Amer. J. Bot. 62(6): 639–643. 1975.

DORMANCY AND GERMINATION OF COMMON RAGWEED SEEDS IN THE FIELD[1]

ROGER W. WILLEMSEN
Department of Botany, Rutgers University, New Brunswick, New Jersey 08903

ABSTRACT

Common ragweed (*Ambrosia artemisiifolia*) seeds were stored under natural environmental conditions by placing them at three soil levels (surface, 5 cm, and 15 cm) in the field on November 1, 1972. Germination tests at 4-week intervals indicated that dormancy was broken by the end of January. Germination was initially greater at high temperatures, but this difference decreased with increasing time in the field. Secondary dormancy was evident in surface seeds by March 21 but not until April 18 at 5 cm and June 13 at 15 cm. Germination in the field was greatest at the surface but was observed at all soil levels by March 21. Seedling survival was 68% at the surface and 0% at 5 and 15 cm on June 13. Maximum and minimum soil temperatures were recorded at each soil level during the experiment and were correlated with the results. Greater germination and survival at the surface supports the evidence for ragweed's dependence on soil disturbance for germination, and the induction of secondary dormancy explains why ragweed does not constitute a dominant part of the vegetation when disturbance occurs after the soil warms to a critical point in the summer.

SEED DORMANCY and germination are very important in determining the success of a species as an invader after soil disturbance. Estimates of the number of seeds (Brenchley and Warington, 1930) and viability of seeds (Crocker, 1938; Toole and Brown, 1946; Darlington and Steinbauer, 1961) in arable soil confirms the maintenance of large populations of seeds for long periods of time. After soil disturbance and subsequent exposure to light, these seeds may give rise to weedy species found in cultivated fields or weedy primary invaders of secondary succession (Saur and Struick, 1964; Wesson and Wareing, 1967, 1969). Germination of the exposed seed after disturbance depends on the existing environmental conditions and the dormancy state of the seed. Seeds of many weedy species under field conditions exhibit cyclic changes in dormancy which follow a seasonal pattern (Courtney, 1968; Taylorson, 1970, 1972; Stoller and Wax, 1974). Secondary dormancy is usually induced during early summer and is broken during the winter, resulting in nondormant seeds in the spring, and if germination doesn't occur the cycle is repeated.

Laboratory germination studies have provided some information regarding the success of common ragweed (*Ambrosia artemisiifolia*) as a primary invader after soil disturbance (Bazzaz, 1968, 1970; Willemsen and Rice, 1972; Willemsen, in press). However, observations on seed germination and dormancy under field conditions would be complementary to these laboratory investigations and would provide a better understanding of this species' natural behavior.

[1] Received for publication 16 July 1974.

Supported by a grant from The Research Council, Rutgers University. I am grateful to Mr. Ralph H. Hofmann, officer in charge of the USDA, Cereal Division Seed Branch, Federal Seed Laboratory in New Brunswick, New Jersey, for his cooperation in the use of this agency's seed germination facilities.

MATERIALS AND METHODS—Ragweed plants bearing mature seeds were collected on October 11, 1972, from a one-year abandoned field on the William L. Hutcheson Memorial Forest property on the Piedmont of New Jersey. Fruits were removed from the plants after 4 days of air drying at 20–25 C. The seed was winnowed and stored in the dark in an air-conditioned laboratory (18–24 C) until burial on November 1, 1972.

For burial, 500 seeds were placed in individual 10×10 cm fiberglass screen envelopes (mesh size 6/cm). These envelopes were then placed on the soil surface and 5 cm and 15 cm below soil surface. Every four weeks four envelopes were collected from each soil level and cleaned under running tap water. The number of seeds which had germinated and the number of seedlings present were counted. The remaining seeds were placed on germination paper in sandwich boxes ($11 \times 11 \times 2.5$ cm) and 12 ml distilled water was added. Small quantities of water were subsequently added if drying became evident. Percent germination (as indicated by root emergence) was determined in continuous darkness and light (8 hr photoperiod) at 5/15, 10/20, 15/25, and 20/30 C ($\pm$ 1 C). The higher temperature of each alternating temperature regime was present during the 8-hr light period. The same alternating temperature regimes were maintained in constant darkness. The seeds placed in constant dark were

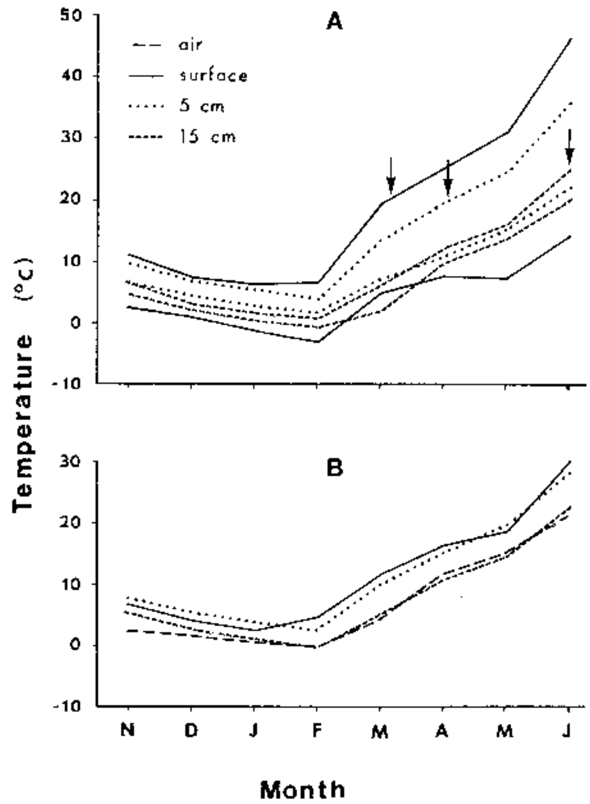

Fig. 1. Air and soil temperature. A, Average monthly maximum and minimum soil temperature. Arrows indicate time of secondary dormancy induction. LSD at the 95% confidence level = 3.68. B, Average monthly soil and air temperature. LSD at the 95% confidence level = 2.12.

exposed to laboratory light for a short time during counting. The number of replicates used at each temperature regime was four plates with 50 seeds each. Germination of freshly harvested nonstratified seeds was determined at the beginning of the experiment (Nov. 1, 1972) by the above procedures. Germination in the light was recorded each week for a period of 3 weeks, and the seedlings were removed after each counting. Germination in the dark was recorded after the 3-week germination period.

The presence of secondary dormancy in seeds collected from the field on July 13, 1973, was determined after the 3-week period in light or dark at the various temperature treatments. The sandwich box germination plates with ungerminated seeds were simply placed in a cold room (4 C) in the dark for 22 weeks, and the seeds were subsequently placed on fresh germination paper and germinated at 15/25 C in the light and dark.

Soil temperature was monitored daily at each level with a maximum-minimum thermometer equipped with a remote sensing device (Palmer Instrument Co.). Average monthly soil temperature at each level was computed by dividing the sum of the maximum and minimum temperature by 2. Air temperature was monitored with a hygrothermograph (Belfort Instrument Co.) placed under a shelter 5 cm above the soil surface. Average air temperature was computed as described above.

The results were analyzed statistically by the analysis of variance test (ANOVAR) with a fixed design, and least significant differences (LSD) were calculated.

Results—The greatest range in soil temperature (Fig. 1A) occurred at the soil surface and decreased with depth. The range in soil temperature was also less at all depths during the winter than in spring months. Average soil temperature (Fig. 1B) was lowest at the 15-cm depth throughout the entire time period. During the winter surface soil was cooler than soil at 5 cm, but this was reversed in the spring. During May and June very little difference in average soil temperature existed at these depths. Average air temperature was very similar to soil temperature at 15 cm.

Freshly harvested ragweed seeds were dormant (Fig. 2), and this dormancy was broken in seeds at all levels by Jan. 24. Initially, germination was best at high temperatures, but by Feb. 21 there was generally no difference in response to the temperatures used. Germination decreased in the spring, and its timing was correlated with depth of burial. The decrease was first observed in seeds at the surface on March 21 but not until April 18 at 5 cm and June 13 at 15 cm. There was no difference in the temperature response of the seeds during the induction of secondary dormancy in contrast to the great differences existing during the breaking of dormancy. Germination in constant darkness was less than in the light, and the difference between light and dark germination generally increased with time of burial. Data for germination of surface seeds in the dark are incomplete after March 21 because of the great amount of germination in the field and, therefore, an insufficient number of seeds.

Ungerminated seeds which were exhumed on June 13 responded to stratification (Table 1), indicating that the decrease in germination during the spring was due to the induction of secondary dormancy. The response was greatest in the light, and buried seeds responded more favorably than seeds at the surface. There was very little difference in germination after restratification of seeds from the 5- and 15-cm levels.

Germination at all soil levels in the field was first observed in packets harvested on March 21 (Fig. 2, Table 2). Germination in these packets had presumably occurred sometime between February 21 and March 21. The greatest amount of

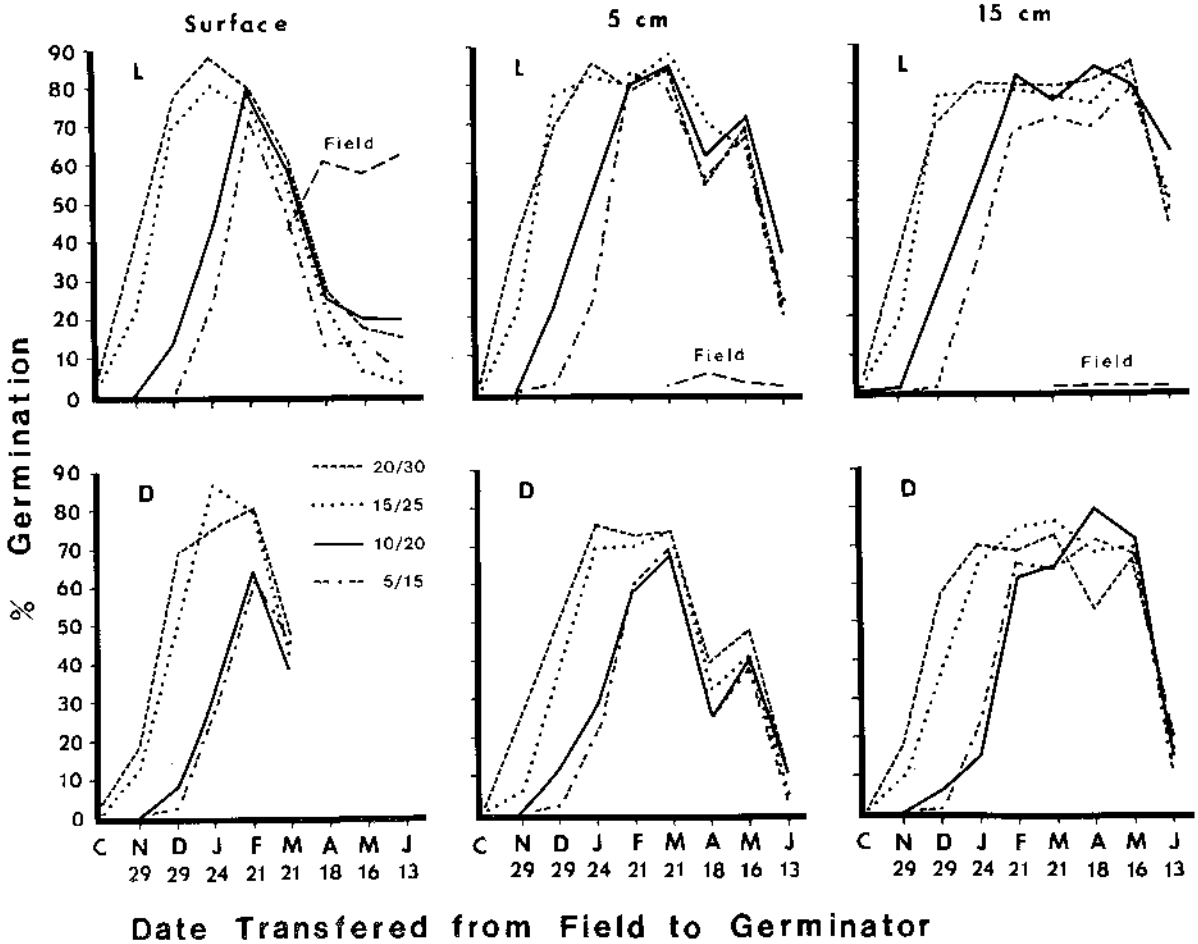

Fig. 2. Germination of freshly harvested (C) and field-stored ragweed seeds in the light (L) and dark (D) at 5/15, 10/20, 15/25, and 20/30 C (LSD at the 95% confidence level = 8.94) and germination of seeds in the field.

germination occurred at the surface followed in decreasing order by the 5-cm and 15-cm levels. All the seedlings from the germinated seeds could be accounted for at this time, indicating 100% survival. During the next 4-week period (April 18) germination at the surface increased but was about the same at the 5-cm and 15-cm levels. Survival was still 100% at all levels. No additional germination occurred during the next 8 weeks (May 16 and June 13), but the number of seedlings surviving was greatly affected. On May 16 survival was still 100% at the surface but only 19.7 and 0% at the 5- and 15-cm levels, respectively. Survival on June 13 decreased to 68.4% at the surface and 0% at the 5-cm level.

Discussion—Innate dormancy in ragweed seeds can be broken by stratification in the laboratory (Willemsen and Rice, 1972; Willemsen, in press). This also occurs in the field during autumn and early winter, resulting in a maximum number of nondormant seeds by the end of January (Fig. 2). Stratification temperature has a great effect on breaking dormancy in ragweed seeds (Willemsen, in press), but in the present study no difference in the time required for this process was found at the soil levels used. This is probably a reflection

Table 1. *Effect of restratification on germination of ragweed seeds exhumed June 13*

	% Germination	
Light		
	June 13[a]	Restratified
Surface	11.11	27.4
5 cm	25.75	58.0
15 cm	40.10	58.1
Dark		
Surface	—	—
5 cm	6.38	39.6
15 cm	15.25	36.6

[a] Value for June 13 is the average % germination for the 4 temperature regimes used.

TABLE 2. *Germination and survival of ragweed seeds in the field*[a]

Date	Depth	% Germination	% Survival
March 21	Surface	43.1	100.0
	5 cm	1.8	100.0
	15 cm	0.2	100.0
April 18	Surface	61.2	100.0
	5 cm	4.9	100.0
	15 cm	0.2	100.0
May 16	Surface	58.1	100.0
	5 cm	2.5	19.7
	15 cm	0.1	0.0
June 13	Surface	62.8	68.4
	5 cm	1.8	0.0
	15 cm	0.2	0.0

[a] Results based on 2,000 seeds at each soil level on each date.

of the rather small differences in soil temperature at the various levels during this time (Fig. 1). Germination in the field did not occur until after February 21, even though a large number of seeds were nondormant and germinated in the laboratory at high temperatures before this date (Fig. 2). Lack of earlier field germination is probably due to low soil temperature (average minimum and maximum February temperatures for all soil levels were −0.22 and 3.61 C, respectively) since germination at 5/15 and 10/20 C in the laboratory was also low before February 21 (Fig. 1, 2). During March soil temperature at all levels warmed to an average minimum and maximum of 5.43/12.85 C, closely approximating the 5/15 C temperature at which substantial laboratory germination occurred during this time.

The induction of secondary dormancy in *Polygonum aviculare* (Courtney, 1968), ragweed, and other weed species (Taylorson, 1970, 1972; Stoller and Wax, 1974) has been correlated with high soil temperature during late spring. Results of the present investigation (Fig. 2, Table 1) agree with these observations and show the induction of secondary dormancy to be closely correlated with depth of burial, with seeds at the surface developing dormancy most rapidly. This is in accord with the spring soil temperature gradient at which time the surface soil was warmer than deeper soil (Fig. 1). The critical minimum soil temperature for the induction of secondary dormancy in ragweed can be estimated by determining the maximum soil temperature at the time germination first decreases. The actual values may be somewhat lower since the first secondary dormancy found in exhumed seeds was presumably induced earlier when the soil was cooler. With this method, Fig. 1A shows that dormancy at all soil levels is not induced until the maximum soil temperature reaches 20 C. Therefore, this is my estimated critical minimum temperature for the induction of secondary dormancy in ragweed seeds. There was no evident correlation of minimum or average soil temperature with the induction of secondary dormancy at the soil levels used.

Secondary dormancy is induced after innate dormancy is broken, and the resulting nondormant seed is exposed to a temperature favorable for germination; but some overriding factor limits germination, causing a temporary state of enforced dormancy which develops into secondary dormancy. Secondary dormancy is induced in ragweed seeds when they are germinated in the dark at a favorable temperature (Bazzaz, 1970; Willemsen, in press). Lack of light may also be partially responsible for the decrease in germination of buried seeds and the subsequent induction of secondary dormancy. Germination of ragweed was less in the dark, and the difference between light and dark germination increased with time in the field (Fig. 2), which agrees with the work of Taylorson (1972) and Stoller and Wax (1974). If the present investigation had been continued to the point of complete secondary dormancy induction, there probably would not have been any difference in germination in the light vs. dark since both would have been very low (Taylorson, 1972). However, all ragweed seeds do not have a light requirement (Fig. 2) since substantial germination takes place in the dark (Taylorson, 1972; Stoller and Wax, 1974). Thus, in situ germination and the induction of secondary dormancy in buried seeds may be a result of some other factor. Holm (1972) suggests that low germination and the subsequent development of secondary dormancy in buried seeds may be due to low oxygen levels and the production of volatile inhibitors. Secondary dormany was also induced in seeds at the surface (Fig. 2, Table 1), and this response cannot be explained by lack of light, low O_2, or volatile inhibitors. In this case, germination may be limited by low moisture levels, leading to the development of secondary dormancy. Evidence for such a mechanism was presented by Justice (1941), who showed that dormancy was induced in nondormant *Polygonum aviculare* seeds which were allowed to become air dry at laboratory temperatures.

Breaking ragweed seed dormancy by stratification in the laboratory generally results in more germination at a wider range of temperatures (Willemsen, in press). This same effect was observed in ragweed seeds stratified in the field (Fig. 2), resulting in high germination at all temperatures after 16 weeks. During the induction of secondary dormancy there was no decrease in the expanded germination-temperature limits. This indicates that the physiological changes taking place during the breaking of dormancy and the induction of secondary dormancy are not the same.

Ragweed is an important primary invader of old fields during secondary succession in many areas of eastern and midwestern U.S. (Oosting, 1942; Keever, 1950; Bard, 1952; Quarterman, 1957; Gebben, 1965; Bazzaz, 1968) and is a semi-important weed in cultivated fields (USDA, 1972). Table 2 shows that ragweed seed germination and survival are greatest at the surface and, thus, its requirement on disturbance for establishment. Small, Buell, and Buell (1971) found ragweed to be an important component of old fields abandoned in April and May, but fields abandoned in June had little ragweed. Stoller and Wax (1973) also reported little emergence of ragweed during June and the following summer months. In light of the present investigation, the lack of ragweed establishment after May is probably due to the presence of secondary dormancy in seeds during this time.

LITERATURE CITED

BARD, G. E. 1952. Secondary succession on the Piedmont of New Jersey. Ecol. Monogr. 22: 195–215.

BAZZAZ, F. A. 1968. Succession on abandoned fields in the Shawnee Hills, southern Illinois. Ecology 49: 924–936.

———. 1970. Secondary dormancy in the seeds of the common ragweed *Ambrosia artemisiifolia*. Bull. Torrey Bot. Club 97: 302–305.

BRENCHLEY, W. E., AND K. WARINGTON. 1930. The weed seed populations of arable soil. I. Numerical estimates of viable seeds and observations on their natural dormancy. J. Ecol. 18: 235–272.

COURTNEY, A. D. 1968. Seed dormancy and field emergence in *Polygonum aviculare*. J. Appl. Ecol. 5: 675–684.

CROCKER, W. 1938. Life span of seeds. Bot. Rev. 4: 235–274.

DARLINGTON, H. T., AND G. P. STEINBAUER. 1961. The eighty-year period for Dr. Beal's seed viability experiment. Amer. J. Bot. 48: 321–325.

GEBBEN, A. I. 1965. The ecology of common ragweed, *Ambrosia artemisiifolia* L. in southwestern Michigan. Ph.D. Thesis. Univ. of Mich., Ann Arbor.

HOLM, R. E. 1972. Volatile metabolites controlling germination in buried weed seeds. Plant Physiol. 50: 293–297.

JUSTICE, O. L. 1941. A study of dormancy in seeds of *Polygonum*. Mem. Cornell Univ. Agric. Exp. Stn. 235: 1–43.

KEEVER, C. 1950. Causes of succession on old fields of the Piedmont, North Carolina. Ecol. Monogr. 20: 231–250.

OOSTING, H. J. 1942. An ecological analysis of the plant communities of Piedmont, North Carolina. Amer. Midl. Nat. 28: 1–126.

QUARTERMAN, E. 1957. Early plant succession on abandoned cropland in the Central Basin of Tennessee. Ecology 38: 300–309.

SAUR, J., AND G. STRUICK. 1964. A possible ecological relation between soil disturbance, light-flash, and seed germination. Ecology 45: 884–886.

SMALL, J. A., M. F. BUELL, AND H. F. BUELL. 1971. Old-field succession on the New Jersey Piedmont—the first year. William L. Hutcheson Memorial Forest Bulletin 2: 26–30.

STOLLER, E. W., AND L. M. WAX. 1973. Periodicity of germination and emergence of some annual weeds. Weed Sci. 21: 574–580.

———, AND ———. 1974. Dormancy changes and fate of some annual weed seeds in the soil. Weed Sci. 22: 151–155.

TAYLORSON, R. B. 1970. Changes in dormancy and viability of weed seeds in soils. Weed Sci. 18: 265–269.

———. 1972. Phytochrome controlled changes in dormancy and germination of buried weed seeds. Weed Sci. 20: 417–422.

TOOLE, E. H., AND E. BROWN. 1946. Final results of the Duvel buried seed experiment. J. Agric. Res. 72: 201–210.

U. S. DEPARTMENT OF AGRICULTURE. 1972. Extent and cost of weed control with herbicides and an evaluation of important weeds, 1968. ARS-H-1.

WESSON, G., AND P. F. WAREING. 1967. Light requirements of buried seeds. Nature 213: 600–601.

———, AND ———. 1969. The role of light in the germination of naturally occurring populations of buried weed seeds. J. Exp. Bot. 20: 402–413.

WILLEMSEN, R. W., AND E. L. RICE. 1972. Mechanism of seed dormancy in *Ambrosia artemisiifolia*. Amer. J. Bot. 59: 248–257.

———. In press. Effect of stratification temperature and germination temperature on germination and the induction of secondary dormancy in common ragweed seeds. Amer. J. Bot.