THE CONTRIBUTION OF CONVENTIONAL PLANT BREEDING TO FORAGE CROP IMPROVEMENT

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ABSTRACT

In terms of harvested dry matter yield, the genetic improvement of forage crops appears to be progressing more slowly than with grain crops. On average, the rate of genetic gain in forage crops is 4% decade^{-1} compared to 13.5% decade^{-1} for grain crops. This reflects greater complexity with regard to the use and evaluation of forage compared to grain crops. Total annual yield may be of secondary importance to seasonal yield distribution or stress tolerance of forages in some situations. Also the ultimate worth of a forage should be measured in terms of the animal output it produces. This may depend more on its nutritive value than its yield. In future, the development of traditional forage breeding methods is likely to involve further widening of gene pools across species boundaries and use of new methods for plant evaluation and multitrait selection to tailor forages to meet animal needs more precisely. Greater control over recombination may become possible and heterosis should be more exploitable through the use of male sterility and apomixis. Traditional breeding methods will increasingly interact with techniques based on novel biotechnology. To exploit this interaction to its full potential, it is essential that traditional breeding experience and expertise is sustained.

KEYWORDS

Genetic gain, yield, nutritive value, stress tolerance, genetic resources, selection, heterosis.

INTRODUCTION

Often during the past decade, plant breeders have been called upon to justify the value of their activities. This is partly in response to world-wide pressure on agricultural research and development funding in the public sector, rationalization in the private sector and a need to ascertain the financial return that may accrue from investment in expensive new biotechnology. It is not easy to isolate the value of genetic improvement in crops from the significant increases in agricultural production which have occurred during the past 50 years. Generally it is considered that cultivar improvement accounts for between 30% and 50% of the observed increases in agricultural output over a range of crops. However, this broad partitioning of gain may underestimate the contribution that plant breeding has made. Improved management practices often demand that crops have specific attributes. The 'Green Revolution' of the 1970's depended on widening the availability of fertilisers, pesticides and modern agricultural techniques to increase the output of developing countries. To benefit from these improved management practices, semi-dwarf cultivars of wheat and rice with high yield potential were required. These were developed by breeders at Institutes such as CIMMYT in Mexico and IRRI in the Philippines. As a result of the combined efforts of breeders and agronomists, agricultural production in the developing countries increased by 33% between 1972 and 1982 (Avery, 1985). The plant breeding strategies adopted to achieve these gains were based on traditional methods involving plant collection, assessment of genetic resources, selfing and/or crossing according to various mating schemes, selection based on phenotypic measurements together with some progeny testing and finally regeneration through seed or vegetative propagation. Some novel techniques such as polyploidy and mutagenesis were also used. In the future, breeding programmes will also exploit the ongoing revolution in biotechnology with the adoption of methodologies based on tissue culture, genetic transformation and DNA markers. These will make significant contributions to breeding progress but will depend on an underlying foundation of traditional methods to realise their full potential. This paper considers past achievements of conventional plant breeding with regard to the improvement of forage crops and assesses the contribution it will make to forage breeding in the future.

PROGRESS IN BREEDING FORAGE CROPS

Total harvested yield of dry matter: Rates of genetic improvement in total annual yield of dry matter due to plant breeding in the 20th Century have been calculated for a number of forage and grain crops (Table 1). It is clear that the average rate of genetic gain for forage crops (4% decade^{-1}) is lower than for grain crops (13.5% decade^{-1}). This has been attributed to:

1. the shorter breeding cycle of annual grain crops compared to perennial forage crops,

2. the major contribution that changing harvest index has had on increasing grain yield without increasing whole plant productivity by reducing vegetative plant parts (Austin et al., 1980; Russell, 1991). In forage crops, because virtually all the above ground production is harvested, changes in harvest index are limited to leaf and stem versus root growth,

3. the exploitation of heterosis, as in breeding hybrid maize (*Zea mays*), is only used indirectly in producing synthetic cultivars of forage crops, and

4. the importance of traits other than total annual dry matter yield in forage crops.

The information in Table 1 also suggests that advances in the dry matter yield of forage crops are more evident in countries which have less stressful climates. For example, improvement in perennial ryegrass (*Lolium perenne*) yield appears greater in the oceanic climate of the UK and Belgium than in the Mediterranean climate of France or Italy. White clover (*Trifolium repens*) shows greater improvement in yield in New Zealand and South Africa than it does in Czechoslovakia or Spain. It has been argued (van Wijk and Reheul, 1991; van Wijk et al., 1993) that total dry matter yield is a sufficient measure of all factors influencing the growth of forages. However in assessing the value of forage cultivars, particular attributes may have greater importance than their effect on total dry matter yield would suggest. Therefore just to consider genetic improvement in total dry matter yield of forage crops can seriously underestimate breeding progress. Also because many forage crops are perennial, they have value in providing a stable ground cover which helps to prevent soil erosion and protects soil water against pollution (industrial and agricultural) and also excessive evaporation resulting in salinity problems. High yield may be of secondary importance in this context and may even be disadvantageous.

Distribution of yield: Yield of forage crops must be considered in relation to animal requirements. The distribution of yield within a year is more relevant in determining the number of animals that can be supported by a grassland system than the total annual yield. There have been few attempts to calculate the value of seasonal forage production although Doyle and Elliot (1983) have indicated a possible approach. This kind of information can be used to assess the true

value of increases in forage production and to determine breeding priorities or construct selection indices (Humphreys, 1991a). Often successful breeding depends on correctly identifying limiting factors which must be overcome to release constraints on seasonal productivity. There may be a lack of persistency, due to poor tolerance of environmental stresses, such as drought, cold, pests, diseases and even the grazing animal, or a lack of seasonal growth potential e.g. in winter, early spring or mid-summer. In many grazed grasslands the ability of swards to recover from the initial flush of primary reproductive growth and produce rapid secondary growth of high nutritive value, is vital to support reasonable stocking rates without overgrazing. In the absence of conserved feed or concentrates, stocking rates are controlled by troughs in the seasonal pattern of sward growth rather than the peaks which tend to dominate overall yields. This is particularly true for many tropical livestock systems but also applies to temperate grassland systems in which mid-summer or winter growth is limiting. Humphreys (1984) demonstrated that improved consistency in seasonal yield of perennial ryegrass could be achieved by crossing early and late flowering plants from different parts of Europe. Wilkins (1985) used similar crosses to improve spring yield without having to impose an early heading date in perennial ryegrass. Selection for stolon survival characteristics improved the overwintering ability and spring growth of white clover (Collins and Rhodes, 1995). As breeders try to get closer to the genotype in their efforts to improve phenotype, the breakdown of total annual yield into component effects will help to simplify genetic analysis and assist in understanding underlying genetic control through interpretation of Quantitative Trait Loci (QTL) expression.

Stress Tolerance: In breeding for marginal conditions, yield is of secondary importance to adaptation (Tigerstedt, 1994) but there is often a negative relationship between these traits. Compared to an unselected control line, the relative dry matter yield of *Dactylis glomerata* plants selected for high yield decreased over a 7-yr period at an average rate of 1.8% yr[-1] in a Norwegian pasture trial (Aastveit, 1985). This was attributed to the impact of natural selection for vegetative fitness with a significant decline in yield occurring during the second year of the experiment.

There have been notable achievements in breeding forages for stress environments, for example in *Agropyron* sp. (Barker and Kalton, 1989) and in *Medicago sativa* (Hill et al., 1988; Falcinelli et al., 1994). However it is of constant concern to breeders (Humphreys 1991b; 1994b) that in official cultivar recommendations sufficient weight is not given to adaptive traits compared to yield under optimum conditions. Cultivar testing is often carried out in non-marginal conditions and usually only over 2 to 3 yr. This places little emphasis on long term persistency under stressful conditions, which may reduce the availability of suitably adapted material to farmers in marginal areas and may ultimately lead to the loss of valuable germplasm (Falcinelli et al., 1994).

Animal Production: The overall measure of success of forage breeding should be measured in terms of the quantity and quality of animal output (milk, meat and wool). Unfortunately these assessments are limited due to restrictions on the funding of animal trials. Animal production can be related to differences in the digestibility of forages in terms of metabolisable energy requirements (ME). A difference of 13% in DOMD (dry organic matter digestibility) of grass can produce a difference of 2MJ ME kg^{-1}. It is estimated that this could result in a difference of as much as 9 kg (45%) in daily milk yield, 0.5 kg (67%) in beef daily gain and 100 g (50%) in lamb daily gain (Holmes, 1989). Clark and Wilson (1993) predicted that a 5% increase in pasture digestibility without loss of yield would increase gross margins of a dairy farm by 5.7%.

In a survey of data from European animal performance trials up to 1984, Walters (1984) estimated that a 1% increase in digestibility on average produces a 5% increase in animal output (milk or meat). Wilman et al. (1992) demonstrated an increase of 0.6 kg d^{-1} in milk production with cows grazing Italian ryegrass (*Lolium multiflorum*) cultivars with superior stem digestibility. Increases in cattle liveweight gains of between 35% and 60% have been achieved by improving digestibility in *Cynodon dactylon* (Burton et al., 1967; Hill et al., 1993) and *Setaria sphacelata* (Evans and Hacker, 1977). Increased leafiness and a dwarfing gene in *Pennisetum americanum* increased cattle liveweight gain by 20% (Burton et al., 1969).

As with adaptation to stress, breeding for improved feeding value may result in a loss of some yield. This may not be important in terms of animal output. In a study of lamb production from contrasting perennial ryegrass cultivars, Munro et al. (1992) showed that the highest yielding grass cultivar produced the lowest lamb output. Their data also indicated that, although digestibility is of central importance, it is not the only forage quality factor governing animal output. The feeding value of forage depends on its chemical constituents. For example the water soluble carbohydrate (WSC) content of grass affects digestibility, palatability, intake, efficiency of digestion and N utilisation by ruminants. Ryegrasses containing 19% and 13% WSC (averaged over 3 yr) supported lamb production of 814 and 700 kg ha^{-1} yr^{-1} respectively (Davies et al., 1989,1991). WSC content is also a major factor in conferring a nutritive quality advantage on tetraploid ryegrasses which has resulted in improved animal production and an increased popularity of tetraploid cultivars in Europe (Reed, 1994). Breeding programmes have also been successful in increasing the mineral content of forage (Moseley and Baker, 1991) and in removing anti-quality factors such as alkaloids in reed canarygrass (*Phalaris arundinacea)* (Marten et al., 1981; Barker and Kalton, 1989). These objectives are important to improving animal health and welfare and hence productivity. For example, lambs grazing a low alkaloid, tryptamine-carboline-free reed canarygrass had up to 95% more liveweight gain d[-1] compared to those grazing commercial cultivars (Marten et al., 1981). Many tropical forage species are virtually undeveloped in terms of improvements in nutritive quality. They present breeders with considerable challenges to improve digestible energy and protein without reducing environmental stress tolerance and resistance to pests and diseases.

DEVELOPING FORAGE CROP BREEDING INTO THE FUTURE

Genetic resources: Domestication of forage crops is relatively recent with serious breeding to improve landraces commencing early in the 20th Century (Harlan, 1992). The collection and exploitation of natural variation from ecotypes and landraces has been important in improving temperate forage grasses in Europe (Davies, et al. 1973) and also many warm-season grasses in the USA (Burton, 1989a). It continues to be important in many forage improvement programmes including temperate grasses and white clover for Europe (Tyler, 1988; Rhodes et al., 1994); alfalfa for North America (Barnes et al., 1988) and the Mediterranean (Falcinelli et al. 1994) and timothy (*Phleum pratense*) for Scandinavia (Helgadottir and Bjornsson, 1994). Novel combinations of traits can be found in specific ecotypes. For example, perennial ryegrass from the Zurich Uplands in Switzerland has rapid spring growth uniquely combined with good winter hardiness and a high water WSC content (Tyler and Chorlton, 1979; Humphreys, 1989) and white clover from the same region has similar characteristics (Collins and Fothergill, 1993; Collins and Rhodes, 1995). It seems likely that these traits are associated with adaptation

to survive prolonged snow cover and to grow rapidly in spring. As breeders attempt to build a greater range of improvements into their cultivars, the possibilities of finding suitable combinations of traits within ecotypes are limited. Also ecotypes often contain disadvantageous traits, such as disease susceptibility (Hides and Wilkins, 1978) which must be removed or negated by breeding. Therefore breeders must consider creating new gene pools by intercrossing divergent genetic resources. In perennial ryegrass, crossing early and late heading plants from different parts of Europe allowed successful selection for improved consistency of seasonal yield and improved nitrogen use efficiency (Humphreys, 1984; Wilkins and Lovatt, 1989). Wide crossing has also been used very effectively in the improvement of bermudagrass (*Cynodon dactylon*) for winterhardiness and digestibility (Burton, 1989a).

Breeders can extend the gene pool available to them by crossing outside species boundaries and using induced polyploidy (Humphreys, 1991d). Successful tetraploid hybrids have been produced between Italian and perennial ryegrass which show flexible response to cutting and grazing managements (Jones and Humphreys, 1993). Tetraploid hybrids between meadow fescue (*Festuca pratensis*) and ryegrass species have extended the ability of grasses with good early growth and high nutritive value to cope with extremes of temperature and moisture (Thomas and Humphreys, 1991; Joks et al., 1994). Good agronomic potential has also been demonstrated in tetraploid hybrids between *L. multiflorum* and *F. arundinacea* var. *glaucescens* (Jadas-Hecart et al., 1992) and octoploid hybrids between *L. multiflorum* and *F. gigantea* have potential to improve summer growth (Humphreys et al., 1989). In *Dactylis*, good yield was combined with high digestibility in hybrids between tetraploid *D. glomerata* subsp. *glomerata* and *D. glomerata* subsp. *marina* (Borrill et al., 1974). An induced tetraploid of *Agropyron cristatum* was crossed with a natural tetraploid of *A. desertorum* to produce the crested wheatgrass cv. 'Hycrest' (Asay et al., 1985).

Interspecific hybrids also provide genetic bridges to allow targeted introgression of genes between species. For example, improved seed production characteristics and rhizome production in white clover has been achieved by introgression from *T. ambiguum* and *T. nigrescens* (Meredith et al., 1995; Marshall et al., 1995). In *Dactylis glomerata* cultivars have been released which contain genes for improved seasonal growth derived from the diploid subspecies *lusitanica* (Rumball, 1982). Introgressive breeding programmes in the *Lolium/Festuca* species complex have been successful in transferring good summer growth from *F. pratensis* into *L. perenne* (Humphreys, 1993), drought tolerance from tall fescue into Italian ryegrass (Humphreys et al., 1993; Thomas et al., 1995) and winter hardiness from *F. pratensis* into ryegrasses (Humphreys and Honne, 1995). There are reports that viable hybrids can be produced between *Dactylis* and *Lolium/Festuca* species which unite the gene pools of the two major polyploid complexes found in humid temperate grasslands (Oertel et al., 1996). Also hybrids with some fertility have been produced between *Lolium* and *Secale* (M. K. Pavlova, personal communication). Dewey (1984) has established genome relationships between many of the perennial Triticeae, including important rangeland species, and has indicated relationships with major arable species. Recent information on synteny between Graminaceous species (Moore et al., 1995) and increasing ability to use genetic transformation techniques considerably widens the gene pool available to breeders to meet the demands of a changing world.

Although new technology may be used to create and introduce new genetic variation into breeding pools much of its subsequent use will be by conventional breeding. The range of genetic variation available in forage crops does not appear to be limiting, but the need to obtain and maintain desirable combinations of genes in stable and well balanced genotypes is challenging. New developments in the control of gene recombination will be of great assistance in achieving this.

Selection methods: Because many forage species are perennial outbreeders, some form of recurrent selection scheme is often used prior to creating a synthetic cultivar based on a variable number of parents. This is an effective way of concentrating desirable genes in an outbreeding gene pool to give sufficiently uniform cultivars based on diverse genetic resources. Oram and Culvenor (1994) consider that recurrent selection in sets of half-sib families selected under spaced plant and realistic sward conditions will continue to be important for *Phalaris* improvement in Australia. Burton (1989a) was very successful in improving yield in Pensacola bahiagrass (*Paspalum notatum*) by recurrent restricted phenotypic selection (RRPS) which increased plant yield by 16% over 15 selection cycles. Similar advances were made by selecting within the progeny of a 2-clone F_1 hybrid (Burton, 1989b) demonstrating that a considerable reserve of genetic variation exists in these species. Humphreys (1995) also indicated good potential for multitrait recurrent selection in the progeny of 2-clone F_1 hybrids from wide crosses of perennial ryegrass and Wilkins (1991) has revealed large amounts of genetic variation for yield in the progeny of early x late perennial ryegrasses.

Phenotypic recurrent selection is the predominant method in breeding white clover and alfalfa (Williams, 1987; Hill et al., 1988) and there is no reason to suppose that this strategy will change in the near future as it is evident that steady progress can be maintained. This will be aided by the development of better screening and evaluation techniques relevant to user needs. Examples include the measurement of biochemical traits, such as enzyme activities associated with carbon and nitrogen assimilation and partitioning, and the use of genetic markers such as RFLPs and AFLPs for marker assisted selection. The identification and use of appropriate companion grasses to test forage legumes in sward conditions will be important in maintaining competitive ability and assessing the value of nitrogen fixation. Evaluation using animals is also important for the realistic assessment of forage legume performance (Evans et al., 1992).

A major challenge in breeding forage crops is to tailor them more precisely to meet animal needs. Animal nutritionists are urging plant breeders to consider the balance between energy and protein supply at various stages of ruminant digestion in addition to overall digestibility (Beever, 1993; Beever and Reynolds, 1994). Humphreys (1994a) indicated that appropriate genetic variation exists to modify the protein and carbohydrate characteristics of ryegrass. Improvements in Near Infrared Reflectance spectroscopy (NIR) technology (Aastveit and Marum, 1993) should help breeders to evaluate a wider range of forage quality characteristics more rapidly, including those associated with the quantity and quality of animal output (such as the yield and composition of milk fat and protein).

As the range of selection criteria facing breeders increases, it is inevitable that forms of multitrait selection will have to be employed to maintain an optimum balance between components of yield, quality and persistence. Godshalk et al. (1988) demonstrated the effectiveness of index selection for forage yield and quality in switchgrass (*Panicum virgatum* L.) while Humphreys (1995) indicated the potential of a selection index based on 10 traits to identify breeding populations with good potential to meet a range of breeding objectives in perennial ryegrass. Ravel and Charmet (1996) showed that a multisite recurrent selection index can produce useful improvements in a range of perennial ryegrass traits. In future the incorporation of

genetic markers into selection indices should help to increase the efficiency of multitrait selection, to avoid undesirable correlated responses and to separate components of specific and general adaptation.

Cultivar construction: Synthetic cultivars have been the main product of breeding in most of the outbreeding forage species. These only make limited use of the heterosis that is apparent when wide crosses are made between diverse gene pools (Humphreys, 1991c). Therefore much of the progress achieved so far in breeding forage crops has relied on the accumulation of additive gene effects with little exploitation of non-additive genetic variation. It is clear that significant improvements in many forage crops could be achieved by more controlled use of hybridity. This strategy is having a large impact on rates of breeding progress in maize (Russell, 1991) and is likely to be an important feature in breeding forage sorghums (*Sorghum* spp. and derived hybrids) for the tropics (Duncan, 1996). Vegetative propagation has been used effectively to exploit heterosis in some perennial forage species such as bermudagrass (Burton, 1989a). Alternatively, polyploidy has been used to stabilize hybrids between closely related ryegrass species. Breese et al. (1981) showed that tetrasomic inheritance, together with some preferential pairing between homologous chromosomes, could reduce genetic segregation sufficiently in tetraploids to maintain hybridity in quantitative traits through four or five generations of seed production. A wide range of tetraploid hybrid ryegrasses have been produced (Jones and Humphreys, 1993) which are proving to be very successful. It may also be possible to impose sufficient control of chromosome pairing in tetraploid hybrids between diverse parents within the same species to allow commercial seed production from F_1s. Preferential pairing of just 34% is sufficient to maintain at least 50% hybridity at seven unlinked loci over six generations compared to less than 1% hybridity in diploid hybrids (Breese et al., 1981). Therefore at the diploid level rapid exploitation of heterosis must depend on some form of pollination control through male sterility or the manipulation of self-incompatibility systems (Hayward, 1988), or by the controlled use of apomixis.

Apomixis is asexual reproduction through seeds. Instead of sexual reproduction through the fusion of male and female gametes with reduced sets of chromosomes, an embryo is formed from an unreduced mother plant cell. It is a feature of a number of polyploid tropical grasses including species of *Brachiaria, Paspalum* and *Cenchrus*. In these species the breeding challenge is often to induce some degree of sexual reproduction so that recombination can generate novel genotypes. Burton (1989a) crossed tetraploid apomictic plants of *Paspalum notatum* with chromosome doubled maternal plants from related sexual diploid species. Out of the highly variable progeny produced by these crosses he was able to select new cultivars with improved winter hardiness. The genetic control of apomixis in tropical forages is now being elucidated more precisely (Hayward, 1995) and provides an example of active interaction between traditional and novel breeding technologies. Whether relevant genes for apomixis can be expressed in diploid temperate forage species remains to be seen.

If suitable methods of hybrid production become available for forage species, then inbreeding is likely to assume greater importance. Inbreeding can reveal useful recessive genetic variation and can be used to remove undesirable recessive genes (genetic load) from parent plants. Partly inbred plants have been used successfully in the production of synthetic cultivars of a number of forage species, particularly alfalfa (Rotili, 1991). However in order to make full use of specific as well as general combining ability, more controlled

systems of hybrid production are necessary. Alternatively if dispersed dominant genes are a major cause of heterosis, it may be possible to produce recombinant inbred lines which have similar performance to F_1 hybrids. The availability of fertile inbred lines in some forage species (e.g. ryegrass and white clover) allows the feasibility of this approach to be assessed. Clonally developed 'artificial seeds', derived from tissue culture, offer another approach if developing technology can reduce production costs to economic levels.

INTERACTION OF TRADITIONAL BREEDING METHODS WITH NEW TECHNOLOGY

Apart from the work on apomixis discussed previously, there are several other areas of active interaction between traditional and novel breeding technology. Exploitation of heterosis in hybrid breeding has benefited from the development of new male sterility systems to control pollination and the use of DNA markers to determine genetic distances between potential parents. Anther culture is being used to produce homozygous lines prior to hybrid or recombinant inbred line development. Genetic maps are being developed in *Lolium* and *Festuca* species and synteny is being established between forage grasses and the genomes of other important Graminaceous crops such as rice (*Oryza* spp.), wheat (*Triticum* spp.), barley (*Hordeum vulgare*) and maize (Moore et al., 1995). Mapping of forage legume species is not very advanced, although some information is available for *Medicago* and *Stylosanthes* and it remains to be seen whether linkage groups are conserved in relation to grain legumes. Genetic maps can be used to locate QTL and careful choice of QTL has potential to speed up breeding progress and minimise undesirable correlated selection responses in marker assisted multitrait selection and introgression. The physical location of introgressed segments and possibly individual genes on chromosomes, using fluorescence in-situ hybridisation (FISH), has been demonstrated in *Festuca/Lolium* (Thomas et al., 1995) and similar work is progressing with *Trifolium* hybrids (Meredith et al., 1995).

Although natural ecotypic variation has traditionally provided the basic raw material for forage breeding programmes, developments in cell culture and transformation techniques provide opportunities to access novel sources of variation. The introduction of novel genes via *Agrobacterium* has been demonstrated in *Lotus, Medicago* and *Trifolium*, and by electroporation, use of polyethylene glycol (PEG) or particle bombardment in *Dactylis, Festuca, Poa* and *Lolium*. However, novel gene expression must be stable and inherited in a predictable way to be useful in cultivar production. Further information is required concerning gene dosage effects, gene silencing and transmission through ovules and pollen. "Trade-offs" in whole plant performance arising from genetic manipulation may be compensated for by using appropriate genetic backgrounds in breeding programmes based on traditional methods. The potential to incorporate new technology into breeding programmes is increasing rapidly but breeders have difficult decisions to face concerning what is most appropriate to their needs in terms of objectives and breeding efficiency. In many tropical perennial forage species which are relatively undeveloped, considerable benefits could result simply from the rapid exploitation of natural variation. Improved technology for the evaluation of existing variation relevant to meeting the nutritional requirements of animals, without jeopardizing tolerance of climatic and biotic stresses, is more likely to be of immediate value than novel gene technology. The exception is probably the genetic control of apomixis and its interaction with environmental effects. The creation of new genetic variation in apomictic forage species such as *Brachiaria* and *Cenchrus* would be of considerable benefit in combating disease and pest problems associated with large scale cultivation of monocultures (e.g. spittle

bug in S. America).

CONCLUSIONS

From the information reviewed above, it is apparent that forage crops have been significantly improved in a variety of ways. However this is not always evident in terms of total dry matter yield and is better considered in relation to the sustainability of animal output.

Experience is essential in making decisions on breeding forage crops. Few crops are more complex in terms of breeding objectives and strategies than forages. Their importance in terms of agricultural output and general environmental protection is often undervalued in relation to arable crops. This has led to a worrying world-wide decline in forage crop breeding and the associated expertise necessary to exploit effectively new breeding technology. The application of young minds to the challenges which lie ahead to improve the genetic potential of the grasslands of this world should be encouraged at every opportunity.

REFERENCES

Aastveit, K. 1985. Genetic aspects of climatic adaptation in plants. Pages 23-42 *in* A Kaurin, O. Juntilla and J. Nilsen, eds. Plant Production in the North. Norwegian University Press, Oslo.

Aastveit A.H. and P. Marum. 1993. Near-infrared reflectance spectroscopy: Different strategies for local calibrations in analyses of forage quality. Appl Spectrosc. **47:** 463-469.

Allerit, R. 1986. Espèces fourragères perennes: progrès réalisés depuis 25 ans, appréciés à travers l'expérimentation officielle. Fourrages **107:**17-33.

Aldrich, D.T.A. 1987. Developments and procedures in the assessment of grass varieties at NIAB 1950-87. J. Natl.. Inst. Agric. Bot. **17:** 313-327.

Asay, K.H., D.R. Dewey F.B. Gomm, D.A. Johnson and J.R. Carlson. 1985. Registration of 'Hycrest' crested wheatgrass. Crop Sci. **25:** 368-369.

Austin, R.B., J. Bingham, R.D. Blackwell, L.T. Evans, M.A. Ford, C.L. Morgan and M. Taylor. 1980. Genetic improvements in winter wheat yields since 1900 and associated physiological changes. J. Agric. Sci. **94**: 675-689.

Avery, D. 1985. U.S. farm dilemma: the global bad news is wrong. Science **230:** 408-412.

Barker, R.E. and R.R. Kalton. 1989. Cool-season forage grass breeding: Progress, potentials and benefits. Pages 5-20 *in* Contributions from Breeding Forage and Turf Grasses, CSSA Special Publication no. 15, Madison, Wisconsin, USA.

Barnes, D.K., B.P. Goplen, and J.E. Baylor, 1988. Highlights in the USA and Canada. Pages 1-24 *in* A.A. Hanson, ed. Alfalfa and alfalfa improvement. Agronomy Monograph no. 29. ASA-CSSA-SSSA, Madison, WI, USA.

Beever, D.E. 1993. Ruminant animal production from forages: present position and future opportunities. Proc. XVII Int. Grass. Cong., New Zealand and Australia pp 535-542.

Beever, D.E. and C.K. Reynolds. 1994. Forage quality, feeding value and animal performance. Pages 48-60 *in* 't Mannetje and J. Frame, eds. Grassland and Society. Proc. 15th General Meeting of the European Grassland Federation, Wageningen, The Netherlands.

Borrill, M., B.F. Tyler and M. Kirby. 1974. Progress in breeding digestible hybrid cocksfoot. Rep. Welsh Plant Breed. Stn for 1974, Aberystwyth, pp 13-15

Breese, E.L., E.J. Lewis and G.M. Evans. 1981. Interspecies hybrids and polyploidy. Philos. Trans. R. Soc. Lond. Biol. Sci. **B 292:** 487-497.

Burton, G.W. 1989a. Progress and benefits to humanity from breeding warm-season forage grasses. Pages 21-29 *in* Contributions from Breeding Forage and Turf Grasses, CSSA Special Publication no. 15, Madison, Wisconsin, USA.

Burton, G.W. 1989b. Great diversity for increased yield within narrow grass populations. Proc. XVI Int. Grass. Cong., Nice, France, pp 301-302.

Burton, G.W., R.H. Hart and R.S. Lowrey. 1967. Improving forage quality in Bermudagrass by breeding. Crop Sci. **7:** 329-332.

Burton, G.W., W.G. Monson, J.C. Johnson, R.S. Lowrey, H.D. Chapman, W.H. Marchant. 1969. Effect of the d2 dwarf gene on the forage yield and quality of pearl millet. Agron. J. **61:** 607-612.

Clark, D. and J.R. Wilson. 1993. Implications of improvements in nutritive value on plant performance and grassland management. Proc. XVII Int. Grass. Cong., New Zealand and Australia, pp 543-550.

Collins, R.P. and M. Fothergill. 1993. A new white clover cultivar of potential importance for cool areas of Europe. Pages 289-294 *in* Crop adaptation to cool, wet, climates. D. Wilson, H. Thomas and K. Pithan eds. Cost 814 Workshop, Aberystwyth.

Collins, R.P. and I. Rhodes. 1995. Stolon characteristics related to winter survival in white clover. J. Agric. Sci. **124:** 11-16.

Davies, W.E., B.F. Tyler, M. Borrill, J.P. Cooper, H. Thomas and E.L. Breese. 1973. Plant introduction at the Welsh Plant Breeding Station. Rep. Welsh Plant Breed. Stn for 1972, Aberystwyth, pp 143-162.

Davies, D.A., M. Fothergill and D. Jones. 1989. Assessment of contrasting perennial ryegrasses, with and without white clover, under continuous sheep stocking in the uplands. 1. Animal production from the grass varieties. Grass Forage Sci. **44:** 431-439.

Davies, D.A., M. Fothergill and D. Jones. 1991. Assessment of contrasting perennial ryegrasses, with and without white clover, under continuous sheep stocking in the uplands. 3. Herbage production, quality and intake. Grass Forage Sci. **46:** 39-49.

Dewey, D.R. 1984. The genomic system of classification as a guide to intergeneric hybridization with the perennial Triticeae. Pages 209-279 *in* J.P. Gustafson, ed. Gene manipulation in plant improvement. Plenum Publ., New York.

Doyle, C.J. and J.G. Elliott. 1983. Putting an economic value on increases in grass production. Grass Forage Sci. **38:** 169-177.

Duncan, R.R. 1996. Breeding and improvement of forage sorghums for the tropics. Adv. in Agron. **57:** 161-185.

Evans, D.R., T.A. Williams and S.A. Evans. 1992. Evaluation of white clover varieties under grazing and their role in farm systems. Grass Forage Sci. **47:** 342-352.

Evans, T.R. and J.B. Hacker. 1977. Growth of cattle grazing six tropical grasses. CSIRO Australia, Division of Tropical Crops and Pastures annual report, 1976-77, p. 26.

Falcinelli, M., L. Russi, V., Negri and F. Veronesi. 1994. Variation within improved cultivars and landraces of lucerne in Central Italy. Euphytica **77:** 199-203.

Godshalk, E.B., D.H. Timothy and J.C. Burns. 1988. Effectiveness of index selection for switchgrass forage yield and quality. Crop Sci. **28:** 825-830.

Harlan, J.R. 1992. Origins and processes of domestication. Pages 159-175 *in* G.P. Chapman, ed. Grass Evolution and Domestication, Cambridge University Press, UK.

Hayward, M.D. 1988. Exploitation of the incompatibility mechanism for the production of F_1 hybrid forage grasses. Euphytica **39:** 33-37.

Hayward, M.D. 1995. The EU/STD Programme, 'The Manipulation of Apomixis for the Improvement of Tropical Forages. Page 53 *in* Harnessing Apomixis, A New Frontier in Plant Science, College Station, Texas, USA.

Helgadottir, A. and H. Bjornsson. 1994. Cooperative breeding for the northern marginal areas. Euphytica **77:** 221-230.

Hides, D.H. and P.W. Wilkins. 1978. Selection for resistance to ryegrass mosaic virus and crown rust (*Puccinia coronata* Corda) in Italian ryegrass populations. J. Br. Grassl. Soc. **33:** 253-260.

Hill, G.M., G.W. Burton and P.R. Utley. 1993. Forage quality and steer performance on Tifton 78 and Coastal bermudagrass pastures. Proc. XVII Int. Grass. Cong., New Zealand and Australia, pp 870-872.

Hill Jr., R.R., J.S. Shenk and R.F. Barnes. 1988. Breeding for yield and quality. Pages 809-825 *in* A.A. Hanson, ed. Alfalfa and alfalfa improvement. Agronomy Monograph no. 29. ASA-CSSA-SSSA, Madison, WI, USA.

Holland, J.B. and E.T. Bingham. 1994. Genetic improvement for yield and fertility of alfalfa cultivars representing different eras of breeding. Crop Sci. **34:** 953-957.

Holmes, W. 1989. Grazing management. Pages 130-171 *in* W. Holmes, ed. Grass - its production and utilisation, British Grassland Society, Blackwell Scientific Publications, UK.

Humphreys, M.O. 1984. Breeding for seasonal consistency in perennial ryegrass for pastures. Pages 57-70 *in* U. Simon ed. Development, construction and multiplication of fodder crop varieties. Proc. 12th Eucarpia Fodder Crops Section Meeting, Freising-Weihenstephan, Germany.

Humphreys, M.O. 1989. Water-soluble carbohydrates in perennial ryegrass breeding. I. Genetic differences among cultivars and hybrid progeny grown as spaced plants. Grass Forage Sci. **44:** 23-236.

Humphreys, M.O. 1991a. A multivariate approach to grass breeding. Pages 41-42 *in* A.P.M. den Nijs and A. Elgersma, eds. Fodder crops breeding: Achievements, novel strategies and biotechnology. Proc. 16th Eucarpia Fodder Crops Section Meeting, Pudoc, Wageningen.

Humphreys, M.O. 1991b. Achievements and prospects in fodder crops breeding - a workshop report. Page 75 *in* A.P.M. den Nijs and A. Elgersma, eds. Fodder crops breeding: Achievements, novel strategies and biotechnology. Proc. 16th Eucarpia Fodder Crops Section Meeting, Pudoc, Wageningen.

Humphreys, M.O. 1991c. A genetic approach to the multivariate differentiation of perennial ryegrass (*Lolium perenne* L.) populations. Heredity **66:** 437-443.

Humphreys, M.O. 1991d. The value of polyploidy in breeding hybrid grasses. Pages 37-44 *in* F. Veronesi, S. Bullitta and S. Caredda eds. Ploidy and chromosome manipulation in forage breeding. Proc. 17th Eucarpia Fodder Crops Section Meeting, Alghero, Italy.

Humphreys, M.O. 1993. Genetic resources for improved climatic adaptation within the ryegrass/fescue complex. Proc. COST 814 Workshop, Aberystwyth, pp 281-287.

Humphreys, M.O. 1994a. Variation in the carbohydrate and protein content of ryegrasses: Potential for genetic manipulation. Pages 165-172 *in* D. Reheul & A. Ghesquiere, eds. Breeding for Quality. Proc. 19th Eucarpia Fodder Crops Section Meeting, Brugge, Belgium.

Humphreys, M.O. 1994b. Why should we breed for marginal conditions - a workshop report. Pages 315-318 *in* O.A. Rognli, E. Solberg and I. Schjelderup, eds. Breeding fodder crops for marginal conditions. Proc. 18th Eucarpia Fodder Crops Section Meeting, Norway, Kluwer, The Netherlands.

Humphreys, M.O. 1995. Multitrait response to selection in *Lolium perenne* L. (perennial ryegrass) populations. Heredity **74:** 510-517.

Humphreys, M.O. and B.I. Honne. 1995. Potential for improved winterhardiness in ryegrass through hybridisation with fescues. Page 79 *in*: Adaptation in Plant Breeding. Proc. XIV Eucarpia Cong., Jyvaskyla, Finland, July 31 - August 4 1995, University of Jyvaskyla.

Humphreys, M.O., H. Thomas and B.F. Tyler. 1989. The potential of *Lolium multiflorum* x *Festuca gigantea* hybrids. Proc. XVI Int. Grass. Cong., Nice, France, pp 253-254.

Humphreys, M.O., M.W. Humphreys and H. Thomas. 1993. Breeding grasses for adaptation to environmental problems. Proc.

XVII Int. Grass. Cong., New Zealand and Australia pp 441-442.

Jadas-Hecart J., C. Poisson, J. Scehovic and Z. Zwierzykowski. 1992. Potential of tetraploid hybrids between *Lolium multiflorum* and *Festuca arundinacea* var. *glaucescens*. Pages 145-147 *in* F. Veronesi, S. Bullitta & S. Caredda, eds. Ploidy and Chromosome Manipulation in Forage Breeding, Alghero, Italy.

Joks, W., Z. Zwierzykowski, E. Joks and T. Nowak. 1994. Agronomic value of *Festulolium (Festuca pratensis x Lolium multiflorum)* strains. Pages 265-266 *in* D. Reheul & A. Ghesquiere, eds. Breeding for Quality. Proc. of 19th Eucarpia Fodder Crops Section Meeting, Brugge, Belgium.

Jones, M. Ll. and M.O. Humphreys. 1993. Progress in breeding interspecific hybrid ryegrasses. Grass Forage Sci. **48:** 18-25.

Marshall, A.H., T.P.T. Michaelson-Yeates, P. Aluka and M. Meredith. 1995. Reproductive characters of interspecific hybrids between *Trifolium repens* L. and *T. nigrescens* Viv. Heredity **74:** 136-145.

Marten, G.C., R.M. Jordan and A.W. Hovin. 1981. Improved lamb performance associated with breeding for alkaloid reduction in reed canarygrass. Crop Sci. **21:** 295-298.

Meredith, M.R., T.P.T. Michaelson-Yeates, H.J. Ougham and H. Thomas. 1995. *Trifolium ambiguum* as a source of variation in the breeding of white clover. Euphytica **82:** 185-191.

Moore, G., K.M. Devos, Z. Wang and M.D. Gale. 1995. Grasses line up and form a circle. Current Biology **5:** 737-739.

Moseley, G. and D.H. Baker. 1991. The efficacy of a high magnesium grass cultivar in controlling hypomagnesaemia in grazing animals. Grass Forage Sci. **46:** 375-380.

Munro, J.M.M., D.A. Davies, W.B. Evans and R.V. Scurlock. 1992. Animal production evaluation of herbage varieties. 1. Comparison of Aurora with Frances, Talbot and Melle perennial ryegrasses when grown alone or with white clover. Grass Forage Sci. **47:** 259-273.

Oertel, C., J. Fuchs and F. Matzk. 1996. Successful hybridisation between *Lolium* and *Dactylis*. Plant Breeding **115:** 101-105.

Oram, R.N. and R.A. Culvenor. 1994. Phalaris improvement in Australia. N. Z. J. Agric. Res. **37:** 329-339.

Paoletti, R. and C. Locatelli. 1989. Seed yield, fodder yield and persistence in white clover cvs of different origins. Results of trials conducted at Lodi (irrigated Po valley). Proc. XVI Int. Grass. Cong., Nice, France pp 655-656.

Ravel, C. and Charmet, G. 1996. A comprehensive multisite recurrent selection strategy in perennial ryegrass. Euphytica **88:** 215-226.

Reed, K.F.M. 1994. Improved grass cultivars increase milk and meat production - a review. N. Z. J. Agric. Res. **37:** 277-286.

Rhind, J.M.L.C., A. Smith, D.C.W. Goodenough, A.R.J. Morrison and J.I. Ellis. 1979. Cultivar evaluation of forage crops. Dep. Agric. Tech. Services. Pietermaritzberg. Cedara Press, Pietermaritzburg, South Africa.

Rhodes, I., R.P. Collins and D.R. Evans. 1994. Breeding white clover for tolerance to low temperature and grazing stress. Euphytica **77:** 239-242.

Rotili, P. 1991. The role of selfing in the synthetic and hybrid varieties constitution in forage crops. Pages 83-88 *in* A.P.M. den Nijs and A. Elgersma, eds. Fodder crops breeding: Achievements, novel strategies and biotechnology. Proc. 16th Eucarpia Fodder Crops Section Meeting, Pudoc, Wageningen.

Rumball W. 1982. Grasslands Kara cocksfoot (*Dactylis glomerata* L.). N. Z. J. Exp. Agric. **10:** 49-50.

Russell, W.A. 1991. Genetic improvement of maize yields. Adv. Agron. **46:** 245-298.

Silvey, V. 1981. The contribution of new wheat, barley and oat varieties to increasing yield in England and Wales 1947-78. J. Natl.

Inst. Agric. Bot. **15:** 399-412.

Thomas, H. and M.O. Humphreys. 1991. Progress and potential of interspecific hybrids of *Lolium* and *Festuca*. J. Agric. Sci., **117:** 1-8.

Thomas, H., M.W. Humphreys, M. Ghesquiere, M.O. Humphreys and C. Mousset. 1995. Improvement of drought resistance in *Lolium* by introgression from *Festuca*. Proc. Cong. Integrated Studies on Drought Tolerance of Higher Plants, Montpellier, France, August 31 - 2 September 1995, Paper IIA, 5 pp.

Tigerstedt, P.M.A. 1994. Adaptation, variation and selection in marginal areas. Euphytica **77:** 171-174.

Tyler, B.F. 1988. Description and distribution of natural variation in forage grasses. Pages13-22 *in* Natural Variation and Breeding for Adaptation. Proc. 14th Eucarpia Fodder Crops Section Meeting, 1987, Lusignan, INRA, France.

Tyler, B.F. and K. Chorlton. 1979. Extending genetic resources. Rep. Welsh Plant Breed. Stn for 1978, Aberystwyth, pp 43-46.

Vacek, V. and I. Zapletalova. 1982. Foreign assortment of Dutch clover (*Trifolium repens* L.) in view of biomass production factors. Sb. UVTIZ Genet. Slechteni **18:** 227-237.

Vaitsis, T.A. 1986. Research programme on alfalfa in Greece. EEC Agrimed Workshop on genetics and Improvement of Alfalfa, Montpellier, France.

Veronesi, F. 1991. Achievements in fodder crop breeding in Mediterranean Europe. Pages 25-30 *in* A.P.M. den Nijs and A. Elgersma, eds. Fodder crops breeding: Achievements, novel strategies and biotechnology. Proc. 16th Eucarpia Fodder Crops Section Meeting, Pudoc, Wageningen**.**

Walters, R.J.K. 1984. D-value: the significance of small differences on animal performance. Proc. 18th NIAB Crop Conference 1984, Cambridge, UK, pp 60-68.

Wijk , A.J.P. van and D. Reheul. 1991. Achievements in fodder crops breeding in maritime Europe. Pages13-18 *in* A.P.M. den Nijs and A. Elgersma, eds. Fodder crops breeding: Achievements, novel strategies and biotechnology. Proc. 16th Eucarpia Fodder Crops Section Meeting, Pudoc, Wageningen .

Wijk , A.J.P. van, J.G. Boonman and W. Rumball. 1993. Achievements and perspectives in the breeding of forage grasses and legumes. Proc. XVII Int. Grass. Cong., New Zealand and Australia, pp 379-384.

Wilkins, P.W. 1985. Breeding for dry matter yield in perennial ryegrass by wide hybridisation and recurrent selection. Pages 25-30 *in* J. Sjodin, ed. New methods, techniques and applications in fodder crop breeding. Proc. 13th Eucarpia Fodder Crops Section Meeting, Svalov, Sweden.

Wilkins, P.W. 1991. Recent yield improvements through recurrent half-sib family selection in diploid perennial ryegrass. Pages 71-72 *in* A.P.M. den Nijs and A. Elgersma, eds. Fodder crops breeding: Achievements, novel strategies and biotechnology. Proc. 16th Eucarpia Fodder Crops Section Meeting, Pudoc, Wageningen

Wilkins, P.W. and A. Lovatt. 1989. Genetic improvement in yield of nitrogen in *Lolium perenne* pastures. Euphytica **43:** 259-262.

Williams, W.M. 1987. Genetics and breeding. Pages 343-419 *in* M.J. Baker and W.M. Williams, eds. White clover. CAB International, Wallingford, Oxon, UK.

Wilman, D., R.J.K. Walters, D.H. Baker and S.P. Williams. 1992. Comparison of two varieties of Italian ryegrass (*Lolium multiflorum*) for milk production, when fed as silage and when grazed. J. Agric. Sci. **118:** 37-46.

Woodfield, D.R. and J.R. Caradus. 1994. Genetic improvement in white clover representing six decades of plant breeding. Crop Sci. **34:** 1205-1213.

Table 1
Genetic gain in harvested annual dry matter yield due to 20th century breeding

Species	Origin of data		Genetic gain % decade -1	Reference
Forage crops				
Perennial ryegrass				
(*Lolium perenne* L.)	UK		6	(Aldrich, 1987)
	Belgium		5	(van Wijk and Reheul, 1991)
	Netherlands		3	(van Wijk and Reheul, 1991)
	France (South)		2.5	(Allerit, 1986)
	Italy		2.5	(Veronesi, 1991)
		(Average	*3.8)*	
Italian ryegrass				
multiflorum Lam.)	Netherlands		3	(Veronesi, 1991)
	France (South)		4.5	(Allerit, 1986)
		(Average	*3.8)*	
Orchard grass/cocksfoot				
(*Dactylis glomerata* L.)	France (South)		1	(Veronesi, 1991)
	Italy		5.5	(Veronesi, 1991)
		(Average	*3.3)*	
Tall fescue				
(*Festuca arundinacea* Schreb.)	France (South)		1	(Veronesi, 1991)
	Italy		5.5	(Veronesi, 1991)
	Spain		3.5	(Veronesi, 1991)
		(Average	*3.3)*	
White clover				
(*Trifolium repens* L.)	New Zealand		6	(Woodfield and Caradus, 1994)
	Czechoslovakia		4.6	(Vacek and Zapletalova, 1982)
	South Africa		6.8	(Rhind et al., 1979)
	Spain		2	(Paoletti and Locatelli, 1989)
		(Average	*4.9)*	
Red clover				
(*Trifolium pratense* L.)	France (South)		3.5	(Allerit, 1986)
Alfalfa				
(*Medico sativa* L.)	USA		1.8	(Holland and Bingham, 1994)
	USA		2.6	(Hill et al., 1988)
	France (South)		5.5	(Veronesi, 1991)
	Greece		3	(Vaitsis, 1986)
	Italy		4.5	(Veronesi, 1991)
	Spain		7	(Veronesi, 1991)
		(Average	*4.1)*	
Grain crops				
Maize				
(*Zea mays* L.)	USA		15	(Russell, 1991)
Wheat				
(*Triticum aestivum* L.)	UK		21	(Silvey, 1981)
Barley				
(*Hordeum vulgare* L.)	UK		10	(Silvey, 1981)
Oats				
(*Avena sativa* L.)	UK		8	(Silvey, 1981)