes in the year of selection, i.e., as sown individuals. The initial selection, although made under competitive conditions, was thus not completely effective, possibly because the genotype of a sown individual could not be replicated, and thus certain local differences in the intensity of competition could have influenced yields. For example, the sown genotype B probably met severe competition from adjacent plants in the row in the year of selection, and was consequently classed as low yielding. This genotype, however, gave the highest average yield when cloned and exposed to full competition, and was even superior to those selected for high yields. Inconsistencies in yield between cloned and sown plants were also found for genotype D.

b) Regression between space and yield

A number of plants died during the first two harvest years, making greater space available for surviving plants. The number and location of spaces were recorded at each cut. The spatial conditions of the surviving plants were scored according to the following scale in which ⊠ represents the plant in question, X a surviving plant and 0 an empty space after a dead plant. Each scale unit is equivalent to 1 cm.

Table 1. Dry matter yield and persistency of selected genotypes with and without competition, 1st harvest year.

| Genotype | Dry matter yield | | | | % surviving plants | |
| | With competition | | | Without competition | With competition (env. 1-3) | Without competition (env. 4) |
	Selected plants (sown) g/pl.	Clone plants (env. 1-3) number	g/pl.	Clone plants (env. 4) g/pl.		
1	42.7	18	2.6	37	90	85
2	32.3	17	2.1	26	49	62
3	24.8	15	2.1	30	35	54
4	23.5	16	1.9	50	54	100
A	0.9	7	1.0	20	10	85
B	0.8	30	2.9	17	84	69
C	0.3	9	1.4	19	32	46
D	14.0	4	0.5	9	13	77

Env. 1-3: mean of environments 1, 2 and 3, 175 plants per clone.
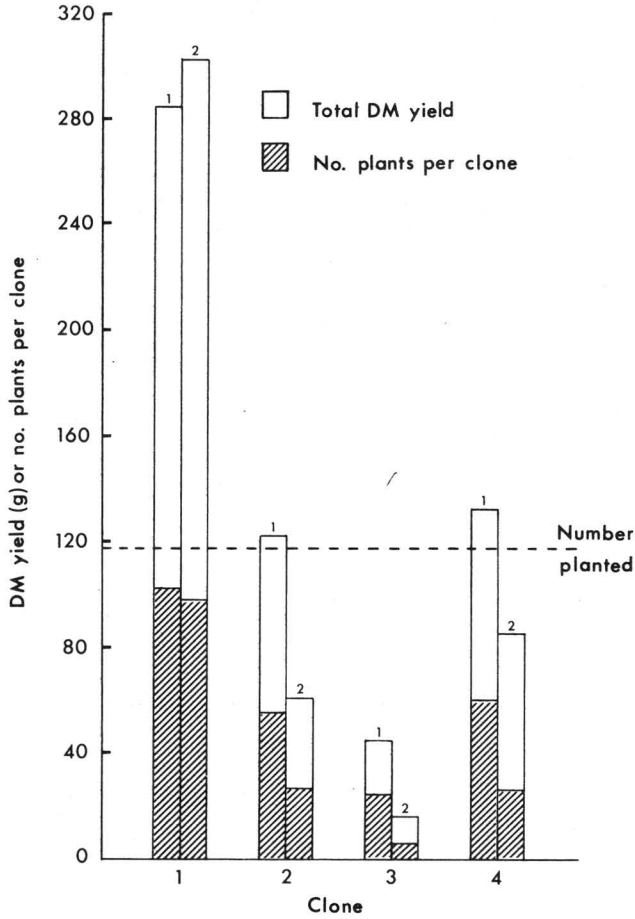Env. 4: environment 4, 13 plants per clone.

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Figure 1.   Total dry matter yield and number of sur-
viving plants per clone in 1st (1) and 2nd
(2) harvest years under competition between
high yielding genotypes (environment 1).

```
Scale
  1            X ⊠ X
  2         X  0 ⊠ X
  3         X  0 ⊠ 0 X
  etc.
```

A small but significant regression was found between spatial scores and yield per plant in the first cut in both first (b = +0.09^{xx}, n = 787) and the second harvest year (b = +0.12^{xxx}, n = 530). This low regression may be partly due to the fact that despite improved competitive conditions, i.e., more space, the ability to increase yield with increasing age differs from genotype to genotype.

c) Competition between high yielding genotypes

Figure 1 shows the effect of competition among clones 1, 2, 3 and 4 (117 plants per clone), selected for high yield (competition environment 1). The number of spaced plants (5 cuts) surviving the first harvest year is compared in table 1 with the survival in swards (3 cuts) averaged over environments. In this table the clones were represented by 13 and 175 plants in spaced plots and microswards, respectively. Survival rates after the first year were in most cases higher in spaced plantings than in swards even though two additional cuts were taken under spaced conditions.

Persistency. Clone 1 showed a high persistency both with and without competition. This genotype showed the highest survival rate in both harvest years and almost maintained its full plant number from first to second year in contrast to clones 2, 3 and 4. Clone 3 lacked persistency under both competitive and non-competitive conditions. With competition survival was 25% in the first year and only 5% in the second (Fig. 1). Without competition only 54% of the plants of this clone survived the first year (Table 1). Clone 4 showed a very high persistency in the absence of competition, but this broke down under competitive stress. A similar tendency, although less pronounced, was also shown by clone 2.

Yield. The percentage yield of each clone in the four-clone mixture is given in table 2 (competition environment 1) in relation to the percentage of the total plant number due to each clone.

The behaviour of the four genotypes in terms of dry matter yield was similar to that observed for persistency. Clone 1 was by far the most productive, and accounted for 49% and 65% of the total yield in first and second years, respectively. In the absence of competition this genotype was fairly high yielding (37 g), but was surpassed by clone 4 (50 g) (Table 1). Although clone 1 gave only a moderate yield under spaced plant conditions, it ranged highest under sward conditions and was even able to increase yield in the second year (Fig. 1).

Clone 4, however, was not able to maintain a high level of productivity under competitive stress. Clone 3 accounted for the lowest share of the total yield in both first and second years due to an extremely low rate of survival. In spaced plantings the yield of clone 2 was only half that of clone 4 (Table 1), but both genotypes showed a similar level of productivity in swards (Fig. 1).

d) Competition between intermediate and low yielding genotypes

Figure 2 shows the effect of competition between clones A, B, C and D. Clones A, B and C were selected for low and D for intermediate yielding ability in swards (competition environment 2). Each clone was represented by 117 plants at the start of the experiment.

Persistency. Although clones A and D showed a high survival rate of approx. 80% in the absence of competition (Table 1), nearly all plants in microswards

Table 2. Percentage contribution of genotypes to total plant number and total dry matter yield in different competition environments over two years. Mean of 3 microplots.

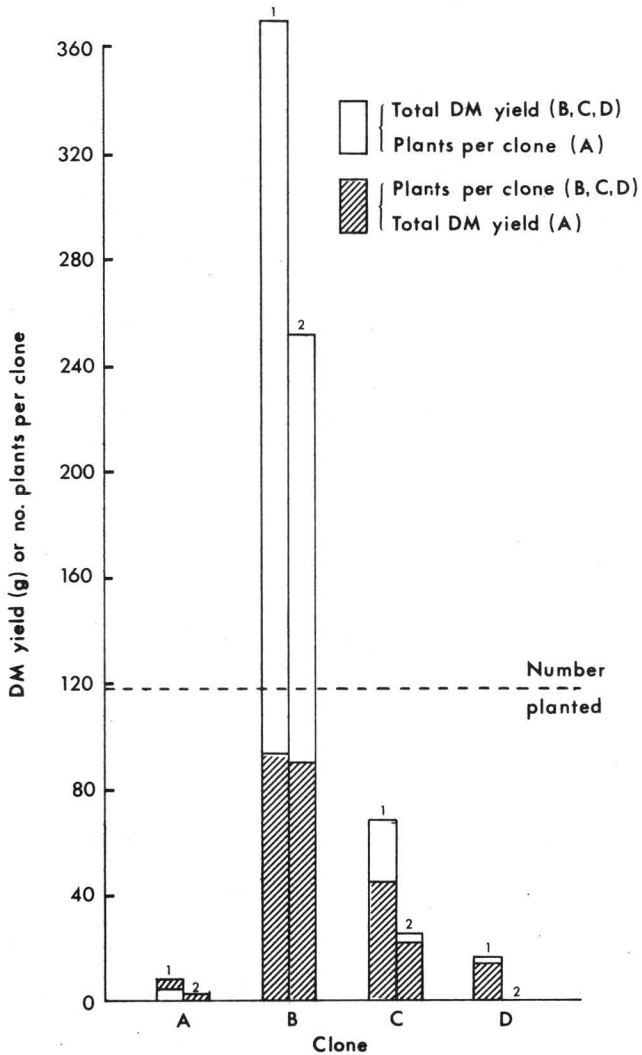| Clone	Harvest year	Competitor	Per cent Number	Yield	Competitor	Per cent Number	Yield
1	1	2,3,4	42	49	2,3,4 & A,B,C,D	23	30
	2		62	65		39	63
2	1	1,3,4	23	21	1,3,4 & A,B,C,D	13	11
	2	(Environment 1)	17	13		11	7
3	1	1,2,4	10	8	1,2,4 & A,B,C,D	15	18
	2		4	3	(Environment 3)	5	4
4	1	1,2,3	25	23	1,2,3 & A,B,C,D	13	10
	2		17	18		14	13
A	1	B,C,D	5	1	1,2,3,4 & B,C,D	4	2
	2	(Environment 2)	2	1		1	0.2
B	1	A,C,D	58	81	1,2,3,4 & A,C,D	24	27
	2		79	91		27	13
C	1	A,B,D	28	15	1,2,3,4 & A,B,D	6	1
	2		19	9		2	1
D	1	A,B,C	9	4	1,2,3,4 & A,B,C	3	1
	2		0	0		1	0.3

Figure 2. Total dry matter yield and number of sur-
viving plants per clone in 1st (1) and 2nd
(2) harvest years under competition between
intermediate and low yielding genotypes
(environment 2).

died during the first year (Fig. 2). It can therefore be concluded that these two clones had a fairly high persistency in the absence of competition, but could not withstand normal competitive conditions. Clone C showed a low survival rate both with and without competition. In swards the plant number was decreased to almost one third already during the first year, and was further reduced during the second (Fig. 2). Under spaced plant conditions about half of the plants died during the first year. Clone B had a survival rate of 84% under sward conditions during the first year (Table 1), and this rate was almost maintained in the following year (Fig. 2). Under spatial conditions only 69% survived. The persistency of this genotype seemed equally adjusted to environments with or without competition.

Yield. Clone D gave the lowest yield per plant under both sward and spatial conditions (Table 1), and due its lack of persistency accounted for only 4% of the total yield in the first harvest year and was competed out of the mixture in the second year (Table 2). Clone A similarly had only 1% of the total yield, although yield per plant was higher for this clone both with and without competition than for D. Yield per plant was almost the same for clones A and C, but the latter was able to contribute 15% of the first year yield due to a higher persistency under competition. Although comparatively low yielding under spaced conditions, clone B showed a high productivity in swards in the first harvest year (2.9 g/plant, Table 1).

In this competitive environment, i.e., under competitive stress from intermediate or low yielding clones, one genotype (clone B) maintained its plant number in both years and was superior in yield to the other three clones in the mixture. It was probably only exposed to a relatively low competitive pressure, especially in the second year. Contrary to clone 1, B was unable to increase productivity from the first to the second year, despite improved spatial conditions.

e) Competition between genotypes of differing yield capacity

Figure 3 shows the effect of competition between all eight selected clones (competition environment 3). Between 57 and 62 plants were planted per clone, i.e., half as many plants as in environments 1 and 2.

Persistency. In the first year clone 1 and clone B were almost equal in terms of persistency, whereas only between two thirds and half of the plants of clones 2, 3 and 4 survived and almost all plants of clones A, C and D died already during the first year (Fig. 3). Under spaced plant conditions clones A and D showed fairly high survival rates of 85% and 77%, respectively. In the second year only clone 1 maintained its plant number whereas all other genotypes showed marked reductions.

Yield. In the first year clones 1 and B ranged highest in yield, clones 2, 3 and 4 were intermediate, and clones A, C and D gave only extremely small yields. In the second year clone 1 showed a pronounced increase in yield whereas the productivity of clone B was greatly reduced. The dry matter yields of all other clones showed similar but less pronounced reductions.

In the first year this environment was dominated by two almost equal competitors, but already in the second year one of these took over the lead in terms of both persistency and yield per plant.

f) Response of genotypes to differences in competitive stress

A comparison of the response of the genotypes to different levels of competitive stress showed that while certain genotypes were clearly affected by the intensity of competition, others appeared to be largely indifferent. Clone 1 appeared to be the strongest competitor, and in both years gave significantly higher yields per plant in environment 3 than in environment 1 (Table 3). As this genotype was highly persistent and maintained an al-

most constant plant number, its contribution to the total yield of environment 3 increased from 30% to 63%, far exceeding the increase expected on the basis of its share of the total plant number, i.e., 23% and 39%, respectively (Table 2). In contrast clone B, although a severe competitor in environment 2 in which it competed with the low yielding clones A, C and D, was evidently suppressed in environment 3 in which the high yielding clones 1, 2, 3 and 4 also participated. In environment 2 this genotype accounted for 81% and 79% of total first and second year yields, respectively, whereas in environment 3 it gave only 27% and 13%. These results suggest that the competitive stress between high yielding plants in environment 1 was more severe than in environment 3 between intermediate and low yielding genotypes, whilst environment 2 was probably intermediate. Furthermore, even strong competitors, such as clone B, were found to respond to changes in competition pressure.

Table 3. The response of genotypes to changes in competitive stress.

Competition environment	1st year		2nd year	
	No. plants	DM g/pl.	No. plants	DM g/pl.
Clone 1				
1	103	2.75	98	3.08
3	56	3.46	55	4.78
Differences between environments		0.71^x		1.70^{xxx}
Clone B				
2	93	4.03	90	2.84
3	58	2.96	38	1.41
Differences between environments		1.07^{xx}		1.43^{xx}
Clone 2				
1	55	2.21	27	2.24
3	32	2.26	16	1.85
Differences between environments		0.05^{ns}		0.39^{ns}
Clone 4				
1	60	2.22	26	3.28
3	34	1.88	19	2.76
Differences between environments		0.34^{ns}		0.52^{ns}

The weakest competitors in environment 2, clones A and D, were unable to withstand the greater competitive stress of environment 3 and were almost eliminated. Clone 3 was the weakest competitor in environment 1, but gave reasonably high yields in environment 3, probably because of a lower competitive pressure from the weak clones A, C and D. Clones 2 and 4 were relatively indifferent to the intensity of competition in terms of dry matter production per plant (Table 3).

Marked differences were observed in the ability of genotypes to exploit the improved conditions caused by plant mortality after the first harvest year. The average yield of clone 1 increased in environment 1 from 2.8 g in the
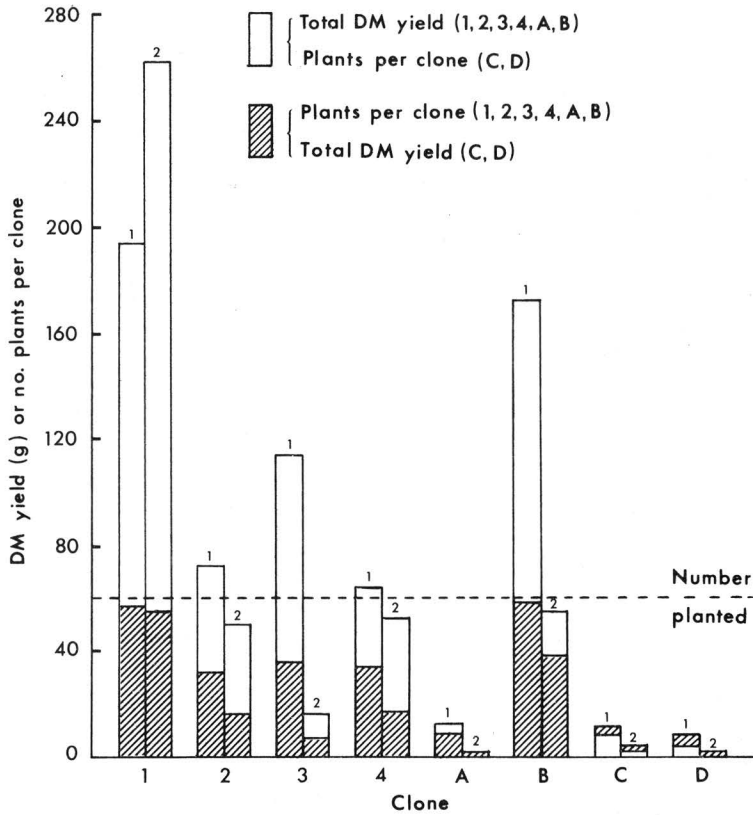
Figure 3. Total dry matter yield and number of surviving
plants per clone in 1st (1) and 2nd (2) harvest years
under competition between high, intermediate and low
yielding genotypes (environment 3).

first harvest year to 3.1 g in the second. In environment 3, i.e., under less severe competitive conditions, the yield of this genotype increased from 3.5 to 4.8 g. Clone B, however, decreased in productivity from first to second years irrespective of the level of competition. In environment 3 the average yield per plant decreased from 3.0 to 1.4 g, and even under the lower competitive stress of environment 2 where this genotype was clearly dominant, yields fell from 4.0 g to 2.8 g per plant. Clone 4 showed a slight tendency to increase in yield, whereas all other clones showed marked yield reductions in the second year.

CONCLUSION

The results obtained from this experiment permit the following observations:

1. After the first harvest year the persistency of most of the clones was greatest in the absence of competition.

2. Certain genotypes possessed low persistency both with and without competition. Others were highly persistent with no competition, but lacked persistency under competitive conditions. Others again possessed high persistency both with and without competition.

3. Som of the genotypes gave high yields in the absence of competition but were unable to maintain this level under competitive stress. Others gave intermediate yields as spaced plants but under competition were among the highest yielders in both harvest years. Other genotypes again gave high yields in the first year, but despite improved spatial conditions yield level decreased in the second year.

4. Competition environments 1, 2 and to a lesser extent 3 were after two years dominated in terms of persistency and yield by one genotype.

5. Under sward conditions some of the genotypes showed greater persistency in one competition environment than in another, whereas other genotypes were indifferent.

6. Even the strongest competitors were found to respond to differences in competitive stress.

7. The variable response of genotypes in terms of both persistency and yield to different competitive conditions clearly demonstrates the necessity of selecting for these characters under sward conditions.

ACKNOWLEDGEMENTS

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EFFECTS OF ASSOCIATION AND DENSITY IN CLONES OF TALL FESCUE (FESTUCA ARUNDINACEA L.) (*)

P. Rotili, L. Zannone and G. Gnocchi

Istituto Sperimentale per le Colture Foraggere, Lodi, Italy.

SUMMARY

As an introduction to a breeding programme in tall fescue (*Festuca arundinacea* L.), a preliminary study was conducted on 32 clones derived from a spontaneous population. In order to determine the importance of the effects of density and association between the plants, the 32 clones were grown in spaced plantings (5 pl/m^2) and in dense swards (100 pl/m^2). In this latter density, 32 pure stands and one global mixture of all the 32 clones were studied. In addition, 28 binary mixtures between 8 clones were studied according to a diallel model. Dry matter yield data are presented; the advantages of the phenotypic selection in dense swards are discussed. The study of binary mixtures has shown that the clone association leads only to situations of competition.

INTRODUCTION

In forage crop species, the performance of an individual plant in the field is not independent from that of the neighbouring plants. The higher the density, the greater the interaction between the different individuals in the culture. Nevertheless, this fact is usually not considered. In fact, spaced plant nurseries are of common use in forage crop breeding procedures, chiefly in the phenotypic selection of mother plants. This is probably due to the fact that the results at present available to the breeders are not sufficient to demonstrate the superiority of the method of selection realized in dense sward. Results obtained at the Institute at Lodi concerning alfalfa have shown that the use of dense sward in a breeding scheme is very efficient (Rotili 1976a, 1976b; Rotili and Zannone 1971; Rotili et al. 1976a).

The present study represents an introduction to a future breeding programme for tall fescue which will be realized in Lodi. The chief aim of such a programme is to improve the yield. The first problem to be resolved was the importance of the effects of density and association between plants, and the consequences of these effects for the practical breeding work. On the basis of the results of the present study, we should be able to decide whether it is more profitable to work on spaced plants or in dense swards.

MATERIAL AND METHODS

32 clones have been studied, derived from a spontaneous population collected in the country around Lodi. This material was made homogeneous during 5 months of growth in pots after two series of cloning, and was then transplanted in the field: 1) in spaced plantings (5 pl/m^2) with 14 replications; 2) in dense swards (100 pl/m^2, distance between plants within rows 4 cm). At this density the experimental units were plots of 14 plants. The experiment involved four blocks. Three types of culture were applied: a) pure stand with 56 plants all derived from the same clone; b) global mixture of all the 32 clones associated at random in the row, with 56 plants per clone; c) binary mixtures of all the combinations between 8 clones, with 56 plants per mixture (28 plants per clone). In the summertime, one irrigation was made during the first week after every cut. The following characters were studied: dry matter weight per plant and per plot, plant height, number of spikes per plant and per plot. The green forage was dried in an oven at 100°C for 40 hours.

This paper presents the data for dry matter yield only in the two first years of trial (8 cuts).

In each culture, the 32 clones were subjected to an analysis of variance of the normal type. Several different approaches were used to analyse the data concerning the 8 clones associated in the binary mixtures:

1. Analysis of situations produced by association effects, through the measurement of the plastic responses, which represent the phenotypic plasticity of clones (Eucarpia 1973). The plastic responses have been calculated by the ratio:

$$\frac{\text{clone performance in mixture}}{\text{clone performance in pure stand}} - 1$$

The most important situations produced by association are: competition, when one partner gains in comparison with its pure stand and the other one shows a disadvantage; contest, when both partners decrease; cooperation, when both partners gain (Mather 1969).

2. Analysis of variance according to a diallel model commonly used in studies of competition (Chalbi 1969, Gallais 1970, Norrington-Davies 1967). The parameters are:

(a) general association ability
(b) specific association ability
(c) general domination ability
(d) specific domination ability

The association abilities are the association effects measured by the analysis of the row and column sums. The domination abilities are the differential effects of competition, measured by the row and column differences.

3. Evaluation af the agronomic value of mixtures, by comparison of each binary mixture to the pure stand of its better partner. Such comparison was made by the ratio:

$$\left(\frac{\text{mixture}}{\text{better partner}} - 1 \right) \cdot 100$$

Table 1. Ranking of clones for forage yield. Average of 8 cuts.

	Spaced plants		Pure stand		Mixture
	g/plant		g/plot		g/plot
13	49.27	11	68.35	3	86.93
12	48.90	3	65.93	11	83.42
3	48.31	13	65.01	13	82.94
17	45.14	-----		-----	
21	45.07	12	51.37	12	68.78
11	42.88	-----		17	60.66
7	41.61	17	50.14	-----	
-----		26	48.64	19	55.45
25	40.65	7	48.44	26	53.83
19	37.40	19	45.72	7	52.05
29	36.10	21	45.54	21	48.41
31	33.66	25	43.61	10	46.64
1	32.32	10	43.44	14	43.85
20	32.31	27	43.13	25	42.85
$\bar{x}$ ———		16	40.35	16	42.60
18	31.92			28	42.41
8	31.15	$\bar{x}$ ———			
26	30.54	6	38.17	$\bar{x}$ ———	
14	30.39	28	37.52	5	38.75
24	29.40	31	37.32	27	37.46
28	29.35	20	35.39	22	33.49
16	28.05	5	34.74	31	33.40
32	27.03	29	34.65	6	32.67
4	26.96	1	34.53	15	32.12
30	26.74	24	34.50	24	31.12
27	26.59	14	33.81	20	30.14
6	26.36	22	32.94	8	29.53
15	25.87	15	32.72	4	29.02
-----		30	30.86	1	27.38
9	21.81	4	30.69	29	24.82
2	21.76	8	29.67	23	23.07
5	21.58	23	28.45	32	22.58
10	20.06	18	27.92	-----	
22	19.77	32	24.18	30	22.26
23	19.58	9	23.55	18	22.19
		2	23.05	9	20.23
				2	18.66
$\bar{x}$	32.14		39.51		41.24
st.dev.	8.98		11.68		18.78
C.V.	27.95		29.56		45.54

RESULTS

1. Association and density effects on the 32 clones

In table 1 the 32 clones are ranked according to their yield in spaced plantings, in pure stand and in global mixture. The yield of spaced plants is expressed in g/plant, while under sward conditions it is expressed in g/plot. The mean, standard deviation and coefficient of variation among clones are also indicated.

The differences between the 32 clones are significant in both spaced plantings and in dense swards; in the latter case the differences are larger in global mixture than in pure stand.

At the level of the variability among clones the effect of density is not important; on the contrary, an important effect of association is evident in the comparison of pure stand with mixture and of spacing with mixture.

The effect of association on the mean is not important, the difference between the means of pure stand and global mixture being not significant. Growing in dense swards allows a better discrimination among the clones, especially in the global mixture. The ranking of clones is about the same in pure stand and in global mixture, but not in spaced plantings. For instance, clones 7 and 21 exceed the mean by one standard deviation when spaced, while in dense swards they are in the middle group.

The correlation coefficients between clones under different growing conditions are presented in table 2. The very good correspondence between pure stand and global mixture is to be underlined.

Table 3 presents the variation coefficients registered at the 2nd and 7th cuts on individual plants. The 7th cut was the first in the second year and was the most productive of the whole trial, as expected. At this cut mortality was only 2% in spaced plants and 3% in dense swards. The effect of density on the variation among the clones is important at the 7th cut only, whereas the effect of association is well evident at both cuts. In terms of the variation within the clones, the effect of density is very important, while no effect of association is evident.

2. Association effects on the 8 clones in binary mixtures

The variance analysis conducted on the eight clones grown in binary mixtures (Table 4) shows in all cases highly significant F values for the "between entries" source of variation, each entry representing a clone either in pure stand or in one of its seven possible associations with the others. The "diallel" analysis shows significant F values for both general association ability and general domination ability, the general domination ability being considerably larger than the general association ability. This is due to the fact that, in general, one clone gains at the expense of the other. The plastic responses (see Material and Methods) confirmed this observation. In Fig. 1 such plastic responses are given for the average of 8 cuts; it is evident that neither significant situations of cooperation, nor of contest are present, while situations of competition are clearly prevailing. In general, the better clones gain in mixture and the worst ones decrease, while the clones of mean type maintain about the same value. This result is demonstrated in table 5, in which the eight clones are ranked according to their performance either in pure stand or in binary mixture and in global mixture.

In terms of the agronomic value of the mixtures (see Material and Methods), it is evident from table 6 that the highest yielding mixtures (derived from the highest yielding clones) are much lower than their better partner in pure stand. A slight advantage over the better partner is observed only for five mixtures showing average or poor yields.

Table 2. Correlation between yield values in different growing conditions.

Correlations	1st Cut	7th Cut	Average of 8 cuts
Spacing/pure stand	0.72**	0.73**	0.76**
Spacing/global mixture	0.72**	0.69**	0.76**
Pure stand/global mixture	0.92**	0.95**	0.95**

Table 3. Coefficients of variation among clones and within clones for yield.

		Spacing	Pure stand	Global mixture
2nd Cut				
Among clones		29	31	50
Within clones	Mean	23	36	38
	Min.	11	25	26
	Max.	55	50	58
7th Cut				
Among clones		33	43	64
Within clones	Mean	32	52	56
	Min.	16	34	41
	Max.	68	73	86

Table 4. F (*) values for forage yield analysis of variance.

Rank of cuts	1	2	3	4	5	6	7	8
Symple analysis (**)								
Between entries	9.99	15.73	15.05	10.35	13.64	10.78	10.71	11.78
Between blocs	ns	ns	ns	7.31	7.78	9.40	5.94	ns
Diallel analysis								
General association ability	30.04	37.65	31.44	28.67	44.03	35.96	30.31	23.38
Specific association ability	ns	ns	ns	ns	ns	ns	ns	ns
General domination ability	54.56	98.50	97.53	55.60	69.72	54.18	61.13	77.00
Specific domination ability	ns	ns	ns	1.72	1.95	ns	ns	ns

(*) ns = not significant
     not underlined = significant at the 5% level
     underlined = significant at the 1% level

(**) analysis performed on the whole of 64 entries, each clone being considered as in pure stand as in
     its seven possible mixtures
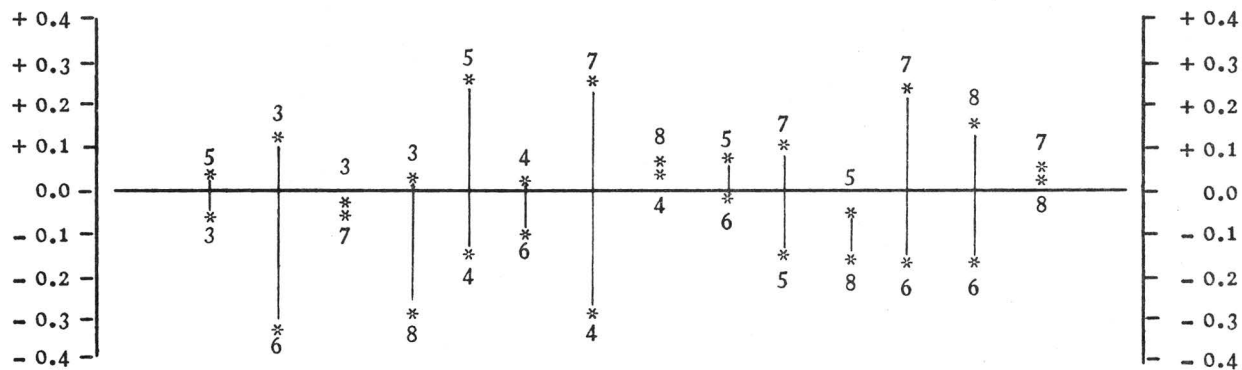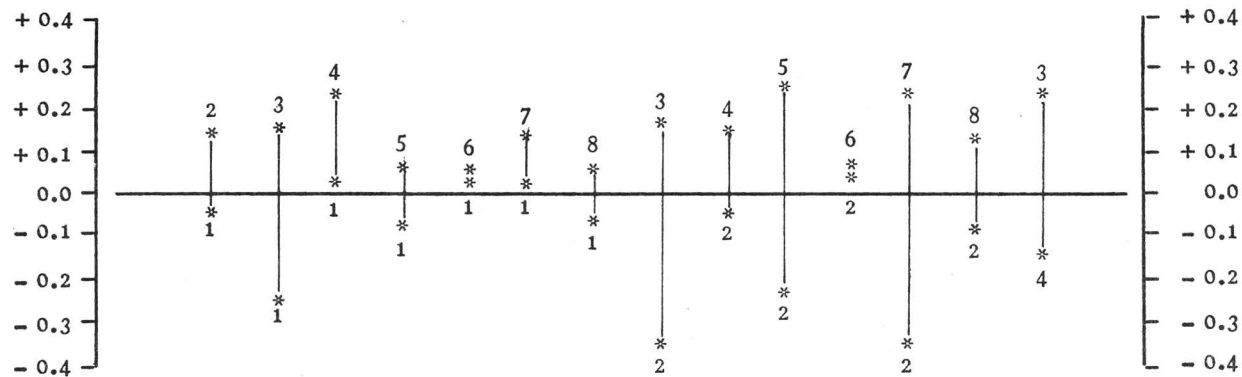
Fig. 1. Plastic responses of clones. Average of 8 cuts.

Table 5. Ranking of 8 clones for yield. Average of 8 cuts.

g/plot

	Pure stand	Binary mixture	Global mixture

100 —

90 —

                                                                        * 3

80 —

                                              * 3

70 —

                    * 3

60 —

                                                              * 7

50 —

                                    * 7

          $\bar{x}$ * 7 $\bar{x}$ * 5

40 — $\bar{x}$ — * 6 $\bar{x}$ — * 5   * 6

                    * 5   * 6   * 8

                    * 1   * 1   * 4

30 —   * 4   * 4   * 1

                    * 8   * 8

                    * 2   * 2   * 2

20 —

10 —

0 —
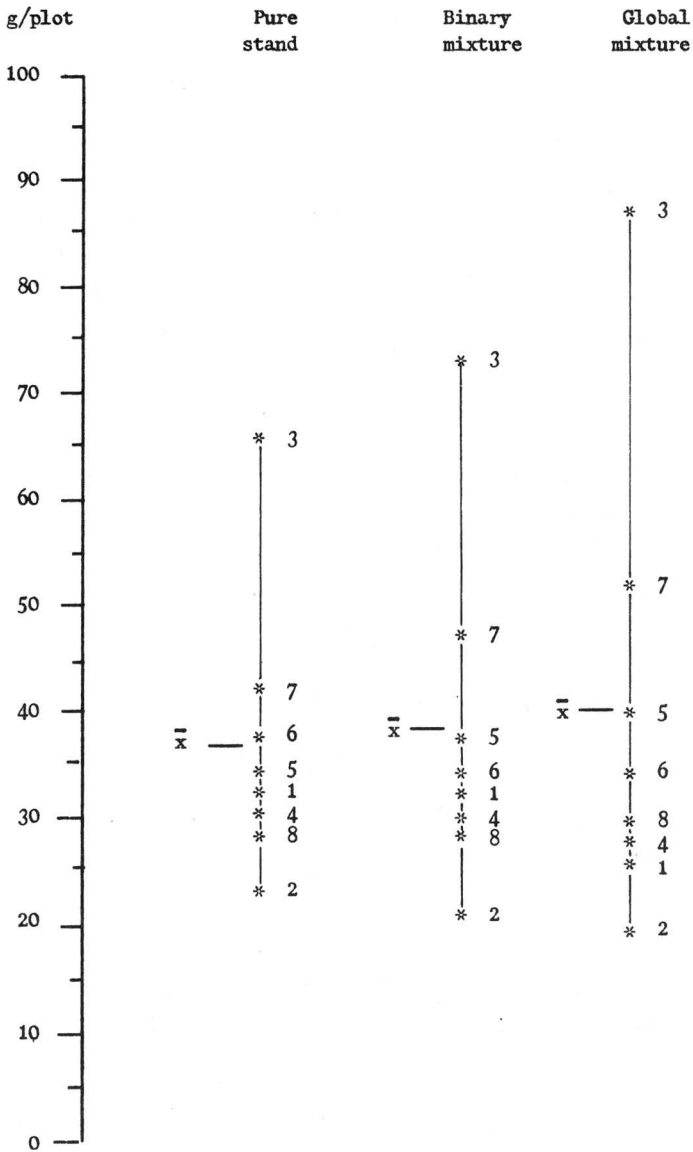
Table 6. Ranking and agronomic value of mixtures. Average of 8 cuts.

g/plot	Mixtures	$100\left(\dfrac{\text{Mixture}}{\text{Better Partner}} - 1\right)$
56		
	3 + 4	− 17
54		
	3 + 7	− 19
52	1 + 3	− 21
50	3 + 6	− 24
	3 + 5	− 25
48		
46	2 + 3	− 30
44	3 + 8	− 33
	6 + 7	0
42	1 + 7	− 4
40		
	5 + 7	− 9
	4 + 7	− 11
38	5 + 6	− 1
	1 + 6	− 2
	7 + 8	− 14
36	1 + 4	+ 6
	4 + 5	+ 1
	1 + 5	0
34	2 + 7	− 20
	6 + 8	− 13
	4 + 6	− 13
32	1 + 8	− 7
	2 + 6	− 16
	4 + 8	+ 3
	2 + 5	− 10
30	1 + 2	− 13
	5 + 8	− 15
	2 + 4	− 7
28		
	2 + 8	− 8
26		

DISCUSSION AND CONCLUSIONS

From these results the following conclusions can be drawn:

1. In the practical breeding, selection within cultivars, families, etc., can be made either in spaced plantings or in dense swards. The latter growing condition corresponds to a global mixture. According to the results presented here the spacing technique seems to be fairly effective, as it gives a clone ranking sufficiently similar to that of the global mixture. By working with spaced plants the breeder can therefore expect a positive result. But such a conclusion must be considered only partly correct because of the following reasons:

a) Selection in spaced plants can give positive results only if the selected plants are subjected to a progeny test. But one has to keep in mind that the sphere of action of a progeny test is limited to the material derived from the phenotypic selection; its efficacy is therefore dependent to some extent, upon the efficacy of phenotypic selection. For example, the progeny test cannot replace the vigorous plants rejected by mistake during the phenotypic selection. In addition, if recurrent phenotypic selection is employed the degree of efficacy of the spaced plant technique will be very low for such a character as forage yield. On the contrary the dense sward condition (global mixture), by emphasizing growth rate differences, allows a more reliable choice than in spacing. This result is due to the fact that the plants in association lead only to situations of competition. Situations of cooperation or contest would lead to a difference in the ranking of clones in pure stand and in mixture; in such a case the phenotypic selection would give rise to many errors. Selection for vigour in dense swards automatically gives a positive result for the other characters; it is for instance automatically accompanied by selection for earliness. In fact, at the 7th cut the coefficient of correlation between forage yield and number of spikes was 0.882** in the global mixture, but only 0.541** in spacing plantings.

b) The use of dense swards has the following practical advantages. It is possible to study a number of plants ten-to-fifteen times greater than in spacing, and on a surface ten-to-fifteen times smaller, and therefore more homogeneous. In this way it is possible to improve at least the experimental procedure. In addition, the study of the same number of spaced plants would take ten-to-fifteen times longer. A breeding programme of reasonable size could therefore not be achieved, not only because of time, but also because of the costs involved.

2. The study of binary mixtures has shown that the clone association leads only to situations of competition. We obtained similar results by studying families and cultivars in alfalfa (Rotili et al. 1976a), red clover (Rotili et al. 1976b) and cocksfoot (Rotili and Zannone 1976). The inference is therefore allowed that also by associating in binary mixtures families of tall fescue, instead of clones, only situations of competition will be produced. In such a case, the same conclusions reached for alfalfa, red clover and cocksfoot might be assumed here: the pure stand is the technique of culture for the progeny test which gives the maximum of information with the minimum of difficulties; the effects of association are not important in the evaluation of the combining abilities of the parents, the performance of a progeny in mixture being predictable from its pure stand.

ACKNOWLEDGEMENT

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TESTING PERENNIAL RYEGRASS AS SPACED PLANTS IN SWARDS

G. E. van Dijk

Foundation for Agricultural Plant Breeding (SVP), Wageningen, Netherlands.

SUMMARY

A method of testing spaced plants in swards of another grass crop is described. The process provides information on sward performance at every stage of the breeding scheme. A large number of entries may be included, together with any cutting frequency.

When used for perennial ryegrass, the method favours the selection of productive and persistent plants.

INTRODUCTION

A well-known problem in grass breeding is the use of widely spaced plants, a condition totally different from those in which the varieties are ultimately grown. This problem has caused a rather comprehensive literature. At Eucarpia Meetings it has been given considerable attention, e.g., in the Meeting of Fodder Crops Section at Dublin, 1972, and the First Meeting of the Section Biometrics at Hannover, 1974. Recently (1975) Les Annales de L'Amélioration des Plantes published a special issue on "Selection and Competition".

This paper describes a method of testing spaced plants already in sward conditions. It was used in the breeding of timothy (van Dijk 1973), perennial ryegrass and smooth stalked meadowgrass. Mainly data on perennial ryegrass are presented.

METHOD

To test plants of ryegrass, first a field of a companion grass such as timothy is broadcast at a usual seed rate, followed by spacing of ryegrass plants (e.g. 50 x 50 cm) in the newly sown timothy crop. If seed lots of perennial ryegrass are to be tested, 6 - 8 weeks old seedlings are planted, which were previously raised in boxes. After the sown and planted species have become fully established, an assessment of individual plants in sward conditions is made. Assessment by eye is most practical and can be done in reliable way (van Dijk 1973), the ease of assessment depending on the species combination. In testing families both the number of surviving plants and the total mean family performance may be taken as criteria.

Exact assessment of heading date is not easy. When heading date is one of the aims, the companion grass should be heading later. Cutting the plants in sward conditions is very easy, and for testing amenity grasses frequent and close cutting can be adopted.

Illustrative figures are taken from two experiments, the first dealing with

154

clones, the second with families.

EXPERIMENT 1. CLONES

On a sandy soil (pH-KCl 4.8, org. matter 6.4%) in 1974 8 clones of late
flowering perennial ryegrass were planted (5 ramets/clone, 2 replications)
at 50 x 50 cm in 8 ways:

a) in monoculture

   in broadcast swards of:

b) *Agrostis tenuis* (cv. Holfior)

c) *Dactylis glomerata* (cv. Holstenkamp)

d) *Festuca rubra* (cv. Koket)

e) *Phleum nodosum* (cv. S 50)

f) *Phleum pratense* pasture type (cv. Pastremo)

g) *Poa pratensis* (cv. Fylking)

In 1975 5 cuts were taken, the last one not weighed. Fertilization/year:
338 kg N, 115 kg P_2O_5, 175 kg K_2O.

RESULTS

The level of suppression suffered by the ryegrass clones depends on the
companion grass. Table 1 gives the relative dry matter yields. In cocks-
foot, ryegrass clones died after two cuts.

Testing in swards more frequently gives significant differences, as ap-
pears from the F-values.

Table 1. F-values and relative figures of dry matter production of 8
          wide-spaced clones of perennial ryegrass, tested in 7 ways.

	Cuts				Total yield	Rel. yield
	1	2	3	4		
monoculture	NS	NS	NS	NS	NS	100
in Agrostis	NS	NS	6.88[x]	7.02[x]	NS	33
in Phl. nod.	NS	4.01[x]	NS	4.05[x]	4.84[x]	22
in Poa prat.	NS	NS	4.60[x]	NS	NS	20
in Phl. prat.	4.09[x]	NS	NS	5.51[x]	4.08[x]	16
in Fest. rubra	6.39[x]	NS	3.85[x]	NS	NS	10
in Dact. glom.	12.01[xx]	NS	--	--	6.95[x]	4

NS = non significant

 x = significant P < 0.05

xx = significant P < 0.01

Correlations for total clonal yields were high (r > 0.9, P < 0.01) in

Phleum pratense, *Poa pratensis* and *Agrostis tenuis*. The same was true
for testing in cocksfoot and red fescue. Testing in *Phleum nodosum* came
closer to the first group, however, the correlations were lower. Whether
testing in red fescue and cocksfoot gives a different ranking from testing
in other grasses needs further investigation. Former results indicated an
effect on production level rather than on ranking of the genotypes (van
den Bergh 1968, van Dijk 1973).

For assessment-by-eye, perennial ryegrass - timothy and perennial ryegrass -
Agrostis were the most easy combinations. The slow establishment of sown
Agrostis is a disadvantage, however.

EXPERIMENT 2. FAMILIES

Time of sowing/planting: March 1972. A total of 56 perennial ryegrass
families from 7 polycross blocks (4 - 15 clones/block) and 8 standard
varieties were laid out for testing in several ways. One way of testing
was: 20 spaced plants per family, 2 replicates a) in monoculture 60 x 60
cm, b) in timothy swards (cv. Pastremo) 50 x 50 cm, c) in cocksfoot
(cv. Holstenkamp) 50 x 50 cm. Performance of plants was assessed by eye,
in September 1974 families in timothy were weighed.

For testing in dense swards family groups were mixed and tested in 4 m^2
plots with 4 replicates; 5 standard varieties were included. In 1973 and
1974 4 cuts/year were weighed.

   Soil: sandy, ph-KCl 5.1, org. matter 6.2%.

   Fertilization/year: 450 kg N, 150 kg P_2O_5, 190 kg K_2O.

RESULTS

Starting with 2560 spaced plants per treatment the percentage of surviving
plants was in the autumn of 1973: in monoculture 99.0, in timothy 94.5, in
cocksfoot 46. Production per plant showed a similar decrease. In testing
in sward, competition will make the weak plants succumb more readily.

In autumn 1974 for number of surviving plants in timothy the range was:
varieties 5.5 - 16.5, families 6.5 - 20 (Q' 0.05 = 6.2). Dry matter pro-
duction for entries ranged from 54 - 466 dry matter (Q' 0.05 = 210 g).
Number of surviving plants per family and dry matter production per family
were significantly correlated (r = 0.772, P < 0.001, n = 64). The plants
in monoculture were not weighed, but differences between families were
much less pronounced. In cocksfoot production per plant was very low and
was not weighed.

The relation between the performance as spaced plants in swards and the
production in a normal dense stand could not be assessed on a single fami-
ly base. To get some idea, Table 2 gives the total two-year production in
normally sown plots of mixed families - called synthetics - and their mean
number of surviving plants in timothy swards. For both family groups and
standard varieties, high production and high plant survival are related.
The same is true for the persistence figure taken from the Dutch De-
scriptive List of Varieties. The survival of spaced plants in swards ap-
pears to be related to production and persistence in normal dense sowings.

Table 2. Dry matter production in g/m^2/year in broadcast plots
          (2 years, 4 cuts/year) and mean plant survival (20 plants/family
          2 replications) of mixed family groups (Syn) and standard va-
          rieties.

	Perennial ryegrass		Persistence[xx])
	dry matter broadcast plots	surviving plants in timothy	
Syn 7(8[x])	1085^C	17.9	
Syn 6(8)	1072^C	19.0	
Syn 5(15)	1060^{bc}	18.4	
Syn 4(5)	1060^{bc}	18.5	
Syn 3(11)	1045^{bc}	18.9	
Var. A	1035^{bc}	16.5	8.5
Syn 2(5)	986^{abc}	17.4	
Var. B	977^{abc}	8.0	8
Var. C	961^{abc}	14.5	8.5
Syn 1(4)	932^{abc}	10.8	
Var. D	886^a	9.5	7
Var. E	880^a	5.5	7
Q' 0,05	140	6.2[xxx])	

x)   number of mixed families

xx) Dutch List of Varieties

xxx) Varieties only

Progenies having a letter in common do not differ significantly.

DISCUSSION

Camlin and Stewart (1976) state rightly that grass varieties should be pro-
ductive and persistent and resist the ingress of other species in the
sward. Testing spaced plants in swards enables selection for these charac-
ters at all stages of the breeding scheme. It discriminates better between
genotypes than widely spaced plants in monoculture. Moreover it is an
easily manageable procedure and can include a high number of entries.

In assessing initial material it combines readily with repeated mass se-
lection. In testing clones, comparison with widely spaced plants in mono-
culture is advisable, e.g., for measuring the exact flowering time. Fami-
lies can be tested in sward conditions even when few seeds are available,
and if more seeds are harvested, it can give information about sward per-
formance in addition to other testing procedures.

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SESSION II: DISCUSSION

O. De Cordova: How many environments did Dr. Hill use in his regression analysis?

J. Hill: How to define and contrive an environment is a very complex problem. The ryegrass experiment included two distinct cutting regimes with successive harvests throughout the growing season, which gave the rather limited number of only six environments. I was surprised, in fact that we got such a good separation between the five perennial ryegrass genotypes with such a small number of environments. Statistically I think that one should aim at more than six environments.

Generally environments should be chosen in such a way that they will be reasonably typical of the conditions under which the crop concerned is likely to be grown in practice. This can be done in a variety of ways, by having, for example, a range of locations or by having different managements or different fertilizer regimes within a single location. Under the conditions of British agriculture we would tend to place more emphasis upon contriving different management regimes within a single location rather than spreading our resources and taking in a broader range of locations. In the UK the grass crop is subjected to a whole host of managements and mismanagements by the farmer, and we feel that it is more important to concentrate on these effects, provided that major regional differences have been catered for.

P. Rotili: Dr. Breese mentioned that we should attach great importance to homogeneity, but I feel that we must distinguish between legumes and grasses in this respect. In lucerne, for example, the effect of the cut is very drastic and the reaction of individual plants to cutting is related to their biological stage of development. In our breeding experiments, the lowest mortality was obtained in genetically more homogeneous material, which also showed higher yield. Homogeneity increases the persistence of a lucerne crop because the majority of plants have restored root reserves by harvest time. In grasses buffering is probably important for natural permanent pastures. However, in our experiments with short term leys (*Dactylis*, *Festuca*), we have observed the same phenomena as in lucerne, i.e., that the more homogeneous material was also the more productive.

E. L. Breese: I would not at this stage wish to put any emphasis on the overall beneficial effect of homogeneity as distinct from heterogeneity. I would agree that there are instances where each has its place. Individual genotype buffering does involve a plastic response which is reversible, whereas synthetic varieties with a wide genetic base or mixtures of varieties lead to potentially unstable situations. These also create problems of variety registration in terms of distinctness, uniformity and stability. I would also like to make a general comment here which I think others will probably bring up in this discussion. How much do we really know about the heterogeneity of a variety in relation to its performance over a number of locations? NIAB or other testing authorities generally might have relevant data available from performance and DUS tests.

F. England: Dr. Hill mentioned in connection with his environmental index graphs that competitive stress had been treated just like any other envi-

ronmental component. Now obviously that worked with his graphs and it has also worked with some of mine, but it does not always work. Were the five ryegrass genotypes of a similar maturity type or was there a very wide range in maturity?

J. Hill: The five genotypes were deliberately chosen to represent a wide range of diverse morphological types. A and B were two contrasting genotypes from an indigenous population from the Monmouthshire moors, C and D were contrasting genotypes from S24 and E was from S23. A, C and E had longer leaves, more erect growth habit and recovered much more rapidly after defoliation than B and D. Indeed after a short period of time genotype B was competed out of many of those mixtures in which it had been originally planted.

F. England: Did you cut after ear emergence, or is this purely vegetative data?

J. Hill: These results relate only to the first year and as the experiment was not started until May there were no flowering effects. In the following year the experiment covered the entire growth period and included flowering effects, and we still obtained a straight line in contrast to some of Dr. England's results where differences were found due to developmental differences in growth rhythms, flowering times, etc.

S. Badoux: Did Dr. Hill find any connection between plant density and the reaction of different clones and genotypes?

J. Hill: This experiment only comprised one density, but other work involving different densities has demonstrated very marked interactions between genotype and density. Under a lower density competitive effects were more obviously expressed because there was more 'space' - in the de Wit sense - for the stronger genotypes to express this strength, whereas under high density the plants tended to be smaller and there was much less variability in response.

S. Badoux: What is the best density for this type of experiment?

J. Hill: If you want to maximize the competitive interactions the results from this one experiment would suggest a lower density.

E. L. Breese: It is very apparent from the way in which Dr. Hill has had to interpret these results that the over-complementation as he called it must represent a density-dependent interaction, i.e., a genotype gets its over-complementation because it has more 'space' available. The other thing that must be emphasized is that this is frequency-dependent, and that maximum expression is generally obtained in 3:1 mixtures favouring the better component and not in the 50:50 mixture.

G. Julén: Dr. Hill mentioned that there was a clear difference in performance depending on the density of the stand. If we have a low density then every genotype will be able to express its own character, but how can results from such experiments be applied to practical conditions where we have a high density from the start?

J. Hill: We obtained this maximum competitive interaction at a low density, of course, but one which could be expected under sward conditions. During establishment phases in the sward there is a pronounced elimination from that sward, and up to 90% of the population may not survive the first winter.

Competition is a very dynamic phenomenon and changes within a growing season and from season to season. This makes the problems of managing a mixed sward for stable performance extremely difficult.

B. Nüesch: I would like to ask Dr. Norrington-Davies if his results are generally applicable to diploid and tetraploid ryegrasses or specific for the two varieties tested.

J. Norrington-Davies: A perfectly valid criticism is that we have only used two varieties, one diploid and the other tetraploid. We should have many diploids and tetraploids in order to see if this is of general application. As we have to work on a limited scale we wanted to try and get a tetraploid that had been derived from a diploid so that we did not confound level of ploidy with a varietal difference. One could also ask whether a small scale experiment like this is going to be applicable in the field, and, in fact, we have set up a field experiment with different managements (conservation and grazing), densities and fertility levels in order to try and repeat this under natural conditions.

P. Rotili: Are the tetraploids and diploids similar in earliness?

J. Norrington-Davies: As far as I know their growth rhythms are about the same; certainly, their heading are similar.

J. Hill: Could Dr. De Cordova explain why the American varieties of lucerne were apparently so well adapted to the High Andes? They yielded more than the local varieties.

O. De Cordova: The better adaptation of the American varieties is related to their origin. In these varieties about 20% of the germplasm is derived from *Medicago falcata*, whereas most of the Peruvian ecotypes are purely *M. sativa*.

D. T. A. Aldrich: Could I ask Dr. Nüesch whether he knows the cause of the variation he found from centre to centre, and if he does know, then what is the factor that is operating? Would it not be more economical, if he has only a few centres, if they were placed at extreme locations? We find in England that the major agricultural regions have a fairly equal climate without extremes, and we therefore get very little experience here of the performance of a variety when temperature or other conditions are unusual. If we place our centres at the extremes of altitude or disease susceptibility, etc., we then get some experience of what will happen in an extreme year.

B. Nüesch: As I mentioned in my paper, there can be many reasons for differences between centres, and some of them may be very unexpected. For example, we have found in tetraploid red clover a reversal of the ranking of varieties at one centre compared to a second centre. This was found to be due to the fact that the most vigorous strains had been eaten by mice and had therefore been given a low ranking. I think we do need to have different locations because there is a marked difference in precipitation between the west and east of Switzerland. We also require localities where we can study disease resistance, and these localities may not be those ideally suited for yield comparisons.

D. Wilson: I think that Dr. Ceccarelli has got a very interesting problem on his hands. The main stresses in his material are obviously water stress in the summer and there is no doubt also a degree of high temperature stress,

and I was interested to see that no significant difference was found between local types and little difference among foreign types. Did you have any ecotypes collected from areas which had similar rainfall patterns or available soil moisture but different temperatures, and conversely similar temperature regimes but different soil moisture availability patterns?

S. Ceccarelli: Unfortunately no such ecotypes were included in our collection. This might have provided a means of evaluating the relative importance of water and heat stresses. We certainly find a higher yield in the first year, due to a very pronounced mortality after the first summer.

G. Julén: A brief question concerning Dr. van Dijk's method. Did you sow and plant at the same time or did you sow first and plant your genotypes into the established sward?

G. E. van Dijk: We sow the sward and then plant immediately. In the past we sowed and planted some weeks later.

G. Julén: Have these two methods given different results due to differences in developmental stage, etc.?

G. E. van Dijk: As we normally plant and sow in the spring and make our assessments the following year, there have been no detectable differences.

O. Bosemark: We have seen here how unpredictable the behaviour of genotypes is in mixture and under competition, and I wonder then how we can find genotypes that are capable of co-operating. Several years ago, Dr. Allard discussed co-operation between genotypes in lima beans and soya beans and suggested that one should look for genotypes that can co-operate in populations where many genotypes have co-existed for a long time. Here one is more likely to find genotypes that co-operate well than if genotypes are picked more or less at random from different populations.

E. L. Breese: A number of ecological studies have considered this question. For example, if ryegrasses which have become adapted to co-exist with *Agrostis* or other species are taken out and studied either as spaced plants or in pure swards, they are usually found to be inferior genotypes. They do not respond to improved pasture fertility. I was particularly intrigued in Dr. van Dijk's work that the ryegrasses did so badly in mixtures with *Festuca rubra* relative to mixtures with *Agrostis*.

G. E. van Dijk: I do not know why *Lolium perenne* was more productive in *Agrostis* than in *Festuca rubra*, but possibly *F. rubra* is capable of growing under drier conditions than *Agrostis* and was a more severe competitor for water. With regard to co-adaptation I wonder if by testing, for example, ryegrass genotypes in timothy and timothy genotypes in ryegrass, one could obtain types better adapted for co-existence than by mixing genotypes at random.

G. Julén: I found Dr. Larsen Petersen's results most interesting, particularly the striking differences he found between clones. There were two aspects that struck me. Firstly, one of the clones selected as a low yielder was found in competition experiments to be high yielding and more persistant than three of the genotypes selected as high yielders. These genotypes were selected from 600 plants in sown swards. Were they tested under non-competitive conditions and selected on this basis? Secondly, in view of this considerable difference in the later behaviour of genotypes after the first selection, how well can we rely on the breeding value of these clones? The

phenotypic appearance of a clone does not always reflect the breeding value of its progeny. Have you carried out experiments to evaluate the behaviour of the progeny of these clones?

H. Larsen Petersen: The genotypes were selected from 600 plants taken at random from a sown sward. The only qualification was that each of these plants had 1 cm on each side to their nearest neighbours and were thus under competitive stress. As the sward was grown from seed there were obviously no replications. Unfortunately, as you mentioned, clone B was selected for very low yield but was subsequently found to be highly productive. The reason for this reversal in behaviour is not known, but this genotype could have been situated between two very high competitors. This simply served to show that one cannot select under these conditions with any degree of certainty. In answer to your second question, we have not been able to evaluate the offspring of these eight clones, but we have an experiment in progress at Højbakkegård to study the inheritance of persistency in offspring from diallel crosses.

S. Badoux: Dr. Zannone has determined DM yields over 8 cuts. Did you find any interrelation between cuts and the response of different clones? We have examined the seedling establishment of tall fescue and have found large differences between varieties. Do you think that the DM yield found after two years is partly or mostly due to the early vigour of the plants?

L. Zannone: In our clones we observed a good stability through cuts, both for vigorous and for weaker plants. In fact, the ranks of the clones remained about the same through eight cuts. We have not yet studied the relationship between seedling and adult plant vigour.

A. J. Kleinhout: I would like to ask a general question. Can we expect a good correlation between genotype-environment interaction and the degree of co-adaptation, i.e., if a variety does well over a large number of environments will this variety also have a good co-adaptation in mixtures?

E. L. Breese: Using Dr. Norrington-Davies' experiments with binary mixtures carried out over a number of cutting treatments, regression analyses for different treatments showed that the kind of sensitivities which genotypes displayed to environmental stresses was of the same order as that displayed to increasing competitive stress. In some of our studies at Aberystwyth it has been possible to look at the behaviour of spaced plants over 2 or 3 years, construct relative response curves, and obtain some idea of the relative performances of composites in swards.

J. Hill: With regard to the cross-predictability of spaced plants and swards, the basic responses to environmental conditions seem to be of the same type, whether they are under competitive or non-competitive conditions, and this can be the case even though there are no actual correlations between the means whatsoever. For example, as we saw in the joint regression analysis referred to earlier by Dr. Breese (see Samuel et al. 1970, J. Agric. Sci., Camb. 75: 1-9), we found that we could predict reasonably accurately the relative performance of three varieties of perennial ryegrass under sward conditions from yields obtained under spaced plant conditions.

Session III

ADAPTABILITY AND UNIFORMITY

A panel discussion

Chairman: Dr. G. Julén

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INTRODUCTION BY PANEL MEMBERS

G. Julén
Swedish Seed Association, Svalöv (S)

The convention for the protection of Plant Breeder's Rights, signed in Paris on the 2nd of December 1961 and later adopted by most West European countries, has greatly influenced plant breeding work.

In article 6 of this convention it is stated that the breeder or the owner of a variety will be given the protection stipulated in the convention if the following are fulfilled:
a) The new variety must be clearly distinguishable from all other varieties known at the time of application. The characters used to describe and distinguish a new variety can be of a morphological or physiological nature. In any case it must be possible to clearly describe and recognize them.
b) The new variety must be sufficiently homogeneous within the limits of the sexual or vegetative reproduction system of the crop concerned.
c) The new variety must be stable with regard to its important characters. This means that the variety shall be in agreement with the description after repeated propagation or, if the breeder has established a specific propagation cycle, at the end of each such cycle.

It is also stated that the concession of protection of a new variety should not depend on anything but these three requirements. Characters which cannot be clearly described and recognized are thus of no importance for registration. Furthermore, there are no requirements for high agronomic value with regard to variety protection.

The background for these regulations is, as we all know, that if an owner of a variety wants to have legal and economic protection for his variety it is necessary to be able to give an accurate description of it, and this description must be true in every field where the variety is grown and in any generation of the variety. From this point of view there can be little discussion of the requirements for distinctiveness, homogeneity and stability. But the ultimate goal for a plant breeder must always be to produce new varieties which are better than existing varieties, and to produce and distribute these varieties without undue delay. Thus the breeder is the servant not only of a seed firm but also of agriculture, and in this connection it might be questioned whether Plant Breeder's Rights and associated regulations will be beneficial for agriculture or whether they might hamper the development.

In forage and pasture plant varieties characters of agronomic importance, such as yield capacity, persistency, winterhardiness, disease resistance, resistance to drought, standing water, and other adverse conditions, seed setting capacity, nutritive quality, etc., should be combined with a very wide adaptability, making it possible to use the varieties over wide areas and secure good yields under varying climatic conditions and different treatment systems. Is it possible to achieve considerable improvement in one or more of these characters and maintain adaptability, and at the same time give the new varieties such an appearance that they can easily be distinguished from all other varieties and be sufficiently uniform to fulfil the requirements

for Plant Breeder's Rights? This might not be a serious problem in self-pollinating crops, but what about the cross-pollinators such as the majority of our fodder crops? If it is possible to combine breeding for agronomic value, adaptability and uniformity, etc., can this be done without considerable delay in time? Furthermore, how long can we continue to produce from these cross-pollinating species new varieties which can be clearly distinguished from all existing varieties?

The Section Board felt that these problems warranted serious consideration and discussion at this meeting. We know that a number of questions are impossible to answer with the knowledge we have today. There are very few factual results to elucidate these problems but we know that there are many among us with a considerable experience in this field. We therefore hope that a discussion inside this group will bring together some ideas about these problems, and the way in which they might be tackled in a scientific way.

We have not invited papers on this subject but we have asked three distinguished persons working on variety control and three equally distinguished plant breeders to start the discussion by giving their ideas on these questions.

H. A. Jönsson
Weibullsholm Plant Breeding Institute, Landskrona (S)

The expression "adaptability" could, for perennial forage crops, be defined as the ability to withstand:
1. Different climatic conditions, e.g., cold winters, hot summers, dry periods, etc.
2. Different soil conditions, such as sandy, clayey or organic soils.
3. Different pathological conditions, i.e., the crop should perform well also when diseases or pests are abundant.
4. Different managements, such as fertilizer level, irrigation, number of harvests, method of harvest, etc.

The crop should not only withstand these different conditions, not only survive under different conditions and treatments, but also yield well. Yielding ability is our ultimate measurement and can be expressed in weight or in money and means something real both for the farmer and for the research worker.

The forage crops, like other perennial plants, have the adaptive advantage that they need not set seed every year. On the other hand, they may during their lifetime be exposed to several periods of extreme conditions such as drought, heat, cold, etc., which requires an adaptability not necessary in annual plants.

Uniformity is easier to define. It could perhaps be considered as self-explanatory, but I do not think it is quite so simple. In general only morphological characteristics have hitherto been taken into consideration. We have now also physiological and biochemical methods at our aid. For instance, resistance tests and electrophoretic investigations could be used. I will not here recommend a more general use of such methods, but they have to be used in some cases when distinctness of a variety is to be ascertained. Then the varietal uniformity will also be assessed. Perhaps methods ultimately could be found by which uniformity and distinctness could be determined faster and cheaper than by the morphological measurements made at present.

With the present breeding methods an absolute uniformity will not be reached in the outbreeding forage crops, there will always be a variability. The

problem is to define the limits. We want as many identifiable varieties as possible in our lists of cultivars, i.e., we want as many individual niches as possible in the array of characteristics. This can be achieved by narrowing the variability of each variety but also by increasing the number of characteristics under observation. That is where new physiological and biochemichal methods can be taken up.

If we look at the points listed above in the definition of adaptability they are all polygenic with the exception of disease resistance which is sometimes governed by just one or a few genes. This implies that our chances of changing any of these characters without a simultaneous change in a morphological trait are small. Thus with the present methods of assessing uniformity we will hardly be able to increase adaptability at the population level and the possibility will be still smaller the more characteristics are included in a variety description. In present forage varieties we have a fairly good adaptability. To a large extent I think this adaptability is dependent on the populational buffering capacity to use the expression of Allard and Bradshaw, but we have also that part of the individual buffering capacity which relies upon the heterozygote.

If in the future we want to widen the adaptability of an outbreeding forage plant without a further increase in variability, the individual buffering capacity has to be exploited. I think we can draw conclusions from autogamous crops where a fair degree of adaptation has been reached. Thus, it should be possible to improve adaptability with the present standards of uniformity. I hope this discussion will lead to the recognition of the common interest of testing authorities and plant breeders, that the best plant material should be brought to the farmers' disposal. A close cooperation between the plant breeders and the testing organizations is desirable.

J. Y. Blanchet
L. Clause S.A., Bretigny-sur-Orge (F)

I find the term adaptability difficult to define because it has a different meaning for geneticists, breeders and farmers. For the farmer adaptability is the capacity of a variety to give high yields at his location independently of how it behaves 50 km away. For the geneticist or ecologist it is the capacity of giving high yields at all locations. I think that adaptability to the method of farming is more important than to climatic conditions. For example, with the present high N usage, the breeder is obliged to breed varieties at high N levels.

For grasses uniformity is also difficult to define. A variety can be uniform for some characters and very heterogeneous for others. It may well be necessary to specify those characters for which a variety must be uniform and those for which uniformity is not necessary.

Our chief task must be to develop methods which give varieties with the highest yields, but not necessarily the highest degree of uniformity. For example, F_1 hybrids generally have good uniformity whereas synthetic varieties show a lesser degree of uniformity in morphological characters. Furthermore, in grasses, for example, morphological characters are not the same at different spacing regimes.

In conclusion it would seem that uniformity is necessary for characters such as disease resistance, growth type, heading date, but not in morphological characters. I think that testing authorities must to a greater degree adapt their methods and requirements according to the progress made by the breeder.

H. Bøgh
Danish Plant Breeding A/S, Børkop (DK)

I would like to attack this problem from the point of view of the practical plant breeder and discuss it not in terms of Plant Breeder's Rights but simply in terms of getting varieties on national lists.

We have seen and still see many varieties refused because of lack of uniformity or distinctness. We also see inconsistencies in the pattern of refusal. In one country a variety may be refused because it cannot be distinguished from variety A, in a second country because it cannot be distinguished from variety B, in a third country from variety C. A fourth country may refuse it because of lack of uniformity, a factor not mentioned by the other three countries. Finally a fifth country may accept the variety as being both distinct and uniform. You will understand that this situation is rather confusing for the breeder.

Distinctiveness is probably a greater problem for the plant breeder than uniformity. A variety may lack uniformity initially but can improve during later stages. Distinctiveness can be very difficult to achieve, and I think that there are only two ways in which we can solve this problem, either by a reduction in the demands for differences between varieties or an improvement in the methods of distinguishing between varieties. Looked at from the point of view of plant breeder's rights it might be difficult to lower the demands for distinctiveness. However, in the case of grasses, clovers and root crops, we could well do without plant breeder's rights; it is more important to get varieties on the national lists, and if this were the only aim the distinctiveness requirements could be reduced.

In most cases when our varieties are refused on the grounds of lack of distinctiveness, we as breeders know these varieties and can see differences between them. Therefore I feel that we should reduce our demands for distinctiveness so that varieties between which we can see differences can be placed on the list. Alternatively we must improve our identification methods so that we can always distinguish between varieties which are visibly different.

We have heard here during the last two days of the excellent work done to improve breeding methods and obtain better varieties. However, these varieties must be registered on the national lists before they are used. It is of little use improving breeding methods if we cannot improve the methods of distinguishing between them.

K. H. Beuster
Bundessortenamt, Hannover (D)

To get plant breeder's rights, respectively to be registered in the variety list, a forage plant variety has to meet the following requirements just as other agricultural crops:
1) It must be new and distinct, sufficiently homogeneous and stable.
2) It must have an agronomic value.

These are requirements according to which the authorities of the UPOV member states (International Union for the protection of new varieties of plants), the EEC member states and many other countries which have introduced, for example, the OECD scheme for the varietal certification of herbage seed, are at present proceeding.

An important basis for this discussion is the question how to integrate adaptability and uniformity. Adaptability cannot be equated with "agronomic value", although they may often be closely related. The characters yield, quality, persistency, resistance, etc., are the primary constituents of ag-

ronomic value, which is an essential prerequisite for registration on variety lists in one or several countries. The value of a variety increases when it has a wide ecological range and hence good adaptability. This is desirable for the widespread use of the variety and for its economic value.

At present the Federal Plant Variety Office (Bundessortenamt) has no data to suggest that good adaptability can only be attained with heterogeneous material or that homogeneous material narrows adaptability.

On the part of the testing authorities there are no objections when the breeder proceeds from different materials and different origins in order to obtain adaptability. But this must not result in a variety which is too heterogeneous in the characteristics which are important for distinctiveness. Even a variety developed from very different genetic materials must be suficiently uniform.

Uniformity and homogeneity are often equated. As a variety tester, I would like to interpret the term "uniformity" as "homogeneity". Homogeneity is an important prerequisite for distinction of varieties and thus for their registration in the variety list. In forage plants, which are mostly cross-pollinating, we have only a few characteristics, as a rule quantitative in nature, with which we can describe a variety. The closer a variety sticks to one state of a characteristic, i.e., the smaller the variation, the better the variety can be defined and the greater the number of varieties which can be distinguished. This is an important argument for the requirement to breed varieties which are as uniform as possible.

According to the UPOV-guidelines a variety is taken as homogeneous when it is as homogeneous as a well known variety with which it is comparable. By judging relatively in this way an adjustment results which avoids too rigid a judgement on the one hand and too wide a variation on the other.

With this in mind the breeders should be able to meet the requirements concerning the uniformity of cross-pollinating varieties of forage plants and combine these requirements with the demands for adaptability now and in future.

D. T. A. Aldrich
National Institute of Agricultural Botany, Cambridge (UK)

I am going to make 3 assumptions. The first is that we are right in aiming for adaptability in our varieties. While this may hinder progress in other directions it buffers a variety against changes in the environment, making the variety more consistent and reliable and it also means that the variety can be sold in more than one country.

I am also going to assume that we agree that new varieties should be distinguishable from existing varieties. It is difficult to see how Plant Breeder's Rights or National Lists could operate without this. I agree with Mr. Bøgh that we must have more and better characters. I think that in many cases, however, the proposal of a character to be used for distinctiveness of a particular variety must come from the breeder, not from the variety testing agencies.

Finally, I am going to assume that we agree that a new variety should be stable during seed production, so that the certified seed will give the same performance as that obtained in the official Value for Cultivation and Use tests.

It is however in the sphere of uniformity that we have been asked to direct our attention in this discussion. There is an implication in the title that the present requirements for uniformity are restricting the breeders

in their attempts to achieve adaptability. Is this really happening? What
is the evidence?

In the UK, in the years 1974 & 1975, we have made decisions on 91 grass
varieties for distinctness, uniformity and stability. The decisions were
as follows:

Accepted	74
Refused on lack of distinctness	11
Refused on lack of stability	4
Refused on lack of distinctness and stability	2
Refused on lack of uniformity	0
	91

There is no evidence of restriction here.

We have been asked, can a variety be both uniform and adaptable? The Common
Catalogue tells us that the perennial ryegrass variety Perma is on the Na-
tional List for all 9 EEC member states, and it must, therefore, be suffi-
ciently uniform in all these countries, but it has also been accepted as
having Value for Cultivation and Use in 8 of these 9 countries, and this
suggests to me that it is also an adaptable variety.

The information from the UK would, therefore, suggest that although a con-
flict between adaptability and uniformity is theoretically possible, it is
not a problem in practice. However, it is important that topics such as
this are discussed from time to time between breeders and those concerned
with official testing and nothing but good can come from a free exchange of
views at a meeting such as this.

R. Duyvendak
IVRO, Wageningen (NL)

Being the last to speak in this series of introductions, I am of course in a
difficult position. If I were to give a balanced review of the subject we
are discussing today, I would have to repeat much of what has already been
said by my colleagues from Germany and Great Britain. I think it would be
of greater value if I concentrate on some major points against the background
of the situation in our country.

1. In the Netherlands it has long been thought that varieties of cross-fer-
tilized crops were not suitable for a plant breeder's rights system as prac-
ticed for potato and cereal varieties under our seed law of 1941.

In the fifties Dr. Nijdam, who was then Head of the Registration Department
of the Institute for Research on Varieties of Field Crops (IVRO) at Wagening-
en, coined the term "Bijzonder Kweekprodukt = Specifik Breeding Product" for
varieties of cross-fertilized crops produced under a closed certification
system. This conception did not in its totality find mercy in the eyes of
those who were responsible for Dutch seed legislation. Part of it is, how-
ever, reflected in our new seed law (Zaaizaad- en Plantgoedwet) of 1967.
Varieties of grasses, legumes, beet and certain other allogamous crops could
enter the Dutch Variety Register under article 18.2 of this law without being
granted plant breeders rights in the sense of the Paris convention, but nev-
ertheless protected by closed certification.

On the initiative of the breeders (and no other party whatsoever) the grasses
were transferred to the plant breeder's rights system in 1970. Our knowledge had by
then sufficiently increased to tackle the problems of distinction and descrip-
tion of grass varieties, so there were no objections from our side.

Red clover and lucerne will follow the grasses as soon as the United Kingdom,
who are now doing the testing work for us, include these species in their

list of species eligible for granting rights. Among the other crops still
under the 18.2 system sugar beet is the most important. Here the discussion
is still in progress.

2. It has been remarked that the Plant Breeder's Rights system complicates
the work of the breeder, and that these complications would not exist if
there were only the National Lists. Most breeders will, however, be aware
of the fact that the wording of the requirements for distinctness, homogene-
ity and stability with respect to Plant Breeder's Rights in the UPOV states
is exactly the same as the wording of the requirements for admission in Vari-
ety Lists in the EEC countries.

It is not to be expected that there will be a difference in the interpreta-
tion of these requirements. Any variety admitted to the National List has
therefore fulfilled the DUS requirements for Plant Breeder's Rights and can
profit from these rights. There is not an extra barrier.

3. Contrary to what has been said by Dr. Julén, we do not think that a vari-
ety needs to be identifiable in every field in which it is sown. We consider
it to be sufficient if a seedlot can be identified when sown in our trial
fields together with the appropriate reference varieties in our collection.

4. The requirement of homogeneity is not a requirement for its own sake. It
is directly related to distinctness and stability, of which stability is the
most important. For recommendation to farmers it is a basic necessity that
the variety is stable and will reproduce the results of the performance trials.
The cultivar must therefore retain its characteristics during seed multipli-
cation and this must be true for each seed lot that is produced and certified
under a blue label.

A gene pool with widely divergent physiological and ecological genotypes
cannot be reproduced as one population. The frequency of the components
would shift in any direction according to the particular conditions of manage-
ment, weather, diseases, etc. It is, however, possible and common practice
to blend different physiological and ecological components under a green label
so as to give the seed sown by the farmer. The stability of a cultivar during
seed multiplication is least threatened in narrow populations in equilibrium.

Restrictions as to the number of generations must be considered for a synthet-
ic variety, especially when it is conceived in the original meaning of the
term, viz. as a variety that is synthesized from genotypes previously select-
ed for hybrid performance (combining ability). It is again easier to guaran-
tee stability when the crossing between the components is postponed to the
last generation and true hybrid varieties or semihybrid varieties are produced.
(A semihybrid variety is the offspring of two strains under open-pollination
with no or weak mechanism to exert influence on the direction of the crossing.
The frequency of hybrids in the offspring can be 50%, together with 25% of
each of the parental sibs).

5. Homogeneity is also linked with distinctness. A smaller variation within
varieties facilitates distinction between varieties. Seed lots of varieties
with agronomically important characters are identified by earmarking charac-
ters that are easily recorded. Such characters can only be used if the dif-
ferences between varieties are large enough in relation to the differences
between individuals within each variety.

6. Since breeders select for agronomic characters such as yield, persistency,
resistance to stress factors (cold, drought, diseases), the new varieties can
be expected to differ in these traits relative to the existing varieties. It
is therefore logical to use these characters for distinctness and description.
In order to do this we need quick and cheap testing methods with which we are
able to classify large numbers of seed lots with respect to these characters

or the morphological or physiological components of these characters. At
our Institute we have devoted much time and energy to find such methods
with some occasional success. Breeders and testing authorities must en-
courage further research in this field.

DISCUSSION

H. Bøgh: I do not think that uniformity is detrimental for a variety, but
I do not like spending too much time or money in obtaining uniformity when
I could be employing these resources more usefully. I admit, however, that
varieties need to be identifiable. We could reduce our demands for differ-
ences, and we could also improve our descriptive methods such that a lower
degree of uniformity could be accepted. Some countries use only spaced
plants in uniformity tests, while others also use swards or single row sow-
ings. Certain characteristics are more easily described in rows, others in
spaced plants.

H. A. Jönsson: I would stress the importance of the exchange of information
between countries which could help in the type of contradictory situation
described by Mr. Bøgh in his introduction. One explanation of differing
DUS decisions in different countries is the differential photoperiodic re-
sponse of varieties. In cereals, for example, varieties showing homogeneous
straw length in Sweden may lack uniformity in Germany. This is something we
have to accept. I would also like to emphasize the importance of using phys-
iological characters, among these agronomic characters such as yield, disease
resistance, etc., in DUS tests.

R. Duyvendak: If a breeder has specifically bred for disease resistance it
is of course desirable that this character is recognised and used in DUS
tests if possible. In UPOV and EEC only diseases capable of artificial in-
fection can be used. This is a considerable restriction as the number of
diseases for which artificial infection methods are available is very limit-
ed. Research instances should be encouraged to develop such methods which
are reproducible in other countries. Rust resistance, for example, is very
important in *Lolium perenne* but no artificial infection method is available,
and resistance cannot be included in DUS tests. (We do in fact use it in
Holland, but will probably be forced to stop due to lack of stable infection
material).

K. H. Beuster: With regard to the exchange of information between countries,
UPOV members are in close contact with one another. The scheme is, however,
fairly new and discrepencies like those described by Mr. Bøgh can occur, but
will gradually become less frequent. Other apparent discrepencies in DUS
decisions are due to differences in daylength, and the breeder will need to
test his new varieties in different countries.

B. S. Ahloowalia: In Ireland, a member of the EEC, we do not yet have Plant
Breeder's Rights, but we have a very good system of seed certification which
gives the farmer the same kind of protection. Apart from the moneymaking
idea behind Plant Breeder's Rights, I find that the breeder is extremely
handicapped in terms of the exchange of genetic material, because he now
tends to hold on to various strains, potential varieties, genotypes, etc. I
wish that some kind of arrangement could be devised whereby we could exchange
material more freely.

E. L. Breese: Both the breeder and the testing authorities seem from the
discussion to be extremely interested in getting out to the farmer good
material having the integrity of a properly constituted variety, and getting
it out in a way which will preserve this integrity. It was encouraging to
hear from the testing authorities that uniformity is regarded very much in

a relative way and with a degree of elasticity. This will help in getting through highly adaptable varieties which have this capacity by reason of genetic heterogeneity. The problem again is thus more a question of distinctness and stability. In this connection David Aldrich rather puts the onus on the breeder to discover or put across distinctiveness points to the testing authorities. Now this is an extra difficulty for the breeder, who is chiefly concerned with performance characteristics which, as we have heard, are not often acceptable as distinctiveness characteristics. Again in breeding stations we are extremely limited in how far we can compare our own material with the necessary range of other varieties. Rather than putting the onus on the breeder for discovering distinguishing features, it would be better for breeders and testing authorities to consider together better ways and means of discriminating between varieties.

D. T. A. Aldrich: From the point of view of the testing authority I do not think we are prepared to take a situation where breeders expect us to decide which characters to use, to do the research, to study the variety, find out all its attributes, and establish it to be distinct. We have neither the money, the staff or the time to do that. At the moment the philosophy is such that in the first two years when a new variety is submitted it goes through the standard tests only. If at the end of the two years it is clear that it is both distinct, uniform and stable based on standard tests there is no need for anybody to spend money on additional tests. But if at the end of the two years it is apparent that there are some varieties from which it cannot be distinguished, then there are discussions with the breeder on which additional tests can be used in that later period. But we have to rely very much on the knowledge that the breeder has of his own material.

E. L. Breese: At the Welsh Plant Breeding Station we accept a responsibility for investigating useful means of identification and are pleased to discuss the acceptability of these with the testing authorities. In this context we have been studying the use of electrophoretic techniques and I wonder if anyone has comments on the possibilities of these.

R. Duyvendak: Taking cereals as an example, the use of electrophoretic characters has demonstrated heterogeneity in certain varieties, which was not otherwise known and which did not bother us at all. Are you not afraid that the use of these characters, which have no direct meaning other than identification, will make it more difficult for the breeder? I would rather take up meaningful characters such as yield and persistency which are not at present used. If we could find a rapid and exact method to measure persistency or yield, this would immediately be included in DUS tests. We have been doing quite a lot of research on persistency, but have not yet found anything of interest. Tillering is difficult to measure exactly for DUS purposes. Our results suggest that the reaction of internode elongation to different light conditions may have some bearing on persistency. As Mr. Aldrich pointed out we are only a very limited staff, and the whole group of interested people must help to find new characters and appropriate methods.

G. Julén: Here we come in on the problems of using physiological characters, which are often more difficult to describe than morphological features, especially for the plant breeder. I would like to ask the crop physiologists here today whether methods could be developed whereby such characters as yield, persistency, or their components, could be used in DUS tests.

D. Wilson: I think this is the converse of the situation with regard to selection criteria which I was talking about earlier, and Mr. Jönsson has already raised the point about the importance of an understanding of the basis of yield. If a variety has some economic value, nutritionally, adaptability or whatever, there will be a physiological or morphological reason for this, and I think that it is up to research stations to try and deter-

mine what this is. A lot of the work currently being done at Aberystwyth and elsewhere on selection criteria could in time be applied to the sort of distinctiveness tests we have been discussing today. Adaptability, for example, is not a single character, it comprises a number of features of the plant that effect adaptability to drought, cold, etc. There are specific adaptations which affect, for example, water use efficiency and often the anatomical features which affect the physiology of the plant, such as stomatal conductance, can be quantifiably measured quite easily. We have, in fact, produced experimental populations which visibly under normal conditions are essentially very similar to the varieties we have selected them from, but they perform very differently under particular sets of water stress conditions. We can, however, distinguish them on the grounds of the criteria we have selected them for, and the population appears to remain very uniform in this respect. On the more physiological level in terms of potential yield or persistency I do not think we yet have sufficient knowledge to use this as a distinctiveness test. Some of our gas exchange studies indicate that certain aspects of respiratory activity do affect plant performance as mature swards, particularly in later years, and we may find this to be related to persistency. Our present techniques are, however, not suited to mass screening of a large number of varieties, but there is little reason why suitable techniques for measuring some of these physiological characters could not be developed in time. It is certainly logical to use such characters as distinctiveness tests. The same sort of thing already applies to nutritive value, since this is always selected for on grounds of a specific quantitative measurement such as *in vitro* digestibility or some character related to intake, and these can always be used as distinctiveness characters.

A. Kleinhout: Could not the registration of varieties be performed after their agricultural value has been established? In this way there would be fewer strains to distinguish between.

D. Aldrich: In the UK it costs a lot more to do the agricultural value tests than the DUS tests, so that this would be an expensive way round. In fact the two tests are run side by side and the decision made at the same time.

R. Duyvendak: In potatoes, of course, agricultural value is assessed first. In our country about 700,000 new seedlings are produced each year, about 200-300 clones enter the first observational value tests, and only some 30-40 are submitted for DUS tests. In potato the chances of a variety being refused on grounds of distinctiveness are negligible, whereas the chances of not reaching the required agricultural value is very much higher. In forage crops we have found, as Mr. Aldrich, that it is very much more expensive to perform yield and grazing trials than to measure a few characters in DUS trials. Yield trials also need quite a number of replications and trial sites to give a good estimate of yield potential, whereas it is much easier to have DUS tests at one site. Dr. Julén stated in his introduction that a variety should be distinctive in each field where it is grown. We have abandoned this idea and we are satisfied when a variety is distinct at one trial site. This has now also been adopted by UPOV and the number of trials for DUS tests will probably be reduced.

M. T. Morales: In the case of a variety which has been shown to be very much better in agricultural value but cannot be distinguished from a variety already on the list, can the testing authorities accept the breeder's observations on characters by which it might be distinguished?

K. H. Beuster: Generally a variety with a much higher agricultural value will have some characters by which it can be distinguished, for example, greater plant height in spring growth or aftermath. In some cases the breeder may need to find other characters, and we are free to add characters to

our selection.

F. Rasmussen: I would like to give some information relating to the question of performing value tests before DUS tests. In Denmark we do have, in fact, such a system. Provisions have been made to enable the breeder to choose whether he wishes to apply for both tests at the same time or for one of the tests first. However, the second alternative has not been used, probably because the breeder does not have time to wait a further two years for a DUS test after obtaining good results for a potential variety in value tests. The second alternative could, however, be taken into account if a breeder has a number of new varieties of similar agricultural value. In this case he could choose to apply for a DUS test first to see which of the varieties could be recognized as distinct and uniform, and then this smaller number of varieties could continue in value tests.

R. Duyvendak: Returning to the uniformity problem in cross-fertilized crops, in the ordinary "population in equilibrium" varieties we expect a normal (Gauss) distribution for all continuous characters that are measured on a linear scale, e.g., date of ear emergence, plant height, etc. The parameters of this frequency distribution are the mean and the standard deviation, the latter being a measure for the homogeneity of the variety. In general varieties resulting from comparable breeding systems have approximately the same standard deviations, e.g., for ear emergence SD = ± 3 days. The coefficient of variation is about 10% for many characters in cross-fertilized varieties. This is not a requirement, but just our experience. For characters under strong selection pressure and in pure lines under inbreeding the variation coefficient can be as low as ± 5%. When selection has been less severe or for characters that are more easily modified by the environment the variation coefficient can be 15% or more. In complex varieties produced by a different breeding system we can find a variation coefficient of 20-30%.

In cross-fertilized forage crop varieties the breeders might want to depart from the simple "population in equilibrium" variety model and breed another type of variety, e.g., a hybrid variety or a semi-hybrid variety. (I define a semi-hybrid variety as one that is produced without the use of male-sterility by simply crossing two strains). I think that a breeder cannot widen the range of variation within the population variety because of the risk of instability.

H. Bøgh: I understand that a significant difference between varieties with respect to a certain character is essential, and that this is why standard deviations have to be taken into account.

R. Duyvendak: What we look for in the first place is a consistent difference, that is a difference that will recur in every trial throughout the years. The difference must not disappear or even reverse. If two varieties are very close together there may be reversals from one year to another. We try to have DUS trials under very uniform environments preferably at one location with as small a residual error as possible.

H. Bøgh: I do not think that you can expect differences in plant height to be consistent. Height will vary in different years and sites, but you cannot always expect two varieties to follow each other.

R. Duyvendak: For distinction purposes only one trial location is needed, i.e., one location for distinctness tests to which we can refer new samples from the same variety for identification.

H. Bøgh: You could have two varieties which are different in Denmark but not in Germany.

R. Duyvendak: We would accept a variety to be distinct even if it is not so

in all countries.

H. Bøgh: We are often advised to concentrate testing for distinctness at one place, but as varieties react differently in different countries it would be unwise for the breeder to rely on testing in only one country. Two varieties might be found not to be distinct in one country, whereas differences could have been found if testing had been performed in another country.

R. Duyvendak: There has been much discussion on the possibility of centralised testing. But, of course, for many crops Europe would have to be divided into several ecological zones, e.g., continental, maritime, north, south. If there is evidence of, for example, a photoperiodic reaction then testing cannot be confined to only one location. There is, however, no reason why testing should be duplicated at stations like Scharnhorst, Wageningen and Cambridge, all of which are located at about 52°N latitude, unless the breeder requests that a variety be tested under specific conditions, e.g., with respect to diseases. In UPOV two different ways of international cooperation have been worked out: a) totally centralised testing, and b) accepting results from different stations. Under the latter system each station continues testing work and the breeder is free to choose the stations at which his varieties are to be tested.

F. Rasmussen: I am not sure that the breeder will always be free to choose. A country may decide to refer all applications for a certain species to another country for testing. In such a case the breeder would not be able to insist on having a variety tested in a specific country if that country does not have provisions for doing so.

R. Duyvendak: That would only be the case when the country that refers testing to another country is convinced that the resolving power for disstinctness is higher in the other country.

F. Rasmussen: The problem of centralised testing could probably be overcome by having sufficient centres to cover certain ecological regions, and in this way we could save testing in each individual country and rely on testing at one centre per region. This would also imply that all varieties submitted in this region would be subjected to the same tests, and especially to the same criteria and same standards of approval or refusal which has been a problem in the past. We have UPOV guidelines, and for member countries also EEC directives, which tell us how testing is to be performed, but we have no standardized criteria on which to base a decision of approval or refusal, and must therefore accept each country's decision. This can lead to the type of inconsistent decision referred to by Mr. Bøgh, and I think that centralized testing would solve this problem.

K. H. Beuster: There is a danger for different decisions on the same variety in different countries, but we do attempt to co-ordinate our testing methods. We have now only very few cases of conflicting decisions.

J. Y. Blanchet: As mentioned by Mr. Duyvendak, the coefficient of variation for distinctness characters is generally about 10%. This is a consequence of the rules for variety registration. Plant breeders are obliged to use breeding methods primarily aimed at fulfilling these rules, and genetic advance becomes of secondary importance. A second point is that the classification criteria chosen are not always used carefully by the testing authorities. For example, the situation for date of heading as described by Mr. Duyvendak is true for Italian ryegrass, but does not apply to hybrid ryegrasses in which a much greater range in heading date is found between plants. It would be interesting to discuss the criteria of classification in terms of the progress that has been made in breeding methods in recent years.

A. J. Kleinhout: The system described earlier by Mr. Duyvendak does permit the use of other breeding methods, especially the use of heterosis. Instead of giving a detailed description of the variety itself, the registration would be mainly based on the submitted components of the hybrid variety. As a breeder I am pleased that we have this chance.

R. Duyvendak: Indeed I do not belief that a complex variety can be reproduced as a stable variety if it is maintained as one population. Our experience is that when there is a wide range of variation, in ear emergence for example, the variety will shift under the severe selection pressure during the cycles of generative multiplication. Either early plants are harvested and late plants are lost or vice versa. It is not possible to reproduce a wide-bodied variety during two or three multiplication cycles..

F. England: It has always struck me as slightly amusing that if you give a numerical taxonomist two wild populations he will guarantee to find them different, and there seems to be no reason why there should be this difficulty about distinguishing between similar varieties. Under the present system you have to find a detectable difference in at least one character for two varieties to be distinguishable. Using numerical taxonomy differences can be established by certain linear combinations of characters which do not themselves show differences. Are numerical taxonomic methods admissible in variety identificantion, and would they meet the legal requirements? There is one other point I would like to make. With a 10% coefficient of variation you would reasonably expect to use about 12 replications with one trial to detect a 5% significant difference. What degree of replication is, in fact, used for characters such as ear emergence, plant height, etc.

R. Duyvendak: It is not so much the numerical taxonomic method itself but the combination of characters that is interesting here. The wording of the plant variety legislations do not, in my opinion, exclude such a procedure. Any two characters may be combined into one character. To take the simple example of green yield and dry matter content, these two negatively correlated characters combined give dry matter yield. This latter character is often less variable than the two component characters taken separately, and may therefore show a significant difference between two varieties whereas the two components do not. The statistical significance of such a difference can be tested in a multivariate analysis, e.g., Hotellings T^2 test, which is a direct extension of Students t-test. If the aim of a breeding programme has been to break a negative correlation between certain characters, then this is a very useful indication for the registration authorities and should be mentioned in the DUS test application.

D. Aldrich: There was a question earlier about the degree of replication in DUS tests. In the UK we use in any one year 60 plants, 6 replications of 10 plants. Normally a variety is grown in three years which gives a total of 18 replications.

R. Duyvendak: Our reasoning is not quite the same as Dr. England's. We have based our tests on a given number of years, trials, replications and plants. To coordinate this in different countries we have pooled our experience and have agreed to 60 plants per trial, taking into account costs and labour requirements. In most characters a difference that is significant at the 1% level within one trial can normally be expected to be consistent over years. We could distinguish between many more varieties if we doubled or trebled the number of plants per trial, but this would be too expensive.

G. Anderson: With regard to uniformity, Dr. Beuster mentioned that a new variety must be at least as uniform as the old varieties. This is not a high demand, and I understand that it is sufficient. However, in this connection I would just point out that there are three steps leading to the release of a

variety:
1) Registration
2) Inclusion on national or international lists
3) Certification
As a rule the demands for certification are much higher and more difficult
to meet than the DUS requirements. A variety of a cross-fertilizing species
will have a certain variation which can be approved by registration in-
stances. Subsequent certification may be more difficult, as under OECD and
EEC rules only one off-type plant is permitted per 10 m^2. This may be out-
side the present discussion, but I think that we should bear in mind that
certification requirements can be more difficult to attain than the require-
ments for distinctiveness, uniformity and stability for registration pur-
poses.

K. H. Beuster: We have different criteria in DUS and certification tests.
Certification employs the frequency of off-types, i.e., plants more than 3s
from the mean. In homogeneity (DUS) trials we look at three general as-
pects: a) whether a variety is a true variety or whether it contains hetero-
geneous fractions, b) measurements of morphological characters, and c) the
distribution of these measurements.

E. L. Breese: In Aberystwyth we are very conscious of the problems of dis-
tinctiveness and stability, just as much as we are of problems of performance.
We do devote quite a lot of research resources towards solving them. First,
as pointed out by David Wilson earlier, any characteristic that the chemist
or the physiologist can identify for us as potentially useful selection cri-
teria we also consider as possible identifying features, and discuss these
with the NIAB. Secondly, we are also looking into the use of electropho-
retic methods and have identified many isozyme polymorphisms which undoubt-
edly are of high potential here. They offer a very high descrimination be-
tween varieties, but we are still looking at how these isozymes change over
multiplicative generations, i.e., we are considering how well they measure
stability, too. Thirdly, I think that methods of statistical analysis,
multivariate or otherwise, are extremely important and form part anyway of
our selection for performance, and research here will be equally applicable
to identification. The direction and ultimate usefulness of this research
will depend on a continuing dialogue and co-operation between the breeders
and the testing authorities.

G. Julén: It is now time to bring this discussion to an end, although there
is much more to be said on the subject. It seems clear that the represent-
atives for variety testing and control authorities have a strong desire to
assist plant breeders in getting good varieties out to the farmer. We are
all working towards the same goal, even if we look at the problems from dif-
ferent angles. This discussion has been valuable, but it must continue. It
is necessary that problems such as these are dealt with in co-operation be-
tween breeders, control authorities and research instances. The breeders
will find new ways to find new and better varieties, and I am sure that the
control authorities will be able to find ways to distinguesh between these
new varieties.

LIST OF PARTICIPANTS

DENMARK

Bøgh, H.	Danish Plant Breeding Ltd., Børkop
Dennis, B.	Dept. of Crop Husbandry & Plant Breeding, Royal Vet. & Agric. University, Taastrup
Flengmark, P.	Statens Forsøgsstation, Roskilde
Frandsen, K. J.	Rødsvingel 16, Store-Heddinge
Fritsen, H.	Danish Plant Breeding Ltd., Store-Heddinge
Jensen, A.	Tystofte forsøgsstation, Skælskør
Lunde, T.	Danish Plant Breeding Ltd., Store-Heddinge
Johansen, B.	Dept. of Crop Husbandry & Plant Breeding, Royal Vet. & Agric. University, Taastrup
Larsen, C. S.	Danish Plant Breeding Ltd., Store-Heddinge
Mortensen, G.	Dept. of Crop Husbandry & Plant Breeding, Royal Vet. & Agric. University, Taastrup
Nielsen, H. M.	Dept. of Crop Husbandry & Plant Breeding, Royal Vet. & Agric. University, Taastrup
Overgaard, S.	Breeding Station Maribo, Holeby
Petersen, H. L.	Dept. of Crop Husbandry & Plant Breeding, Royal Vet. & Agric. University, Copenhagen
Rasmussen, F.	Sekretariatet for Sortsafprøvning, Tystofte Skælskør
Rasmussen, K.	Danish Plant Breeding Ltd., Børkop
Rasmussen, P.	Statens Forsøgsstation, Roskilde
Ritzema, D.	Danish Plant Breeding Ltd., Børkop
Sebro, C.	Danish Plant Breeding Ltd., Store-Heddinge

FINLAND

Juuti, T.	Hankkija Plant Breeding Institute, Hyrylä

FRANCE

Blanchet, J. Y.	L. Clause S.A., Bretigny-sur-Orge
Chosson, J. F.	Société R.A.G.T., Rodez
Gayraud, P.	Amélioration Fourragere, Provins
Jadas-Hecart, J.	Station d'Amélioration des Plantes Fourrageres, Lusignan

GERMANY

Baukloh, H.	Kleinwanzlebener Saatzucht AG, Einbeck
Berner, P.	Saatzucht Steinach, Steinach

Beuster, K. H.	Bundessortenamt, Scharnhorst, Neustadt
Bugge, G.	Inst. f. Pflanzenbau u. Pflanzenzüchtung, Göttingen
Entrup, E. L.	Landsbergerstrasse 2, Lippstadt
Klinzmann, B	Norddeutsch Pflanzenzucht, Hohenlieth Post Holtsee
Kobabe, G.	Inst. f. Pflanzenbau u. Pflanzenzüchtung, Göttingen
Lichter, R.	Max-Planck-Institut f. Pflanzengenetik, Ladenburg-Rosenhof
Morgner, F.	Hessische Lehr- und Forschungsanstalt, Bad Hersfeld
Scheller, H.	Bayerische Landesanstalt für Bodenkultur und Pflanzenbau, Freising
Ziegenbein, G.	Hessische Lehr- und Forschungsanstalt, Bad Hersfeld

HUNGARY

Bócsa, I.	Agricultural Research Institute, Kompolt

IRELAND

Ahloowalia, B. S.	The Agricultural Institute, Carlow
Ribeiro, M. Valle	The Agricultural Institute, Carlow

ITALY

Ceccarelli, S.	Istituto di Allevamento Vegetale, Perugia
Gnocchi, G.	Istituto Sperimentale Colture Foraggere, Lodi
Lorenzetti, F.	Istituto di Allevamento Vegetale, Perugia
Rotili, P.	Istituto Sperimentale Colture Foraggere, Lodi
Zannone, L.	Istituto Sperimentale Colture Foraggere, Lodi

NETHERLANDS

Baerends, B.	Barenbrug Holland B.V., Arnhem
Bakker, J.	IVRO, Wageningen
Bogaert, C. W. van den	Zelder B.V., Ottersum
Dijk, G. E. van	Foundation for Agricultural Plant Breeding, Wageningen
Dijkstra, J.	Foundation for Agricultural Plant Breeding, Wageningen
Duyvendak, R.	IVRO, Wageningen
Hendrickx, J.	Mommersteeg International B.V., Vlijmen
Kleinhout, A. J.	Barenbrug Holland B.V., Arnhem
Korsten, L. H. J.	Veredelingsbedrijf Cebeco, Lelydtad
Morales, M. T.	Van der Have Plant Breeding Station, Rilland
Post, J.	Foundation for Agricultural Plant Breeding, Wageningen

Regt, A. de	Cebeco-Handelsraad, Vlijmen
Werkman, W. J.	Zwaan & de Wiljes B.V., Scheemda

NORWAY

Aastveit, K.	Institute of Genetics & Plant Breeding, Agricultural College of Norway, Ås
Honne, B. I.	Institute of Genetics & Plant Breeding, Agricultural College of Norway, Ås

PERU

De Cordova, O.	Universidad Agraria, La Molina, Lima

POLAND

Lipinski, J.	Hodowla Buraka Pastewnego, Krakow

SWEDEN

Andersson, G.	Swedish Seed Association, Svalöv
Bosemark, O.	Hilleshög Seed Co., Ltd., Landskrona
Julén, G.	Swedish Seed Association, Svalöv
Jönsson, H. A.	Weibullsholm Plant Breeding Institute, Landskrona
Magyarosi, T.	Swedish Seed Association, Svalöv
Nilsson, I.	Swedish Seed Association, Svalöv
Nilsson, L. B.	Weibullsholm Plant Breeding Institute, Landskrona
Sjödin, J.	Swedish Seed Association, Svalöv

SWITZERLAND

Nüesch, B.	Swiss Fed. Research Station for Agronomy, Zurich
Badoux, S.	Station Federale de Recherches Agronomiques de Changins, Nyon

UNITED KINGDOM

Aldrich, D.	National Institute of Agricultural Botany, Cambridge
Bassi, F.	Hurst Gunson Cooper Taber Ltd., Witham
Breese, E. L.	Welsh Plant Breeding Station, Aberystwyth
Dickie, P. G.	Rothwell Plant Breeders Ltd., Lincoln
England, F. J. W.	Scottish Plant Breeding Station, Roslin
Gowers, S.	Scottish Plant Breeding Station, Roslin
Hill, J.	Welsh Plant Breeding Station, Aberystwyth
MacKay, G. R.	Scottish Plant Breeding Station, Roslin
Norrington-Davies, J.	University of Wales, Aberystwyth
Wilson, D.	Welsh Plant Breeding Station, Aberystwyth