THE MEDITERRANEAN WEEDY VEGETATION AND ITS ORIGIN

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ABSTRACT - An overview on the origin and evolutionary trends in the Mediterranean weedy vegetation is presented, with reference to the phytosociological units to which they are ascribed: *Stellarietea mediae*, *Papaveretea rhoeadis, Oryzetea sativae*. It is postulated that the "Neolithic revolution" was more likely a "Neolithic evolution", *i.e*. the result of a process of selection and demographic growth that lasted for at least 10000 yrs, before leading to the domestication of plants and animals. During this very long time, wild crop relatives were simply growing together with the wild weed relatives, in their original milieu. At the beginning of agriculture, fields were obtained to the detriment of oak-woods and maquis-vegetation; the deforestation had probably a patchy pattern, resulting from the burn-beating practice, and the annual plants from the vegetation around the fields were probably quite abundant also within the fields, at least those having the most prolific seed set, the most durable seeds and the most effective dispersal strategies, together with a diachronic, life-long, flowering and seed-dispersal. These features, apparently in contrast with the achievement of a within-population- organizational hierarchy, are in reality an extreme expression of the attitude of weedy plant species in "amplifying adaptation", or, in other words, of its "adaptation to adapt", which is the cornerstone of the opportunistic life strategy. The Mediterranean weedy vegetation is therefore a flexible system, able to cope with changes and disturbances: species frequency and composition may undergo great variations, but the functional role of any weedy community keeps.
KEY-WORDS - Adaptation, weeds, Mediterranean region, evolutionary trends.

INTRODUCTION

The Mediterranean agriculture started about 12000 years ago in the Middle East and begun its westward expansion not before 9000 yrs b.p. (Diamond, 1997). It is likely that the setting of the first cultures was triggered by the observation of the after-fire biological successions, in areas where the annual vegetation is characterized by high frequency of edible legumes and cereals. The transition from the simple, tribal social structures of hunters and gatherers towards more complex and technologically developed cultures was probably related to the setting of the first agricultural techniques: increased fire frequency, superficial plugging, (eventually) hoeing.

The setting of agriculture, transformed the human societies, which from scattered and erratic became sedentary, stationed in larger settlements. The archeological findings from the “fertile halfmoon” (namely in Mesopotamia and Egypt) testify a radical transformation in the housing habits and the social relationships among the members of each single community.

The origin of agriculture was more a process than an event, resulting from a progressive changing of the behavioral schemes of the men towards the available resources of its territory (Cohen, 1977). When the agriculture started in the Mediterranean area, fire was already commonly used since many thousand years for driving out the game, for directing the herds of herbivores and for creating grasslands, where the hunt is easier and where the domestication of useful plants and animals probably occurred. The Mediterranean grasslands were not only pasturelands for domesticated livestock, but also fields for the collection of wild legumes, oily seeds, cereals, bulbs, native of the Mediterranean region, which at a certain point of the human history became the ancestors of cultivars that are still grown. Much earlier than the first agricultural practices became established, the Mediterranean landscape started to be dominated by versatile but poorly competitive species, whose ecological fitness took advantage from the human disturbance (Guarino, 2006).

The floristic settlement and productivity of the Mediterranean dry grasslands are naturally subject to great variations, often driven by stochastic, unpredictable events and climatic crisis (Naveh, 1998), that forced the human populations to have recourse to simple agricultural practices, such as the sowing of edible species and the killing of weedy species, for getting over the periodical alimentary crisis which were induced, on one hand, by the mentioned quantitative variability of the native populations of the wild crop relatives, on the other hand, by the demographic growth of the human population. The selection and domestication of the most productive breeds originated from these practices, their seeds and the associated agricultural practices spread thanks to the human migrations and the establishment of a network of exchanges between neighboring human populations.

The development of agriculture and the spreading of the agricultural practices selected an opportunistic, poorly competitive, specialized flora, dominated by species with prolific seed sets and efficient dispersal strategies. The Mediterranean weedy communities progressively increased their species richness during the westward spreading of the cultivation techniques, and reinforced as soon as commercial routes become established. From the Mediterranean agriculture, several polyploid populations of weedy species are deriving, that often crossed the limits of the distribution ranges of their ancestors and in some cases (such as *Poa annua* and *Veronica persica*) achieved a worldwide success.

Basing on literature and personal unpublished data, this paper aims to summarize the main features and adaptations of the Mediterranean weedy vegetation, with reference to the phytosociological units to which this vegetation is traditionally ascribed.

Adaptations and functional consequences

Each agricultural practice operates a selective pressure on the weedy communities, and this is also influencing the phytosociological classification of the Mediterranean weedy vegetation. Depending on the kind of tillage, the Mediterranean weedy vegetation can be ascribed to three main functional groups: the one combined with the cereal growing (*Papaveretea rhoeadis*), where the agricultural practices were traditionally limited to a pre-sowing superficial ploughing and after-yield fire, the one combined with the hoed crops (*Stellarietea mediae*) and the one associated to the paddy fields (*Oryzetea sativae*). Relevant physiognomic, adaptive and floristic differences are featuring the three mentioned typologies that will be commented separately in the following paragraphs. As a whole, the adaptations and functional consequences to the environmental stresses and agricultural practices of the plants growing in the Mediterranean weedy vegetation are reported in Tab. 1.

Seed dispersal, life-cycle and harvesting-time, interacting with environmental disturbance and management across heterogeneous landscape, result in irregular weed spatial distribution (Cardina *et al.*, 1997). Therefore, a prerequisite to study and describe the weedy vegetation is the understanding of the origin of weeds and what determines their frequency and distribution at present time. Few generalizations can be drawn, however, because spatial patterns, heterogeneity and species composition of the weedy communities are highly influenced by stochasticity, that's why the phytosociological associations describing these communities often do have a narrow range and a very short metastability. This is a main result of the intense and frequent disturbances affecting the weeds, which impede to the vegetation at issue to reach their own internal organization. For weeds, the adaptation to the environmental disturbances is obtained through the adoption of a therophytic habit and of a diachronic, life-long, flowering and seed-dispersal. These features, apparently in contrast with the achievement of an organizational hierarchy, are in reality an extreme expression of the attitude of each single weedy plant species in "amplifying adaptation", or, in other words, of its "adaptation to adapt" (Ashby, 1947), which is the cornerstone of the opportunistic (or ruderal, *sensu* Grime, 1979) life strategy. The weedy vegetation is therefore a flexible system, able to cope with changes and disturbances: species frequency and composition may undergo great variations, but the functional role of any weedy community keeps.

Papaveretea rhoeadis

Irano-Turanian and pan-Mediterranean vegetation, sporadically spread, as well, in the temperate and Atlantic Europe, Macaronesia and Saharo-Sindic region. It is dominated by annual grasses, among which the scapose growth-form is prevailing. Some geophytes (*Ornithogalum, Allium*) may also occur. This vegetation is usually ascribed to the phytosociological class *Papaveretea rhoeadis* Brullo, Scelsi & Spampinato 2001 (= *Secalietea* Br.-Bl. in Br.-Bl., Roussine & Negre 1952) (Ferro, 1990, Brullo *et al.*, 2001).

In the Mediterranean region, cereal crops are an extensive winter-growing cultivation, traditionally harvested in May-June, ignited in summer, ploughed and

TABLE - 1: Synopsis of the main adaptations to stresses of the weedy plants occurring in the Mediterranean crops.

Stress	Adaptation	Functional consequence
Generic disturbance	Therophytic/Geophytic habit	Increased versatility
	Anemochory	Long-distance dispersal
	Asexual reproductive attitude	Proliferation under optimal conditions
	Allelopahty	Increased ecological fitness
Ploughing	Persistent, soil-stored seeds	Maintenance of viable populations for many yrs.
Hoeing	Rapid root growth	Rapid re-establishment
	Rooting nodes	Reduced physical damage
	Small size	Minimization of the attack layer
	Creeping habit	Stress avoidance
	Precocity	Stress avoidance
Trampling	Prostrate, caespitose growth form	Reduced physical damage
	Low stature of plants	Minimization of the attack layer
Harvesting	Diacronic flowering and seed dispersal	Long reproductive period
	prolific seed set	Higher reproduction rate
	Precocity	Stress avoidance
	Polichory	Diversification of risk
	Seed mimicry	Minimization of risk
Chemical fertilization	Rapid growth	Sequestration of nutrients
	C4 metabolism	Cost-effective metabolism
	Cluster roots	Increased exchange surface
Herbicides	Crop-weed hybridisation	Increased resistence to the treatment
	Introgression / genetic variability	Increased probability of developing resistence
Flooding (Oryzetea sativae only)	Thin cuticle	Optimal light absorption
	Maximized surface area	Optimal light absorption
	Chloroplasts on the top of leaves	Increased metabolic fitness
	High stomatal density	Increased exchange surface
	Extended canopy architecture	Increased competitiveness for space
	Hydrochory	Optimal dispersal strategy
Summer drought (Chenopodion bo-tryos & Diplotaxion erucoidis only)	Epidermal trichomes, waxes, thick cuticle	Reduced evapotranspiration
	Sunken stomata, conduplicate leaves	Increased boundary layer resistance
	Reduced leaf area	Reduced water loss
Summer heat (Chenopodion bo-tryos & Diplotaxion erucoidis only)	Rapid root growth of seedlings	Adequate water supply
	Serotine germination	Avoidance of extreme temperatures
	Reduced leaves	Reduced heat loading
	Open canopy architecture	Sensible heat removal
	Epidermal trichomes, waxes, thick cuticle	Increased reflectance

seeded after the first fall-rains. Frequent fires cause a sudden de-hydratation of soils and a sudden increase of cations (K^+, Ca^{2+}, Mg^{2+}). Therefore pH increases as well, at least next to the soil surface (De Bano *et al.*, 1977; De Lillis, 1995). That's why the segetal vegetation can be neutro-basiphilous (*Ridolfion segeti*), also when it occurs on soils deriving from acidic substrata. Acidophilus segetal communities (*Scleranthion annui*) are found, however, in the most rainy areas of the Mediterranean region, especially where the condensation of orographic clouds along the mountain slopes creates relatively fresh and moist microclimatic conditions.

As we will better see in the final chapter, the Mediterranean agriculture probably begun with cereal growing, thus the segetal vegetation is likely to be the first appeared in the Mediterranean region, originating from plants having an Irano-Turanian distribution (archeophytes). Even at present times, this vegetation is better expressed and shows higher species richness in the SE-part of the Mediterranean region.

Stellarietea mediae

Eurosiberian and pan-Mediterranean vegetation, dominated by annual plants linked to disturbed habitats, chiefly in agrarian and urban ecosystems. This vegetation is ascribed to the phytosociological class *Stellarietea mediae* Tx., Lohmeyer & Preising ex v. Rochow 1951(=*Chenopodietea* Br.-Bl. in Br.-Bl., Roussine & Nègre 1952) (Brullo & Marcenò, 1985). Within this class, three main groups of weedy communities, linked to non-watered hoed crops, are found in the Mediterranean region. Most of the weeds growing in this context originated from plants belonging to Mediterranean or sub-Meditrerranean chorotypes. To the hoeing-practice, a seasonal alternation of plant communities is associated, depending on the life-cycle and harvesting-time of the crop: one group includes the weeds growing in winter-spring (*Fumarion wirtgenio-agrariae*) and two include those growing in summer-fall, either on carbonatic (*Diplotaxion erucoidis*) or siliceous (*Chenopodion botryos*) soils. The chemical reaction of the soils has got a strong influence on the weed distribution during the dry season, because soils richer in carbonates and clay are on average more compact and their surface dries up faster (Fierotti, 1997). The combined influence of the soil chemistry and texture is negligible during the rainy season, due to the hydratation of the soil surface that buffers the physical stress in the rhizosphere. Hoeing is also practiced in the agrume-groves, where the shadowing of the canopy facilitates the development of a sciaphilous-nitrophilous weedy vegetation (*Veronico-Urticion urentis*), rich in geophytes and short-lived hemicryptophytes, that protract their growing season well into the summer.

In relatively recent times, another kind of weedy communities appeared in the Mediterranean region, together with the cultivation of corn and many species of *Solanaceae*. In the dry Mediterranean summer, these are the only watered crops. Warm temperatures and abundant water favour a weedy vegetation dominated by fast-growing tropical species (*Digitario ischaemi-Setarion viridis*), among which the neotropical chorotype is often prevalent (neophytes), due to the American origin of the cultivated species.

Oryzetea sativae

Rice has a minor importance in the Mediterranean region, even if paddy fields are commonly occurring in NW-Italy, SE-Spain and W-Sardinia, where they started between the mid-17th century and the early 20th century. The weedy vegetation of Mediterranean paddy fields includes several species with an E-Asiatic origin, that's why phytosociologists use to ascribe it to the class *Oryzetea sativae* Miyawaki 1960, i.e. to the same class to which the weedy plant communities of the Asian paddy fields belong to. In all Mediterranean countries where paddy fields occur, the traditional hand methods of cultivating and harvesting rice have undergone mechanization at all stages of cultivation and harvesting, that's why the typical *Oryzetea sativae*-vegetation is at present time poorly represented. The main reason for the rarefying of this weedy vegetation is, however, the use of herbicides, recently combined with the increasing tendency to keep the paddy fields flooded in fall and winter, for the resting of migratory birds (Smith & Fox, 1973). The last practice favours the predation of seeds and is particularly detrimental for *Eragrostis* and *Echinochloa* spp., the commonest and most abundant *Oryzetea sativae*- elements in the Mediterranean region. That's why at present time, the only serious weedy competitors of the rice cultivated in the Mediterranean region is the red rice, i.e. *O. sativa* L. var. *sylvatica* (Vidotto *et al*., 1998). The fight against red rice is particularly difficult because of its phenotypic variability and because of its physiologic and genetic proximity to the cultivated rice.

Hypothesis on the origin of the Mediterranean weedy vegetation

It is well known that in the SE proximities of the Mediterranean region, i.e. in the so-called fertile half-moon, the domestication of many cultivated plants took place, among which barley, wheat, pea, lentil, cicer, broad been, chickling, flax (Harlan, 1971). The first unequivocal evidence of "Neolithic revolution", i.e. the transformation of the human settlements and societies associated with the development of agriculture in the SE Mediterranean and neighboring territories, dates to 9000 yrs. ago (Zohary & Hopf, 1973). Abundant seeds of the above-mentioned plants have been found, however, in much earlier human settlements, such as in Wadi Kabbaniya (W-Egypt), dated from 18500 and 17000 yrs b.p. (Wendorf et al., 1982).

A common feature of all the Mediterranean wild crop relatives is that they are adapted to disturbed and rather unstable natural habitats, such as clearings, land sliding slopes, riverbeds and open shrub lands, where only a feeble or null interspecific competition occurs. They are relatively exigent, however, for what concerns the soil fertility, since their ecological function is to be involved in the post-disturbance (post-fire, post-flood) processes of recolonization through which a wooden potential vegetation can recover (Hawkes, 1969).

One of the first effects of the human colonization of the Mediterranean lands was an increased fire frequency: wildfires were the easiest way to obtain grass-dominated terrains, which attract wild herbivores and can be used as "hunting reserves". In the same sites, seasonal camps were also settled and most of the human foraging activities were probably accomplished. As a consequence of the standing of herds and hordes, soils were locally enriched with nitrogen and phosphates (Harlan & de Wet, 1965) and the plants growing there were providing most of the harvest of hunters and gatherers, because it was easy to identify them and because they were found in dense and homogeneous populations. Therefore, the "Neolithic revolution" was more likely a "Neolithic evolution", i.e. the result of a process of selection and demographic growth that lasted for at least 10000 yrs, before leading to the domestication of plants and animals.

During this very long time, wild crop relatives were not cultivated: they were simply growing together with the wild weed relatives, in their original milieu. *Linum bienne*, *Triticum boeoticum*, *T. dicoccoides, Aegylops longissima, A. squarrosa, Hainardia villosa, Hordeum spontaneum*, i.e. the wild relatives of flax, wheat and barley (Scossiroli, 1984), have their ecological optimum in neutro-basiphilous therophytic dry grasslands which are classified by phytosociologists in the order *Stipo-trachynietalia distachyae* Brullo 1985. On the other hand, *Avena ludoviciana*, *Cicer pinnatifidum, C. echinospermum, Lens orientalis, Pisum elatius, P. humile Vicia narbonensis, V. galilea*, i.e. the wild relatives of oats and the Mediterranean legumes (Scossiroli, *l.c.*), have their ecological optimum in more mesophilous and subsciaphilous therophytic vegetation, commonly occurring in small niches and micro-ledges, on substrata rich in organic matter, often under the canopy of shrubs and trees in the Mediterranean maquis, classified by phytosociologists in the order *Geranio-Cardaminetalia hirsutae* Brullo 1985.

One of the ecological differences between the chief species of *Papaveretea-* and *Stellarietea-* vegetation is that the former are more frequent on poorly tilled and non-fertilized dry soils, the latter on looser and fertilized soils, due to the hoeing practice less exposed to withering. This might be related to the different ancestral habitats of the two groups of species. Actually, most of the species characterizing the *Papaveretea-* vegetation progressively become less frequent moving from the SE-Mediterranean territories NW-wards, since under cooler and moister climatic conditions they are replaced by *Stellarietea*-elements. For this reason, in central-European and NW-Mediterranean- phytosociological studies, the order *Papaveretalia rhoeadis* (= *Centaureetalia cyani*) is often framed in the class *Stellarietea mediae*.

After the beginning of agriculture, the first agro-pastoral societies migrated East- and Westwards (Fig. 1), under the spur of the demographic pressure and the environmental degradation, determined by the frequent burning off associated with the pristine farming activities. Archeological findings show that the speed of the expansion of the farming activities throughout Europe and Northern Africa had an average speed of about 1 km/yr (Menozzi *et al.*, 1978). This expansion was not simply a cultural transmission, but happened as a real migration of human beings, with the typical traits of an invasion, with the new settlers getting mixed or, more often, totally substituting the indigenous populations (Cavalli-Sforza, 1975).

The sites to be subjected to agriculture were carefully selected, their ecological and structural traits being the most similar to the original ones: Mediterranean maquis and oak-woods. But the available technologies for deforesting and weed killing were not efficient enough to avoid that some seeds and plants accidentally outlived the tillage and joined the ones unintentionally transported and spread with the cultivated seeds. At the beginning of agriculture, the deforestation had probably a patchy pattern, resulting from the burn-beating practice, and the annual plants from the vegetation around the fields were probably quite abundant also within the fields, at least those having the most prolific seed set, the most durable seeds and the most effective dispersal strategies. It must be noted, however, that the weedy plant communities currently ascribed to the classes *Papaveretea rhoeadis* and *Stellarietea mediae* are not simply the result of an *in situ* selection of weedy plants: the agricultural expansion had been enough slow for letting the annual weeds to migrate and to occupy the ecological niches suitable for them.

To the post-industrial modernization of the agricultural practices, two main trends are associated: on one side, the ingression in the Mediterranean region of weeds from other continents (like the vegetation of *Oryzetea sativae* and *Digitario ischaemi-Setarion viridis*); on the other, an overall impoverishment of the weedy plant communities, due to the increased energy employed in the weed-control (Roberts & Feast, 1972; Radosevich *et al.*, 1997).

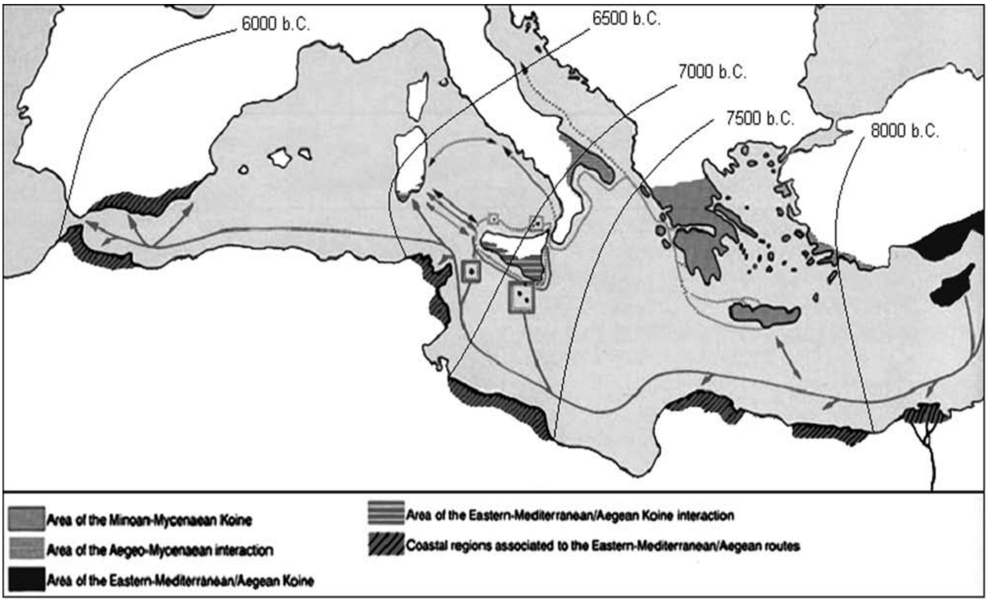

FIGURE 1 - Mediterranean trading routes in the Bronze age and isochrones of the agricultural expansion (after Cavalli-Sforza, 1975, modified).

References

Ashby W. R., 1947 - *Principles of the Self-Organizing Dynamic System*. Journ. General Psychology, **37**: 125-128.

Brullo S. & Marcenò C., 1985 - *Contributo alla conoscenza della vegetazione nitrofila della Sicilia*. Coll. Phytosoc., **12**: 23-148.

Brullo S., Scelsi F. & Spampinato G., 2001 - La vegetazione dell'Aspromonte. Studio fitosociologico. Laruffa – Reggio Calabria.

Cardina J., Johnson G.A. & Sparrow D.H., 1997 - *The nature and consequence of weed spatial distribution*. Weed Sci., **45**: 364-373.

Cavalli-Sforza L. L., 1975 - *La genetica delle popolazioni umane*. Le Scienze, **14**: 56-64.

Cohen M.N., 1977 - The food crisis in prehistory. Yale Univ. Press, New Haven and London.

De Bano L.F., Dunn P.H., Conrad C.E., 1977 – *Fire's effects on physical and chemical properties of chaparral soils*. Proceed. Environm. Consequences of Fire and Fuel Management in Mediterranean Ecosystems. USDA For. Serv. Gen. Tech. Rep., **WO-3**: 65-74.

De Lillis M., 1995 – Ecologia del fuoco. In: Pignatti S. (ed.): Ecologia Vegetale. UTET, Torino.

Diamond J., 1997 – Guns, germs and steel: the fates of the human societies. Norton & Company, New York.

Ferro G., 1990 - *Revisione della vegetazione segetale mediterranea ed europea dell'ordine Secaletalia*. Braun-Blanquetia, **6**: 1-59.

Fierotti G., 1997 - I suoli della Sicilia. D. Flaccovio Editore, Palermo.

Grime J.P., 1979 - Plant strategies and vegetation processes. John Wiley & Sons Ltd.

Guarino R., 2006 - *On the origin and evolution of the Mediterranean dry grasslands*. Ber. Reinhold Tüxen Gesell., **18**: 195-206.

Harlan J.R., 1971 - *Agricultural origins: centers and noncenters*. Science, **174**: 468-474.

Harlan J.R. & de Wet, J.M.J., 1965 –*Some thought about weeds*. Econ. Bot., **19**: 16-24.

Hawkes J.G., 1969 - The ecological background of plant domestication. In: Ucko P.J. & Dimbleby (eds.): The domestication and exploitation of plants and animals. Duckworth, London, p. 19-27.

Menozzi P., Piazza A. & Cavalli-Sforza L. L., 1978 - *Synthetic maps of human gene frequency in Europeans*. Science, **201**: 786-792.

Naveh Z., 1998 - *From Biodiversity to Ecodiversity*. In: Rundel P.W., Montenegro G. & Jaksic F.M. (eds.): *Landscape disturbance and Biodiversity in Mediterranean-type ecosystems*. - Ecological studies, **136**: 23-53.

Radosevich S.R., Holt J.S. & Ghersa C., 1997 - Weed Ecology: Implications for Management. 2nd ed. John Wiley & Sons, New York. 589 p.

Roberts H.A. & Feast P.M., 1972 - *Fate of seeds of some annual weeds in different depths of cultivated and undisturbed soil*. Weed Research, **12:** 316-324.

Scossiroli R. E. 1984 - L'uomo e l'agricoltura: Il problema delle origini. Edagricole, Bologna.

SMITH R.J. & FOX W.T. 1973 - *Soil water and growth of rice and weeds*. Weed Science, **21**: 61-63.

VIDOTTO F., FERRERO A. & TABACCHI M., 1998 - Lotta al riso crodo (*Oryza sativa* L. var. *sylvatica*) con la tecnica della falsa semina. Proc. Giornate Fitopatologiche, p. 369-374. Scicli e Ragusa, Italy.

WENDORF F., SCHILD R. & CLOSE E. E., 1982 – *Un antichissimo raccolto sul Nilo*. Scienza, **82(2)**: 38-43.

ZOHARY D. & HOPF M., 1973 – *Domestication of pulses in the Old World*. Science, **182**: 887-894.