

A Review on the Root System of *Argania spinosa*

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Abstract

The Argane tree [*Argania spinosa* (L.) Skeels] is a remarkable essence by its botanical interest, ecological services, and its socio-economic value. This endemic species is known by its adaptive behavior to arid and semi-arid regions where it grows naturally in vast forests in Southwestern Morocco. Although its adaptation has been commonly attributed to various mechanisms in different organs and tissues, whose the root system has a primary role in this whole process. However, the increased aridity and desertification in the Mediterranean region appear to affect the health, growth and functioning of the root system of *A. spinosa*. In this review, we highlighted morphological aspects and physiological and biochemical mechanisms related to the roots and involved in the abiotic stress tolerance in the Argane tree. The mycorrhizal symbiosis in Argane tree plays a vital role in nutrient uptake and growth of this woody species, as well as in the adaptation to its environment. Despite the difficulties encountered in rooting during its *In Vitro* propagation, this technique seems to be an attractive alternative for the regeneration of the selected Argane tree.



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Introduction

The Argane tree [*Argania spinosa* (L.) Skeels] is an essential species in Southwestern Morocco; it contributes to the preservation of the forest's ecosystem by promoting the existence of a floristic and faunistic biodiversity¹ and plays a considerable socio-economic role through the production of Argane oil. Significant efforts combining chemical, agronomic, and human sciences have led to the international recognition and marketing of this oil.² *A. spinosa* is the only representative of the tropical family of Sapotaceae in Morocco. The climate in its natural distribution area is of arid Mediterranean type, where the rainfall is distributed unequally over the year.³ According to McGregor *et al.*,⁴ the Argane forests are part of a transitional zonation: Mediterranean-Saharan.⁴ The Argane tree grows naturally and abundantly in this transitional region in Southwestern Morocco, which is characterized by an arid and semi-arid climate. It displays a wide morphological diversity, which is evident even within the same locality and under similar eco-geographical conditions. This diversity provides a broad genetic basis for domestication and breeding programs.⁵⁻¹⁰

Since December 1998, the Moroccan Argane forests have been part of the worldwide network of biosphere reserves supported by UNESCO. The forests formed by Argane tree are the most extensive forests in Morocco after holm oak and red cedar. The main area of Argane forest, which create vast natural regions also known as "Arganeraie", is estimated at 900 000 hectares.¹¹ It originally covered a much larger area by extending over coastal, inland, and mountainous regions. The main area of *A. spinosa* forests distribution is limited to Southwestern Morocco, in the region of Agadir city, north of Oued Draa and south of Oued Tensift¹ between 29° and 32° north. The argane forest offers multiple functions (creation of a favorable microclimate for many fauna and flora, soil erosion protection, climate change mitigation, desertification control, etc.) and uses for local populations whose socio-economic activities are strongly linked to the various products that provides (oil, soap, shampoo, cosmetic creams, livestock feed, etc.).^{2,12,13} The Argane tree is a "multipurpose" tree; each part or production of the tree (wood, leaves, fruits, oil) is usable and is a source of income or food for the user.¹⁴ The Argane tree adapts to all kinds of soils, presenting a wide

range of soils in Western Morocco, except mobile sand. Thus, this tree can be found on poor and shallow soils due to its roots, acting as a support for its development.¹⁴

The roots are the underground parts of the plant. They generally move downward in a positive geotropism and thus responding to gravity. The main functions of the roots are the anchoring of the plant in the soil, the absorption, and then the conduction of water and mineral nutrients. They must transport water and mineral nutrients to the stems and leaves, but also import the organic molecules from stems and leaves through the phloem and xylem. Besides absorption and conduction functions, the roots produce hormones and other substances that regulate the development and structuring of the plant. Early in evolution, plants have acquired the ability to associate with soil fungi symbiotically.¹⁵ Despite the few studies on Argane root system, the results found showed important adaptive mechanisms to some abiotic stress, especially drought stress¹⁶⁻¹⁸ and an excellent ability to establish a mycorrhizal symbiosis.¹⁹⁻²⁵ This review highlights various morphological, physiological and biochemical aspects relating to the functioning of the Argane root system in the face of different biotic and abiotic factors.

Roots of Argane Tree

A. spinosa is a long-lived tree species.¹ This woody species is characterized by an original growth pattern that allows the elongation of stems and roots and the replacement of damaged or dead tissue. Like many perennial species, this tree also has a secondary growth, thus having a secondary meristem. Primary extension allows the Argane tree to explore, through its roots, the immediate surroundings to get what they need. These roots can also absorb water and mineral elements from new soil layers, deep and lateral, still rich in resources.²⁶ While the shallow roots are generally dedicated to nutritional inputs, the deep ones allow hydration and enhance the stability of sloping soils. Like some plant species, *A. spinosa* possesses a dimorphic root system that seems related to flexible water uptake pattern.^{27,28} In adult Argane trees, the root system is gradually and slightly being substituted by the lateral root system through to trap water in the surface soil. The presence of these both roots, those that continue

the proliferation in-depth (taproots) and roots that develop horizontally, allows for nutrient uptake near the surface and water uptake from deep soil layers when the surface dries.¹⁸ This species plays an essential ecological role in its territory, threatening by some biophysical processes as the advance of desertification.^{29,30} Also, it protects against rain erosion especially in mountainous regions. Due to its dimorphic root system, Argane tree is an effective stabilizer of soils in the mountains. In addition, the hydraulic redistribution in soil mediated by its root system (especially deep roots) contributes to lift or redistribute water from layers of wetter soil to layers of dryer soil, which allows the maintenance of soil moisture.^{1,26} These characteristics make it an interesting tree for developing arid zones. The soil remains relatively moist under the tree, and microbial activities are more important, especially regarding nitrogen mineralization and phosphorus availability.^{22,31} From the point-of-view of morphology, the Argane tree is characterized by magniloid roots, devoid of absorbing root hairs. The latter is not essential for symbiosis because of the roots of Argane tree associated with arbuscular mycorrhizae.³² Many mycelial hyphae, visible only under the microscope, emerge from the root and explore a considerable volume around this magniloid roots.²⁴

Impact of Changing the Climate on Argane Tree

The phenological shifts in plant communities are one of the most sensitive indicators of global warming, which can have multiple impacts on ecosystem processes.^{33,34} The Intergovernmental Panel on Climate Change (IPCC) concluded that plant phenology is the easiest way to track the ecological effects of climate change.³⁵ Since the roots are an important part of plant biomass and phenology roots may not respond to warming in the same way as the shoots, this constitutes a significant scientific knowledge gap on the impact of climate change on phenology and performance of plants. But root phenology, as a function of depth, can be influenced by environmental factors, such as humidity and temperature,³⁶⁻³⁸ and limiting water resources are the main risk factors responsible for tree loss and forest dieback.³³ In Morocco, the scarcity of water resources is the main factor limiting productivity, particularly in the arid and semi-arid regions, which represent over two-thirds of the country.³

The main area of distribution of Argane forests is characterized by low and variable rainfall and frequent droughts. The prolonged drought has had adverse ecological consequences, including loss of vegetation cover in some areas, removal of shrubs, and lowering of groundwater. Monitoring the evolution of forest ecosystems through many parameters (growth, phenology, nutrition and health of the forest treesb ...), while considering the environmental variations in one hand and the other hand management of natural resources in the face of climate change require the search for indices and evaluation methods.³⁹ According to an integrated conceptual model of degradation in the Argane woodlands, le Polain de Waroux and Lambin²⁹ found that the Argane tree density decreased by 44.5% in the Awluz region between 1970 and 2007, as part of a long decline since the 18th century.⁴ The increasing aridity due to climate variability or change was the primary cause of this loss of Argane forest.^{29,30} Besides the effect of climate change, Zhao *et al.*,⁴⁰ demonstrated that the human impact on Argane woodlands increases, leading to a sparse vegetation cover and increased erosion.

Effect of Drought Stress on The Roots of Argane Tree

The Argane tree is a species adapted to arid and semi-arid climatic regimes in Southwestern Morocco due to its deep root system compared to species adapted to mesic climatic conditions.^{26,41} Generally, tree species adapted to arid climatic conditions are characterized by a higher root/shoot ratio. In a study of 62 tropical tree species, dry forest seedlings have been shown to have underground biomass and deeper roots than seedlings from moist forests.⁴² Under dry conditions, adapted tree species invest more and sustainably in the root organ biomass, thus optimizing water absorption while minimizing water loss through transpiration. The Argane tree has developed effective physiological strategies to adapt to drought conditions via mechanisms related to water status and its regulation. It limits water loss through stomatal closure, increased leaf water potential and solute accumulation.⁴³⁻⁴⁷ But to reduce consumption and enhance water absorption, trees respond to drought stress by contributing to increase root-to-shoot ratio and rooting depth^{15,48,49} further. The change in dry root / shoot biomass ratio is one of mechanisms involved in drought avoidance.¹⁵ Until

today the root system has been the subject of few studies (Table 1). Given the high genetic variability of the Argane tree, a study conducted on eight selected genotypes of *A. spinosa* has shown that under drought stress, even a severe stress, some Argane tree genotypes have significantly increased their fresh and dry root-to-shoot biomass ratio, while maintaining larger investments in the primary root and lateral roots.¹⁶ However, Chakhchar *et al.*,¹⁸ reported in Argane seedlings subjected to severe drought stress, by withholding the irrigation for 40 days, that root length and diameter, and root-to-shoot ratio did not change significantly in comparison with control. These findings demonstrate the capacity of Argane seedlings to maintain root elongation despite the decline in root biomass under drought stress. As a water-use strategy, Argane root system can maintain its growth in length to explore deeper soil horizons.^{26,41} Physiologically (Table 1), a significant decrease in root-relative water content has been recorded in Argane seedlings under drought stress conditions.¹⁷ Nonetheless, Chakhchar *et al.*,¹⁸ showed a considerable reduction in root hydraulic conductivity in Argane seedlings under

severe drought stress. This reduction could be a biophysical response to minimize water loss by *A. spinosa* roots through water channels⁵⁰ and to maintain leaf hydration,⁵¹ and it could also be due to cell wall suberization.⁵² The recourse to these strategies may allow the Argane tree to conserve and maintain the growth and functioning of its roots under drought conditions. However, this physiological response was associated with an increase of root electrolyte leakage, signaling an injury to root cell membranes¹⁸. In addition, significant accumulation of malondialdehyde, as an indication of lipid peroxidation, was observed in the root of Argane seedlings under drought stress.¹⁷ Thus, at the biochemical level (Table 1), proteins and proline contents increased in roots of *A. spinosa* seedlings, as well as the peroxidase activity in response to severe drought stress.¹⁷ These changes were related to the duration of drought stress applied. These traits that occurred at the cellular level seem to be considered as heritable adaptive traits constituting the internal mechanism of tolerance to drought stress in *A. spinosa*.

Table 1: Summary of different root traits from studies conducted on *Argania spinosa* root system under different abiotic and biotic conditions

Root trait	Factors	Root traits	Reference
Morphological and growth	Drought stress	- Root length	- Chakhchar <i>et al.</i> , ¹⁸
		- Root dry biomass	- Meslem <i>et al.</i> , ¹⁷
		- Fresh root biomass	- Zahidi <i>et al.</i> , ¹⁶
		- Root diameter	
		- Root/shoot biomass ratio	
		- Root water content	
		- Number of lateral roots	
	Salt stress	- Root length	- Reda Tazi <i>et al.</i> , ⁵³
	- Root dry biomass		
	Morphological and growth	Mycorrhizal inoculation	- Root length
- Root fresh biomass			- Elmaati <i>et al.</i> , ²³
- Root dry biomass			- El Mrabet <i>et al.</i> , ²²
Germination and in vitro techniques (cuttings, grafting, micropropagation,...)		- Root dry weight	- Boussemame <i>et al.</i> , ⁵⁴
		- Root length	- Nouaim and Chaussod ^{19,20}
		- Rooting percentage	- Lamaoui <i>et al.</i> , ⁵⁵
		- Number of roots	- Zunzunegui <i>et al.</i> , ⁴¹
		- Root/ shoot elongation ratio	- Justamante <i>et al.</i> , ⁵⁶
			- Metougui <i>et al.</i> , ⁵⁷
			- Nouaim <i>et al.</i> , ⁵⁸
	- Boussemmane <i>et al.</i> , ⁵⁴		

Physiological	Drought stress	- Root hydraulic conductivity	- Chakhchar <i>et al.</i> , ¹⁸
		- Root relative water content	- Meslem <i>et al.</i> , ¹⁷
Biochemical	Drought stress	- Root cell membrane injury	- Chakhchar <i>et al.</i> , ¹⁸
		- Proline content	- Meslem <i>et al.</i> , ¹⁷
		- Protein content	
		- Peroxidase activity	
		- Lipid peroxidation (malondialdehyde content)	
Architectural and geophysical	Field conditions (from early spring till midsummer)	- Electrical resistivity imaging	- Ain-Lhout <i>et al.</i> , ²⁶
Chemical	Mycorrhizal inoculation	- Macroelements content (N, P, K)	- El Mrabet <i>et al.</i> , ²²
		- Microelements content (Fe, Mn, Cu and Zn)	- Boussemmane <i>et al.</i> , ⁵⁴
			- Nouaim <i>et al.</i> , ³¹
Anatomical	Mycorrhizal inoculation	- Relative mycorrhizal dependency index	- Ouallal <i>et al.</i> , ²⁵
		- Percentage of roots mycorrhizal	- Sellal <i>et al.</i> , ²⁴
		- Microscopic examination of root	- Elmaati <i>et al.</i> , ²³
			- El Mrabet <i>et al.</i> , ²²
			- Echairi <i>et al.</i> , ²¹
			- Nouaiml and Chaussod ¹⁹
Genetic	Chloroplast DNA phylogeography	- Polymorphisms in chloroplast DNA	- El Mousadik and Petit ⁵

Effect of Salt Stress on The Roots of Argane Tree

The impact of salinity with different concentrations of NaCl on root growth in young seedlings of *A. spinosa* was tested by Reda Tazi *et al.*,⁵³ *In Vitro*. These authors reported decreasing of the root length with increasing concentration of NaCl in the medium. They also observed a decrease in root biomass of approximately 57.6% compared to the control, for the concentration 9 g/l NaCl.⁵³ The Argane tree seems to be a species sensitive to salt stress.^{53,59} In an *In Vitro* study, negative correlation was reported between *A. spinosa* callus growth and salt stress severity.⁵⁵ The obtained results showed that concentration over 128 mM (NaCl) had noticeably inhibited calli growth. Nevertheless, the authors of the quoted study proved the efficiency of salt stress in boosting the Argane cell's antioxidant status, which could be commercially applied in the field of tissue engineering and regenerative therapy.⁵⁵

Mycorrhizal Symbiosis in Argane Tree

Most forest trees in the arid and semi-arid regions benefit from this symbiosis between their roots and specialized endophytic fungi.⁶⁰ The Argane tree is

characterized by a vital dependence (mutualism).²⁴ This species is a good model of a host plant for root symbioses in arid woody plants. The Argane tree can associate with arbuscular mycorrhizae (AM) fungi belonging to the *phylum Glomeromycota*. Nine provenances of Argane tree from Southwestern Morocco have been the subject of a study focused on the assessment of the mycorrhizal potential of soils and determination of the community structure of the fungi in different edapho-climatic situations.²⁵ The results of this study showed that the cytological organization of the mycorrhizae observed in *Argania spinosa* is arbuscular mycorrhizae in all samples analyzed with a broad dominance of the genus *Glomus* (approximately 80%).

When the fungus reaches the internal cortical cells of the Argane roots, the hyphae branch out and colonize the intercellular space. Once internal tissue colonization is substantial enough, the hyphae penetrate the inner cortical cells by invagination of the root cells (membrane level), forming fine branched complex structures called arbuscules (Fig. 1).²⁴ These developed structures

are a metabolic exchange interface between the root of the Argane tree and the fungus. Inoculation of young Argane seedlings with a strain of *Glomus intraradices* showed a beneficial and significant effect on plant size and biomass compared with non-mycorrhizal plants.^{19,20,21,24} Thus, Boussemmane *et al.*,⁵⁴ reported that endomycorrhization of Argane plants by *Glomus* strains significantly improved height growth, dry biomass of shoot and root parts, and mineral nutrition. Sellal *et al.*,²⁴

tested endomycorrhizal composite inoculum effect composed of arbuscular mycorrhizae fungi belonging to six genera: *Acaulospora*, *Glomus*, *Scutellospora*, *Entrophospora*, *Pascispora* and *Gigaspora* on Argane plants under nursery conditions. The results obtained by these authors also showed a positive and significant effect on the growth of inoculated plants (shoot and root biomass) compared with controls.

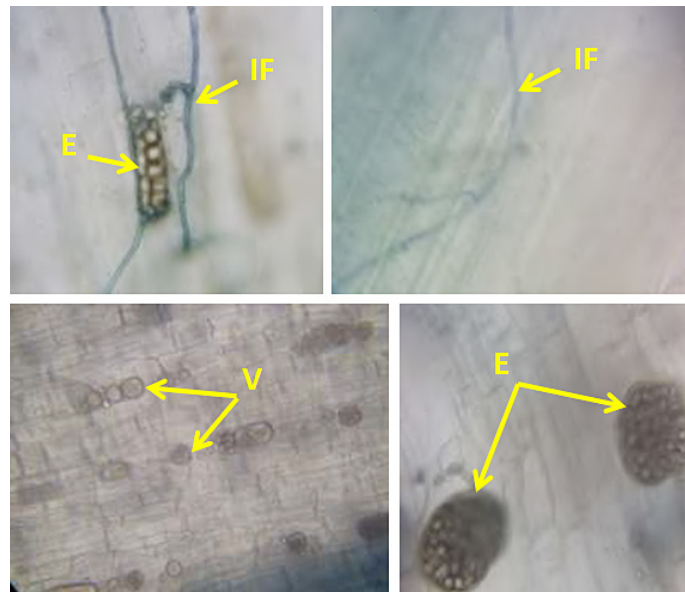


Fig. 1: Microscopic observation of some of arbuscular mycorrhizae structures in the roots of inoculated Argane plants. IF, internal hyphae, E, endophyte and V, vesicule. (Sellal *et al.*,²⁴)

In addition, the relative mycorrhizal dependence index of inoculated Argane plants reached 80% after 6 months of growth under controlled conditions, in the presence of mineral nutrition and suitable irrigation.¹⁹ This mycorrhizal symbiosis has stimulated the absorption of macroelements, in particular nitrogen, phosphorus, potassium and calcium, and microelements such as iron, zinc, manganese and copper.^{22,31,58} This dependency is all the more important as the soils of Argane forests are low in phosphorus and sometimes reach the thresholds of deficiency for micronutrients. Improved mineral nutrition of Argane plants has resulted in significant biomass production.⁵⁴ This mycorrhizal symbiosis is essential for the Argane tree; it allows a good recovery of plants in the natural environment,

limiting the stress of transplantation and promoting initial growth through the improvement of mineral nutrition and water supply. Mycorrhization in the Argane tree has shown a long-term positive effect on inoculated and transplanted Argane plants in their natural environment.⁶¹ The beneficial effect of mycorrhization has been confirmed on several phenotypic and genotypically different Argane plants propagated by cuttings.^{20,54} Controlled and early inoculation of young seedlings of *A. spinosa* by a strain of *Glomus intraradices*, showed that mycorrhizal plants grow better than non-mycorrhizal controls, thus confirming the strong mycorrhizal dependence of the Argane tree.²¹ This also justifies the importance of inoculating the Argane tree with selected fungus strains early, at the nursery stage

Rooting of Argane Tree by different Culture Techniques

Assessment of the multiplication mode of the Argane tree consists in considering the state of the root system, i.e. above all the integrity and the length of the pivoting system, but also its architecture and branching, as well as the degree of mycorrhization of the secondary roots which carry the bulk of mycorrhizal symbiosis.^{20,21,54} Regarding the different multiplication techniques involved in the Argane tree, both rooting and growth rates of the root system are highly variable and depend primarily on the multiplied genotype.⁵⁷ The genetic diversity of the Argane tree is a significant difficulty in its micropropagation, and it proves impossible to develop a single medium or combination allowing the multiplication and rooting of all genotypes. There were also problems related to Argane root formation *In Vitro* culture, such as apical necrosis, absence of secondary roots and blocking of root elongation. However, a significant rooting rate (over 50%) have been recorded in Argane *In Vitro*-plants.^{55,56,58} This technique provides the opportunity to produce genetically identical Argane plants by capturing attractive adaptive and productive traits of selected genotypes to ensure successful conservation and move from an exclusively wild plantation to an oilseed crop. Lamaoui *et al.*,⁵⁵ pointed out that well-rooted Argane *In Vitro*-plants were successfully acclimatized and then transferred to the field with a 100% survival rate.

The other methods of vegetative propagation of the Argane tree by cuttings, grafting, and layering (marcotting) are possible, despite the difficulty of rooting which depends on several endogenous and exogenous factors. In the natural environment of the Argane tree (Argane forest), the marcotting process is more common than suckering, especially along the Oueds, in the plains and very windy areas. In the latter case, the Argane trees are lying down by the sea winds, and their lower branches are rooted. Adventitious roots, often few, appear at the base of these branches. However, it is impossible to take advantage of these natural marcots to regenerate

the Argane tree.^{62,63} Given the ability to develop suckers of one to two meters around the trunk in some stations, *A. spinosa* is therefore very apt to be propagated by cuttings of root segments.^{62,63} But new cultivation techniques used in the nursery have made it possible to produce seedlings with several pivoting roots and a dense network of lateral roots, which in plantations will then develop vigorously.⁶⁴

Conclusion

Adaptation of *A. spinosa* to its environment in Western Morocco is mostly due to its root system. Despite the few studies performed on the roots of this species, these last reveal essential physiological and biochemical potentialities allowing Argane tree to overcome specific abiotic stresses and establish important mycorrhizal symbiosis. These innate and acquired features of the root system ensure the development and natural regeneration of the species in the Moroccan Argane forest. However, natural regeneration remains insufficient to maintain its existence and conservation. So, *In Vitro* culture, after control and improvement of its rhizogenesis, seems to have many advantages for the production of selected and elite Argane genotypes with high yield oil production, and consequently, the development of an agroforestry system based on Argane tree.

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Conflict of interest

The authors declare that they have no competing interests.

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