

Early Growth and Development of Horseweed (*Conyza canadensis* (L.) Cronq.)

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Abstract

Horseweed (*Conyza canadensis* (L.) Cronq.) produces thousands of small elongated seeds which are botanically defined as achenes; yet, relative to the quantity of achenes produced, few seedlings survive to produce mature plants. The developmental progression from achene to 4 mm seedlings was documented, and seedling response to moisture deprivation was described. Radical protrusion through the pericarp occurred between 18 and 30 hours after onset of imbibition in water or when germinated on soil at or greater than field capacity. A ring of root hair initials formed immediately after radical emergence at the interface of what was to become the separation between the root and hypocotyl. By 48 hours post imbibition, radicals differentiated into a distinct root with root cap and a hypocotyl, and root hairs elongated. By 72 hours post imbibition, seedlings had emerged from the pericarp, and had: expanded photosynthetic cotyledons, a clearly defined hypocotyl, a ring of elongated root hairs exceeding 1 mm in length, and a root equal or longer than the hypocotyl. The epicotyl had not yet emerged, and the total seedling length was approximately 3 to 4 mm. Germination was delayed on soil at or below field capacity. More than 95% of two- and four-day-old seedlings that had been desiccated for more than 24 hours died after being rehydrated.

Keywords

Horseweed, *Conyza canadensis*, Germination

1. Introduction

Horseweed (*Conyza canadensis* (L.) Cronq.) is a native North American weed species found in over 40 crops and in 70 countries [1] [2]. Horseweed has become a significant threat to soybean, cotton, and vegetable crops production by reducing yields, and may also interfere with harvesting operations [3] [4] [5].

Horseweed is also a host for tarnished plant bug (*Lygus lineolaris* (Palisot de Beauvois)), a primary pest of economic concern in cotton production [2] [6]-[11], *Adelphocoris lineolatus* (Geoze), a major pest in alfalfa [12], and numerous bacteria, fungi and viruses [2]. Thus, gaining insight into horseweed establishment and development may reveal new control options thereby reducing yield losses and curbing the buildup of insect pests and diseases.

The increase in horseweed populations in cropping systems was the result of several factors. Most important was the shift to conservation tillage land management programs and the evolution and rapid spread of herbicide resistant biotypes [13] [14]. Horseweed produces thousands of seeds with single plant estimates greater than 200,000 plant⁻¹ [15]. The seeds, botanically defined as achenes, do not require after-ripening and germination may exceed 80% [16]. The pericarp of the achene has a modified calyx, called the pappus, consisting of awns approximately 2 mm in length which enables wind dissemination up to 500 m from source populations [17]. Furthermore, horseweed may behave as a biennial germinating in the fall and growing to an overwintering rosette stage which bolts in the spring, or as a summer annual, germinating in spring, and completing its life cycle in a single season [2]. The biennial growth format affords early growth when favorable fall conditions persist positioning horseweed to resume growth from the more difficult to control rosette stage in the spring. Fortunately, from a management perspective, rosette survival in the following spring is highly variable with estimates between 3% and 91% depending on fall growth conditions [18] [19]. Rosette survival was highly correlated with rosette size [19].

Control options for emerged horseweed are most effective prior to planting and tillage alone can significantly reduce horseweed populations [20] [21]. Shallow fall tillage was reported to effectively prevent it from becoming a serious weed problem [3]. Spring cultivation as tandem-disked once or twice in conventional and minimum-tillage soybeans controlled horseweed [22]. Horseweed rosettes beginning to bolt were more difficult to control necessitating control by mechanical destruction like disking [3]. Herbicides, such as glyphosate, 2,4-D, chlorimuron, and paraquat applied postemergence were effective means of controlling seedlings and rosettes [13]. However, plants not killed by cultivation or chemical burn down may re-grow and sprout multiple stems resulting in increased seed production and be less susceptible to later herbicide applications [23].

No-tillage and conservation tillage practices favor horseweed survival because the soil surface is undisturbed, and horseweed has since emerged as a problem in these production systems [13] [14]. Conservation tillage practices expanded because effective pre- and post-emergence herbicides were readily available that could control horseweed [13] [22]. The introduction of glyphosate-resistant soybean in 1996 followed by corn and cotton a few years later resulted in a dramatic increase in use of glyphosate [24]. Within five years of commercialization of transgenic soybeans, glyphosate resistant horseweed was reported in Delaware

and in Arkansas a year later [25]. Since then 27 other states have reported glyphosate resistant horseweed [26]. The evolution of herbicide resistance especially to postemergence herbicides such as glyphosate and paraquat has contributed to horseweed becoming a significant weed control problem. Herbicide resistant populations of horseweed are found across the USA and Canada [26]. Horseweed has also evolved resistance to acetolactate synthase inhibitor herbicides (9 states reporting) and photosystem I and II herbicides (4 states reporting) [26], and some populations have multiple resistances to glyphosate and ALS herbicides, and glyphosate and paraquat [27].

Considering the importance of limiting horseweed survival because of its high seed production and germination capacity, its capacity to overwinter as rosettes, its resistance to herbicides and its role as host for insects and disease, gaining further insight into its most sensitive growth stages may lead to improved control strategies. Knowledge of seedling germination characteristics and seedling survival under adverse conditions may aid in development of improved horseweed management systems [28]. The objectives of this research were to describe the early stages of horseweed development from onset of germination to seedling pegging in soil and to characterize the effects of water deprivation on seedling survival following a period of desiccation when grown on soil. Identifying how quickly seedlings succumb to desiccation and their ability to re-establish after a period of desiccation will aid farmers in timing the use of tillage to reduce horseweed infestations.

2. Materials and Methods

Horseweed rosettes were collected from a soybean field in Stoneville, MS in October 2017, and grown in a greenhouse with a 35°C/26°C day night temperature ($\pm 2^\circ\text{C}$) and at a day/night cycle of 16/8 h supplemented with high pressure sodium lamps until seed heads were mature. Humidity was not regulated. Pots containing the plants were watered weekly and fertilized biweekly with a pelleted fertilizer (Osmocote Plus 15-9-12, Everis NA Inc., P. O. Box 3310 Dublin OH 43016). Once mature, seeds were harvested using a hand-held vacuum cleaner fitted with a thin cloth filter inserted between the hose and attachment to catch the seeds. Once collected, the seeds were stored in plastic bags in the laboratory at room temperature (approximately 28°C).

To study the early stages of horseweed development, seeds were sown in 2 ml of water in 5 cm plastic Petri dishes which were sealed with Parafilm. Due to the small size of horseweed seed, the amount of seed sown per dish was based on seed mass. The seed mass consisted of a mixture of achenes with pappus' and pedicels. A 6 mg seed mass provided approximately 100 seeds per plate. Dishes were seeded with 6 mg of seed mass and seed number per dish was immediately determined by counting seed under the microscope. Petri dishes were placed under a bank of three cool fluorescence tubes centered 10 cm above the Petri dishes which provided $63 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ of white fluorescent light. Dark conditions were created by wrapping the dishes in aluminum foil. Germination per-

centages were calculated by counting the number of viable seedlings per petri dish with the aid of a dissecting microscope. Seedlings were considered viable when they had emerged from the pericarp and began to acquire chlorophyll in the cotyledons. Each treatment had four replications, and each experiment was repeated once. Seedlings were stained with aqueous 0.01% toluidine blue to provide contrast to translucent anatomical features. Photographs were taken with a Leica Z16 APO microscope. The early growth stages were monitored for 96 hours.

To determine the effects of soil moisture on seedling development, the field capacity of the soil was first measured. The soil to be used in experiments (300 g) was added to 1 L of distilled water and the mixture was filtered on Whatman #1 filter paper under mild vacuum. When water stopped being removed from the soil cake, the soil was removed, weighed and then dried in an oven at 60°C for 24 hours and weighed again. This procedure was applied to 6 batches of soil.

The germination percentage was determined in 5 cm diameter Petri dishes with soil (3 g) at 0.67 (2 ml distilled water), 1.0 (3 ml), and 1.5 (4.5 ml) of the field capacity, or in distilled water in the light (63 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ of white fluorescent light) and dark (foil wrapped dishes). The germination percentage on soil at 1.5 X field capacity was slightly less than germination in water so 1.5 X field capacity was used to obtain the highest germination for experimental purposes without overly saturating the soil. The drying rate of the soil at 1.5 X field capacity (4.5 mL per 3 g soil) was determined on 6 replicate dishes placed under fluorescent light without lids and the drying rate determination was repeated once. The weight of the wet soil in petri dishes was measured at 6-hour intervals, and by 24 hours of dehydration. The rate of water loss was described by the equation: $y = -0.195x + 4.56$ ($R^2 = 0.99$), where x = hours after removal of lids and y = soil water weight in grams.

To estimate horseweed survival following drying, as would occur in field conditions following a rain event, experiments were performed with field soil at 1.5 X field capacity. At 48 and 96 hours from onset of imbibition, the Petri dish lids were removed, the number of germinated seedlings was determined, and dishes allowed to dry for an additional 24, 48, 72 and 96 hours at which time dishes were weighed to determine water loss and rehydrated to 1.5 X field capacity. The dishes were then resealed and placed back in the light for four days at which time survival was determined by counting the number of seedlings that rehydrated as a percentage of the seedlings that originally germinated.

3. Results and Discussion

3.1. Horseweed Germination and Early Growth

Horseweed produces achenes which are small, dry one-seeded fruits that do not open to release the seed. The achene is ellipsoidal being approximately 1 mm in length and 0.3 mm in width and has small ciliated awn-like structures approximately 2 mm in length, called pappus, protruding from the distal end of the pericarp (**Figure 1a**). The achene was roughly 1/3 the size of an *Amaranthus pal-*

meri S. Watson seed (**Figure 1a**). Radical emergence occurred between 18 and 30 h post imbibition. Differentiation into primary root and hypocotyl began almost immediately after emerging from the proximal end of the pericarp (**Figure 1b**). A dense ring of root hair initials developed immediately behind the root apex at the intersection of what was to become the hypocotyl and root (**Figure 1b** and **Figure 1c**).

The pericarp was translucent allowing light to penetrate and cotyledons to initiate chlorophyll accumulation before emerging from the pericarp (**Figures 2a-c**). Root hairs and the primary root elongated to about 1mm in length (**Figures 2a**). Newly formed roots exhibited strong gravitropism and were observed to rapidly penetrate the soil surface (**Figure 2b**). The dense ring of root hairs elongated fanning out radially across the soil surface appearing to anchor the seedling to the soil (**Figure 2b**). After emerging from the pericarp, the cotyledons expanded (**Figure 2c**) and unfolded exposing the adaxial surface towards the light (**Figure 2c**). Cotyledons emerged from the pericarp between 48 and 72 hours post imbibition.

Root hairs (arrow) gradually formed along the elongating primary root and primary root length surpassed the length of the hypocotyl and cotyledons which did not increase in length (**Figure 3**).

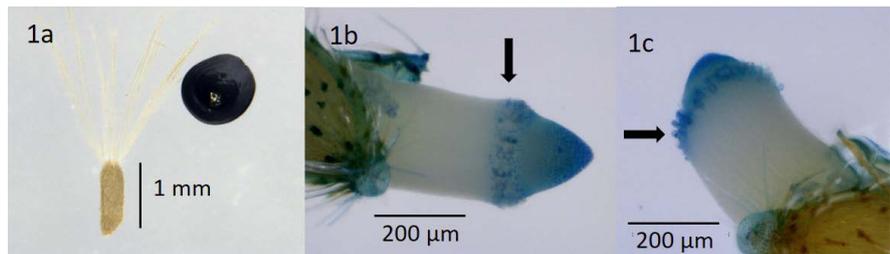


Figure 1. a: Horseweed achene (seed) with barbed awn-like structures approximately 2 mm in length, called pappus, protruding from the distal end of the pericarp compared to an *Amaranthus palmeri* seed; b: Recently emerged radical showing immature root cap demarcated from the hypocotyl by the root hair initials (arrow); c: Root hair initials beginning to elongate (arrow).



Figure 2. a: Seedling with cotyledons still encased in the pericarp and synthesizing chlorophyll. Root tip beginning to differentiate and root hairs elongating; b: Seedlings anchored to the soil by the primary root and root hairs spread out across the soil surface (black arrow). Cotyledons emerging from pericarp; c: Cotyledons enlarging and becoming photosynthetic as root hairs spread out across the soil surface (white arrow).

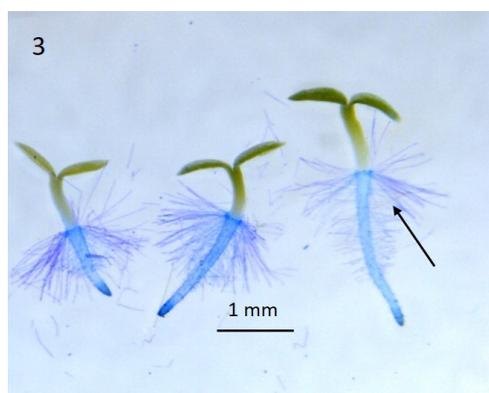


Figure 3. Comparison of seedlings showing growth of the primary root relative to the hypocotyl and cotyledons and development of the root hairs along the primary root axis.

3.2. Horseweed Seed Germination Requirements

The field capacity of the local field soil was found to be 3 ml water per 16 g soil. Horseweed seed germinated readily in tap water or on the soil surface when soil moisture exceeded the field capacity (**Table 1**). Radicle emergence began between 18 and 30 hours after initiation of imbibition in water or on soil at 1.5 X field capacity. Water levels at or below field capacity reduced germination (**Table 1**). Germination was greatest in white light and was much reduced in the dark (**Table 1**). These results indicate that in nature the initial stages of seedling growth and establishment may be delayed by lack of adequate moisture at the earliest stages of establishment resulting in a sparse stand. If drying conditions persist, then the growth may be inhibited to the point of death. Without adequate moisture, the root hairs being fragile single cells will become dehydrated and the root will be deprived of moisture to elongate. From a management perspective, in fields having high horseweed populations, extending the drying period after a rain event before tillage may help reduce infestations by severing root contact with the soil.

3.3. Seedling Response to Dehydration

The drying rate of soil at 1.5 X field capacity was 0.195 ml water lost per hour ($P < 0.0001$) and by 24 hours after removing Petri dish lids, soil lost 4.56 ml water. After germination, seedlings were very susceptible to dehydration. Desiccation treatments (drying dishes without sealed lids in the air for 24 to 96 hours before rehydration to 1.5 X of field capacity) resulted in nearly complete seedling death between 24 and 48 hours after exposure to drying (**Figure 4**). These data showed that at 24 hours post dehydration seedling viability could be re-established whereas between 48 to 96 hours seedling death was greater than 95%. The soil in the Petri dishes dried within 24 hours following removal of lids by visible estimation and measurement of Petri dish weight. This sensitivity to dehydration was similar for plants that were either 48, 72 or 96 hours old and

Table 1. Effects of light and water levels on percentage germination of horseweed seeds in water or on soil hydrated at, above and below field capacity (2 ml, 3 ml (field capacity) and 4.5 ml per 16 g soil in 5 cm diameter Petri dishes) in the dark or under white fluorescent light ($63 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) at 48 hours after onset of imbibition. Within columns, values followed by the same letter were not significantly different at $P \leq 0.05$.

Water per 16 g soil	Percent Germination	
	No light	Light ($63 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)
2 ml	0a	8b
3 ml (field capacity)	0a	28b
4.5 ml	0a	71a
Water only	18a	89a

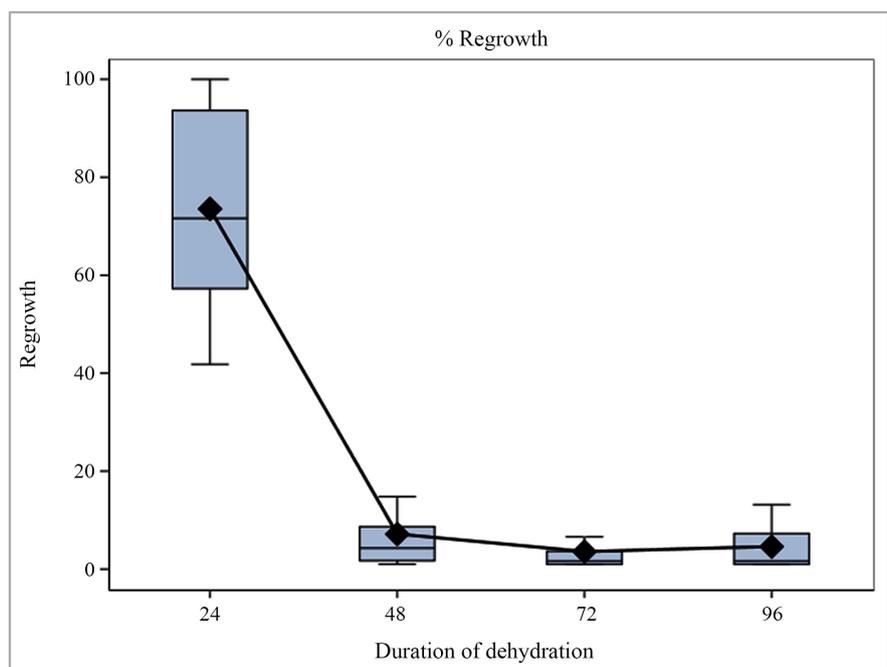


Figure 4. Box plot of the effect of dehydration and rehydration on survival of horseweed seedlings. 48 and 96 hours (two and four day) old seedlings were desiccated for 24, 48, 72 and 96 hours at which time soil was rehydrated to 1.5 X field capacity and dishes were covered and sealed with Parafilm. Dishes were seeded with 6 mg of seed mass (approximately 100 achenes) and seed number per dish was immediately determined by counting seed under the microscope. 96 hours after rehydration percentage survival was determined. Results between experiments were not significantly different ($P > F = 0.22$) so data were combined. The F value for duration of dehydration was F 156 (Prob > F 0.0001).

indicated that older seedlings were not more resilient to dehydration. These data indicated that the combined effect of a shallow tillage event to dry soil and a sufficient soil drying period after dislodging seedlings from the soil may improve horseweed control in infested fields. Tillage should be avoided right before a rain event to prevent rehydration, resumption of growth and seedling re-establishment.

3.4. Horseweed Management

Light tillage of an intensity to dislodge and bury seedlings and rosettes will exclude light which may also lessen seedling survival. Horseweed germination was stimulated in light compared to germination in the dark [29] but was limited to less than 5% by burial in as little as 0.25 cm of soil [29]. Germination was reduced more than 50% when buried in soil but placed on a surface receiving sunlight but was almost completely inhibited when buried in soil and placed in the dark [15]. The small size of seedlings, their propensity to make chlorophyll rapidly, and probable limited stored food reserves within the seed, may accentuate the requirement for rapid establishment and lack of emergence when light is compromised. The higher seedling and rosette populations found in no-till fields where seeds remain on the soil surface may similarly reflect the requirement of light for germination [30]. Germinating in the shade of other species or underneath plant litter below the level from which they can emerge may reduce seedling survival.

Figure 5 shows a dense cluster of horseweeds growing along the edge of a soybean field shortly after harvest in Lake Village, AR, 2019, and shows the practical application of horseweed management. Not observable was that the entire border had horseweed allowing continuous seed rain to be added to a field. Seeds falling along the field edges repopulate the borders and some seedlings establishment among the soybean debris may be expected. Prevailing winds may also scatter seeds well into the center of the field.

The loss of seedling viability in horseweed has been associated with post germination drying [29] which might be encountered in nature on sunny days between rain events [31]. Imbibed seeds and seedlings at 48 hours after onset of imbibition and then dried for 72 hours steadily lost viability at a rate of 3% per hour [31]. These experiments were performed with seed germinated in water on filter paper and may not adequately reflect desiccation on soil where germination and growth may be influenced by soil moisture or changes in osmotic stress. Horseweed germination decreased from 25% to 2% as osmotic potential increased from 0 (distilled water) to -0.8 MPa [29].



Figure 5. Mature (1.8 m tall) horseweed growing along the edge of a soybean field following harvest in Lake Village, AR, 2019. This field had horseweed along the entire border which allowed continuous seed rain in the field. A few stalks of horseweed were evident in the field post-harvest.

4. Conclusion

Under suitable conditions, horseweed rapidly transitioned through the early stages of development to having photosynthetic cotyledons, a well-developed root and hypocotyl as well as numerous root hairs combing the surface of the soil. These early stages of horseweed establishment were extremely sensitive to dehydration, which if of sufficient duration resulted in high seedling death. From a management perspective, the goal should be to prevent seedlings advancing to the rosette stage. Shallow tillage should occur as soon as it is feasible following a rain event in fields subject to horseweed contamination to dislodge seedlings from the soil but at a time with an anticipated drying period sufficient to dehydrate seedlings before the next rain event. Timely tillage operations performed in the fall and spring based on seedling and rosette presence, and the chances for sufficient drying period to kill horseweed would provide farmers an opportunity to improve control of horseweed.

Author Contributions

Writing-original draft preparation, review and editing, W.T.M., K. P. and C. L. B.; experimental procedures, W.T. M. and C. L. B.; photography, K. P. and W. T. M.

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Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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