Definition and Classification of Halophytes as an Ecological Group of Plants

Marius-Nicusor Grigore

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Abstract

The definition of halophytes is manifold. The concept evolved from the broader ecological definition of halophytes to specialize physiological and biochemical definitions; they are often arbitrarily based on numerical values of salinity thresholds. Classifications of halophytes are mainly focused on the affinity of plants for salts, for instance, their "obligatory" requirement for high salinity, in the case of euhalophytes (obligatory halophytes). Definitions of halophytes and their classification in an ecological frame are very important for establishing a correlation between halophytes and xerophytes, through the concept of physiological drought.

Keywords

Halophyte · Euhalophyte · Glycophyte · Salinity

M.-N. Grigore (✉)
Faculty of Biology, Alexandru Ioan Cuza University of Iasi, Iasi, Romania
e-mail: mariusgrigorepsyche@yahoo.com; mariusgrigore80@gmail.com; nicusor.grigore@uaic.ro

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1 Introduction

There are many definitions of halophytes that were attributed to them during time; halophytes are very diverse from taxonomical, morphological, anatomical, and even ecological point of view, so it is very problematic to find a unique definition of halophytes (Grigore 2008a, b, 2012; Grigore et al. 2010, 2012, 2014; Grigore and Toma 2010a, 2017; Grigore 2019).

Grigore et al. (2010) discussed several aspects on the difficulty of approaching a "standard" definition of halophytes. While halophytes have been mentioned since the time of Theophrastus (see Grigore's chapter on ► "A Botanical History of Halophytes: From Theophrastus to Nowadays," in this handbook), they were rigorously taken into scientific attention through the papers of Schimper (1903) and especially Warming (1909 and his previous publications). Although the history of halophytes is somewhat longer, their definition remains unclear (Grigore 2019). Within so many definitions of halophytes, it may be observed that some of them reflect the scientific profile of researchers who had defined these plants (Grigore et al. 2010).

2 Definition of Halophytes

Table 1 summarizes definitions of halophytes, following a chronological order (Grigore et al. 2010, 2014; Grigore 2019, 2012; Grigore and Toma 2017).

As seen from Table 1, definitions of halophytes are very diverse; several explanations were suggested to explain this large heterogeneity regarding the concept of halophyte (Grigore et al. 2010, 2014; Grigore and Toma 2017; Grigore 2019):

(a) *Halophytes represent a contrasting ecological group of plants.* This would imply that salinity is not the single environmental factor involved in projecting a complete definition of halophytes. Water regime of soil and plant is very relevant, and despite halophytes are subjected to physiological dryness, there are halophytes vegetating in unlike saline environments: seashore, inland saline, saline steppes and deserts, and mangroves. Therefore, some halophytes may be exposed to salt spray, others to high temperatures and others to tides and water logging. Consequently, botanists who had worked during time with halophytes from a specific and restricted point of view defined halophytes according to their particular interest.
(b) *The concept of salinity himself and hence those terms related to saline habitats are relative and equivocal*. *Salinity* is not a biological term, and this complicated ecological sciences, when it has been used for defining saline environments and consequently the species vegetating within. Defining halophytes as those species vegetating in saline environments is convenient, but perhaps without further questions of what is a saline environment and how salinity does affects them.
(c) *There is a historical diversification of research interest in halophytes, reflected by the progressively accumulated knowledge about them.* At the beginnings the

Table 1 Definitions of halophytes (for other definitions, here not included, see Grigore et al. 2014 and Grigore and Toma 2017)

Definition or short descriptions of halophytes	Author/s	Comments
Those (plants) growing near the sea [have a large proportion of soda in their composition, while those growing inland contain more potash. Various species of *Salsola*, *Salicornia*, *Halimocnemum*, and *Kochia*, yield soda for commercial purposes] and are called halophytes [Plants] *grow in salt marshes and are called halophytes* [Maritime or saline plants. These are plants which grow on the border of the sea, or of salt lakes, and require salt for nourishment, as *Salicornia*, glasswort, *Salsola*, saltwort. *Anabasis*.] Such plants are often called halophytes [Marine plants, such as seaweeds, lavers, etc., which are either buried in the ocean, or float on its surface: also, such plants as *Ruppia* and *Zostera*]	Balfour (1851)	A distinction between maritime and marine plants is being operated. This specialized distinction suggest that the most (exclusive) halophytic species are those that are in direct contact with seawater, while the others (maritime) are in relation to salinity, but not immersed in seawater
Plants growing in salty regions	Sorauer (1895)	An ecological definition
Plants which only flourish abundantly on soils rich in alkaline salts are called halophytes. The same name has also been applied to plants which only thrive in seawater	Von Marilaun (1894)	An ecological definition
[Halophytes] are essential xerophytes produced by the abundance of salt solutions in the soil and should be properly classed among xerophytic plants. A few, however, *Ruppia*, *Zostera*, etc., are aquatic, and in the event of the division of the group should be classed as halophilous hydrophytes	Pound and Clements (1900)	An ecological and physiological definition – taking into account the physiological drought of soil
[Some soils contain such an abundance of certain salts that only certain plants grow there]. These plants are known as halophytes (salt loving)	Atkinson (1900)	An ecological and physiological definition – taking into account the physiological drought of soil
Salt plants	Coulter (1900)	Brief ecological definition
Strand plants	Ward (1901)	Brief ecological definition
[Root absorption may also be diminished by the presence of salts dissolved in large quantities in the water about the root. Such an effect is wrought in salt marshes and on seashores above the tide, where the plants show characteristic xerophytic adaptations]. Plants fitted to life in such conditions are termed halophytes	Leavitt (1901)	An ecological and physiological definition – taking into account the physiological drought of soil
Saltwater plants [evergreen shrubs] preferring a saline soil (halophytes)	Mohr (1901)	An ecological definition

(continued)

Table 1 (continued)

Definition or short descriptions of halophytes	Author/s	Comments
[] seaside sort [plants]	Robinson (1902)	An ecological definition
Salt marsh plants and "alkali" plants, species which can flourish in a very saline soil	Bergen (1904)	An ecological and physiological definition
All saline plants	Clements (1905)	Brief ecological definition
A halophyte is a plant which can thrive in a soil containing much common salt or other saline substances	Bergen and Davis (1906)	An ecological and physiological definition
[Sand-dunes, sea-marshes, deserts, and old lake bottoms are more or less impregnated with salts of sodium, calcium, magnesium, and potassium]. Plants growing in such situations are termed halophytes	Laing and Blackwell (1907)	An ecological and physiological definition
Species of saline and alkaline soils (salt plants)	Clements (1907)	Saline and/or alkaline soils are terms more precise than other words designating saline environments
[If the water or saturated soil in which the plant lives contains salts, such as sea salt or the alkali salts of some of our Western lakes, then the conditions are said to be halophytic], and a plant living under such conditions is known as a halophyte	Hunter (1907)	An ecological and physiological definition
[At the same time, plants vary in this respect, and there are many (usually known as halophytes)] which can thrive on saline soil and are able to recover the necessary water from concentrated solutions of salts	Hole (1909)	An ecological and physiological definition
Many true halophytes, of course, occur on the seashore, [but the strand flora as such must rather be classified as a halophile flora], while the true halophytes are those plants which are confined to saline situations in the interior	Olsson-Seffer (1909)	An ecological definition
[Halophytes], which possess great power of resisting the action of sodium chloride in solutions as strong as seawater]	Harshberger (1909–1910)	A physiological definition
A certain amount of soluble salts must be present before halophytic vegetation is called into existence	Warming (1909)	How precise the term "certain" could be?
Plants which tolerate a larger proportion of mineral salts in the soil than can be endured by most plants	Bergen and Caldwell (1911)	A physiological definition
[Resembling in many respects, the true xerophytes] are the halophytes, or salt-marsh plants	Campbell (1911)	An ecological definition – taking into account the physiological drought of soil

(continued)

Table 1 (continued)

Definition or short descriptions of halophytes	Author/s	Comments
[The soil is saturated with saltwater], and the plants are typical halophytes	Bevis and Jeffery (1911)	An ecological definition – taking into account the physiological drought of soil
[Plants] which belong to saline habitats – halophytes – as they are called	Farmer (1911)	An ecological definition
Halophytes include plants growing by the seashore and the vegetation around salt springs and lakes and that of alkali deserts. The name halophyte applies more particularly to land plants that have adapted themselves to the presence in the soil or in the atmospheric vapor, of certain minerals, popularly known as salts, which cause them to take on many xerophyte characteristics	Andrews and Lloyd (1911)	An ecological and physiological definition – taking into account the physiological drought of soil
[The salt marshes possess a characteristic vegetation of what are termed halophytes], plants capable of resisting a considerable quantity of salt in the medium in which they grow	Hall (1912)	An ecological and physiological definition – taking into account the physiological drought of soil
Salt-loving plants	Horwood (1915)	Brief ecological definition
Salt-marsh plants are known as halophytes	Woodhead (1915)	Ecological definition
Halophytes are merely a form of xerophytes, as much salt in the soil renders it physiologically very dry	Stomps (1915)	An ecological and physiological definition – taking into account the physiological drought of soil
Halophytes, i.e., adapted for soils rich in saline constituents	Armstrong (1917)	A physiological definition – taking into account the physiological drought of soil
[Halophytes] The plants of this group live in a soil which is rich in soluble salt, usually common salt (NaCl), and, on account osmotic overcome to such physiologically dry. A halophyte, in fact, is one form of xerophytes	Youngken (1918)	An ecological and physiological definition – taking into account the physiological drought of soil
Plants growing in regions of much salt, though called xerophytes, are also conveniently termed halophytes to distinguish them from other xerophytes	Widtsoe and Stewart (1918)	An ecological and physiological definition – taking into account the physiological drought of soil
Plants which grow in salt water and salt marshes	Cook (1919)	An ecological definition
The seacoast plants, or halophytes []	Day (1920)	An ecological definition
The plants of this group live in a soil which is rich in soluble salt, usually common salt (NaCl), and on account of the fact that the osmotic force of the root is nearly inadequate to overcome that of the concentrated solution of the soil, the soil to such plants is physiologically dry. A halophyte in fact is one form of xerophytes	Youngken (1921)	An ecological and physiological definition – taking into account the physiological drought of soil

(continued)

Table 1 (continued)

Definition or short descriptions of halophytes	Author/s	Comments
[Halophytes] grow where saltwater is the governing factor	John (1922)	An ecological definition
[While seawater contains two and a half percent, and the soil of salt marshes, on which all these] halophytes, or salt-loving plants, grow, may contain even more salt	Townsend (1925)	A physiological definition – taking into account the physiological drought of soil
Salt-loving plants	Rendle (1925)	Brief ecological definition
Plants that tolerate salt water	Bailey and Coleman (1925)	A physiological definition
Halophytes or maritime species	Weatherby and Adams (1945)	Brief ecological definition
1. Plants which grow and complete their life cycle in habitats with a high salt content. 2. Usually, the term is reserved only for plants which appear in salty habitats constantly and specifically	Waisel (1972)	An ecological and physiological definition 1. It's very difficult to precisely say what high salt content represents 2. This remark of Waisel suggest that the term to be applied only to euhalophytes ("true halophytes")
Plants that can tolerate seawater, pure or diluted	Duncan (1974)	The seawater concentration is not a universal standard, so pure or diluted could be regarded as quite relatively adjectives
Salt-marsh plants are all halophytes, that is, plants that live in saline soils	Ornduff (1974)	An ecological definition
[The inland saline wetlands occur in poorly drained, semiarid regions, where high temperature evaporates much of the water, leaving the salts behind. Where insufficient leaching occurs the salts accumulate, forming alkali soils]. Plants on such sites are known as halophytes and are characteristic of saline flats and marshes that may be permanently or periodically flooded	Goodwin and Niering (1975)	An ecological and physiological definition
Plants of salty environments; plants adapted to live in a saline environment, be it seawater, a saltwater marsh, or a salt-desert. Plants found growing under naturally saline conditions; for terrestrial plants, this means a minimum salt concentration of about 100 mM in the soil solution. Plants adapted to complete their life cycles in salinities about that of seawater	Flowers et al. (1986)	An ecological and physiological definition

(continued)

Table 1 (continued)

Definition or short descriptions of halophytes	Author/s	Comments
The term halophyte literally means salt plants, but is used specifically for plants that can grow in the presence of high concentrations of Na salts	Sharma and Gupta (1986)	Perhaps referring also to the character of euhalophytes
Those species for which salt marsh is a major and, in any cases, only habitat	Adam (1990)	A good ecological definition
Halophytes are defined as those plants which grow and complete their entire life cycle in saline habitats. Coping with salinity needs adaptations on all levels from the autecological, the tissue, and cellular level to subcellular and biochemical adaptations	Breckle (1995)	"Entire" means inclusively producing seeds for assuring plant survival, colonization, and stabilization in any habitat A holistic definition
Halophyte species are those occurring in naturally saline conditions *only*	Aronson and Le Floc'h (1996)	Also suggesting the "obligate" character of (some) halophytes
Salt-tolerant plants (halophytes, including salt marsh and mangrove plants) are highly evolved and specialized organisms with well-adapted morphological and physiological characteristics allowing them to proliferate in the soils possessing high salt concentrations	Khan and Duke (2001)	A good holistic definition
Halophytes are able to adapt faster and to tolerate extreme salinity	Schulze et al. (2005)	A deeper physiological definition
Plants that survive to reproduce in environments where the salt concentration is around 200 mM NaCl or more	Flowers and Colmer (2008)	A physiological definition.
Plants able to complete their life cycle on saline substrates	Koyro et al. (2009)	An ecological and physiological definition
Plants that are tolerant of excess salt	Quinn (2009)	A physiological definition
Halophytes are plants that are adapted to saline environments and are able to survive and reproduce at salt concentrations of 200 mM or greater	(2018)	A physiological definition

attention was focused on halophytes ecology and distribution; thence, first definitions were the simplest in the direction of defining them as plants occurring in saline areas. Gradually, many aspects focused on physiology, salt tolerance, cellular and molecular biology, or genetics were revealed, and subsequently definitions of halophytes changed in this direction.

(d) *There is a semantic field related to halophytes* (especially regarding their classification). This field is composed by different terms, formulated by various authors, and these terms are more or less synonymous with each other. Sometimes, researchers have adopted previous established terms without new contributions to clarify them; in this way the "new" terminology does not implies a new clarification in the language referring on halophytes.

(e) *Many studies on halophytes were conducted in experimental conditions*, especially when trying to establish artificial salt-tolerance thresholds. However, as shown many times (Grigore et al. 2012), experimental design never completely reproduce natural ecosystem, where there is a subtle continuum of interactions between environmental factors. Sometimes, results derived from experimental approaches indicate unexpected or contradictory patterns of halophytes behavior as compared to natural situations (Grigore et al. 2012). Adversely, studies on salinity thresholds measured in plants in natural conditions may reveal unanticipated high salinity tolerance for species usually designated as glycophytic (Bucur et al. 1957 and discussions in Grigore 2013).

(f) The large diversity of saline environments and their terminology contributed to a lack of agreement on definition of halophytes. Ecologically, halophytes were linked to these saline environments that evolutionarily speaking had a formative effect on halophytes (Grigore 2008a; Grigore and Toma 2010a). Each saline habitat has different concentrations and composition of salts; "salinity" term seems to refer rather to the concentration than to composition of the soil solution. Some halophyte species are included in plant associations that have been described as chloride, sulphatic, carbonate (Șerbănescu 1965), but this would be applicable only for a given geographical area, while a species included in a such association may be found as well in another, from different geographical area.

(g) *Linguistics aspects*. Every language uses its own terms designating a halophyte, and Latin and Old Greek established some origin for many of the terms used today; some of them may be precise, while others less accurate. Often, terms or syntagms related to halophytes are not perfect synonyms, and slight differences may in fact cover large differences in respect with the ecology of halophytes. For instance, *marine* and *maritime* plants were described (Balfour 1851), but the first are restricted to those species submerged in seawater, while maritime plants refers to seashore species.

As can be observed, definitions of halophytes are based on ecological, physiological, ecological, and physiological criteria; many definitions have a background supported by the hypothesis of physiological drought of soil that would impose particular ecological conditions to soil and physiological responses in halophytes, respectively. Some of definitions are purely descriptive (brief ecological descriptions), and in this case, the evolution of halophytes definition started from descriptive, implicit characterization of plants to more sophisticated terms covering restricted definitions (for instance, the term euhalophyte) (see Table 2).

Table 2 Semantic field with different words related to halophytes (Grigore 2012)

Romanian	English
Halofite; plante de sărătură; plante halofile; plante iubitoare de săruri (sare); plante de locuri sărate; plante salifere	Halophytes; salt-tolerant plants; salt plants; high salinity tolerant plants; salt loving plants; halophylous plants; halophytic plants; maritime plants

Short ecological definitions were convenient at the beginning of study of halophytes, since authors needed to quickly discriminate halophytes from other ecological groups of plants and this without going to deep in their study. They would open further new directions of research and new ways in approaching halophytes' definition. For the sake of simplicity, an ecological definition of halophytes seems the more convenient option, and consequently halophytes must be considered all species hat vegetate in saline habitats (Grigore 2008a, b; Grigore and Toma 2010a).

A powerful example is that of *maritime plants* (*plante maritime*, in French), a term that has been indicated for more than 150 years to designate a halophyte. It was further translated or nominated as "halophyte," but this would be true only in part; while maritime plants were associated first with littoral (seashores) plants as strongly influenced by sea salinity, it has been proved thereafter that halophytes can also vegetate in inland salines, not necessarily in connection with sea. Therefore the initial definition of maritime plants would have not been applicable anymore for the rest of halophytes.

Some ecological definitions include the need of halophytes to "completing life cycle." This implies that the plant needs to flowering, in order to produce fruits with seeds; they will germinate, and thus the stability of a species will be ensured within its habitat. However, it has reported that seeds of many halophytes can germinate better rather under freshwater conditions or low salinity concentration (under 100 mM NaCl). Despite large diversity of seed germination responses of halophytes under salt conditions, most halophytes reduce germination rate under high sodium chloride concentration (Grigore et al. 2012). Therefore, the success of halophyte populations, especially for *annuals* that have only one opportunity in their life history to reproduce, is greatly dependent on seed germination responses (Ungar 1991). In a salt marsh, many halophyte species are in fact perennial, and this would imply different survival strategies than annual species; relatively few species of annuals have become adapted to the true salt marsh habitat (Ranwell 1972). This means that many perennial halophytes have rhizomes, which are be able to assure the persistence of a species at a location on the salt marsh for several decades. Therefore, following the above mentioned ecological definition, perennial species could survive in a saline habitat, without "completing the entire life cycle," namely, without producing seeds that will germinate.

Here is another definition of halophytes: halophytes are those species growing in saline habitats *only* (or in conditions of an excess of salts, high levels of salt, or plants that need a high concentration of salts in their media for an optimal growth). This definition applicable to euhalophytes is based on the assumed obligatory presence of salts for growth and development of halophytes. Nevertheless, many halophytic species can germinate and develop better in nonsaline or low salinity conditions, perhaps even under the established border between halophytes and glycophytes.

"Physiological" definitions of halophytes are based on established concentration boundary that separate glycophytes from halophytes; according to such definitions, halophytes are plants that can survive and complete their life cycle in media containing more than 200 mM NaCl (Flowers and Colmer 2008). These definitions are mainly the result of experimental approaches and have the potential advantage of being operational when trying to discriminate among various species. However, in natural conditions the situation is completely different, and it would be difficult to identify a static and unchangeable value of salt concentration.

Therefore, in time, the emphasis has moved from halophytes perception in the broadest sense to a narrower sense of terms that finally overlapped with the definition of obligatory (true) halophytes (*euhalophytes*).

In this way, we accept that a more extensive meaning of halophytes, in an environmental way (also based on field data) would be increasingly fitting in an operational sense. Plants that grow in saline conditions can be viewed as halophytes, since there is constantly a susceptible influence of soil salinity. The basic view is predisposed to consider as halophytes only those corresponding in fact to euhalophytes ("true" halophytes); however halophytes assigned as preferential, supporting, and accidental should be also placed next to euhalophytes within a saline environment.

Nevertheless, soil salinity, and – of course, excessive salinity – that many plants, the so-called glycophytes, cannot face, is the main factor that influences halophyte distribution. This explains the universal taxonomical occurrence of halophytes in very different ecological and climatic areas of the globe. For instance, several genera, and even species (*Atriplex halimus*, *Salicornia herbacea*, and *Juncus maritimus*) occur in salt marshes from temperate to tropical and subtropical zone (Waisel 1972). It is amazing how so many plants, different in taxonomical, evolutionary, and geographically ways adapted to extreme soil conditions, expressed by a significant high salinity.

3 Halophytes and Glycophytes

In 1676 Grew advanced the next question: *Whether any plant growing in a Garden or the Field, doth not yield a lesser quantity of Lixivial Salt, that another of the same kindred growing on the Sea-Coast; and with what difference?* To answer this naive, but legitimate scientific question, he used in his experiments individuals of *garden* and *sea scurvy grass* species having the same weight. After calcinations and weight measurements, he found more than four times salt in sea scurvy grass that in garden form. Actually, it is worth reading all the chapters included in his essay: *An essay of the various proportions wherein the lixivial salt is found in plants*, read before the Royal Society in March, 1676.

In the past decades, a clear distinction between halophytes and glycophytes has been advanced and described; glycophytes were traditionally assimilated to crop plants, considered sensitive to high salinity conditions (especially NaCl salt). In the common language, the opposite is a *halophyte* that etymologically means "salt-loving plant" (*hals – salt; phyton – plant; philein – to love*), while *glycophytes* is a "sweet" plant, because it prefers fresh, nonsaline substrates (*glykos – sweet*). In fact, there is a very broad spectrum of salt tolerance in plants, ranging from the most sensitive plants that are severely affected even by a lower concentration of 50 mM NaCl (about a tenth of the concentration of seawater) to those able to complete their life cycle in terms of a concentration of 500 mM NaCl or even above, close to seawater concentration (Sharma and Gupta 1986).

Other ecological definitions refer to halophytes as those plants that can grow satisfactorily and can compete with other species in the same habitat, and thus completing their life cycle (Waisel 1972). Frey and Basan (1985) consider the presence of halophytes as a necessary part of salt-marsh definition. Glycophytes from maritime flora of salt marshes would include those species regarded as occurring in nonsaline inland habitats (this approach proposes an external, nonbiological definition of maritime salt marshes, sometimes contradicting the suggestion offered by Frey and Basan 1985).

The term “halophyte” should be applied to species that are more or less confined to maritime or other saline habitats; the use of this term should be made in the broadest sense for all species occupying saline environments (Adam 1990).

Despite the term “glycophyte” has been traditionally used for the species generally vegetating in nonsaline than in saline habitats, the border between glycophytes and halophytes is very subtle. This distinction does not exclude that glycophytes can be tolerant to salt; moreover, it has been shown that frequently populations of glycophytes from salt marshes are genetically adapted to saline habitats (Adam 1990).

A more recent definition of a glycophyte is a species which has evolved by adaptation under natural selective pressures in ecosystems with low soil sodium levels and which maintains low sodium levels in its above ground tissues, especially in its leaves (Cheeseman 2015). As in the case of halophytes definitions, some terms involved in glycophytes definitions (such as low sodium levels) need further clarification.

Traditional crop plants are glycophytes; their selective advantage over halophytes on nonsaline soils is the higher growth rate (Sharma and Gupta 1986).

In contrast to glycophytes, halophytes (salt marshes and mangroves species) are well-specialized organisms that can survive and reproduce in saline environments grace to their morphological, anatomical, biochemical, and physiological traits (Khan and Duke 2001).

Poljakoff-Mayber and Gale (1975) define halophytes as plants that normally grow on salt marshes, in seawater or saline soils.

From the physiological point of view, halophytes are recognized as plants that can survive at high concentrations of electrolytes in their environments (Flowers et al. 1977); these substrates are typically dominated by NaCl, which is mainly used in experimental assays, but they can also contain other various salts, such as Na_2SO_4, Mg SO_4, $CaSO_4$, $MgCl_2$, KCl, and Na_2CO_3.

Flowers et al. (1986) established a minimum salt concentration of about 100 mM in the soil solution for definition of terrestrial halophytes, as plants found growing under naturally saline conditions. According to this definition, the criterion for separating the halophytes from glycophytes is the ability of halophytes to complete its life cycle at salt of 100 to 200 mM NaC1.

Distinction between glycophytes and halophytes occurred in agronomy from the necessity of reclamation of saline soils and finding crop species with certain degree of salinity tolerance; this distinction is based on the value of electrical conductivity (EC) of the saturation extract. According to the definition of US Salinity Laboratory Staff (Richards 1954), a soil is considered saline when EC is above 4 dS m^{-1}, which corresponds to approximately 40 mM NaCl. For a quick evaluation of the suitability of saline soils for crop production, the measurement of EC offers a rapid and accessible method for characterizing the salt content (Marschner 2012). Electrical conductivity of seawater corresponds to about 44 dS m^{-1}; the salt concentration of seawater (3%: 480 mM Na^{+}, 50 mM Mg^{2+}, and 560 mM Cl^{-}) corresponds to an osmotic potential of −2.7 MPa (Schulze et al. 2005).

Osmotic potential of the saturation extract can be calculated as follows: osmotic potential (MPa) = EC x −0.036. According to Richards (1954), the salt tolerance of a crop (glycophyte) may be evaluated according to three criteria:

(a) The ability of the crop to survive on saline soils
(b) The yield of the crop on saline soils
(c) The relative yield of the crop on a saline soil as compared with its yield on a nonsaline soil under similar growing conditions

Kovda (1973) reviewed the literature and proposed three types of salt tolerance of plants, according to values of electrical conductivity (dS/m) and to total content of soluble salts:

(a) High tolerance: EC from 10 to 16 dS/m and a total content of soluble salts between 0.5 and 1.0 grams/100 grams of soil
(b) Moderate tolerance: EC from 4 to 10 dS/m and a total content of soluble salts between 0.2 and 0.5 grams/100 grams of soil
(c) Low tolerance: EC from 2 to 4 dS/m and a total content of soluble salts between 0.1 and 0.2 grams/100 grams of soil

Accordingly, several ways in which glycophytes and halophytes respond in relation to soil salinity (EC) have been proposed by Romanian research (compare data from Figs. 1 and 2).

Bucur et al. (1957) conducted an impressive study on interrelationships between salt-tolerant plants and soil salinity; his accurate results (commented by Grigore 2013) show, among other interesting conclusions, that in a group of halophytes (called true halophytes, obligate halophytes, euhalophytes), the increase in plant biomass occurs at high salinity levels (over 100 mg soluble salts %) (Fig. 3). Some other species (*Aster punctatus, Festuca arundinacea, Heleocharis palustris, B. eruciformis*) – not strictly related to salt environments – but frequently found on them registered a decrease in biomass in line with increasing salinity in their rhizosphere (Fig. 4).

Increase of plant biomass occurs at high salinity levels (100–300 mg soluble salts %) and was observed in several halophytes from wet saline environments such as *Oenanthe silaifolia*, *B. eruciformis*, *Alopecurus geniculatus*, *Polygonum persicaria* (Fig. 5), where salts have a stimulative effect on plant growth, because in diluted soil solution salt uptake is high and may contribute to development of plant biomass.

In other halophytes (called neohalophytes), plant biomass increases only under lowered salinity thresholds (usually below 100 mg soluble salts %) (Fig. 6).

In other major group of halophytes, plant biomass decreases in line with increasing salinity level; in a delineated subgroup, decreasing biomass occurs at increasing salinity levels (high concentrations of salts) (Fig. 7), while in another subgroup,

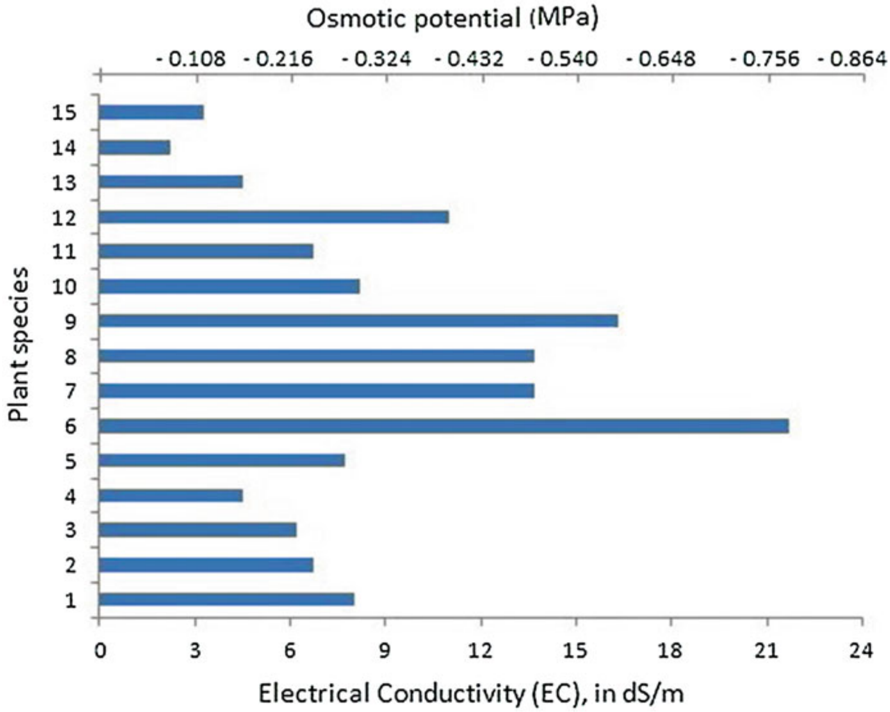

Fig. 1 Several Romanian crop species and their relation to soil salinity (1 – barley; 2 – wheat; 3 – oat; 4 – rye; 5 – maize; 6 – castor bean; 7 – sunflower; 8 – sugar beet; 9 – beet; 10 – sorghum sudangrass; 11 – common sainfoin; 12 – alfalfa; 13 – spring vetch; 14 – common garden pea; 15– been. (Based on Măianu et al. 1965)

decreasing biomass was recorded even at low salt concentrations (Fig. 8). These are facultative (adapting) halophytes.

A detailed picture of salinity thresholds from several halophytic species from salt meadows of Jijia-Bahlui (Romania) is shown in Fig. 9 (Bucur et al. 1957).

Halophytes are species that typically grow in soils with high levels on NaCl and, therefore, on a low water potential; they accumulate NaCl in their vacuoles (Lambers et al. 2008). Glycophytes have a limited capacity to transport NaCl into their vacuoles and are unable to tolerate high salinity levels. However, cytoplasmic enzymes of both glycophytes and halophytes are very similar with respect to their sensitivity to high concentrations of inorganic solutes.

4 Classification of Halophytes

Classifications of halophytes are very discrepant, a logical reality if considering the large diversity of definitions attributed to these plants and to saline environments. As a result, there is no unique classification of halophytes entirely satisfactory, because

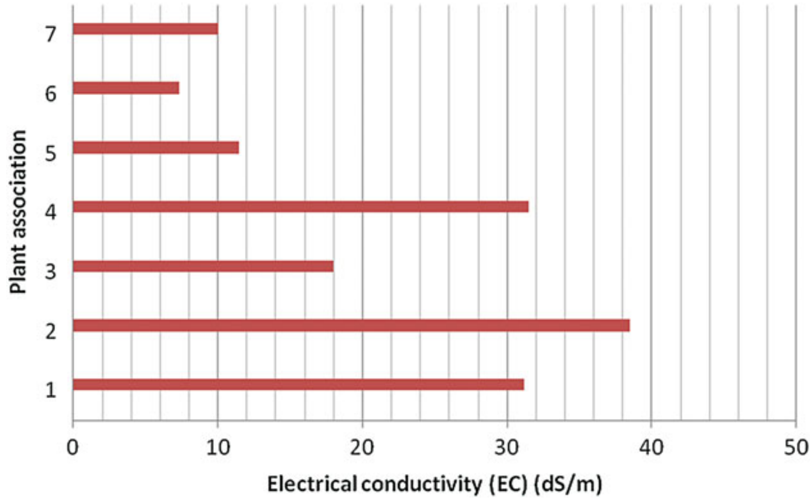

Fig. 2 Relation between soil salinity (EC) and Romanian halophytic plant associations; 1 – *Salicornia europaea*; 2 – *Salicornia europaea, Salsola soda, Halimione pedunculata*; 3 – *Salicornia europaea, Suaeda maritima, Bassia hirsuta, Salsola soda;* 4 – *Suaeda maritima, Salicornia europaea, Salsola soda, Halimione pedunculata*; 5 – *Puccinellia distans*; 6 – *Atriplex tatarica, Camphorosma annua, Bassia hirsuta*; 7 – *Poa bulbosa*. (Based on Sandu et al. 1983)

there is no unique criterion of classification. Three major criteria were considered in order to classify halophytes: salt content of native habitats, the importance of origin of salts, and plant responses to salinity (Waisel 1972).

Attempts to classify halophytes were made early in the history of botany. Hedenberg in his PhD thesis from 1754 (published in 1788) included *marine* (*marinae*) and *maritime* (*maritimae*) species in aquatic stations of plants. Marine plants are those species vegetating in seawater, found in a continuous movement of seawater. In this group many algae were included, but also several vascular genera: *Najas*, *Zostera*, *Potamogeton, Ruppia*. Maritime plants vegetate in saline seashores, irrigated sometimes by seawater; they are sub-succulent species: *Atriplex portulacoides*, *Aster tripolium*, *Glaux maritima*, *Rumex maritimus*, *Artemisia maritima*, *Salicornia europaea*, and *Salsola kali*.

Poiret (1820) distinguishes:

1. Maritime (saline) species are those that – without being submersed in saline waters or floating on their surface – need often to live close to saline waters in order to uptake a necessary amount of it, for their nutrition. According to Poiret, some species from salt marshes (*Salicornia*) can absorb salts by their roots and leaves, while others (*Eryngium campestre*) do not require salt, but may vegetate on seashore as in other common places, due to their robust constitution, allowing to alleviate the action of harmful salts.
2. Marine plants grow immersed in saline water or float its surface.

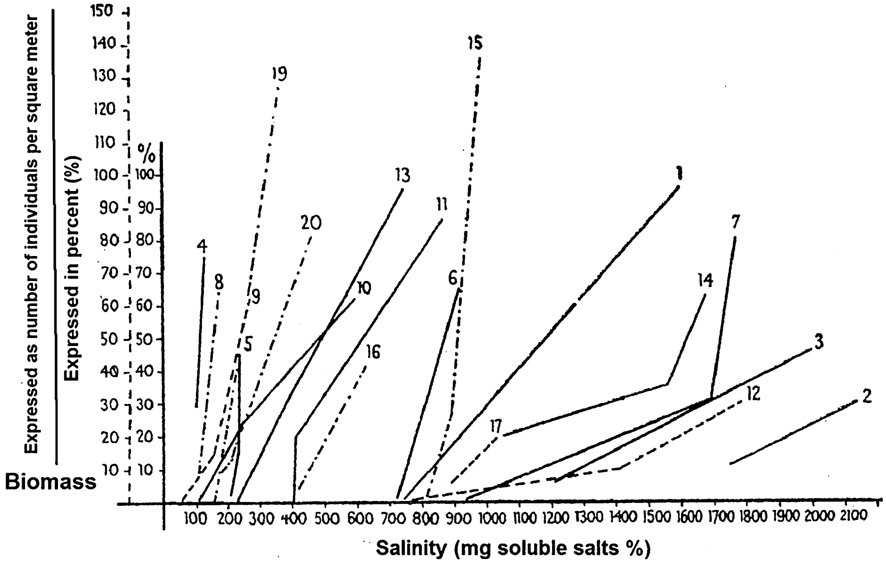

Fig. 3 Relationship between increase plant biomass and increasing soil salinity in the rhizosphere of several halophytes (euhalophytes): 1 – *Atriplex hastata;* 2 – *Scorzonera austriaca;* 3 – *Atriplex littoralis;* 4 – *Heleochloa schoenoides;* 5 – *Podospermum canum;* 6 – *Aster tripolium;* 7 – *Camphorosma ovata;* 8 – *Silaum flavescens;* 9 – *Aster cinereus;* 10 – *Artemisia maritima;* 11 – *Taraxacum bessarabicum;* 12 – *Kochia prostrata;* 13 – *Puccinellia distans;* 14 – *Limonium gmelini;* 15 – *Salicornia europaea;* 16 – *Plantago schwarzenbergiana;* 17 – *Lepidium cartilagineum;* 18 – *Peucedanum latifolium;* 19 – *Leuzea salina;* 20 – *Plantago tenuiflora.* (Modified after Bucur et al. 1957)

Contejean (1874) underlined the importance of soil and its chemical composition in defining ecological groups of plants; in relation to sodium chloride, he stated that it acts either as an attraction factor for maritime plants or as a rejecting factor for other species (inland species). Maritime plants are confined to seashore proximity because they need sodium chloride, while other species avoid occupying habitats of maritime plants, because they are rejected by sodium chloride. According to Contejean's theory, there are a maritime flora (determined by sodium chloride), an inland flora (rejected by the same factor) and an indifferent flora, which grow on all types of soils. Consequently, he divided maritime plants in:

1. Xerophytes: *Crithmum maritimum*, *Statice ovalifolia*, and *Asplenium marinum.*
2. Hygrophytes
   (a) Clay soil species (*péliques*, French term): *Cirsium anglicum*, *Limosella aquatica*, and *Scirpus acicularis.*
   (b) Psammophytes (on sandy soils): *Scleranthus perennis.*
   (c) Species vegetation both on clay soils and sandy soils (*pélopsammiques*, French term): *Pulicaria vulgaris*, *Hypericum humifusum.*

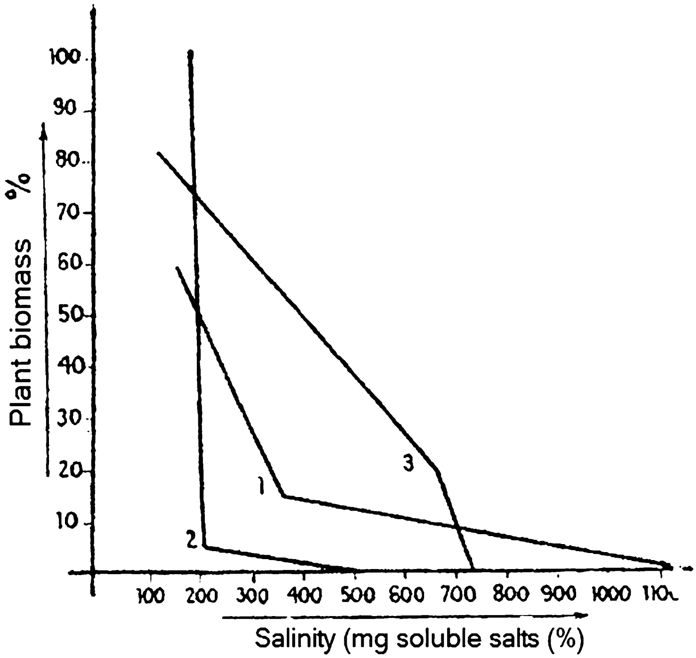

Fig. 4 Decrease of plant biomass in respect to increased soil salinity (1 – *Heleocharis palustris*; 2 – *Festuca arundinacea*; 3 – *Aster punctatus*) (Bucur et al. 1957)

Contejean (1881) classified maritime (halophyte) species in:

1. Exclusive (or almost exclusive) maritime species, which only accidentally vegetate outside littoral zones and which cannot propagate in nonsaline soils.
2. Less exclusive maritime species that generally occur outside littoral area and often grow in soils less saline or completely nonsaline.
3. Almost indifferent maritime species that often are found more in inland areas than in littoral regions; most of them are found next to the sea and seem not to really need the salt influence derived from the sea.

Casu (1905) offered an interesting classification of halophytes, taking into account the features of saline environments: water, salt, and organic substances. Thus, halophytes were divided in:

1. Succulent species who vegetate exclusively in contact with salt solution: *Salicornia fruticosa*, *S. herbacea*, *Arthrocnemum macrostachyum*, *Halopeplis amplexicaulis*, *Halocnemum strobilaceum*, *Suaeda fruticosa*, *S. maritima*, *S. setigera*, and *Mesembryanthemum nodiflorum.*
2. Less succulent species, which vegetate usually in wet environments, but can be also found in dry areas: *Obione portulacoides*, *Atriplex rosea*, *A. halimus*, *Frankenia laevis*, *Cakile maritima*, and *Plantago maritima.*

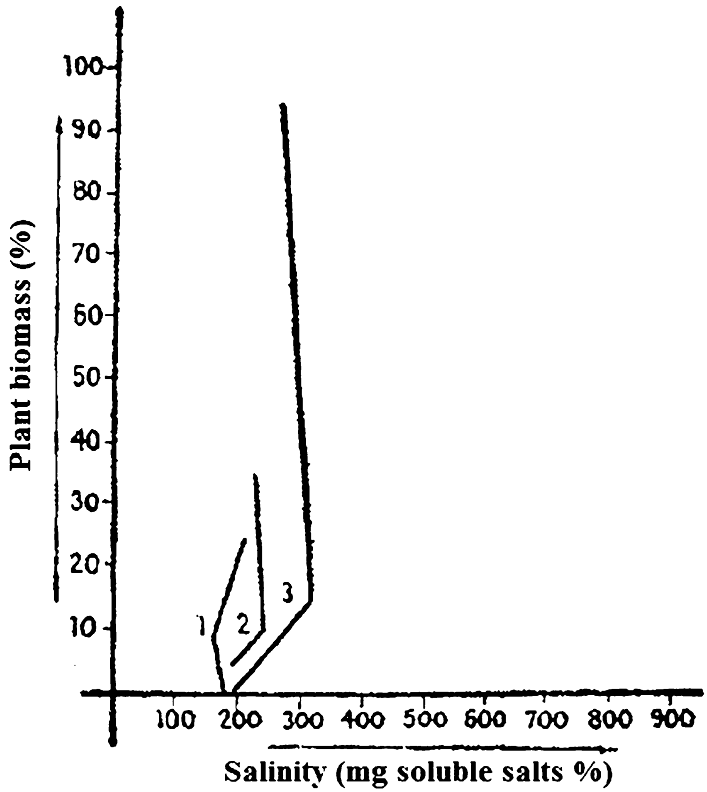

Fig. 5 Increase of plant biomass in respect to increased soil salinity (1 – *B. eruciformis*; 2 – *Polygonum persicaria*; 3 – *Alopecurus geniculatus*) (Bucur et al. 1957)

3. Non-succulent species that vegetate usually in dry places, but may migrate also in humid places, coming in some contact with salt water: *Phalaris canariensis*, *Polypogon monspeliensis*, *Stipa tortilis*, *Juncus maritimus*, and *Plantago coronopus*.

Based also on experimental observation, Casu came to several conclusions in respect with halophytes: succulent halophytes are exclusively related to wet and salt environments; succulence diminishes in line with water from habitats; and succulent species do not vegetate in dry, despite saline places. Casu (1905) has been also interested in the influence of salts upon halophytes germination and development and suggested that a halophyte needs added salt for an optimum growth (Fig. 10).

Chermezon (1910) divided first littoral flora in xerophilous and halophilous, and plants vegetating on seashore were classified accordingly:

1. Flora of the beaches (seashores), occupying a restricted area, where there are few or no continental species; the most characteristic species are: *Cakile maritima*,

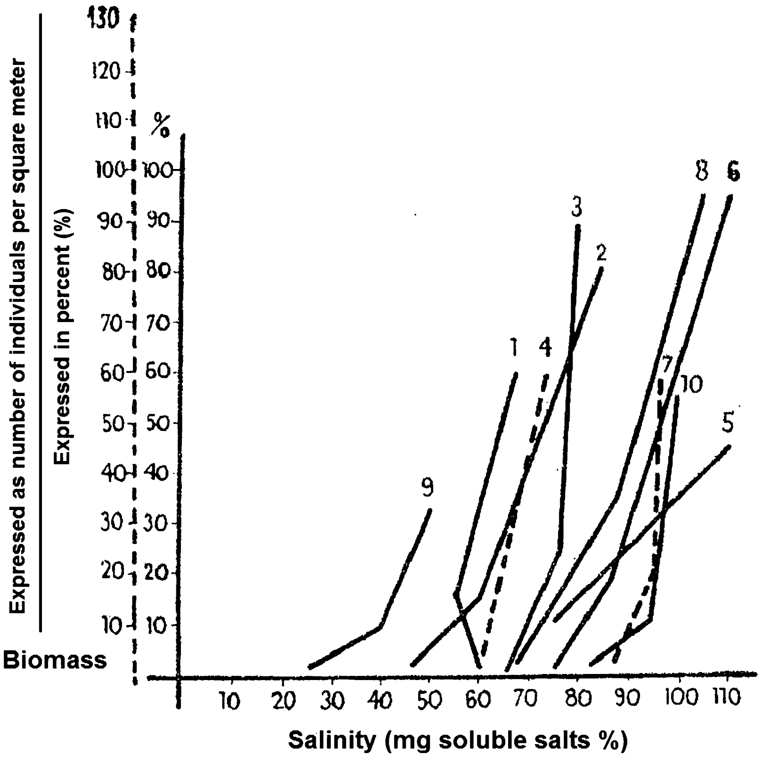

Fig. 6 Increase of plant biomass occurs at the slight increase of soil salinity in the rhizosphere of several halophytes (neohalophytes): 1 – *Trifolium hybridum;* 2 – *Lythrum virgatum;* 3 – *Gratiola officinalis;* 4 – *Medicago lupulina;* 5 – *Festuca pratensis;* 6 – *Phalaris arundinacea;* 7 – *Glyceria aquatica;* 8 – *B. eruciformis;* 9 – *Plantago lanceolata;* 10 – *Taraxacum officinale*. (Modified after Bucur et al. 1957)

Eryngium maritimum, *Statice bellidifolia*, *Polygonum maritimum*, etc. These plants make the transition between psammophytes and other halophyte species.

2. Flora of the cliffs is confined to a small area consisting of rocks exposed to salt spray derived from the sea. Influence of seawater is greater here than on beaches, and this confers to plants an obvious halophilous character: *Crambe maritima*, *Silene maritima*, *Plantago macrorhiza*, *State dodartii*, etc.;
3. Flora of salt marshes occupy considerable areas within halophytic vegetations; it forms a band on lower shores and along estuaries whose width varies with terrain profile and has a large number of characteristic species: *Frankenia pulverulenta*, *Spergularia marginata*, *Aster tripolium*, *Plantago maritima*, *Atriplex littoralis*, *Salsola soda*, *Triglochin maritimum*, etc. This is the well-individualized flora of the coastal region and the most halophilous. Salinization is here quite considerable, which explains the rarity of continental species. Plants are clearly halophilous in this area.

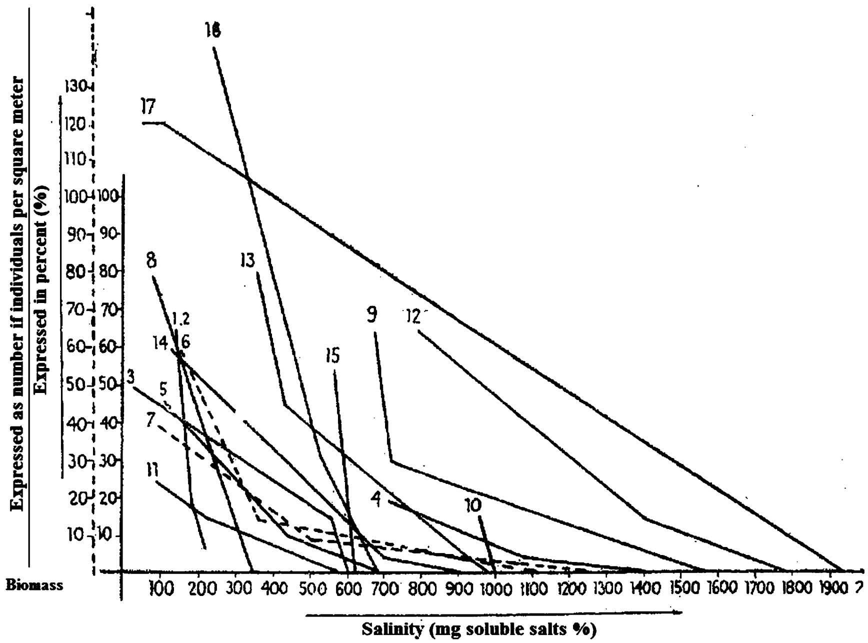

Fig. 7 Decrease of plant biomass in line with increasing soil salinity (1 – *Matricaria inodora*; 2 – *Lepidium ruderale*; 3 – *Achillea setacea*; 4 – *Rumex crispus*; 5 – *Melilotus officinalis*; 6 – *Heleocharis palustris*; 7 – *Lotus corniculatus*; 8 – *Inula britannica*; 9 – *Schoenoplectus lacustris*; 10 – *Atriplex tatarica*; 11 – *Alopecurus pratensis*; 12 – *Agropyron cristatum*; 14 – *Bromus commutatus*; 15 – *Carex nutans*; 16 – *Gypsophila muralis*; 17 – *Iris halophila*) (Bucur et al. 1957)

Prodan (1922) offered an intriguing classification of halophytes, based on ecological conditions of saline environments, meaning that "natural saline environments which, according to their degree of humidity and partly, to characteristic plants can be divided into: dry salt areas, salt marshes and salt lakes." Consequently, he distinguished halophytes from dry salt areas, salt marshes, and salt lakes (littoral salt lakes from Black Sea and steppes lakes) (Figs. 11, 12, 13, and 14).

Prodan (1922) also proposed another classification of halophytic flora: spring flora, including plants that bloom in spring and last until summer; autumn flora, including plants that bloom in summer and last until late autumn.

Perhaps one of the first modern classifications of saline habitats was proposed by Stocker (1928):

1. *Aquatic-haline*
2. *Terrestro-haline*
   Hygrohaline
   Mesohaline
   Xerohaline
3. *Aero-haline*

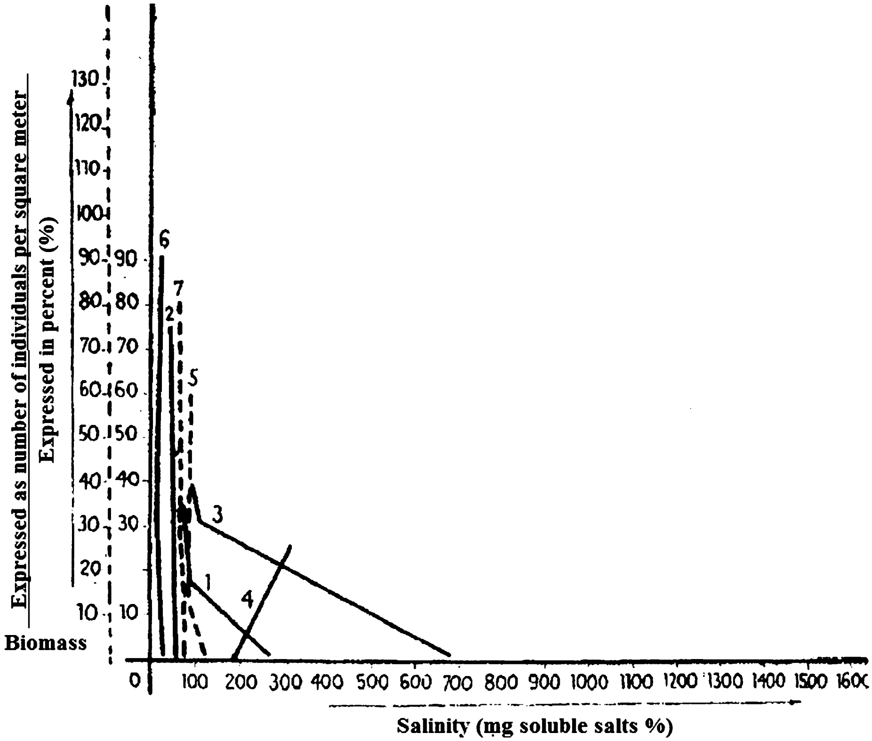

Fig. 8 Decrease of plant biomass in line with increasing soil salinity (1 – *Erysimum repandum*; 2 – *Festuca pseudovina*; 3 – *Agropyron cristatum*; 4 – *Plantago cornuti*; 5 – *Trifolium hybridum*; 6 – *Daucus carota*; 7 – *Trigonella caerulea*) (Bucur et al. 1957)

Habitats affected by salt spray (maritime).
Habitats affected by salt dust (salt-deserts).

This classification is based on the sources of salts and on the plant organs which they affect. Plants are divided according to their respective habitats and later subdivided according to their water relations.

Van Eijk (1939), using a classification based on plant distribution as well as on several plant responses, divided halophytes into:

1. Plants which tolerate salts, but whose optimal development is in nonsaline habitats
2. Plants which have an optimal development in saline habitats

Each of these two groups has been divided in plants which appear only in saline habitats and plants which appear also in nonsaline habitats.

Kovda (1939) divided plants from salt marshes and soils with lower salinity in:

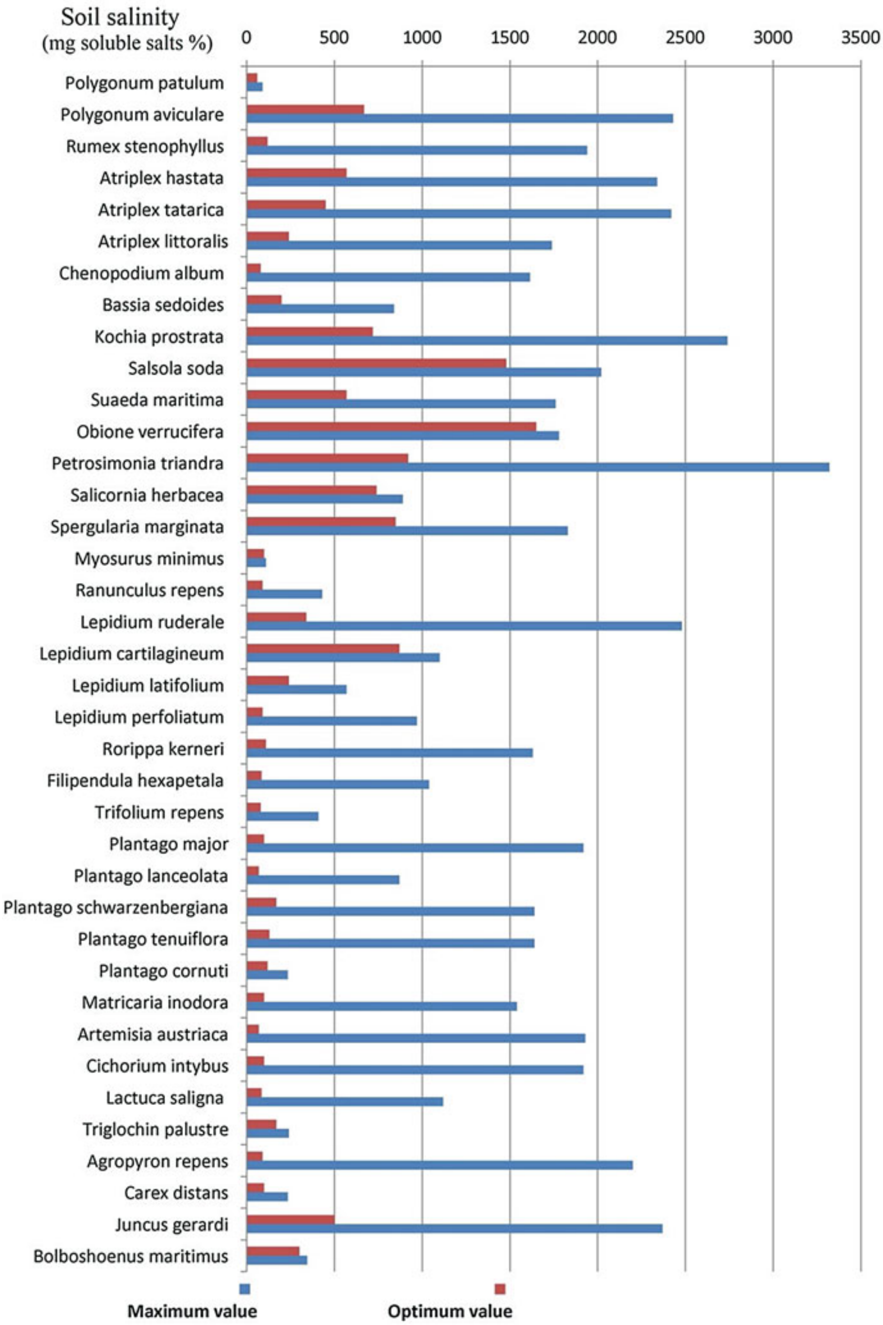

Fig. 9 Salinity thresholds of halophytic species from salt meadows from Jijia-Bahlui (Romania) (measured at the top of the roots). (Based on Bucur et al. 1957)

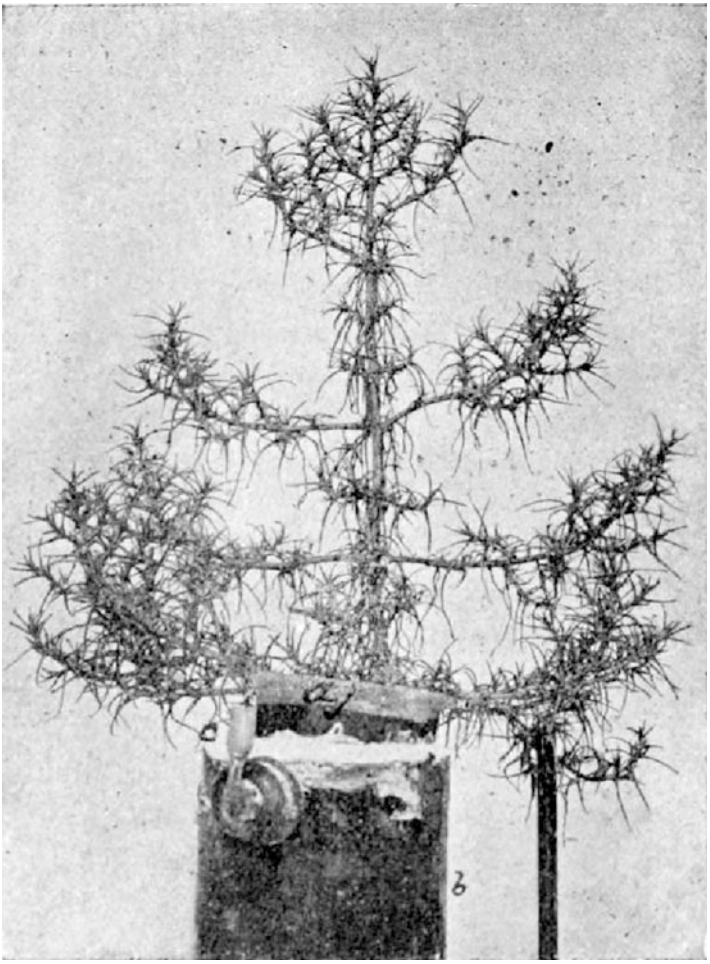

Fig. 10 *Salsola soda*, grown with supplement of salt solution (Casu 1905)

1. *Typical halophytes, succulent Salsola-like species*, characteristic to humid solonchaks, with very high water table; they contain 40–55% salts, where NaCl predominates. For this reason, these species maintain the salinity in upper layers of salt-affected areas.
2. *Semi-dried halophytes*, from dry solonchaks and other intensely salinized soils, with lower level of water table; they contain 20–30% salts, where chlorides and sulphates are in close proportion. They maintain salinity, but also enrich soil with Ca, Mg, K, and SiO_2, in the detriment of sodium.
3. *Haloxerophytes or dry Salsola-like species*, several *Artemisia* species, and other xerophyte species, which grow on less (or not) salinized solonetzs; they have a mineral content of 10–20%, where P, S, Ca, and K predominate. They contribute to desalinization and de-solonizing of solonetzs.

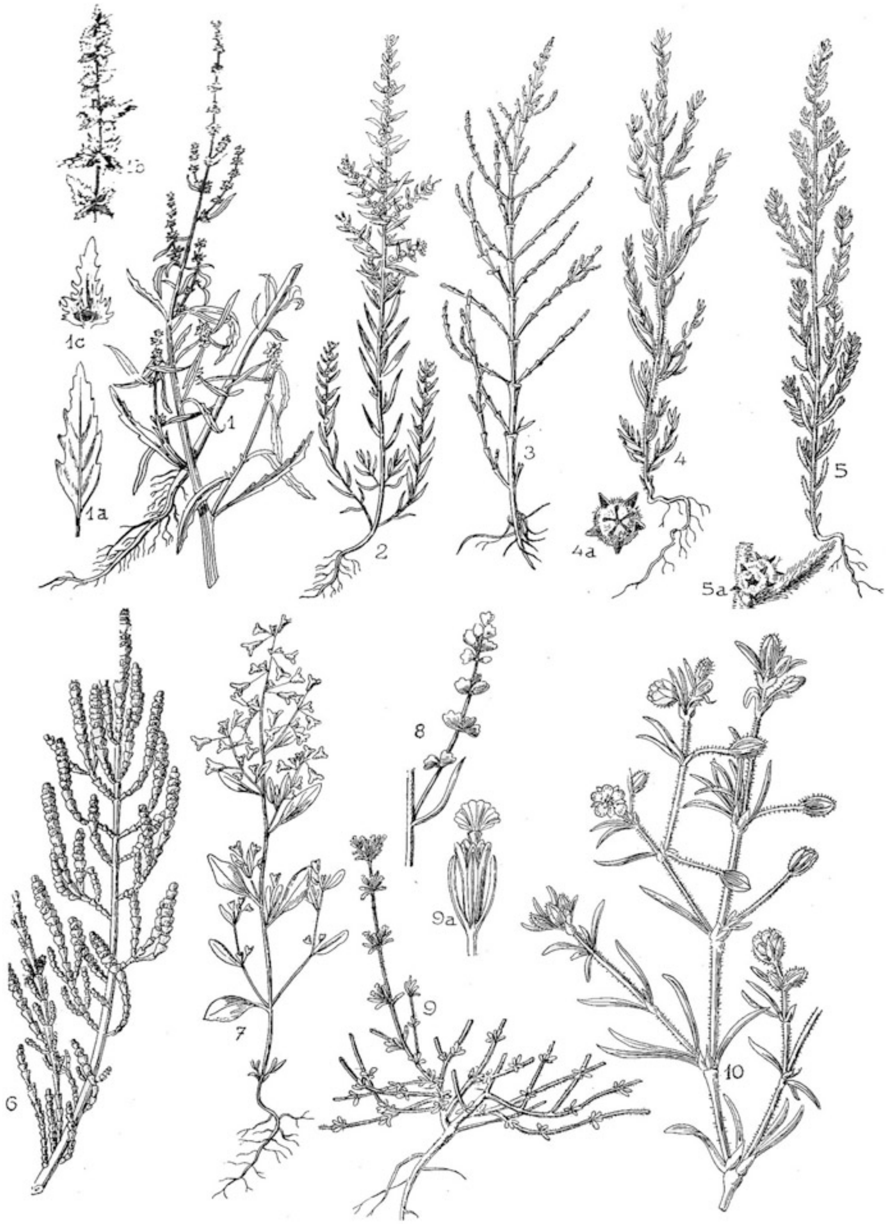

Fig. 11 Romanian halophytes: *Atriplex littoralis* (Fig. 1; 1a – basal leaf; 1b – fruiting shoot; 1c – fruit), *Suaeda maritima* (Fig. 2), *Salicornia herbacea* (Fig. 3), *Bassia hirsuta* (Fig. 4; 4a – fruiting perianth), *B. sedoides* (Fig. 5; 5a – fruiting perianth), *Arthrocnemum glaucum* (Fig. 6), *Obione pedunculata* (Fig. 7), *O. portulacoides* (Fig. 8), *Frankenia hispida* (Fig. 9), *Spergularia rubra* (Fig. 10) (Prodan 1922)

Fig. 12 Romanian halophytes: *Statice gmelini* (Fig. 1), *S. caspia* (Fig. 2; 2a – a bract from flowering shoot), *Camphorosma ovata* (Fig. 3), *Plantago tenuiflora* (Fig. 4), *P. maritima* (Fig. 5) (Prodan 1922)

4. *Poaceae*, *Fabaceae species*, several *Artemisia* species, characteristic to steppic soils, and dry less salinized steppes. They have a mineral content under 10%, where $SiO_{2,}$ P, Ca, and K predominate. They complete the de-solonizing process and enrichment of complex with calcium.

Prodan (1939) suggested a classification of halophytes, using as criterion *the way in which plants withstand salt.* He delineated three categories of halophytes:

1. "First category" of halophytes includes species that *grow exclusively in salt areas and only exceptionally in other places*: *Zostera marina*, *Ruppia rostellata*, *Juncus gerardi*, *Atriplex hastata*, *Aster tripolium*, and *Artemisia salina*.
2. "The second category" of halophytes represents *the species which besides salty areas can also vegetate in several habitats (waters, marshes, sands)*: *Najas minor*, *B. eruciformis*, *Carex distans*, *Spergularia marginata*, etc.

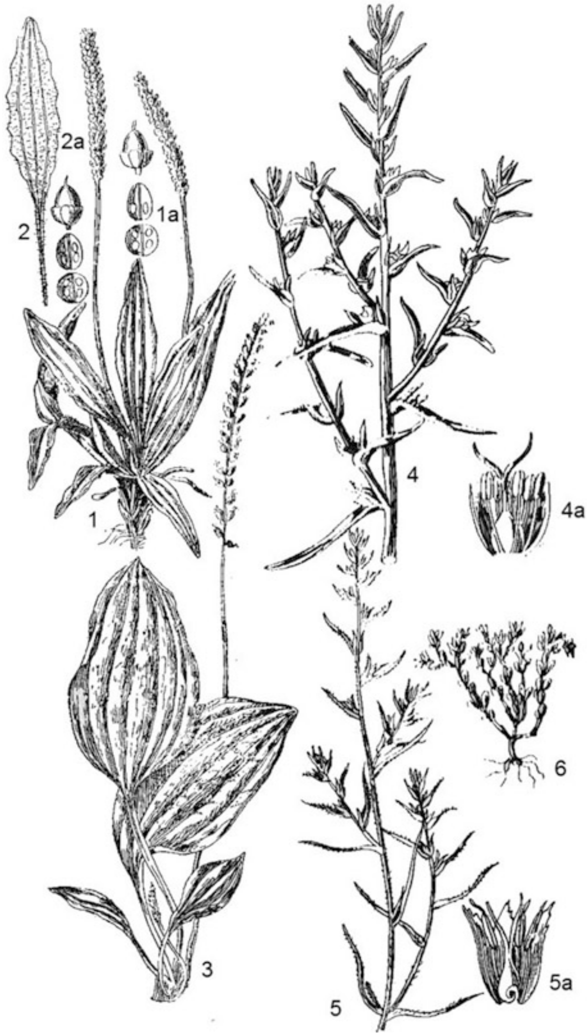

Fig. 13 Romanian halophytes: *Plantago schwarzenbergiana* (Fig. 1; 1a – covered and uncovered fruits), *P. sibirica* (Fig. 2; 2a – covered and uncovered fruits), *P. cornuti* (Fig. 3), *Salsola soda* (Fig. 4; 4a – flower), *Petrosimonia triandra* (Fig. 5; 5a – flower), *Sedum caespitosum* (Prodan 1922)

3. "Third category" of halophytes comprises species that *grow in other environments and can pass only rarely or exceptionally in saline areas.* Some of them suggest an incipient halophilous affinity: *Triglochin palustris*, *Andropogon ischaemum*, *Polygonum aviculare*, and *Tamarix pallasii*.

Ţopa (1939) offered perhaps the first Romanian work (s) where the "standard" classification of halophytes is explicitly given with appropriate definitions (see Grigore 2013).

1. *Obligatory halophytes* as those plants growing in salty habitats requiring a considerable amount of salt for their development, at least for a short period of the year:

Fig. 14 (continued)

Camphorosma annua, *Halocnemum strobilaceum*, *Salicornia herbacea* and *Suaeda maritima*.
2. *Preferential halophytes* **prefer** the saline environments where they find the *optimal living conditions*: *Atriplex tataricum*, *Lotus tenuifolius*, *Tamarix ramosissima*.
3. *Supporting halophytes* endure the salts but do not manage to compete with local vegetation: *Rumex maritimus*, *Polygonum aviculare*, and *Atriplex hastata*.
4. *Accidental halophytes* occur **accidentally** in the salty habitats, but are not able to survive there: *Rumex hydrolapathum*, *Poa annua*, and *Molinia caerulea.*

Chapman (1942) proposed the following system, including different groups of halophytes:

Miohalophytes
1. Glyco-mesohalophytes. Plants that grow in habitats with a range of 0.01–1.0% NaCl
2. Euryhalophytes. Plants that grow in habitats with a range of 0.1 < 1.0% NaCl

Euhalophytes
1. Mesohalophytes. Plants that grow in habitats with a range of 0.5–1.0% NaCl
2. Meso-euhalophytes. Plants that grow in habitats with a range of 0.5 to <1.0% NaCl
3. Euhalophytes. Plants that grow in habitats with more than 1.0% NaCl

Sennikov (1950) pointed that different groups of plants vegetating on saline environments have specific structural and physiological features. Thus, he divided these species in:

1. *Typical halophytes* are plants that exclusively grow on salt areas; they can endure higher concentration of salts due to typical halomorphic adaptations such as succulence, reduced leaves: *Salicornia herbacea*, *Suaeda maritima*, *Halocnemum strobilaceum*, and *Salsola soda*. They accumulate in their tissues large amount of salts, especially chlorides and sulphates as an adjustment to very high osmotic pressure; for typical halophytes, the salinity is required and even can stimulate their growth.
2. *Semi-dried halophytes*: *Petrosimonia crassifolia*, and some species of *Suaeda*, which have a halomorphic structure, with subtle adaptations of xerophytic nature (small trichomes).
3. *Haloxerophytes: Obione verrucifera* and *O. canum*, from salt areas that moderately dry during summer; they have a deeper root system than typical halophytes,

Fig. 14 Romanian halophytes: *Crypsis alopecuroides* (Fig. 1), *C. aculeata* (Fig. 2), *C. schoenoides* (Fig. 3), *Atropis distans* (Fig. 4), *Beckmannia eruciformis* (Fig. 5), *Alopecurus littoralis* (Fig. 6), *Triglochin palustris* (Fig. 7), *Polygonum bellardi* (Fig. 8), *Rumex odontocarpus* (Fig. 9), *Atriplex hastatum* (Fig. 10), *Atriplex microspermum* (Fig. 11) (Prodan 1922) are succulent, and sometimes possess reduced leaves, covered by a layer of water-storage hairs (vezicular hairs).

4. *Xerophytes less halophilous*, characteristic to deep desalinized solonetzs that are dry during summer: *Artemisia* spp. and *Camphorosma monspeliaca.* They have a xeromorphic nature, not succulent, but with strong shoot and leaves intensely divided in narrow segments or lacinia.

Bucur and collaborators (1957) gave a very consistent bioecological classification of halophytes (Table 3), based on interrelationships between plants and saline environments; they established salinity tolerance thresholds for about 350 species vegetating in natural salinized meadows and pastures from Jijia-Bahlui depression (Romania).

With respect to other major Romanian classifications previously made by Prodan (1939) and Ţopa (1939), a system to harmonize all these classifications has been figured (Grigore 2012) (Table 4). Following the obtained results by Bucur et al. (1957), several general patterns were described:

1. In several species, the biomass increases according to the increasing soil salinity in the rhizosphere (Figs. 3, 5, and 6); here are described two subgroups.
2. In other species, the biomass decreases according to the increasing soil salinity nearby the roots (Figs. 4, 7, and 8); two subgroups are also described.

Table 3 Classification of halophytes according to Bucur and collaborators (1957)

Halophytes (Plants vegetating on saline environments)	1. **Euhalophytes:** halophytes strictly adapted to salinity (strictly *obligate* to salinity) are *exclusively preferential* and grow *only* on salinized environments, with the entire or a part of the radicular system, both as seedlings and as mature plants 2. **Neohalophytes:** plants able to adapt to salinity; plants to be adapted to halophytic environment; they are *supporting* and *preferential*, living both on non-salinized and salinized media, with the entire or a part of the radicular system
Non-halophytes (Plants that do not grow on saline environments)	Plants non-adapted to salinized media, non-tolerant to high concentrations of salinity. In relation to concentrations more than 30–40% milligrams of soluble salts, they could be tolerant and preferential

Table 4 Equivalence between major Romanian systems of halophytes classification (Grigore 2012)

Prodan (1939)	Ţopa (1954)	Bucur et al. (1957)		
"First category"	Obligatory	Obligatory	Euhalophytes	Halophytes
"Second category"	Preferential	Facultative halophytes (plants able to adapt to salinity)	Neohalophytes	
	supporting			
"Third category"	Accidental	Supporting (tolerant to salinity)		Non-halophytes

Table 5 Hierarchy of euhalophytes, taking into account the soil salinization degree in the rhizosphere (Bucur et al. 1960)

Euhalophyte	Soil salinity in the rhizosphere (% mg soluble salts)
Very weak	75–95
Weakly/less	95–150
Moderately	150–450
Strongly	450–1400
Very strongly	1400–3400
Excessively	3400–5500

According to these general observations, salt plants are divided in:

(a) *Obligatory halophytes* (*strictly halophytes*, or halophytes); plants that grow only in saline environments: *Salicornia herbacea*, *Salsola soda*, *Atriplex hastata*, *Plantago schwarzenbergiana*, and *Petrosimonia triandra*.
(b) *Facultative halophytes* (adaptable halophytes, plants adaptable to salinity); species that develop both in saline habitats and in normal soils. In saline soils, they have a fragile development and can desiccate faster, during the dry season or severe droughts: *Lepidium ruderale*, *Poa bulbosa*, *Matricaria chamomilla*.
(c) *Halophobous*: plants whose biomass decreased according to increasing soil salinity.

Consequently, Bucur and collaborators proposed a classification within euhalophytes (Table 5) and neohalophytes (Table 6; see also Figs. 3, 4, 5, 6, 7, and 8), in respect to the intensity of soil salinization.

In addition, according to available water from soil during vegetation season, xero-halophytes, hygrohalophytes, and mesohalophytes can be delineated; xero-halophytes are strictly adapted to salinity and drought in the maximal period of plant development; hygrohalophytes are adapted to salinity and constant humidity in the soil, and mesohalophytes are adapted to soil salinity and humidity.

Moreover, following the analysis of plant-salinity relationships established in plants from salinized meadows and pastures, Bucur et al. (1957) proposed a classification of soils (layers of soils) based on the intensity of salinization (Table 7). It is important that this classification is based on analysis of soil salinity distribution within plant associations.

Şerbănescu (1965) classified halophytic plant associations according to the preferences of species for chemical composition of salts:

1. Plant associations of chloride salt areas: *Bassia hirsuta*, *Salicornia herbacea*, *Suaeda maritima*, *Salsola soda*, *Halimione pedunculata*, *H. verrucifera*, *Aeluropus littoralis*, *Puccinellia distans, Agropyron elongatum*, *Taraxacum bessarabicum*, *Aster tripolium*, *Cyperus pannonicus*, *Spergularia marginata*, *Crypsis aculeata*, *Petrosimonia triandra*, *Cerastium anomalum*, *Juncus gerardii*, *B. eruciformis*, *Trifolium angulatum*, *Iris halophila*, *Pholiurus pannonicus*, *Leuzea salina*, *Atriplex littoralis*, *Erysimum repandum*, and *Tamarix ramosissima.*

Table 6 Hierarchy of neohalophytes, taking into account the soil salinization degree in the rhizosphere (Bucur et al. 1961)

Tolerant neohalophyte	Soil salinity in the rhizosphere (% mg soluble salts)
Very weak	55–75
Weakly/less	75–95
Moderately	95–150
Strongly	150–450
Very strongly	450–1500
Excessively	1500–3500

Table 7 Classification of soils (layers of soils) according to the degree of salinization (Based on Bucur et al. 1957)

Soil (layers of soil) salinity	Group of salinization
<75 mg soluble salts %	Non-salinized
75–95 mg soluble salts %	Non-perceptibly salinized
100–220	Sensible salinized
220–450	Less salinized
450–1400	Moderately salinized
1400–2400	Strongly salinized
2400–3500	Very strong salinized
>3500	Excessively salinized

2. Plant associations of sodium salt areas: *Carex divisa*, *Camphorosma annua*, *C. monspeliaca*, *Plantago maritima*, *Lepidium crassifolium*, and *Hordeum maritimum*.
3. Plant associations of sulphate salt areas: *Artemisia maritima* and *Limonium gmelini*.

Waisel (1972) proposed an integrated classification of plants from saline habitats, as an attempt to unify the plant-salt relationships into one scheme and to underline internal salt-resistance mechanisms rather than the external salt relationships (Table 8).

Breckle (1995) offered an ecophysiological classification of halophytes taking into consideration the salt uptake and metabolism of the salt in the interior of plant:

1. Most plants are non-halophytes, vegetating in terrestrial regions where salt concentration in soil is low. They are very selective with their root cell membranes and thus are able to exclude the great majority of NaCl from being uptake.
2. Pseudohalophytes are plants that can withstand higher amount of salts without possessing any special adaptations, besides a very good electivity at their root membranes and in other plant tissues. They often tend to accumulate NaCl in the roots and the lower shoot parts (xylem parenchyma).
3. Euhalophytes are plants where a higher uptake of salts and transport to the shoot can be observed; either the leaves and/or the stems become succulent.
4. Some halophytes eliminate salt via special structures (salt glands and salt hairs) outside aerial plant organs. This phenomenon is called recreation, and it is observed in several halophytes species (Grigore and Toma 2017).

Table 8 Classification of plants of saline habitats. (Adapted from Waisel 1972)

Euhalophytes					Pseudohalophytes
Salt-requiring halophytes		**Salt-resistant halophytes**			Salt-avoiding plants
Obligatory halophytes	Preferential halophytes	Salt-enduring halophytes (salt tolerant)	Salt-excluding halophytes	Salt-evading halophytes	
Plants dependent upon salts for their survival, e.g., *Salicornia* sp. and various bacteria and algae	Plants whose growth and development are improved in the presence of salts, e.g., *Arthrocnemum* sp., *Aster* sp., *Nitraria* sp., *Salicornia* sp., *Suaeda* sp.	Plants enduring a high protoplasmic salt content, e.g., *Suaeda monoica*	Plants accumulating salts in special hairs, e.g., *Atriplex* sp. Plants secreting salts from their shoot, e.g., *Aeluropus* sp., *Limonium* sp., *Tamarix* sp. Plants are transporting salts from the shoot into the root, e.g., *Salicornia* sp.	Plants evading salt uptake, e.g., *Rhizophora* sp. Plants evading salt transport into the leaves, e.g., *Prosopis farcta*	Ephemers Niche plants

Yensen and Biel (2006) divided plants according to their ability to remediate salty soils:

1. *Excluders* include plants that exclude salts at the level of the roots. Most terrestrial plants are excluders despite many have limited abilities to exclude salts; they die if the salt load into their tissues increases. However, some euhalophytes as the mangrove *Rhizophora* spp. are salt-excluding plants, but their capacity to remediate saline soil is very limited or has no ability to remediate saline soils. They selectively absorb water but exclude salts at the root level and tend this way to accumulate salts in soil to the point that the salt tolerance of the plant is exceeded.
2. *Accumulators* are plants that uptake salts and accumulate them in the vacuoles of the plant cells. Glycophytes, salt-tolerant or euhalophyte plants may be accumulators. In general, these plants have remediation value only if they, or their parts, are removed from the fields.
3. *Conductor* plants that absorb salts from the soil transport the salt through the plant to the shoot surface and, with the aid of wind, disperse the salt away from the area. These plants potentially have great ability to remove salt from the soil and widely distribute the salt via wind dispersal.

Grigore and Toma (2010b) suggested a classification of halophytes based on anatomical adaptations of more than 70 species of halophytes (see Grigore et al. 2014; Grigore and Toma 2014 and references therein) and their ecological and functional value in respect with environmental factors:

1. **Extreme halophytes** (well adapted to salinity grace due their morphological and anatomical adaptations) vegetate exclusively (or almost exclusively) in saline environments. Two types of extreme halophytes were subsequently described:
   (a) Irreversible extreme halophytes having the most typical and pronounced anatomical adaptations: succulence, Kranz anatomy, salt-secreting devices, successive cambia phenomenon (*Petrosimonia oppositifolia*, *P. triandra*, *Salicornia europaea*, *Suaeda maritima*, *Halimione verrucifera*, *Sarcocornia fruticosa*, *Arthrocnemum macrostachyum*, *Halocnemum strobilaceum*, etc.).
   (b) Reversible extreme halophytes: *Atriplex tatarica*, *Atriplex littoralis*, *Atriplex prostrata*, *Bassia hirsuta*, *Camphorosma annua*, and *C. monspeliaca*. The adaptations displayed by these species are a little bit less developed than irreversible halophytes, and some of them may have large ecological spectra, thus occurring in less salinized habitats.
2. **Mesohalophytes** are species with intermediary anatomical adaptations between extreme halophytes and glycophytes: *Aster tripolium*, *Lactuca saligna*, *Scorzonera cana*, *Lepidium cartilagineum*, *Lepidium latifolium*, *Lepidium perfoliatum*, *Iris halophila*, *Plantago schwarzenbergiana*, and *Trifolium fragiferum*. In this group a separated group, *amphibious halophytes* (that have bulliform cells) have been included; they are hygrophilous, sometimes growing in flooded areas, but are subjected often to seasonal droughts: *Scirpus maritimus*, *Carex distans*, *Juncus gerardi*, *Puccinellia distans* subsp. *limosa*, *Carex vulpina*, and *Alopecurus arundinaceus*.

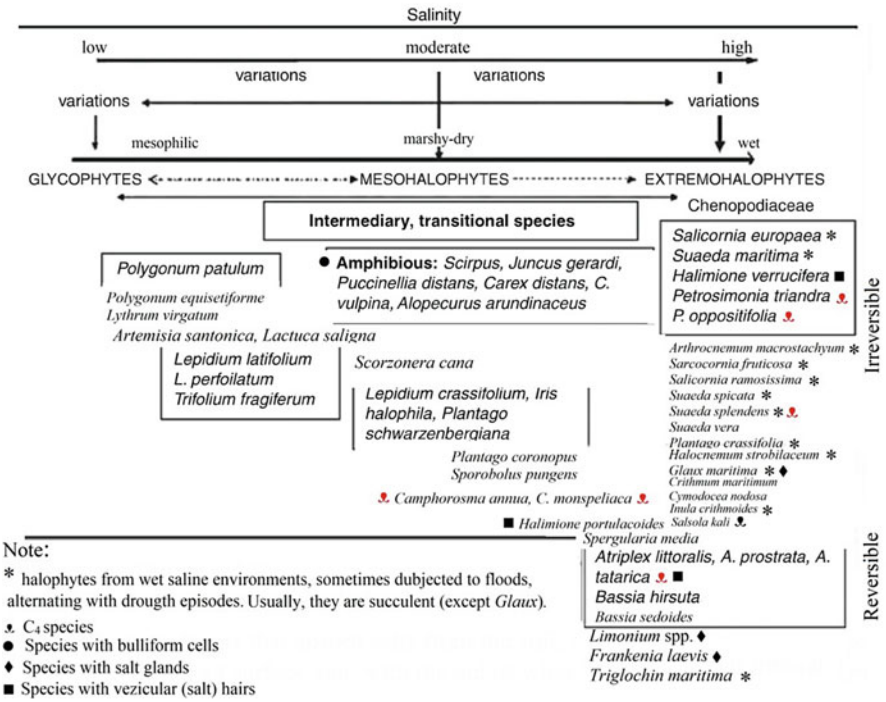

Fig. 15 An integrated classification of halophytes, based on their anatomical adaptations and ecological requirements (Adapted and improved after Grigore and Toma 2010b)

3. **Glycophytes** are conventionally plants that normally cannot grow in saline environments. Their place in this classification is just to have a conventional border in respect with halophytes categories (Fig. 15).

5 What Is an "Obligatory" Halophyte?

The term obligatory halophyte(s) occurs in many papers dealing with halophytes, and sometimes it is used in contrast with non (not)-obligatory or facultative halophyte concepts. Barbour (1970) questioned if any angiosperm is an obligate halophyte, and ever since, especially under experimental conditions, halophytes started to be classified either as obligatory or facultative halophytes. However, definitions of obligatory halophytes were suggested earlier, at the end of the nineteenth century, despite without clearly using the term *obligatory*; for instance, definitions such as "[plant] which thrives **best** in salty places" or "[plants] which **only** flourish abundantly on soils rich in alkaline salts" can be found already in the last decade of nineteenth century (see Table 1, this chapter; Grigore et al. 2014; Grigore 2019). From our knowledge, it looks like Backer was first who use the term "obligatory halophytes" in 1888.

Grigore et al. (2012) observed that some definitions of halophytes imply that salts, especially NaCl, are compulsorily required during the life cycle of halophytes, due to their stimulating effect upon several biological processes in this type of plants. To emphasize this requirement, a subcategory of halophytes has been described: *euhalophytes*, sometimes called "absolute halophytes," "exclusive halophytes," or "obligatory halophytes"; however, by extrapolation or by misinterpretation of the original definition, the term "euhalophytes" is about to be used for all categories of salt-tolerant plants.

Apart from terminology and definitions, earlier botanists have been interested in the role of salt in plant life, how salt content is regulated and, finally, if salt is really required by halophytes to achieve a better growth and development. The Grew's (1676) experiments were already mentioned in this direction.

A good example is that offered by Linné and his collaborators; Hedenberg (1754/1788), supervised by Linné, in a dissertation about plants' environments, underlined the importance of salt for plants. He offered the example of *Nitraria schoberi* (an interesting Romanian halophyte species, restricted only to Buzau county, Fig. 16) that has been cultivated for 20 years under conditions of Uppsala (Sweden) without flourishing, remaining sterile. The plant was able to flourish only when salt was added to the culture medium; the same was expressed by Linné in a letter of from 1759 to François Boissier de La Croix de Sauvages: "this year, after an assiduous attempt, (I) finally obtained fruiting of Nitraria schoberi (. . .) whose flowers were not seen in Europe, despite it is found in all gardens; I obtained (flowers) only after salt has been added."

Fig. 16 *Nitraria schoberi* (Photo: Marius-Nicuşor Grigore)

Chapman (1975) defined obligatory halophytes as those species that reach their optimal growth under conditions of salinities exceeding 0.5% NaCl.

Some authors refer explicitly or implicitly to halophytes that (obligatory) require for their growth high levels of salt. Barbour (1970) suggests that an obligatory halophyte is a species with optimal growth at moderate or high salinity and incapable of growth at low salinity (low salinity meaning in this case more than 2% salt).

Obligatory halophytes are defined as plants that thrive when given water having greater than 0.5% NaCl (Koyro and Lieth 1998). Other authors gave indirect definitions of obligatory halophytes; for instance, *Batis* is considered an obligatory halophyte, as it "requires NaCl to express maximum growth capacities," and in contrast, *Crithmum maritimum* is considered a facultative halophyte (its growth was decreased progressively as NaCl levels were raised in the medium from 100 to 300 mM NaCl) (Ben Hamed et al. 2008). Duarte et al. (2019) consider that obligatory halophytes demand saline environments for optimal growth; for instance, *Aster tripolium* has been reported as obligatory halophyte, as it has its optimum salinity around 250 mM NaCl, corresponding approximately to natural salinity from estuarine habitats.

However, it is a matter of debate if halophytes really require salt for their growth and development or they just can face high salinity concentrations, over other species, considered as non-halophytic, which have not refined adaptations to tolerate high amount of salt. In fact, many halophytes can germinate in nonsaline conditions; Schimper (1903) was among the first who recognized that most halophytes can grow quite well in nonsaline conditions. In this context, it seems unlikely that an obligatory requirement for high levels of salts occurs in angiosperms.

Many typical halophytes are found to vegetate in natural conditions under salinity thresholds that are sometimes very variable (Table 9). The underlined species and their values show important differences within multiple soil samples from the rhizosphere of the same species – a fact that reinforces the idea of difficulty in managing concept as soil salinity and plant-soil relationships (Grigore 2008a, 2012; Grigore et al. 2010, 2014).

Sharma and Gupta (1986) suggested that many halophytes are perfectly able to grow normally in environments with low salinity, or even nonsaline, and are called

Table 9 Values of pH and EC for several halophytes vegetating in Valea Ilenei nature reserve (Grigore and Toma 2014)

Halophyte species	pH	EC (dS/m^{-1})
Halimione verrucifera	8.58	1.54
Suaeda maritima	9.3	4.03
Salicornia europaea	**8.55–8.87**	**8–11.82**
Atriplex littoralis	9.2	2.49
Limonium gmelinii	7.92	2.29
Lepidium crassifolium	**9.04–9.78**	**4.54–10.56**
Artemisia santonicum	8.01	0.57
Aster linosyris	8	0.35
Bolboschoenus maritimus	8.95	2.39
Juncus gerardii	9.05	4.92

facultative halophytes. They, despite having optimal growth without salt, have the ability to tolerate high NaCl concentrations (Duarte et al. 2019).

In addition to the term "obligatory" (halophyte), Grigore (2008a) suggested that expression *preferential halophytes* is also a little bit inconvenient, from semantic point of view, but also from purely biological consideration; according to all given definitions of halophytes, they do *prefer* salt as compared to glycophytes.

Grigore et al. (2012) indicated that salts are not compulsorily required for development of halophytic species; they suggest that limitation of water and nutrients, rather than soil salinity per se, are the most important restrictive factors for plant growth in saline habitats. In two halophyte species (*Plantago crassifolia* and *Inula crithmoides*) and a psammophyte (*Medicago marina*), specific for sand-dunes, measurements of growth parameters (number of leaves, plant length, fresh, and dry weights) showed that all three species grew much better on the salt-free and nutrient-rich substrates, peat, and garden soil, than on saline soil and dune sand (Figs. 17 and 18). Obtained results suggest that distribution of halophytes in nature is probably dependent on their limited ability to compete with glycophytes in nonsaline areas. Contrarily, in stressful (saline) conditions, they would remain highly competitive as non-tolerant species cannot cope with these harsh environmental factors.

However, data regarding the effect of salts on halophytes are not homogeneous. In many halophytic species, growth is inhibited by increasing salt concentrations; on the contrary, in several genera, such as *Salicornia*, *Suaeda*, or *Atriplex*, a stimulation of growth in the presence of salt has been observed, although no species has been shown to grow optimally at seawater or higher salt concentrations (Ungar 1991; and references therein). In euhalophytes, such as *Aster*, *Salicornia brachystachya*, *S. patula*, *S. europaea*, *Spartina anglica*, *Suaeda monoica*, and *S. salsa*, dry mass production is stimulated by salinity. In other species, which could be considered less halophytic, a decrease in dry mass has been observed under salt treatment, for example, in *Atriplex gmelini*, *A. hastata*, *A. nummularia*, *A. inflata*, *A. triangularis*, *A. vesicaria*, or *Spartina alterniflora* (data summarized by Grigore et al. 2012).

However, as already underlined, these results should be regarded with caution, as they are derived from experimental conditions; in nature, it is likely that salinity stress would rather affects plants by its indirect effects, such as hydric stress or nutritional imbalance.

6 Physiological Drought of Soil and the Position of Halophytes Within Ecological Groups of Plants

Halophytes were perceived and described as a heterogeneous ecological group of plants, as recognized and discussed today (Grigore 2008a, 2012; Grigore and Toma 2010a, 2017; see Grigore and Toma's chapter on ▶ "Morphological and Anatomical Adaptations of Halophytes: A Review," in this handbook).

Early in the history of botany and especially in that of halophytes, they started to be approached firstly as maritime plants (halophytes restricted to sea vicinity), and later the concept has been extended to inland halophytes (Grigore 2019).

Fig. 17 Relative size of representative individual plants of *Inula crithmoides*, after 12 weeks of growth in different substrates: peat (**a**), garden soil (**b**), saline soil (**c**), and dune sand (**d**) (plants of the different species are not shown at the same scale) (Grigore et al. 2012)

Ever since, halophytes have been clearly defined as an ecological group of plants by iconic contributions of ecologists such as Schimper, Clements, and Warming who continuously refined this vision in terms of adopted physiological drought theory (see Grigore and Toma 2011). With the works of Warming (1895 – followed by multiple translations and editions) and Schimper (1903) – based on their anatomical and morphological features and characteristic of saline environments – halophytes started to be considered as a (special) case of xerophytes.

Stevens (1908), writing about the character of halophytes, underlined that they have essentially the same character as the xerophytes; despite they grow in soils abundantly supplied with water, their roots absorb it with great difficulty. However, the ways of

Fig. 18 Relative size of representative individual plants of *Plantago crassifolia*, after 12 weeks of growth in different substrates: peat (**a**), garden soil (**b**), saline soil (**c**), and dune sand (**d**) (plants of the different species are not shown at the same scale) (Grigore et al. 2012)

adaptation to the unfavorable conditions for absorbing water are essentially the same, as can observed by comparing a plant from the Algerian desert, another growing on wet, salt, tropical beaches, and one growing in the cold soil of Greenland. In each of these plants, the reduction of the transpiring surface is very marked.

Many handbooks of botany from the beginning of twentieth century deal with halophytes in close relation with xerophytes; classification of halophytes is being integrated in the large spectra of xerophytes, as a clear evidence for the theory of physiological drought of the soil (Coulter 1900; Bevis and Jeffery 1911; Farmer 1911; Stevens 1908).

Schimper (1903) emphasized that apart from structural features of halophytes or xerophytes, also characteristics of the environment (water and soil, especially) are of great importance for establishing the nature of adaptations in plants. Schimper (1903) concluded that physiological drought is caused by external factors that either reduce water uptake or which favor transpiration; frequently, there is a combination of these influences (Grigore and Toma 2011, 2017; Grigore et al. 2014). Among the factors that reduce water uptake, abundance of soluble salts in the soil must be mentioned for the case of halophytes.

The most important natural regions and habitats, where physiological dryness prevails and only xerophytes therefore thrive, are grouped as follows, according to their physical characters (Schimper 1903):

Fig. 19 North American desert species: *Bigelowia graveolens* (1); *Sarcobatus vermiculatus* (2–3); *Halostachys occidentalis* (4); *Graya polygaloides* (5–6); *Eurotia lanata* (7) (Schimper 1903)

1. Deserts (Fig. 19), steppes, and other districts with a dry substratum and dry air, occasional or persistent great heat, and intense illumination.
2. The bark of trees, rocks where there is rapid drying up of the substratum, owing to deficient depth.
3. Sandy soil, gravel, and the like, on account of the rapid drying up of the substratum owing to its great permeability (Fig. 20).
4. Seashores, solfataras, which have abundance of soluble salts in the soil (see Figs. 11, 12, 13, and 14).
5. Peat bogs, because of the humic acids in the soil (Fig. 21).
6. Polar zones (Fig. 22), vicinity of glaciers in high mountains, where the temperature of the soil is low.
7. Alpine highlands (Fig. 23), which are under rarefied air and strong insolation characteristic of the alpine climate.

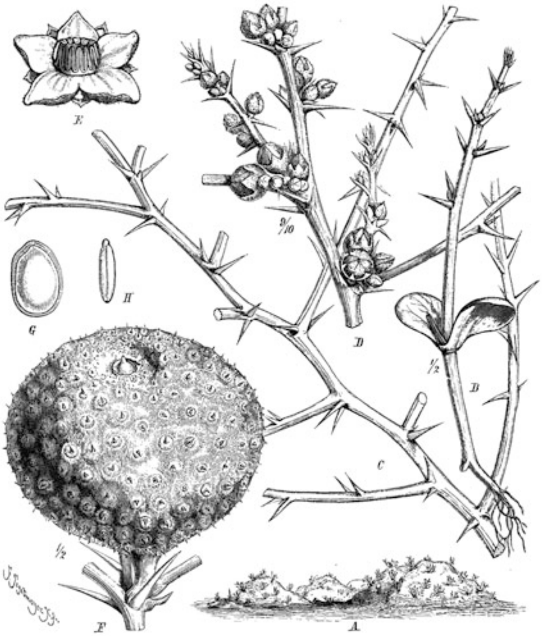

Fig. 20 Plant from sand dune: *Acanthosicyos horrida* (A: habitat; B: seedling; C-D: branches; E: flower; F: fruit; G-H: seed) (Müller and Pax 1894)

All these types of habitats were mentioned to better understand how one common factor (physiological drought) found in various environments can induce similar xeromorphic traits to plants thus vegetating in habitats that seem to be so different (Grigore et al. 2014).

Based on these details, together with some experiments aimed to show plant behavior in saline condition, Schimper concluded that halophytes' morphological characteristics are consistent with those of xerophytes.

Therefore, it would be correct to consider a halophyte a special form of xerophytes (Warming 1909; Grigore and Toma 2010a, 2011). This statement seems well supported by the features of environments that are affected by physiological drought and especially by morphological and anatomical adaptations of halophytes.

Kearney (1904) believes that even halophytes should be regarded as a subdivision of xerophytes (referring especially on succulence, Kearney considered that in halophytes, this feature is of xerophytic nature). He states that in using the term "halophyte," it should not be forgotten the fact that halophytes do not constitute an ecological class coordinate with hydrophytes and xerophytes, but are properly only a subdivision of the xerophytes. Like other xerophytes, they are characterized in general by the possession of various adaptations for reducing transpiration, as promoters of physiological drought – Warming (1895, 1897) and Schimper (1903) have pointed out. Kearney (1904) underlined that halophytes are such xerophytes as owe

Fig. 21 Peat bog plant *Vaccinium oxycoccos* (Fitch and Smith 1880)

their necessity for a reduction of transpiration largely to the presence in the soil of an excessive amount of readily soluble salts.

Despite he believed that the character of the soil is the final criterion which decides whether the vegetation should be called halophytic or non-halophytic, halophytes and xerophytes may actually occupy similar habitats. According to Kearney (1904), no ecological characters can be cited as exclusively halophytic, although halophytes seem to show a more marked tendency than other xerophytes toward a development of water-storage tissue. The well-marked succulence in halophytes has been discussed in detail in their ecological frame (Grigore 2008a; Grigore et al. 2014; Grigore and Toma 2017). In halophytes, the xerophytic habit is often developed to an extreme; this could be explained by the fact that in saline environments, a cumulus of stressing factors occur, and drought and high salinity in the soil are synergic factors that induced xeromorphic character of anatomical adaptations in halophytes.

Fig. 22 *Vaccinium uliginosum*, plant from polar environment (Schimper 1903)

Henslow (1895), in his important works on plant adaptations to living environments, stressed also the similarities between anatomical characteristics of halophytes and xerophytes. Taking into account especially plant' succulence and pubescence, he concluded that there are certain peculiarities common with desert plants and with some alpine and subalpine species. Henslow (1895) believed that resemblances in plants from widely different localities, such as seashores, alpine regions, and desert areas can be explained by the fact that certain elements of the environments are found in excess. Through a simplest deduction, he states that these elements act upon the plants and they respond accordingly, so that much the same results occur. For instance, the succulence from plants of deserts, especially where the soil is saline, arises from identically the same cause as in plants from seashores. He correctly concluded that since the moisture of the air and soil is charged with saline matters in maritime regions and salt marshes, the presence of salts is in some extent responsible for succulence in many halophytes.

Fig. 23 Alpine rosette-plants: *Carmelita formosa* (1); *Eryngium humile* (2); *Calycera eryngioides* (3) (Schimper 1903)

The introduction and operational use of physiological drought complicated in some extent ecological classification of plants and especially of halophytes (Warming 1895, 1909), Schimper (1903), and Clements (1907).

7 Conclusion

Definitions of halophytes date back to the middle of nineteenth century when started to be ecologically approached by botanists. As knowledge about them accumulated, their definitions and classifications became more complicated. Nowadays, definitions and classifications based on the real salt requirement of halophytes for their growth and development are still questionable. There is a need for further and detailed studies conducted on halophytes in their natural habitats, as some definitions of "obligatory" halophytes are based on salinity tolerance value established under experimental NaCl treatments.

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