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Ecophysiological aspects and photosynthetic pathways in 105 plants species in saline and arid environments of Tunisia

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Abstract: In Tunisian arid regions, plant life forms, ecotypes, physiological types and photosynthetic pathways (C_3, C_4 or CAM) remain unclear. Understanding the characters of these plant species could be important for land restoration. A literature survey was conducted for 105 plants species in arid regions of Tunisia. These plant species belong to several ecotypes: halophytes, xerophytes, gypsophytes, psamophytes, xero-halophytes, gypso-halophytes, psamo-halophytes, psamo-xerophytes, xero-gypsophytes and hygro-halophytes. The variation of photosynthetic pathway types in the 105 studied species shows that 56.2% were C_3, 41.0% were C_4, 1.9% were CAM and 1.0% were C_3-CAM. The C_3 pathway was more abundant in the halophytes, whereas the C_4 one was more common in the xerophytes, gypsophytes, gypso-halophytes and psamo-halophytes. The ratio of C_3 to C_4 species (C_3/C_4 ratio) was 0.2 in the psamo-halophytes, 0.8 in the gypso-halophytes, 1.1 in the xerophytes, 1.6 in the xero-halophytes, 1.8 in the hygrohalophytes, 2.0 in the psamophytes and 3.8 in the halophytes. The annuals were mainly C_3 plants whereas most of perennials were C_4 ones. The C_3/C_4 ratio was 1.3 in succulent species and 1.4 in non-succulent species. Thus, succulence seems not to affect the distribution of C_3 and C_4 pathways within the studied plants. This investigation shows high percentages of C_4 plants occurred in Tunisian arid regions. However, there were significant differences in their abundance among ecotypes. Basing on C_3/C_4 ratio, we can find that the abundance of the C_4 pathway was in the following order: psamo-halophytes, gypso-halophytes, xerophytes, xero-halophytes, hygro-halophytes, psamophytes and halophytes. In Tunisian arid regions, C_4 species were most abundant in xerophytes and less abundant in halophytes. In the Chenopodiaceae the number of C_3 plants was 13 and the number of C_4 species was 20 and in the Poaceae the number of C_3 was 23 and the number of C_4 was 19 species. Thus, the most C_4 proportion was in the Chenopodiaceae and Poaceae species. This confirms the fact that the Chenopodiaceae and the Poaceae were the leading families that tolerate salinity and aridity.

Keywords: C_3; C_4; CAM; life form; ecotype; physiological type; Tunisian arid regions

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In arid and saline regions, plants develop different forms of photosynthetic pathways to cope with the extreme conditions. There are three types of photosynthesis on earth, which are C_3, C_4 and CAM. The most common and the most primitive is C_3 pathway (or Calvin-Benson cycle). The C_4 pathway (or Hatch-Slack cycle) is a more evolutionarily recent photosynthetic pathway. The third one is the crassulacean acid metabolism (CAM). The majority of terrestrial plant species (about 95%) use the C_3 photosynthetic pathway (Osborne and Freckleton, 2009). And only 5% of species have C_4 or CAM photosynthetic pathways. However, C_4 photosynthetic pathway accounts for approximately 18% of the total global

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photoproductivity (Ehleringer et al., 1997). In saline and arid areas, the efficiency of C_3 photosynthetic pathway is compromised by the increase of photorespiration and its rate is strongly limited by CO_2 diffusion from the atmosphere. Under arid climate conditions, photorespiration increases at low CO_2 concentrations and high temperatures. The reduction of stomatal aperture decreases CO_2 diffusion, which limits photosynthesis activity (Osborne and Freckleton, 2009). C_4 photosynthetic pathway draws mesophyll CO_2 down to lower concentrations than that C_3 pathway. It also allows stomatal conductance to be reduced, leading to greater water use efficiency under the same environmental conditions (Downes, 1969). In addition, C_4 photosynthetic pathway has the potential to achieve higher rates of photosynthesis than that C_3 pathway. It also maximizes dry matter production in water shortage conditions (Osborne and Freckleton, 2009). The mechanism should therefore confer significant selective and competitive benefits for C_4 plants over C_3 species in arid climates. CAM plants were shown to be the least abundant. In these species, CO_2 uptake occurs at night, when stomata open. They typically grow in semi-arid regions, where water deficit is frequent. Indeed, it is widely accepted that CAM photosynthetic pathway is an adaptive mechanism which optimizes water use under conditions of deficient water supply (Herrera, 2009).

It is well known that saline and arid environments are characterized by specific vegetation mainly composed of halophytes, xerophytes, gypsophytes, xero-halophytes, gypso-halophytes and psamo-halophytes. They exhibit morphological and physiological adaptations that allow them to accomplish their life cycle in these environments (Atia et al., 2011). For instance, xerophytes are characterized by a low area/volume ratio and a high palisade tissue/spongy tissue ratio (Wang et al., 2004). Additionally, xerophytes have few relatively large stomata, a thick cuticle, a well-developed water storing tissue, dense epidermal hairs and well-developed water transporting tissues. These adaptations reduce transpiration rate (Wang et al., 2004). Two main groups of halophytes can be distinguished according to their tolerance mechanisms: excluders and includers (Koyro et al., 2008). Excluders minimize ion toxicity and nutritional imbalances by salt exclusion, i.e. avoiding toxic ions by secreting them via salt glands. They are mainly subject to osmotic stress and are non-succulent halophytes. In contrast, includers reduce water deficit by loading toxic ions in vacuoles. They are mainly subject to ion toxicity and nutritional imbalances. The latter two factors can be counteracted, e.g. by salt restriction in the vacuole or by re-translocation via phloem. The osmotic balance between the cell compartments and organs is maintained by the accumulation of compatible organic solutes, such as proline, glycine-betaine and inorganic solutes such as potassium in the cytoplasm (Hafsi et al., 2010). The includers are generally known as succulent halophytes. These mechanisms permit halophytes to survive in extreme environments. Thus, both xerophytes and halophytes have the highest water holding capacities.

However, in Tunisian arid regions, the relationships among plant life form, ecotype, physiological type and photosynthetic pathway remain unclear, and these data are important for land restoration.

This study aims to (1) present an overview about the photosynthetic pathways of arid vegetation in Tunisian and (2) determine the distribution of photosynthetic pathways (C_3, C_4 and CAM) within plant ecotypes, physiological types and life forms in arid environments in Tunisia.

1 Study area and methods

1.1 Study area

In Tunisia, 65% of the terrestrial surface is arid. In these regions, climatic and soil conditions are commonly harsh and unfavourable for plant growth as a result of high evaporation, limited water supply and nutrient availability, low soil organic matter content and high salinity. The climate is characterized by an extreme spatiotemporal irregularity of precipitations. In these areas, the annual precipitation is lower than 300 mm and erosion is intensive. The highest evaporation in these regions is varied between 900–1,200 mm/a while the annual average temperature is 18–21°C. The maximum daily temperature reached 55°C. Furthermore, the increase of anthropogenic disturbances contributes to desertification. For instance, the clear-cutting of native vegetation and the replacement cropland has led to underground water table rising thereby enhancing soil evaporation and salt deposition.

In Tunisia, the flora of arid regions groups about 1,630 species (Chaieb and Boukhris, 1998) essentially composed of therophytes (43%), chamephytes (30%) and hemicryptophytes (20%). Geophytes and phanerophytes are less abundant, which represent only 4% and 2% of total species, respectively. However, there are a few data about the ecophysiological aspects and photosynthetic pathways of these floras in Tunisia. It is well known that high light intensity, high temperature and frequent water shortage are common characters of arid regions. These conditions favour the presence of the C_4 plants.

1.2 Methods

A literature survey study was conducted. Information regarding species, life form, ecotype, and physiological type (succulent or no-succulent) were obtained from the following references: Flora of Tunisia (Cuénad et al., 1954; Pottier-Alapetite, 1979; 1981) and Flora Succinct and Illustrated of Arid Zones of Tunisia (Chaieb and Boukhris, 1998). Some were from internet sites: www.efloras.org and an official site of the Botanical Society of French: www.bium.parisdescartes.fr/sbf/. The photosynthetic pathways were determined by using the following references: Winter (1981), Ziegler et al. (1981); Collins and Jones (1985), Batanouny et al. (1988), Akhani et al. (1997) and Yensen database (http://www.ussl.ars.usda.gov/pls/caliche/halophyte.query.). In this work the studied ecotypes, halophytes, xerophytes, gypsophytes, psamophytes, xero-halophytes, gypso-halophytes, psamo-halophytes, psamo-xerophytes, xero-gypsophytes and hygro-halophytes were commonly found in arid and saline zones (Chaieb and Boukhris, 1998; Alegro et al., 2004; Khadri et al., 2013).

2 Results

Out of the 105 studied species, the percentage of five ecotypes was higher than 10% for halophytes, xerophytes, xero-halophytes, psamo-halophytes and hygro-halophytes (Table 1; Fig. 1). The analysis of the photosynthetic pathway in the 105 studied species showed that 56.2% were C_3, 41.0% were C_4, 1.9% were CAM and 1.0% were C_3-CAM (Table 1). Thus, the C_4 form is highly represented in all studied ecotypes. In the halophyte, the species with C_4 form were less abundant in comparison to the abundance in the other ecotypes (Fig. 2). In this ecotype the C_3/C_4 ratio was 3.8 (Fig. 3). However, in the xerophytes the C_4 form was more abundant (Fig. 2). The C_3/C_4 ratio was 1.12 (Fig. 3). Surprisingly, all gypsophytes were C_4 (Fig. 2). A percentage of 2.9% of the studied species were psamophytes, of which 34.4% were C_4 types (Fig. 2). In these species, the C_3/C_4 ratio is 2.0 (Fig. 3). The

Table 1 Species, photosynthetic pathway, ecotype, succulence and life form

Species	C_3/C_4	Ecotype	Succulence	Life form
Aizoaceae				
Aizoon canariense	C_3	Hal	Succulent	Annual
Mesembryanthemum cristallinum	C_3-CAM	Hal	Succulent	Annual
Mesembryanthemum nodiflorum	CAM	Hal	Succulent	Annual
Apiaceae				
Crithmum maritimum	C_3	Hal	Succulent	Perennial
Asteraceae				
Inula crithmoides	C_3	Hyg-hal	Succulent	Perennial
Brassicaceae				
Cakile maritima	C_3	Hal	Succulent	Annual
Boraginacae				
Heliotropium curassavicum	C_4	Hal	Succulent	Perennial
Cactaceae				
Opuntia ficus-barbarica	CAM	Xer	Succulent	Perennial
Chenopodiaceae				
Anabasis aphylla	C_4	Psam-hal	Succulent	Perennial
Anabasis oropediorum	C_4	Hal	Succulent	Perennial

To be continued

Continue

Species	C_3/C_4	Ecotype	Succulence	Life form
Arthrocnemum macrostachyum	C_3	Hal	Succulent	Perennial
Atriplex coriacea	C_4	Psam-hal	Non-succulent	Perennial
Atriplex dimorphostegia	C_4	Xer	Non-succulent	Annual
Atriplex glauca	C_4	Hal	Non-succulent	Perennial
Atriplex halimus	C_4	Xer-hal	Non-succulent	Perennial
Atriplex mollis	C_3	Xer-hal	Non-succulent	Perennial
Atriplex tatarica	C_4	Gyp-hal	Non-succulent	Perennial
Atriplex portulacoides	C_3	Hal	Non-succulent	Perennial
Atriplex hastata	C_3	Hal	Non-succulent	Perennial
Bassia indica	C_4	Hal	Non-succulent	Annual
Beta maritima	C_3	Hal	Succulent	Annual
Chenopodium ambrosoides	C_3	Hal	Succulent	Annual
Cornulaca monacantha	C_4	Xer-hal	Succulent	Annual
Halocnemum strobilaceum	C_3	Hal	Succulent	Perennial
Halopeplis amplexicaulis	C_3	Hyg-hal	Non-succulent	Annual
Hammada scoparia	C_4	Gyp	Non-succulent	Perennial
Salicornia arabica	C_3	Hal	Succulent	Perennial
Salicornia europea	C_3	Hal	Succulent	Annual
Salsola vermiculata	C_4	Hal	Succulent	Perennial
Salsola kali	C_4	Psam-hal	Succulent	Annual
Salsola longifolia	C_4	Gyp-Hal	Succulent	Perennial
Salsola tetragona	C_4	Xer	Succulent	Perennial
Salsola tetandra	C_4	Xer-hal	Succulent	Perennial
Salsola sieberi	C_4	Psam-hal	Succulent	Perennial
Salsola villosa	C_4	Psam-hal	Succulent	Perennial
Suaeda maritima	C_3	Hal	Succulent	Annual
Suaeda fruticosa var. *langifolia*	C_3	Hal	Succulent	Perennial
Suaeda fruticosa var. *brevifolia*	C_3	Hal	Succulent	Perennial
Suaeda vermiculata	C_4	Hal	Succulent	Perennial
Traganum nudatum var. *abtusatum*	C_4	Gyp-Hal	Succulent	Perennial
Traganum nudatum var. *microphyllum*	C_4	Gyp-Hal	Succulent	Perennial
Cypreceae				
Cyperus capitatus	C_4	Hyg-hal	Non-succulent	Perennial
Frankeniaceae				
Frankenia pulverulenta	C_3	Hal	Succulent	Annual
Juncaceae				
Juncus maritimus var. *typicus*	C_3	Hyg-hal	Non-succulent	Perennial
Juncus maritimus var. *arabicus*	C_3	Hyg-hal	Non-succulent	Perennial
Juncus acutus	C_3	Hyg-hal	Non-succulent	Perennial
Poaceae				
Aegylops geniculata	C_3	Xer	Non-succulent	Annual
Aeluropus littorlis var. *intermedius*	C_4	Gyp-hal	Non-succulent	Perennial
Aristida coerulescens	C_4	Psam-hal	Non-succulent	Perennial
Bromus madritensis	C_3	Xer	Non-succulent	Annual
Catapodium regidum	C_3	Hal	Non-succulent	Annual
Cenchrus ciliaris	C_4	Xer	Non-succulent	Perennial
Crypsis aculeata	C_4	Hyg-hal	Non-succulent	Annual
Cutandia dichotoma	C_3	Xer	Non-succulent	Annual

To be continued

Continue

Species	C_3/C_4	Ecotype	Succulence	Life form
Cutandia maritima	C_3	Psam-hal	Non-succulent	Annual
Cutandia philistaea	C_3	Psam-xer	Non-succulent	Annual
Cymbopogon schoenanthus	C_4	Xer-hal	Non-succulent	Perennial
Cynodon dactylon	C_4	Xer-hal	Non-succulent	Perennial
Dactylis glomerata var. *hispanica*	C_3	Xer	Non-succulent	Perennial
Dactylis glomerata var. *maritima*	C_3	Xer-hal	Non-succulent	Perennial
Digitaria nodosa	C_4	Xer	Non-succulent	Perennial
Eragrostis barrelieris	C_4	Psam	Non-succulent	Annual
Hordeum marinum	C_3	Hal	Non-succulent	Annual
Cutandia philistaea	C_3	Psam-xer	Non-succulent	Annual
Hypparrhenia hirta	C_4	Xer	Non-succulent	Perennial
Imperata cylindrica	C_4	Psam-hal	Non-succulent	Perennial
Koeleria pubscens	C_3	Xer	Non-succulent	Annual
Lagurus ovatus	C_3	Xer-hal	Non-succulent	Annual
Lamarckia aurea	C_3	Hal	Non-succulent	Annual
Lolium rigidum	C_3	Psam	Non-succulent	Annual
Lygeum spartum	C_3	Xer-gyp	Non-succulent	Perennial
Oryzopsis miliacea	C_3	Xer	Non-succulent	Perennial
Panicum turgidum	C_4	Psam-hal	Non-succulent	Perennial
Panicum repens	C_4	Hyg-hal	Non-succulent	Perennial
Pennisetum setaceum	C_4	Xer	Non-succulent	Perennial
Polypogon monspelensis	C_3	Hyg-hal	Non-succulent	Annual
Schismus barbatus	C_3	Psam	Non-succulent	Annual
Spartina patens	C_4	Hyg-hal	Non-succulent	Perennial
Sporobolus pungens	C_4	Psam-hal	Non-succulent	Perennial
Sphenopus divaricatus	C_3	Hal	Non-succulent	Annual
Sphenopus syrticus	C_3	Hyg-hal	Non-succulent	Annual
Stipa capensis	C_3	Xer	Non-succulent	Annual
Stipa lagascae	C_3	Xer	Non-succulent	Perennial
Stipa parviflora	C_3	Gyp-hal	Non-succulent	Perennial
Stipa tenacissima	C_3	Xer	Non-succulent	Perennial
Stipagrostis ciliata	C_4	Gyp	Non-succulent	Perennial
Stipagrostis obtusa	C_4	Xer	Non-succulent	Perennial
Stipagrostis plumosa	C_4	Xer	Non-succulent	Perennial
Stipagrostis pungens	C_4	Psam-xer	Non-succulent	Perennial
Plumbaginaceae				
Limoniastrum monopetalum	C_3	Gyp-hal	Non-succulent	Perennial
Limonium sinuatum ssp. *eu-sinuatum*	C_3	Psam-hal	Non-succulent	Perennial
Limonium sinuatum ssp. *bonuelli*	C_3	Xer-hal	Non-succulent	Annual
Plantaginaceae				
Plantago coronopus	C_3	Hal	Succulent	Annual
Plantago crassifolia	C_3	Hyg-hal	Succulent	Perennial
Polygonaceae				
Polygonum patulum	C_4	Psam-hal	Non-succulent	Annual
Portulacaceae				
Portulaca oleracea L.	C_4	Hyg-hal	Succulent	Annual
Primulaceae				
Anagallis arvensis	C_3	Xer-hal	Non-succulent	Annual

To be continued

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Tamaricaceae				
Tamarix africana	C_3	Xer-hal	Non-succulent	Perennial
Tamarix aphylla	C_3	Xer-hal	Non-succulent	Perennial
Tamarix gallica ssp. *nilotica*	C_3	Xer-hal	Non-succulent	Perennial
Tamarix gallica ssp. *gallica*	C_3	Hal	Non-succulent	Perennial
Tamarix boveana	C_3	Hyg-hal	Non-succulent	Perennial
Zygophyllaceae				
Nitraria retusa	C_3	Gyp-hal	Succulent	Perennial
Peganum harmala	C_3	Hal	Succulent	Annual
Zygophyllum album ssp. *album*	C_3	Gyp-hal	Succulent	Annual
Zygophyllum album ssp. *geslini*	C_3	Hal	Succulent	Annual

Note: Hal, Halophyte; Xer, Xerophytes; Xer-hal, Xero-halophytes (desert species suspected as halophytes). Gyp, Gypsophytes; Psam, Psamophyte; Psam-hal, Psamo-halophytes; Gyp-Hal, Gypso-halophytes; Xero-gyp, Xero-gypsophytes; Psam-xer, Psamo-xerophytes.

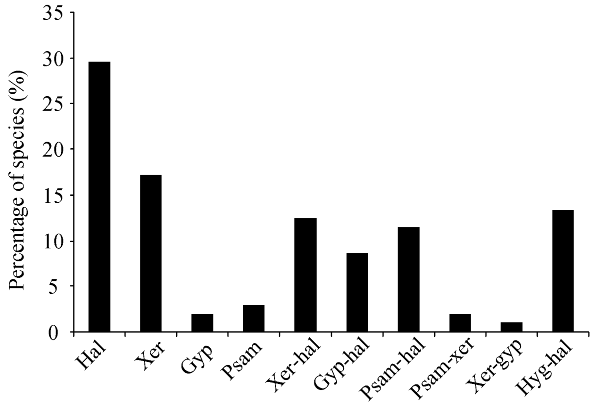

Fig. 1 Percentage of different ecotypes in the studied species. Hal, Halophyte; Xer, Xerophytes; Xer-hal, Xero-halophytes (desert species suspected as halophytes). Gyp, gypsophytes; Psam, Psamophyte; Psam-hal, Psamo-halophytes; Gyp-Hal, Gypso- halophytes; Xero-gyp, Xero-gypsophytes; Psam–xer, Psamo- xerophytes. Symbols are the same as in Figs. 2 and 3.

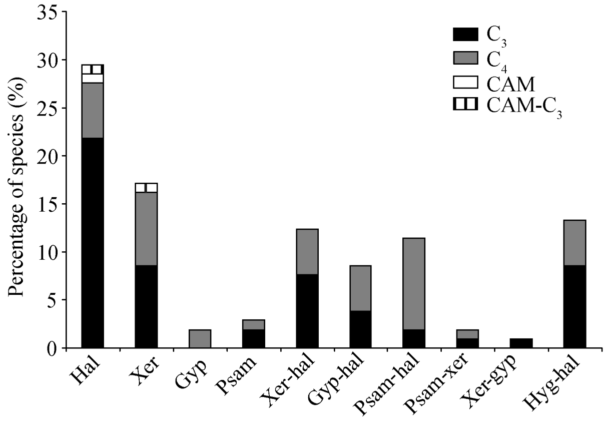

Fig. 2 Variations of photosynthetic pathway in different ecotypes

xero-halophytes represent 12.4% of the studied species, 4.8% of them were C_4 (Fig. 2). Their C_3/C_4 ratio is 1.6 (Fig. 3). In the gypso-halophytes the dominant form was C_4 (Fig. 2). The percentage of C_4 psamo-halophytes species reached 9.5% (Fig. 2). In these species, the C_3/C_4 ratio was 0.2 (Fig. 3). The percentage of the psamo-xerophytes was about 2% and the C_3/C_4 ratio was about 1 (Fig. 2). The xero-gypsophytes was represented by 1 species and had C_3 photosynthetic pathway (Fig. 2). The percentage of hygro-halophytes was 13.2% and 4.8% of them was C_4 (Fig. 2). And their C_3/C_4 ratio was 1.8 (Fig. 3). As concerns physiological type, there were two types in the 105 studied species: 38 species were succulent and 67 species were non-succulent (Table 1). Among the succulent species, 19.0% were C_3, 14.3% were C_4, 1.9% were CAM and 1.0% were C_3-CAM (Fig. 4). Among the non-succulent species, there were 37.1% C_3 and 26.7% C_4 (Fig. 4). The C_3/C_4 ratio is 1.3 and 1.4 respectively for succulent and non-succulent species (Fig. 6a). Of the studied vegetation, there were 40

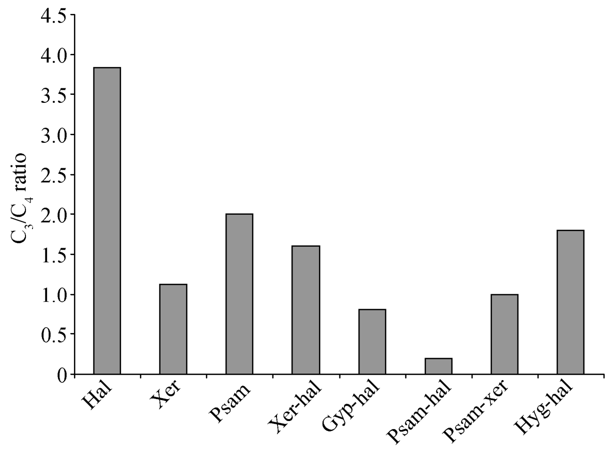

Fig. 3 Composition of different photosynthetic pathways (C_3/C_4 ratio) in different ecotypes

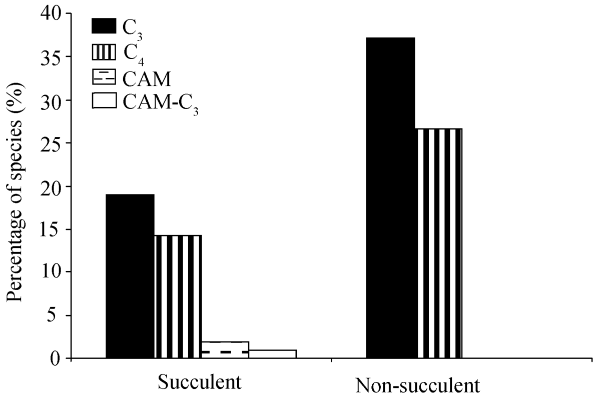

Fig. 4 Variations of photosynthetic pathway between succulent and non-succulent species

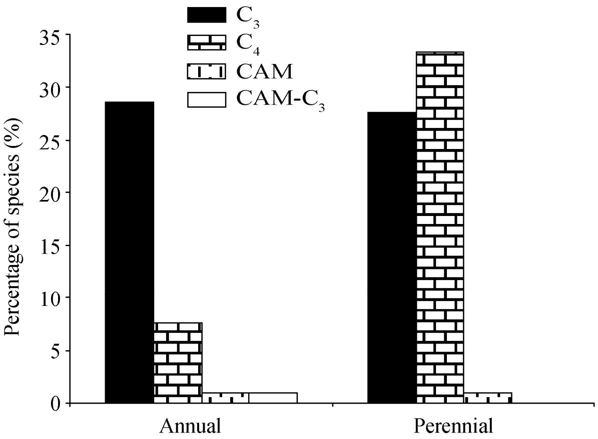

Fig. 5 Photosynthetic pathways variation between annual and perennial species

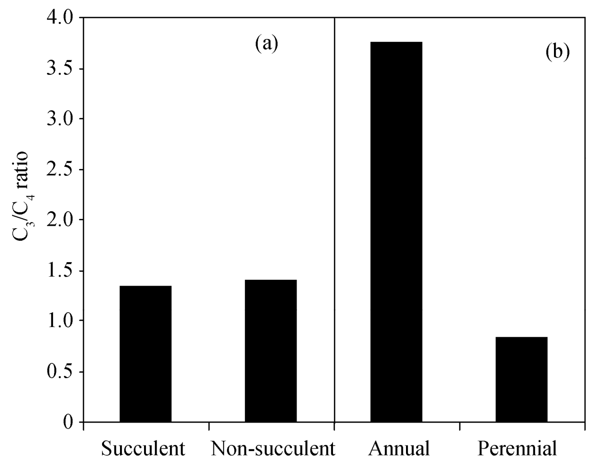

Fig. 6 Variations of C_3/C_4 ratio between succulent and non-succulent species (a) and between annual and perennial species (b)

annual and 65 perennial species (Table 1). Among the annual species, 28.6% were C_3, 7.6% were C_4, 1.0% were CAM and 1.0% were C_3-CAM. As regards the perennial species, 27.6% were C_3, 33.3% were C_4 and 1.0% were CAM (Fig. 5). The C_3/C_4 ratio was 3.8 and 0.8 for the annual and perennial species, respectively (Fig. 6b).

3 Discussion and conclusion

In this paper, the studied species were classified according to their life forms (annual or perennial), physiological types (succulent or non-succulent) and photosynthetic pathways (C_3, C_4 or CAM). However, the classification of plant species on the basis of photosynthetic pathways is the fundamental knowledge for a true understanding of the differences in ecophysiological responses among plants (Wang, 2007).

Terrestrial vegetation is composed of about 95% C_3 plants and only about 5% C_4 plants (Warrick et al., 1986). Thus, for total world vegetation, the C_3/C_4 ratio is about 19. This paper showed that there was an abundance of the C_4 group in the arid regions of Tunisia. This is a common property in all arid zones throughout the world. However, the composition of photosynthetic pathways differs greatly among ecotypes, life forms and physiological types (succulent and non-succulent species).

In the halophyte species, there is more abundance of C_3 species in comparison to their abundance in the other ecotypes. Relatively, more C_4 species were previously identified in halophytes around the world. For instance, Wang (2007) observed that in 61 halophytes, 18 species were C_4 and 43 species were C_3. However, in northeastern China, the number of C_4 species in saline grasslands was higher than in the other areas (Wang, 2002). The abundance of C_4 species was very common in saline regions because they had relative higher saline tolerance and water use efficiency (Wang, 2004).

In the xerophyte species, the C_3/C_4 ratio was 1.1. This ratio is very low when compared to C_3/C_4 world ratio. Thus, the dominance of C_4 plants among the xerophytes is evident. Our results are consistent with previous researches conducted in other arid areas in the world such as Xilingol steppes and Hunshandake Desert in China (Wang, 2002). This was mainly due to greater ability of C_4 species to maintain high photosynthetic activity during the dry season (Wang, 2004). In arid areas, the efficiency of C_3 photosynthetic pathway is influenced by the increase of photorespiration and its rate is strongly limited by CO_2 diffusion from stomata. However, C_4 photosynthesis minimises mesophyll CO_2 and reduces stomatal conductance for higher water-use efficiency than that of C_3 pathway under the same environmental conditions (Osborne and Freckleton, 2009).

In the xero-halophytes, the C_3/C_4 ratio was 1.6. Thus, the C_4 photosynthetic pathway was also abundant in the xero-halophytes. This is mainly due to the high tolerance of C_4 species to environmental stresses and the great ability to maintain high photosynthesis activity under harsh environment, e.g. drought and salinity (Wang, 2004). In the psamophytes, the C_3/C_4 ratio was 2.0. However, in the psamo-halophytes, there was a higher proportion of C_4 species, the C_3/C_4 ratio being 0.2. Indeed, these species are subjected to extreme conditions like sandy soil, e.g. fixed dunes and mobile dunes, salinity, low moisture conditions and low nutrient availability. These plants can be used for the vegetation recovery in arid areas in Tunisia. The occurrence of the hygro-halophytes under the arid climate was observed near the littoral zones and in salty marshes. In these conditions, plants are subjected to anoxia, high salinity and poor nitrogen nutrition (Drake, 1989). These results confirm the fact that C_4 is abundant (C_3/C_4 ratio=1.8) in the extreme conditions. Hence, photosynthetic pathway types, especially the occurrence of C_4 species, could be efficient indicators of stress tolerance.

A significant difference is observed between the annual and the perennial species in C_3/C_4 ratio. The C_4 pathway is more abundant in the perennial species than in the annual species. This is related to the fact that the formers should survive through dry season and consequently they need the C_4 photosynthetic pathway to overcome the severe conditions. The higher abundance of the C_3 pathway in the annual species is due to the fact that they are mainly winter annual species. They achieve their cycle during winter season and evade dry conditions. They go through the severe dry seasons in the form of seed.

In the Chenopodiaceae family, the number of C_3 plants is 13 and the number of C_4 species is 20 and in the Poaceae family the number of C_3 was 23 and the number of C_4 was 19 species (Table 1). Thus, the most C_4 proportion is in the Chenopodiaceae and Poaceae species. Although the latter species were more abundant, the formers had higher proportion of C_4. This confirmed the fact that the Chenopodiaceae (Winter, 1981; Pyankov et al., 2000) and the Poaceae (Wang, 2004) are the leading family that tolerate salinity and aridity and constitute the most abundant species in the studied region.

In conclusion, the C_4 photosynthetic pathway was evidently the abundant form in the flora of Tunisian arid regions. Most of C_4 species were found in Chenopodiacieae and Poaceae families. However, there are significant differences among ecotypes. According to the C_3/C_4 ratio, the abundance of the C4 pathway in Tunisia was in the order of psamo-halophytes>gypso-halophytes>xerophytes> xero-halophytes>hygro-halophytes>psamophytes> halophytes (Fig. 3). The annual species were essentially C_3 whereas most perennials are C_4 species. For succulent and non-succulent species, C_3 and C_4 photosynthetic pathways are similar in both physiological types.

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