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Chapter

Biodiversity of the Genus Medicago from Africa

Mounawer Badri and Ndiko Ludidi

Abstract

The genus Medicago has its primary center of diversity in the Caucasus, northwestern Iran and northeastern Turkey. It occurs widely in Africa, where it constitutes a rich and diversified heritage. In addition to their ecological importance, Medicago species are an important source of feed for livestock. These species show significant diversity in genetic composition, symbiotic interactions, and tolerance to abiotic and biotic stresses. At the morphological level, some species show a high diversity of biomass and flowering precocity. Characterization using molecular markers (isozymes, random amplified polymorphic DNA (RAPD), amplified fragment length polymorphism (AFLP), single sequence repeats (SSR), etc.) shows significant variation within and among different populations. The differentiation of populations based on phenotypic traits and molecular markers emphasizes a role of the site of origin as the basis of natural selection. Furthermore, a broader-to-narrow symbiotic specificity is demonstrated, where some species are nodulated by both species of Ensifer meliloti and E. medicae while others are nodulated only by E. medicae or by a restricted group of E. meliloti. Different Medicago species show diverse levels of tolerance to biotic and abiotic stresses, which enable selection of lines displaying good agronomic performance. This review summarizes the current status of the characterization of the Medicago species in Africa and their use in breeding programs.

Keywords: Medicago species, populations, lines, morphological traits, molecular markers, symbiotic specificity, Medicago-fungi interactions, abiotic and biotic stresses, Africa

1. Introduction

The world population is increasing rapidly and estimates predict 9.6 billion humans on earth in 2050, which emphasizes the need to produce enough food for the entire population. However, our environment is increasingly affected by the intensification of agriculture with, according to an estimate by the Millennium Ecosystem Assessment [1], 60% of ecosystem services being degraded due in particular to the massive use of pesticides and fertilizers. It is therefore becoming urgent to rethink our agricultural systems [2] in order to make them more sustainable while remaining productive. One possibility considered is to increase the diversity of cultivated species as a way to increase resilience and reduce agricultural impacts on the environment while maintaining productive systems [3]. Increasing the diversity of cultivated species can be done by selecting new varieties from spontaneous species. The existence of a large
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reservoir of useful genes in wild species is evident if we take into account the adaptation of these species to very different environments. Their possible use in genetic improvement programs is therefore of great interest. The *Medicago* genus is endemic to Africa where it constitutes a rich and highly diversified heritage. The majority of the species of this genus are pastoral in nature and few species are cultivated, including the perennial alfalfa *M. sativa* and the two annual species *M. polymorpha* and *M. truncatula*. Several biodiversity analysis studies have been carried out in *Medicago* species in Africa, particularly in Morocco, Algeria, Tunisia, and South Africa, and few studies in Egypt and Libya.

Characterization of genetic diversity within and between natural populations of *Medicago* species was done using phenotypic traits [4], iso-enzymatic analyses [5, 6], and SSR markers [7–14]. The results showed a high level of polymorphism, the highest values of which are recorded within populations in annual *Medicago* species in Tunisia [4, 8–11].

In addition, to fix atmospheric nitrogen, *Medicago* species, like other legumes, have the ability to enter into a symbiotic association with soil bacteria belonging to the genus *Ensifer*. These species show broad to narrow spectra of symbiotic specificity. The perennial alfalfa *M. sativa* has a broad spectrum of symbiotic specificity and is nodulated by *Ensifer meliloti* [15] while *M. truncatula* is nodulated by both species *E. meliloti* and *E. medicae* [16, 17], *M. laciniata* is nodulated by a new biovar of *E. meliloti* [18, 19], whereas *M. ciliaris* [20] and *M. polymorpha* [21] are preferentially nodulated by *E. medicae*.

Furthermore, it has been reported that *Medicago* species are infected by nine species in their natural habitat in Tunisia, such as *Erysiphe polygoni*, *Uromyces striatus*, *Pseudopeziza medicaginis*, *Pseudopeziza trifolii*, *Cercospora medicaginis*, *Alternaria* sp., *Fusarium* sp., *Phoma medicaginis*, and *Stemphylium* sp., powdery mildew (*Erysiphe polygoni*) and rust (*Uromyces striatus*) [22]. In addition, more than 60 species of fungi have been isolated from diseased roots of *Medicago* spp. in South Africa [23].

Finally, *Medicago* species showed a high level of variability in responses to abiotic and biotic stresses. Diversity within and among populations has been noted for water deficit [24], salinity [25–27], nutritional deficiencies [28], and resistance to pathogens [29–32].

In this review, the genetic and symbiotic characterization and diversity of abiotic and biotic stress responses in *Medicago* species are discussed. We also describe and discuss the nutritional value in the perennial alfalfa *M. sativa* and the analysis of the genetic determinants of agronomic traits of interest in the model legume *Medicago truncatula*.

2. Phenotypic and molecular genetic variation

Genetic characterization of natural populations of *Medicago* species was performed using quantitative vegetative and reproductive traits and molecular markers. The genetic diversity within and between Tunisian populations of *M. truncatula* [8, 11, 12], *M. laciniata* [9], *M. ciliaris* [10], and *M. polymorpha* [4, 14] was made using quantitative characters and microsatellite markers. A high level of portability of microsatellites, developed on the genome of *M. truncatula*, was noted in *M. laciniata*, while a moderate percentage of transfer of these markers was recorded in *M. ciliaris* [10] and *M. polymorpha* [14]. *M. truncatula* showed significantly higher levels of quantitative (*Q*\textsubscript{ST}) and molecular (*F*\textsubscript{ST}) differentiation between populations than in the three species *M. laciniata* [9], *M. ciliaris* [10], and *M. polymorpha* [4, 14]. Natural
selection represents the main evolutionary force responsible for maintaining polymorphism between the natural populations of these four species. The site of origin explains a moderate part of the quantitative genetic variability between populations for *M. truncatula*, *M. laciniata*, *M. ciliaris*, and *M. polymorpha*. The results obtained in these studies could be useful to breeders who plan to introduce certain lines of these four species into breeding programs.

Additionally, Jabri et al. [33] analyzed genetic diversity in 14 Tunisian populations of *M. ciliaris* using morphological characters and two combinations of amplified fragment length polymorphism primers (E-AGC/M-CAA; E-AAG/M-CTG). Molecular data indicated a significant difference between the studied populations. *M. ciliaris* populations were clustered into three main groups according to their geographical origin. The populations of the first group come from high and cold inland areas, and those of the second group come from low areas with mild winters while those of the third come from low coastal areas.

Furthermore, Zitouna et al. [13] studied six Moroccan *Medicago* species using SSR markers. A high level of gene flow was noted between the studied species with significant intraspecific variation. The results showed that *M. polymorpha* and *M. orbicularis* are closely related and that *M. truncatula* is probably the ancestral species. There are no correlations between the geographical distribution of Moroccan species and genetic similarities.

In addition, Haddioui et al. [6] studied molecular polymorphism in nine Moroccan populations of *M. truncatula* using enzyme markers. The results showed a large genetic variability between populations, which argues in favor of the autogamous breeding system in this species. The phylogenetic relationships between the studied populations appear to be independent of the geographical origins of the populations. Conservation programs for this species should consider the levels of genetic diversity within and between populations revealed using enzyme markers.

Finally, Laouar et al. [34] studied the ecology of the taxa *M. ciliaris* and *M. intertexta* in Algeria. Their distribution showed ecological specificities where *M. ciliaris* is more common on heavy, saline soils and has a wider dispersal, and its climatic requirements are less stringent than those of *M. intertexta*. The geographical distribution of *M. intertexta* is limited to the northeast of Algeria, under a subhumid and humid bioclimate, on soils poor in calcium and at altitudes lower than 250 m on average.

### 3. Symbiotic host specificity

Species of the *Medicago* genus belonging to the Fabaceae family have the ability to fix atmospheric nitrogen (N₂) and transform it into NH₃ following a symbiotic association with soil bacteria of the *Rhizobium* genus. Some species of the *Medicago* genus have a broad spectrum of symbiotic specificity such as the perennial alfalfa (*M. sativa*), while other species have a narrow spectrum of nodulation.

The genetic characterization of a collection of 299 isolates of rhizobia that nodulate *M. truncatula*, isolated from 10 Tunisian soils, was made by polymerase chain reaction restriction fragment length polymorphism analysis (PCR/RFLP) of 16S rRNA genes [16]. The results showed that 227 isolates belong to the genus *Ensifer meliloti*, while 72 isolates belong to the species *E. medicae*. The species *E. meliloti* exists in 9 soils among the 10 soils analyzed, while *E. medicae* was only detected in 5 soils among the 10. Genetic characterization, by repetitive extragenic palindromic-PCR (REP-PCR), of 48 isolates of each of the two species showed that the isolates
belonging to the species *E. meliloti* are the most polymorphic. Data from a crossing test between plant populations and the soils of origin showed no significant correlation between the origin of the lines and the type of isolates trapped [17]. Additionally, Zribi et al. [20] reported that *M. ciliaris* is preferentially nodulated by *E. medicae* and, even if it is sometimes nodulated with *E. meliloti*, this association remains ineffective. The co-inoculation experiment of *M. ciliaris* with *E. medicae* and *E. meliloti* showed that *E. medicae* is the most competitive in terms of nodulation.

Furthermore, analysis of the symbiotic properties, nodulation spectrum, and nitrogen fixation efficiency (EFA) in two sympatric populations of *M. laciniata* and *M. truncatula* revealed that *M. laciniata* is symbiotically different from *M. truncatula* even if it occupies the same habitat [19]. *Sinorhizobium* strains that form effective symbioses with *M. ciliaris* and *E. medicae* showed that *E. medicae* is the most competitive in terms of nodulation.

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Molecular characterization of a collection of rhizobium isolates from *M. sativa* by PCR/RFLP of 16S genes showed that almost all isolates (158 out of 160 isolates) belong to *E. meliloti* [15]. Strains isolated from soil in northern Tunisia were more efficient and produced fewer nodules than those on southern soil. A significant interaction between plant genotypes and those of *E. meliloti* was also noted.

In addition, the analysis of responses to saline and thermal stresses in a Tunisian collection of strains of *Ensifer* sp. isolated from four *Medicago* species (*M. sativa*, *M. ciliaris*, *M. polymorpha*, and *M. minima*) showed that five isolates of *M. sativa*, three of *M. ciliaris*, and three of *M. minima* continued to grow at 45°C [35]. However, only two *M. sativa* isolates grew at 4% NaCl. Genetic analyzes have made it possible to suggest that there is a horizontal transfer of genes between *E. meliloti* and *E. medicae*.

On the other hand, the genetic characterization of a collection of strains isolated from the nodules of the spontaneous species of *Medicago* in Egypt shows that they belong to *E. meliloti* and *E. medicae*, with a predominance of *E. meliloti* [36].

Furthermore, the genetic characterization of a set of strains nodulating *Medicago littoralis* in Algeria showed that they all belong to the *E. meliloti* species [37].

The nodulation study of *M. polymorpha* and *M. minima* following an association with *E. meliloti* in Libya showed the formation of indeterminate elongated nodules with an apical meristem and containing different central tissues [38].

Finally, the evaluation of the response of *M. sativa* to arbuscular mycorrhizal (AM) inoculation under water deficit in Tunisia showed a positive effect of inoculation on plant growth and biomass production [39]. The maximum mycorrhizal intensity was recorded in the roots of plants subjected to severe water deficit. Therefore, it appears that natural mycorrhization would be as effective as mycorrhizal addition for growth stimulation and tolerance to drought stress.

### 4. Fungi-plant interactions

Annual species of the *Medicago* genus are an important source of fodder for livestock in Africa. In addition to their detrimental effects on productivity, pathogens can also affect the forage quality of *Medicago* species. Nine species belonging to eight genera of fungi have been identified as pathogens of the aerial parts of *M. truncatula*, *M. ciliaris*, and *M. polymorpha* in Tunisia [22, 29, 40]. These are *Erysiphe polygoni*, *Uromyces striatus*, *Pseudopeziza medicaginis*, *Pseudopeziza trifolii*, *Cercospora medicaginis*, *Alternaria* sp., *Fusarium* sp., *Phoma medicaginis*, and *Stemphylium* sp. Powdery mildew (*Erysiphe polygoni*) and rust (*Uromyces striatus*) are widespread on these species, especially in northern and central Tunisia. *Cercospora medicaginis* was
isolated from the three species in various regions ranging from the north to the south of the country. This fungus is characterized by a very important diversity. Indeed, analysis of several isolates of *C. medicaginis* showed a diversity in the dimensions of the conidia, the morphology of the cultures, and the degree of infection [40].

*Phoma medicaginis* was isolated from *M. truncatula* and *M. ciliaris* in the northern regions of Tunisia. This fungus causes necrosis on leaves and stems [29]. Twelve of the 14 strains of this pathogen tested on *M. truncatula* were virulent, nearing those initially isolated on *M. ciliaris*. The results showed a high level of diversity in the aggressiveness of *P. medicaginis* strains, which depends on the inoculated organ. It thus could be important to inoculate the aerial and root parts in order to select resistant lines.

On the other hand, the other pathogens noted on the leaves of *Medicago* spp. in the winter rain region of South Africa are *Phoma medicaginis*, *Leptosphaerulina briosiana*, *Colletotrichum trifolii*, *Colletotrichum destructivum*, *Erysiphe polygoni*, *Cercospora medicaginis*, and *Stemphylium vesicarium* [41]. Symptoms on leaves and stems caused by *Phoma medicaginis* var. medicaginis are the most common disease symptoms and include formation of small, dark brown to black spots that can enlarge to eventually result in leaf chlorosis and defoliation. In addition, *Colletotrichum trifolii* caused leaf infection of *Medicago* spp. in a number of areas in the south and southwest of the Western Cape province of South Africa [42]. Seedlings are more susceptible than older plants. Representative isolates of *Colletotrichum* have been collected from *M. sativa* in South Africa [43]. *C. dematium*, *C. destructivum*, *C. trifolii*, and *C. truncatum* are pathogenic on *M. sativa*, and a diversity of disease aggressiveness on this host has been noted. *C. trifolii* is the most pathogenic species on *M. sativa*.

In addition, more than 60 species of fungi have been isolated from diseased roots of *Medicago* spp. in the winter rain region of South Africa [23]. The predominant fungi isolated are *Fusarium acuminatum*, *F. avenaceum*, *F. equiseti*, and *F. oxysporum*. The pathogenicity test of 23 species in *Medicago truncatula* cv. Jemalong showed that the most aggressive agents are *F. avenaceum*, *F. culmorum*, *F. graminearum* Group I, *F. lateritium*, *Pythium irregular*, *P. ultimum*, and *P. spinosum*. Among these species, *F. avenaceum* appears to be the most important pathogen for root rot because it is widespread and virulent.

Finally, the diversity of *Ichneumonidae* (Hymenoptera) was studied in *M. sativa* in Bahariya and Farafra in Egypt. A total of 206 specimens belonging to 8 subfamilies, 14 genera, and 24 species were collected. Seven species were recorded for the first time in Egypt, in addition to the 11 species that were newly reported in association with *M. sativa* [44].

5. Adaptation to abiotic and biotic constraints

Several approaches are used to improve the productivity of plants under abiotic and biotic stress, while the selection of varieties tolerant to these constraints remains one of the most promising ways to sustain productivity. Several studies have been carried out on the biodiversity of responses to abiotic stresses in *Medicago* species in Africa.

A significant diversity of responses was noted within and between 11 Tunisian populations of *M. truncatula* under water deficit [24] and salt stress [25]. This large phenotypic variation in *M. truncatula* can be used to identify genes and alleles important for the trait of tolerance to drought and salinity stress.

5
Analysis of morpho-physiological variability of responses to salt in four Tunisian natural populations of *M. ciliaris* showed that the 46 lines studied form three groups under control treatment and 100 mM NaCl, and their genetic structure is dependent on the treatment factor [27]. The results of this study can be used in the identification and selection of salt-tolerant *M. ciliaris* lines.

In addition, evaluation of the variation of tolerance to water deficit in 47 lines of *M. truncatula*, *M. ciliaris*, and *M. polymorpha* showed that *M. ciliaris* is the latest to flower under water deficit, and it gives the most biomass under both control treatments and 30% of field capacity [45]. The lines were classified into five groups on the basis of their differing responses to drought. Tolerant lines of the three species may be good candidates for future breeding programs for drought tolerance.

Analysis of the responses at the germinal stage in 10 local varieties of *M. sativa* from the Algerian oases and a commercial cultivar (Giulia) under a range of NaCl concentrations (0 mM, 85.6 mM, 171.1 mM, 256.7 mM, and 342.2 mM) showed a high level of diversity between the varieties studied under control treatment and salt stress [46]. In addition, a germination study in the Tunisian variety El Hamma and a Californian variety of *M. sativa* under a range of NaCl (100, 150, 200, and 250 mM) revealed that the latter variety is less affected by salt stress for length and fresh weight of roots, while the local variety of El Hamma has the lowest reduction for fresh leaf weight [47]. Further work is needed to validate the behavior of tolerant varieties in the field in the presence of salt.

The inoculation of *M. sativa* with a consortium of arbuscular mycorrhizal (AM) fungi with or without autochthonous strains of rhizobium (RhLO1) showed that these autochthonous microorganisms are effective in mitigating the damage caused by salinity and improve plant growth and productivity [48].

In addition, an exploration of tolerance to Fe deficiency was carried out in 20 Tunisian lines of *M. truncatula* [28]. The results showed a high level of response diversity between these 20 genotypes, of which TN8.20 and Jemalong A17 are tolerant, while TN1.11 and TN6.18 are the most sensitive ones. Tolerant genotypes showed the lowest decreases in chlorophyll content and photosynthetic activity (CO₂ assimilation) compared to sensitive genotypes.

To elucidate the genetic determinants of abiotic stress tolerance in the model forage legume *M. truncatula*, different approaches including quantitative trait loci (QTLs), functional genomics, and association genetics have been used.

Genetic analysis of tolerance to water deficit [49] and salt stress [50, 51] was carried out using an LR5 population of recombinant inbred lines (RILs) at the F8 generation derived from a cross between the line Jemalong A17 and F83005.5. The RILs and the two parental lines were cultured under control treatment and water deficit (in tubes under 75 mM mannitol (D-) and in pots under 33% of field capacity) and salt stress (45 mM NaCl). In addition, a second population of RILs was also used for the analysis of the genetic determinants of tolerance to water deficit [52] and salinity [53]. This RILs population comes from the cross between the Tunisian line TN1.11 and the reference line Jemalong A17. Several QTLs were identified under water deficit and salt stress, suggesting their multigenic nature. The set of QTLs identified under water deficit and salt stress are generally different, with only a few QTLs in common. Overall, the majority of QTLs were mapped to chromosomes 1, 5, and 8.

In addition, an expression study of two candidate genes, *DREB1B* under water deficit [54] and the *MtERF1* gene [55] under salt stress in four lines (TN1.11, TN6, 18, JA17, and A10) of *M. truncatula* was done. The results of the expression analysis by
RT-qPCR revealed differential tissue expression of the DREB1B gene in the four lines under osmotic stress, with a higher induction rate in the roots of TN6.18 and Jemalong A17 than in A10 roots, suggesting a key role for DREB1B in water-deficit tolerance in M. truncatula. Moreover, the MtERF1 gene is mainly expressed in the roots and is inducible by NaCl and low temperature. A higher level of MtERF1 expression was noted in TN1.11 plants than in TN6.18. Therefore, both DREB1B and MtERF1 genes can be used as selection markers to obtain Medicago lines with osmotic stress tolerance.

The evaluation of the responses in 39 Tunisian lines of M. truncatula, whose genomes are fully sequenced, in greenhouse and in the field under control conditions and salt stress revealed that there is an ongoing migration of genomic region candidates for salt tolerance [26]. These regions contain genes that regulate physiological acclimation to salt stress, such as abscisic acid and jasmonic acid signaling. They also contain genes linked to biotic stress tolerance and some involved in early flowering. These candidates emphasize the importance of both tolerance and avoidance in natural populations of M. truncatula.

In another study, analysis of responses in 14 Tunisian natural populations of M. truncatula to infection with Aphanomyces euteiches showed that most of the phenotypic variation (65.4%) is found within populations [29]. Significant correlations were noted between quantitative traits and ecological factors, suggesting the existence of local adaptation. The populations studied form three groups, based on their responses to this pathogen. The first group contains resistant lines from populations originating from central Tunisia. The second group is made up of partially resistant lines from populations in southern Tunisia and the mountainous region of Thala. The third group is formed by susceptible lines from populations in the north of the country and saline soils. Overall, the results revealed that the studied lines are more sensitive (71.3%) than resistant (28.7%) to attack by A. euteiches. However, resistant lines have shown several forms of reactions to attack by this pathogenic agent, which can be used for the identification of potentially new resistance genes.

Furthermore, analysis of the responses of 10 varieties of M. sativa to infection by P. medicaginis revealed that the studied varieties are classified into three large groups [32]. The tolerant variety Gabès2355 and the susceptible variety Magna-601 form a contrasting pair following infection by P. medicaginis. These two varieties can be used to analyze the physiological and genetic determinants of M. sativa tolerance to infection by this pathogen.

In addition, screening a collection of M. truncatula lines against infection by Fusarium oxysporum, Fusarium solani, and Rhizoctonia solani strains showed a diversity of disease responses with resistant and highly susceptible phenotypes [30]. The Jemalong A17 line showed relative resistance to all the fungal strains studied, while TN1.11 was sensitive. The results showed increased antioxidant activities in Jemalong A17 plants in leaves and roots.
6. Fodder quality

Despite the importance of Medicago species as a source for livestock feed, few studies have been conducted on their forage quality in Africa. The study of the nutritive value of M. sativa hay in South Africa showed that the highest recorded moisture content (140 g/kg) is below the critical moisture level of 160 g/kg for efficient storage [56]. The average ash content is a mean of 130 g/kg (73 to 295 g/kg), indicating soil contamination. Furthermore, according to acid detergent fiber-crude protein (ADF-CP) contents, 6% of the samples were damaged by heat. High mean values of Ca (13.5 g/kg), P (25.3 g/kg), and Fe (874 mg/kg) were noted.

7. Conclusions and future perspectives

A high level of genetic and symbiotic diversity within and among natural populations of Medicago species in Africa exists. Most of this genetic variation resides within populations. A specificity of interaction has been recorded between plant species and rhizobial or pathogen genotypes, indicating that there is a certain level of coevolution between plants and their associated microorganisms.

Moreover, a large diversity of responses to abiotic and biotic stresses was found within or among natural populations of Medicago species. Importantly, this variability in responses is associated with the site of origin from which the genetic material was collected.

Further work is needed to establish an African consortium for the conservation and valorization of Medicago species and their associated microbes. This consortium will strengthen efforts to enhance the ecological and agronomic interests of endemic species of this genus. In this context, organization of new prospecting and collection campaigns for the genetic material of endemic Medicago species, especially those that have become rare or endangered, will be of great benefit. It will also be interesting to evaluate the agronomic performance of Medicago accessions in multi-local field trials in different African countries with a view to selecting new varieties that are tolerant to abiotic and biotic constraints and have good nutritive value.

Additionally, it is important to take advantage of the genetic and genomic tools that have been developed by the international scientific community to improve endemic perennial and shrub Medicago species in Africa by developing new molecular markers for selection.

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Conflict of interest

The authors declare no conflict of interest.
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