Biology, life-strategy and invasiveness of Amaranthus retroflexus L. (Amaranthaceae) in central Italy: preliminary remarks

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ABSTRACT: A review of biological, ecological and chorological information is provided for Amaranthus retroflexus L. (Amaranthaceae). The species is a noxious weed introduced in Italy from North America. It exhibits a high phenotypic plasticity and easily adapts to a multitude of agricultural and ruderal habitats. A. retroflexus has variable degrees of dormancy and germination rates as a result of environmental factors. Growth is rapid and plants produce a large number of viable seeds. The species has developed resistance to several herbicides and other chemicals. It is alternate host to nematodes, viruses, bacteria and fungi that usually affect cultivated plants.

Key words: Alien species, Amaranthus, biology, invasiveness, life-strategies

INTRODUCTION

Amaranthus L. (Amaranthaceae) is a genus of about 70 species of monoecious and dioecious usually annual species of worldwide distribution, about 40 of which are native to America, while the remaining ones are native to the other continents (Costea et al. 2001a). This genus is represented in the Italian flora by 21 species (23 taxa if we consider species and subspecies) (Conti et al. 2005; Conti et al. 2007; Iamonico 2008a, 2008b; Celesti-Grapow et al. 2009); most of these entities are considered aliens and some are naturalized and invasive species (Celesti-Grapow et al. 2009). Several amaranths can have ecological and/or economic impact (Camarda et al. 2005). In latter case, they strongly compete with crops, and their detrimental effects are: reduction in productivity and crops quality, toxicity, production of damages by secondary chemicals or diffusion of pathogens.

During my research on the genus Amaranthus in Italy, aiming to clarify its taxonomy aspect and distribution, I observed several ecological character of A. retroflexus.

In this paper, ecological, morphological and chorological informations on A. retroflexus in central Italy are given, in order to highlight the characters that allow the naturalization and invasion of this species.

STUDY AREA

The study area includes the five regions of central Italy: Toscana (Alpi Apuane excepted), Umbria, Marche, Lazio and Abruzzo (Fig.1). The total area covered is about 68000 Km² and it is characterized by a high landscape diversity: geolithologic (limestone, marls, clay and silt, sandstone, flysch, drift), geomorphologic (from coastal to mountain sectors up to 3,000 m a.s.l.), climatic (from mediterranean to alpine climates), habitats (beach and coastal dune, maquis, thermophilous and mesophilous forests, meadows, wetlands, cliff, altitude grassland, synanthropic habitats and wastelands) and landscape [with anthropic, seminatural matrix (urbanized or agricultural) or natural matrix].
MATERIAL AND METHODS

Ecological and biological data were collected both during field surveys and from literature. I examined the specimens kept in the following herbaria, as well: APP, AQUI, FI, PESA, PERU, RO and URT.

Based on Noble (1989), Rejmánek (1999) and Celesti-Grapow et al. (2005), the following characters were chosen for the study:

- morphology;
- plant life form;
- native country, chorotype and abundance in study area;
- phenology;
- pollination mode;
- seed dispersal;
- habitat;
- landscape matrix;
- reference syntaxa;
- phytoclimatic regions.

Moreover, the following information is given:

- hybrids;
- floral biology;
- fruit;
- germination;
- soil;
- photosynthetic path;
- response to herbicides;
- response to herbivory, nematodes, fungi, bacteria, viruses and higher plants parasites.

RESULTS

Morphology, life form and hybridization. *A. retroflexus* includes herbaceous annuals (*T* scap *sensu* Pignatti 1982), 5-160 cm tall (occasionally more). Stem usually erect (sometimes prostrate), green and typically densely pubescent. Leaf blade rhomboid, ovate or lanceolate, ± glabrous (pubescent on the veins abaxially), base cuneate, margins entire (sometimes undulate) and inferior veins very protruding, white-green, apex usually acute and mucronate. Inflorescence composed of green, erect, condensed spikes; the terminal spike usually equal or shorter than the lateral spikes. Flowers with lanceolate, thick and long pointed bracts longer than the perianth; tepals five, spathulated, with apex obtuse, truncate or emarginate. Fruit circumscissile, elliptic, equal or shorter than the perianth. For further details on the morphology and phenotypic variability, see Iamonico (2008c).

*A. retroflexus* easily hybridizes with other entities from subgen. *Amaranthus* (*sensu* Mosyakin & Robertson, 1996). Costea et al. (2001a) also reported hybrids with dioecious species of the subgen. *Acnida* (L.) Aellen ex K. R. Robertson [in Italy one species is reported for this subgenus: *A. tuberculatus* (Moq.) J.D. Sauer (= *A. rudis* J. D. Sauer) (Celesti-Grapow et al. 2009). *A. tamariscinus* Nutt. (that was indicated by Conti et al. 2005; Conti et al. 2007) was reported as *Name in previous floras* by Celesti-Grapow et al. (2009)].

Most of the natural hybrids in subgen. *Amaranthus* were described by Aellen (1959) and Priszter (1958),
two eminent specialist of the genus *Amaranthus* in Europe in 1950s and 60s. In our study area the following hybrids have been reported: *A. × galili* Sennen et Gonzalo (= *A. retroflexus* L. × *A. cruentus* L.), *A. × ozononii* Priszter (= *A. retroflexus* L. × *A. hybridus* L.), *A. × ralletii* Contré (= *A. retroflexus* L. × *A. bouchonii* Thell. var. *cacciatoi* Aellen ex Cacciato).

**Origin, corology and abundance in the study area.** *A. retroflexus* is native to North America (Sauer 1950; Sauer 1967; Costea et al. 2001a) and is considered cosmopolitan at present (Aellen 1964; Bojan et al. 2003; Brenan 1981; Mosyakin & Robertson 2003). The oldest Italian specimen is kept in the Biblioteca Angelica (Rome) and was collected by Gherardo Cibo in 1532 (Saccardo 1909).

Based on personal observations and examination of herbarium specimens, *A. retroflexus* can be considered a common or very common species in central Italy. However, further studies are needed in order to verify its actual distribution.

**Phenology.** Young plants usually emerge from the end of May to June. Growth can be very rapid (about ten days to generate the first flowers in optimal ecological conditions). Flowers appear from June to October. The first fruits can be developed in July, although I observed plants that fructified in January. Senescence stage is from November to December.

Phenological stages are slightly dephased for different latitudes. All stages are shorter at higher latitudes (northern sectors of Toscana and Marche) and the emerging of the young plants is late in June, while they die back in December.

**Floral biology and pollination.** The inflorescence structure of *A. retroflexus* (the same of the other *Amaranthus* species) is quite complex (Weaver & McWilliams 1980; Costea et al. 2001a). Flowers are small, usually green, unisexual and are grouped in dense clusters (cymes). Each cyme has a central axis with a terminal male flower followed by a pair of opposite lateral branches of female flowers. The cymes are arranged in spike structures. At anthesis new male flowers develop at the end of the inflorescence branches; these flowers may pollinate the lower female flowers (Costea et al. 2004).

This structure described above is typical of the self-pollinated plants (Brenner et al. 2000; Costea et al. 2001a). However, pollination is performed mainly by the wind. In fact, the flowers lack the nectar glands and the pollen grain is small (diameter 18-28 μm) with 30-45 pores uniformly distributed on its surface (Costea et al. 2004). Franssen et al. (2001b) suppose that this distribution of the pores generate a high air turbulence that decreases the friction between the pollen grain and the air, maximising the distance at which the pollen grain can be dispersed.

The pollen grains also contain starch (up to 7.5%) protecting them against desiccation (Roulston & Buchmann 2000).

The adherence to the stigma hairs is favoured by the presence of the granules and/or spinules on the pollen surface (Costea et al. 2004).

Costea et al. (2004) observed that the reproduction is indirectly favoured by insects. In the amaranths, in fact, developing of the flowers and production of the seed proceed simultaneously because of the high density of the inflorescence. Certain predators may accidentally pick up or carry the pollen grains, favouring the dispersal.

**Fruit.** The fruit is a circumsiscle capsule containing one seed. The ripe pericarp has two layers, between which is a large intercellular space filled with air allowing the floating of the fruit (Costea et al. 2001b).

**Production, dispersal and germination of the seeds.** The seeds are subelliptic (diameter 1-1,5 mm) and their surface is more or less smooth, water-proof and resistent to chemical and physical atmospheric agents (Costea et al. 2004).

Each plant may produce up to 100,000 seeds, in optimal ecological conditions (Mohler & Callaway 1995). The amount of the seeds produced by one plant can be estimate by measures of the height of the plant and by the diameter of the stems. Cacciato (1966) reported the investigation by Priszter (1950), who collected as much as 506,000 seeds from a single plant!

The dispersal of the seeds is performed by four main factors (Costea et al. 2004):

- wind, though seed weight prevents long distance dispersal (seeds typically fall near the mother plant, up to 2 m);
- water, typically river, water courses and irrigation channels;
- animals, in particular mammals and birds (birds excrements; seed structure is not damaged by digestion);
- humans, by sewage works.

Seed initially show a high vitality (>90%) (Weaver & McWilliams 1980), but when they are buried, their survival period is variable in relation to depth, temperature and texture of the soil, frequency of disturbance, dormancy (Costea et al. 2004). Taylorson (1970) reported that the dormant seeds of *A. retroflexus* have a high vitality (up to 93%) after 12 months of burial, while the not-dormant seeds have lower vitality (25%).
Temperature and length of the photoperiod are the main ecological factors that influence the production of the dormant seeds. Laboratory experiments have shown that the production is directly correlated to the length of the day, while the production and temperature are inversely correlated (Kigel et al. 1977; Chadoeuf-Hannel & Barralis 1983). Low concentration of nitrogen in soil also enhances the production of dormant seeds (Costea et al. 2004).

The germination is influence by several factors:
- photoperiod and temperature: minimum temperature required increases from summer to autumn and winter (Kigel et al. 1977; Weaver & Thomas (1986) verified that the ideal percentage for germination is achieved at 20-35 °C with a 14 h photoperiod;
- water: germination is inhibited in very dry soils (Ghobani et al. 1999);
- nitrogen: high concentration of nitrogen compounds (nitrates and ammonium) increase the emergence of seedlings (Hurtt & Taylorson 1980);
- oxygen: germination of dormant seed is inhibited by atmospheric O₂ lower than 10-15%; dormant seeds do not germinate in water probably because of low O₂ concentration (Costea et al. 2004);
- carbonic anhydride: higher level of CO₂ stimulate the germination (Schonbeck & Egley 1981);
- presence of other therophytes: laboratory experiments have shown that the germination of A. retroflexus decreases when the soil is mixed with aqueous extracts of tissues of some plants (Helianthus annuus L., Sorghum halepense L., Rumex crispus L., Cirsium arvense (L.) Scop., Artemisia annua L.) (Costea et al. 2004). Other experiments have as well shown that A. retroflexus inhibits the germination of other species (such as: Sinapis alba L. s.l., Setaria verticillata L., Trifolium repens L. s.l., Dactylis glomerata L., s.l.) (Reigosa et al. 1999; Costea et al. 2004).

Photosynthesis. A. retroflexus has the C₄ photosynthesis path and it exhibits the typical C₄ anatomy of leaves and bracts (Wang et al. 1993; Costea & Tardif 2003). Mesophyll contains several types of chloroplast (differing from one another in their ultrastructure), each one associated with different types of cell (Fischer & Evert 1982; Groe et al. 1989).

In common with other C₄ species A. retroflexus shows a high photosynthetic rate at high temperature and light intensity and a lower CO₂ compensation than C₃ species. Nielsen & Anderson (1994) produced an equation that relates the carbon exchanged and transpiration rates with the temperature and the photon flux; they observed that the carbon percentage and the transpiration rates increase at temperatures between 20 and 35°C and at a 0-2000 μmol·m⁻²·s⁻¹ photon flux density.

Three main factor influence the biomass accumulation:
- nitrogen: high levels of nitrates in the soil increase photosynthetic rates and assimilative process, while low levels of nitrogen causes a reduction of leaf mass (sometimes inferring the necrosis or the premature senescence) and an increase of stem and root masses (Gebauer et al. 1987). The presence of the nitrogen in the leaves also favours a better water circulation (Sage & Pearcy 1987);
- photoperiod: stem length, flowering, reproductive dry weight and number of seeds are rapid in short-day conditions (8-12 h) (Huang et al. 2000). In particular, the flowering response allows the plants to emerge later in the summer and to produce the seeds before winter. The plants germ early in the summer (under long-day conditions) have a longer vegetative period and they attain a larger size and produce a greater number of seeds than the plants emerging in short-day conditions.

Preferential habitats and substratum. A. retroflexus is a pioneer species which rapidly colonizes synanthropic areas with medium-low environment quality. It frequently occurs in roadsides, railways, rubbish dumps, fallow fields and wastelands, both as isolated plants or in dense populations (4-7 plants/m²). A. retroflexus can also be found on banks or in coastal habitats, while its presence is rare in meadows and it was never found in mature shrublands and forest.

A. retroflexus can be found at altitudes between 0-1600 m a.s.l. Poor populations (more common isolated plants) were observed up to 1700 m a.s.l.

As regards the substratum, this species can tolerate a wide range of soil types and pH levels (Weaver & McWilliams 1980). Dieleman et al. (2000) pointed out that the distribution of Amaranthus spp. is associated with high levels of nitrates and low levels of phosphate and potassium, in agricultural fields in Nebraska. Based on personal observations, I also suppose that A. retroflexus tolerates medium levels of salinity (however, no laboratory experiments were carried out).

Landscape matrix and vegetation communities. Preferential habitats of A. retroflexus (see previous paragraph) are fragmented landscapes characterized by a low connection between the natural or semi-natural patches. The matrix is antrophic and is made of cities, industrial/commercial areas or wastelands; the matrix extends as far as 80-90% of the total area.
**Chenopodium ambrosioidis**

- **Stellarietea mediae**
- **Amaranthaceae**
- **Phytoclimatic region.** According to classification made by Blasi (2007), *A. retroflexus* occurs in all Italian phytoclimatic regions, though the species is more common in Mediterranean regions.

**Response to herbicides.** *A. retroflexus* is susceptible to herbicides and other chemicals (glyphosate, glufosinate, paraquat) that control invasive plants (Costea et al. 2004).

However, it was observed that *A. retroflexus* has evolved resistance to herbicides in Canadian and German populations (Heap 2003). Resistant populations probably developed in response to repeated use of the same herbicide or different herbicides with the same mode of action. Franssen et al. (2001a) reported that the resistance to some herbicides was transferred through hybridization and introgression.

**Response to herbivory, nematodes, fungi, bacteria, viruses and parasitic vascular plants.** Domestic herbivores (especially sheeps and cows) eat young plants of *A. retroflexus*, while the seeds complete the diet of small rodents (*Mus* spp.) and birds. Costea et al. (2004) reported some insect species (incl. Coleoptera, Hymenoptera and Orthoptera) as predators of the seeds of *A. retroflexus*. No predator insect is observed in Italy.

As regards Nematodes, Fungi and Bacteria, Costea et al. (2004) reported three lists. As regards Nematodes, a selection of the lists by Costea et al. (2004) follows [I considered the species recorded for Italy, according to Checklist Fauna (2003)], while no scientific paper is available for Fungi and Bacteria for Italy [see Costea et al. (2004)]:

- **Nematodes:** Ditylenchus dipsaci Filipjev, Heteroder a schachtii (Schmidt), Heteroder a zeae Koshy, Swarup & Sethi, Meloidogyn e chitwoodi Golden, O’Bannon, Santo & Finley, Meloidogyne incognita (Kofoid and White), Pratylench us penetrans (Cobb- Sher-Allen), Punctodera puntata (Thorne) Mulvey & Stone and Tylenchorhynchus claytoni Steiner.
- Some of these organisms are potential herbicides, causing the decrease in growth of *A. retroflexus*, leaves and roots necrosis (by direct penetration in their tissues) or producing compounds that inhibits the germination of the seeds (Costea et al. 2004).

Here follows a list of viruses found in *A. retroflexus* [only the viruses recorded for Europe (Brunt et al. 2003) are reported]: Alfamosaic alfamovirus (AMV), Amaranthus leaf mottle potyvirus (AmLMV), Apple mosaic ilavirus (ApMV), Beet curly top hybrigenimivirus (BCTV), Beet mosaic potyvirus (BtMV), Beet yellows closterovirus (BYV), Cactus X potexvirus (C VX), Celery latent potyvirus, Cucumber mosaic cucumovirus (CMV), Elm mottled ilavirus (EMoV), Ribgrass mosaic tobamovirus (RMV), Strawberry latent ringspot nepovirus (SLRSV), Tobacco rattle tobravirus (TRV), Tobacco streak ilavirus (TSV), Tobacco black ringspot nepivirus (TRSV), Tomato top necrosis nepivirus (ToTNV), Tomato ringspot nepivirus (ToRSV), Tomato spotted wilt tospovirus (TSWV).

Finally, as regards higher vascular plants, Mitich (1993) recorded Orobanche ramosa L. as parasitic on *A. retroflexus* for North America, while Costea et al. (2004) indicate Cuscuta campestris Yuncker. Pignatti (1982) does not specify *A. retroflexus* in his lists of plants parasited by these species and he reported O. ramosa as a parasite on several cultivated plants (Fabaceae, Lamiaceae and Asteraceae), while C. campestris as parasitic on Fabaceae.

**DISCUSSION**

*A. retroflexus* has several different biological and ecological characters that distinguish it as a synanthropic alien species. Some of these characters (e.g. its huge size and wind pollination) are also peculiar of the so-called “apophytes” (native Mediterranean species occurring on a secondary habitat), that are considered important invasive species in several geographycal areas (Celesti-Grapow et al. 2005).

Naturalization-invasion process of *A. retroflexus* is favoured by the following features:

- **short life cycle (therophyte):** allowing a good adaptation to human-made habitats (Viegi 2001);
- **huge size** (height of plants, stem diameter, leaf area): favouring high competitive ability in relation to some ecological factors (e.g. light and soil organic matter);
- **habitus** and population structure: erect and very branched plants or dense populations, successfully compete against native species and apophytes reducing their population size and dispersal ability;
- **phenology:** time of emergence (late May to beginning of June), speed growth (young plants can even grow flowers in only ten days) and late flowering (up to October-November) decrease the competition against native species (Viegi 2001; Celesti-Grapow et al. 2005);
- **wind and self pollination** are considered advantageous in dispersal and invasion processes in open environments (Rejmánek 1999);
• production, morphological characters and not specialized dispersal seeds mode: huge production of seeds, high vitality of dormant seeds and diverse dispersal modes (wind, water, animals, humans) aid a rapid colonization of the environment (Andersen 1995);
• soil and light characteristics: nitrates and high photon flux levels are necessary for an optimal growth. According to Pyšek et al. (1995) this should permit the colonization of open eutrophic habitats;
• habitats: A. retroflexus colonizes any habitat in made environments, therefore increasing its invasive potential.

As regards the ecology, A. retroflexus shows a high plasticity, since it does not have specialized ecological characters that allows it to colonize open environment and successfully compete with apophytes and other alien species. This clearly causes a high invasiveness.

The altitude appears to be the only limiting factor. In fact, the number and density of the populations considerably decreases above 1500 m a.s.l. So the invasiveness also decreases. This is probably caused by the temperature that is an important ecological factor for growth and for production and vitality of the dormant seeds.

Under 1500 m a.s.l., the main ecological factors for the growth are light and soil organic matter. A. retroflexus is an heliophyte and pioneer species that is rare in shady environments (such as shrubs or forest). Like other invasive species it is characterized by a high photosynthetic rate at high radiation intensity, while the compensation light point is for higher radiation values respect to non-heliophyte species (Bullini et al. 1998).

The rule of soil nitrogenous compounds is very important for the biology of A. retroflexus. The increase of nitrates in the soil enhances the photosynthetic process, the assimilation of organic matter, the circulation of the water in the leaves and the emergence of young plants. So the presence of this species in synanthropic environments is considerable. The species also occurs in seminatural areas, while it is never reported from high quality habitats, such as hill and mountain meadows and maquis (this is also true for communities that represent patches included in very anthropic landscape, such as the Natural Reserves of Rome).

Therefore, A. retroflexus can be considered a synanthropic species that colonizes open spaces in anthropic landscapes, at medium and low altitudes.

Two types of impacts emerge:
• economical impact: the dispersal in fields and the successful competition with cultivated plants causes a reduction of the agricultural income. In addition, the possibility to develop resistance to herbicides and other chemicals must also be considered. On the other hand, this and other alien species are favoured by the indirect attention by the farmer and by the increase in density of the populations;
• ecological impact: large and dense communities of A. retroflexus caused a loss of biodiversity both in decreasing floristic richness (on a small scale) or in loss of landscape diversity (on a large scale). In fact, some anthropic habitats (e.g. wastelands) have an important rule in urbanized areas since they represent the areas with the higher floristic pool in these environments (Fanelli 2002).

Therefore, according to Pyšek et al. (2004), A. retroflexus needs to be considered an invasive species for central Italy causing economical and ecological impacts.

The future aims are to give a complete account of biology, ecology and chorology of all amaranths that are reported for Italy. This is very important both because the genus Amaranthus includes globally invasive species and because the study of the characters that favour the alien species in naturalization-invasion process is the main object in the biological invasions researches.

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REFERENCES


Biologija, životne strategije i invazivnost vrste *Amaranthus retroflexus* L. (Amaranthaceae) u centralnoj Italiji: preliminarna zapažanja

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U radu je dat pregled horoloških, ekoloških i bioloških podataka za *Amaranthus retroflexus* L. (Amaranthaceae). Ova vrsta je štetan korov introdukovan u Italiju iz Severne Amerike. Pokazuje visoku fenotipsku plastičnost i lako se adaptira na brojna i raznovrsna poljoprivredna i ruderalna staništa. *A. retroflexus* ima različit stepen dormancije i klijavosti u zavisnosti od ekoloških faktora. Rast je brz, a biljka produkuje veliki broj vijabilnih semena. Ova vrsta je razvila otpornost na više tipova herbicida i drugih hemikalija. Ona je jedan od domaćina nematodama, virusima, bakterijama i gljivama koje napadaju i useve.

Ključne reči: introdukovana vrsta, *Amaranthus*, biologija, invazivnost, životne strategije