

Ecological classification of white lupin landrace genetic resources

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Abstract Information on the adaptation of germplasm pools to specific agroclimatic conditions is essential for ensuring high genetic progress while broadening the genetic base of breeding programmes. This study aimed to provide an ecological classification of global white lupin (*Lupinus albus* L.) landrace genetic resources on the basis of their adaptation pattern, verifying whether region of origin could conveniently contribute to such a classification. Some 113 landraces representing 11 regional pools were evaluated in three major agroclimatic conditions, i.e., Mediterranean and subcontinental climate in Italy under autumn sowing, and suboceanic climate in France under spring sowing. The classification of regional pools by pattern analysis suggested the presence of five major ecological groups composed as

follows: A = Azores, Greece and Italy; B = Madeira and Canaries; C = Maghreb, Portugal and Spain; D = East Africa, Egypt and West Asia; and E = Turkey. This classification implied specific adaptation ranging from the cold-prone, autumn-sown environment (group A) to the spring-sown environment (groups D and E). Ecological grouping accounted for about half of the overall genotypic variation and genotype × environment interaction variation in just 3.6% of its degrees of freedom in an analysis of variance. It reflected largely the entry groups issued by pattern analysis classification of the individual accessions. Our classification of ecological groups can drive the incorporation of exotic genetic resources in European breeding programmes as a function of the targeted agroclimatic conditions. In addition, it can contribute to the definition of global or user-specific core collections.

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Introduction

Despite their acknowledged importance for long-term crop improvement, exotic genetic resources are poorly utilized in breeding programmes (FAO 1998). Various reasons may account for this trend.

Narrowly-based genetic pools may still provide selection gains (Rasmusson and Phillips 1997). Introgression through backcrossing procedures can be envisaged only for specific traits controlled by one or a few genes and, particularly for vertical resistance to pests and diseases, has often proved of limited usefulness (Spoor and Simmonds 2001). Large-scale incorporation of exotic germplasm in the genetic base through crossing with locally-adapted, elite material followed by selection for adaptation may fail to provide genetic progress, especially when exotic material is markedly misadapted to the target region (Duvick 1984; Kannenberg and Falk 1995). In this context, information on the adaptation of germplasm pools to specific agroclimatic conditions is essential for ensuring high genetic progress while broadening the genetic base of breeding programmes. Germplasm evaluation networks encompassing major agroclimatic conditions can produce this information by exploring genotype \times environment interaction for production traits and generating an ecological classification of germplasm types on the basis of their adaptation pattern. An ecological group may pool landraces (or wild populations) featuring different regions of origin but similar adaptation patterns, as a result of convergent evolutive adaptation to similar growing environments which does not necessarily imply same genetic mechanisms (Arendt and Reznick 2008).

Passport data are limited or almost nil for most accessions in major world collections (Plucknett et al. 1987). Country of origin is the most accessible information and is frequently used, as such or pooled into geographical regions, as a classification criterion for summarizing characterization or evaluation data (e.g., Perry and McIntosh 1991; Pecetti et al. 1992) or for establishing core collections (e.g., Knüpfper and van Hintum 1995). This classification criterion confirmed to be a useful indicator of morphophysiological or ecological diversity in some studies (Peeters and Martinelli 1989) but not in others (Spagnoletti-Zeuli and Qualset 1987).

White lupin (*Lupinus albus* L.) is a traditional food legume with high potential as a high-protein feed crop in several European regions (Papineau and Huyghe 2004; Annicchiarico 2008) and increasing interest also as an ingredient of functional or healthy food products (Arnoldi 2005). It is usually autumn-sown in Mediterranean environments and spring-

sown in cold-prone temperate regions. However, widening its autumn-sown area through selection of winter-hardy varieties is being pursued as a means to raise grain yields through the longer crop cycle and/or the escape from terminal drought and heat stress (Huyghe 1997; Papineau and Huyghe 2004). The main ecological limitation to white lupin cropping probably lies in its poor adaptation to calcareous or alkaline soils (Jayasundara et al. 1998). White lupin was probably domesticated in ancient Greece from the locally-occurring wild type var. *graecus*, spreading thereafter eastward, southward and westward (Gladstones 1998). Genetic resources for white lupin breeding are largely represented by cultivated landraces because of the limited distribution of var. *graecus* (Gladstones 1998), and are limited to the primary gene pool because of effective genetic barriers to interspecific hybridization (Atkins et al. 1998).

Specific-adaptation responses proved widespread in a world collection of white lupin landraces across three major European cropping conditions, i.e., Mediterranean and subcontinental climate in Italy under autumn sowing and suboceanic climate in France under spring sowing (Annicchiarico et al. 2010). That study also documented the agronomic value of landrace germplasm relative to variety material, the variation among and within landrace and variety germplasm pools for several morphophysiological traits, the impact of evaluation environments on entry responses, and the relation between adaptive responses and morphophysiological characteristics. Those experimental data are exploited here with the specific objective to provide an ecological classification of global white lupin landrace genetic resources on the basis of their adaptation pattern, verifying whether region of origin could conveniently contribute to such classification.

Materials and methods

Detailed information on germplasm accessions, test environments and experimental procedures was provided in an earlier report (Annicchiarico et al. 2010). The current study included 113 lupin landrace accessions belonging to seven national pools (Greece; Italy; Egypt; Spain; Portugal; Turkey; Azores) and four transnational pools, each pool being represented

by at least eight accessions (Table 1). Transnational pools were contemplated for four regions placed far apart from the putative area of domestication, namely: (i) Maghreb (Algeria and Morocco); (ii) East Africa (Ethiopia, Kenya and Sudan); (iii) West Asia (Syria, Lebanon, Israel and Jordan); and (iv) Canaries and Madeira, i.e., the mid North Atlantic islands. Accessions within pools were randomly chosen from INRA's global white lupin collection at Lusignan (France), ensuring that they sampled adequately the within-pool morphophysiological variation which emerged from data of previous characterization or evaluation work. The Italian pool also included four recently collected landraces.

The evaluation was performed during the 2004–05 cropping season in three cropping conditions: (i) autumn sowing (October 14) in Lodi (northern Italy), representative of the subcontinental climate with extended frosts in winter and moderate terminal drought which is typical of northern Italy and some inland areas of the Iberian and Balkan peninsulas; (ii) autumn sowing (October 29) in Sanluri (Sardinia), representative of the Mediterranean climate with fairly mild winters and terminal drought and heat stress which is widespread in southern Italy and other Mediterranean areas; and (iii) late-winter sowing

(March 9; considered as spring-sown hereafter) in Saint Sauvant (western France), representative of the suboceanic climate with extended frosts in winter and cool, fairly humid summers which features various areas of western Europe. In agreement with the expected climatic characteristics of the test sites, winter frost was severe in Lodi (78 frost days; -9.0°C absolute minimum temperature) and absent in Sanluri, whereas total rainfall from March 1 to harvesting date was 186 mm in Lodi, 131 mm in Sanluri, and 196 mm in Saint Sauvant. All soils were suitable for white lupin ($\text{pH} \leq 7.4$; active lime $\leq 0.4\%$). Their texture was sandy-loam in Lodi, clay-loam in Sanluri, and silty-clay in Saint Sauvant. The experiments were designed as a randomized complete block with three replications. The plot size was two rows 1.53 m long and 0.5 m apart, with 18 seeds spaced 8.5 cm on each row (sowing density ≈ 23.5 seeds/m²). Prior to sowing, seeds were treated with Germipro UFB (350 g/l iprodione + 177 g/l carbendazim) at the rate of 2.6 ml/kg of seed, and were inoculated with NPPL HiStick (Becker Underwood, Toulouse, France). The fertilization was site-specific. Dry grain yield was assessed on a plot basis, estimating seed moisture on 250 random seeds per plot.

A preliminary analysis of variance (ANOVA) including the fixed factors regional pool and environment and the random factors landrace within pool and block within environment aimed to compare the landrace pools for mean yield across environments, holding entry within pool as the error term. Ecological groups were identified by classifying the regional pools according to their average adaptive response through pattern analysis. Cooper et al. (1996) described this technique and highlighted its ability to account for the two determinants of genotype adaptive response, i.e., mean yield and genotype \times environment interaction effects. The analysis implied a hierarchical cluster analysis of germplasm pools (acting as individuals) as a function of their mean yields in the three cropping environments (acting as variables) standardized within environment to zero mean and unit standard deviation. It adopted a squared Euclidean distance as the dissimilarity measure, and Ward's clustering method (Cooper et al. 1996).

A second ANOVA aimed to verify the amount of genotypic and genotype \times environment interaction

Table 1 Number of accessions and mean dry grain yield of 11 regional pools of white lupin landraces evaluated in northern Italy and Sardinia under autumn sowing and western France under spring sowing

Regional pool	Number of accessions	Grain yield (t/ha)
Madeira and Canaries	8	4.30a
Spain	10	3.77a
Portugal	8	3.71a
Italy	15	3.64a
Maghreb	10	3.46a
Greece	10	3.28a
Azores	10	3.21
West Asia	10	2.97
East Africa	10	2.89
Egypt	12	2.17b
Turkey	10	1.74b

Means followed by letters 'a' and 'b' do not differ from the top- and the bottom-ranking mean, respectively, according to Bonferroni's test ($P < 0.05$; landrace within pool as error term)

variation accounted for by the classification into ecological groups. It included the fixed factors ecological group (EG), regional pool within EG, and environment, as well as the random factors landrace within EG and regional pool, and block within environment. Accordingly, landrace within EG and regional pool acted as the error term for the other genotypic effects, and its interaction with environment as the error term for the other genotype \times environment interaction effects. Separate ANOVAs compared the ecological groups for yield response in each environment. A second pattern analysis was performed on the matrix of landrace accession by environment yields. While classifying the individual landraces for adaptation pattern, this analysis further verified the ability of ecological groups and regional pools to account for entry diversity in adaptation pattern.

Pattern analysis was performed through CropStat (IRRI 2008), whereas ANOVAs were performed through Statistical Analysis System software (SAS 1999).

Results

The landrace pool from Madeira and Canaries was top-yielding across the three European environments, but several regional pools were not statistically inferior ($P < 0.05$) because of the sizeable within-pool entry variation which acted as the error term (Table 1). The regional pools from Turkey and Egypt were lower-yielding than the other pools ($P < 0.05$).

The clustering stages of pattern analysis performed on regional pools are summarized in Fig. 1. The germplasm pools from Europe, Maghreb and Atlantic islands were distinctly separated from the other extra-European pools. The pools from Greece, Azores and Italy formed a rather homogeneous group for ecological response. The landrace pools from Maghreb and the Iberian countries formed a second EG somewhat distinct from Madeira and Canaries germplasm, which tended to form a distinct EG. The fairly different adaptation pattern of the Turkish material relative to Egyptian, East African and West Asian germplasm suggested the presence of two additional ecological groups. The geographical definition of these five groups is reported in Fig. 2.

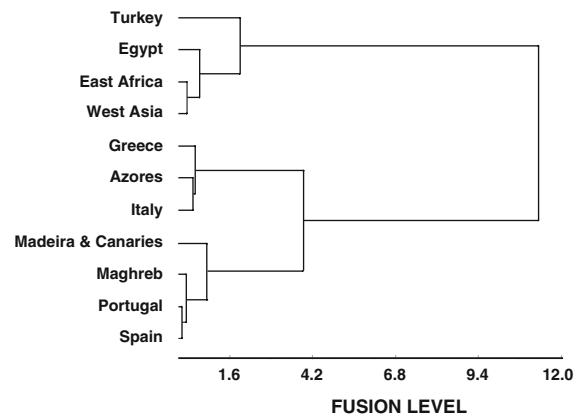


Fig. 1 Pattern analysis classification of 11 regional pools of white lupin landraces based on dry grain yield responses in northern Italy and Sardinia under autumn sowing and western France under spring sowing

The EG factor and its interaction with environment were significant ($P < 0.01$) in the ANOVA and accounted for a remarkable portion of entry variation for adaptive response (Table 2). In particular, EG accounted for 47.6% of the overall genotypic sum of squares while accounting for just 3.6% (4/112) of its degrees of freedom; whereas EG \times environment interaction accounted for 51.5% of the overall genotype \times environment interaction variation in just 3.6% (8/224) of its degrees of freedom (Table 2). The proportion of variation accounted for by regional pools within EG was only 6.6% of the genotypic variation and 7.1% of the genotype \times environment interaction variation, highlighting the modest loss of diversity for adaptive response obtained by pooling the 11 pools into 5 EGs. The remaining variation, i.e., 45.8% of the genotypic variation and 41.4% of the genotype \times environment interaction variation, was due to diversity for adaptive response among accessions within EG and regional pools.

The yielding ability of the five ecological groups varied markedly depending on the cropping environment. The EG codes ranging from A to E in Table 3 implied specific adaptation ranging from the cold-prone, autumn-sown environment to the spring-sown environment. EG A, including landraces from Azores, Greece and Italy, was specifically adapted to the cold-prone environment. EG B, including material from Madeira and Canaries, was fairly widely-adapted, being top-performing in both autumn-sown environments. EG C, pooling germplasm from Maghreb and

Fig. 2 Geographical representation of the ecological classification of 11 regional pools of white lupin landraces into five groups by pattern analysis of dry grain yield responses in northern Italy and Sardinia under autumn sowing and western France under spring sowing, and preferential utilization of each ecological group by European breeding programmes as a function of the targeted agroclimatic conditions

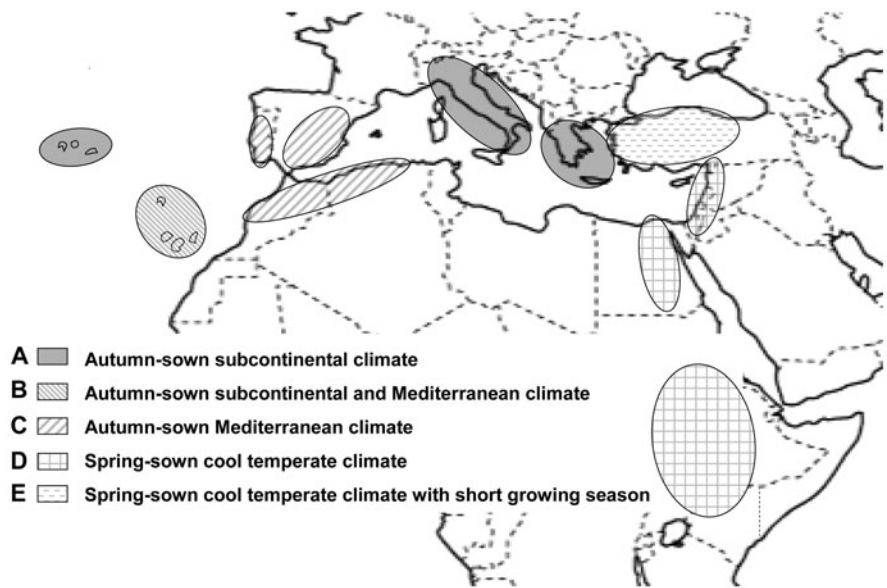


Table 2 Analysis of variance for dry grain yield in northern Italy and Sardinia under autumn sowing and western France under spring sowing of 113 white lupin landraces belonging to 11 regional pools. Sum of squares (SS) for landrace and for

landrace × environment interaction partitioned into variation among ecological groups (EG), among regional pools within EG, and within regional pools

Source of variation	Degrees of freedom	SS	Proportion of SS	Mean square
Environment	2	1296.2	–	648.10**
Block (Environment)	6	267.0	–	44.50
Landrace	112	838.2	–	–
EG ^a	4	399.1	0.476	99.78**
Pool (EG)	6	55.0	0.066	9.16*
Landrace (EG pool)	102	384.1	0.458	3.77**
Landrace × Environment	224	1127.5	–	–
EG × Environment	8	580.5	0.515	72.56**
Pool × Environment (EG)	12	79.8	0.071	6.65**
Landrace × Environment (EG Pool)	204	467.2	0.414	2.29**
Pooled error	672	651.2	–	0.97

ns not significant; * $P < 0.05$; ** $P < 0.01$

^a For 5 EG levels defined by pattern analysis classification of regional pools (see Fig. 1)

the Iberian peninsula, was specifically adapted to the autumn-sown Mediterranean environment. The ecological groups D and E were specifically adapted to the French spring-sown environment and quite misadapted to the cold-prone autumn-sown environment, but this adaptive response was more accentuated in EG E including the Turkish landraces (Table 3).

The high number of accessions prevented a clear graphical representation of the classification tree outputted by pattern analysis of the individual entries. The first clustering stage separated one accession group (AG 1) of 21 entries, whereas the next stage divided the remaining entries into two groups (AG 2, with 23 entries; AG 3, with 59 entries). AG1 and AG3 were further divided into two and three

Table 3 Mean dry grain yield (t/ha) in three autumn-sown (AS) or spring-sown (SS) environments, for five ecological groups (EG) of white lupin landraces defined by pattern analysis classification of 11 regional pools across the three environments

Ecological group		Lodi (Northern Italy), AS	Sanluri (Sardinia), AS	Saint Sauvant (western France), SS
Member regional pools	EG			
Azores/Greece/Italy	A	5.52ab	3.71b	0.94c
Madeira and Canaries	B	6.18a	5.20a	1.36b
Maghreb/Portugal/Spain	C	4.84b	4.58a	1.44b
East Africa/Egypt/West Asia	D	2.75c	3.49b	1.67a
Turkey	E	1.21d	2.12c	1.92a

Mean values followed by different letter differ according to Bonferroni's test ($P < 0.05$; landrace within group as error term)

Table 4 Frequency of white lupin entries from each regional pool and ecological group (EG), for each accession group (AG) or subgroup (ASG) issued by pattern analysis classification of 113 landraces for dry grain yield responses in northern Italy and Sardinia under autumn sowing and western France under spring sowing

EG ^a	Regional pool	AG 1		AG 2	AG 3			Total
		ASG 1	ASG 2		ASG 3	ASG 4	ASG 5	
A	Azores	0	0	9	0	1	0	10
A	Greece	0	0	8	2	0	0	10
A	Italy	0	1	4	3	6	1	15
B	Madeira and Canaries	0	0	1	0	3	4	8
C	Maghreb	0	2	0	5	1	2	10
C	Portugal	0	0	0	3	4	1	8
C	Spain	0	0	1	4	3	2	10
D	East Africa	0	5	0	4	1	0	10
D	Egypt	1	10	0	1	0	0	12
D	West Asia	2	1	0	5	0	2	10
E	Turkey	7	2	0	0	1	0	10
	Total	10	21	23	27	20	12	113

^a Coded as in Table 3; defined by pattern analysis classification of regional pools

accession subgroups (ASG), respectively, whereas any further subgrouping had limited practical interest because it implied distinctly lower distance between novel clusters (data not reported). The contribution of ecological groups and regional pools to each of the six groups or subgroups of accessions is summarized in Table 4. AG 2 was mainly composed of (91%), and included most (60%), accessions belonging to the EG formed by Azorean, Greek and Italian germplasm. ASG 1 was mainly composed of (70%), and included most (70%), entries belonging to the Turkish EG. ASG 2 was mainly composed (76%), and included half, of the landraces belonging to the EG formed by Egyptian, East African and West Asian

germplasm. Landraces of the EG formed by Maghrebian and Iberian material were largely included (89%) into AG 3, especially ASG 3 (which also included several entries from East Africa and West Asia). Finally, the EG formed by germplasm from Madeira and Canaries was largely included (87%) in ASG 4 and ASG 5 of AG 3. These results confirmed the fairly good ability of the ecological groups issued by pattern analysis classification of regional pools to summarize the ecological response of major groups of individual accessions. They also highlighted, however, the difficulty of classifying the accessions belonging to the Italian, East African or West Asian pool into a single ecological group, because of the

large within-pool diversity for entry adaptive response of these pools reflected by the large spreading of their accessions into different entry groups (Table 4).

Discussion

The large extent of genotype \times environment interaction effects for yielding ability of the ecological groups (Table 3) confirms the importance of a careful selection of exotic genetic resources when broadening the genetic base of European white lupin breeding programmes. A previous report (Annicchiarico et al. 2010) provided essential information on the adaptive responses of the regional landrace pools and the individual accessions, and the morphophysiological characteristics underlying these responses. Flowering time emerged as a crucial adaptive trait, with a different optimal level for each cropping condition. In particular, specific adaptation to the autumn-sown subcontinental-climate environment was strictly related to late phenology and its contribution to lower winter plant mortality. Conversely, early flowering was important for adaptation to the French spring-sown environment, owing to its short growing season and the absence of cold stress on the seedlings. The EG codes ranging from A to E in Table 3 implied not only specific adaptation ranging from the cold-prone, autumn-sown environment to the spring-sown environment but also mean flowering date progressively decreasing from EG A through EG E, on the ground of phenological data for their component regional pools (Annicchiarico et al. 2010). The more specific adaptation pattern and the distinctly earlier phenology of EG E (including Turkish germplasm) relative to EG D (including Egyptian, East African and West Asian material) concurred to define the preferential utilization of each ecological group by European breeding programmes as a function of the targeted agroclimatic conditions that is reported in Fig. 2. This information, which summarizes the implications of our findings for germplasm users, indicates the special interest of genetic resources from EG E for spring-sown, continental-climate environments characterized by a short growing season. The Turkish germplasm exhibited earlier phenology than Egyptian material also in Simpson (1986) although the vernalization

requirement, which is the major determinant of white lupin flowering time (Huyghe 1997), proved similar and substantially nil in all regional pools included in EG E and EG D (Noffsinger and van Santen 2005).

Our classification of ecological groups differs in various respects from the ecogeographic classification of landrace germplasm reported by Kurlovich (1998), which contemplated the following six major plant types: (i) the Balkan-Asian (inclusive of Greek and Turkish material); (ii) the Palestinian (i.e., West Asian); (iii) the Egyptian-Abyssinian; (iv) the Algerian (i.e., Maghrebian); (v) the Iberian; and (vi) the Italian. This latter classification was based on morphophysiological characteristics rather than adaptive responses, and implied a geographical criterion preventing to group material with contrasting geographical origin but similar adaptation pattern. The current attribution to contrasting ecological groups of the Greek and Turkish germplasm pools reflected their distinct phenology which emerged in our evaluation (Annicchiarico et al. 2010), in Simpson (1986) and, to a somewhat lesser extent, in Noffsinger and van Santen (2005). As a matter of fact, most current Turkish landraces originated in inland areas, while those originated in coastal areas may be less dissimilar from Greek material (Papineau and Huyghe 2004). The interest of genetic resources from Azores and Italy when targeting cold-prone autumn-sown environments had already been reported (Huyghe 1997; Papineau and Huyghe 2004), while that of germplasm from Madeira and Canaries for a wide range of autumn-sown European environments is a novel important finding.

The current usefulness of regional pools for classifying sets of accessions into ecological groups is comforting because of its practical importance. Country or region of origin provides a simple and widely-accessible criterion for choosing subsets of germplasm accessions to be studied, for classifying tested and non-tested accessions into entry groups with distinct characteristics, and for locating genetic resources with desired characteristics. Compared with germplasm classification based on regional pools, that of individual accessions has the advantage of maximizing the genetic diversity between groups but the disadvantage of preventing any inference on the expected characteristics and the group membership of non-tested accessions which have been or may be collected. These aspects have special importance

when defining ecological groups for global crop germplasm collections, because the high costs entailed by the necessary multi-environment testing usually prevent to evaluate the entire germplasm collection. In our case, the evaluated entries represented about 8% of INRA's global white lupin collection, which is the largest world collection (Buirchell and Cowling 1998) and currently exceeds 1400 accessions. The lower ability of the East African and West Asian pools to account for the diversity in adaptation pattern of their component accessions reflected their high within-pool diversity for entry adaptation, which probably descended from the wide heterogeneity of landrace collecting environments featuring these vast regions.

Besides driving the incorporation of exotic genetic resources in breeding programmes, the information on major ecological groups can also contribute to the definition of global core collections of germplasm. Although the genetic diversity for molecular markers has been advocated as the most useful information layer for establishing these collections (e.g., van Hintum 1995), its combination with other information layers is supported by the possible inconsistency between marker-based and morphophysiological diversity (Gepts 1995), especially when the former cannot rely on high numbers of markers. This may imply the inconsistency of marker-based diversity also with the diversity for adaptation pattern of germplasm accessions, as verified in one study where molecular, morphophysiological and adaptive information layers were jointly compared (Annicchiarico et al. 2009). The importance of ecological response to cropping environments has been acknowledged in some core collections by including a few crucial adaptive traits or collecting variables among the classification criteria used for defining germplasm groups for stratified sampling (e.g., Tohme et al. 1995). When available, ecological classification could conveniently be used as a major information layer contributing to define global core collections.

There is second, possibly even more important exploitation of an ecological classification of global crop germplasm in the context of core collections. Evaluating a core collection may be less cost-efficient than evaluating a carefully-chosen working collection for breeding programmes, because of the high frequency of locally-misadapted exotic germplasm that also a core collection is expected to include (Jana

1999). Accordingly, it has been proposed to establish multiple core collections for germplasm users characterized by different sets of crucial adaptive traits (Mackay 1995), or to envisage a criterion for further germplasm choice within a core collection as a function of user-specific priorities (van Hintum 1999). Ecological classification could conveniently act as a major information layer for defining user-specific sets of accessions which could maximize the locally-useful genetic variation, by meeting simultaneously two needs: (i) maximizing the crop genetic diversity according to conventional criteria used for a core collection (e.g., the combination of molecular-based and morphophysiological variation); and (ii) excluding accessions of ecological groups whose definite misadaptation to the targeted agroclimatic conditions is highly probable.

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