CHAPTER 13

WEED GERMINATION, SEEDLING GROWTH AND THEIR LESSON FOR ALLELOPATHY IN AGRICULTURE

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INTRODUCTION

The question of paradigm in the science of allelopathy is under discussion in the latest years (Reigosa et al. 1999; Inderjit, 2002; Mallik, 2002). Although it is well known that the plant physiologist Hans Molisch in 1937 coined the term allelopathy, the actual subject of his work has been negleted. Indeed, he was caught by an horticultural problem: the induction of ripening by early-ripening apples and pears on fruits from late-ripening varieties when stored together. Molisch demonstrated that the substance responsible for ripening induction was ethylene. He also demonstrated that root growth of vetch (*Vicia sativa* L.) and pea (*Pisum sativum* L.) seedlings is inhibited when seeds were germinated under a jar together with some apples. Molisch in his book reported: *The described phenomenon that one plant can influence another, play an important role in physiology, so it deserves an appropriate term. For this I coin the word allelopathy from the Greek words "allelon", meaning mutual and pathos, meaning harm or "affection". The shorter word allopathie is appropriate too but it is already present in literature as opposite of homeopathy* (Molisch, 1937).

Successively, Molisch's definition was adopted in a broader view by the botanist Elroy Rice who was encouraged by some studies that demonstrated the role of allelopathy in the field. Rice formal definition of the term was: *any direct or indirect harmful or beneficial effect by one plant (including microorganisms) on a another through production of chemical compounds that escape into the environment* (Rice, 1984). This shift of paradigm implies a growing complexity to ascertain an allelopathic

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phenomenon in the ecosystems where a dynamic web of surprising interelationships among organisms exists at all scales. Indeed, the term allelopathy is perceived differently by researchers of different specializations and his differences in worldview has created much confusion. For example, an ecologist's perspective of allelopathy is quite different from that of natural product chemist, biochemist, plant physiologist, agronomist, weed scientist, microbiologist, and experimental botanist (Mallik, 2002). Unfortunately only rarely have these varied professional talents been assembled in experimental programmes. By way conclusive proofs of allelopathy in the field remain few, and use af field relevant bioassay has been regularly called for (Inderjit, 2002).

Seed germination is the most widely used bioassay in allelopathy and the literature pertaining to the use of this bioassay and its general suitability for the determination of allelopathic activity among species has been reviewed by Leather and Einhellig (1986), Inderjit (1995) and Romeo and Weidenhamer (1988). These authors pointed out that there is little standardization governing seed germination bioassays. Most research is centered on a few plants, especially agricultural seeds to discover biochemical and physiological aspects of seed germination. This raises the question as to what extent do the results obtained in the lab with these seeds which have been subjected to man's selection can be extrapolated to the wild plants in the field.

This chapter reviews the biological characteristics and germination responses of three major weeds: Purslane (*Portulaca oleracea* L.), Lambsquarter (*Chenopodium album* L.) and Redroot pigweed (*Amaranthus retroflexus* L.), with a focus on how their reproductive strategies indicate a vulnerability to allelopathic control. We have also included some unpublished data obtained in our lab.

WEEDS FROM A BOTANICAL PERSPECTIVE

Weed species may be defined as those plants "out of place" from an anthropocentric point of view. A fundamental basis for sound weed management in agriculture is to know:

a) the species present and the level of infestation;
b) biology and ecology of the prevalent species;
c) interference of the prevalent weed species;
d) technically effective, economically viable and environmentally safe methods of control (Labrada and Parker, 1994).

Table 1 lists 14 species considered as the most serious weeds from a worldwide perspective on the basis of their distribution and prevalence in crops. It is difficult to classify weeds on a narrow set of botanical (e.g., morphological, phenological or taxonomic) criteria. However, a look at the table with taxonomic and ethnographic evidence shows that important weeds and crops are closely related and took origin from a common ancestor (i.e., *Avena fatua* and *A. sativa*; *Sorghum halepense* and *S. vulgare*). Moreover, some weed seeds such as Barnyard grass, Goosegrass, Lambsquarter, and Redroot pigweed were important sources of food in the past (Harlan, 1992). Most of monocot crops and weeds are Gramineae therophytes whose seeds are the only overwintering living structures. The two worst weeds Purple nutsedge and Bermuda grass are geophytes. Finally, dicot weeds such as Purslane, Lambsquarter, and Redroot pigweed are taxonomically related belonging to the same order of Centrospermae.

REPRODUCTIVE STRATEGIES OF THREE MAJOR WEEDS: Purslane (*Portulaca oleracea* L.), Lambsquarter (*Chenopodium album* L.) and Redroot pigweed (*Amaranthus retroflexus* L.)

Seed dispersal and seed germination are critical phases in the life-cicle of the plant, during these phases the forces of natural selection have a maximum opportunity to exert their influence. These clues will be evaluated into three annual weeds: purslane, lambsquarter and redroot pigweed.

Portulaca oleracea L

Purslane is a succulent herb with stems that may grow erect or prostrate, depending on light conditions. It is one of the weeds which have been most successful in colonizing arable lands worldwide (Allard, 1965). The plant is a major obnoxious weed of 45 crops in 81 countries and the ploughable layer of the soil cropped with maize contains about 220.000 purslane seed per m^2. Purslane fruit is a capsule apparently simple structured with a pyxidium and a caliptra. Indeed, its inner structure reveals the contrivance of the plant in order to reach an effective seed dispersal, which contribute to its weediness in arable lands. Figure 1 shows the morpho-functional aspects of the purslane fruit. The ovaric cavity is divided in two chambers, the lower one is wide, dehiscent and contains numerous seeds (50-70). The upper chamber is tiny, globous, and contains few seeds. During ripening this tiny chamber is included in the nipple-shaped operculum of the capsule, by means of a tight narrowing across the ovaric apex. The capsule is circumscissed in hot days when the operculum falls, retaining inside 2-4 seeds, along with the calyx, dried petals, stamen and styles (together called “the caliptra”). Moreover, the withering petals, stamens and styles produce a glue-like substance turning the operculum into a fruit absolutely indehiscent.

Table 1. The Worst Weeds of the World (from Holm et al. 1977, modified)

Rank	Species	Taxa and Biological Form
1	*Cyperus rotundus* L. (Purple nutsedge)	Monocot., Cyperales, Cyperaceae, Geophyte
2	*Cynodon dactylon* (L.) Pers. (Bermuda grass)	Monocot., Graminales, Gramineae, Geophyte
3	*Echinochloa crus-galli* (L.) Beauv. (Barnyard grass)	Monocot., Graminales, Gramineae- Therophyte
4	*Echinochloa colonum* (L.) Link. (Jungle rice)	Monocot., Graminales, Gramineae, Therophyte
5	*Eleusine indica* (L.) Gaertner (Goosegrass)	Monocot., Graminales, Gramineae, Therophyte
6	*Eichhornia crassipes* (Mart.) Solms. (Water hyacinth)	Monocot., Liliiflorae, Pontederiaceae, Hydrophyte
7	*Portulaca oleracea* L. (Purslane)	Dicot., Centrospermae, Portulacaceae, Therophyte
8	*Chenopodium album* L. (Lambsquarter)	Dicot., Centrospermae, Chenopodiaceae, Therophyte
9	*Digitaria sanguinalis* (L.) Scop. (Crabgrass)	Monocot., Graminales, Gramineae, Therophyte
10	*Convolvulus arvensis* L. (Field bindweed)	Dicot., Tubiflorae, Convolvulaceae, Hemicryptophyte
11	*Sorghum halepense* (L.) Pers. (Johnson grass)	Monocot., Graminales, Gramineae, Geophyte
12	*Imperata cylindrica* (L.) Beauv. (Cogon grass)	Monocot., Graminales, Gramineae, Geophyte
13	*Avena fatua* L. (Wild oat)	Monocot., Graminales, Gramineae, Therophyte
14	*Amaranthus retroflexus* L. (Redroot pigweed)	Dicot., Centrospermae, Amaranthaceae, Therophyte

Legend: Geophyte: a perennial plant that is deeply embedded in the soil substrate.
Hemicryptophyte: a plant having buds at the soil surface and protected by scales, snow, or litter.
Hydrophyte: aquatic plant, floating or rooting in the mud.
Therophyte: an annual plant whose seed is the only overwintering structure.

This phenomenon was discovered by the Italian botanist Federico Delpino, who

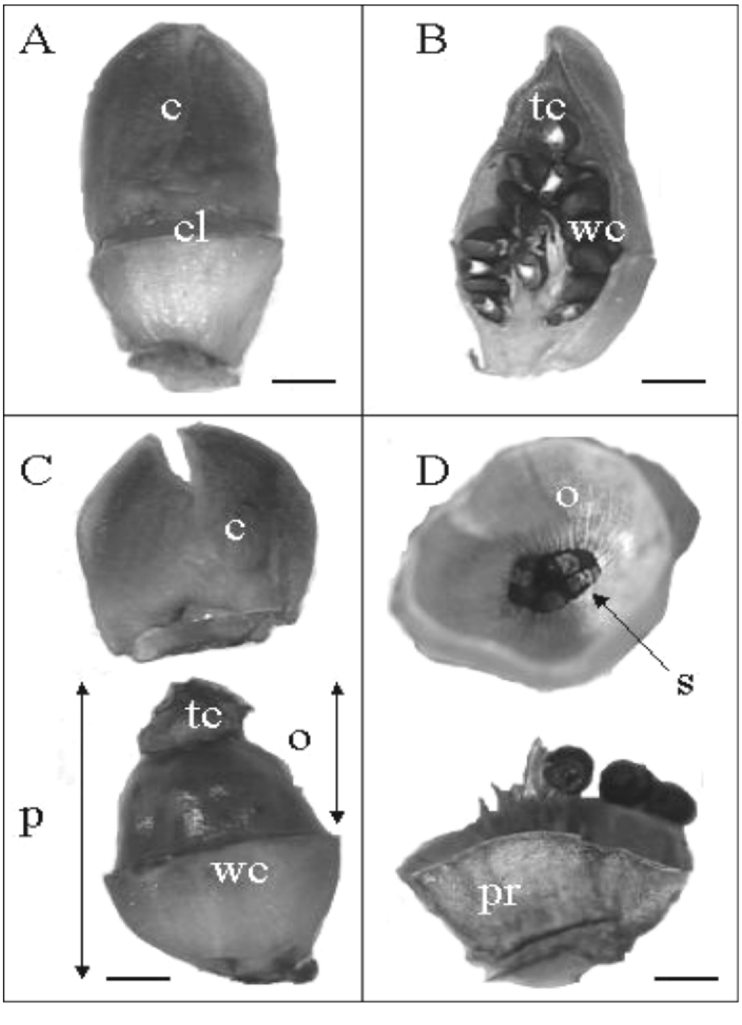

Figure 1. Stereomicrographs showing the morpho-functional aspects of purslane fruit. A) Capsula with the calyptra (c) and the circumscission line (cl); B) Longitudinal section of the capsule with the upper tiny chamber (tc), containing few seeds and the lower wide chamber (wc), containing numerous seeds; C) Unripened capsule with the calyptra (c), the pyxidium (p), with a tiny chamber (tc) narrowing at the apex and a lower wide chamber (wc); the operculum (o) covers the pyxidium. D) The operculum (o) retainings few seeds (s); pyxidium remnant (pr); Bars = 1mm.

referred it by the term Heteromericarpia, providing the first evidence that one of the ten most widespread weeds has fruits with effective seed dispersal (Delpino, 1903). In fact, the seeds in both chambers are the same but their fate is different. Those from the wide chamber of the pyxidium gradually spread around the plant while those of the opercule will fly away from the plant. Paradoxally, most of the worst weeds of the cultivated fields have seeds with no obvious dispersal aids (Zimmerman, 1976).

We have also studied the anatomical and ultrastructural aspects of *in vitro* germination of the purslane seeds using scanning electron microscopy (Figure 2). A dry quiescent purslane seed and the successive changes when it is moistened have been reported here. The outer integument (testa) of the seed coat is formed by dead cells sculptured on the surface with stellulae (Figure 2A). The peripheral face of the testa presents an opening: the micropyle and a residue of the funiculus of the placenta which functions as elaiosome, an edible appendage of seeds dispersed by ants. Surprisingly, the first structure that protrudes from the micropyle of the moistened seed, is not the radicle, as happens in seeds of other species, but the endosperm (Figure 2B). When germination proceeds further, the radicle breaks the endosperm and protrudes, completing rapidly the early stages of primary structure development viz., root hairs and hypocotyl elongation (Figure 2C). Usually these three phases require 25, 30 and 40 hours respectively. The radial section of purslane seed shows the embryo surrounded by a thin endosperm layer and curved around the starch hard perisperm (Figure 2D).

Weed scientists were not aware of the endosperm protrusion. Perhaps the phenomenon was overlooked because they recorded only the end of germination, when the radicle emerges, which is visible with the naked eye. Our step by step morphological investigations of purslane germination process, has revealed the endosperm protrusion (Aliotta et al. 1996).

Chenopodium album L

As purslane lambsquarter is reported to be one of the most successful colonizing species. The plant is an erect, rigid, pale-green herb growing to 2 meter in rich, moist soil, strongly tap-rooted. During the long photoperiods of 16 to 18 hours in the temperate zone, the plant grow vigorously for a long time and attains great size before it is induced to flower by oncoming short days. Because the plant has no special seed dispersal system, most of its seeds are deposited near the mother plant: such deposition causes it to grow in patches in crops. The seeds are commonly distributed as impurities in crop seeds. Lambsquarter thrives on all soil types. It attains its greatest size on fertile heavy soils rich in nitrate. Fruit is an utricule (a seed covered by the thin papery pericarp which often persists). Propagation of *Chenopodium album* L. is always from seeds. There is considerable heteromorphy in the seeds. Their color in one plant may be black and shiny, brown, and brownish green. It is believed that there is a correlation between the amount of dormancy in a seed and its color (Holm et al. 1977). A needle puncture on the seed coat in the micropylar region of the seeds overcome their dormancy (Aliotta et al. 2002). Figure 3 shows the morphology of lambsquarter seed and its germination after scarification. Germination begins 24 hours of moistening and the first structure that protrudes from the micropyle of the seed is the endosperm layer which covers the radicle. When the germination proceeds further, the radicle breaks the endosperm and protrudes. After 96 hours the seedling is well developed.

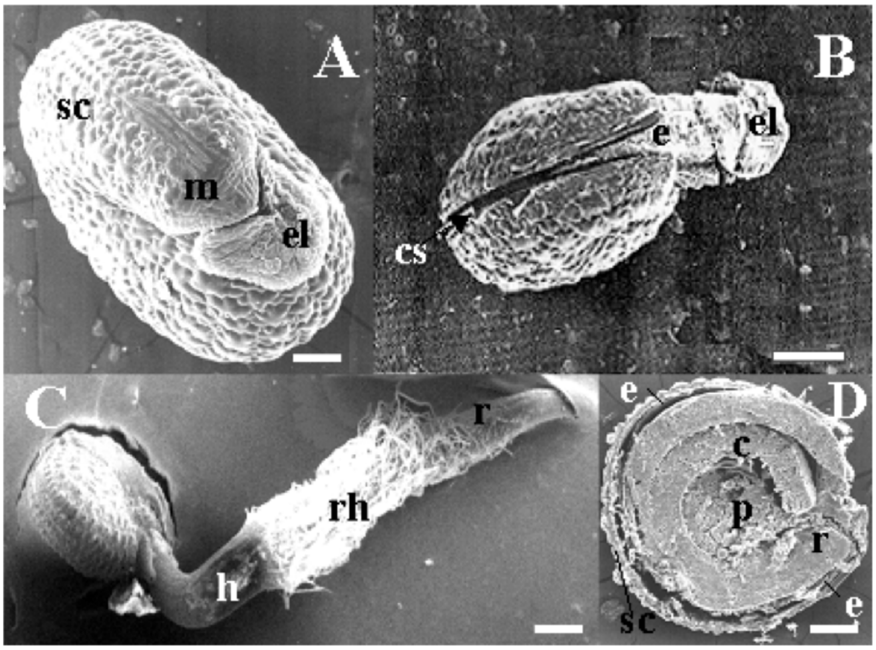

Figure 2. SEM micrographs of the whole purslane seed (A), Bar = 200µm. Endosperm protrusion (B), Bar = 250 µm. Seedling growth (C), Bar = 250µm. Radial section (D), Bar = 150 µm. sc, seed coat; m, micropyle; el, elaiosome; e, endosperm; cs, circumscission line; h, hypocotyl; r, radicle; rc, root cap; c, cotyledons; p, perisperm; rh, root hairs.

Amaranthus retroflexus L

Some species of the genus *Amaranthus* are serious weeds worldwide viz., *Amaranthus retroflexus, A. spinosus, A. viridis, A. hybridus, A. lividus* and *A. blitoides*.

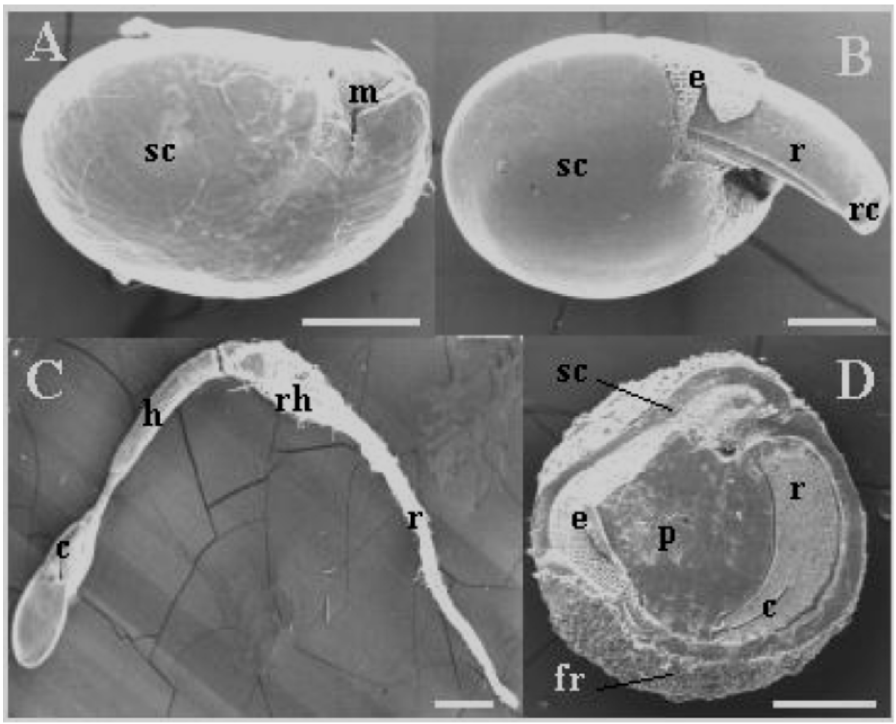

Figure 3. SEM micrographs of the whole lambsquarter seed (A), Bar = 300 µm. Endosperm and radicle protrusion (B), Bar = 300 µ m. Seedling growth (C), Bar = 1mm. Radial section (D), Bar = 350 µm.m, micropyle; e, endosperm; fr, fruit residue; h, hypocotyl; r, radicle; rc, root cap; c, cotyledons; p, perisperm; rh, root hairs; s, seed coat.

The *A. spinosus, A. retroflexus* and *A. viridis* are among the worst weeds. *A. retroflexus* and *A. spinosus* compete with other weeds and grasses in pastures, crop and roadsides.

A. retroflexus is the species most widespread. It has exhibited resistance to triazines herbicides and has developed resi stant biotypes, therefore since 1990's, its biology and allelopathyc properties are intensely studied (Suma et al. 2002). *A. retroflexus* is a monoecious, erect, finely hairy, freely-branching, herbaceous annual growing to 2 m tall; taproot pink or red, depth varies with soil profile; leaves alternate, egg-shaped upto 10 cm long; flowers numerous, small, borne in dense blunt spikes 1 to 5 cm long, densely crowded onto terminal panicle 5 to 20 cm long; tepals 5, much

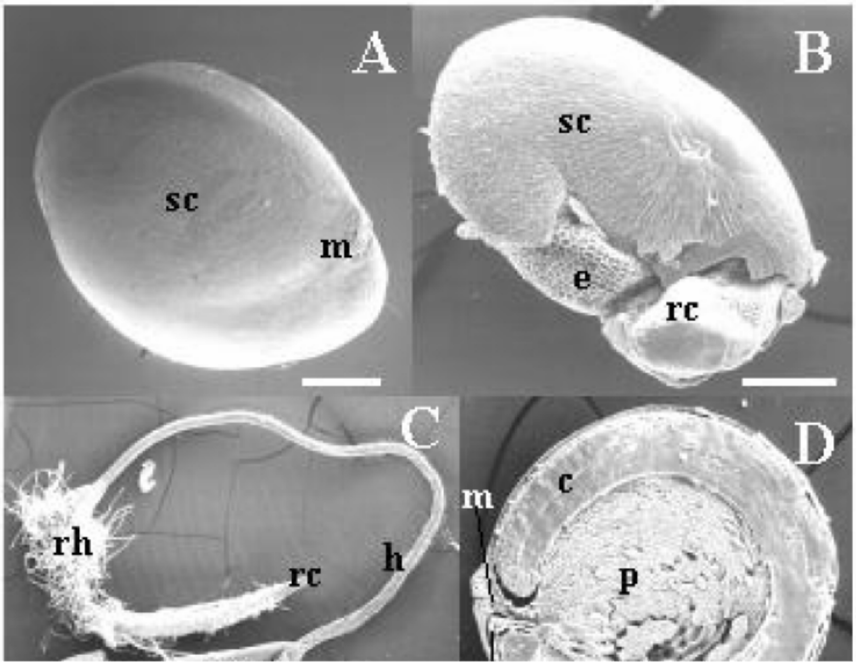

Figure 4. SEM micrographs of the whole redroot pigweed seed (A), Bar = 250 µm. Endosperm and radicle protrusion (B), Bar = 250 µm. Seedling growth (C), Bar = 300 µm. Radial section (D), Bar = 100 µm.m, micropyle; e, endosperm; h, hypocotyl; r, radicle; rc, root cap; c, cotyledons, p, perisperm; rh, root hairs; s, seed coat.

longer than fruit, 1 pistil and 5 stamens; style branches erect or a bit recurved; fruit a utricle, membranous, flattened, 1.5 to 2 mm long, dehiscing by a transverse line at the middle, wrinkled upper part falling away; seed oval to egg-shaped, somewhat flattened, notched at the narrow end, 1 to 1.2 mm long, shiny black or dark red-brown. Figure 4 shows the morphology of redroot pigweed seed and its germination after scarification.

It should be noted that the three weeds have the same seed embryology. In fact, the seeds are lenticulars, seed coat usually black and its peripheral face presents an opening: the micropyle. The embryo is curved around the starchy hard perisperm and covered by a thin endosperm. It is interesting the role of endosperm, which during germination protrudes covering the radicle. Recently, we have demonstrated that phenolic compounds of olive oil mill wastewater and the aqueous extract of Rue (*Ruta* *graveolens* L.), induce an inhibitory growth delaying, modifying, and locking cellular activity of endosperm of purslane, lambsquarter and redroot pigweed. Our studies suggest that the outermost living structures of the seed (i.e., seed coat or endosperm) are the primary subject of the allelochemicals (Aliotta et al. 1999, 2000, 2002).

ALLELOPATHY AND WEED CONTROL

Seed and growth parameters of the three weeds studied are reported in table 2. They are discussed considering eventual vulnerability points. Seed size and weight of purslane, lambsquarter and redroot pigweed are very small and the numerous seedlings emerge best from a depth of 0.5 to 1.0 cm. By contrast, most agronomic crops have much larger seeds and they are usually planted at 3 to 5 cm of depth. These difference in emergence depth and seed size between weeds and crops makes possible the implementation of allelopathy for natural weed management (Mohler, 2001). Crop residues can provide selective weed control through their physical presence on the soil surface and through the release of allelochemicals. A more fruitful approach has been to use waste products from plants that are processed for food or oil (Aliotta et al. 2001; Duke et al. 2002; Bhowmik and Inderjit, 2003).

The suppression of smaller-seeded weeds by allelochemicals may be the result of two processes. First, at least from germination until emergence, the surface-to-volume ratio of a small seeded species is usually greater, and therefore its exposure per unit mass to allelochemicals in the soil is also greater. Second, when residue is used as a mulch, the allelopathic toxins are released onto the soil surface and may not diffuse very deeply into the soil profile (Mohler, 2001), Barnes and Putnam (1986) showed that percent germination and root elongation of several species decreased as the layer of soil separating seeds from rye residue decreased from 15 to 0 mm. To have any potential for emergence, a small-seeded weed or crop must germinate near the soil surface, but under an allelopathyc mulch, this is where the toxins are most concentrated. In contrast, larger-seeded crops are planted more deeply, and thus germination and initial root growth may occur in a less toxic environment. Both hypotheses require testing by careful experimentation (Mohler, 2001).

Once small-seeded weeds have germinated and established in the field starts the crop-weed interference. As can be seen in table 2 Purslane, lambsquarter and redroot pigweed have higher values of growth parameters such as: biomass added per unit time (RGR), and leaf weight ratio (LAR), than sunflower. The values of net assimilation rate (NAR), are almost similar. That is, differences in growth rate due to seed size were attributable to morphology rather tha physiology. Because small-seeded weeds have a higher RGR than larger seeded crops, they tend to catch up in size eventually. As an extreme example, the initial 500-fold difference in the seed size of maize and redroot pigweed, may be reduced to a two-fold difference in the size of the mature plants if each species is allowed to grow without competition (Mohler, 1996). At the emergence, the crop has a greater leaf area and a larger root system than the weed. Therefore the crop's absolute growth rate is initial greater, and usually remains greater for at least several weeks (Zimdahl, 1980).

Table 2. Seed and growth parameters of three major weeds in arable lands and sunflower.

Parameters	***Portulaca oleracea* L.**	***Chenopodium album* L.**	***Amaranthus retroflexus* L.**	***Heilanthus annuus* L.**
Seed weight (mg)	0,12±0.01	0.38±0.02	0.37±0.03	61±2.3
Number seeds m^{-2}	120000	4000	68000	-
Seedlings m^{-2}	420±15	90±5	300±10	-
Seedling type	Epigeal	Epigeal	Epigeal	Epigeal
RGR*	0.461	0.298	0.349	0.197
LAR*	180	224	198	140
NAR*	0.220	0.254	0.298	0.241
LWR*	0.430	0.674	0.597	0.495

Notes: RGR: relative growth rate = g increase in plant weight g^{-1} plant weight day^{-1}.
LAR: leaf area ratio = cm^2 leaf area g^{-1} plant weight.
NAR: net assimilation rate = g increase in plant weight dm^{-2} leaf area day^{-1}.
LWR: leaf weight ratio = g leaf weight g^{-1} plant weight.
*Correlation with ln (seed weight), significant at $p < 0.05$ level.
Sources: From Aliotta et al. 2001; Seibert and Pearce, 1993; and Zimmerman, 1976.

Use of the initial advantage conferred to the crop by relatively large size and high absolute growth rate is a key concept in ecological weed management. A major strategy in most annual crops is to design the cropping system so that the initial size advantage still holds at the time the crop and weeds grow into physical contact. With few exceptions, both crops and weeds are adapted to open habitats, and both are intolerant of shade (Bello et al. 1995). Consequentely if the crop is in the superior position, it will suppress the growth of the weeds, whereas if the weeds grow above the crop canopy, then yield reduction is likely to be severe.

Recently, it has been examined the role of allelopathic crop residues, natural compounds and weed-suppressing cultivars, as well as rhizosphere interactions involving higher plants (Birkett et al. 2001; Duke et al. 2002; Bhowmik and Inderjit, 2003). Results suggest that allelopathy offers a real promise for practical weed management, especially if we join the different expertise involved.

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