Bot. Rev.
https://doi.org/10.1007/s12229-017-9194-1

Biology of Amaranths

Rezwana Assad[1] · Zafar A. Reshi[1] · Snober Jan[1] · Irfan Rashid[1,2]

[1] Department of Botany, University of Kashmir, Srinagar, J&K 190 006, India
[2] Author for Correspondence; e-mail: ecoirfan@yahoo.co.in

Abstract *Amaranthus*, a cosmopolitan genus including endangered species, restricted endemics and widespread weeds, is often difficult to characterize taxonomically and thus has generally been considered by systematists as a "difficult" genus. Species in this genus have high genetic variability, with diversity in growth form, plant height, number of inflorescences, seed colour, protein content, seed yield, resistance to pests and diseases, and adaptation to soil type, pH, climate, rainfall and day-length. The combination of various anatomical characteristics of *Amaranthus*, such as Kranz anatomy, well developed root system, stomatal conductance, and maintenance of leaf area, results in increased efficiency of using CO_2 under a wide range of temperatures, and higher light intensity and moisture stress environments which enables this plant to adapt under diverse geographic and environmental conditions. Buried seeds of *Amaranthus* constitute an important part of the soil seed bank and position, distribution and dormancy type of these seeds in the soil play an important role in their germination and subsequent emergence, which is further influenced by factors like temperature, soil moisture, and light availability. The current review highlights the positive as well as negative role of the various species of genus *Amaranthus*. Many species of the genus are medicinally important and bear antiallergic, anticancer, antihypertensive and antioxidant properties, thus being used in the treatment of several aliments. Amaranthus being a rich source of fatty acids, proteins, micronutrients, vitamins and squalene, are used as cereals, dye plants, forages, medicinal plants, ornamentals, and as vegetables. However some of the *Amaranthus* species are noxious weeds which are known to compete with many economic crops in different parts of the world and cause great yield losses. Thus, further research is warranted to strike a balance between the beneficial and harmful species of this Pseudocereal. Moreover, understanding the weedy behaviour of these plants would provide valuable information for improving our mechanistic models of crop-weed competition and weed population dynamics.

Keywords Allelopathy · Biological control · Amaranthus · Pseudocereal · Seed biology · Weed

Published online: 26 October 2017

Introduction

Amaranthus is a cosmopolitan genus of annual or short-lived perennial plants (Dorling, 2008), including domesticated and endangered species, restricted endemics and wide-spread weeds (Sauer, 1950), which are commonly referred as 'Amaranths' or 'Pig-weeds' (Bensch et al., 2003). The genus name, *Amaranthus* comes from the Greek word "amarantos", (Αμάραντος) which means "unfading", "immortal", "everlasting" or "non-wilting", in view of the fact that its flowers last for a long time.

It has been reported that genus *Amaranthus* consists of 87 species, of which 14 are distributed in Australia, 17 in Europe, and 56 in America (Jacobsen et al., 2000). However, due to fewer studies on *Amaranthus* systematics, the number of species is still tentative. There is some disagreement regarding the number of species in this genus with different reports like 60 species (Uphof, 1968; Singh et al., 1983; National Research Council, 1984; Budin et al., 1996; Wiersema & Leon, 1999), 70 species (Pratt et al., 1999; Costea & DeMason, 2001; Mosyakin & Robertson, 2003), over 75 species (Sauer ,1993), 86 species (USDA, ARS, 1999) and 100 species (Hanf, 1984) [Table 1- Appendix].

Presently, *Amaranthus* is distributed in many parts of the world, including Central and South America, Africa, China, India, and the United States (Budin et al., 1996). Approximately 25 species of Amaranthus have been reported in Asian region (Das, 2016). In India the species of genus *Amaranthus* are mainly found in Himalayas - from Kashmir to Bhutan - and in South Indian hills.

Morphology

Genus *Amaranthus* is characterized by the following traits: Annual or (rarely) short-lived perennial life history, herbaceous habit with prostrate to erect stem. Leaves are alternate, ovate to linear and have an indented or notched apex and smooth margins. Flowers are imperfect, in compound dichasia packed into inflo-rescences. The plants of *Amaranthus* are monoecious (*A. albus, A. blitum, A. caudatus*, *A. hybridus*, *A. powellii*, *A. retroflexus* and *A. spinosus)* or dioecious (*A. tuberculatus*, *A. palmeri* and *A. rudis*). The inflorescence is terminal and/or axillary with three to five tepals and stamens. Monoecious species are generally self-pollinated, wind pollinated. Fruit is utricle or pyxidium. Seeds are lenticular and tiny (0.9 to 1.7 mm diameter and 1000-seed weights from 0.6 to 1 g) that are typically dispersed by wind, water, or birds, having extended period of germination with prolific seed production and a base chromosome number of 16 or 17 (Stevens, 1932; Sauer, 1967; Kigel, 1994; Pratt et al., 1999; Franssen et al., 2001b; Costea & Tardif, 2003; Mosyakin & Robertson, 2003; Costea et al., 2004; Steckel, 2004). In addition, this genus has C_4 photosynthesis, unlike its closest related genera (Weaver, 1984; Mitich, 1997; Bensch et al., 2003; Sage et al., 2007). Morphological terminology in *Amaranthus*, as used in different floristic and taxonomic treatments, is rather confusing, especially regarding the terms applied to flowers and inflorescence. Within each *Amaranthus* species there are several races defined by their common branching pattern, height, inflorescence size and form, days to maturity, seed size and colour, and other morphological characteristics (Espitia-Rangel, 1994; Brenner et al., 2000).

Taxonomy

Genus *Amaranthus* is often difficult to characterize taxonomically, due to few distinguishing characters among its species, small and difficult-to-see diagnostic parts, broad geographical distribution, large number of hybrid forms, complicating the taxonomy and thus has generally been considered by systematists as a "difficult" genus (Costea & DeMason, 2001). The genus *Amaranthus* was first reported by Linnaeus (1753). Various species of the genus were at one time recognized as separate genera, particularly the dioecious species and the monoecious species with dehiscent or indehiscent fruits (Linnaeus, 1753; Kunth, 1838). These genera were later placed within *Amaranthus* by Sauer (1955), and Robertson (1981), and are presently recognized as subgenera. In the most recent taxonomic work, the genus has been divided into three subgenera: Acnida, Amaranthus, and Albersia (Mosyakin & Robertson, 1996; Costea et al., 2001). Subgenus Acnida is generally delimited to include all the dioecious species of *Amaranthus*, whereas subgenus Amaranthus and subgenus Albersia split the monoecious species using combination of inflorescence position, number of tepals, and fruit dehiscence (Mosyakin & Robertson, 1996). Several authors have suspected that this infrageneric taxonomy may not correspond well to evolutionary history (Eliasson, 1988; Mosyakin & Robertson, 2003) but, despite its wide geographical distribution and close association with human activities, currently there is no well-sampled, well-supported phylogenetic study of this genus. Müller and Borsch (2005) and Sage et al., (2007) placed *Amaranthus* in the order Caryophyllales, family Amaranthaceae, subfamily Amaranthoideae, tribe Amarantheae, sub-tribe Amaranthinae, genus *Amaranthus* and according to Sauer (1967) into the section Amaranthus.

Origin

The centre of origin of *Amaranthus* is believed to be Central America, with evidence of its cultivation dating back as far as 6700 BC (Myers & Putnam, 1988; Putnam et al., 1989; Sauer, 1993; Kigel, 1994; Mposi, 1999). The Aztec civilization of central Mexico represents the first recorded instance of *Amaranthus* use, and the crop figured prominently in Aztec culture during the 1400 to 1500 AD. *Amaranthus*, which the Aztecs called 'huautli' was their staple food and was incorporated into their religious ceremonies. Its seeds were ground by Aztec women and mixed with honey, other sweets, and sometimes with human blood (National Research Council, 1984), then molded into various forms (including animals, natural features, and Gods) for consumption at religious ceremonies and other occasions (Brenner et al., 2000). Despite the known Aztec custom of human sacrifice, the association of human blood with the figures is unclear (National Research Counci,l 1984).

After the arrival of the Spanish conquistadors in Mexico in the early 1500 AD, Spanish attempted to suppress Aztec culture and religion; so upon their conquest *Amaranthus,* as a crop almost disappeared in America (Sauer, 1950). However, according to Spanish missionaries, the use of *Amaranthus* as food and in traditional cultural practices continued at a reduced level until some 50 years after the Spanish conquest, but subsequently declined (Early, 1992). Even today *Amaranthus* is grown in limited quantity in that area, most of which is popped and mixed with honey to make a confection called, "alegría" which means "happiness".

Sauer (1967) reports the introduction of *Amaranthus* into Spain in sixteenth century, from where it had spread throughout the Europe. Around 1700 AD, it was known as a minor grain plant in central Europe and Russia and by the early nineteenth century it reached Africa and Asia. Till mid-1990s, South Asia was the world's only region where *Amaranthus* production was increasing (Brenner et al., 2000). It was in 1970s that research on this plant began in the US, only after new evidence revealed grain amaranth protein to be of high quality (Senft, 1980; Lehmann, 1996). Today, it has spread around the world in different regions of Europe, Asia and Africa (Myers & Putnam, 1988; Putnam et al., 1989; Mposi, 1999). Thus *Amaranthus* is a historic as well as a contemporary plant.

Habitat Preference

Amaranthus has high genetic variability, with diversity in plant form (erect to prostrate), plant height, number of inflorescences (one to several), seed colour, protein content, seed yield, resistance to pests and diseases, and adaptation to soil type, pH, climate, rainfall and day-length (Kulakow, 1990). Although *Amaranthus* can grow on a wide range of soil types and soil moisture levels, it has been reported to grow well in loamy or sandy-loam or silty-loamy soils with good water holding capacity (Whitehead & Singh, 1993; Ghorbani et al., 1999; Palada & Chang, 2003) with pH range between 4.5 and 8.0 (National Research Council, 1984; Stallknecht & Schulz-Schaeffer, 1993; Palada & Chang, 2003).

Amaranthus is extremely adaptable to adverse growing conditions and tolerates drought and low fertility (O'Brien & Price, 1983). Field studies have shown that it grows well on soils varying widely in levels of soil nutrients (National Research Council, 1984; Myers, 1998) and responds well to good soil fertility and organic matter (Schippers, 2000). Agricultural fields are a great habitat for annual plants like *Amaranthus*, which grow naturally in open or disturbed areas and receive full sunlight (Pratt et al., 1999). Dieleman et al., (2000) pointed out that the distribution of *Amaranthus* species in agricultural fields is associated with high levels of nitrates and low levels of phosphate and potassium.

Phenology

Phenology is the study of periodic biological events that take place at different levels, for example in organs, tissue or cells (Alm et al., 1991). The analysis of phenological stages makes it possible to accurately estimate crop-weed competition (Ghersa & Holt, 1995). Thus phenological surveys are of great importance in weed science (Brainard et al., 2005) and can help us in the development of a realistic and practical model for weed control (Elmore, 1996; Swanton et al., 1999).

Phenology of various *Amaranthus* species has been reported by several workers. Forcella et al. (1997) reported that emergence of *Amaranthus* species begins in early

April and continues until the end of May. Emergence of *A. tuberculatus* commences from late May and continues to early August (Hartzler et al., 1999), while as flowering and seed set continue until the first frost. Germination of *A. albus* and *A. blitoides* occurs from the middle of May to the beginning of June. The first seeds of *A. blitum* germinate at the end of June or beginning of July. Flowering of *A. albus* and *A. blitoides* begins at the end of June or beginning of July, and of *A. blitum* at the end of July or early August, continuing until senescence is induced by the first fall frost (Stevens, 1924). Shedding of seeds (*A. albus* and *A. blitoides*) and of fruits enclosing the seeds (*A. blitum*) extends throughout the rest of the growing season, due to the indeterminate growth pattern of inflorescences and the continuous formation of new flowers (Costea & Tardif, 2003). *A. retroflexus* emerges at the end of May and its senescence stage is from November to February; however its phenological stages are slightly dephased for different latitudes, with shorter developmental stages at higher latitudes (Huang et al., 2000; Iamonico, 2010). *A. spinosus* emerges in June, flowers in July, fruit develops in August, followed by seed dispersal in September and finally shows senescence in November (Chakravorty & Ghosh, 2012).

Physiology

Amaranthus is a dicotyledonous, herbaceous mesophyte that utilizes specialized C_4 carbon-fixation pathway for photosynthesis in which the first photosynthesis product is a four carbon-compound (National Research Council, 1984; Stallknecht and Schulz-Schaeffer, 1993; Myers, 1998; Wang et al., 1999). *Amaranthus* belongs to the group of NAD-malic enzyme-type of C_4 metabolism and it exhibits the typical Kranz anatomy (C_4 anatomy) of leaves, cotyledons and bracts (Wang et al., 1993; Costea & Tardif, 2003). Their photosynthetic pathway is characterized by the use of the mitochondrial NAD-ME to decarboxylate malate in the Kranz bundle-sheaths (Long et al., 1994; Long & Berry, 1996). The combination of various anatomical characteristics of *Amaranthus*, such as C_4 metabolism, well developed root system, stomatal conductance, and maintenance of leaf area (Spreeth et al., 2004), results in increased efficiency of using CO_2 under a wide range of temperatures (from 25 °C to 40 °C), with higher light intensity and moisture stress environments (Williams & Brenner, 1995) which enables this plant to adapt under diverse geographic and environmental conditions (Kigel, 1994). Plants that use the C_4 carbon fixation pathway tend to require less water than the more common C_3 carbon-fixation pathway plants (National Research Council, 1984). This is the reason that *Amaranthus* performs well under adverse temperature and moisture conditions as compared to many C_3 plants such as wheat and soybeans (Stallknecht & Schulz-Schaeffer, 1993; Schippers, 2000; Spreeth et al., 2004), indicating that *Amaranthus* can be grown in areas that are not suitable for other crops (Breene, 1991; Lehmann, 1996; Brenner et al., 2000; Rana et al., 2007). Previous studies showed that C_4 weed species like *A. palmeri*, *A. retroflexus* and *A. rudis* respond positively to elevation in temperature (Guo & Al-Khatib, 2003), thus temperature elevation due to climate change could promote the invasion potential of C_4 weed species like *A. retroflexus* by enhancing their growth and seed production (Hyvönen, 2011).

Amaranthus has been referred to as drought tolerant (Grubben & van Sloten, 1981; Liu & Stützel, 2002) and this drought tolerance is due to its C_4 photosynthetic pathway, a deep and extensive root system, ability to go dormant under extreme drought conditions (O'Brien & Price, 1983) and ability to shut down transpiration through wilting and then recovering easily when moisture is available (Myers, 1996). Plant height, dry matter production, and leaf area expansion of *Amaranthus* species respond positively to increasing day/night mean temperature (Flint & Patterson, 1983). Flower initiation depends on photoperiod and most of the *Amaranthus* species flower when day-length is shorter than 12 h (Fuller, 1949; Huang et al., 2000; Palada & Chang, 2003). Plants grown under short-day conditions (8 h) require 14 to 16 days to initiate flowering, whereas plants grown under long-day conditions (16 h) need approximately 45 days (Costea et al., 2004). O'Brien and Price (1983) reported that short days and water stress may promote flowering in this plant.

Simbolon and Sutarno (1986) studied responses of *Amaranthus* species to reduced light intensity and found them to be moderately tolerant to shade. Previous research shows that C_4 plants have higher light-saturated photosynthetic rates and are better adapted to high levels of irradiance compared to C_3 plants that saturate at relatively lower light intensities (Stoller & Myers, 1989; Regnier & Harrison, 1993). Shading affects the survival and growth of plants by altering their physiological and morphological response to light environment. Weeds like *Amaranthus* show physiological and morphological adaptations to reduced irradiance and the "adaptive plasticity" to adjust to a light-limited environment (Stoller & Myers, 1989). Stoller and Myers (1989) reported that *A. albus* respond to shade by decreasing light saturated photosynthesis, dark respiration rates, and leaf thickness, while increasing chlorophyll content per unit leaf volume and specific leaf area. *A. powellii*, *A. retroflexus* and *A. tuberculatus* respond to shade by reducing biomass and leaf appearance rates and by increasing specific leaf area and stem elongation (McLachlan et al., 1993a, b; Steckel et al., 2003; Brainard et al., 2005). Characterizing these physiological and morphological responses of this genus to shading are likely to provide valuable information for improving our mechanistic models of crop-weed competition and weed population dynamics (Brainard et al., 2005).

Chromosome Analysis

The genus *Amaranthus* provides fascinating material for geneticists to work with. Basic genetic studies of this genus were initiated in late 1950s with chromosomal counts (Grant, 1959b; Pal, 1964) and identification of polyploids (Khoshoo and Pal 1972).

Chromosome number varies among *Amaranthus* species (Table 2). In *A. albus*, *A. palmeri* and *A. retroflexus* chromosome counts of $2n = 34$ (Grant 1959b; Sharma and Banik, 1965; Weaver & McWilliams, 1980) and $2n = 32$ (Heiser & Whitaker, 1948; Mulligan, 1984; Rayburn et al., 2005) have been reported. In *A. spinosus*, somatic counts of $2n = 34$ (Baquar & Olusi 1988; Al-Turki et al., 2000) and the gametic counts of $n = 17$ (Koul et al., 1976; Behera & Patnaik, 1977; Behera & Patnik, 1982) have been reported. *A. palmeri* and *A. spinosus* may share a recent common ancestor (Wassom & Tranel, 2005; Riggins et al., 2010), as they have the same chromosome number ($2n = 34$), pollen morphological similarities (Grant, 1959b; Franssen et al., 2001b; Gaines et al., 2012), and similar genome sizes (Rayburn et al., 2005). Pal et al. (1982) reported that, within the *Amaranthus* genus, both $n = 16$ and $n = 17$ occasionally occur in the same species. The chromosome number of *A. blitum* and *A. powellii* is 2n = 34 (Weaver & McWilliams, 1980; Pal & Pandey, 1989; Greizerstein et al., 1997). The chromosome number for *A. caudatus*, *A. hypochondriacus*, *A. cruentus*, and *A. hybridus* is normally 2n = 32, but occasionally it is 34 (National Research Council, 1989), i.e. these species are diploids with a basic chromosome number of 16 or 17. There are no major chromosomal differences between the genomes of *A. hypochondriacus, A. caudatus* and *A. edulis* (Ramesh & Kumar, 2009).

Hybridization

Amaranthus is a predominantly self-pollinated plant (Murray, 1938), with varying amounts of outcrossing (Hauptli & Jain, 1985; Liu et al., 2012). Hybridization among different species has been widely reported within the genus *Amaranthus* (Saue,r 1950; Trucco et al., 2005b). The possibilities for interspecific hybridization among most of the *Amaranthus* species have been documented (Murray, 1938; Sauer, 1950; Pal & Khoshoo, 1973), and some have even referred to the genus as 'promiscuous' (Trucco et al., 2005b). The identification of three sources of cytoplasmic male sterility in *Amaranthus* paves the way for additional hybridization techniques (Peters & Jain, 1985, 1987; Gudu & Gupta, 1988).

A. retroflexus occasionally forms natural hybrids with other species of the same genus (Murray, 1938). It has been reported that hybridization between *A. palmeri* and *A. tuberculatus* following controlled pollinations yield practically no fertile offspring (Wetzel et al., 1999b; Franssen et al., 2001a; Steinau et al., 2003; Trucco et al., 2007). Hybridization between *A. hybridus* and *A. tuberculatus* produce some fertile F1 individuals (Murray, 1940; Trucco et al., 2007; Trucco et al., 2009), although genetic introgression between these species occurs only in one direction, from *A. hybridus* to *A. tuberculatus* (Trucco et al., 2005a, b; Trucco et al., 2009). Based on reported interspecific hybridizations in *Amaranthus*, equal chromosome number is not a prerequisite for hybridization; however, hybrid progeny appears to be more viable and fertile when their parental species have the same chromosome number, as in the case of hybridization between *A. hybridus* and *A. tuberculatus* (Trucco et al., 2009).

There is a concern that glyphosate resistance owing to EPSPS gene amplification could be introgressed from glyphosate resistant *A. palmeri* to other weedy *Amaranthus* species (Culpepper et al., 2006). The potential interspecific transfer of EPSPS gene amplification and glyphosate resistance within the genus *Amaranthus* has considerable evolutionary and agronomic significance (Gaines et al., 2012).

Seed Biology

The detailed understanding of seed biology helps in the development of effective integrated weed management systems (Bhowmik, 1997). Kigel (1994) has compiled much of the available information on seed biology of the genus *Amaranthus*, including research on effects of light (Oladiran & Mumford, 1985; Gutterman et al., 1992;

Gallagher & Cardina, 1998a, b), temperature (Baskin & Baskin, 1977; Weaver, 1984; Oladiran & Mumford, 1985; Weaver & Thomas, 1986; Ghorbani et al., 1999), water availability, osmotic potential and salinity (Ghorbani et al., 1999), hormones (Holm & Miller, 1972; Weaver, 1984; Kępczyński et al., 1996), soil types, burial depth (Webb et al., 1987; Oryokot et al., 1997a; Ghorbani et al., 1999), and other environmental parameters (Bibbey, 1935; Siriwardana & Zimdahl, 1984; Habib & Morton, 1987; Wiese & Binning, 1987; Forcella et al., 1997) on seed germination.

Seed Dormancy

Weed seed dormancy is often induced and regulated by a compliment of genetic, physiological, and environmental factors (Karssen, 1982; Baskin & Baskin, 1998), including day length and plant age (Gutterman & Genotypic, 1997; Castor et al., 2000), harvest date (Ghosh & Bruin, 1997) and temperature (Marayama et al. 1997). During seed development, *A. retroflexus* seed dormancy is affected by various environmental conditions like parental photoperiod, temperature environments, fertilization of soil, competition with other plants (Kigel et al., 1977; Costea et al., 2004), and shading of the maternal plant or in fact by the aid of natural infrared light (Doroszeweski, 2001). Induction of secondary dormancy (thermodormancy) in seeds due to higher temperatures has been reported in *A. retroflexus* (Baskin & Baskin, 1977, 1985a, 1990; Egley, 1989), *A. caudatus* (Kępczyński & Bihun, 2002), *A. quitensis* (Faccini & Vitta, 2005), and *A. palmeri* seeds (Jha et al., 2010), indicating that this behaviour of seeds kept in soil is characteristic of the genus *Amaranthus*. The occurrence of such temporal changes in dormancy of buried *Amaranthus* seeds has been interpreted as an adaptation to enhance survival when seeds are in the soil, especially when they are deeply buried (Omami et al., 1999).

Effect of Temperature

The effect of temperature and light on seed germination of *Amaranthus* species have been studied by previous researchers (Baskin & Baskin, 1977, 1998; Gallagher & Cardina, 1998a, b; Leon & Owen, 2003; Steckel et al., 2004). The high temperature requirement for germination of *Amaranthus* species was reported by Bibbey (1935), Kadman-Zahavi (1960), McWilliams et al. (1968), Baskin and Baskin (1977), Washitani and Takenaka (1984), Habib and Morton (1987), Gutterman et al. (1992), Ghorbani et al. (1999), and Guo and Al-Khatib (2003) (Table 3).

Mature *Amaranthus* seeds remain dormant during autumn and winter (Baskin & Baskin, 1977, 1987; Jha et al., 2007, 2008c; Norsworthy & Oliveira, 2007), since temperatures during that period are below those required for germination. Following after-ripening during winter, seeds of *Amaranthus* species, like most summer annuals, require high fluctuating temperatures for germination and do not germinate in the field at lower temperatures until late spring to summer (Baskin & Baskin, 1977, 1987; Karssen, 1982; Benech-Arnold et al., 1990; Bouwmeester & Karssen, 1992; Faccini & Vitta, 2005), while as after-ripening for few more months after winter leads to decline in the minimum temperature requirements, or broadening of thermal range for seed germination (Baskin & Baskin, 1977, 1987; Benech-Arnold et al., 1990; Bouwmeester & Karssen, 1992). Thus, seeds gain the ability to germinate equally well at temperatures below the optimum range of 25 to 35 °C (Wright et al., 1999; Guo & Al-Khatib, 2003).

Temperature fluctuations like alternating temperature regimes have been shown to reduce dormancy, decrease time to onset of germination and increase germination rates in various *Amaranthus* species, like *A. cruentus*, *A. gangeticus, A. hybridus*, *A. palmeri*, *A. paniculatus*, *A. retroflexus*, *A. rudis*, *A. spinosus*, and *A. viridis* (Santelmann & Evetts, 1971; Weaver, 1984; Oladiran & Mumford, 1985; Guo & Al-Khatib, 2003; Leon et al., 2004, 2007; Steckel et al., 2004; Thomas et al,. 2006; Chauhan and Johnson 2009; Jha et al., 2010) because alternating temperatures are most similar to diurnal temperature responses and can break seed coat-imposed physical dormancy of seeds (McKeon & Mott, 1982).

Minimum germination temperature for *A. palmeri* and *A. retroflexus* was >5 °C, but the optimal temperature for maximum germination has been reported to be from 25 to 40 °C (Evans, 1922; McWilliams et al., 1968; Baskin & Baskin, 1977; Habib & Morton, 1987; Wiese & Binning, 1987; Kępczyński et al., 1996; Ghorbani et al., 1999; Wright et al., 1999; Kępczyński & Bihun, 2002; Guo & Al-Khatib, 2003). Dormant *A. retroflexus* seeds cannot germinate in darkness at 25 °C and can either germinate partially at 35 °C (Schonbeck & Egley, 1981a, b; Kępczyński et al., 2003b), or fully at 35–40 °C (Kępczyński et al., 1996). Optimum germination of *A. caudatus* and *A. blitum* has been reported at 35 °C while as of *A. hybridus* seeds was reported to be between 32 and 34 °C (Washitani & Takenaka, 1984; Teitz et al., 1990; Gutterman et al., 1992; Kępczyński & Bihun, 2002). Oladiran and Mumford (1985) reported optimum germination between 30 and 35 °C for *A. cruentus*, *A. hybridus*, *A. paniculatus* and *A. gangeticus*. High temperatures (≥25 °C mean), thermal amplitudes (≥7.5 °C) and high soil moisture favour germination of *A. palmeri* and other *Amaranthus* species (Hartzler et al., 1999; Wright et al., 1999; Guo & Al-Khatib, 2003; Steckel et al. 2004; Jha et al., 2008b, c, 2010).

A. spinosus seeds respond positively under an alternating temperature regime of 20, 25 and 30 °C and adversely at 35 °C and no germination occurs at 15 °C but, when the temperatures were held constant, significant germination was recorded at 30 °C and 35 °C (Steckel et al., 2004). *A. viridis* seeds germinated over a range of 20 to 40 °C with 30 °C as the optimum temperature for germination (Thomas et al., 2006), while as no germination was observed at 10 °C (Cristaudo et al., 2007).

Effect of Light

Kigel (1994) reported that most species of *Amaranthus* respond to light, but the response level varies among the species (Gallagher & Cardina, 1998a, b; Cristaudo et al., 2007), depending upon the dormancy level of seeds, which is further influenced by factors such as burial and temperature (Gallagher & Cardina, 1998a; Leon & Owen, 2003). Light requirement for germination has been reported in various *Amaranthus* species like *A. blitum*, *A. caudatus*, *A. hybridus*, *A. retroflexus*, *A. rudis*, *A. spinosus*, and *A. viridis* (Baskin & Baskin, 1977; Schonbeck & Egley, 1981a, b; Teitz et al., 1990; Gallagher & Cardina, 1998a, b; Leon & Owen, 2003; Cristaudo et al. 2007). Seeds of *A. spinosus, A. retroflexus* and *A. viridis* germinate better in light than in darkness, implying that the buried seeds will germinate following soil disturbance (Baskin & Baskin, 1977, 1985b, 1998; Omami & Medd, 1992; Gallagher & Cardina, 1998a, b;

Benvenuti et al., 2001; Cristaudo et al., 2007). The ecological significance attributed to the light response in various species of *Amaranthus* is that light acts as a soil depth "indicator," or depth-sensing mechanism for seeds, allowing greater germination of surface seeds than seeds buried in soil (Ghorbani et al., 1999; Schütz et al., 2002).

Phytochrome-regulated seed germination of various *Amaranthus* species like *A. arenicola*, *A. caudatus*, *A. hybridus*, *A. palmeri, A. retroflexus*, and *A. rudis* has been documented (Hendricks et al., 1968; Kendrick & Frankland, 1969; Kendrick et al., 1969; Taylorson & Hendricks, 1969, 1971; Gallagher & Cardina, 1998a, b; Leon & Owen, 2003; Jha et al., 2010). Exposure to red (R) light induces germination in dormant seeds (Jha et al., 2010), and this effect is more pronounced in chilled seeds (moist stratification at 4 °C) compared to non-chilled seeds, suggesting an interaction of low temperatures with phytochrome in dormancy alleviation (Taylorson & Hendricks, 1969; Gallagher & Cardina, 1997, 1998a, b; Leon & Owen, 2003). However, high temperatures (30 °C or above) during summer can reduce the photosensitivity of *Amaranthus* seeds and overcome the phytochrome mediated red light requirement for enhanced germination in various *Amaranthus* species like *A. hybridus*, *A. retroflexus*, and *A. rudis* (Gallagher & Cardina, 1998a; Hartzler et al., 1999; Leon & Owen, 2003). On the other hand FR light inhibits germination and induces dormancy (Kendrick & Frankland, 1969; Taylorson & Hendricks, 1971; Gallagher & Cardina, 1998a; Leon & Owen, 2003; Jha et al., 2010). This inhibitory effect of FR light is due to decrease in Pfr/Pr of the phytochrome, thus causing photo dormancy in seeds (Hendricks et al., 1968; Kendrick & Frankland, 1969; Taylorson & Hendricks, 1969, 1971).

Effect of Soil Types, Seed Burial Depth and Duration of Seed Burial

Percent emergence of *A. retroflexus* is greater in lighter soils (sandy clay loam, Loamy sand and Sandy loam) than heavier soils (silty clay and sandy clay). Maximum emergence occurs at 0.5 cm depth in the three lighter soils, between 0.5 and 2 cm in the sandy clay, and 3 cm deep in the silty clay (Ghorbani et al., 1999), possibly due to poor gas exchange, poor light, and lower temperature in heavier soils (Gallagher & Cardina, 1998a).

Buried weed seeds constitute an important part of the soil seed bank (Baskin & Baskin, 1985b, 1998; Benvenuti et al., 2001) and position, distribution and dormancy level of these seeds in the soil play an important role in their germination and subsequent emergence (Burnside et al., 1981; Benvenuti & Macchia, 1997; Benech-Arnold et al., 2000), which is further influenced by factors like soil temperature, soil moisture, and light availability. Small-seeded weeds such as *Amaranthus* species can germinate only from shallow soil-depths of 0.5 to 2.5 cm (Baskin & Baskin, 1977, 1998; Buhler et al., 1996; Oryokot et al., 1997a; Gallagher & Cardina, 1998a, b; Ghorbani et al., 1999; Benech-Arnold et al., 2000; Leon & Owen, 2003).

Santelmann and Evetts (1971) examined emergence for several *Amaranthus* species and found that germination decreases at depths below 1.9 cm. Increase in dormancy of seeds buried at a depth of 5 to 10 cm for 3 to 12 months has been reported in other *Amaranthus* species (Baskin & Baskin, 1977; Omami et al., 1999). Ghorbani et al. (1999) observed in-situ emergence patterns of *A. retroflexus* and concluded that the optimal burial depth was between 0.5 and 3 cm, with no emergence at 5 cm. Under field conditions also *A. retroflexus* seeds showed a decline in germination with an increase in burial depth from 0 to 10 cm (Wiese & Davis, 1967; Omami et al., 1999). Benvenuti et al. (2001) also reported a decrease in *A. retroflexus* seedling emergence with an increase in burial depth and the emergence was found to be less than 10% at a burial depth of 8 cm. Furthermore, the seeds of *A. viridis* on the soil surface had reduced emergence compared to the seeds placed just below the surface and germination was optimum from shallow soil depths of 0.5 to 2 cm, but some seedlings emerged from as deep as 6 cm (Thomas et al., 2006). Limited soil-to-seed contact, light conditions on the surface, and water availability or lower soil water potential close to the seed are some environmental conditions that may limit germination of seed on the soil surface (Ghorbani et al., 1999). Seedling emergence on the soil surface was lower than germination observed in Petri dishes in the light (Chauhan & Johnson, 2009). This difference could be due to poor soil-seed contact or more limited availability of moisture on the soil surface than on the filter papers (Ghorbani et al., 1999).

Seeds of *A. spinosus* and *A. viridis* emerge at the same rate from 0.5 cm to 2 cm but, as the burial depth increases, *A. spinosus* emergence declines more rapidly than that of *A. viridis*, with no emergence from 4 cm in the former and only 6% emergence in the later, while as no emergence was observed at a depth of 6 cm in either species (Chauhan & Johnson, 2009). Larger seeds with greater carbohydrate reserves have increased ability to emerge from greater burial depths compared to those with lower reserves (Baskin & Baskin, 1998). The greater seed mass of *A. viridis* (more than twice than that of *A. spinosus*) could explain its ability to emerge from deeper in the soil than *A. spinosus* (Chauhan & Johnson, 2009). Small-seeded broadleaf weed species, such as *A. retroflexus*, *A. spinosus*, *A. viridis* and several other *Amaranthus* species have a similar pattern of emergence due to limited carbohydrate reserves to support germination and seedling emergence, thus limiting the depth from which these seedlings can emerge (Webb et al., 1987; Santelmann & Evetts, 1971; Ghorbani et al., 1999; Thomas et al., 2006; Chauhan & Johnson, 2009) (Table 4).

The acquisition of depth-mediated dormancy of weed seeds (Milberg & Andersson, 1997; Benvenuti et al., 2001) is an important strategy that allows longevity and perpetuation of weed seeds in the soil seed bank (Thompson, 1987; Benvenuti et al., 2001), and is known to occur due to lack of light transmittance, decrease in thermal fluctuation, decrease in oxygen, increase in carbon dioxide, and low rates of gaseous diffusion with increasing soil depth (Holm, 1972; Woolley & Stoller, 1978; Baskin & Baskin, 1985b; Drew, 1990; Benvenuti & Macchia, 1997, 1998; Gallagher & Cardina, 1998a; Benvenuti et al., 2001; Benvenuti, 2003).

,Furthermore, temperature fluctuations, which have been reported to have effect on seed dormancy alleviation of *Amaranthus* species (Baskin & Baskin, 1977, 1985b; Omami et al., 1999; Guo & Al-Khatib, 2003; Leon & Owen, 2003; Steckel et al., 2004; Cristaudo et al., 2007), decrease with increasing soil depth, thus acting as a depth-sensing mechanism for weed seeds (Ghersa et al., 1992; Baskin & Baskin, 1998; Kegode et al., 1998). Gutterman et al. (1992) and Kępczyński et al. (1996) reported that the non-dormant seeds of *Amaranthus* need at least 10% oxygen for germination. But with an increase in burial depth, there is a decrease in oxygen concentration, leading to hypoxia and germination inhibition in seeds of some weed species (Holm, 1972).

Milberg and Andersson (1997) reported that burial in soil induced a light requirement in some weed seeds. Burial induced red-light requirement for germination, resulted in a shift from low fluence response (LFR) to very low fluence response (VLFR) of the phytochrome in *A. retroflexus* and *A. hybridus* seeds (Scopel et al., 1991; Smith, 1995; Gallagher & Cardina, 1998a, b), which may also be expected in other species of *Amaranthus*.

Duration of seed burial also plays an important role in dormancy and germination of weed seeds like *A. patulus* (Baskin & Baskin, 1985b, 1998; Washitani, 1985) (Table 4). Washitani (1985) reported that only a negligible number of buried seeds of *A. patulus* maintained their germinability after 3 years of burial. Omami et al. (1999) reported cyclic changes in dormancy and germination of *A. retroflexus* seeds during a 12 month burial period. Seed germination of *A. retroflexus* and *A. palmeri* declined after 1 to 3 months of seed burial; peak germination occurred after 9 months and again declined at 12 months after seed burial (Omami et al., 1999; Jha et al., 2010). Buried seeds of *A. retroflexus* can remain viable for at least 6–10 years (Chepil, 1946a; Weaver & McWilliams, 1980; Burnside et al., 1981, 1996; Costea et al., 2004). In Beal's experiment in Michigan, 2% of seeds of *A. retroflexus* germinated after 40 years of burial (Telewski & Zeevaart, 2002).

Effect of Shade and Tillage

Subtle differences in the soil microclimate may have large affects on seed germination of weeds including *Amaranthus* species (Mohler, 1993; Buhler et al., 1996; Oryokot et al., 1997a). Effects of shade and tillage on emergence characteristics of *Amaranthus* species such as *A. retroflexus* and *A. rudis* has been previously studied (Anderson & Nielsen, 1996; Oryokot et al., 1997a; Hartzler et al., 1999; Cardina et al., 2002; Leon & Owen, 2006).

Effect of Scarification and Stratification

Santelmann and Evetts (1971) observed that *A. spinosus* seeds germinated best when treated with sulfuric acid. Mechanical or chemical scarification with sulphuric acid for 1 to 5 min resulted in germination of the secondary dormant *A. caudatus* seeds at 25 °C (Kępczyński & Bihun, 2002). Treatment with different concentrations of acetone, ethanol, ethylene, hydrogen peroxide, potassium cyanide, sodium azide, and sulfuric acid were very effective in breaking *Amaranthus* seed dormancy and promoting germination (Taylorson & Hendricks, 1973; Mahmudzadeh et al., 2003). Soomarin et al. (2010) treated the seeds of *A. retroflexus* with sulfuric acid and reported that with the increase in the duration of treatment the germination rate of *Amaranthus* seeds increased from 2% (in control) to 78.5% (in 25-min pre-treatment). Radicle length and weight, however, decreased (Evans, 1922; Mahmudzadeh et al., 2003; Soomarin et al., 2010).

Stratification, an effective way of alleviating seed dormancy (Bewley & Black, 1994), releases *A. retroflexus* and *A. rudis* seed dormancy gradually over time (Leon & Owen, 2003; Kępczyński & Sznigir, 2012) and increased seed germination percentage but the rate of germination at 35 °C was higher than at 25 °C after every period of stratification (Taylorson & Hendricks, 1969; Kępczyński & Sznigir, 2012). Seeds of *A. retroflexus* grown under a short-day length had higher germination in response to cold stratification than those grown under long-day lengths (Kigel et al., 1977).

Stratification at a constant temperature was less effective in releasing dormancy than autumn–winter burial of seeds due to the reason that in the soil, seeds are exposed not only to fluctuating temperatures, but also to several other factors such as compounds solutions, gases and soil microorganisms, which may affect the dormancy state of *Amaranthus* seeds (Kępczyński & Sznigir, 2012). Moore (1979) pointed out that chilling at 4 °C increases endogenous GA and decreases ABA concentration, therefore, it is possible that dormancy alleviation in seeds of some species by stratification or partial burial is associated with changes in ABA/GA and ethylene balance and/or sensitivity to these hormones (Cadman et al., 2006; Rodríguez-Gacio et al., 2009).

Economic Importance of Genus *Amaranthus*

Composition and Nutritional Value of *Amaranthus*

The role of *Amaranthus* as an under-exploited plant with promising economic value was recognized by the National Academy of Sciences, USA (NAS, 1975), after which it's nutritional value has been extensively studied (Becker et al., 1981; Teutonico & Knorr, 1985; Petr et al., 2003).

Amaranthus leaves show significant energy value ranging from 27 to 53 kcal/100 g of fresh leaves and high nutrient value ranging from 4 to 6 g of protein, 0.2 to 0.6 g of fat, and 4 to 7 g of carbohydrates per 100 g of fresh leaves (Uusikua et al., 2010) and are known to be rich in micronutrients and vitamins particularly chlorine, copper, iron, manganese, sodium, vitamin A, vitamin C and vitamin B-12 (Mnkeni, 2005). *Amaranthus* leaves taste much like spinach but, are nutritionally superior as they contain 3 times more vitamin C, calcium and niacin than spinach (Mnkeni, 2005). As compared to lettuce, *Amaranthus* leaves contain 18 times more vitamin A, 13 times more vitamin C, 20 times more calcium and 7 times more iron (Mnkeni, 2005; Srivastava, 2011).

Amaranthus seeds have protein content of about 12.5 to 17.6% (Becker et al., 1981; Teutonico & Knorr, 1985), with significantly higher content of lysine (0.73 to 0.84% of the total protein content) and the sulphur-containing amino acids (methionine and cysteine) than other cereal grains (Becker et al., 1981; Saunders & Becker, 1984; Railey, 1993; Lehmann, 1996; Petr et al., 2003) except soybeans (Petr et al. 2003), thus having potential to improve world food situation as an alternative source of protein (Oliveira & de Carvalho, 1975).

Amaranthus seeds have an excellent amino acid profile which, when combined with maize or rice, would approximate the modern standard protein recommended by the FAO/WHO (FAO, 1973; Senft, 1980; Teutonico & Knorr, 1985; Singhal & Kulkarni, 1988) and is useful in supplementing nutritive food and amelioration of protein deficiency strictly in the vegetarian diet people (Downtown, 1973; Senft, 1980; Railey, 1993).

The lipid content of *Amaranthus* seed is typically 6 to 20% (Lorenz & Hwang, 1985; Garcia et al., 1987a; Budin et al., 1996). Both *Amaranthus* seeds as well as leaves are a good source of unsaturated fatty acids like palmitic, oleic, linoleic, and linolenic acids (Fernando & Bean, 1984; Jahaniaval et al., 2000; Leon-Camacho et al., 2001). Although *Amaranthus* seed is not considered a typical oilseed crop, it has been identified as a rich source (2.4 to 8%) of squalene (2,6,10,15,19,23-hexamethyl-2,6,10,14,18,22-

tetracosahexaene) and tocotrienols (a form of vitamin E) (Budin et al., 1996; Lehmann, 1996; Sun et al., 1997). Squalene is an expensive terpenoid compound, derived primarily from liver of shark (*Cantrophorus squamosus*) and whale (*Physeter macrocephalus*) oils. Due to the concern for marine animal protection, attention has been focused on identifying crop sources of squalene (Sun et al., 1997). Squalene is an important ingredient in cosmetics, pharmaceuticals, and lubricants for computer disks (Sun et al., 1997; Budin et al., 1996). Both squalene and tocotrienols can play an important role in lowering LDL-cholesterol in blood (Railey, 1993; Budin et al., 1996; Lehmann, 1996) and thus acts as protective factors against cardiac infarction which is caused by isoproteronol (Farvin et al., 2006).

Amaranthus seeds are a rich source of calcium (1300 to 2850 mg/kg), iron (72 to 174 mg/kg), magnesium (2300 to 3360 mg/kg), sodium (160 to 480 mg/kg) and zinc (36.2 to 40 mg/kg); sterols (0.27–0.32 mg/g); as well as vitamin riboflavin (0.19–0.23 mg/100 g of flour) and ascorbic acid (4.5 mg/100 g of flour), niacin (1.17 to 1.45 mg/100 g of flour), thiamine (0.07 to 0.1 mg/100 g of flour) and other microelements (Becker et al., 1981; Plate and Areas, 2002).

Some *Amaranthus* species, when grown under conditions of stress, are known to accumulate toxic levels of oxalate and nitrate (Der Marderosian et al., 1980; Saunders & Becker, 1984; Wills et al., 1984) and these nitrates upon consumption may be chemically changed in the digestive tract into poisonous/carcinogenic nitrosamines.

Applications of *Amaranthus*

Amaranthus is one of the few highly nutritious multi-purpose crops and is used as vegetable, cereal, medicinal plant, dye plant, forage, fuel and as an ornamental. (Sauer ,1950; Oke 1983; Saunders & Becker, 1984; Railey, 1993; Mlakar et al., 2009; Sheikh & Singh, 2013).

The red dye from the leaves of various species of *Amaranthus* is used to color foods, alcoholic beverages and maize dough (Sauer, 1950). In Mexico, *Amaranthus* seeds are used chiefly for making alegria candies from popped seeds and molasses (Early, 1977) and for preparing atole, a drink from roasted and powdered seeds mixed with syrup and water (Oke, 1983). In India, *A. hypochondriacus*, commonly known as “rajgeera” (the King’s grain), is extensively cultivated as subsidiary food crop from Kashmir to Arunachal Pradesh and is often popped to be used in confections called “laddoos,” (Vietmeyer, 1978) which are very similar to Mexican ‘alegria’. In Nepal, *Amaranthus* seeds are eaten as gruel called “sattoo” or milled into a flour to make chappatis (Vietmeyer, 1978; Singhal & Kulkarni, 1988). *Amaranthus* leaves are used in custards, pastes, soups, stews, salad, boiled and mixed with a groundnut sauce (Oliveira & de Carvalho, 1975; National Research Council, 1984).

Various species of *Amaranthus* (*A. blitum*, *A. caudatus* and *A. spinosus*) are consumed as vegetable in Africa, Caribbean, China, Greece, India, Italy, Nepal and South Pacific Islands (Stallknecht & Schulz-Schaeffer, 1993). Based on utilisation of cultivated *Amaranthus* for human consumption, species can be divided into grain and vegetable *Amaranthus*. Grain *Amaranthus* is not a “true cereal” rather it belongs to a group of cereal-like grain crops or “pseudo-cereals” (O’Brien & Price, 1983). Pseudocereals are dicotyledonous species which are not closely related to each other or to the monocotyledonous true cereals (Shewry, 2002).

The *Amaranthus* seeds can be ground and included as a flour ingredient in different mixtures for biscuits, bread, cookies, crackers, crepes, dumplings, muffins, noodles, pancakes, puddings, and other confectioneries (National Research Council, 1984; Mlakar et al., 2009; Sanz-Penella et al., 2013) and also the combination of amaranth and wheat flour increases the nutritional value of baked products (Saunders & Becker, 1984; Segura-Nieto et al., 1994; Mlakar et al., 2009).

Amaranthus has antiallergic, anticancer, antihypertensive and antioxidant properties (Conforti et al., 2005; Castelano-Sousa & Amaya-Farfán, 2012) and protects against several disorders such as bleeding tendencies, brain stroke, celiac disease, defective vision, diabetes, digestion disorder, functional sterility, haemorrhage, heart diseases, HIV/AIDS, hypertension, kwashiorkor, leucorrhoea, liver disease, marasmus, premature ageing, recurrent colds, respiratory infections, retarded growth, skin diseases, TB and wound healing (Thompson, 2001).

Phytoremediation Potential of Genus *Amaranthus*

The uptake of heavy metals by *Amaranthus* species has been recently studied in soils at refuse dump sites, animal waste dumpsites and other forms of contaminated soils (Adekunle et al., 2009; Adefila et al., 2010; Adefemi et al., 2012; Akubugwo et al., 2012; Shagal et al., 2012). *A. caudatus* plants grown on dump sites contain higher concentration of heavy metals like Fe, Cu, Pb, Zn, Mn, Cd (Adewuyi et al., 2010). *A. hybridus* grown on dumpsites possessed higher concentration of heavy metals like Fe, Zn, Cd, Cr, Cu, Ni, Pb, Mn and Hg (Akubugwo et al., 2012). The assessments of the heavy metal content of plants grown on dumpsites provide precious data on the heavy metals phytoaccumulation potential of such plants (Mclntyre & Lewis, 1997). *A. retroflexus* has been identified as metal accumulator (Bigaliev et al., 2003; Mellem, 2008). *A. spinosus* is a potential agent for accumulation and translocation of heavy metal like Cu, Zn, Cr, Pb and Cd (Chinmayee et al., 2012). *A. tricolor* has high cadmium-accumulating ability (Watanabe et al., 2009). *A. viridis* has a method of concentrating heavy metals especially Pb and Cd in its tissues (Atayese et al., 2009). This suggests that these *Amaranthus* species can serve as phytoaccumulators of heavy metals and can be used for the purpose of Phytoremediation.

Amaranthus as a Weed

Genus *Amaranthus* consists of some of the worst C_4 weeds of the world (Holm et al., 1977), and its several species are consistently ranked among the top 10 most troublesome weeds in the southeast United States (Dowler, 1995; Webster, 2009), which have been causing problems for farmers since the mid-1990s. Nine *Amaranthus* species are listed as “invasive or noxious weeds” in the USDA Plants Database, and an additional 20 species are listed as “agricultural weeds” in the Global Compendium of Weeds (Randall, 2007; USDA, NRCS, 2010).

Several *Amaranthus* species such as *A. retroflexus, A. spinosus* and *A. viridis* (Yan et al., 2001), *A. blitum* (Costea & Tardif, 2003), *A. albus, A. powellii* and *A. rudis* (Ortiz Ribbing & Williams, 2006) and *A. palmeri* (Kendig, 2009), are known to compete with many economic crops including cereals and vegetables in different parts of the world and cause great yield losses (Holm et al., 1977; Menges, 1988; Monks & Oliver, 1988). The weedy *Amaranthus* species are referred to as "opportunists" (Sauer, 1955) because of the fact that they thrive in disturbed soils and tend to be associated with agricultural practices. They are able to compete with crops for water, nutrients and light, causing severe reductions in yield, quality and harvest efficiency (Vangessel & Renner, 1990) and their high competitiveness may be related to their prolific seed production, prolonged seed viability, seed dormancy, speed and timing of germination, long germination period, aggressive growth at higher temperatures due to its extensive root system, thermostability of the C_4 photosynthetic mechanism, high water use efficiency, and high density of infestation (Weaver & McWilliams, 1980; Knezevic & Horak, 1998; Horak & Loughin, 2000; Aguyoh & Masiunas, 2003; Massinga et al., 2003), which is further enhanced due to evolution of herbicide-resistant *Amaranthus* biotypes (Heap 2014). Besides, their competitiveness varies with species, density, and time of emergence relative to the crop (Klingaman & Oliver, 1994; Knezevic & Horak, 1998). Allelopathic effects may also interact with competition for resources between some *Amaranthus* species and the crop in which they are growing (Connick et al., 1987; Bradow & Connick, 1988; Menges, 1988).

A. blitum is listed by as a serious or principal weed in ten countries, mainly across Europe and Asia (Holm et al., 1979; Takabayashi & Nakayama, 1981; Walter & Dobes, 2004) and occurs in a wide range of field and horticultural crops, grassland, orchards, plantations and vineyards.

A. palmeri is the most troublesome weed in southeastern United States (Dowler, 1995; Norsworthy, 2003), and is known to cause severe interference and yield loss in various agronomic crops like *Arachis hypogaea* (Horak & Loughin, 2000; Burke et al., 2007), *Glycine max* (Monks & Oliver, 1988; Klingaman and Oliver 1994; Dieleman et al., 1995; Bensch et al., 2003; Norsworthy, 2003), *Gossypium hirsutum* (Keeley & Thullen, 1989; Dowler, 1995; Morgan et al., 1997; Rowland et al., 1999; Smith et al., 2000; Morgan et al., 2001), *Ipomoea batatas* (Meyers et al., 2010), *Sorghum bicolor* (Moore et al., 2004), and *Zea mays* (Massinga et al., 2001; Massinga & Currie, 2002; Massinga et al., 2003).

A. retroflexus, one of the ten weed species of greatest economic importance in Europe (Schroeder et al., 1993) is a common weed of cultivated fields in many agricultural areas of the world (Weaver & McWilliams 1980; Horak & Loughin, 2000), which is capable of infesting and reducing yields of crops such as *Beta vulgaris*, *Brassica napus* (Hendrick et al., 1974), *Glycine max* (Orwick & Schreiber, 1979; Dieleman et al., 1995; Cowan et al., 1998; Bensch et al., 2003), *Gossypium hirsutum* (Buchanan et al., 1980), *Helianthus annus* (Heidarian et al., 2012), *Phaseolus* sp. (Aguyoh & Masiunas, 2003), *Solanum tuberosum* (Vangessel & Renner, 1990), *Zea mays* (Knezevic et al., 1994), and other vegetables (Weaver & McWilliams, 1980).

A. spinosus has been reported as a weed in 28 crops and 44 countries in India, Southeast Asia and the west and south of Africa (Waterhouse, 1994; Chauhan and Johnson 2009). It occurs as a weed of varying significance in a variety of crops like *Ananas comosus*, *Arachis hypogaea*, *Celosia argentia*, *Corchorus olitorius*, *Glycine max, Gossypium hirsutum*, *Oryza sativa*, *Saccharum officinarum*, *Sorghum bicolor*, *Zea mays* (Ogunyemi et al., 2000; Ogunyemi et al., 2005; Chauhan & Johnson, 2009) and horticultural enterprises (Waterhouse, 1994). A remarkable example of recent weed invasion is that of *A. tuberculatus* in corn and soybean fields in the central United States over the past two decades (Steckel, 2007). *A. tuberculatus* was first recorded as an agricultural weed in Illinois cornfields in the early 1950s (Sauer, 1957) and has become a weed of major concern since 1990s (Trucco et al. 2009). Yield losses caused by interference from various other species of *Amaranthus* have been reported for numerous crops (Moolani et al., 1964; Rushing et al., 1985; Bensch et al., 2003; Hartzler et al., 2004).

Allelopathy

Allelopathic effects of different *Amaranthus* species on various plants have been reported (Table 5**)**. Dry residues of the aerial part of *A. retroflexus* reduced the germination of *Beta vulgaris*, *Brassica oleracea*, *Brassica oleracea* var. *brotrytis*, *Capsicum annuum*, *Carthamus tinctorius*, *Cucumis sativus*, *Cucurbita ovifera*, *Daucus carota*, *Glycine max, Gossypium hirsutum*, *Helianthus annus*, *Hordeum vulgare*, *Lactuca sativa*, *Lycopersicon lycopersici*, *Phaseolus vulgaris, Solanum melongena*, *Sorghum bicolor* and *Zea mays* (Munger et al., 1983; Qasem, 1995a, b; Alam et al., 2001; Aguyoh & Masiunas, 2003; Costea & Tardif, 2003; Dos Santos et al., 2004; Rezaie & Yarnia, 2009; Souza et al., 2011).

Shoot residues of *A. retroflexus* inhibited radicle and hypocotyl elongation, interfered with photosynthesis, reduced growth, nutrient uptake and productivity of *Zea mays* (Bhowmik & Doll, 1980, 1982, 1984) and decreased respiration, relative growth rate (RGR), net assimilation rate (NAR), root fresh weight (FWR), nitrogen fixation of nodules, chlorophyll content and biomass production in *Glycine max* (Bhowmik & Doll, 1980, 1982, 1984; Chaniago et al., 2006); reduced growth and yield in *Nicotiana tabacum* (Lolas, 1981; Lolas, 1986); affected common bean growth and establishment (Shimi & Termeh, 2004) and decreased safflower yield (Williams et al., 2005) through release of allelochemicals, but, the inhibition was not appreciably affected by temperature or light (Bhowmik & Doll, 1983). Dried shoot residues of *A. retroflexus*, *A. blitoides* and *A. gracilis* reduced germination, coleoptile length, root length, root dry weight, plant height, grain and straw yield of *Triticum aestivum* (Qasem, 1995b; Shahrokhi et al., 2012) and caused reductions in the productivity of *Hordeum vulgare* (Qasem, 1994, 1995a).

Allelopathic effects of *A. palmeri* have been reported on seedling emergence of several species (Menges, 1987, 1988). Extracts of *A. palmeri* inhibited seed germination and growth of *Daucus carrota* and *Allium cepa* (Altieri and Doll 1978; Bradow & Connick, 1987; Menges, 1987). Vapours of 2-heptanone and 2-heptanol, isolated from *A. palmeri*, inhibited the germination of onion, carrot, tomato, and palmer amaranth seeds (Connick et al., 1987). Menges, (1988) reported phytotoxicity of *A. palmeri* residues on growth of several crop species including *Sorghum bicolor*, *Brassica oleracea* var. Capitata, *Daucus carrota* and *Allium cepa*. Water-soluble extracts of *A. palmeri* were more phytotoxic than were extracts of *A. retroflexus* (Hicks et al., 1986).

Allelopathic effects of *A. spinosus* have been reported (Shrefler et al., 1996). Extract of leaves and inflorescence of *A. spinosus* drastically reduced the vegetative and reproductive phases of *Sinapis alba* and *T. aestivum* (Datta & Bandyopadhayay, 1981). Leached components of *A. spinosus* showed strong allelopathic effect over the growth and establishment of *Parthenium hysterophorus* (Chikkalingaiah & Mahadevappa, 1998) and also over the growth of some cultures (Suma, 1998).

Burned residues of *A. viridis* diminished growth and productivity of *Pennisetum americanum* (Singhal & Sen, 1981). Also the aqueous extracts of *A. dubius* were found inhibitory to seedling emergence and growth of several plant species (Altieri & Doll, 1978). Dry shoot extracts *of A. hybridus* negatively affected the total chlorophyll content, number of developed leaves, stem length, and total plant dry matter of dry beans (Amini et al., 2013).

Allelochemicals such as aldehydes, alkaloids, apocarotenoids, flavonoids, steroids, xyloids, clerogenic acid and saponins (Anaya et al., 1987; Alm et al., 2002), secreted by aerial organs of *Amaranthus* plants were found to be released through washing by rain or irrigation water to the soil (Anaya et al., 1987; Al-Khatib, 1995; Khanh et al., 2005).

Fischer and Quijano (1985) isolated phytol, chondrillasterol, vanillin, 3-methoxy-4-hydroxy nitrobenzene, and 2, 6-dimethoxy-benzoquinone from *A. palmeri*. Coumarins have been isolated from *A. retroflexus* (Rezaie & Yarnia, 2009). The principal allelochemicals present in *A. spinosus* were phenolic acids, alkaloids belonging to the quinolizidine class, steroid, indol and sesquiterpene lactones (Narwall 1994; Qasem 1995a; Velu & Ali, 1995; Suma, 1998). The quantity of phenolic acids in *A. spinosus* was greatest in plants growing in soils polluted with domestic, industrial and vehicle residues (Suma, 1998) while as the concentration of phenolic acids within the plant was highest in the leaves, followed by stems, inflorescence and the lowest in the roots (Souza et al., 2011).

Management

Weedy *Amaranthus* species are difficult to control due to their prolific seed production (200,000 to 600,000 seeds/female plant), small seed size, ability to cross successfully with other *Amaranthus* species, long germination period, high density of infestation, ability to rapidly evolve herbicide resistance, and difficulty in proper identification (Stevens, 1932; Keeley et al., 1987; Dillon et al., 1989; Horak, 1997; Wetzel et al., 1999a, b; Sellers et al., 2003; Vigueira et al., 2013). Although, proper identification of *Amaranthus* species can be difficult, it is important due to varying responses to herbicides and weed management practices (Pratt et al., 1999).

Shade can have a suppressive effect on weed seed germination, as it dampens the soil thermal amplitude and alters the light quality perceived by seeds lying on the soil surface (Fortin & Pierce, 1990; Batlla et al., 2000; Norsworthy, 2004). Under a canopy, besides reductions in PAR, seeds experience a reduction in the red: far-red (R:FR) ratio as a result of an increase in far-red (FR) transmitted light (Taylorson &Borthwick, 1969; Thompson & Grime, 1983; Sattin et al., 1994; Norsworthy 2004), which is inhibitory to germination of various *Amaranthus* species like *A. hybridus*, *A. palmeri*, *A. retroflexus*, and *A. rudis* (Taylorson & Borthwick, 1969; Gallagher & Cardina, 1998a, 1998b; Hartzler et al., 1999; Leon & Owen 2003; Jha et al., 2008c). Shading of the maternal plant in *A. retroflexus* resulted in reduced seed dormancy under short day (8 h light) and increased seed dormancy under long day (16 h light) conditions (Kigel et al., 1977). Washitani (1985) and Brainard et al. (2005) also reported a leaf canopy effect on increased seed dormancy of *A. patulus.* The germination percentage of *A. powellii* seeds was 50% lower for seeds maturing on plants grown under shade than in open sunlight (Brainard et al., 2005).

Tillage is a major mechanism for vertical movement of weed seeds in soil (Buhler et al., 1997, 2001). In a no-tillage system, weed seeds are concentrated in the upper 5 cm of the soil profile relative to conventional tillage systems (Cardina et al., 1991; Buhler, 1992; Clements et al., 1996), which allows small-seeded weeds such as pigweeds to emerge more easily from shallow depths (Webb et al., 1987; Buhler et al., 1996; Oryokot et al., 1997a; Ghorbani et al., 1999). Stimulation of germination and subsequent emergence following tillage was possibly due to increased soil aeration, improved soil-seed contact, and elevated soil temperatures (Litch and Al-Kaisi 2005; Leon and Owen 2006; Norsworthy and Oliveira 2007). Although high reduction of *Amaranthus* by the tillage system is promising, yet it is not sufficient. A control of approximately 90% is not satisfactory because in low densities the surviving *Amaranthus* plants produce more seeds per plant than in high densities (Bürki et al., 1997).

Mowing is also not an effective option for control of various *Amaranthus* species because once mowed they bounces back and start growing prostrate, produces viable seed and complete their life cycle if mowing is not maintained. Therefore, herbicides can be a more effective option to control these species, than mowing.

Herbicides are cost-effective and efficient tools for weed control in modern agriculture. 2,4-D (Szmedra, 1997), Aminocyclopyrachlor (DuPont, 2009), Aminopyralid (Burch et al., 2005), Dicamba (Senseman et al., 2007), Pendimethalin (Malefyt and Duke, 1984), are some of the widely used herbicides for broadleaf weed control in the world. Early to mid-season (early May to late June) herbicide applications (Dieleman et al. 1996) with an early crop canopy closure would be a promising strategy to manage different *Amaranthus* species (Jha et al., 2008a, 2008b). Steckel (2004) reported that *Amaranthus* species in various row crops can be best managed when a pre-applied herbicide is followed by a post applied herbicide or when a post applied herbicide is followed by another post applied herbicide, which contains a residual product. Although many currently labelled soil-applied herbicides like 2,4-D, Banvel® or Clarity® (dicamba), Cimarron® (metsulfuron), Cimarron Max® (metsulfuron +2,4-D+ dicamba), Distinct® (diflufenzopyr + dicamba), Grazon P + D® (picloram +2,4-D), Milestone® (aminopyralid) or ForeFront R&P® (aminopyralid +2,4-D), Roundup® (glyphosate), Surmount® (picloram + fluroxypyr), and Weedmaster® (dicamba +2,4-D) provided good control of various *Amaranthus* species, difficulties in control have been reported (Fritz & Hartwig, 1986; Fuerst et al., 1986; Mayo et al., 1995; Grichar, 1997; Steckel, 2004; Green et al. 2006; Boyd, 2008). With proper herbicide selection, 90% control of *A. albus*, *A. palmeri*, *A. retroflexus*, and *A. rudis* is possible (Sweat et al., 1998). Besides, it may be necessary to make two to three herbicide applications to effectively control them all season long (Ferrell & Sellers, 2007).

Herbicide Resistance in Amaranthus Species

Sole reliance on herbicides has resulted in evolution of herbicide resistance in weeds (Heap, 2014). Herbicide-resistant biotypes of *Amaranthus* species have developed in many countries (Barralis & Gasquez, 1987). At least one *Amaranthus* weed species is reported to be resistant to one or more herbicide groups in twenty-nine U.S. States (Sellers et al., 2003). The presence of herbicide tolerance traits raises questions of how to address management issues at a grower, county, and regional level (Cardina et al., 1999). Evolution of resistance to glyphosate, the world's most widely used herbicide with effective broad-spectrum weed control, is a significant problem facing world agriculture (Powles, 2008; Webster & Sosnoskie, 2010).

Herbicide-resistant biotypes of *A. blitum* have been reported from North America, Europe and Asia which have developed resistance to different herbicides including ALS inhibitors, Atrazine and Paraquat (Itoh et al., 1992; Manley et al., 1996; Heap, 2014). *A. palmeri* has developed resistance to several different herbicides, including acetolactate synthase (ALS) inhibitors, dinitroaniline, glyphosate, imidazolinone, sulfonylurea, and triazine (Gossett et al., 1992; Horak & Peterson, 1995; Sprague et al., 1997; Peterson, 1999; Franssen et al. 2001a; Culpepper et al. 2006; Steckel et al., 2008; Vencill et al., 2008; Wise et al. 2009; Price et al., 2011; Heap, 2014). Also *A. rudis* and *A. retroflexus* biotypes with resistance to glyphosate, triazine or acetolactate synthase-inhibiting herbicides have been reported (Horak & Peterson, 1995; Peterson, 1999; Price et al., 2011). Prior to the recent occurrence of glyphosate resistance in *A. palmeri* (Culpepper et al., 2006; Mueller et al., 2006; York et al., 2007; Culpepper et al., 2008; Norsworthy et al. 2008; Steckel et al., 2008; Gaines et al., 2010; Price et al., 2011), glyphosate had been highly effective in controlling this weed (Scott et al., 2002; Norsworthy, 2004, 2005; Bond et al., 2006), which contributed to rapid adoption of glyphosate-resistant soybean and cotton throughout the southern United States. A survey of Georgia growers revealed that the presence of Glyphosate resistant *A. palmeri* in fields increased management costs by 58%, from $81 ha21 to $129 ha21 (Culpepper & Kichler, 2009).

A. tuberculatus have evolved resistance to five different chemical classes of herbicides: Acetolactate synthase (ALS) inhibitors (Horak & Peterson, 1995; Foes et al., 1998; Tranel & Wright, 2002; Patzoldt & Tranel, 2007; Nordby et al., 2010), glyphosate (Legleiter and Bradley 2008; Nandula et al. 2013), p-hydroxyphenylpyruvate dioxygenase (HPPD) inhibitors (Hausman et al. 2011), Photosystem II (PSII) inhibitors, also called triazines (Anderson et al., 1996), and Protoporphyrinogen oxidase (PPO) inhibitors (Shoup et al., 2003), furthermore its some populations have developed resistance to multiple herbicide classes (Tranel et al., 2004; Falk et al., 2005; Patzoldt et al., 2005; Mcmullan & Green, 2011; Bell et al., 2013). Simultaneously, ALS resistance appears to have no fitness cost in herbicide-free environments in some *Amaranthus* species (Sibony & Rubin, 2002; but see Tardif et al., 2006).

Biological Control of Amaranthus Species

Excessive use of herbicides has resulted in problems, including contamination of surface and groundwater resources (Guzzella et al., 2006; Spalding et al., 2003), and various human health risks (EPA, 2007). The growing public concerns about pesticide residues in our food and environment, and the increasing public pressure for more sustainable crop production methods have led to an increasing interest in integrated weed control strategies for *Amaranthus* species (Bürki et al., 1997), based on mechanical, physical, or biological control. Numerous weedy *Amaranthus* species were chosen for biological control research within the framework of COST (European Cooperation in the Field of Scientific and Technical Research)–Action (Müller-Schärer, 1993).

Various insects which are being promoted as biological control agents for various *Amaranthus* species (like *A. caudatus*, *A. hybridus*, *A. retroflexus*, *A. spinosus*, *A. viridis*) are: *Disonycha glabrata* (Garman, 1892; Vogt & Cordo, 1976; Balsbaugh et al., 1981; Tisler, 1990), *Chaetocnema tibialis* (Cagán et al., 2000), *Cassida nigriventris* and *Coleophora versurella* (Khan et al., 1978), *Hypolixus truncatulus* (Napompeth, 1982, 1989, 1992; Julien, 1992), *Hypolixus nubilosus* (Kolaib et al., 1986; López et al., 2011; Torres et al., 2011; Kagali et al., 2013), *Haplopeodes minutes* (Spencer & Steyskal, 1986), *Epicauta leopardina* (Schuester, 1987), *Melanagromyza amaranthi* (Spencer & Havranek, 1989), *Pellucidus Vittula* (Cagán et al., 2000), and *Hepertogramma bipunctalis* (López et al., 2011; Kagali et al., 2013).

Erwinia carotovora var. *rhapontici* (Kataryan, 1975; Mendoza & Rodriguez, 1990), *Gliocladium virens* (Howell & Stipanovic, 1984) are some examples of bacteria which can be used as bio control agents for various *Amaranthus* species. Promising pathogens that can be used as potential bioherbicide or mycoherbicide for *Amaranthus* include: *Aposphaeria amaranthi* (Mintz & Weidemann, 1992); *Microsphaeropsis amaranthi* (Ortiz Ribbing & Williams, 2006), *Phomopsis amaranthicola* (Charudattan, 1994; Ortiz Ribbing & Williams, 2006) and *Alternaria alternata* (Ghorbani et al., 2000).

Allelopathy may also be a useful means of biological weed control, especially when integrated into pest management systems, reducing dependence upon synthetic herbicides. A recent screening for inhibiting activity against *A. spinosus* identified several plants with herbicidal activity (Rizvi & Rizvi, 1992). Macharia and Peffley (1995) reported the allelopathic effect of *Allium fistulosum* and *A. cepa* genotypes on plant growth and seed germination of *A. spinosus*. Aqueous extracts of tissues of some plants like *Artemisia annua*, *Cirsium arvense*, *Fagopyrum esculentum*, *Helianthus annuus*, *Rumex crispus and Sorghum halepense* decreases germination of *A. retroflexus* (Costea et al., 2004; Haramoto & Gallandt, 2005). Thus these plants can act as biological control agents.

The potential conflict of interest between the need for effective biological control of noxious *Amaranthus* species to prevent major crop losses and reduce herbicide application in systems of sustainable agriculture, on the one hand and the potential economic value of certain *Amaranthus* species as crops, on the other, needs to be discussed and resolved. The important point is that agents used in the inundative bio control of noxious *Amaranthus* species should not endanger crop *Amaranthus* (Bürki et al., 1997).

Conclusion

The high nutritional value of *Amaranthus* seeds, functional potential, short lifecycle, rapid growth, adaptability to unfavourable climate and soil condition, drought tolerance and the food use of the entire plant is the reason for increasing research interest in this pseudocereal. This is a food for future crop for many developing countries, particularly in drought-prone areas of Africa and Asia. However, Genus *Amaranthus* consists of some of the troublesome invasive or noxious weeds of the world which are known to compete with many economic crops in different parts of the world resulting in great yield losses. Hence, extensive research is required to choose between the good and bad Amaranths.

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Appendix

Table 1 Accepted plant names of the species for the genus *Amaranthus* with their synonyms

Name	Synonyms
Amaranthus acanthobracteatus Henr.	
Amaranthus acanthochiton Sauer	• *Acanthochiton wrightii* Torr.
Amaranthus × *adulterinus* Thell.	
Amaranthus albus L.	• *Amaranthus albus* var. *albus* • *Amaranthus albus* var. *monosepalus* Thell. • *Amaranthus albus* var. *parviflorus* Moq. • *Amaranthus albus* var. *puberulus* Thell. • *Amaranthus albus* var. *pubescens* (Uline & W.L.Bray) Fernald • *Amaranthus albus* var. *rubicundus* Thell. • *Amaranthus gracilentus* H.W.Kung • *Amaranthus graecizans* Cutanda • *Amaranthus graecizans* var. *pubescens* Uline & W.L.Bray • *Amaranthus littoralis* Hornem. • *Amaranthus pubescens* (Uline & W.L.Bray) Rydb. • *Galliaria albida* Bubani • *Glomeraria alba* (L.) Cav.
Amaranthus anderssonii J.T.Howell	• *Scleropus urceolatus* Andersson
Amaranthus arenicola I.M.Johnst.	
Amaranthus asplundii Thell.	• *Amaranthus affinis* Thell. • *Amaranthus buchtienianus* Thell.
Amaranthus atropurpureus Roxb.	
Amaranthus aureus F.Dietr.	
Amaranthus australis (A.Gray) Sauer	• *Acnida alabamensis* Standl.

Table 1 (continued)

Name	Synonyms
	• *Acnida australis* A.Gray • *Acnida cannabina* var. *australis* (A.Gray) Uline & W.L.Bray • *Acnida cuspidate* Bertero ex Spreng.
Amaranthus bahiensis Mart.	
Amaranthus bigelowii Uline & W.L.Bray	• *Amaranthus bigelowii* var. *emarginatus* (Torr.) Uline & W.L.Bray • *Sarratia berlandieri* var. *emarginate* Torr.
Amaranthus blitoides S.Watson	• *Amaranthus blitoides* var. *crassius* Jeps. • *Amaranthus blitoides* var. *densifolius* Uline & W.L.Bray • *Amaranthus blitoides* var. *halophilus* Aellen • *Amaranthus blitoides* var. *reverchonii* Uline & W.L.Bray • *Amaranthus reverchonii* (Uline & W.L.Bray) Kov. • *Galliaria blitoides* Nieuwl.
Amaranthus blitum L.	• *Albersia arenaria* Schur • *Albersia ascendens* Fourr. • *Albersia blitum* Kunth • *Albersia livida* Kunth • *Amaranthus adscendens* auct. • *Amaranthus albus* Rodschied ex F.Dietr. • *Amaranthus alius* K.Krause • *Amaranthus ascendens* Loisel. • *Amaranthus berchtoldii* Seidl ex Opiz • *Amaranthus blitonius* St.Lag. • *Amaranthus blitum* var. *ascendens* (Loisel.) DC. • *Amaranthus blitum* var. *blitum* • *Amaranthus blitum* var. *polygonoides* Moq. • *Amaranthus blitum* subsp. *polygonoides* (Zoll. ex Moq.) Carretero • *Amaranthus diffusus* Dulac. • *Amaranthus gangeticus* Wall. [Invalid] • *Amaranthus graecizans* var. *blitum* (L.) Kuntze • *Amaranthus lividus* Hook.f. [Illegitimate] • *Amaranthus lividus* subsp.*ascendens* (Loisel.) Wacht. • *Amaranthus lividus* subsp. *ascendens* (Loisel.) Heukels • *Amaranthus lividus* var. *ascendens* (Loisel.) Thell. • *Amaranthus lividus* var. *ascendens* (Loisel.) Hayw. & Druce • *Amaranthus lividus* subsp. *lividus* • *Amaranthus lividus* var. *polygonoides* (Moq.) Thell. • *Amaranthus lividus* subsp. *polygonoides* (Moq.) Probst • *Amaranthus minor* Gray • *Amaranthus mucronatus* Poir. • *Amaranthus oleraceus* Rodschied • *Amaranthus pallidus* M.Bieb.

Table 1 (continued)

Name	Synonyms
	• *Amaranthus polygonoides* Zoll. Ex Moq. [Invalid] • *Amaranthus prostratus* T.Bastard [Illegitimate] • *Amaranthus ruderalis* Koch ex Moq. • *Amaranthus tenuiflorus* Fisch. ex Moq. • *Amaranthus tenuifolius* Roxb. • *Amaranthus viridis* All. [Illegitimate] • *Blitum maius* Scop. • *Euxolus alius* (E.H.L.Krause) E.H.L.Krause • *Euxolus ascendens* (Loisel.) H.Hara • *Euxolus viridis* var. *ascendens* (Loisel.) Moq. • *Glomeraria blitum* (L.) Cav. • *Pyxidium graecizans* Moq.
Amaranthus blitum subsp. *emarginatus* (Salzm. Ex Uline & Bary) Carretero, Muñoz Garm. & Pedrol	• *Albersia emarginate* (A.Braun & C.D.Bouché) Asch. ex Hausskn. • *Amaranthus ascendens* var. *polygonoides* (Moq.) Thell. • *Amaranthus ascendens* subsp. *polygonoides* (Moq.) Thell. ex Priszter • *Amaranthus blitum* var. *emarginatus* (Moq. ex Uline & W.L.Bray) Lambinon • *Amaranthus emarginatus* Salzm. ex Uline & Bray • *Amaranthus emarginatus* Salzm. ex Moq. • *Amaranthus lividus* subsp. *ascendens* Heukels. • *Euxolus emarginatus* A.Braun & C.D.Bouché • *Euxolus viridis* var. *polygonoides* Moq.
Amaranthus blitum subsp. *oleraceus* (L.) Costea	• *Albersia blitum* var. *oleraceus* (L.) Hook.f. • *Albersia oleracea* (L.) Kunth • *Amaranthus ascendens* var. *oleraceus* (L.) Thell. ex Priszter • *Amaranthus blitum* var. *oleraceus* (L.) Hook.f. • *Amaranthus circinnatus* Poir. • *Amaranthus lividus* L. • *Amaranthus lividus* subsp. *oleraceus* (L.) Soó • *Amaranthus lividus* var. *oleraceus* (L.) Thell. • *Amaranthus obtusiflorus* (Mart.) Kov. • *Amaranthus officinalis* Gromov ex Trautv. • *Amaranthus oleraceus* L. • *Amaranthus olitorius* Besser • *Blitum lividum* (L.) Moench • *Blitum oleraceum* (L.) Moench • *Glomeraria livida* (L.) Cav. • *Glomeraria oleracea* (L.) Cav. • *Pentrius oleraceus* Raf.
Amaranthus blitum var. *pseudogracilis* (Thell.) Lambinon	• *Amaranthus emarginatus* subsp. *pseudogracilis* (Thell.) Hügin • *Amaranthus lividus* f. *pseudogracilis* Thell. • *Amaranthus pseudogracilis* (Thell.) G.H.Loos
Amaranthus brandegeei Standl.	
Amaranthus brasiliensis Moq.	
Amaranthus brownii Christoph. & Caum	
Amaranthus × *budensis* Priszter	

Table 1 (continued)

Name	Synonyms
Amaranthus californicus (Moq.) S.Watson	• *Amaranthus albomarginatus* Uline & W.L.Bray • *Mengea californica* Moq.
Amaranthus campestris Willd.	
Amaranthus cannabinus (L.) Sauer	• *Acnida cannabina* L. • *Acnida cannabina* var. *concatenate* Moq. • *Acnida cannabina* var. *cuspidate* (Bertero ex Spreng.) Moq. • *Acnida cannabina* var. *lanceolate* Moq. • *Acnida cannabina* var. *salicifolia* Moq. • *Acnida elliotii* Raf. • *Acnida obtusifolia* Raf. • *Acnida rhyssocarpa* Spreng. • *Acnida ruscocarpa* Willd. • *Acnida salicifolia* Raf. • *Amaranthus macrocaulos* Poir.
Amaranthus capensis Thell.	• *Amaranthus capensis* subsp. *capensis* • *Amaranthus capensis* subsp. *uncinatus* (Thell.) Brenan • *Amaranthus dinteri* var. *uncinatus* Thell.
Amaranthus caracasanus Kunth	• *Amaranthus coracanus* Mart.
Amaranthus cardenasianus Hunz.	
Amaranthus caturus Roxb.	
Amaranthus caudatus L.	• *Amaranthus abyssinicus* L.H.Bailey • *Amaranthus alopecurus* Hochst. ex A.Br. & C.D.Bouché • *Amaranthus cararu* Moq. • *Amaranthus caudatus* var. *albiflorus* Moq. • *Amaranthus caudatus* var. *alopecurus* Moq. • *Amaranthus caudatus* subsp. *mantegazzianus* (Pass.) Hanelt • *Amaranthus caudatus* var. *maximus* (Mill.) Moq. • *Amaranthus caudatus* subsp. *saueri* V.Jehlík • *Amaranthus dussii* Sprenger • *Amaranthus edulis* Speg. • *Amaranthus edulis* var. *spadiceus* Hunz. • *Amaranthus hybridus* var. *leucocarpus* (S.Watson) Hunz. • *Amaranthus leucocarpus* S.Watson • *Amaranthus leucospermus* S.Watson • *Amaranthus mantegazzianus* Pass. • *Amaranthus maximus* Mill. • *Amaranthus pendulinus* Moq. • *Amaranthus pendulus* Moq. • *Euxolus arvensis* Rojas Acosta
Amaranthus celosioides Kunth	• *Amaranthus hybridus* var. *pergaminensis* Covas
Amaranthus centralis J.Palmer & Mowatt	
Amaranthus chihuahensis S.Watson	
Amaranthus clementii Domin	
Amaranthus cochleitepalus Domin	
Amaranthus commutatus A.Kern.	

Table 1 (continued)

Name	Synonyms
Amaranthus congestus C.C.Towns.	
Amaranthus crassipes Schltdl.	• *Amaranthus crassipes* var. *crassipes*
Amaranthus crassipes var. *warnockii* (I.M.Johnst.) Henrickson	• *Amaranthus warnockii* I.M.Johnst.
Amaranthus crispus (Lesp. & Thévenau) A.Terracc.	• *Albersia crispa* Asch. Ex Hausskn. • *Amaranthus cristulatus* Speg. • *Celosia crispus* Lesp. & Thev. • *Euxolus crispus* Lesp. & Thévenau
Amaranthus cruentus L.	• *Amaranthus anacardana* Hook.f. • *Amaranthus arardhanus* Sweet • *Amaranthus carneus* Moq. • *Amaranthus chlorostachys* Moq. • *Amaranthus esculentus* Besser ex Moq. • *Amaranthus farinaceous* Roxb. ex Moq. • *Amaranthus guadeloupensis* Voss • *Amaranthus guadelupensis* Moq. • *Amaranthus hybridus* subsp. *cruentus* (L.) Thell. • *Amaranthus hybridus* var. *paniculatus* (L.) Uline & W.L.Bray • *Amaranthus hybridus* var. *patulus* (Bertol.) Thell. • *Amaranthus hybridus* subsp. *patulus* (Bertol.) Carretero • *Amaranthus incarnates* Moq. • *Amaranthus montevidensis* Moq. • *Amaranthus paniculatus* L. • *Amaranthus paniculatus* var. *cruentus* (L.) Moq. • *Amaranthus paniculatus* var. *longispicatus* Moq. • *Amaranthus paniculatus* var. *monstrosus* Moq. • *Amaranthus paniculatus* var. *sanguineus* (L.) Moq. • *Amaranthus paniculatus* var. *speciosus* L.H.Bailey • *Amaranthus paniculatus* var. *strictus* (Willd.) Moq. • *Amaranthus purgans* Moq. • *Amaranthus rubescens* Moq. • *Amaranthus sanguineus* L. • *Amaranthus sanguinolentus* Schrad. Ex Moq. • *Amaranthus speciosus* Sims • *Amaranthus spicatus* Wirzén • *Amaranthus strictus* Willd. • *Amaranthus violaceus* Moq.
Amaranthus cuspidifolius Domin	
Amaranthus deflexus L.	• *Albersia deflexa* (L.) Fourr. • *Albersia prostrate* (Bastard) Kunth • *Amarantellus argentines* Speg. • *Amaranthus deflexus* var. *rufescens* (Godr.) Thell. • *Amaranthus deflexus* f. *rufescens* (Godr.) Thell. & Probst • *Amaranthus minor* (Moq.) Sennen • *Amaranthus perennis* Bellardi ex Colla

Table 1 (continued)

Name	Synonyms
	• *Amaranthus prostrates* Balb. • *Euxolus deflexus* var. *ascendens* Moq. • *Euxolus deflexus* var. *major* Moq. • *Euxolus deflexus* var. *minor* Moq. • *Euxolus deflexus* var. *rufescens* Godr. • *Galliaria prostrate* (Bastard) Bubani • *Glomeraria deflexa* (L.) Cav.
Amaranthus dinteri Schinz	• *Amaranthus dinteri* subsp. *brevipetiolatus* Brenan • *Amaranthus dinteri* subsp. *dinteri*
Amaranthus dubius Mart. ex Thell.	• *Amaranthus dubius* var. *flexuosus* Thell. • *Amaranthus dubius* var. *leptostachys* Thell. • *Amaranthus dubius* var. *xanthostachys* Thell. • *Amaranthus tristis* Willd. • *Amaranthus tristis* var. *flexuosus* Moq. • *Amaranthus tristis* var. *xanthostachys* Moq.
Amaranthus fimbriatus (Torr.) Benth.	• *Amblogyna fimbriata* (Torr.) A.Gray • *Sarratia berlandieri* var. *denticulate* Torr. • *Sarratia berlandieri* var. *fimbriata* Torr.
Amaranthus floridanus (S.Watson) Sauer	• *Acnida floridana* S.Watson
Amaranthus furcatus J.T.Howell	
Amaranthus globosa L.	
Amaranthus graecizans L.	• *Amaranthus angustifolius* Lam. • *Amaranthus angustifolius* M.Bieb. ex Willd. • *Amaranthus angustifolius* subsp. *aschersonianus* Thell. • *Amaranthus aschersonianus* (Thell.) Chiov. • *Amaranthus blitum* Moq. • *Amaranthus blitum* var. *graecizans* (L.) Moq. • *Amaranthus blitum* var. *nanus* Moq. • *Amaranthus graecizans* subsp. *aschersonianus* (Thell.) Costea, D.M. Brenner & Tardif • *Amaranthus graecizans* subsp. *graecizans* • *Amaranthus graecizans* var. *pachytepalus* Aellen • *Amaranthus graecizans* subsp. *thellungianus* (Nevski ex Vassilcz.) Gusev • *Amaranthus hierichuntinus* Vis. • *Amaranthus roxburgianus* var. *aschersonianus* (Thell.) N.C.Nair • *Amaranthus thellungianus* Nevski ex Vassilcz. • *Blitum graecizans* (L.) Moench • *Galliaria graecizans* (L.) Nieuwl. • *Glomeraria graecizans* (L.) Cav.
Amaranthus graecizans subsp. *silvestris* (Vill.) Brenan	• *Amaranthus angustifolius* var. *silvestris* (Villiers) Thell. • *Amaranthus angustifolius* subsp. *silvestris* (Vill.) Wacht. • *Amaranthus graecizans* var. *silvestris* (Vill.) Asch. & Schweinf. • *Amaranthus silvestris* Vill.
Amaranthus grandiflorus (J.M.Black) J.M.Black	

Table 1 (continued)

Name	Synonyms
	• *Amaranthus mitchellii* var. *grandiflorus* J.M.Black
Amaranthus greggii S.Watson	• *Amaranthus annectens* S.F.Blake • *Amaranthus greggii* var. *muelleri* Uline & W.L.Bray • *Amaranthus muelleri* (Uline & W.L.Bray) Kov. • *Amaranthus myrianthus* Standl.
Amaranthus haughtii Standl.	
Amaranthus hunzikeri N.Bayón	
Amaranthus hybridus L.	• *Amaranthus aureus* Moq. • *Amaranthus batalleri* Sennen • *Amaranthus bellardii* Moq. • *Amaranthus berchtholdii* Moq. • *Amaranthus catechu* Moq. • *Amaranthus chlorostachys* Willd. • *Amaranthus chlorostachys* var. *hybridus* (L.) S.Watson • *Amaranthus cruentus* var. *patulus* (Bertol.) Lambinon • *Amaranthus eugenii* Sennen • *Amaranthus flavescens* Moq. • *Amaranthus hecticus* Willd. • *Amaranthus hybridus* f. *aciculatus* Thell. • *Amaranthus hybridus* var. *batalleri* (Sennen) Carretero • *Amaranthus hybridus* var. *bellardii* Moq. • *Amaranthus hybridus* var. *chlorostachys* (Willd.) Beck • *Amaranthus hybridus* var. *chlorostachys* (Willd.) Thell. • *Amaranthus hybridus* var. *densus* Farw. • *Amaranthus hybridus* var. *hecticus* (Willd.) Moq. • *Amaranthus hybridus* subsp. *hybridus* • *Amaranthus hybridus* var. *hybridus* • *Amaranthus hybridus* subsp. *incurvatus* (Trimen ex Gren. & Gord.) Brenan • *Amaranthus hybridus* var. *laetus* (Willd.) Moq. • *Amaranthus hybridus* var. *prostratus* Moq. • *Amaranthus hybridus* var. *rubricaulis* Moq. • *Amaranthus hybridus* var. *sanguineus* (L.) Farw. • *Amaranthus incurvatus* Trimen ex Gren. & Gord. • *Amaranthus intermedius* Guss. ex Moq. • *Amaranthus laetus* Willd. • *Amaranthus laxiflorus* Comelli ex Pollini • *Amaranthus neglectus* Moq. • *Amaranthus nepalensis* Moq. • *Amaranthus paniculatus* var. *sanguineus* Regel • *Amaranthus patulus* Bertol. • *Amaranthus patulus* f. *multispiculatus* (Sennen) Priszter • *Amaranthus patulus* var. *multispiculatus* Sennen • *Amaranthus pseudoretroflexus* (Thell.) Almq.

Table 1 (continued)

Name	Synonyms
	• *Amaranthus retroflexus* var. *chlorostachys* (Willd.) A.Gray • *Amaranthus retroflexus* var. *hybridus* (L.) A.Gray • *Amaranthus spicatus* Rchb. • *Amaranthus timeroyi* Jord. Ex Moq. • *Amaranthus trivialis* Rota • *Galliaria hybrida* (L.) Nieuwl. • *Galliaria patula* Bubani
Amaranthus hybridus subsp. *quitensis* (Kunth) Costea & Carretero	• *Amaranthus hybridus* var. *quitensis* (Kunth) Covas • *Amaranthus quitensis* Kunth • *Amaranthus quitensis* f. *rufescens* Thell. • *Amaranthus quitensis* var. *stuckertianus* Thell. • *Amaranthus retroflexus* subsp. *quitensis* (Kunth) O.Bolòs & Vigo
Amaranthus hypochondriacus L.	• *Amaranthus anardana* Buch.Ham. ex Moq. • *Amaranthus atrosanguineus* Moq. • *Amaranthus aureus* Besser • *Amaranthus bernhardii* Moq. • *Amaranthus flavus* L. • *Amaranthus frumentaceus* Buch.Ham. ex Roxb. • *Amaranthus hybridus* Vell. • *Amaranthus hybridus* var. *erythrostachys* Moq. • *Amaranthus hybridus* f. *hypochondiacus* (L.) B.L. Rob. • *Amaranthus hybridus* f. *hypochondriacus* (L.) H.Rob. • *Amaranthus hybridus* var. *hypochondriacus* (L.) H.Rob. • *Amaranthus hybridus* subsp. *hypochondriacus* (L.) Thell. • *Amaranthus hypochondriacus* var. *macrostachys* Moq. • *Amaranthus hypochondriacus* var. *monstrosus* Moq. • *Amaranthus hypochondriacus* var. *racemosus* Moq. • *Amaranthus hypochondriacus* var. *tortuosus* Moq. • *Amaranthus macrostachyus* Mérat ex Moq. • *Amaranthus monstrosus* Moq.
Amaranthus hypochondriacus var. *powellii* (S.Watson) Pedersen	• *Amaranthus hybridus* subsp. *powellii* (S.Watson) Karlsson • *Amaranthus obovatus* S.Watson
Amaranthus induratus C.A.Gardner ex J.Palmer & Mowatt	
Amaranthus interruptus R.Br.	• *Amaranthus lancifolius* Delile ex Moq. • *Amaranthus lineatus* R.Br. • *Amaranthus rhombeus* R.Br. • *Amaranthus spathulatus* Desf. Ex Moq. • *Amaranthus undulates* R.Br.
Amaranthus kloosianus Hunz.	

Table 1 (continued)

Name	Synonyms
Amaranthus leptostachyus Benth.	
Amaranthus lepturus S.F.Blake	
Amaranthus lombardoi Hunz.	
Amaranthus looseri Suess.	
Amaranthus macrocarpus Benth.	• *Amaranthus macrocarpus* var. *pallidus* Benth.
Amaranthus minimus Standl.	• *Goerziella minima* (Standl.) Urb.
Amaranthus mitchellii Benth.	• *Amaranthus mitchellii* var. *strictifolius* Domin
Amaranthus muricatus (Gillies ex Moq.) Hieron.	• *Euxolus muricatus* Gillies ex Moq.
Amaranthus × *ozanonii* Piszter	• *Amaranthus* × *ralletii* Contré
Amaranthus pallidiflorus F.Muell.	• *Amaranthus pallidiflorus* var. *viridiflorus* Thell.
Amaranthus palmeri S.Watson	• *Amaranthus palmeri* var. *glomeratus* Uline & W.L.Bray
Amaranthus paolii Chiov.	
Amaranthus paraguayensis Parodi	
Amaranthus parvulus Peter	
Amaranthus persimilis Hunz.	
Amaranthus peruvianus (Schauer) Standl.	• *Mengea peruviana* Schauer
Amaranthus polygamus L.	• *Albersia polygama* Boiss. • *Amaranthus angustifolius* subsp. *polygonoides* Maire & Weiller • *Amaranthus polygonoides* Roxb. • *Amaranthus roxburgianus* Nevski • *Amaranthus roxburgianus* var. *angustifolius* (Moq.) N.C.Nair • *Amaranthus tenuifolius* Wall.
Amaranthus polygonoides L.	• *Albersia polygonoides* (L.) Kunth • *Amaranthus berlandieri* (Moq.) Uline & W.L.Bray • *Amaranthus polygonoides* subsp. *berlandieri* (Moq.) Thell. • *Amaranthus taishanensis* F.Z.Li & C.K.Ni • *Amaranthus verticillatus* Pav. ex Moq. • *Amblogyna polygonoides* (L.) Raf. • *Euxolus polygonoides* Nakai • *Glomeraria polygonoides* (L.) Cav. • *Roemeria polygonoides* (L.) Moench • *Sarratia berlandieri* Moq. • *Sarratia polygonoides* (L.) Moq.
Amaranthus polystachyus Willd.	• *Albersia polystachya* Kunth
Amaranthus powellii S.Watson	• *Amaranthus chlorostachys* var. *powellii* (S.Watson) Priszter • *Amaranthus chlorostachys* var. *pseudoretroflexus* Thell. • *Amaranthus hybridus* f. *pseudoretroflexus* (Thell.) Thell. • *Amaranthus hybridus* var. *pseudoretroflexus* (Thell.) Carretero • *Amaranthus retroflexus* var. *powellii* (S.Watson) B.Boivin

Table 1 (continued)

Name	Synonyms
	• *Amaranthus retroflexus* var. *pseudoretroflexus* (Thell.) B.Boivin
Amaranthus powellii subsp. *bouchonii* (Thell.) Costea & Carretero	• *Amaranthus bouchonii* Thell. • *Amaranthus hybridus* subsp. *bouchonii* (Thell.) O.Bolòs & Vigo
Amaranthus praetermissus Brenan	
Amaranthus pringlei S.Watson	
Amaranthus pumilus Raf.	
Amaranthus retroflexus L.	• *Amaranthus bulgaricus* Kov. • *Amaranthus bullatus* Besser ex Spreng. • *Amaranthus chlorostachys* Willk. • *Amaranthus curvifolius* Spreng. • *Amaranthus delilei* Richt. & Loret • *Amaranthus johnstonii* Kov. • *Amaranthus recurvatus* Desf. • *Amaranthus retroflexus* var. *delilei* (Richt. & Loret) Thell. • *Amaranthus retroflexus* subsp. *delilei* (Richt. & Loret) Tzvelev • *Amaranthus retroflexus* var. *retroflexus* • *Amaranthus retroflexus* var. *rubricaulis* Thell. • *Amaranthus retroflexus* f. *rubricaulis* Thell. Ex Probst • *Amaranthus retroflexus* var. *salicifolius* I.M.Johnst. • *Amaranthus rigidus* Schult. Ex Steud. • *Amaranthus spicatus* Lam. • *Amaranthus strictus* Ten. • *Galliaria retroflexa* (L.) Nieuwl. • *Galliaria scabra* Bubani
Amaranthus rosengurttii Hunz.	
Amaranthus roxburghianus H.W.Kung	• *Amaranthus blitum* var. *angustifolius* Moq.
Amaranthus scandens L.f.	
Amaranthus scariosus Benth.	• *Amaranthus floridus* Benth. • *Amblogyna scariosa* (Benth.) A.Gray • *Sarratia scariosa* (Benth.) Moq.
Amaranthus schinzianus Thell.	
Amaranthus scleranthoides (Andersson) Andersson	• *Amaranthus scleranthoides* f. *abingdonensis* A.Stewart • *Amaranthus scleranthoides* f. *albemarlensis* A.Stewart • *Amaranthus scleranthoides* f. *chathamensis* B.L.Rob. & Greenm. • *Amaranthus sclerantoides* f. *abingdonensis* Stewart • *Amaranthus sclerantoides* f. *hoodensis* B.L. Rob. & Greenm. • *Amaranthus sclerantoides* f. *rugulosus* Howell • *Euxolus scleranthoides* Andersson
Amaranthus scleropoides Uline & W.L.Bray	• *Amaranthus blitoides* var. *scleropoides* (Uline & W.L.Bray) Thell.

Table 1 (continued)

Name	Synonyms
	• *Amaranthus blitoides* f. *scleropoides* (Uline & W.L.Bray) Thell. Ex Probst
Amaranthus × *sopronìensis* Priszter & Kárpáti	
Amaranthus sparganicephalus Thell.	
Amaranthus spinosus L.	• *Amaranthus spinosus* var. *basiscissus* Thell. • *Amaranthus spinosus* var. *circumscissus* Thell. • *Amaranthus spinosus* var. *indehiscens* Thell. • *Amaranthus spinosus* f. *inermis* Lauterb. & K.Schum. • *Amaranthus spinosus* var. *purpurascens* Moq. • *Amaranthus spinosus* var. *pygmaeus* Hassk. • *Amaranthus spinosus* var. *rubricaulis* Hassk. • *Amaranthus spinosus* var. *viridicaulis* Hassk. • *Galliaria spitosa* (L.) Nieuwl.
Amaranthus squamulatus (Andersson) B.L.Rob.	• *Amaranthus squarrulosus* (Andersson) Uline & W.L.Bray • *Scleropus squamulatus* Andersson
Amaranthus standleyanus Parodi ex Covas	• *Amaranthus parodii* Standl. • *Amaranthus vulgatissimus* var. *sublanceolatus* Thell.
Amaranthus tamariscinus Nutt.	• *Acnida tamariscina* (Nutt.) Alph.Wood
Amaranthus tamaulipensis Henrickson	
Amaranthus tenuifolius Willd.	• *Mengea tenuifolia* Moq.
Amaranthus × *texensis* Henrickson	
Amaranthus thellungianus Nevski	
Amaranthus thunbergii Moq.	• *Amaranthus albus* Thunb.
Amaranthus tricolor L.	• *Amaranthus amboinicus* Buch.Ham. ex Wall. • *Amaranthus bicolor* Nocca ex Willd. • *Amaranthus cuspidatus* Vis. • *Amaranthus dubius* Mart. • *Amaranthus flexuosus* Moq. • *Amaranthus gangeticus* L. • *Amaranthus gangeticus* var. *angustior* L.H.Bailey • *Amaranthus gangeticus* var. *angustior* Bailey • *Amaranthus inamoenus* Willd. • *Amaranthus incomptus* Willd. • *Amaranthus japonicas* Houtt. Ex Willd. • *Amaranthus japonicas* Houtt. Ex Steud. • *Amaranthus lanceolatus* Roxb. • *Amaranthus lancifolius* Roxb. • *Amaranthus lividus* Roxb. • *Amaranthus mangostanus* L. • *Amaranthus mangostanus* Blanco • *Amaranthus melancholicus* L. • *Amaranthus melancholicus* var. *obovatus* Moq. • *Amaranthus melancholicus* var. *parvifolius* Moq. • *Amaranthus melancholicus* var. *tricolor* (L.) Lam. ex Moq. • *Amaranthus mucronatus* Hook.f.

Table 1 (continued)

Name	Synonyms
	• *Amaranthus oleraceus* Roxb. • *Amaranthus polygamus* Roxb. • *Amaranthus polygamus* Thwaites • *Amaranthus rotundifolius* Moq. • *Amaranthus salicifolius* H.J.Veitch • *Amaranthus tricolor* var. *gangeticus* (L.) Fiori • *Amaranthus tricolor* var. *mangostanus* (L.) Aellen • *Amaranthus tricolor* var. *melancholicus* (L.) Lam. • *Amaranthus tricolor* var. *tristis* (Willd.) Mehrotra, Aswal & Bisht • *Amaranthus tricolor* var. *tristis* (L.) Thell. • *Amaranthus tristis* L. • *Amaranthus tristis* Wall. • *Amaranthus tristis* var. *leptostachys* Moq. • *Blitum gangeticum* Moench • *Blitum melancholicum* Moench • *Glomeraria bicolor* Cav. Ex Moq. • *Glomeraria tricolor* (L.) Cav. • *Pyxidium gangeticum* Moq. • *Pyxidium melancholicum* Moq.
Amaranthus tuberculatus (Moq.) Sauer	• *Acnida altissima* Moq. • *Acnida altissima* var. *prostrate* (Uline & W.L.Bray) Fernald • *Acnida altissima* var. *subnuda* (S.Watson ex A.Gray) Fernald • *Acnida cannabina* var. *prostrate* (Uline & W.L. Bray) Fernald • *Acnida cannabina* var. *subnuda* (S. Watson) Fernald • *Acnida concatenate* (Moq.) Small • *Acnida subnuda* (S.Watson) Standl. • *Acnida tamariscina* var. *concatenate* (Moq.) Uline & W.L.Bray • *Acnida tamariscina* var. *prostrate* Uline & W.L.Bray • *Acnida tamariscina* var. *subnuda* (S.Watson) J.M.Coult. • *Acnida tamariscina* var. *tuberculata* (Moq.) Uline & W.L.Bray • *Acnida tuberculata* Moq. • *Acnida tuberculata* var. *prostrate* (Uline & W.L.Bray) Lunell • *Acnida tuberculata* var. *prostrate* (Uline & W.L. Bray) B.L. Rob. • *Acnida tuberculata* var. *subnuda* S.Watson • *Amaranthus altissimus* Riddell • *Amaranthus ambigens* Standl. • *Amaranthus cannabinus* var. *concatenates* Moq. • *Amaranthus miamiensis* Riddell • *Amaranthus rudis* J.D.Sauer • *Amaranthus tuberculatus* var. *prostrates* (Uline & W.L.Bray) Mohlenbr.

Table 1 (continued)

Name	Synonyms
	• *Amaranthus tuberculatus* var. *rudis* (J.D.Sauer) Costea & Tardif • *Amaranthus tuberculatus* var. *subnudus* (S.Watson) Mohlenbr. • *Montelia tamariscina* (Nutt.) A. Gray • *Montelia tamariscina* var. *concatenate* (Moq.) A. Gray
Amaranthus tucsonensis Henrickson	
Amaranthus urceolatus Benth.	• *Amaranthus jonesii* (Uline & W.L.Bray) Kov. • *Amaranthus urceolatus* var. *jonesii* Uline & W.L.Bray • *Amaranthus urceolatus* var. *obcordatus* Uline & W.L.Bray • *Amblogyna urceolata* (Benth.) Andersson • *Amblogyna urceolata* (Benth.) A.Gray • *Amblogyna urceolata* var. *obcordata* A.Gray • *Euphorbia gracilis* Pav.ex Moq. • *Sarratia urceolata* Moq.
Amaranthus venulosus S.Watson	• *Amaranthus fimbriatus* var. *denticulatus* Uline & W.L.Bray
Amaranthus viridis L.	• *Albersia caudate* (Jacq.) Boiss. • *Albersia gracilis* (Desf.) Webb & Berthel. • *Amaranthus acutilobus* Uline & W.L.Bray • *Amaranthus fasciatus* Roxb. • *Amaranthus gracilis* Desf. • *Amaranthus littoralis* Bernh. Ex Moq. • *Amaranthus polystachyus* Buch.Ham. ex Wall. • *Chenopodium caudatum* Jacq. • *Euxolus caudatus* (Jacq.) Moq. • *Euxolus caudatus* var. *gracilis* Moq. • *Euxolus caudatus* var. *maximus* Moq. • *Galliaria adscendens* Bubani • *Glomeraria viridis* (L.) Cav. • *Pyxidium viride* (L.) Moq.
Amaranthus vulgatissimus Speg.	• *Amaranthus ataco* Thell.
Amaranthus watsonii Standl.	• *Amaranthus torreyi* (A.Gray) Benth. ex S.Watson • *Amaranthus torreyi* f. *prostrates* Farw. • *Amaranthus torreyi* var. *suffruticosus* Uline & W.L.Bray • *Amblogyna torreyi* A.Gray
Amaranthus wrightii S.Watson	

Source: http://www.theplantlist.org/browse/A/Amaranthaceae/Amaranthus/ (Accessed on November 20, 2016)

Table 2 Chromosome number(s) of various *Amaranthus* species

Amaranthus species	Chromosome number	Ploidy	Reference
A. albus	32 34	Diploid	Heiser and Whitaker (1948) Grant (1959b) Sharma and Banik (1965) Mulligan (1984) Song et al. (2002)
A. arenicola	32	Diploid	Grant (1959b)
A. asplundii	34	Diploid	Grant (1959b)
A. atropurpureus	34	Diploid	Sharma and Banik (1965)
A. aureus	32 34	Diploid	Grant (1959b) Milan (2008)
A. australis	32	Diploid	Murray (1940) Grant (1959b)
A. blitoides	32	Diploid	Song et al. (2002) Sheidai and Mohammadzadeh (2008)
A. blitum	28 34	Diploid	Takagi (1933) Murray (1940) Grant (1959b) Pal et al. (2000) Srivastava and Roy (2012)
A. caturus	64	Tetraploid	Behera and Patnaik (1974)
A. caudatus	30 32 34	Diploid	Takagi (1933) Grant (1959b) Behera and Patnaik (1974) National Research Council (1989) Greizerstein and Poggio (1995) Song et al. (2002) Ramesh and Kumar (2009) Bonasora et al. (2013)
A. crispus	34	Diploid	Grant (1959b)
A. cruentus	32 34	Diploid	Takagi (1933) Grant (1959b) National Research Council (1989) Greizerstein and Poggio (1995) Song et al. (2002) Lanta et al. (2003) Milan (2008) Ramesh and Kumar (2009) Bonasora et al. (2013)
A. deflexus	34	Diploid	Grant (1959b)
A. dubius	64	Tetraploid	Grant (1959a) Pal (1971) Madhusoodanan and Nazeer (1983) Greizerstein and Poggio (1992) Greizerstein et al. (1997)
A. fimbriatus	34	Diploid	Ward and Spellenberg (1986)
A. graecizans	32 34	Diploid	Heiser and Whitaker (1948) Grant (1959b) Pal (1972)
A. hybridus	32 34	Diploid	Covas and Schnack (1946) Grant (1959b) Behera and Patnaik (1974) Weaver and McWilliams (1980) Pal et al. (1982) National Research Council (1989)

Table 2 (continued)

Amaranthus species	Chromosome number	Ploidy	Reference
			Song et al. (2002) Ramesh and Kumar (2009)
A. hypochondriacus	32 34	Diploid	Grant (1959b) Pal and Khoshoo (1974) Pal et al. (1982) National Research Council (1989) Greizerstein and Poggio (1995) Song et al. (2002) Milan (2008) Ramesh and Kumar (2009) Bonasora et al. (2013)
A. mangostanus	32 34	Diploid	Takagi (1933) Behera and Patnaik (1974)
A. muricatus	34	Diploid	Covas and Hunziker (1954)
A. palmeri	32 34	Diploid	Heiser and Whitaker (1948) Grant (1959a) Grant (1959b) Pal et al. (1982) Mulligan (1984) Rayburn et al. (2005) Gaines et al. (2012)
A. polygonoides	32 34	Diploid	Song et al. (2002)
A. powellii	32 34	Diploid	Murray (1940) Grant (1959b) Pal and Khoshoo (1974) Weaver and McWilliams (1980)
A. retroflexus	32 34	Diploid	Murray (1940) Heiser and Whitaker (1948) Grant (1959b) Weaver and McWilliams (1980) Mulligan (1984) Song et al. (2002) Lanta et al. (2003)
A. roxburghianus	34	Diploid	Song et al. (2002)
A. spinosus	n = 17		Koul et al. 1976 Behera and Patnaik 1977 Behera and Patnik 1982
	34	Diploid	Takagi (1933) Murray (1940) Grant (1959b) Behera and Patnaik (1974) Baquar and Olusi (1988) Greizerstein and Poggio (1995) Al-Turki et al. (2000) Song et al. (2002) Rayburn et al. (2005) Srivastava and Roy (2012)
A. standleyanus	34	Diploid	Grant (1959b) Covas and Hunziker (1954)
A. tamariscinus	32	Diploid	Grant (1959b)
A. tenuifolius	28	Diploid	Pal et al. (2000)
A. tricolor	34	Diploid	Takagi (1933) Grant (1959b) Sharma and Banik (1965)

Table 2 (continued)

Amaranthus species	Chromosome number	Ploidy	Reference
			Behera and Patnaik (1974) Madhusoodanan and Nazeer (1983) Song et al. (2002) Srivastava and Roy (2012)
A. tuberculatus	32	Diploid	Murray (1940) Grant (1959b) Wetzel et al. (1999b) Franssen et al. (2001b) Steinau et al. (2003) Trucco et al. (2007)
A. viridis	32 34	Diploid	Covas and Hunziker (1954) Grant (1959b) Sharma and Banik (1965) Behera and Patnaik (1974) Madhusoodanan and Nazeer (1983) Greizerstein and Poggio (1995) Song et al. (2002)

Table 3 Effect of temperature on seed germination of *Amaranthus* species

Parameters	*Amaranthus* species	Results (Optimum germination)	Reference
Effect of temperature	*A. blitum*	35 °C	Teitz et al. (1990)
	A. caudatus	35 °C	Gutterman et al. (1992) Kępczyński and Bihun (2002)
	A. cruentus	30 to 35 °C	Oladiran and Mumford (1985)
	A. gangeticus	30 to 35 °C	Oladiran and Mumford (1985)
	A. hybridus	32 to 34 °C	Washitani and Takenaka (1984) Oladiran and Mumford (1985)
	A. palmeri	25 to 40 °C	Wright et al. (1999) Guo and Al-Khatib (2003) Jha et al. (2008c) Jha et al. (2010)
	A. paniculatus	30 to 35 °C	Oladiran and Mumford (1985)
	A. retroflexus	25 to 40 °C	Evans (1922) McWilliams et al. (1968) Baskin and Baskin (1977) Habib and Morton (1987) Kępczyński et al. (1996) Ghorbani et al. (1999) Guo and Al-Khatib (2003)
	A. rudis	25 to 40 °C	Guo and Al-Khatib (2003)
	A. spinosus	30 to 35 °C	Steckel et al. (2004) Chauhan and Johnson (2009)
	A. viridis	30 °C	Thomas et al. (2006) Chauhan and Johnson (2009)

Table 4 Effect of various environmental parameters on seed germination of *Amaranthus* species

Parameters	*Amaranthus* species	Results (Optimum germination)	Reference
Effect of seed burial depth	*A. albus*	1.9 cm	Santelmann and Evetts (1971)
	A. graecizans *A. hybridus* *A. palmeri*		
	A. retroflexus	0.5 cm to 4 cm	Wiese and Davis (1967) Baskin and Baskin (1977) Ghorbani et al. (1999) Omami et al. (1999) Benvenuti et al. (2001)
	A. spinosus	0.5 to 2 cm	Santelmann and Evetts (1971) Chauhan and Johnson (2009)
	A. viridis	0.5 to 2 cm	Thomas et al. (2006) Chauhan and Johnson (2009)
Effect of duration of seed burial	*A. palmeri*	peak germination occurred after 9 months of burial	Jha et al. (2010)
	A. patulus	remain viable upto 3 years	Washitani (1985)
	A. retroflexus	peak germination occurred after 9 months of burial	Baskin and Baskin (1985b) Baskin and Baskin (1998) Omami et al. (1999)
	A. retroflexus	remain viable for 6–10 years	Chepil (1946) Burnside et al. (1981) Burnside et al. (1996)
	A. retroflexus	germinated even after 40 years of burial	Telewski and Zeevaart (2002)

Table 5 Allelopathic effect of *Amaranthus* species on other plants

Amaranthus Species	Allelopathic effect against	Effect	Reference
A. blitoides *A. gracilis*	*Triticum aestivum*	• Reduced germination, coleoptile length, root length, root dry weight, plant height, grain and straw yield.	Qasem (1995b)
A. hybridus	*Phaseolus* spp.	• Negative effect on total chlorophyll content, number of developed leaves, stem length, and total plant dry matter.	Amini et al. (2013)
A. palmeri	*A. palmeri* seeds	• Inhibit growth and seed germination.	Altieri and Doll (1978)
	Allium cepa *Brassica oleracea* var. Capitata		Bradow and Connick (1987) Connick et al. (1987) Menges (1987)

Table 5 (continued)

Amaranthus Species	Allelopathic effect against	Effect	Reference
	Daucus carrota *Lycopersicon lycopersici* *Sorghum bicolour*		Menges (1988)
A. retroflexus	*Beta vulgaris* *Brassica oleracea* var. *brotrytis* *Capsicum annuum* *Cucumis sativus* *Cucurbita ovifera* *Daucus carota* *Helianthus annus* *Lycopersicon lycopersici* *Solanum melongena*	• Decrease chlorophyll content. • Decrease nitrogen fixation of nodules. • Decrease respiration. • Decrease RGR, NAR and FWR. • Inhibit radicle and hypocotyl elongation. • Interfere in photosynthesis. • Reduce coleoptile length, root length, root dry weight, plant height, grain and straw yield. • Reduce germination, nutrient uptake, growth and yield.	Bhowmik and Doll (1980) Qasem (1995a) Alam et al. (2001) Souza et al. (2011)
	Carthamus tinctorius		Williams et al. (2005) Rezaie and Yarnia (2009)
	Glycine max		Bhowmik and Doll (1982) Bhowmik and Doll (1984) Chaniago et al. (2006)
	Gossypium hirsutum		Munger et al. (1983)
	Hordeum vulgare		Lolas (1981) Lolas (1986) Qasem (1994)
	Lactuca sativa		Dos Santos et al. (2004)
	Nicotiana tabacum		Lolas (1981) Lolas (1986)
	Phaseolus vulgaris		Aguyoh and Masiunas (2003)
	Sorghum bicolour		Bhowmik and Doll (1983)
	Triticum aestivum		Qasem (1995b) Shahrokhi et al. (2012)
	Zea mays		Bhowmik and Doll (1982) Bhowmik and Doll (1984)
A. spinosus	Cultures	• Negative impact on growth. • Reduce time duration of vegetative and reproductive phases.	Suma (1998)
	Lactuca sativa		Shrefler et al. (1996)
	Parthenium hysterophorus		Chikkalingaiah and Mahadevappa (1998)
	Sinapis alba *Triticum aestivum*		Datta and Bandyopadhayay (1981)
A. viridis	*Pennisetum americanum*	• Decrease growth and productivity	Singhal and Sen (1981)

Web-Links

http://www.theplantlist.org/1.1/browse/A/Amaranthaceae/*Amaranthus*/ (Accessed on November 20, 2016).