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BREEDING FOR IMPROVED DIGESTIBILITY IN TEMPERATE FORAGE GRASSES

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ABSTRACT

Variability and inheritance of digestibility and yield characters were studied in clonal populations of perennial ryegrass and cocksfoot, and in the F_1 and F_2 progenies derived from crosses between selected clones.

Variation in digestibility is described and the stability of digestibility estimates over harvests and years is discussed. Negative correlations were generally found between digestibility and earliness and between digestibility and yield, but these correlations were not of such a magnitude as to preclude the selection of plant types of different earliness and growth patterns with higher digestibility and dry matter production.

Narrow-sense heritabilities were generally within the range 0.4-0.6 for digestibility and for rate of decrease in digestibility in primary growth. Triple test crosses showed the relative magnitudes of additive and dominance components of genetic variance to vary between harvests, but dominance and epistasis were generally of limited importance to additive gene effects for digestibility.

It is concluded that selection for high yield, high digestibility and a slow rate of decrease in digestibility is a valid approach to breeding for improved digestibility in cocksfoot and perennial ryegrass.

KEYWORDS

Perennial ryegrass, cocksfoot, genetic variability, growth and production character.

INTRODUCTION

In selecting for digestibility the breeder is faced with a number of problems. The availability of additive genetic variation is of major interest, as is the question of the efficiency of individual plant selection. Likewise, the relationships between digestibility and dry matter yield, and between digestibility and such traits as earliness, leafiness and growth type are of importance in terms of correlated selection effects and the possibilities of employing indirect selection methods during preliminary stages of the breeding programme.

The aim of the present investigation was to evaluate the variation and inheritance of digestibility in populations of perennial ryegrass, cocksfoot and meadow fescue adapted to Danish conditions, to obtain information on the structure of the genetic variability in these populations and to determine the relationship between digestibility and important growth and production characters.

This paper reviews some of the results obtained in the perennial ryegrass and cocksfoot populations, and evaluates the possibilities of improving overall digestibility in these two species.

MATERIALS AND METHODS

Parental clones from populations of different origin, chiefly north western European varieties and local populations, were selected on the basis of three digestibility criteria:

- in vitro digestibility
- content of neutral detergent fibres
- the ratio between detergent lignin and acid detergent fibre.

F_1 and F_2 progenies from pair-crosses between clones with high and low values for these criteria were compared in spaced plant trials over two harvest years. The primary growth was sampled at three growth stages from late May to early June, and in a further 2-3 harvests of secondary growth. The behaviour of spaced plants was also compared with plants grown in dense swards (drilled in rows 12 cm apart).

The pepsin-hydrochloric acid method, corresponding approximately to the 2nd stage of the Tilley and Terry (1963) 2-stage method, was used for the routine determination of digestibility in the F_1 and F_2 progeny. The methods of digestibility analysis and the origin of the plant material are described in detail by Frandsen and Fritsen (1982) and Frandsen (1986).

RESULTS AND DISCUSSION

Variation in digestibility

Mean values for digestibility are given in Table 1 for F_1 progeny in the first harvest year. Perennial ryegrass showed

Table 1. Digestibility estimates in F_1 progeny of perennial ryegrass and cocksfoot (pepsinhydrochloric acid method).

Cut and growth stage	Ryegrass mean	Ryegrass range	Cocksfoot mean	Cocksfoot range
1st cut, stage 1	54.1	49.3-57.8	44.4	40.2-47.1
stage 2	53.4	48.7-57.7	37.8	33.7-41.0
stage 3	48.0	45.1-53.1	34.2	29.3-37.6
2nd cut	35.5	33.3-38.6	36.4	30.9-39.4
3rd cut	39.7	35.2-46.3	36.8	34.8-39.8
4th cut	44.9	42.0-47.7	38.6	34.5-42.0

an overall higher digestibility than cocksfoot. Differences between progeny were highly significant in most harvests over both generations and harvest years. Digestibility was highest at the first growth stage and decreased with increasing maturity through the second and third growth stages, increasing again in the 3rd and 4th regrowth cuts.

The rate of decline in digestibility of primary growth was higher in cocksfoot than in perennial ryegrass (Table 2). Decreases in digestibility of a similar magnitude have been reported by Tilley and Terry (1963) and Pritchard *et al.* (1963). Considerable variation was found in the rate of decline, and differences between progenies were in most cases significant, suggesting that selection for improved capacity to maintain a high level of digestibility over a longer period might be a possible approach to breeding for improved digestibility.

Table 2. Rate of decline in digestibility (%D per day).

	Ryegrass mean P	Cocksfoot mean P
F_1 1st harvest year	0.47***	0.73***
F_1 2nd harvest year	0.30***	0.79*
F_2 2nd harvest year	0.36***	0.89 ns
F_2 1st harvest year (swards)	0.67***	0.61*

P: significance levels for family differences.

Stability over harvests and years

One of the problems faced by the plant breeder is to decide which growth stages or harvests to include in an evaluation of digestibility. In the present study progeny x growth stage and progeny x cut interactions were highly significant, particularly in perennial ryegrass. Correlation coefficients between cuts were highly variable, ranging for example, from r = 0.94*** to −0.35* in perennial ryegrass. Heritability estimates and correlations between digestibility and yield likewise showed considerable variability, emphasizing the necessity of basing selection on digestibility analyses carried out over several harvests.

Within growth stages and harvests, estimates of digestibility were fairly consistent when F_1 progenies were compared in different years (Table 3). Improvements made in one year can be expected to be retained in subsequent years.

Table 3. Correlation between digestibility estimates in F_1 progeny in 1st and 2nd harvest years.

Cut & growth stage	Ryegrass	Cocksfoot
1st cut, stage 1	0.61***	0.37*
stage 2	0.86***	0.73***
stage 3	0.53***	0.62***

Spaced plants vs. swards

Analyses of digestibility are frequently performed on spaced plants, particularly in the initial stages of breeding programmes when potential parent genotypes are evaluated. Information on the correlation between digestibility estimates under spaced plantings and under sward conditions is therefore of considerable value to the breeder of forage grasses. A comparison of digestibility estimates of F_2 progenies grown as spaced plants (50 x 50 cm) and in drilled swards showed significant positive correlation coefficients, ranging from 0.64** in cocksfoot to 0.89*** in perennial ryegrass, suggesting that digestibility is probably less affected by competition than traits such as dry matter yield.

Correlation between digestibility and yield

Digestibility has often been found to be negatively correlated with dry matter productivity. Table 4 lists correlation coefficients between digestibility and yield among F_1 progeny in the 1st harvest year. In the majority of cases highly significant negative correlation coefficients were obtained, most pronounced in perennial ryegrass. These correlations were, however, highly variable, and not of such a magnitude as to preclude the simultaneous selection for dry matter yield and digestibility. Shenk and Westerhaus (1982) also found correlations between yield and quality to be inconsistent in magnitude and sign, and a number of workers have likewise concluded that both yield and quality characters can be included in the same selection programme (for example, Ross *et al,* 1970, Tan *et al,* 1978). No consistent correlation pattern was found in either perennial ryegrass or cocksfoot between yield and rate of decrease in digestibility of primary growth.

Table 4. Correlation between dry matter yield and digestibility in F_1 progenies.

Cut & growth stage	Ryegrass	Cocksfoot
1st cut, stage 1	−0.79***	−0.32
stage 2	−0.70***	−0.30
stage 3	−0.60**	−0.18
2nd cut	0.11	−0.39*
3rd cut	−0.10	−0.42**
4th cut	−0.47**	−0.49**

Correlation between earliness and digestibility

Earliness of ear emergence was generally found to be negatively correlated with digestibility (Table 5), although the correlation coefficients varied considerably in size, and

Table 5. Correlation between digestibility and earliness of ear emergence in F_1 progenies.

Cut & growth stage	Ryegrass	Cocksfoot
1st cut, stage 1	−0.56***	−0.68***
stage 2	−0.84***	−0.50**
stage 3	−0.88***	−0.23
2nd cut	0.32*	−0.12
3rd cut	−0.22	0.14
4th cut	−0.36*	−0.17

in some cases a positive relationship was found. The highest correlation was obtained in the primary growth, whereas the effect of earliness on digestibility estimates was less marked in regrowth harvests.

As the progenies were harvested on the same day irrespective of differences in maturity, the close relationship between earliness and digestibility could imply that the significant differences found between progenies may have been due in part to differences in earliness. Mason (1975) found, for example, that most of the variation in both yield and quality in a cocksfoot population could be explained in terms of differences in maturity. In the present study covariance adjustments of digestibility data to eliminate the direct effects of differences in earliness reduced progeny variances to a varying degree, but this reduction was generally of a minor magnitude, and the remaining difference in digestibility between progenies was in most cases still highly significant.

Degree of genetic control

Genetic variation for digestibility has been found in both cocksfoot and perennial ryegrass (Cooper *et al.* 1962, Julen and Lager 1966, Christie and Mowat 1968, Stratton *et al.* 1979). Several studies have shown additive gene effects to be a significant source of variation in digestibility, although Harrison *et al.* (1984) found no evidence of additive genetic variation in nine populations of perennial ryegrass.

Table 6. Estimates of narrow-sense heritabilities derived from parent-progeny regression.

Trait	Ryegrass	Cocksfoot
Earliness	0.82-0.93	0.61-0.71
Dry matter	0.26-0.50	0.21-0.43
Digestibility	0.34-0.57	0.38-0.79
Rate of decline in digestibility	0.64	0.52

Narrow-sense heritabilities, computed from parent-progeny regressions for individual growth stages and harvests, showed considerable variation (Table 6), but there was a fairly close agreement between different estimates. Most values were within the range 0.4-0.6, which is in good agreement with the values reported by Cooper *et al.* (1962), Stratton *et al.* (1979) and others.

The rate of decline in digestibility was also found to be under genetic control, and heritability values of 0.52*** and 0.64*** were obtained in cocksfoot and perennial ryegrass, respectively. The variation found in this character and the predominance of additive genetic effects suggests that selection for a slow rate of decrease in digestibility of primary growth could be exploited as a means of improving overall digestibility.

More detailed information on the nature of genetic variation in the F_1 progenies was obtained from a triple test cross. Twenty cocksfoot and eight perennial ryegrass genotypes were crossed with two testers from each population and with the F_1's between these testers. Epistasis was detected only for dry matter yields in the first growth stage, but not in later harvests, and no evidence of epistasis was found for digestibility. The relative magnitudes of additive and dominance components varied between harvests, but dominance was generally of limited importance compared to additive gene effects for both yield and digestibility.

CONCLUSION

The investigations outlined here have demonstrated that sufficient additive genetic variation is available for digestibility in both perennial ryegrass and cocksfoot to warrant improvement by suitable selection methods. Although digestibility tends to be negatively correlated with dry matter productivity and with earliness, these correlations were found to be inconsistent and not of such a magnitude as to preclude the simultaneous improvement of digestibility and yield. Selection for high dry matter production, high digestibility and a slow rate of decline in digestibility would appear to be a valid approach to breeding for improved quality in both cocksfoot and perennial ryegrass.

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SYMPOSIUM DISCUSSION

Dr H.S. Easton, Grasslands Division, DSIR

The covariance analysis showed that even when you took the earliest variation out, you still had variation in digestibility. Have you any idea if the earliest variation would account for a large part of the unfortunate correlation between digestibility and yield.

Dennis

We have looked at the correlation between the adjusted means of these values for digestibility, adjusted for differences in earliness. We still find a significant correlation. There are real differences between them and not just differences in earliness.

Dr G.W. Burton, USDA, Georgia

How does your stage 2 correlate with your stage 1 for those two cool season grasses?

Dennis

In the parent material we looked at originally we did stage 1, stage 2, and various other analyses. As far as I can remember the correlation between stage 1 and stage 2 was something like 0.8. We felt confident that we could use the stage 2 alone. This has been adopted in the past 4 or 5 years by the majority of Danish plant breeders, for screening breeding material.

Mr G.D. Hill, Lincoln College

We had a gentlemen here from Holland a few years ago who showed that even with the same ryegrass cultivars, there were very significant differences in digestibility by growing them at different temperatures. So with your later cuts which were obviously taken when temperatures were higher, it would be interesting to do a covariance using temperature against digestibility.

Dennis

Yes, it would be interesting to look at — we have not done it.

Dr M.J. Carson, Forest Research Institute

In forestry we would be a bit alarmed by the size of the negative correlation with the two selected traits. How do you plan to select against them?

Dennis

From the correlation diagrams we are getting, it is fairly easy to pick out families that combine high digestibility and high dry matter production, within any area of earliness that we happen to be interested in. One suggestion that has been made by Danish plant breeders is that in fact what we are really interested in is the yield of digestible dry matter. We tried using the values for yield of digestible dry matter but these values seem to be more or less dependent on dry matter production and digestibility seems to have very little effect. The variation in dry matter production is masking the effect of the variation in digestibility. What we have had to do is to look at both traits at the same time and try to combine them in digestible dry matter production.

Carson

That would seem to suggest that dry matter should have a much stronger economic weighting or selection than digestibility?

Dennis

Yes.