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EFFECT OF STRATIFICATION TEMPERATURE AND GERMINATION TEMPERATURE ON GERMINATION AND THE INDUCTION OF SECONDARY DORMANCY IN COMMON RAGWEED SEEDS[1]

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ABSTRACT

Stratification of common ragweed (*Ambrosia artemisiifolia*) seeds at 4 C was most successful for breaking dormancy, whereas –5 C was least effective and 10 C was intermediate. Germination in the light exceeded that in the dark at all stratification and germination temperatures. The optimum temperatures for germination in the light were 10/20, 15/25, and 20/30. Maximum germination in the dark occurred at 20/30 C for seeds stratified at 4 and 10 C but the optimum temperatures for seeds stratified at –5 C were 10/20, 15/25, and 20/30. Seeds stratified at –5 and 10 C germinated best after 15 weeks of stratification, whereas 12 weeks of stratification at 4 C resulted in maximum germination. Secondary dormancy was induced in seeds which did not germinate in the dark. This was affected by stratification temperature and duration and germination temperature. The ecological significance of these germination characteristics is discussed.

COMMON RAGWEED, *Ambrosia artemisiifolia* L., is a successful primary invader of old fields during secondary succession in many areas of eastern and midwestern U.S.; e.g., North Carolina (Oosting, 1942; Keever, 1950), New Jersey (Bard, 1952), Tennessee (Quarterman, 1957), Michigan (Gebben, 1965), and Illinois (Bazzaz, 1968). The success of ragweed as a primary invader may be largely attributable to its seed germination characteristics, for the seeds are dormant at harvest and require a period of stratification to break the dormant state. These nondormant seeds germinate best in the light, which could be adaptive in disturbed sites (Bazzaz, 1968; Willemsen and Rice, 1972). If the seed remains in the dark and is exposed to an optimum germination temperature after stratification, it enters into a state of secondary dormancy (Bazzaz, 1970). This insures a continual supply of viable seed in the field.

Various authors have also found the time of disturbance to affect the resulting population of ragweed. Bazzaz (1970) found denser populations of ragweed when the fields were plowed in the spring. Small, Buell, and Buell (1971) also reported greater cover and frequency of ragweed in fields abandoned in April and May. However, fields plowed and abandoned in June had the smallest ragweed population. The present study was designed to investigate the effects of stratification duration and temperature, subsequent germination temperature, and light on germination and induction of secondary dormancy in common ragweed. These germination characteristics are related to the population behavior of this species.

MATERIALS AND METHODS—Plants bearing mature seeds of common ragweed 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. A General Seed Blower was used to separate chaff from the seed. The seed was stored in a closed dark bottle in an air-conditioned laboratory (approx. 18–24 C) until stratification was initiated on November 15, 1972.

The effect of stratification temperature was determined by mixing seeds with moist sand in plastic bags and immediately chilling in the dark at –5, 4, and 10 C (± 1 C). Seeds were removed from stratification after 3, 6, 9, 12, and 15 weeks, placed on germination paper in 11 × 11-cm sandwich boxes and 12 ml of distilled water was added. Percent germination (as indicated by root emergence) was determined in continuous darkness and light (16 hr photoperiod) at 5/15, 10/20, 15/25, and 20/30 C (± 1 C). The higher temperature of each alternating temperature regime was present during the 16-hr light period. The same alternating temperature regimes were maintained in constant darkness. Germination was recorded each week for a period of 3 weeks in

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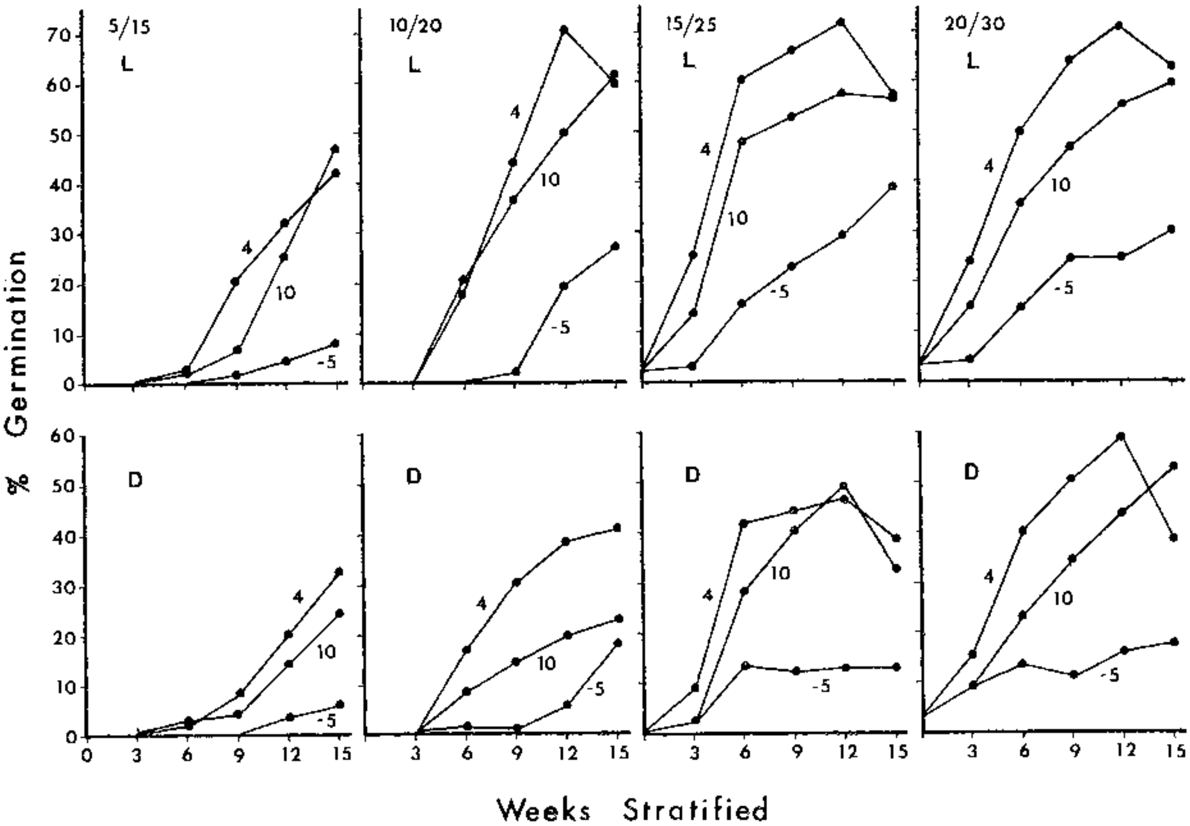

Fig. 1. Germination of ragweed seeds at 5/15, 10/20, 15/20, and 25/30 C in the light (L) and dark (D) after stratification at –5, 4, and 10 C. LSD at the 95% confidence level = 8.08.

the case of the light experiments and after the 3-week period for seeds germinated in the dark. Each test consisted of three replicates with 50 seeds each. Germination of nonstratified seeds was determined at the beginning of the experiment with the above procedures.

The induction of secondary dormancy was investigated by transferring the seeds which did not

TABLE 1. *Germination of ragweed seeds in the dark expressed as fraction of germination in the light*

Germination Temperature	Stratification Temperature	Weeks of Stratification					
		0	3	6	9	12	15
5/15	– 5	—[a]	—	—	—	.71	.75
	4	—	—	.75	.39[b]	.62[b]	.75[b]
	10	—	—	1.33	.60	.52[b]	.51[b]
10/20	– 5	—	—	—	.33	.26[b]	.54[b]
	4	—	—	.92	.69[b]	.55[b]	.69[b]
	10	—	—	.41[b]	.39[b]	.39[b]	.37[b]
15/25	– 5	—	.50	.87	.53[b]	.44[b]	.33[b]
	4	—	.36[b]	.70[b]	.67[b]	.65[b]	.69[b]
	10	—	.16[b]	.59[b]	.76[b]	.86[b]	.58[b]
20/30	– 5	1.00	2.16	.91	.47[b]	.64[b]	.59[b]
	4	—	.64[b]	.80[b]	.78[b]	.83[b]	.61[b]
	10	—	.59	.65	.74[b]	.79[b]	.89

[a] Dash indicates no germination in light and/or dark which made the calculation of a fraction impossible.
[b] Germination significantly less than in light (95% confidence level).

TABLE 2. *Total germination of ragweed seeds in the dark plus germination of these seeds after transfer to the light expressed as fraction of total germination in the light*

Germination Temperature	Stratification Temperature	Weeks of Stratification					
		0	3	6	9	12	15
5/15	−5	—[a]	—	—	4.51	3.14[b]	2.92[b]
	4	—	—	6.52[b]	1.16	1.00	.94
	10	—	—	5.66[b]	1.80	.78	.67[c]
10/20	−5	—	—	—	13.33[b]	1.76	1.56[b]
	4	—	—	1.88[b]	1.89[b]	.73[c]	.99
	10	—	—	1.21	2.41[b]	.93	.77[c]
15/25	−5	—	7.27[b]	1.78[b]	1.62[b]	1.00	.78
	4	—	1.75[b]	.91	1.07	.73[c]	.84[c]
	10	—	2.26[b]	.94	.95	.95	.76[c]
20/30	−5	—	5.83[b]	1.73[b]	.92	1.00	.84
	4	—	1.28	.99	.89	.92	.64[c]
	10	—	1.68[b]	.64[c]	.68[c]	.94	.97

[a] Dash indicates no germination in light and/or dark-light which made the calculation of a fraction impossible.
[b] Germination significantly greater than in light (95% confidence level).
[c] Germination significantly less than in light (95% confidence level).

germinate in continuous darkness after the initial 3-week period to light at the same temperature. Germination was recorded each week for an additional 3 weeks.

The results were analyzed statistically by the analysis of variance test (ANOVAR) with a fixed design.

RESULTS—Seeds used in this experiment were initially dormant (Fig. 1). Stratification at 4 C generally resulted in superior germination at all temperatures in both the light and constant darkness. Stratification at 10 C was not as effective as 4 C and stratification at −5 C resulted in the least germination. Germination in the light exceeded that in the dark at all germination and stratification temperatures (Fig. 1; Table 1). The optimum temperatures for germination in the light were 10/20, 15/25, and 20/30 C and were not dependent on stratification temperature (Fig. 1). Maximum germination in the dark occurred at 20/30 C for seeds stratified at 4 and 10 C but germination at 10/20, 15/25, and 20/30 C of seeds stratified at −5 C did not differ significantly and was more than germination at 5/15 C. Fifteen weeks of stratification at −5 and 10 C usually resulted in maximum germination, but seeds stratified at 4 C germinated best after 12 weeks of stratification at the higher temperatures.

Transfer of seeds which did not germinate in the dark to the light resulted in additional germination of both nonstratified and stratified seeds at all temperatures. The results (Table 2) show an interaction between stratification temperature, stratification time, and germination temperature. Transfer of seeds stratified at −5 C stimulated germination (compared to seeds germinated in the light) except after 15 weeks of stratification and subsequent germination at 15/25 and 20/30. Transfer of seeds stratified at 4 and 10 C also stimulated germination but at lower germination temperatures and shorter stratification periods as compared with −5 C stratification. Germination was inhibited (less than light) at high germination temperatures in seeds stratified for a long time at 4 and 10 C.

DISCUSSION—Dormancy in seeds of many temperate species can be broken by stratification under artificial conditions in the laboratory. The natural mechanism of breaking dormancy in these seeds is simply moist winter chilling. Stratification temperatures used in the laboratory are generally between 3 and 5 C (Stokes, 1965). Results of the present investigation show that 4 C was the most effective temperature for breaking dormancy in ragweed seeds. The possibility of seeds from different local populations or geographical areas responding differently exists (Justice, 1944; Varasova, 1956; Lindauer and Quinn, 1972) but was not investigated in the present research. Dormancy was broken less effectively by stratification at 10 C, and −5 C was least successful. These results are consistent with the work of Schander (Stokes, 1965), who found lower stratification temperatures of 3 and 5 C more effective in breaking dormancy in apple and pear seeds. Others (Davis and Rose, 1912; Eckerson, 1913; Roberts, 1924; Flemion, 1931; Haut, 1933; Choate, 1940) have also shown below-freezing temperatures (−3 and −5 C) to be ineffective in breaking dormancy in *Crataegus mollis*, *Sorbus aucuparia*, *Echinocystis lobata*, and species of *Ferula*. In fact, freezing had deleterious effects on *Berberis thunbergii* and other species (Davis, 1927). In the case of ragweed an injurious effect was not evident during the 15-week stratification period since germination usually increased steadily once it started (Fig. 1). The below-freezing temperature did delay initial germination and dormancy was not broken as rapidly as in stratification at higher temperatures.

Stratification temperature also affected the range of the germination response to germination temperature. Stratification at 4 and 10 C resulted in more germination at a wider range of germination temperatures than stratification at –5 C (Fig. 1). It is also evident that as stratification was increased (at any temperature) more seeds became able to germinate at a wider range of temperatures. Germination at lower temperatures was increased by stratification at 4 and 10 C and by lengthening the time of stratification. A correlation between range in germination temperature and stratification time was also observed in apple (Luckwill, 1952) and *Danthonia sericea* (Lindauer and Quinn, 1972). The responses of seeds in the dark were similar to those in the light except for the general decrease in germination in the dark (Fig. 1). Germination in the dark became significantly less than in the light as stratification time was increased, and this seems to be positively correlated with high germination temperatures and possibly stratification at 4 and 10 C (Table 1). However, these results may be misleading because of low germination in both the light and dark of seeds stratified for a short period at –5 C and germinated at low temperatures.

The decrease in germination at higher temperatures 15 weeks after the initiation of stratification may be due to the induction of secondary dormancy induced by exposure to dark at an optimum temperature for germination (Bazzaz, 1968). The decrease in germination in both the light and dark with 15 weeks of stratification also indicates an induction of secondary dormancy. The effect was greatest in seeds stratified at 4 C and was not evident in seeds stratified at –5 C. Stratification at this lower temperature resulted in very low germination and the increase in germination with stratification was less, especially in the dark, which would mask any induction of secondary dormancy. The induction of secondary dormancy in seeds germinated in the light was not investigated and the decrease in germination of these seeds after an extended period of stratification may be attributed to some other factor such as a decrease in viability. The presence of secondary dormancy in seeds which did not germinate in the dark was investigated by transferring them to light conditions. The combined germination of these transferred seeds and germination of seeds in the dark would be expected to be the same as germination in the light. However, Table 2 shows many cases of stimulated germination and this seems to be positively correlated with low stratification temperature, low germination temperature, and short stratification periods. Less germination of these transferred seeds compared with germination in light may indicate secondary dormancy. This was positively correlated with high germination temperatures, higher stratification temperatures (4 and 10 C), and long periods of stratification (Table 2). Davis (1930) also found secondary dormancy induction in *Ambrosia trifida* and *Xanthium* seeds in response to high germination temperatures.

These germination characteristics supply additional information explaining the success or failure of ragweed as a primary invader of old fields. Disturbance (plowing) in the spring results in exposure to light and subsequent germination of stratified seeds. This exposure of buried seeds to light conditions may actually stimulate germination beyond that expected for seeds maintained in the light or dark. Transferral to light did stimulate germination especially at low germination temperatures and after short stratification periods (Table 2). Exposing ragweed seeds to the light in early spring, when the soil temperature is low, may have the same effect.

Since stratified seeds germinated well at high temperatures (20/30 C), ragweed might be expected to establish dense populations even when fields are abandoned in late spring or early summer. Contrary to this, Small et al. (1971) found a small population of ragweed after June abandonment. This discrepancy may be due to the low moisture potential of the soil during the summer. However, ragweed was found to germinate at fairly low water potentials (Raynal and Bazzaz, 1973). Another possibility is the induction of secondary dormancy by late spring. Ragweed seeds were found, in the present study, to exhibit secondary dormancy after exposure to warm temperatures in the dark (Table 2). The effect was influenced by the length of stratification but a temperature of 10/20 C was adequate. The presence of secondary dormancy would insure the maintenance of a viable source of seed year after year (Bazzaz, 1970).

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