

CHARACTERIZATION OF FORAGE GENETIC RESOURCES CONSTRAINTS AND OPPORTUNITIES

G. Charmet, F. Balfourier and C. Ravel

INRA, station d'amélioration des plantes, F63039 Clermont-Ferrand cedex, France

ABSTRACT

This introductory paper attempts to provide a picture of the current state of the art of the characterization and evaluation of forage genetic resources. Highlight is given to the ecological approach, successfully used in the past decades. New developments on this approach have been facilitated by statistical tools or by the use of genetic markers. It appears however, that the genetic variability of forage plant populations cannot be entirely predicted by ecogeographical factors. Moreover, the dissection of complex quantitative traits into marker-labelled mendelian ones is at a very preliminary stage. Therefore a breeder-oriented evaluation of germplasm collections appears to be a prerequisite to their extensive use in applied breeding programmes. The main specificity of forage plants are reviewed: GxE interaction, intra and interspecific competition, phenotypic plasticity and *Rhizobium* and *Neotyphodium* symbionts. The most recent papers dealing with these aspects are briefly reviewed. It is concluded that the development of core subsets of limited size (core collections) could enhance the use of forage germplasm collection by permitting a more in depth evaluation at a reasonable cost.

KEYWORDS

Forage grasses, forage legumes, ecology, genetic markers, adaptation, breeding potential, core collection.

INTRODUCTION

In the XVII International Grassland Congress in New-Zealand, Hadley (1993), reported that grasslands cover about 3 billions hectares, about one fifth of the world's land area. "Natural" grassland ecosystems, which historically accounted for about half of total grasslands, have been converted on large-scale into crop lands, while forests, either temperate or tropical, are converted into grasslands and pastures. Thus even if the grassland area remains globally stable, its nature is changing from natural to "artificial", i.e. planted by man. This has consequences on farmers' requirements of plant resources for establishing grassland.

For many centuries since the spread of agriculture in Europe and the extensive deforestation that followed, grassland established itself naturally from native herbage plants, some species being then favoured by selection pressures imposed by farming practices such as cutting or grazing (a similar figure is likely to have occurred in tropical regions, although less is known about it). This history favoured grasses, legumes and a few other genera. Voluntary sowing of grassland species is reported first in Northern Italy in the XII century for Italian ryegrass (*Lolium multiflorum*). This species spread over continental Europe, then was introduced to the British Isles in 1831 (Borrill, 1976). Perennial ryegrass (*Lolium perenne*) was first used for intentional sowing in England in the XVII century, and therefore is called "English" ryegrass in many European languages.

The first known example of long distance forage seed transportation by man is that of lucerne (*Medicago sativa*), which was introduced from Mesopotamia to Greece by Medes and then by Romans across their empire. Its culture disappeared in the early middle ages, before its re-introduction by Arabs from North Africa through Spain (Michaud et al., 1988). A few centuries later (in the XIX), it was introduced in New World countries of America and Oceania by settlers, along with the main European grasses (fescues *Festuca*,

cocksfoot *Dactylis* and ryegrass *Lolium*), which form most of grassland areas in USA, New-Zealand and Argentina, among others (Buckner et al., 1979).

At that time, it is likely that the availability and the cost of seeds were the main criteria of choice, although unconscious selection may already have been applied for productivity, forage quality or adaptation.

The first record of genetic improvement of forage species appears to be that of perennial ryegrass at the Welsh Plant Breeding Station, Aberystwyth, in 1919 (Breese and Davies, 1969). In this early age of scientific selection, plant breeders tried to exploit the genetic variation of indigenous material through an ecological or population genetics approach. This approach, pioneered by Stapledon (1933), took advantage of material from natural grasslands already adapted by natural selection to specific environments and management systems. The aim was to provide the means to raise the general standard of grassland in Britain to that of the best existing grassland. Wild populations were therefore collected in ryegrass dominant permanent grazing pastures of Wales and screened as spaced plants for uniformity of type and vigor, followed by progeny testing for combining ability. Selected parents formed the basis of a synthetic cultivar. The highly successful, multi-tillering perennial ryegrass cultivar S23 was developed in this way.

In a similar way, useful hay-type perennial ryegrasses were obtained by selection from indigenous leafy, early flowering types from unusual shade habitats, such as gorse brakes (Stapledon, 1933, in Breese, 1983). In New Zealand, where perennial ryegrass and white clover are not indigenous, this ecological approach was applied, either to "naturalized" populations (Suckling and Forde, 1978), or to European material with collections targeted to areas which showed climatic features similar to those of New Zealand (Easton et al., 1989, Caradus et al., 1990).

The success of these ecologically based cultivars resulted in increased intensification of grassland usage and thereby created requirements beyond the scope of indigenous material. One good example is by the extension of growing season. To this end, Welsh breeders collected ryegrass populations adapted to grow in the milder winters of south-western France or northern Spain. Although considerable success in early spring growth was achieved (e.g. cv S321), there was some reduction in winter hardiness. This illustrates a limit of the ecological approach: that the potential of the material is constrained within the framework of its adaptation, whether to climate, soil or management. Nevertheless many of the cultivars obtained in this way showed a relatively wide range of adaptability over various soil types, climatic conditions or intensity of utilization. This highlights the necessity of a more accurate evaluation of collected wild populations for use in genetic improvement programmes of forage species. In this paper we will attempt to review the main advantages and disadvantages of the use of collection of wild populations in forage plant breeding.

AN INCREASING INTEREST IN PLANT GENETIC RESOURCES

Computerized world bibliographic databases now allow the scientist to extensively search all papers referring to a given topic. The main difficulty arises from the choice of appropriate key-words to be

reasonably certain of identifying most of the information. The concept of “genetic resource(s)” is a typical example of this difficulty. Although the pioneering work of A. de Candolle last century and N.I. Vavilov in the 1920’s led to the widespread recognition of the “centers of diversity” of crops, and then H.V. Harlan stressed that such diversity was endangered, it was only after World War II that a possible widespread loss of diversity was recognized. The wording genetic resources started to be used in the 1960s, then more extensively by the early 1970’s (Harlan, 1972). However the number of references recovered by searching the key-words “genetic resource(s)” or “germplasm” with “forage or fodder crop or grass or legume”, was still very small in the 1970’s, then increased dramatically in the 1980s and is still growing, although more slowly, in the 1990s, as illustrated in Figure 1. Moreover many of these papers report results on collection, ‘conservation or database management. Studies related to evaluation, characterization or utilization of forage genetic resources appear more frequently after 1984. This latter type of study has even doubled in number in the last 3-year period compared to the preceding decade, probably indicating a great increase in the interest of forage plant breeders in the utilization of forage genetic resources.

We must keep in mind that such an analysis may be biased by a “fashion” effect. Indeed the pioneering work of Stapledon on Welsh ryegrass populations would be referred today as a genetic resources concern. However we can consider that the comparisons made in Figure 1 are valid for the period beginning in 1979.

Going into more details in this bibliometric analysis, we divided the data into two time groups, separated by the year 1990. This rough grouping was chosen in order to get enough data to smooth some possible “year effects, which can be caused for example by the organization of a big congress in a given region of the world. Data were then distributed according to the country or continent of origin of the first author and to the topic. Again to obtain significant figures to allow comparisons among world regions, we retained only four classes of subject matter (Figure 2). Although the distinction between single trait and multitrait evaluation is quite clear, often in the title, it is less easy to differentiate between multitrait evaluation and breeding application. We used this last category only when breeding was explicitly referred to, but it is obvious that many references classified under multitrait analysis do concern plant breeding too. One should add that this topic of use of genetic resources in applied plant breeding is likely to be underestimated when only counting the number of papers. Everybody knows that most plant breeders in private seed companies are required to breed and provide new cultivars rather than to publish scientific papers, and that this is also sometimes the case in public research institutes.

The most important findings in Figure 2 are: 1) the overall increase in paper numbers is attributable to multitrait evaluation or germplasm classification studies, with the more specialized studies and those strictly applied to breeding remaining stable in numbers, 2) the contribution of each defined geographic region of the world is more balanced for the last 6 years than in the past, 3) there is an increasing use of biochemical and molecular markers in the description of forage genetic resources since 1990.

From an overall, although probably too limited analysis of the original papers published since 1990, we would like to highlight a few points. Sometimes very old questions have been addressed recently with new biological or mathematical methods, or with a renewed, integrated approach.

A REFINEMENT OF THE ECOLOGICAL APPROACH

From 1990 to 1995, we found 75 reports on ecogeographic surveys or on characterization/evaluation of ecologically oriented collections of natural population. Compared to previous studies, most papers not only report descriptive work but also describe the geographic patterns of variation, use more intensively agro-ecological data, relate agronomic traits more precisely to ecological characteristics of the site of origin, or model the geographic patterns of variation.

Correlation analyses and multivariate descriptive methods: Many studies used principal component analysis of agro-morphologic data with geographic or ecological groups as illustrative variable. Results of such studies are very contradictory, depending on the species and the geographic region surveyed. Examples of “successes” are given by Abdelguerfi et al. (1988) or Bounejmate et al. (1992), who found that the distribution of annual *Medicago* species fits ecogeographic factors well, in Algeria and Morocco, respectively. Similarly Smith et al. (1991) on alfalfa (*Medicago sativa*) obtained phenotypically distinct geographic groups using multivariate clustering. On *Medicago polymorpha*, Loi et al. (1995) reported that all morpho-agronomic variables were related to collection site parameters, and Bullitta et al. (1994) found soil pH to be positively correlated with 1000 seed weight in Sardinia. A similar relationship between soil characteristics and seed yield was found by Akundabweni et al. (1991) in *Trifolium temense* from Ethiopia, while Smith et al. (1995) reported that patterns of morph distribution of *Trifolium glomeratum* in southern Australia were related to summer maximum temperatures, winter minimum temperatures and spring rainfall. In grasses, Balfourier and Charmet (1991a) were able to discriminate perennial ryegrass from different mediterranean countries for agronomic traits, and Charmet and Balfourier (1991) obtained through multivariate clustering distinct geographic groups throughout Europe, with the notable exception of Norwegian populations which were disseminated among all clusters. Balfourier and Charmet (1991b) showed that both climatic and management data of the site of origin were related to genetic components of growth and persistence of perennial ryegrass from France. Again in perennial ryegrasses from Europe, Loos (1994a) reported that correlations between morphology and environmental factors of the site of origin were significant in several cases but were generally weak. Fujimoto (1993) found that fresh weight and leaf size of Japanese cocksfoot populations were related to average rainfall.

On the other hand other studies reported a lack of relationships between agromorphological traits and ecogeographic factors of the site of origin. In white clover, Caradus (1990) obtained heterogeneous geographic groups, and Jahufer et al. (1995) found no correlation between herbage yield in dry summer environments of Australia and amount of rainfall from passport data. Similarly, Johnson et al. (1989) obtained clusters of *Hedysarum boreale* which were not clearly related to characteristics of the collection site. In alfalfa, Smith et al. (1994) reported that mean salt tolerance did not differ between accessions from six basic climate groups, and that the effects of agronomic practices represented a major limitation to use of climatological data. In grasses, Luchin et al. (1990) on cocksfoot and Solberg et al. (1994) on perennial ryegrass found no general relationships between winter mortality and the climatic origin of the populations. Looking at the microgeographic differentiation of perennial ryegrass populations from adjacent site pairs in Ireland, we found no effect of directional selection by ecological factors, but a possible reproductive isolation caused by genetic drift (Charmet and Balfourier, 1994a).

It seems that the efficiency of the ecological approach of selecting

germplasm of forage species from the possible action of past selection pressure is highly dependent on the origin of the material and on the variable considered. A possible source of inefficiency may be in some cases the inadequacy of the ecological variables available in passport data. To remedy this problem, Steiner and Green (1996) proposed a flexible set of ecological descriptors that capture the most important ecological features of the collection site to give a standardized description of the natural conditions where accessions are found. They also proposed a revised data collection form and a method to retroclassify poorly documented accessions that do not have detailed descriptions of the collection site. Another case of poor relationships between agronomic traits and ecological traits may occur when the effect of natural selection is hidden by other mechanisms of plant evolution such as genetic drift. The use of sophisticated statistical methods may help to resolve this confusion. For example, methods of geostatistics allowed Monestiez et al. (1994) to discriminate between two spatial structures, one due to the isolation-by distance phenomenon and the second one, which explained 30% of the total genotypic variance, presumably caused by natural selection for a complex climatic adaptation.

Consequently, although the ecological approach can in some instances be very useful, either *a priori* for determining the collection area, or *a posteriori* to select a subset of accessions for a given breeding objective, it does not exempt the breeder from a complementary characterization or a breeding oriented evaluation of genetic resources.

Use of genetic markers: Genetic markers offer a tool for a complementary characterization of genetic resources of forage species. Their main advantage is their high heritability (theoretically 100%) and the small amount of plant material usually required. During the period 1990-1995 there were 45 papers reporting on the use of genetic markers in the description of forage genetic resources. These studies used mostly seed storage proteins (Forde and Gardiner, 1991; Konarev et al., 1995) or isozymes. Isozymes have been used for the description of collections in relation with ecogeographic factors in a range of forage species: perennial ryegrasses (Balfourier and Charmet, 1994; Loos, 1994b; Hayward et al., 1996), fescues (Weibull et al., 1991), buffalo clover (Hickey et al., 1991), *Leucaena* (Harris et al., 1994), *Hedysarum* (Baatout et al., 1990) and sainfoin (Kidambi et al., 1990). However these studies are mostly descriptive and provide little information for the use of genetic resources. Charmet et al. (1993a) and Loos (1994b) on *Lolium perenne*, and Bullitta et al. (1994) on *Medicago polymorpha* reported significant correlations (although generally not very high) between allelic frequencies of isozymes and climatic data, which may contribute to the improvement of the classification of germplasm collections on an ecological basis. The use of isozyme data for conservation purposes is discussed by Francisco-Ortega et al. (1992) for tagasaste *Chamaecytisus proliferus* and by Balfourier et al. (1994) for perennial ryegrass.

In fact, many studies with either isozyme or molecular DNA markers are devoted to taxonomy and phylogenetic relationships among species or subspecies. We can mention, among others, studies of the *Lolium-Festuca* complex by isozymes (Loos, 1993; Aiken et al., 1993; Charmet and Balfourier, 1994b), by RFLP (Xu and Sleper, 1994), RAPD (Stammers et al., 1995) or restriction analysis of cpDNA (Darbyshire and Warwick, 1992). RAPD or RFLP have also been used for phylogenetic reconstruction in *Trifolium* (Bullitta, 1995), *Lotus* (Campos et al., 1994), *Stylosanthes* (Glover et al., 1994; Curtis et al., 1995), *Leucaena* (Harris, 1995) and annual *Medicago* (Brummer et al., 1995; Mariani et al., 1996), and for within species

variation studies in buffalograss *Buchloe dactyloides* (Huff et al. 1993), tagasaste (Francisco-Ortega et al., 1993), alfalfa (Kidwell et al., 1994) and red clover *Trifolium pratense* (Kongkiatngam et al., 1995).

Again these studies are very useful for germplasm classification and management, but have little predictive value of general or specific adaptation of accessions to regional environments or farming practices. This last objective could only be achieved after a complete dissection of adaptive characters, which are mostly quantitative traits under polygenic control, into discrete genes, each labelled by a specific marker. Even so, the application of genetic markers in germplasm evaluation would first require the establishment of the state of linkage disequilibrium between marker and gene-of-interest alleles in the collection considered, unless the marker probe was itself the gene. This may appear to be somewhat futuristic, although some genetic mapping and/or QTL analyses are currently in progress for some species such as alfalfa (Brummer et al., 1993; Kiss et al., 1993; Echt et al., 1994,), tall fescue (*Festuca arundinacea*) (Xu et al., 1995), *Stylosanthes* (Kazan et al., 1993a, 1993b; Liu and Musial, 1995), *Pennisetum* (Smith et al., 1993) and ryegrass (Hayward et al., 1994).

We can thus conclude that, with current knowledge, neither the ecological approach nor the use of genetic markers are sufficient to choose appropriate germplasm for applied breeding programmes, which are the main potential users of genetic resource collections of forage populations.

A NEED FOR A BREEDING-ORIENTED EVALUATION OF GENETIC RESOURCES

What we mean by “breeder-oriented evaluation” is not only the measurement of a range of morphological or agronomic traits aimed primarily at the classification of collections and the supply of databases. To be of real use to plant breeders, germplasm databases (to which we do not deny their usefulness) should contain information about the range of adaptation of each accession, either to environmental conditions or to farm management practices; and also about their ability to be genetically improved, i.e. their potential responsiveness to selection.

Evaluation for environmental or management adaptation: There has been a long debate around the words adaptation, adaptedness, adaptability or adaptive value (see Tigerstedt, 1994). From the breeder’s point of view, we assign “broad adaptation” for accessions which are “stable” across a wide range of environments, and “narrow adaptation” for those which are highly interactive, i.e. which perform well in some specific conditions only. This meets the concept of ecological amplitude as defined by Campbel (1993). Several recent studies report genotype-by-environment (GxE) interactions in germplasm evaluation of forage plants (e.g. Santen and Casler, 1990 on cocksfoot; Jahufer et al., 1994 on white clover...). Reviews on these concepts of stability or GxE interactions are numerous (e.g. Becker, 1988; Eeuwijk, 1995). It would take several books to simply summarize all research, both methodological or applied, on GxE interactions. Among the most recent methodological developments, two are of particular interest for forage plants: the use of environmental covariates and multivariate modelling.

The use of environmental variables in the interpretation of GxE interaction was first proposed by Wood (1976), then formalized by Denis (1980, 1988) under the name “factorial regression”. This method uses variables associated to both genotypes and environments. When a significant amount of interaction variance is

accounted for by linear regression on covariate products, it leads to interesting biological interpretations, such as that given by Baril et al. (1995) for potato. We applied this method to summer growth scores of natural populations of perennial ryegrass (Charmet et al., 1993b) and found that the interaction component, rather than population main effect, was explained by climatic data of the site of origin (i.e. populations from dry sites show positive interactions in dry conditions), which fits a natural selection hypothesis.

The great majority of forage breeding programmes have multiple objectives, e.g. dry matter and seed yield, consistency of seasonal production, nutritive quality and a wide range of resistance or tolerance to various pests or climatic and edaphic limiting factors. Selection must therefore be multitrait, and so the evaluation of genetic resources should be too. In this context, the use of a multivariate approach to GxE modelling would be highly recommended. Such methods have been proposed by Kroonenberg (1983) as three-mode principal component analysis, and applied to GxE interaction by Kroonenberg and Basford (1989). However Crossa et al. (1995) said that the implementation of such methods for analysing large datasets such as required for germplasm description (>500 accessions, >10 attributes) needs further investigation. A pragmatic solution to overcome present limitations of three-mode methods could be to restrict its use to subsets of data such as those provided by the evaluation of core collections.

Interactions between plant genotype and the type of agronomic management are also major in forage species, making it necessary to evaluate germplasm under a range of agronomic conditions as close as possible to realistic farming practices. A noteworthy example is given by Cameron et al. (1995), who evaluated new introduced forage germplasm (representing 18 grass and 23 legume species) in Indonesia, Malaysia, the Philippines and Thailand: "Evaluation was on smallholder farms, which resulted in more realistic and relevant selection". Moreover the material identified as being broadly adapted and high yielding was distributed directly to farmers. Testing of genetic resources under grazing is also highly desirable whenever the intended use is for pastures (Caradus, 1991).

Other kinds of interaction can be encountered in forage plant evaluations, namely intra and interspecific competition between plants and symbiotic relationships with *Rhizobium* (legumes) or *Neotyphodium* endophyte (grasses).

The effect of within species interplant competition is generally estimated by evaluating accessions as monospecific dense swards, which requires a sufficient amount of seeds, and often implies a pre-multiplication of genetic resource collections, as reported by Paul et al. (1994) for a German collection of perennial ryegrass. Performance under competition sometimes agrees with non-competitive evaluation (Negri et al., 1995 on *Lotus corniculatus*), but there are many reports of disagreement. Interspecific competition can be tested in the same way by sowing a mixture. This approach is widely used in legume germplasm evaluation (e.g. Caradus, 1994 on white clover; Smith et al., 1992 on lucerne). Competition for light can also be studied in a greenhouse or growth chamber by simulation techniques such as that proposed by Evers (1994). Phenotypic plasticity is another factor of the adaptability of forage species (Hay and Baxter, 1989). It may often lead to the masking or to the overestimation of true genetic variation, and should therefore be taken into account. It is important to not confound genetic variation with a purely plastic response. But on the other hand, phenotypic plasticity was reported to be under genetic control (Jain, 1978), and could thus be improved by selection (Scheiner, 1993), however this would require a specific protocol,

which is not, to our knowledge, routinely used by forage breeders.

Interactions of forage plants with their symbionts is also a vast field of research. In the past five years, more than 350 papers relate to the *Neotyphodium* (formerly named *Acremonium*) endophyte of grasses. Out of them, 22 describe studies of genetic resources of fodder or turf grasses for the presence or effect of fungus endophyte, mostly for tall fescue (e.g. Santen et al., 1991; Cagas, 1993; Holder et al., 1994) or perennial ryegrass (e.g. Widdup and Ryan, 1991; Oldenburg, 1994; Siegel et al., 1995; Lewis and Ravel, in press). Significant plant-endophyte interactions have been reported for alkaloid synthesis and pest resistance (Clement et al., 1994), and for drought tolerance of *Neotyphodium*-bearing plants (Hill et al., 1996). This should encourage both plant breeders and gene bank managers to further consider the endophyte companion of grasses in the collection and evaluation of genetic resources. Many similar studies have also been carried out on the legume-*Rhizobium* association (e.g. Howieson and Ewing, 1989, Howieson et al., 1994). In the future, molecular biology may provide tools for a better understanding of nodule formation and for evaluating the effectiveness of nitrogen fixation (Kiss et al., 1995). Collection and evaluation of *Rhizobium* strains appears as necessary as that of *Neotyphodium* (e.g. Hartel et al., 1991; Chen et al., 1993).

Evaluation of the breeding potential of genetic resources: At the boundary of genetic resources evaluation and actual breeding programmes, studies should take place on the estimation of genetic parameters, namely heritabilities and genetic correlations among traits. These studies are useful to choose the germplasm which shows the highest theoretical response to selection, and also to devise the most efficient selection scheme. We found 32 reports of such quantitative genetics oriented evaluation of forage genetic resources published since 1990, including white clover (Caradus and Woodfield, 1990; Annichiarico and Piano, 1995), alfalfa (Johnson and Rumbaugh, 1995), perennial ryegrass (Charmet and Debote, 1995), cocksfoot (Tronsmo, 1992) or *Panicum coloratum* (Young, 1994). As discussed above, these evaluation of genetic parameters must take into account the effects of GxE interactions (Rowe and Brinks, 1993) or competition. Several breeding designs have been recently proposed for selecting stable cultivars from broad based populations derived from genetic resources (Helgadottir et al., 1995 on timothy; Ravel and Charmet, 1995 on perennial ryegrass). The effect of between plant competition generally leads to the buffering of the differences between families, thus reducing heritabilities and the response to selection (Devey et al., 1989). Moreover, Hebert et al. (1994) showed that competition also modified genetic correlations, thus affecting the correlated responses in multitrait selection.

Again such labour and time consuming analyses would profitably be carried out on representative subsets of large collection, that are now referred to as core collections.

DEVELOPMENT AND USE OF FORAGE CORE COLLECTIONS

Seventeen recent papers present studies of core formation and/or evaluation in forage species. Many studies are applications of principal components or multivariate clustering to the sampling of a core collection, i.e. a representative subsample. The most illustrative in this respect are the studies carried out on USDA collections of Medicago (Basigalup et al., 1995; Diwan et al., 1994, 1995; Brummer et al., 1995), white clover (Pederson et al., 1996), red clover (Kouame and Quesenberry, 1993) and ryegrass (Casler, 1995). They used a range of sampling strategies based on different levels of collection structuring (stratified sampling), according to various clustering

methods, pre-selection of a reduced set of variables. *etc.*. The criterium used to check the efficiency of core sampling methods was generally the ratio of the core variance to whole collection variance for a quantitative trait, or its lower confidence limit estimated through Monte-Carlo resampling.

We used a slightly different method of hierarchical multivariate clustering with a geographic contiguity constraint (Charmet et al., 1994). This method enabled us to obtain geographically compact clusters without an a-priori classification by country of origin or other criteria. Similar to the American studies, we found that a stratified sampling according to this clustering was the most efficient sampling method, even for a very small "core" of 25 populations (Charmet and Balfourier, 1995)

Reports on the use of core collection in pre-breeding or breeding programmes are still scarce (Charmet et al., 1993b on perennial ryegrass; Bouton, 1996 on alfalfa), but their number is likely to increase in the future. Such core subsets and their evaluation could profitably be developed within the framework of existing international cooperative networks, as illustrated by the European core collection created and currently under study in 18 countries of the European Cooperative Programme on Genetic resources (ECPGR) (Gass et al., 1995; Sackville-Hamilton et al., present congress).

CONCLUDING REMARKS

We would like to end this paper with an optimistic conclusion. Plant breeders are now aware worldwide of the necessity to preserve natural populations of forage species, both well known or still not used, for the future needs of sustaining an increasing number of humans. Much progress has been achieved on the collection and maintenance of these valuable genetic resources, although this effort must be continued. We reviewed some strengths and present limitations to the use of natural populations of genetic resources. However, despite limitations, new improved cultivars have been created from natural populations, with the general aim of reducing inputs, and providing plant resources for a sustainable, durable agriculture. We will mention a single example of a natural population based variety obtained in Switzerland from an adapted upland ecotype (Boller and Nuesh, 1992)

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Figure 1

The number of published papers recovered from CAB plant breeding abstracts CD-rom database using (“genetic resources” or “germplasm”) and (“forage” or “fodder “plant” or “legume” or “grass”) as keywords. The black subdivisions are references dealing with characterization or evaluation of forage genetic resources.

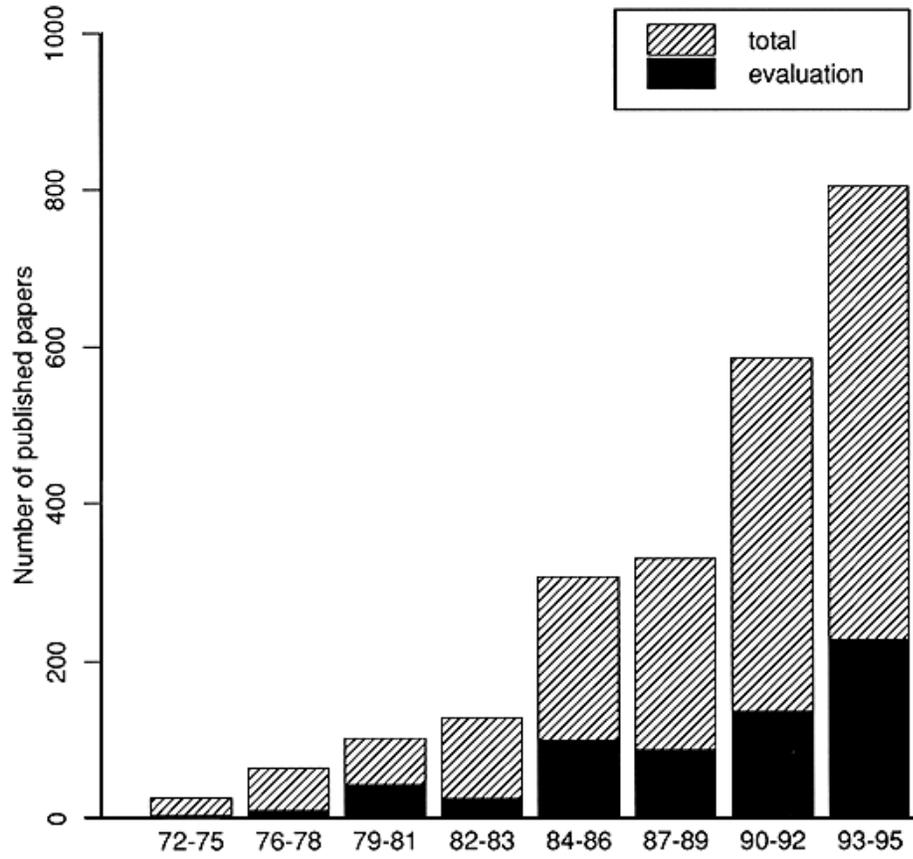


Figure 2

Geographic representation of the number of papers related to forage genetic resource characterization or utilisation, split by topic and continent or country of origin of the first author. Pie size is proportional of the total number of references for the period. Figure 2a: 1980-1989; (187 papers) Figure 2b: 1990-June 1996 (309 papers).

Figure 2a

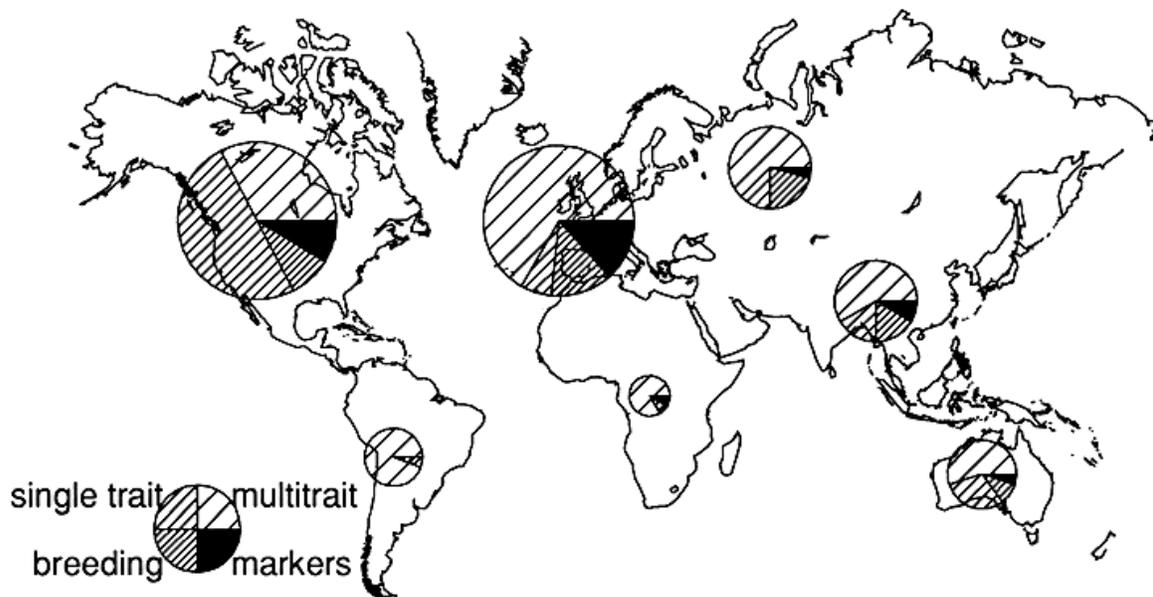


Figure 2b

