Germination characteristics of eight weed species from the dry tropics[1]

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Abstract: This research investigated the germination of eight tropical weeds in response to seed development position on the mother plant, storage, and GA_3 (90% (+)-gibberellic acid). Seeds were collected from agricultural fields during the dry and rainy seasons and germinated in darkness at 30 °C for two weeks. Tetrazolium (2,3,5-triphenyl tetrazolium chloride) tests were conducted to assess seed viability. Also, the effect of three wounding positions on the seed were investigated for *Bidens pilosa* L. and *Sorghum halepense* (L.) Pers. Effect of polymorphism in *B. pilosa* achenes on germination was assessed. In the dry season, *Portulaca oleracea* L. seeds that developed on the upper 20% of the plant were less dormant than seeds from the lower 20%. *Chloris virgata* Swartz produced more germinable caryopses from the lower 20% of the spike. *B. pilosa*, *P. oleracea* and *S. halepense* seeds were less dormant after storage, while *C. virgata* germination was reduced with storage. Exogenous GA_3 enhanced the germination of *Amaranthus hybridus* L., *P. oleracea*, *Tithonia tubaeformis* (Jacq.) Cass., *C. virgata*, and *Eleusine indica* (L.) Gaertner, while no effect was found in *B. pilosa*, *Cenchrus echinatus* L., and *S. halepense*. *T. tubaeformis* achenes germinated more two weeks after collection with the application of 10 µM GA_3 than 24 weeks after storage. However, *E. indica* caryopses germinated more when 10 µM GA_3 was applied 24 weeks after storage. Wounding the distal region of *B. pilosa* and *S. halepense* seeds increased germination. Long-thin *B. pilosa* achenes were less dormant that short-thick ones. Germination was highly variable within species and season. This variation may help explain seasonal emergence and adaptive features that contribute to their success as weeds.

Key words: dormancy, gibberellic acid, scarification, seed storage, somatic polymorphism, tetrazolium.

Resumen: Esta investigación evaluó la germinación de ocho malezas de los trópicos en respuesta a la posición de desarrollo de la semilla en la planta, almacenamiento y GA_3 (90% (+)-ácido giberélico). Las semillas fueron colectadas en campos agrícolas durante la estación seca y la estación lluviosa. Estas semillas fueron germinadas en oscuridad a 30 °C por dos semanas. Se realizaron pruebas de Tetrazolium (2,3,5-trifenil cloruro de tetrazolium) para determinar la viabilidad de la semilla. El efecto de lesiones en tres sitios de la semilla también fue investigado para *Bidens pilosa* L. y *Sorghum halepense* (L.) Pers. Se evaluó el efecto del polimorfismo en la germinación de *B. pilosa*. En la estación seca, las semillas de *Portulaca oleracea* L. que se desarrollaron en el 20% superior de la planta tuvieron menor latencia que las semillas desarrolladas en el 20% inferior. *Chloris virgata* Swartz produce cariopses con menor latencia en el 20% inferior de la espiga. Las semillas de *B. pilosa*, *P. oleracea* y *S. halepense* fueron menos latentes después del almacenamiento, sin embargo la germinación de *C. virgata* se redujo con el almacenamiento. Aplicaciones exógenas de GA_3 incrementaron la germinación de *Amaranthus hybridus* L., *P. oleracea*, *Tithonia tubaeformis* (Jacq.) Cass., *C. virgata* y *Eleusine indica* (L.) Gaertner, sin embargo no se encontró diferencia en la germinación de *B. pilosa*, *Cenchrus echinatus* L. ni *S. halepense*. Los aquenios de *T. tubaeformis* germinaron más dos semanas después de colectados al aplicar 10 µM GA_3 que 24 semanas después de almacenamiento. Sin embargo, los cariopses de *E. indica* germinaron más cuando 10 µM GA_3 fueron aplicados 24 semanas después de almacenamiento. Las lesiones en la región distal de semillas de *B. pilosa* y *S. halepense* incrementaron la germinación. Los aquenios largos y delgados de *B. pilosa* germinaron más que los aquenios cortos y gruesos. La germinación entre especies y estaciones fue muy variable durante la investigación. Esta variación puede ayudar a explicar la emergencia estacional y las cualidades de adaptación que contribuyen al éxito de las malezas.

Palabras claves: ácido giberélico, almacenamiento de la semilla, escarificación, latencia, polimorfismo somático, tetrazolium.

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INTRODUCTION

While weeds are the most important pest complex in tropical agriculture (Akobundu, 1987), little information exists regarding the impact of weed biology on management. Better knowledge about the germination of important tropical weed species may aid in the development of alternative weed management strategies, and improve current control tactics. Importantly, some tropical weeds are also important in the temperate agriculture and behavioral comparisons between regions could expand our understanding about their biology. The objective of this study was to assess the effects of seed developmental positions on the mother plant, season, storage, and GA_3 on the germination of eight important weed species from the dry tropics.

Seed dormancy. Seed dormancy is a period in which metabolism declines and germination does not occur even under adequate environmental conditions (Bewley and Black, 1994). Dormancy is common in many weed species and is an evolutionary strategy for survival. Dormancy can be described as dissemination in time because seeds can delay germination for several years until environmental conditions are suitable for plant growth (Bradbeer, 1988; Simpson, 1990).

Dormancy can occur because of an immature embryo, hormonal balance, mechanical restrain or seed coat impermeability to water and oxygen. Much research has investigated the hormonal control of dormancy by interaction of gibberellins and abscisic acid (ABA). Literature indicated that gibberellins release seeds from dormancy and enhance seed germination, while an antagonistic effect on germination is described for ABA (Groot and Karssen, 1992; Hsiao, 1993; Ni and Bradford, 1993).

Dormancy variation on the mother plant. Dormancy variation related to the seed development position on the mother plant has been reported for several grass species (Simpson, 1990). Wellington (1956) showed that *Triticum aestivum* L. seed dormancy increased from the apex toward the base of the spikes and was correlated with variations in grain moisture content. In addition, Gosling *et al.* (1981) discovered that extended anthesis and maturity periods increased the temperature range for *T. aestivum* germination. Temperature and photoperiod can affect gene expression of inflorescence morphology and thus influence the degree of dormancy in caryopses (Simpson, 1990). Twentyman (1974) reported that *Cenchrus longispinus* (Hack.) Fern. seeds in the upper section of the raceme germinated within one year of collection, while lower ones remained dormant. Basipetal or acropetal dormancy within the floral structure has been reported for *Avena fatua* L. (Raju and Ramaswamy, 1983), *Aegilops kotschyi* Boiss. (Wurzburger and Koller, 1973), *Cenchrus longispinus* (Hack.) Fern. (Twentyman, 1974), *C. tribuloides* L. (Anderson, 1968), and *Poa pratensis* L. (Phaneendranath *et al.*, 1978).

Somatic polymorphism. Somatic polymorphism refers to the production of different seed morphologies on the same plant and is reported in Asteraceae, Chenopodiaceae, Poaceae, and Brassicaceae (Harper, 1977). Pitty and Muñoz (1991) reported that *Bidens pilosa* L. produced two achene morphisms. Achenes from the circumference of the capitulum were longer than the ones developed in the interior of the capitulum. Forsyth and Brown (1982) discovered that shorter achenes were more dormant than longer ones and reported that exposure to red light, hormones or scarification was needed to break short achene dormancy. A single *Chenopodium album* L. plant can produce black and brown seeds; brown seeds have a thinner seed coat and are less dormant than black ones (Williams and Harper, 1965). Somatic polymorphism has been described for *Xanthium strumarium* L., *Calendula* spp., *Avena fatua*, *Rumex crispus* L., and *Atriplex heterosperma* Bunge (Harper, 1977).

MATERIALS AND METHODS

Seeds from eight weed species were collected at El Zamorano, Yegüare Valley, Department of Francisco Morazán, Honduras. This area is 800 m above sea level and has an average temperature range of 18 °C to 29 °C and annual mean precipitation of 1100 mm. The region is characterized as a dry tropical environment where the dry season extends from December to April and the rainy season from May to November.

Seed collections. Four broadleaf and four grass species were selected because of their weedy importance in the dry

tropics (Table 1). Seeds were collected from arbitrarily selected plants from corn fields or horticultural crops. The field was divided in quadrants and random numbers were generated to determine the sampling area within the field; all mature plants in the sampling area were harvested. Seeds were collected from June to July, 1995 in the rainy season and from December, 1995 to January, 1996 in the dry season. *Cenchrus echinatus* and *Tithonia tubaeformis* were collected only in June and December, 1995, respectively (Table 1). Plant height of broadleaves and lenght of the inflorescence of grasses was measured and seed collections were taken from the upper and lower 20% of the plant or inflorescence measurements. Seeds that shed from the mother plant when gently rubbed were considered physiologically mature, collected in plastic bags, cleaned and air dried for two weeks at room temperature. Seed cleaning for *Chloris virgata* Swartz and *Eleusine indica* (L.) Gaertner included separating caryopses from glumes, lemma and palea, and in *C. echinatus*, removing the caryopses from the concealed spiny bur. For *Sorghum halepense* (L.) Pers., caryopses were incubated with the glumes. After the drying period, seeds were tested for initial germination and then stored in glass containers under dark conditions at 5 °C.

Table 1. Dates and crops were seed collections occurred at El Zamorano, Honduras.

Weed species	1995 rainy season	1996 dry season	Crop
Broadleaf weeds			
Amaranthus hybridus	Jun, 23	Jan, 22	Tomato
Bidens pilosa	Jun, 19	Jan, 15	Tomato
Portulaca oleracea	Jun, 12	Jan, 17	Cucumber
Tithonia tubaeformis	Unknown	Dec, 13	Corn
Grasses			
Cenchrus echinatus.	Jun, 6-7	Not done	Corn
Chloris virgata	Jul, 7	Jan, 29	Pepper
Eleusine indica	Jul, 3	Jan, 25	Carrot
Sorghum halepense	Jun, 27	Jan, 19	Citrus

Germination tests. Tests were conducted on samples arbitrarily selected from the seed collections. Some seeds produce allelopathic chemicals that are detrimental to the germination of other seeds (Rice, 1974). Thus, to reduce potential allelopathic interactions, seeds were evenly distributed in 100 x 15 mm plastic petri dishes and processed in batches of 50 seeds with two batches representing one replication. Three replications of 100 seeds were used per treatment and percent germinated, dormant and non-viable seeds was determined. The experiment consisted of five main treatments: a scarification treatment, three concentrations of 90% (+)-gibberellic acid (GA_3) and a control treatment.

The control treatment consisted of seeds placed in test tubes for 12 hr with 10 ml of distilled water. The test tubes were drained, seeds dried in a paper towel and placed in 100 mm diameter sterile plastic petri dishes on a #1 Whatman filter paper. Two ml of distilled water were added to moisten the filter paper and the petri dishes placed in a growth chamber under darkness at 30 °C.

The GA_3 concentration treatments were 0.1, 1.0 and 10 µM . For each treatment, 100 seeds were placed in test tubes with 10 ml of a GA_3 solution for 12 hours. Test tubes were drained and seeds handled as described previously.

Seeds were considered germinated when the radicle was observed. The petri dishes were inspected every two days for two weeks, germinated seeds were counted, removed and distilled water added as needed. Seeds that did not germinate were dissected and placed in a 1% tetrazolium (TZ) staining solution to determine viability (Moore, 1985) (Table 2). Seeds were completely covered with the TZ solution and stained in darkness at 30 °C. After the staining period, seeds were placed in cold distilled water and evaluated for viability. Seeds that displayed a light pink to red stain in the embryonic axis and scutellum were considered dormant, but seeds without stains were considered non-viable.

Seed development position on the mother plant and treatments were considered main plots and germination dates subplots. Data were analyzed as repeated measures. Data analysis was conducted by analysis of variance (ANOVA) and means were separated with Fisher's least significant difference (LSD) test ($P \leq 0.05$) (SAS, 1987).

Effect of wounding position on *S. halepense* and *B. pilosa* germination. This experiment investigated the effect of wounding position on the germination of *S.*

halepense caryopses and *B. pilosa* achenes. The treatments consisted of a control and seeds punctured through the proximal, central, or distal section. Proximal location was the section where seeds adhere to the mother plant and distal location referred to the seed apex. The experiment was conducted in May, June and July of 1996 for *B. pilosa*, and in June and July for *S. halepense*. Seed samples were drawn from collections made in January 15, 1996 for *B. pilosa* and January 19, 1996 for *S. halepense* (Table 1). Each treatment had three replications of 100 seeds. The germination test was conducted as described previously. The data were analyzed as repeated measures with treatments as the main plots and germination dates as subplots. Data analysis was conducted as previously described. This experiment was only realized in 1996.

Table 2. Staining period and seed cutting procedure for the eight weed species (adapted from Moore 1985).

Species	Staining hours	Seed cutting procedure
Amaranthus hybridus	18-24	Center and outward between radicle and cotyledons
Bidens pilosa	8-12	Longitudinal and completely through mid section
Portulaca oleracea	18-24	Center and outward between radicle and cotyledons
Tithonia tubaeformis	8-12	Transversal and completely through mid section
Cenchrus echinatus	10-16	Longitudinal and completely through mid section
Chloris virgata	14-18	Longitudinal and completely through mid section
Eleusine indica	10-16	Longitudinal and completely through mid section
Sorghum halepense	10-16	Longitudinal and completely through mid section

Germination of dimorphic *B. pilosa* achenes. Achenes developing in the peripheral region of the capitulum are short-thick and less numerous than the ones developing in the middle of the capitulum. This experiment investigated the germination of these two morphisms and was conducted from achenes collected in January 15, 1996 (Table 1). Treatment were both achenes morphisms and was replicated four times. The germination test was conducted as described previously and repeated in June, July, and August of 1996. Data were analyzed as repeated measures with seed morphisms as the main plots and germination dates the subplots. Data were analyzed as previously described. This experiment was only realized in 1996.

RESULTS AND DISCUSSION

Effect of seed development position on seed dormancy. Germination of seeds developed on the lower or upper strata of the plant was similar for *A. hybridus*, *B. pilosa*, and *T. tubaeformis* nor was any difference found for the effect of inflorescence strata for *C. echinatus*, *E. indica*, and *S. halepense*. Germination position differences were only found for collections made in the dry season for *P. oleracea* and *C. virgata*.

P. oleracea seeds that developed on the upper strata of the mother plant had greater germination and were less dormant than the ones from the lower strata (Table 3). These results contradict Egley (1974) who reported that variations in *P. oleracea* seed dormancy were not a result of the developmental position on the plant. In the tropics, *P. oleracea* can germinate at various dates (Miyanishi and Cavers, 1980) and flowers throughout the year (Matthews *et al.*, 1993) which results in seed that have experienced different maturation conditions. Dunn (1970) indicated that seed maturation started from the center of the plant and extended toward the peripheral branches. The above literature supports the notion that *P. oleracea* dormancy is highly variable and that changes in dormancy are attributable to environmental conditions or intrinsic characteristics of the species.

C. virgata caryopses from the lower 20% of the spike germinated 15% more and tended to be less dormant than ones from the upper strata (Table 3). Spikelet maturation and spike abscission in *C. virgata* starts from the apex and extends toward the base of the spike, thus upper spikelets may experience different environmental conditions resulting in dormancy differences. Variation in seed water content and environmental conditions influence the degree of dormancy within wheat spikes (Wellington, 1956; Gosling *et al.*, 1981). Temperature and photoperiod can

interact with the genes to determine inflorescence morphology and influence the degree of dormancy in caryopses (Simpson, 1990).

While environmental conditions during seed maturation were not monitored during this investigation, these conditions may have influenced the results. Climatic conditions (Koller, 1962; Guttermann, 1973), defoliation (Mann and Cavers, 1971), or hormone treatments (Black and Naylor, 1959) during seed development have been demonstrated to influence seed germination.

Table 3. Effect of two seed development positions on germination of *Portulaca oleracea* L. and *Chloris virgata* Swartz seeds collected during the dry season, El Zamorano, 1995-1996.

Species	Development position	Germination	Dormant	Non-viable
		% [1]		
P. oleracea	upper strata	35 a	39 b	26 a
	lower strata	25 b	49 a	26 a
C. virgata	upper spike	53 b	22 a	25 a
	lower spike	68 a	8 a	24 a

[1] Means in columns within species followed by the same letter are not significantly different at the $P \leq 0.05$ level determined by Fisher's LSD test.

seeds (Table 4). Several investigations indicate that storage increases *P. oleracea* germination (Cantoria and Gacutan, 1972). Fresh *P. oleracea* seeds require a light stimulus to germinate, however this requirement vanishes after three months of storage (Cantoria and Gacutan, 1972). In addition, Zimmerman (1977) obtained 90% germination of 2.5 years old *P. oleracea* seeds and Darlington and Steinbauer (1961) determined that seeds remained viable after 40 years of burial.

Table 4. Effect of season and storage on *Bidens pilosa* L. and *Portulaca oleracea* L. germination, El Zamorano, 1995-1996.

Species	Season	Storage (weeks)	Germination	Dormant	Non-viable
			% [1]		
B. pilosa	dry	2	69 b	6 a	25 a
		24	75 a	3 b	22 b
	rainy	2	50 b	16 a	34 a
		24	66 a	5 b	29 a
P. oleracea	dry	2	21 b	52 a	27 a
		24	39 a	36 b	25 a
	rainy	2	6 b	71 a	23 b
		24	33 a	39 b	28 a

[1] Means in columns within species and season followed by the same letter are not significantly different at the $P \leq 0.05$ level determined by Fisher's LSD test.

Effect of seed storage on germination. The storage period affected *B. pilosa*, *P. oleracea*, *C. virgata* and *S. halepense* germination, but not *A. hybridus* and *C. echinatus*. Also, interactions between storage and seed treatments were found for *T. tubaeformis* and *E. indica*.

Experiments on *B. pilosa* were conducted on natural ratios of long-thin and short-thick polymorphic achenes. Storage enhanced the germination of *B. pilosa* achenes (Table 4). Holm *et al.* (1977) reported that fresh seeds may germinate from 35 to 60%, however, three years after storage their germination increased by at least 20%. Forsyth and Brown (1982) reported that storage enhanced the germination of long achenes of *B. pilosa* more than short achenes.

Storage also enhanced germination of *P. oleracea*

C. virgata germination decreased with the storage period. Seeds collected in the rainy season germinated twice as much and were 10% less dormant than before the storage period (Table 5). This tropical species seldom experiences temperatures below 10° C, thus cold storage may have induced secondary dormancy in the caryopses. Lodge and Whalley (1981) stored *Chloris truncata* R.Br. seeds at room temperature and observed no significant changes in germination during a three-year period.

S.halepense seeds germinated more after 24 weeks of storage for the dry season collections (Table 5). More dormant seeds were found after two weeks of storage compared to 24 week, regardless of season. These seeds are highly dormant when shed from the mother plant (Monaghan, 1979; Warwick and Black, 1983). Harrington

(1916; 1917) reported that four or five months of dry storage at room temperature overcame the dormancy of most *S. halepense* seeds. Nevertheless, Huang and Hsiao (1987) had almost half of the seeds dormant after six months of dry storage. Taylorson and Brown (1977) recommended storage at 50 °C for 14 days to improve the germination of fresh *S. halepense* seeds.

Loss of light requirement for gemination and biosynthesis of germination promoters may explain the enhanced germination after storage. Germination was enhanced over time because seeds no longer required a light stimulus (Cantoria and Gacutan, 1972). Seed hormone balance may also change over time and decreased dormancy of several grass species has been attributed to increased gibberellic acid biosynthesis (Simpson, 1965; Mott, 1974).

Table 5. Effect of season and storage on *Chloris virgata* Swartz and *Sorghum halepense* (L.) Pers. germination, El Zamorano, 1995-1996.

Species	Season	Storage (weeks)	Germination	Dormant	Non viable
			---------- % [1] ----------		
C. virgata	dry	2	58 a	19 a	23 b
		24	63 a	11 a	26 a
	rainy	2	20 a	53 b	27 b
		24	7 b	63 a	30 a
S. halepense	dry	2	9 b	69 a	22 a
		24	15 a	63 b	22 a
	rainy	2	9 a	72 a	19 b
		24	11 a	59 b	30 a

[1] Means in columns within species and season followed by the same letter are not significantly different at the P ≤ 0.05 level determined by Fisher's LSD test.

Effect of GA_3 on germination. No significant interactions between storage and GA_3 treatment were obtained for *A. hybridus*, *P. oleracea*, *B. pilosa*, *C. echinatus*, *C. virgata*, and *S. halepense*, thus results are presented as the means of both storage treatments.

***A. hybridus*.** Seeds had a high degree of dormancy (Table 6). Baskin and Baskin (1987a) and Fenner (1980a) indicated that fresh *A. hybridus* seeds are highly dormant. Taylorson (1970) observed no germination from one lot of fresh *Amaranthus retroflexus* L. seeds and reported that this dormancy was overcome when exposing seeds to red light. Scarification enhance germination of *A. retroflexus* L. (Kigel *et al.*, 1977), *A. albus* L., and *A. spinosus* L. (Santelmann and Evetts, 1971). Pal *et al.* (1990) found that seed coat formation in *A. hybridus* occurred from the outer integument and suggested that tanniniferous deposits in seed coat cells could be related to the low germination. Kigel (1994) reported that the seed coat imposed dormancy was not a result of reduced water uptake.

Table 6. Effect of season and GA_3 on *Amaranthus hybridus* L. germination, El Zamorano, 1995-1996.

Season	Treatments	Germination	Dormant	Non viable
		---------- % [1] ----------		
dry	control	5 b	80 a	15 a
	0.1 µM	5 b	80 a	15 a
	1 µM	5 b	83 a	12 a
	10 µM	50 a	33 b	17 a
rainy	control	3 b	83 a	14 a
	0.1 µM	7 a	81 a	12 a
	1 µM	8 a	78 a	14 a
	10 µM	11 a	74 a	15 a

[1] Means in columns within season followed by the same letter are not significantly different at the P ≤ 0.05 level determined by Fisher's LSD test.

Compared to the control, 10 µM GA_3 enhanced germination by 45% for dry season seeds (Table 6). Similar GA_3 responses have been described in *A. lividus* L. (Teitz *et al.*, 1990) and *A. retroflexus* L. (Holm and Miller, 1972). These investigations suggest that activation of germination in pigweed species requires the presence of GA_3. Potassium nitrate (Engelhardt *et al.*, 1962) and sodium hypochlorate (Santelmann and Evetts, 1971) have also been reported to enhance *A. hybridus* germination.

Low germination rates in the control treatment may be

in part attributable to the incubation conditions. Several investigations indicated that dark conditions limited the germination of several pigweed species. Most pigweed species produce photoblastic seeds and their germination is controlled by phytochrome and temperature (Taylorson and Hendricks, 1969; 1971; Kigel, 1994). Kigel (1994) reported that light and temperature synergism was required to promote the germination of fresh seeds. Optimum germination conditions for fresh pigweed seeds include 20 to 40 °C and light (Weaver and McWilliams, 1980).

B. pilosa. Experiments on *B. pilosa* were conducted on natural ratios of long-thin and short-thick polymorphic achenes. Achenes were almost 80% viable and germination was at least 59% for dry and rainy season achenes (Table 7). GA_3 had no effect on the germination of *B. pilosa* achenes, nevertheless the control had more dormant achenes when compared to the 10 mM GA_3. The incubation conditions may have affected the response of *B. pilosa* achenes to GA_3. Forsyth and Brown (1982) obtained greater responses to GA when achenes were germinated under illumination. *B. pilosa* achenes can germinate under dark conditions (Reddy and Singh, 1992) but white and red light considerably enhanced germination (Forsyth and Brown, 1982).

Table 7. Effect of season and GA_3 on *Bidens pilosa* L. germination, El Zamorano, 1995-1996.

Season	Treatments	Germination	Dormant	Non viable
		---------- % [1] ----------		
dry	control	77 a	10 a	13 a
	0.1 µM	80 a	7 b	13 a
	1 µM	85 a	3 c	12 a
	10 µM	86 a	1 c	13 a
rainy	control	59 a	18 a	23 a
	0.1 µM	65 a	15 a	20 a
	1 µM	68 a	12 ab	20 a
	10 µM	70 a	8 b	22 a

[1] Means in columns within season followed by the same letter are not significantly different at the $P \leq 0.05$ level determined by Fisher's LSD test.

P. oleracea. Seeds demonstrated a high degree of dormancy but compared to the control, 10 µM GA_3 enhanced *P. oleracea* germination 19% for seeds collected during the dry season (Table 8). Most studies indicate that *P. oleracea* seeds are dormant when shed from mother plant (Cantoria and Gacutan, 1972; Baskin and Baskin, 1987b). The dark incubation conditions may have prevented seeds from germinating because of a red light requirement (Cantoria and Gacutan, 1972; Duke *et al.*, 1977). Singh (1973) germinated seeds under dark conditions and obtained little response to various temperature ranges. Duke *et al.* (1977) found that the red light irradiation periods that gave high germination rates also resulted in high phytochrome far-red (Pfr) activity. Guttermann (1974) reported that the photo-stimulus required for *P. oleracea* germinations may be affected by the light conditions during seed maturation and suggested that seed germination was influenced by the photoperiod during the last eight hrs of seed development.

Table 8. Effect of season and GA_3 on *Portulaca oleracea* L. germination, El Zamorano, 1995-1996.

Season	Treatments	Germination	Dormant	Non viable
		---------- % [1] ----------		
dry	control	21 b	59 a	20 a
	0.1 µM	24 b	58 a	18 b
	1 µM	27 b	53 ab	20 a
	10 µM	40 a	43 b	17 b
rainy	control	15 a	66 a	18 a
	0.1 µM	17 a	66 a	16 a
	1 µM	15 a	69 a	15 a
	10 µM	21 a	64 a	15 a

[1] Means in columns within season followed by the same letter are not significantly different at the $P \leq 0.05$ level determined by Fisher's LSD test.

T. tubaeformis. Achenes collected in the dry season were highly dormant and viability was at least 87% (Table 9). Muñoz *et al.* (1995) reported high dormancy rates in *T. tubaeformis* achenes collected from three locations in Honduras. Compared to the control treatment, 10 µM GA_3 increased *T. tubaeformis* germination 52% and 15% for two and 24 weeks of storage. Ortíz (1991) enhanced

T. tubaeformis germination with a prechilling treatment and GA immersions for five days. GA_3 has also been reported to enhance *Tithonia rotundifolia* Mill. germination (Upfold and Staden, 1990). In addition, *T. tubaeformis* achene response to GA_3 decreased with the dry-cold storage. Compared to 24 weeks of storage after collection, achenes with two weeks of storage germinated more when 10 µM GA_3 was applied (Table 9). Upfold and Staden (1990) discovered that storage induced a light requirement for germination of *T. rotundifolia* achenes.

Table 9. Effect of storage and GA_3 on the germination of *Tithonia tubaeformis* (Jacq.) Cass. after 2 and 24 weeks on seeds collected during the dry season, El Zamorano, 1995.

Treatment	Germination		Dormant		Non viable	
	2	24	2	24	2	24
	---------- % [1] ----------					
control	1 b	3 c	90 a	84 a	9 a	13 a
0.1 µM	3 b	2 c	86 a	86 a	11 a	12 a
1 µM	3 b	4 b	87 a	86 a	10 a	10 a
10 µM	53 a	18 a	34 b	73 b	13 a	9 a

[1] Means in columns within storage period followed by the same letter are not significantly different at the $P < 0.05$ level determined by Fisher's LSD test.

C. echinatus. Caryopses collected in the rainy season were at least 93% viable and compared to the control, no response to GA_3 was observed (Table 10). Bhupathi *et al.* (1983) reported no effect of GA_3 on the germination of *Cenchrus ciliaris* L. seeds. Nevertheless, they obtained good germination when applying potassium nitrate and thiourea to *C. ciliaris* seeds. Pandeya and Lieth (1993) suggested that anthocyanins in sandbur glumes may be responsible for the dormancy in fresh seeds and indicated that seed storage may help overcome dormancy in several sandbur ecotypes.

C. virgata. Caryopses collected in the rainy season demonstrated higher dormancy than caryopses collected in the dry season (Table 11). Compared to the control, 10 µM GA_3 enhanced *C. virgata* germination 20% and 13% for caryopses collected in the dry and rainy seasons, respectively. Lodge and Whalley (1981) reported 20% germination from *Chloris truncata* R.Br. seeds collected in April and indicated that seed storage enhanced germination. Anderson (1968) enhanced the germination of *C. truncata* Swartz 60% when seeds were incubated under illumination. The presence of glumes, lemma and palea determines the germination of fingergrasses (Anderson, 1968; Lodge and Whalley, 1981). In other grass species, the lemma and palea reduced oxygen uptake or mechanically restrained radicle protrusion (Mott, 1974).

Table 10. Effect of GA_3 on the germination of *Cenchrus echinatus* L. collected during the rainy season, El Zamorano, 1995.

Treatments	Germination	Dormant	Non viable
	---------- % [1] ----------		
control	33 a	61 a	6 a
0.1 µM	43 a	51 a	6 a
1 µM	31 a	62 a	7 a
10 µM	32 a	64 a	4 a

[1] Means in columns followed by the same letter are not significantly different at the $P \leq 0.05$ level determined by Fisher's LSD test.

Table 11. Effect of season and GA_3 on *Chloris virgata* Swartz germination, El Zamorano, 1995-1996.

Season	Treatments	Germination	Dormant	Non viable
		---------- % [1] ----------		
dry	control	69 b	25 a	6 a
	0.1 µM	66 b	27 a	7 a
	1 µM	75 ab	18 a	7 a
	10 µM	89 a	4 a	7 a
rainy	control	14 b	72 a	14 a
	0.1 µM	13 b	76 a	11 a
	1 µM	14 b	76 a	10 a
	10 µM	27 a	63 b	10 a

[1] Means in columns within season followed by the same letter are not significantly different at the $P \leq 0.05$ level determined by Fisher's LSD test.

E. indica. Caryopses were highly dormant and viability was at least 84% (Table 12). Hawton and Drennan (1980) reported that *E. indica* caryopses were highly dormant when shed from the mother plant. *E. indica* caryopses viability was approximately 90% after 18 months (Horng and Leu, 1978) and 2.5 years (Egley and Chandler, 1978) of storage. In Africa, seeds have been reported to remain viable after five years of burial (Schwerzel, 1976).

Compared to the control, 10 µM GA_3 enhanced *E. indica* germination for caryopses with 24 weeks of storage 82% in collections during the dry season (Table 12). This promotion of germination by GA_3 was affected by the dry-cold storage period. Hawton and Drennan (1980) enhanced *E. indica* germination with 0.1% solution of GA_3. Other seed-applied chemicals have been reported to enhance *E. indica* germination (Toole and Toole, 1940; Hawton and Drennan, 1980).

Table 12. Effect of season, storage (2 and 24 weeks), and GA_3 on *Eleusine indica* (L.) Gaertner germination, El Zamorano, 1995-1996.

Season	GA_3	Germination 2	Germination 24	Dormant 2	Dormant 24	Non viable 2	Non viable 24
		% [1]					
dry	control	13 a	1 b	80 a	86 b	7 a	12a
	0.1 µM	13 a	2 b	82 a	89 a	5 a	9a
	1 µM	12 a	3 b	82 a	87 ab	6 a	10a
	10 µM	40 a	83 a	53 a	5 c	7 a	13a
rainy	control	1 a	7 a	88 a	77 a	11 a	16a
	0.1 µM	0 a	7 a	94 a	77 a	6 a	16a
	1 µM	1 a	7 a	89 a	80 a	10 a	13a
	10 µM	2 a	20 a	87 a	66 a	11 a	14a

[1] Means in columns within season followed by the same letter are not significantly different at the $P \leq 0.05$ level determined by Fisher's LSD test.

S. halepense. Seeds demonstrated a high degree of dormancy and were at least 82% viable (Table 13). Several investigations indicated that *S. halepense* seeds have high innate dormancy when shed from the mother plant (Weir, 1959; Warwick and Black, 1983). Taylorson and McWhorter (1969) reported great variation in the germination characteristics of 43 *S. halepense* ecotypes. The low germination rate obtained in this investigation may be a result of the incubation conditions because dark conditions have been demonstrated to reduce germination (Monaghan, 1979; Warwick and Black, 1983). McWhorter (1972) reported that phytochrome activation was an important component of *S. halepense* dormancy.

No significant effect on *S. halepense* germination was observed for GA_3 (Table 13). The seed coat may have prevented the diffusion of GA_3 into the embryo. Huang and Hsiao (1987) promoted *S. halepense* germination by exposing seeds to 5µM GA_3, 16 hr light, and 35° C. Further studies by Hsiao and Huang (1988) reported that the interaction between light, GA_3, and sodium hypochlorite produced a synergistic effect on *S. halepense* germination.

Table 13. Effect of season and GA_3 on *Sorghum halepense* (L.) Pers. germination, El Zamorano, 1995-1996 .

Season	GA_3	Germination	Dormant	Non viable
		% [1]		
dry	control	6 a	82 a	12 b
	0.1 µM	3 a	81 a	16 a
	1 µM	4 a	82 a	14 ab
	10 µM	5 a	82 a	13 b
rainy	control	2 a	82 a	16 a
	0.1 µM	2 a	80 a	18 a
	1 µM	1 a	85 a	14 b
	10 µM	3 a	80 a	17 a

[1] Means in columns within season followed by the same letter are not significantly different at the $P \leq 0.05$ level determined by Fisher's LSD test.

Effect of wounding position on *S. halepense* and *B. pilosa* germination. More *B. pilosa* germination was obtained with the control treatment and wounding the distal region of the achene (Table 14). Compared to the control, wounding the proximal and central region of *B.*

pilosa achenes reduced the germination and increased the proportion of non-viable achenes. Henry-Vian *et al.* (1995) reported that wounding the cotyledon of *B. pilosa* seedlings enhanced polysomal mRNA that signaled the inhibition of hypocotyl development. Central wounding may have damaged the embryo axis and possibly promoted the synthesis of plant growth inhibitors.

S. halepense seeds demonstrated high degrees of dormancy and less than 10% germinated in the control treatment (Table 14). Wounding enhanced *S. halepense* germination and but also increased the number of non viable seeds. At least 16% more germination was obtained when wounding the distal section of *S. halepense* seeds compared to other wounding positions (Table 14). Harrington (1923) associated *S. halepense* dormancy with the presence of glumes during germination. Bennett (1973) reported that *S. halepense* dormancy was largely imposed by the seed coat which contained tannins that reduced water permeability. In addition, Taylorson and McWhorter (1969) indicated that seed dormancy resulted from a mechanical restraint imposed by the seed coat and suggested the dormancy was genetically controlled by the integuments during seed development.

Germination of dimorphic *B. pilosa* achenes. Long-thin *B. pilosa* achenes germinated five times more and were twice less dormant than short-thick achenes (Table 15). Forsyth and Brown (1982) reported that long achenes germinated under a wider range of environmental conditions and suggested red light or scarification enhanced short achene germination. Compared to long achenes, short achenes have a thicker seed coats that may limit imbibition, oxygen diffusion or radicle protrusion. In addition, seedlings originating from short achenes displayed lower survival rates and slower initial growth development (Forsyth and Brown, 1982).

Zelaya (1997) suggested that germination differences between dimorphic achenes
may be evolutionarily advantageous because *B. pilosa* germination could extend throughout the growing season. Under crop canopies, long achenes may be favored to germinate because exposure to far-red radiation inhibited the germination of short achenes. However, Fenner (1980a; 1980b) reported that *B. pilosa* germination was reduced by shading. Fenner (1980c) indicated that one hr exposure to leaf shade promoted the development of a light requirement for gemination and thus prevented direct competition with established plants. Fenner (1980b) suggested that seed sensitivity to canopy shading is an important determinant of changes in the composition of *B. pilosa* populations.

Table 14. Effect of wounding positions on *Bidens pilosa* L. and *Sorghum halepense* (L.) Pers. germination, El Zamorano, 1996.

Species	Wounding position	Germination	Dormant	Non viable
		% [1]		
B. pilosa	no wounding	63 a	9 a	28 c
	distal	63 a	11 a	26 c
	central	32 c	2 b	66 a
	proximal	50 b	3 b	47 b
S. halepense	no wounding	7 c	75 a	18 d
	distal	48 a	14 b	38 c
	central	26 b	1 d	73 a
	proximal	32 b	5 c	63 b

[1] Means in columns within species followed by the same letter are not significantly different at the P ≤ 0.05 level determined by Fisher's LSD test.

Table 15. Germination and dormancy of dimorphic *Bidens pilosa* L. achenes, El Zamorano, 1996.

Morphism	Germination	Dormant	Non viable
	% [1]		
short and thick	11 b	56 a	33 a
long and thin	56 a	23 b	21 b

[1] Means in columns followed by the same letter are not significantly different at the P ≤ 0.05 level determined by Fisher's LSD test.

CONCLUSIONS

The germination characteristics varied within the eight weed species and may result in greater plasticity of the weed community to emerge at different times of the growing season. *B. pilosa* and *C. virgata* seeds

demonstrated little dormancy, thus represent species that emerge readily with the arrival of the rainy season. *A. hybridus*, *T. tubaeformis*, *E. indica*, and *S. halepense* had high percentage of dormancy thus their seeds may remain viable in the soil seed bank for several years. Seed developmental position on the mother plant only had an effect on *P. oleracea* and *C. virgata* germination. *P. oleracea* seeds that developed on the upper 20% of the mother plant were less dormant that seeds developed in the lower 20%. However, *C. virgata* caryopses germinated more when developed on the lower 20% of the spike. The seed storage conditions promoted the germination of *B. pilosa*, *P. oleracea* and *S. halepense* but were detrimental to that of *C. virgata*.

The germination of *A. hybridus*, *P. oleracea*, *T. tubaeformis*, *C. virgata*, and *E. indica* was promoted by GA_3. *A. hybridus*, *P. oleracea*, and *E. indica* collections in the rainy season were less responsive to GA_3. *T. tubaeformis* achenes germinated more when 10 µM GA_3 was applied to achenes with two weeks of storage after collection than 24 weeks of storage after collection. *E. indica* caryopses germinated more when 10 µM GA_3 was applied to caryopses with 24 weeks of storage. Wounding the distal region of *B. pilosa* and *S. halepense* seeds resulted in more germination. Long-thin *B. pilosa* achenes germinates better than short-thick ones.

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LITERATURE CITED

Akobundu, I.O. 1987. Weed science in the tropics: principles and practices. John Wiley and Sons, Great Britain. pp 522.

Anderson, R.N. 1968. Germination and establishment of weeds for experimental purposes. Weed Science Society of America, W.F. Humphrey Press Inc, Geneva, New York. pp 236.

Baskin J.M., and C.C. Baskin. 1987a. Temperature requirements for after-ripening in buried seeds of summer annual weeds. Weed Research 27:385-389.

Baskin J.M., and C.C. Baskin. 1987b. Role of temperature in regulating the timing of germination in *Portulaca oleracea*. Canadian Journal of Botany 66:563-567.

Bennett, H.W. 1973. Johnsongrass, carpetgrass and other grasses for the humid south. Pag. 286-293. *In* M.E. Heath,; D.S. Metcalfe, and R.F. Barnes (eds.) Forages. Iowa State University Press, Ames, Iowa.

Bewley J.D., and M. Black. 1994. Seeds: physiology of development and germination. Plenum Press, New York. pp 445.

Bhupathi, P., J.A. Selvaraj, and K.R. Ramaswamy. 1983. A note on seed dormancy in *Cenchrus ciliaris* L. Seed Research 11:232-234.

Black, M., and J.M. Naylor. 1959. Prevention on the onset of seed dormancy by gibberellic acid. Nature 184:468-469.

Bradbeer, J.W. 1988. Seed dormancy and germination. Blackie and Son Ltd, London. pp 146.

Cantoria, M., and N.V.C. Gacutan. 1972. Germination behavior of *Gynura crepidioides* Beeth., *Portulaca oleracea* L. and *Dactyloctenium aegyptium* (L.) Ascress and Schwein. Plant Physiology 79(supp.):14.

Darlington, H.T., and G.P. Steinbauer. 1961. The eighty-year period for Dr. Beal's seed viability experiment. American Journal of Botany 48:321-325.

Duke, S.O., G.H. Egley, and B.J. Recer. 1977. Model for variable light sensitivity in imbibed dark-dormant seeds. Plant Physiology 59:244-249.

Dunn, S. 1970. Light quality effects on the life cycle of common purslane. Weed Science 18:611-613.

Egley, G.H. 1974. Dormancy variation in common purslane seeds. Weed Science 22:535-540.

Egley, G.H., and J.M. Chandler. 1978. Germination and viability of weed seeds after 2.5 years in a 50-year buried seed study. Weed Science 26:230-239.

Engelhardt, M., M. Vicente, and K. Silberschmidt. 1962. The stimulating effect of light and potassium nitrate on the germination of seeds of *Amaranthus hybridus* L. Revista Brasileira de Biologia 22:1-7.

Fenner, M. 1980a. Germination test on thirty-two east African weed species. Weed Research 20:135-138.

Fenner, M. 1980b. The inhibition of germination of *Bidens pilosa* seeds by leaf canopy shade in some natural vegetation types. New Phytologist 84:95-101.

Fenner, M. 1980c. The induction of light requirement in *Bidens pilosa* seeds by leaf canopy shade. New Phytologist 84:103-106.

Forsyth, C., and N.A.C. Brown. 1982. Germination of the dimorphic fruits of *Bidens pilosa* L. New Phytologist 90:151-164.

Gosling, P.G., R.A. Butler,, M. Black, and J.M. Chapman. 1981. The onset of germination ability in developing wheat. Journal of Experimental Botany 32:621-627.

Groot, S.P.C., and C.M. Karssen. 1992. Dormancy and germination of abscisic acid-deficient tomato seeds. Plant Physiology 99:952-958.

Guttermann, Y. 1973. Differences in the progeny due to day-length and hormone treatment of the mother plant. Pag. 59-80 *In* W. Heydecker (ed.) Seed Ecology. The Pennsylvania State University Press, University Park, Pennsylvania.

Guttermann, Y. 1974. The influence of the photoperiodic regime and red-far red light treatments of *Portulaca oleracea* plants on the germinability of their seeds. Oecologia 17:27-38.

Harper, J.L. 1977. Population biology of plants. Academic Press Inc, Great Britain. pp 892.

Harrington, G.T. 1916. Germination and viability tests of johnsongrass seed. Proceedings of the Association of Official Seed Analysts 9:24-28.

Harrington, G.T. 1917. Further studies of the germination of johnsongrass seeds. Proceedings of the Association of Official Seed Analysts 10:71-76.

Harrington, G.T. 1923. Use of alternating temperature in the germination of seeds. Journal of Agricultural Research 23:295-332.

Hawton, D., and D.S.H. Drennan. 1980. Studies on the longevity and germination of seed of *Eleusine indica* and *Crotalaria goreensis*. Weed Research 20:217-223.

Henry-Vian, C., A. Vian, A. Dietrich, G. Ledoigt, and M.O. Desbiez. 1995. Changes in the polysomal mRNA population upon wound signal expression or storage in *Bidens pilosa*. Plant Physiological Biochemistry 33:337-344.

Holm, R.E., and M.R. Miller. 1972. Weed seed germination responses to chemical and physical treatments. Weed Science 20:150-153.

Holm, L.G., D.L. Plucknett, J.V. Pancho, and J.P. Herberger. 1977. The world's worst weeds: distribution and biology. The University Press of Hawaii, Honolulu. pp 609.

Horng, L.C., and L.S. Leu. 1978. The effect of depth and duration of burial on the germination of ten annual weed seeds. Weed Science 26:4-10.

Hsiao, A.I., and W.Z. Huang. 1988. Induction of germination of skotodormant seeds of Johnson grass, *Sorghum halepense* (L.) Pers. Weed Research 28:163-174.

Hsiao, A.I. 1993. Actions of acid immersion, red light and gibberellin A_3 treatments on germination of thermodormant lettuce seeds. Environmental and Experimental Botany 33:397-404.

Huang, W.Z., and A.I. Hsiao. 1987. Factors affecting seed dormancy and germination of Johnsongrass, *Sorghum halepense* (L.) Pers. Weed Research 27:1-12.

Kigel J., M. Ofir, and D. Koller. 1977. Control of the germination responses of *Amaranthus retroflexus* L. seed by their parental photothermal environment. Journal of Experimental Botany 28(106):1125-1136.

Kigel, J. 1994. Development and ecophysiology of amaranths. Pag. 39-73. *In*: O. Paredes-López (ed.). Amaranth Biology, Chemistry, and Technology. CRC Press Inc, Boca Raton, Florida.

Koller, D. 1962. Preconditioning of germination in lettuce at time of fruit ripening. American Journal of Botany 49:841-844.

Lodge G.M., and R.D.B. Whalley. 1981. Establishment of warm- and cool-season native perennial grasses on the north-west slopes of the new south wales. I. dormancy and germination. Australian Journal of Botany 29:111-119.

Mann, M.A., and P.B. Cavers. 1971. Seed production and dormancy in *Rumex crispus*. I. The effect of cauline leaves at anthesis. Canadian Journal of Botany 49:1123-1130.

Matthews J.F., D.W. Ketron, and S.F. Zane. 1993. The biology and taxonomy of the *Portulaca oleracea* L. (Portulacaceae) complex in North America. Rhodora 95(882):166-183.

McWhorter, C.G. 1972. Factors affecting johnsongrass rhizome production and germination. Weed Science 20:41-45.

Miyanishi, K., and P.B. Cavers. 1980. The biology of Canadian weeds. 40. *Portulaca oleracea* L. Canadian Journal of Plant Science 60:953-963.

Monaghan, N. 1979. The biology of Johnson grass (*Sorghum halepense*). Weed Research 19:261-267.

Moore, R.P. 1985. Handbook on tetrazolium testing. The International Seed Testing Association, Switzerland. pp 120.

Mott, J.J. 1974. Mechanisms controlling dormancy in the arid-zone grass *Aristida contorta*. I. physiology and mechanisms of dormancy. Australian Journal of Botany 22:635-645.

Muñoz, R., A. Pitty, and V. Ortíz. 1995. Algunos aspectos biológicos de la maleza *Tithonia tubaeformis* (Jacq.) Cass en el Zamorano, Honduras. Ceiba 36(2):255-261.

Ni, B.R., and K.J. Bradford. 1993. Germination and dormancy of abscisic acid- and gibberellin-deficient mutant tomato (*Lycopersicon esculentum*) seeds. Plant Physiology 101:607-617.

Ortíz, V.J. 1991. Biología y control químico de la maleza *Tithonia tubaeformis* (Jacq.)Cass. Ing. Agr. Thesis, Escuela Agrícola Panamericana, El Zamorano, Honduras. pp 48.

Pal, A.; R.P. Singh, and M. Pal. 1990. Development and structure of seeds in *Amaranthus hypochondriacus* L. and its wild progenitor *A. hybridus* L. Phytomorphology 40:145-150.

Pandeya, S.C, and H. Lieth. 1993. Ecology of cenchrus grass complex. Environmental conditions and population differences in Western India. Kluwer Academic Publishers, Dordrecht, Netherlands. pp. 175-222.

Phaneendranath, B.R., R.W. Duell, and C.R. Funk. 1978 Dormancy of Kentucky bluegrass seed in relation to color of spikelet and panicle branches at harvest. Crop Science 18:683-684.

Pitty, A., and R. Muñoz. 1991. Guía práctica para el manejo de malezas. Escuela Agrícola Panamericana, El Zamorano, Honduras. pp. 148-149.

Raju, M.V.S., and S.N. Ramaswamy. 1983. Studies on the inflorescence of wild oats (*Avena fatua* L.). Canadian Journal of Botany 61:74-78.

Reddy, K.N., and M. Singh. 1992. Germination and emergence of hairy beggarticks (*Bidens pilosa*). Weed Science 40:195-199.

Rice, E.L. 1974. Allelopathy. Academic Press, New York. pp. 353.

Rojas-Garciduenas, M., and T. Kommedahl. 1960. The effects of 2,4-D on germination of pigweed seeds. Weeds 8:1-5.

Santelmann, P.W., and L. Evetts. 1971. Germination and herbicide susceptibility of six pigweed species. Weed Science 19:51-54.

SAS Institute Inc. 1987. SAS user's guide: statistics. SAS Institute Inc., Cary, North Carolina. pp 113-138.

Schwerzel, P.J. 1976. The effect of depth of burial in soil on the survival of some common Rhodesian weed seeds. Rhodesian Agricultural Journal 73:97-99.

Simpson, G.M. 1965. Dormancy studies in seed of *Avena fatua*. 4. the role of gibberellin in the embryo dormancy. Canadian Journal of Botany 43:793-816.

Simpson, G.M. 1990. Seed dormancy in grasses. Cambridge University Press, Great Britain. pp 297.

Singh, K.P. 1973. Effect of temperature and light on seed germination of two ecotypes of *Portulaca oleracea* L. New Phytologist 72:289-295.

Taylorson, R.B., and S.B. Hendricks. 1969. Action of phytochrome during prechilling of *Amaranthus retroflexus* L. seeds. Plant Physiology 44:821-825.

Taylorson, R.B., and S.B. Hendricks. 1971. Changes in phytochrome expressed by germination of *Amaranthus retroflexus* L. seeds. Plant Physiology 47:619-622.

Taylorson, R.B., and C.G. McWhorter. 1969. Seed dormancy and germination in ecotypes of Johnsongrass. Weed Science 17:359-361.

Taylorson, R.B., and M.M. Brown. 1977. Accelerated after-ripening for overcoming seed dormancy in grass weeds. Weed Science 25:473-476.

Taylorson, R.B. 1970. Changes in dormancy and viability of weeds seeds in soils. Weed Science 18:265-269.

Teitz, A.Y., S.F. Gorski, and M.B. McDonald. 1990. The dormancy of livid amaranth (*Amaranthus lividus* L.) seeds. Seed Science and Technology 18:781-789.

Toole, E.H., and V.K. Toole. 1940. Germination of seed of goosegrass, *Eleusine indica*. Journal of the American Society of Agronomy 32:320-321.

Twentyman, J.D. 1974. Environmental control of dormancy and germination in the seeds of *Cenchrus longispinus* (Hack.) Fern. Weed Research 14:1-11.

Upfold, S.J., and J.V. Staden. 1990. The germination characteristics of *Tithonia rotundifolia*. Annals of Botany 66:57-62.

Warwick, S.I., and L.D. Black. 1983. The biology of Canadian weeds: 61. *Sorghum halepense* (L.) Pers. Canadian Journal of Plant Science 63(4):997-1014.

Weaver S.E., and E.L. McWilliams. 1980. The biology of Canadian weeds. 44. *Amaranthus retroflexus* L., *A. powellii* S. Wats. and *A. hybridus* L. Canadian Journal of Plant Science 60:1215-1234.

Weir, H.L. 1959. Germination of Johnson grass. Proceedings of the Association of Official Seed Analysts 49:82-83.

Wellington, P.S. 1956. Studies on the germination of cereals. 1. The germination of wheat grains in the ear during development, ripening and after-ripening. Annals of Botany 20:105-120.

Williams. J.T., and Harper, J.L. 1965. Seed polymorphism and germination. 1. The influence of nitrates and low temperatures on germination of *Chenopodium album*. Weed Research 5:141-150.

Wurzburger, J., and D. Koller. 1973. Onset of seed dormancy in *Aegilops kotschyi* Boiss.-itsexperimentalmodification. New Phytologist 72:1057-1061.

Zelaya, I.A. 1997. La reproducción de malezas. Pag. 27-48. *In*: A. Pitty (ed.) Introducción a la Biología, Ecología y Manejo de Malezas. Zamorano Academic Press, Honduras.

Zimmerman, C.A. 1977. A comparison of breeding systems and seed physiologies in three species of *Portulaca oleracea* L. Ecology 58:860-868.