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Comparing Physical, Chemical, and Cold Stratification Methods for Alleviating Dormancy of Giant Ragweed (*Ambrosia trifida*) Seeds

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Giant ragweed has become an increasingly important weed of arable land in many parts of North America. It is now a common weed of row crop production systems, a fact that can be attributed to earlier crop planting dates, reduced tillage, and the development of resistance to Group 2 and 9 herbicides. The propagation of giant ragweed seedlings for experimental purposes is a lengthy process because up to 90 d of stratification is often required to alleviate primary seed dormancy. The objective of this research was to evaluate physical, chemical, and cold stratification methods for alleviating seed dormancy in giant ragweed and reducing the length of cold stratification required. Results indicate that the most effective method for alleviating dormancy in seed of giant ragweed is to excise the embryo from its covering structures. By excising the embryo, 96% of viable giant ragweed seeds germinated with no stratification. In contrast, untreated seeds required a minimum of 6 wk of stratification to alleviate dormancy in a similar proportion of the population. Although excising embryos requires time and effort, the time savings relative to stratification make it an attractive method for propagating giant ragweed seedlings.

Nomenclature: Giant ragweed, *Ambrosia trifida* L. AMBTR.

Key words: Cumulative germination, excised embryo, gibberellic acid, physiological seed dormancy, Weibull function.

Ambrosia trifida se ha convertido en una maleza cada vez más importante en terrenos arables en muchas partes de Norteamérica. Esta maleza es ahora común en sistemas de producción de cultivos, un hecho que puede ser atribuido a fechas de siembra de cultivos más tempranas, labranza reducida, y el desarrollo de resistencia a herbicidas de los Grupos 2 y 9. La propagación de plántulas de *A. trifida* para fines experimentales es un proceso largo porque frecuentemente se requieren hasta 90 d de estratificación para aliviar la dormición primaria de la semilla. El objetivo de esta investigación fue evaluar métodos físicos, químicos, y de estratificación con frío para aliviar la dormición de la semilla en *A. trifida* y así reducir la duración de la estratificación con frío requerida. Los resultados indican que el método más efectivo para aliviar la dormición en semillas de *A. trifida* es extraer el embrión de las estructuras de cobertura de la semilla. Al extraer el embrión, 96% de las semillas viables de *A. trifida* germinaron en ausencia de estratificación. En contraste, semillas sin tratamiento requirieron un mínimo de 6 semanas de estratificación para aliviar la dormición en una proporción similar de la población. Aunque extraer los embriones requiere tiempo y esfuerzo, el ahorro relativo de tiempo en comparación con la estratificación, hace este método atractivo para la propagación de plántulas de *A. trifida*.

Giant ragweed has become an increasingly important weed of arable land in many parts of North America (Gibson et al. 2005; Johnson et al. 2009). Although it has historically been considered a weed of roadsides, fence rows, and ditches (Abul-Fatih et al. 1979; Alex 1964; Bassett and Crompton 1982), giant ragweed is now more common in row crop production systems, a fact that can be attributed to earlier crop planting dates, reduced tillage, and the development of resistance to Group 2 and 9 herbicides (i.e., inhibitors of acetolactate synthase/acetohydroxyacid synthase [ALS/AHAS] and EPSP [5-enolpyruvylshikimate-3-phosphate] synthase, respectively; Dinelli et al. 2013; Gibson et al. 2005; Patzold and Tranel, 2002;; Vink et al. 2013).

Giant ragweed biotypes resistant to glyphosate [*N*-(phosphonomethyl)glycine; Group 9] were first documented in the United States and Canada in 2004 and 2008, respectively (Heap 2014). As the acreage of glyphosate-resistant crops have increased over the past decade, so too have the number of suspected cases of glyphosate-resistant weed biotypes. Seed samples from plants suspected to be resistant are often submitted for testing in early

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Figure 1. Physical modifications of giant ragweed seeds prior to cold stratification: (left to right) untreated, snipped, and excised.

autumn. For weed species with little to no seed dormancy, such as Canada fleabane [*Conyza canadensis* (L.) Cronq.], the propagation of seedlings large enough to facilitate resistance testing can proceed without impediment following seed maturation (Weaver 2001). In contrast, seeds from weed species possessing an innate primary dormancy may require additional procedures, such as after-ripening, scarification, or several months of stratification, to alleviate dormancy, which can lead to lengthy delays in the process of resistance testing.

The dispersal unit of giant ragweed is an involucral achene (hereafter referred to as a seed) that possesses a physiological primary dormancy at maturity (Baskin and Baskin 2001, 2004; Davis 1930; Schutte et al. 2012). Germination is primarily inhibited by structures covering the embryo, which include a thick-walled involucre and a membranous seed coat. Dormancy of freshly collected giant ragweed seeds can be alleviated through exposure to cool, moist conditions (i.e., stratification); however, this is a lengthy process, often requiring up to 90 d of stratification (Davis 1930).

Although several authors have investigated methods for alleviating dormancy of giant ragweed seeds (Ballard et al. 1996; Davis 1930; Schutte 2007), none of these studies have reported a notable increase in germination (> 50%) without at least 10 to 12 wk of stratification. The development of a more rapid method to alleviate seed dormancy would facilitate the propagation of giant ragweed seedlings for experimental purposes and enable a more timely evaluation of suspected cases of herbicide resistance. Therefore, the objective of this research was to evaluate physical, chemical, and cold stratification methods for alleviating seed dormancy in giant ragweed and reducing the length of cold stratification required.

Materials and Methods

Mature seeds of giant ragweed were collected over several weeks in autumn 2011 from a natural, nonagricultural population. The seeds from each harvest were cleaned and combined to create a composite sample representing the range of giant ragweed maturation dates in a natural population. Seeds were stored at 4 C and 40% relative humidity for 9 to 10 mo prior to the start of the experiment.

A randomized complete block design was used to test the interaction of five cold stratification periods (0, 2, 4, 6, or 8 wk at 4 C) and five seed treatments on the germinability of giant ragweed seed. The five seed treatments tested were: (1) a untreated control of intact seed, (2) a snipped seed treatment, in which the crown of the involucre was sliced off with a razor blade (Figure 1), (3) complete excision of the embryo from the involucre and seed coat, (4) exogenous application of 0.02% gibberellic acid (GA_3) to intact seed, or (5) exogenous application of 0.1% potassium nitrate (KNO_3) to intact seed. Physical modifications to the seeds (i.e., the snipped and excised treatments) were made prior to cold stratification, whereas GA_3 and KNO_3 were applied following stratification.

Experimental units consisted of Petri dishes containing 15 giant ragweed seeds for each stratification period by seed treatment combination. In preparation for stratification, giant ragweed seeds were screened for visible signs of insect predation (Amatangelo 1974) prior to being placed in Petri dishes, lined with blue blotter paper (i.e., steel blue germination blotters, Anchor Paper Company, St. Paul, MN), and moistened with 8 ml of reverse osmosis (RO) water. Following each cold stratification treatment, seeds were transferred to new Petri dishes, moistened with RO water, GA_3, or KNO_3 where appropriate, and placed in an a controlled-environment chamber (model G30, Conviron, Controlled Environments Ltd., Winnipeg, MB, Canada) with a photoperiod of 14 h and an alternating thermoperiod of 25/15 C (day/night). This chamber was outfitted with two banks of four cool white fluorescent tubes, which provided an average photosynthetic photon flux density of 100 $\mu mol\ m^{-2}\ s^{-1}$ and a red to far-red ratio of 5.

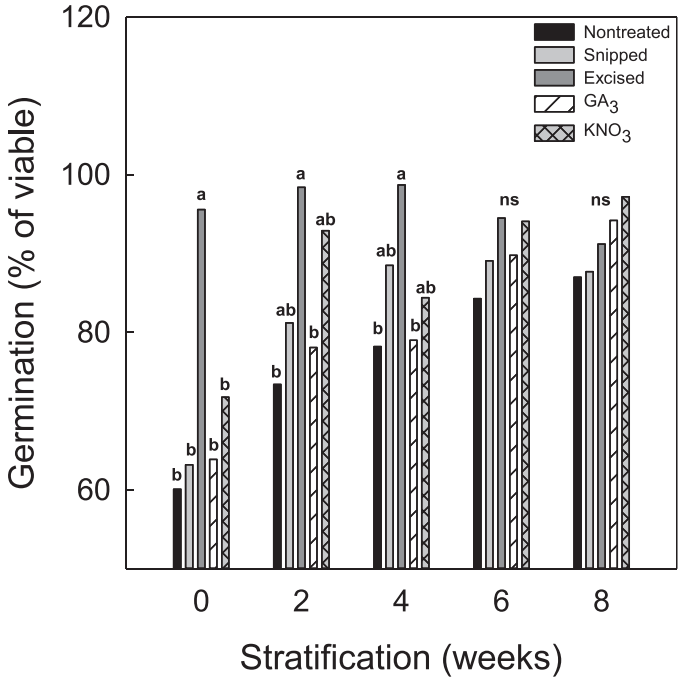

Figure 2. Germination (% of viable) of giant ragweed seeds after 14 d of incubation. Analysis of variance of arcsine square root–transformed data indicated a significant seed treatment by stratification time interaction ($P < 0.05$). Letter groups indicate significance differences ($P < 0.05$) within a stratification period; ns, nonsignificant.

Germination was defined as the protrusion of the radicle through the involucre by more than 20 mm and was recorded daily for 14 d. Viability of nongerminated seeds was determined using 0.1% tetrazolium chloride solution (Peters 2000).

The experiment was repeated twice in time, with five replicate shelves in the growth cabinet within each repetition. Statistical analyses were carried out using a mixed model ANOVA (PROC MIXED, SAS Institute, Cary, NC). The total number of viable seeds after 14 d (i.e., germinated and nongerminated but viable seeds) were expressed as a percentage of total seeds initially set to germinate and were arcsine square root–transformed prior to analysis. Replicate and replicate within repetition were treated as random effects, whereas seed treatments and stratification periods were considered fixed effects. The COVTEST option of PROC MIXED indicated no difference between repetitions of the experiment ($Pr > Z = 0.3576$).

Cumulative percent germination over the 14-d period was fit to a four-parameter Weibull function (Weibull 1951) using PROC NLIN in SAS:

$$f(t) = M\Big(1 - \exp[-\{k(t-l)\}c]\Big) \qquad (1)$$

where M is the upper asymptote (maximum percent germination) and is constrained to ≤ 100, l is the lag phase between the start of incubation and the start of germination and is constrained to > 0, c is the shape parameter, and k is the rate of germination (Brown 1987; Brown and Mayer 1988).

Results and Discussion

As the length of the stratification period increased, dormancy in seeds of giant ragweed was alleviated and the number of seeds capable of germination increased ($P < 0.0001$; Figure 2). For untreated, intact seeds, germination increased from 60 to 87% of viable seeds as the period of stratification increased from 0 to 8 wk. The number of viable seeds did not differ among stratification periods or seed treatments ($P < 0.0001$), with each Petri dish having an average of 10 viable seeds or 67% viability.

The total number of giant ragweed seeds capable of germinating during the 14-d incubation period was influenced by the interaction of stratification period and the physical or chemical treatments applied to the seeds ($P = 0.0015$). At 0 wk of stratification, the percent germination of embryos that had been excised from their involucres and seed coats was notably greater than that of all other treatments (Figure 2). After 2 and 4 wk of stratification, percent germination was still highest for excised embryos, although it was not significantly different from that in the snipped and KNO_3 treatments. After 6 and 8 wk of stratification, there were no differences in the percentage germination among treatments.

The pattern of cumulative germination in giant ragweed was also influenced by the length of the stratification period and the physical and chemical treatments applied to the seeds (Table 1; Figure 3). Notably, at 0 wk of stratification, the lag phase from the start of incubation to the initiation of germination was reduced from an average of 5 d in treatments where the involucre and seed coat were snipped or left intact to 1 d for excised embryos (Figure 3A). After 2 wk of stratification, the lag phase was reduced to < 1 d for all treatments.

Table 1. Parameter estimates (± SE) of the Weibull function.[a]

Stratification	Treatment[b]	M		k		l		c	
0 wk	Untreated	55	(4.1)	0.2	(0.11)	4.0	(1.95)	1.7	(1.19)
	Snipped	60	(12.6)	0.5	(0.28)	6.0	(0.10)	0.7	(0.44)
	Excised	84	(22.9)	0.2	(0.06)	1.0	(2.13)	1.1	(0.90)
	KNO_3	66	(18.1)	0.4	(0.29)	6.0	(0.14)	0.8	(0.47)
	GA_3	62	(6.5)	0.2	(0.11)	4.0	(2.14)	1.6	(1.24)
2 wk	Untreated	71	(2.7)	0.1	(0.01)	0.0	(0.00)	2.4	(0.30)
	Snipped	78	(2.7)	0.2	(0.01)	0.0	(0.00)	2.7	(0.41)
	Excised	86	(9.1)	0.3	(0.09)	1.0	(0.00)	0.8	(0.23)
	KNO_3	74	(1.9)	0.1	(0.00)	0.0	(0.00)	4.6	(0.63)
	GA_3	93	(4.7)	0.1	(0.01)	0.0	(0.00)	1.9	(0.25)
4 wk	Untreated	74	(2.8)	0.2	(0.01)	0.0	(0.00)	2.2	(0.31)
	Snipped	89	(2.4)	0.2	(0.04)	0.7	(0.71)	1.6	(0.40)
	Excised	100	(0.0)	0.7	(0.13)	0.8	(0.14)	0.7	(0.11)
	KNO_3	73	(2.9)	0.2	(0.00)	0.0	(0.00)	2.2	(0.32)
	GA_3	83	(2.3)	0.2	(0.01)	0.0	(0.00)	2.2	(0.25)
6 wk	Untreated	86	(2.1)	0.2	(0.04)	0.5	(0.66)	1.6	(0.37)
	Snipped	90	(2.4)	0.3	(0.04)	0.7	(0.38)	1.2	(0.25)
	Excised	96	(2.9)	0.6	(0.09)	0.0	(0.00)	0.9	(0.20)
	KNO_3	89	(2.3)	0.2	(0.01)	0.0	(0.00)	1.9	(0.20)
	GA_3	94	(2.2)	0.2	(0.01)	0.0	(0.00)	1.9	(0.24)
8 wk	Untreated	91	(8.9)	0.4	(0.18)	1.0	(1.32)	0.8	(0.52)
	Snipped	88	(2.0)	0.3	(0.06)	0.5	(0.42)	1.2	(0.29)
	Excised	84	(5.4)	0.4	(0.10)	0.0	(0.00)	0.9	(0.32)
	KNO_3	95	(3.9)	0.4	(0.08)	1.5	(0.43)	0.9	(0.28)
	GA_3	98	(1.8)	0.3	(0.01)	0.0	(0.00)	1.4	(0.12)

[a] The Weibull function: $f(t) = M(1 - \exp[-\{k(t - l)\}c])$, where M is the upper asymptote (maximum percent germination) and is constrained to ≤ 100, l is the lag phase between the start of incubation and the start of germination and is constrained to be > 0, c is the shape parameter, and k is the rate of germination.

[b] GA_3, gibberellic acid.

From 2 to 6 wk of stratification, the rate of germination was the primary factor distinguishing the patterns of cumulative germination among treatments (Table 1). For example, after 6 wk of stratification, the rate of germination in excised embryos was approximately double that in all other treatments (Table 1; Figure 3B). Excised embryos reached 50% germination after 1.5 d, whereas a minimum of 4 d was required for all other treatments. After 8 wk of stratification, there were no differences in the rates of germination among treatments.

Results of this experiment indicate that excising giant ragweed embryos from their covering structure was the most effective method for overcoming seed dormancy. Even with no stratification, 96% of these viable embryos (or 69% of the total number of embryos) were able to germinate during the 14-d incubation period (Figure 2). Conversely, a minimum of 6 wk of stratification was required to alleviate dormancy in a similar proportion of giant ragweed seeds that were left intact (i.e., untreated seeds). Similarly, snipping the tip of the involucre or adding exogenous GA_3 or KNO_3 did not reduce the requirement for at least 6 wk of cold stratification.

The effect of excising the embryo of giant ragweed from its covering structure has been previously examined by Davis (1930) and Schutte et al. (2012). While the results of these studies clearly indicated that the inhibitory effect associated with the embryo covering structures in giant ragweed is primarily associated with the membranous seed coat rather than the hardened involucre, the effect of removing these structures on the germinability of embryos was less consistent. For example, Schutte et al. (2012) reported that embryos excised from nearly fresh seeds (i.e., stored dry at 4 C for 45 d) were still highly dormant and that a period of stratification (i.e., moist storage at 4 C) was an absolute requirement for dormancy loss. Alternatively, Davis (1930, pg. 59) stated: "Al-

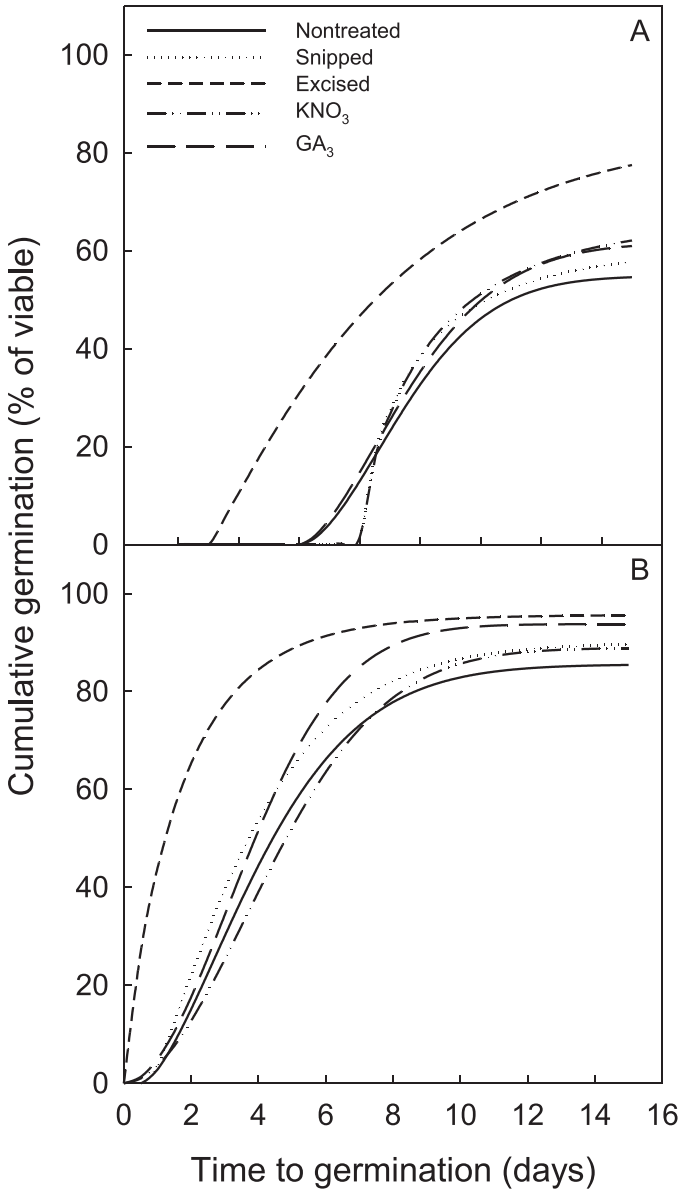

Figure 3. Cumulative germination following (A) 0 and (B) 6 wk of stratification. Four-parameter Weibull functions [$f(t) = M(1 - \exp[-\{k(t - l)\}c])$] were fitted to sample cumulative germination data for the five treatments applied to seeds of giant ragweed. Parameter values for the presented curves are reported in Table 1.

though all embryos are dormant at maturity, the dormancy is not equally deep seated in all." Our results indicate that the embryo covering structures were the primary factor contributing to seed dormancy in giant ragweed and that this was alleviated once the embryo was excised. Although we did not test the germinability of embryos excised from freshly harvested seed, the results of Schutte (2007) suggest that there would have been little change in seed dormancy during the period of dry storage that preceded the start of our experiment (i.e., 9 to 10 mo dry at 4 C).

It is likely the population of giant ragweed used in the present study had lower levels of innate dormancy than populations used in previous studies (Ballard et al. 1996; Davis 1930; Schutte 2007). For instance, our results indicate that, regardless of the treatment applied, a majority of the viable seeds in our population were capable of germinating without stratification (Figure 2). Although this suggests that stratification was not an absolute requirement for dormancy loss in our population of giant ragweed, increasing durations of stratification did influence the parameters of the cumulative germination curves for all of our tested treatments. In particular, the cumulative germination curves of untreated seeds and excised embryos were distinguished by the effect of stratification on the lag phase (l) and the shape parameter (c) of their respective Weibull functions (Table 1).

One of the most notable effects of excising the giant ragweed embryo from its covering structures was a reduction in the duration of the lag phase (from the start of the incubation to the first occurrence of germination) relative to the control treatment of untreated seeds (Figure 3A; Table 1). The predicted lag phase of 4 d for untreated seeds with no stratification, however, could also be reduced by stratifying the seeds for a period of 2 wk. Indeed, the lag phase in all nonexcised treatments was decreased after 2 wk of stratification, suggesting that some of the inhibitory influence of the embryo covering structure can be quickly alleviated under the cool, moist conditions of stratification (Table 1).

A second feature that distinguishes the cumulative germination curves of untreated seeds and excised embryos is the decline in shape parameter with increasing periods of stratification (Table 1). The shape parameter of the Weibull function describes the underlying distribution of germination times and approximates a normal distribution at values between 3.25 and 3.61 (Brown and Mayer 1988; Dubey 1967). When the value of the shape parameter falls below this range, it indicates that the distribution of germination time (in days) displays positive skewness (i.e., the median germination time falls below the mean, and a tail of late germinating seeds is drawn out to the right of these

measures of central tendency). For untreated seeds, as the shape parameter declined from 2.4 at 2 wk of stratification to 0.8 at 8 wk, the distribution of germination time became more positively skewed, and a larger proportion of the population approached the mean germination time. In contrast, the shape parameter for the cumulative germination curves of excised embryos changed little with any duration of stratification and indicated that the distribution of germination times was positively skewed throughout the experiment. These results provide further evidence of the inhibitory influence of the embryo covering structures and suggest that stratification may slowly alleviate dormancy by breaking down a mechanical constraint to the growth of the embryo or perhaps indicates a leaching of germination-inhibiting compounds from these covering structures as the duration of stratification increases. Ballard et al. (1996) investigated the effects of stratification on proteins in the embryo axis and cotyledons of giant ragweed seeds and found that three proteins present in dry, afterripened seeds and briefly stratified seeds (i.e., 30 d) were absent in seeds that were stratified for 60 d. Although this extra 30 d of stratification coincided with an increase in the germinability of the seeds from 5 to 33%, there was no causative evidence presented to link the presence of these proteins to the inhibition of germination. To the best of our knowledge, no further studies have investigated the inhibitory mechanism(s) of the embryo covering structures in seed of giant ragweed.

Based on the results, as well as those of previous studies, we hypothesize that giant ragweed seeds possess an intermediate level of physiological dormancy (sensu Baskin and Baskin 2004). Physiological dormancy can involve a hardened covering layer that acts as a mechanical restriction of the embryo (Finch-Savage and Leubner-Metzger 2006). Germination can proceed when the embryo is released from this layer either through excision or by an increase in the embryo growth potential that exceeds the mechanical constraint imposed by the hardened covering layer. This later process may also involve enzymes released from the endosperm or radicle, facilitating the rupture of the seed coat layer (Finch-Savage and Leubner-Metzger 2006). When seeds are enveloped in hardened covering structures, as is the case for giant ragweed, physiological dormancy can often be mistaken for physical dormancy (Baskin et al. 2001; Baskin and Baskin 2004). However, the defining feature of physical dormancy is the presence of "one or more water-impermeable layers of palisade cells in the seed or fruit coat" (Baskin and Baskin 2004, pg. 7). In our experience, the covering structures of giant ragweed seeds are not impermeable to water (E Page, personal observation). For instance, excised embryos, snipped and untreated, intact seeds of giant ragweed (per Figure 1) gained on average 24, 48, and 42% of their dry weight, respectively, following 24 hr of imbibition at 4 C. Conversely, scarified and untreated, intact seeds of velvetleaf [*Abutilon theophrasti* (Medic.)], a species with well-documented physical dormancy (Warwick and Black 1988; Winter 1960), gained 70 and 6% of their dry weight, respectively, during the same period of imbibition. Thus, we contend that primary dormancy in seed of giant ragweed should be classified as a physiological rather than a physical dormancy.

In conclusion, the results of this research demonstrate that the most effective method for alleviating dormancy in seed of giant ragweed is to excise the embryo from its covering structures. Although excising embryos requires significant time and effort, the time saving relative to weeks of cold stratification make embryo excision an attractive method for propagating small numbers of seedlings for experimental purposes.

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