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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

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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 Km^2 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].

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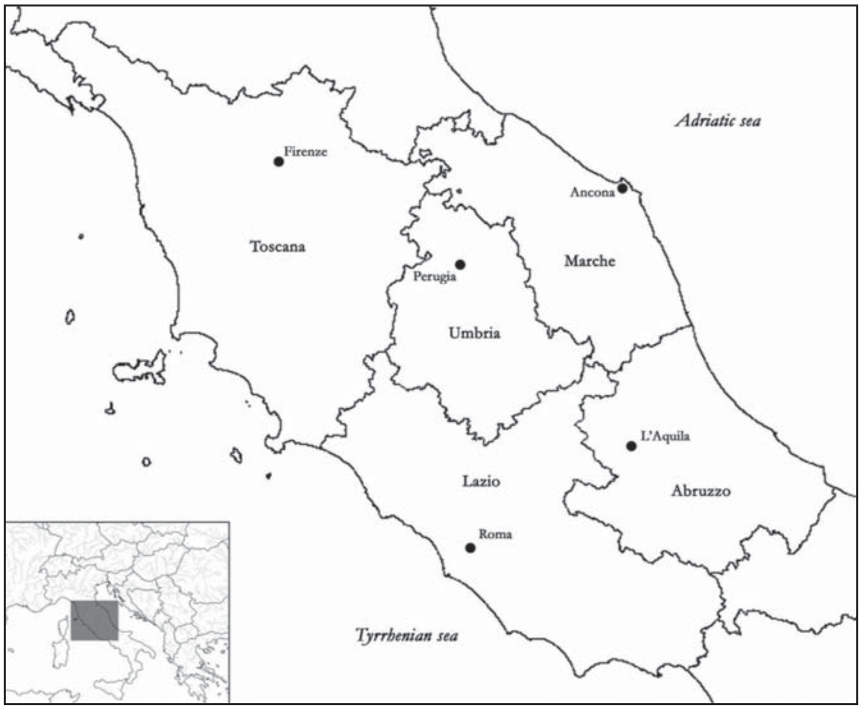

Fig. 1 Study area.

MATERIAL AND METHODS

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

Based on Noble (1989), Rejmànek (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;
- photosynthesic 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), 5-160cm 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 protuding, 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 circumscissle, 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 1950's and 60's. In our study area the following hybrids have been reported: *A.* × *galii* Sennen et Gonzalo (= *A. retroflexus* L. × *A. cruentus* L.), *A.* × *ozanonii* 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; Bojian *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 February.

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 uniformely 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 dintance 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 circumscissle 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 lenght 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 lenght 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 (Ghorbani *et al.* 1999);
- nitrogen: high concentration of nitrogen compounds (nitrates and ammonium) increase the emergence of seedlings (Hurtt & Taylorson 1980);
- oxigen: germination of dormant seed is inhibited by atmospheric O_2 lower than 10-15%; dormant seeds do not germinate in water probably because of low O_2 concentration (Costea *et al.* 2004);
- carbonic anhydride: higher level of CO_2 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 C_4 photosynthesis path and it exhibits the typical C_4 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; Grof *et al.* 1989).

In common with other C_4 species *A. retroflexus* shows a high photosynthetic rate at high temperature and light intensity and a lower CO_2 compensation than C_3 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 $\mu mol \cdot m^{-2} \cdot s^{-1}$ 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);
- light: low values of red/far-red light ratio stimulate the growth of the stems of *A. retroflexus*, while the number of branches seems to be directly correlated to photosynthetic photon flux density (Rajcan *et al.* 2002);
- photoperiod: stem lenght, 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/m^2). *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.

A. retroflexus occurs in synanthropic plant communities and it is frequent or dominat in some syntaxa including in *Stellarietea mediae* R. Tx., Lohm. et Preising ex Rochow 1951 (Fanelli 2002), such as: *Conyzetum albido-canadensis* Baldoni et Biondi 1993 and *Euphorbio-Chrozophoretum tinctoriae* Ferro 1980 (as a frequent species), *Amarantho-Chenopodietum ambrosioidis* O. Bolós 1976 and *Xanthio italici-Daturetum stramonii* Fanelli 2002 (as a dominant species).

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, glucosinate, 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 are 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, *Heterodera schachtii* (Schmidt), *Heterodera zeae* Koshy, Swarup & Sethi, *Meloidogyne chitwoodi* Golden, O'Bannon, Santo & Finley, *Meloidogyne incognita* (Kofoit and White), *Pratylenchus 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 hybrigeminivirus (BCTV), Beet mosaic potyvirus (BtMV), Beet yellows closterovirus (BYV), Cactus X potexvirus (CVX), Celery latent potyvirus, Cucumber mosaic cucumovirus (CMV), Elm mottled ilarvirus (EMoV), Ribgrass mosaic tobamovirus (RMV), Strawberry latent ringspot nepovirus (SLRSV), Tobacco rattle tobravirus (TRV), Tobacco streak ilarvirus (TSV), Tobacco black ringspot nepovirus (TRSV), Tomato top necrosis nepovirus (ToTNV), Tomato ringspot nepovirus (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 Asteracae), while *C. campestris* as parisitic 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 (Rejmànek 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 euthrophic 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 descrease 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 anthrophic 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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Botanica SERBICA

REZIME

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

Duilio Iamonico

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