SEED GERMINATION OF HIERACIUM PRATENSE, A SUCCESSIONAL PERENNIAL

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Hieracium pratense (hawkweed) becomes established from seeds the second spring after disturbance during old-field succession. Hawkweed is a perennial, and its seeds mature and are dispersed in June. Germination of buried and dry-stored seeds of hawkweed was investigated over a 1-yr period. Freshly harvested seeds showed some innate dormancy which was broken by a short period of afterripening. Germination of dry-stored seeds in light remained high throughout the testing period except at low temperatures (5-15 C). Germination of seeds buried at 2, 5, and 15 cm was similar to that of the dry-stored seeds, but germination at low temperatures in light increased during the winter months. Laboratory stratification also resulted in increased germination at low temperatures. Germination of dry-stored and buried seed in the light was greater than in the dark. The burial experiments indicated short-term viability of hawkweed seeds in the soil. High-temperature drying had no harmful effect on germination, but solutions of high osmotic potential caused a decrease in germination. Increased far-red to red ratio of light passing through a vegetation canopy had little effect on germination. The ecological implications of these results are discussed.

Introduction

Hieracium pratense (hawkweed) is a weedy perennial with a rosette habit which requires long days for bolting and flowering (Peterson and Yeung 1972). On the Piedmont of northern New Jersey, hawkweed flowers during late May and June, with seed maturation and dispersal taking place shortly after flowering. It ranges from Quebec south to Georgia and west to West Virginia, where it grows in fields, pastures, and along roadsides (Gleason and Cronquist 1963).

Germination studies of many annual weedy species show adaptations which allow seed germination to coincide with times when environmental conditions are optimal for seedling survival, ensuring a highprobability that the plant can complete its life cycle (Newman 1963; Courtney 1968; Taylorson 1970; STOLLER and WAX 1974; WILLEMSEN 1975). However, the seed stage is less important to the survival of a perennial species than an annual species except as a means of colonizing new areas. This has probably led to the relatively small number of investigations concerning the germination ecology of perennial weeds or herbs in relation to establishment during secondary succession. Вымвоки (1973) investigated germination of Solidago nemoralis, a secondstage successional perennial on the Piedmont of New Jersey. The freshly matured seeds of this species are nondormant at high temperatures in the fall but would not germinate at lower temperatures. Germination at lower temperatures increased with stratification, resulting in seeds capable of germinating at low temperatures in the spring.

SMALL et al. (1971) noted that *H. pratense* is not a principal species on first-year old fields which were set aside for natural revegetation at Hutcheson Memorial Forest on the Piedmont of New Jersey. Hawkweed cover remained low the second year but

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then increased rapidly in subsequent years, reaching 55% cover 6 yr after abandonment (SMALL, personal communication). Once it is established in a field, the main cause of hawkweed's increase in cover is vegetative reproduction (Kott 1962). Its initial establishment after disturbance, however, depends on seed germination.

The objectives of this research were (1) to determine the time of hawkweed establishment during old-field succession and (2) to determine the effects of selected environmental factors on seed germination in an attempt to explain the time of establishment.

Material and methods

"Seeds" (fruits) of *Hieracium pratense* were collected from plants on the old fields at Hutcheson Memorial Forest (HMF), East Millstone, New Jersey, June 11–19, 1974. Seeds were cleaned, mixed thoroughly, and stored in an envelope at room temperature (hereafter referred to as dry-stored seed). Except where noted below, the germination tests were carried out by placing seeds on a single layer of blotter paper in plastic trays (11 × 11 × 2.5 cm) with lids and moistening them with 12 ml of distilled water. Each experimental treatment consisted of three replicates with 50 seeds each.

Germination tests were conducted in seed germinators set at four alternating temperature regimes: 5–15, 10–20, 15–25, and 20–30 C. The higher temperature of each regime coincided with the 8-h photoperiod. Seeds to be kept in darkness were counted under a green safelight (500–600 nm; peak at 550 = .036 μ W cm⁻² nm⁻¹ at 70 cm), and the trays were wrapped in a double layer of aluminum foil. Germination (radicle emergence) in the light was counted once a week for 3 wk, and the seedlings were removed after each counting. Germination in the dark was recorded after the 3-wk germination period.

The effect of burial on hawkweed seed germination was tested by placing freshly harvested seeds at

depths of 2, 5, and 15 cm beneath the soil surface in plastic tubes (5 × 20 cm), with four 6.4-mm diameter drainage holes drilled at 8- and 18-cm depths. The tubes were filled with screened soil (a silty clay loam derived from the Triassic red shales of the Piedmont in New Jersey), and the seeds were placed on a thin layer of sand which acted as a marker. The tubes were buried completely in soil in the courtyard of the Rutgers University Botany Department greenhouse (on the Piedmont), July 6-7, 1974. Every 6 wk for a 1-yr period 12 tubes were randomly removed; the seeds from each depth from all tubes were pooled for the germination tests. The germination of drystored seeds was determined at the same time.

Emergence of seedlings from buried seed was tested by placing approximately 200 seeds in soil as a single layer in a 10-cm diameter plastic tube. Four tubes for each depth (surface, 2, 5, and 15 cm), one depth per tube, were deployed in a random manner on July 4, 1974. Model 35-B soil thermometers (Palmer Instruments, Inc., Cincinnati, Ohio) recorded the maximum and minimum temperatures at 2-, 5-, and 15-cm soil depths.

Fifteen 0.5×0.5 -m quadrats were laid out in a 5×3 design every 10 m on two fields at HMF; one field was plowed in the spring, 1974, and the other in the spring, 1975. The number of hawkweed rosettes in each quadrat was counted in the fall of 1974 and in the spring of 1975 on the 1974 field and in the spring of 1975 on the 1975 field. Any hawkweed plants found in these plots were assumed to have arisen from seeds.

The effect of drying imbibed seeds was determined by placing wetted, previously dry-stored seeds in plastic petri dishes in an oven at 45 C during October 1974. Seeds were dried for 3 days under a 16-h photoperiod, remoistened, and then placed in the germinators.

Simulated soil drought conditions were created in March 1975 with the use of polyethylene glycol

(PEG) solutions, following the procedure of PARMAR and MOORE (1966). Germination of dry-stored seed was determined at solution osmotic potentials of 0 (distilled water), 3, 5, 6, 8, and 10 bars (12 ml of solution were used per tray). Germination was tested only at 20–30 C, since drought conditions most likely occur during the higher temperatures of the summer months.

The effect of light transmitted through vegetation was examined by placing hawkweed seeds under a ragweed (Ambrosia artemisiifolia) canopy. Ragweed was grown in two flats at a density comparable to that found in the first-year HMF fields (16 m⁻²; J. R. Jackson, unpublished data). The plants were grown on a greenhouse bench where sunlight was supplemented by a bank of incandescent floodlamps. providing a minimum photoperiod of 16 h from April 15 to July 17, 1975. On July 17 a black cloth was placed around the flats, allowing no scattered light to penetrate the sides of the canopy. Four seed trays with lids (lids did not affect the far-red [FR]/red[R] ratio) containing 50 dry-stored seeds were wetted and placed under the canopy, and germination was monitored for 2 wk. Controls were placed on the same bench but were not shaded and also under green 3-mm mesh plastic shading material. A similar experiment was performed in the field in July 1975. Light intensity was measured with a Weston illumination meter, and light quality was measured by a Model SR Spectroradiometer (Instrument Specialties Co., Lincoln, Nebraska).

The germination data obtained were analyzed statistically by the analysis of variance. Arcsine transformation of percentage germination was used for the statistical analysis; *F*-values and least-significant differences (LSD) were determined.

Results

Freshly harvested seeds (0 wk) were tested for germination on June 27, 1974 (fig. 1). At this time,

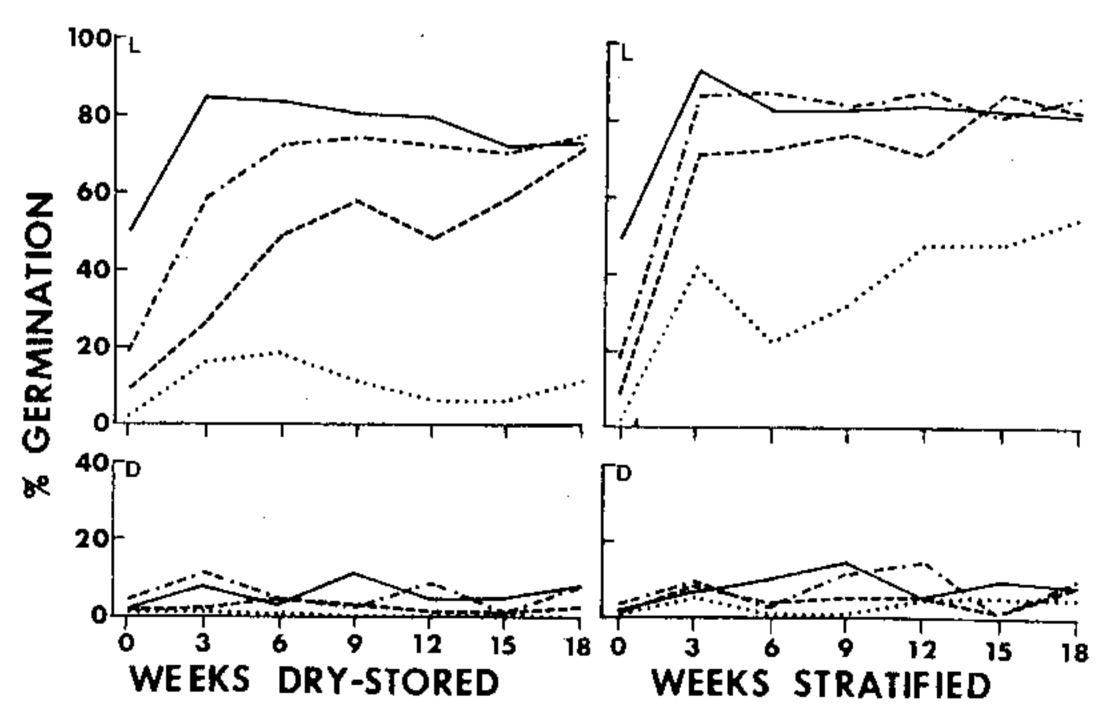


Fig. 1.—Germination of dry-stored and stratified hawkweed seeds in light (L) and dark (D) at 5–15 (\cdots), 10–20 (\cdots), 15–25 (\cdots), and 20–30 C (\cdots). LSD at 95% confidence level = 6.1. Seeds first placed in germinators (0 wk) on June 27, 1974.

germination increased with increasing temperature in the light, reaching 50% at 20-30 C. Germination in the dark was near zero at all temperatures.

Comparison of the germination of dry-stored and stratified seeds showed a marked increase in germination of stratified seed at lower temperatures (especially at 5–15 C) in the light after only 3 wk, whereas the dry-stored seed showed a more gradual increase in germination except at 5–15 C, which never exceeded 20%. After 18 wk, germination in the light at 20–30, 15–25, and 10–20 C was almost the same for both stratified and dry-stored seed. Germination in the dark remained very low in both treatments. About 2% of the seeds germinated during stratification.

Germination of seeds at 5-15 C in the light from all three soil depths increased steadily to the point where, at 36 wk (March 14), germination at 5-15 C was in the same range as that occurring at the higher temperatures (fig. 2). After 36 wk, germination at 5-15 C of seeds from the 2- and 5-cm depths decreased, but the 15-cm depth showed no decrease until 54 wk (July 21). The expansion of the germination-temperature limits (more germination at a wider temperature range) was more rapid in buried seed than those stored dry. Germination of buried seeds showed no differences when the various depths were compared. Germination in the dark generally in-

creased with increasing temperature but was variable with respect to the period of time buried. A sudden increase in dark germination occurred at 20–30 C after 48 wk (June 12) of burial. Germination results at 15 cm were incomplete due to in situ germination (table 1).

The percentage of empty seed coats from buried seeds increased with depth and time, especially during the spring and summer months (table 1). The number of seeds with radicles attached did not show a similar increase. During the germination testing of the buried seeds, we noticed that many of the seedlings in the dark in the 20-30 C germinator lacked vigor and probably would not survive. Drystored seeds, however, produced vigorous seedlings at 20-30 C in the dark. This seedling mortality of the buried seeds decreased rapidly with decreasing temperature so that most seedlings occurring at 10-20 C were healthy.

No seedlings emerged from the tubes set aside for that purpose, although several hawkweed seedlings were found in the immediate area in the spring of 1975.

Maximum and minimum soil temperatures for 2, 5, and 15 cm, averaged for each month, are shown in figure 3. The degree of fluctuation between maximum and minimum temperatures decreased with increasing depth.

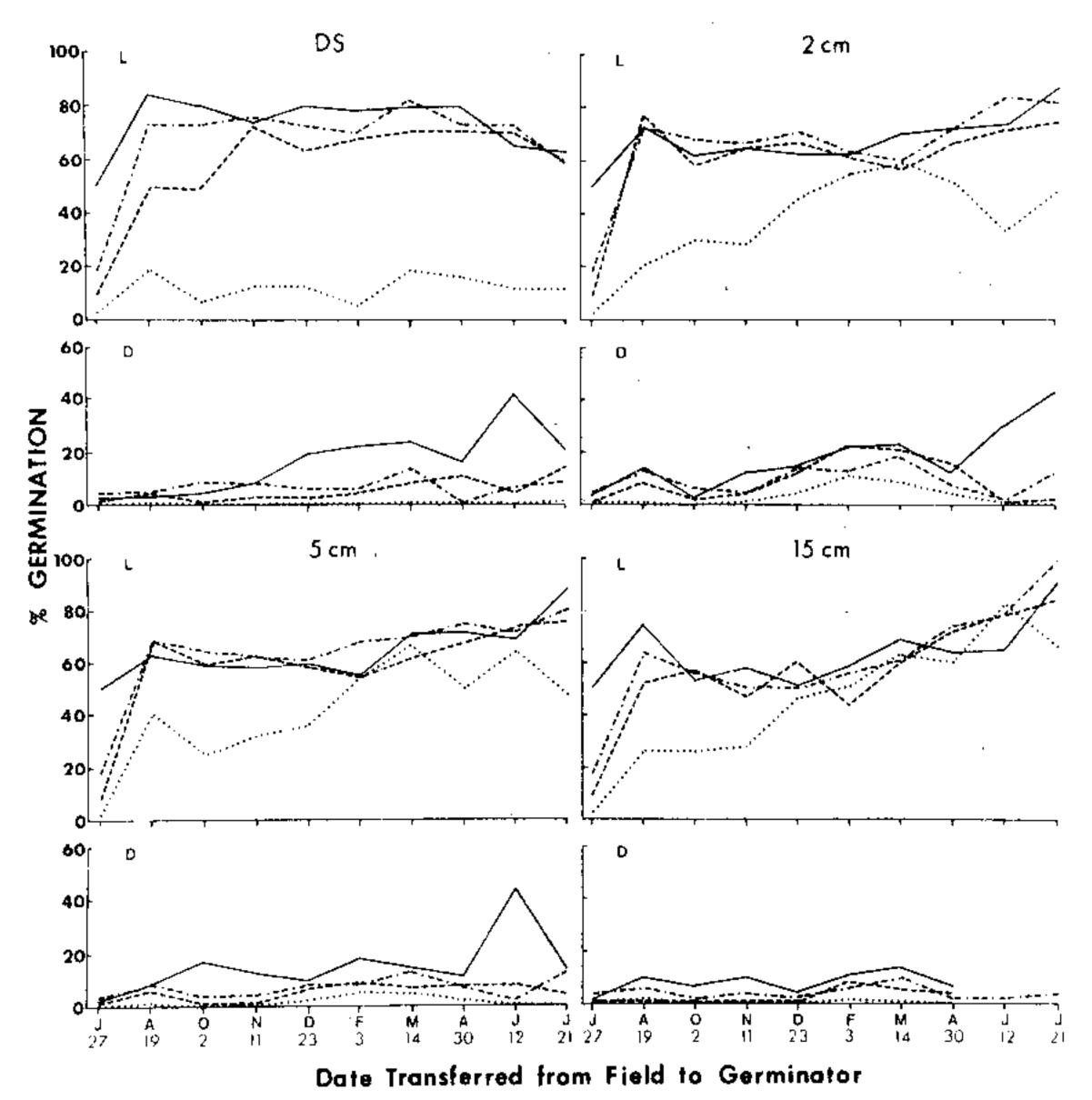


Fig. 2.—Germination of dry-stored (DS) hawkweed seeds and of seeds buried at 2, 5, and 15 cm in light (L) and dark (D) at 5-15 (\cdots), 10-20 (\cdots), 15-25 (\cdots), and 20-30 C (\cdots) at 6-wk intervals. LSD at 95% confidence interval = 7.7.

Examination of the quadrats on October 7, 1974 and April 10, 1975 in the field plowed and abandoned in the spring, 1974, showed only one hawkweed plant in the 15 quadrats (0.27 m⁻²). This number increased to 10 (2.7 m⁻²) on May 22, 1975 and to 12 (3.2 m⁻²) on June 14, 1975, the increase between the last two dates being due to vegetative reproduction. No hawk-

TABLE 1

NUMBER OF SEEDS WITH RADICLES (R) AND EMPTY SEED COATS (SC) (% OF TOTAL SEEDS COUNTED) FOUND AT 2-, 5-, AND 15-CM BURIAL DEPTHS

| DATE AND SEEDS | BURIAL DEPTH (cm) | | |
|--|-------------------|-----------------|-------|
| | 2 | 5 | 15 |
| October 2: | | | |
| SC, | 1.2 | 4.0 | 2,7 |
| R | 1.0 | 3.0 | 6.0 |
| November 11: | | | * * * |
| SC | 1.0 | 2.8 | 0.7 |
| R | 2.0 | 3.0 | 0.0 |
| December 23: | | 0.0 | 0.0 |
| SC | 0.7 | 2.4 | 2.3 |
| R | 1.0 | $\frac{1}{4}.0$ | 1.0 |
| February 3: | ••• | 1.0 | 1.0 |
| SC | 1.0 | 2.4 | 2.3 |
| R | 0.0 | 2.0 | 2.0 |
| Aarch 14: | W. O | | 2.0 |
| SC | 1.1 | 3.2 | 8.1 |
| R | 4.0 | 4.0 | 2.0 |
| pril 30: | 1.0 | *.0 | 2.0 |
| SC | - 5.5 | 10.7 | 12.3 |
| R., | 10.0 | 2.0 | 0.0 |
| une 12: | 10.0 | 2.0 | 0.0 |
| SC | 9.8 | 22.5 | 38.6 |
| R | 2.0 | 2.0 | 0.0 |
| uly 21: | 2.0 | 2.0 | 0.0 |
| SC | 30.7 | 35.3 | 35.9 |
| A second control of the control of t | | | |
| Ř | 0.0 | 1.0 | 0. |

weed was found on June 14, 1975 in the field plowed and abandoned in the spring, 1975.

Seeds which were allowed to dry at 45 C showed more of a linear decrease in germination than the dry-stored seeds which were not dried, but otherwise drying does not harm the germination capability of these seeds, except perhaps at 10–20 C (fig. 4). Germination decreased almost linearly with increasing osmotic potential (fig. 5), and the length of time needed for germination increased with increasing osmotic potential.

Germination in the open in the greenhouse (table 2) was similar to that of dry-stored seeds in the germinators (fig. 2). No seeds germinated in the open in the field due to drying in the seed trays. The high FR/R ratio under the ragweed canopy in both the field and greenhouse had little effect on the germination of hawkweed seeds. Germination at low light intensities seemed to be restricted.

Discussion

Seeds of *Hieracium pratense* germinated well at high temperatures after only a short period of afterripening (figs. 1, 2). However, establishment in first-year fields was not detected at the time of dispersal (mid-June) nor through the remainder of the growing season during which soil temperatures (fig. 3) were comparable to those which promoted germination in the laboratory. The absence of seedlings at this time is probably not due to the lack of a seed source, since hawkweed produces great numbers of seeds which are capable of being transported over great distances (Wagner 1965), and hawkweed was a component of nearby adjacent fields on the HMF property. The small number of seedlings could be

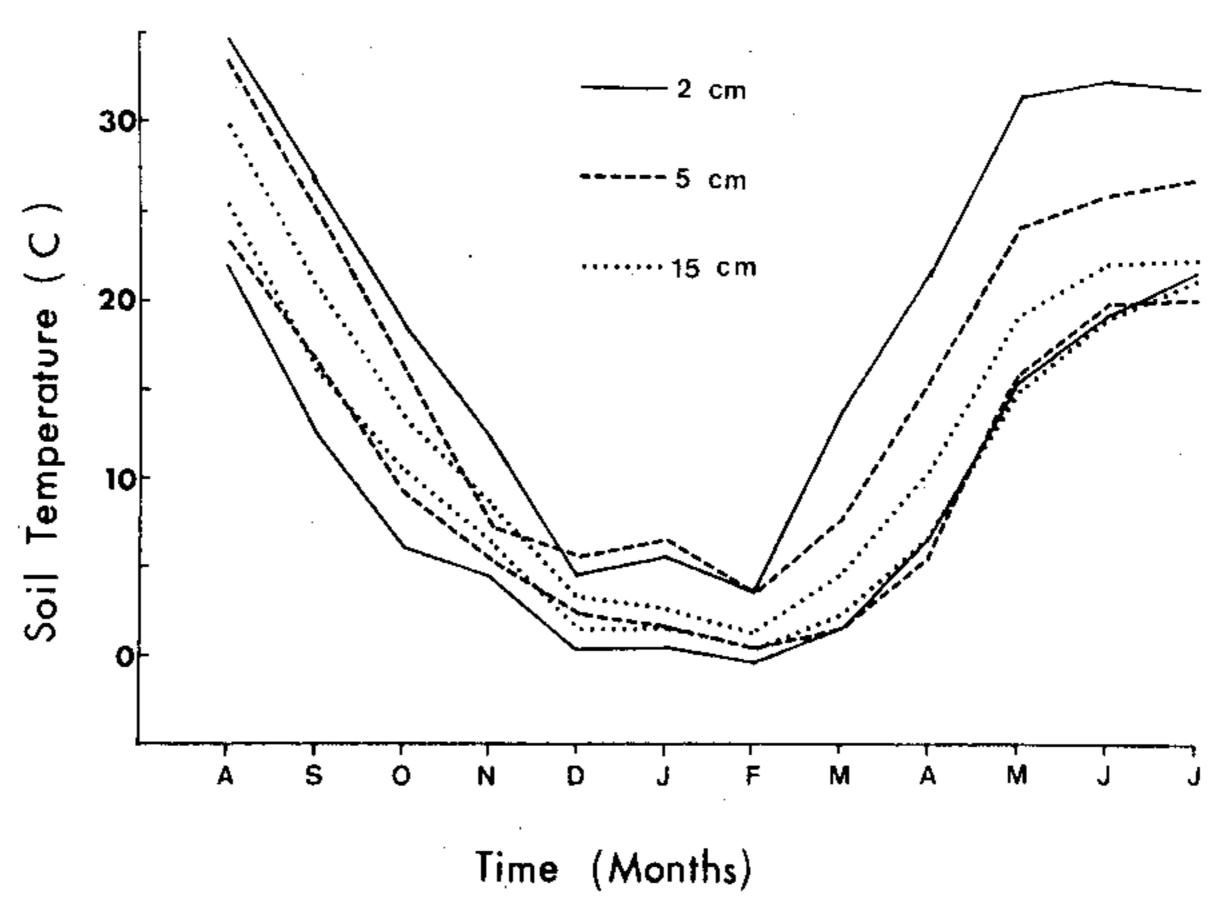


Fig. 3.—Mean monthly maximum and minimum soil temperatures at 2-, 5-, and 15-cm burial depths

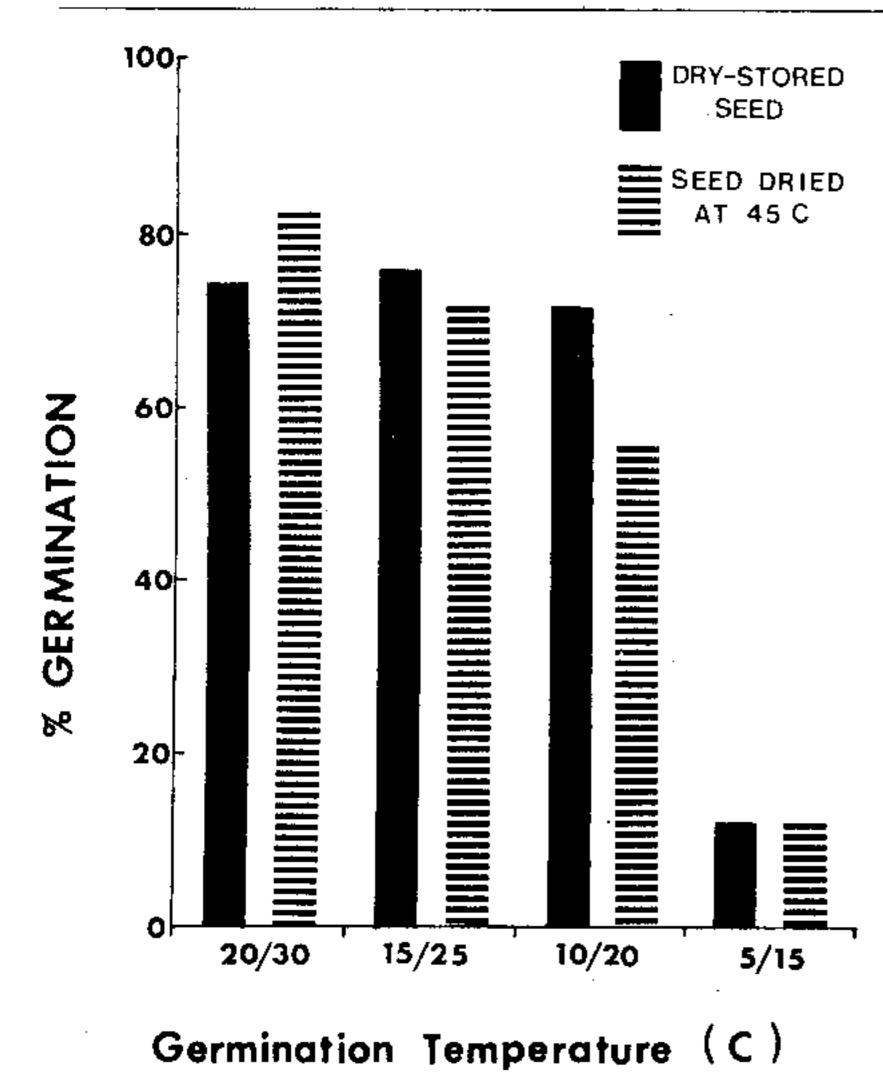


Fig. 4.—Germination of dry-stored seed and seed dried at 45 C for 4 days at 5-15, 10-20, 15-25, and 20-30 C in October 1974. USD at 95% confidence level = 8.7.

TABLE 2
GERMINATION OF SEEDS PLACED IN THE OPEN AND UNDER GREEN-MESH SHADING MATERIAL AND A RAGWEED CANOPY IN THE FIELD AND IN THE GREENHOUSE

| Treatment | FR/Rª | Light Intensity (1x) | Germination ^b (%) |
|-------------------|-------|----------------------------|---------------------------------|
| Greenhouse: | | | |
| Open | 0.95 | 14,208 | 54.0 |
| Green mesh | 1.08 | [′] 549 | 24.5 |
| Ragweed Field: | 2.11 | 786 | 69.5 |
| Open | 0.72 | 91,493 | 0.0 |
| Green mesh | 2.17 | 3,229 | 49.5 |
| Ragweed | 4.72 | 3,165 | 51.5 |

Note,—Germination of dry-stored seeds at 20-30 C on July 21 in light and dark was 64% and 22%, respectively.

due to lack of germination and/or establishment. Low water potential inhibited hawkweed germination in the laboratory (fig. 5), which is typical of many of the species tested by Hoveland and Buchanan (1973), and this may restrict germination in the field since less moisture is available during the summer months, and July 1974 was especially dry. Direct drying by high temperature, however, is not harmful to the seeds and did not induce dormancy (fig. 4). Soil moisture should be adequate for germi-

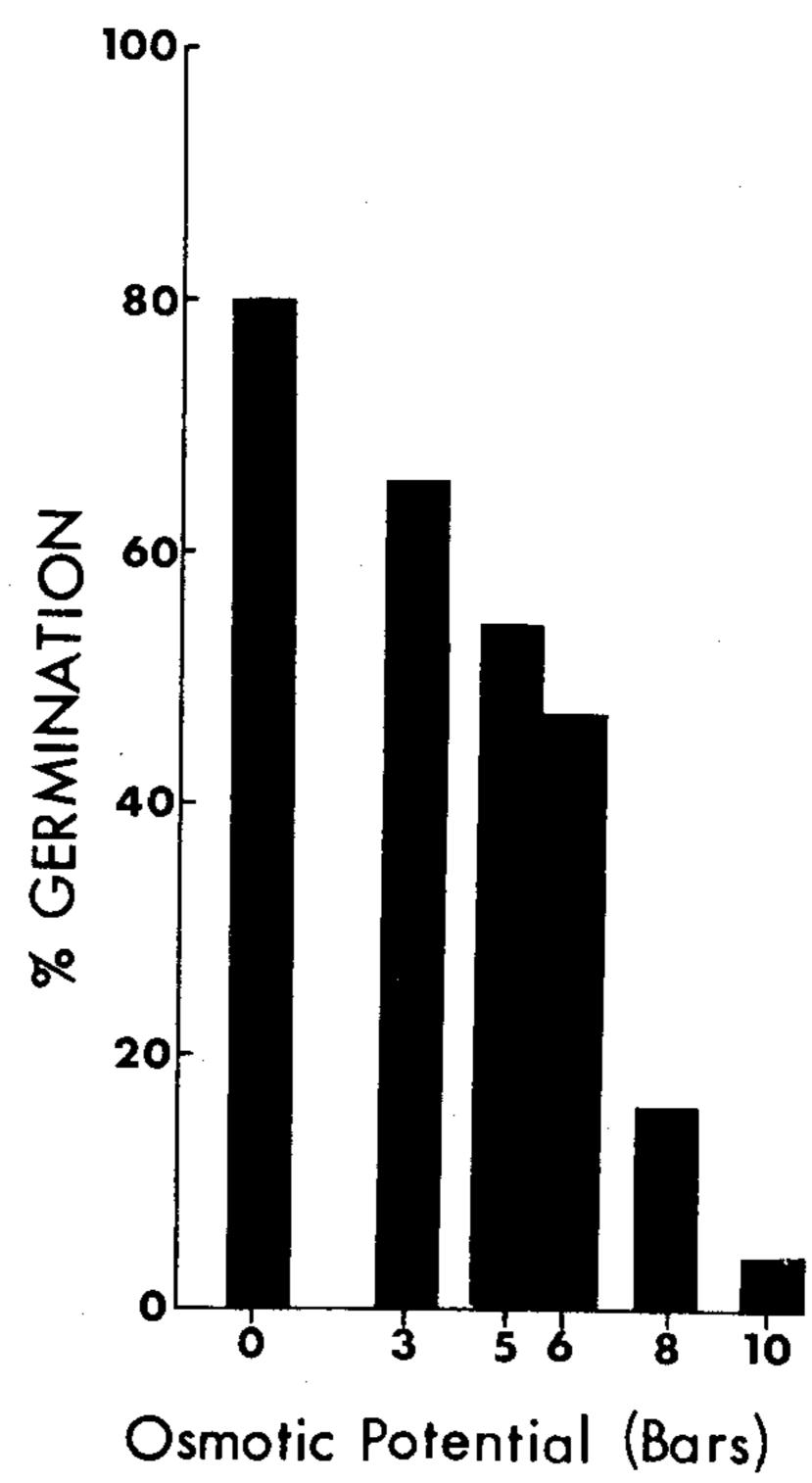


Fig. 5.—Germination of hawkweed seeds at 0, 3, 5, 6, 8, and 10 bar osmotic potential solutions at 20-30 C in March 1975. LSD at 95% confidence interval = 8.1.

nation later in the growing season when air and soil temperature decrease (fig. 3). However, field germination during the late fall and winter may be restricted by these low soil temperatures since hawkweed seed germination was poor at 5-15 C until after stratification or overwintering (figs. 1, 2). A few seeds germinated during laboratory stratification, which may indicate some field germination during this time; however, little seedling growth would be expected at these low soil temperatures. Germination of buried seeds at 5-15 C increased during the winter to at least 50% by early February (fig. 2), indicating that seeds in the field could germinate early in the spring when soil temperatures are still low (fig. 3). Germination did occur in the second-year field in the spring following seed dispersal, and once a rosette is established, an increase in cover may be effected by vegetative reproduction (Kott 1962).

Several researchers (FEDERER and TANNER 1966;

 $^{^{}n} FR/R = far red (730 nm)/red (660 nm).$

^b LSD at 95% confidence interval = 9.8.

TAYLORSON and BORTHWICK 1969; FLEET 1972; SMITH 1973; RAYNAL and BAZZAZ 1975) noted an increase in the FR/R ratio after sunlight passed through a vegetation canopy. A spring-plowed field is rapidly revegetated during the following summer, so there is little bare ground left when hawkweed seeds are dispersed. The effects of this phenomenon could be important for germination in the field. Since FLEET (1972) showed that ragweed caused a FR enrichment of light which passed through its leaves, and because of its dominance in first-year fields, this plant was used to test the effect of FR enrichment on hawkweed seed germination. The results (table 2) indicate that light with a high FR/R ratio has relatively little effect on germination of hawkweed compared to seeds placed in the open or in the 20-30 C germinator. Therefore, this factor should not greatly affect germination in the field. However, the high FR/R ratio of light passing through a vegetation canopy may inhibit germination of freshly harvested seeds. The seeds used for this test were over 1 yr old, and TAYLORSON (1970) showed that Amaranthus retroflexus seeds only became capable of germinating after a R/FR treatment following a period of burial. There is some evidence that germination at reduced light intensities is inhibited (table 2), and this could also limit field germination beneath a vegetation canopy during the summer and fall.

Hawkweed seeds would be expected to be present in the spring in soil of the first-year fields used in this investigation, since hawkweed comprised part of the previous season's vegetation of these and adjacent fields. Seeds from the previous season are nondormant the following spring (fig. 2). Thus, germination would be expected, but we did not observe successful establishment in first-year fields. Hawkweed seedlings were found in June by Jackson (1976) in the field plowed and abandoned in the spring, 1974 (the same field we used for fall observations), but were gone by September. BASKIN and BASKIN (1971, 1972) showed that an unusually heavy summer rain caused many winter annuals to germinate in July, but the following drought period resulted in very high seedling mortality. Also, we found seedling survival of hawkweed to be poor at high temperatures. The work of FLEET (1970, 1972) provided evidence that hawkweed seedlings are competitively inferior to yellow foxtail, a common plant on first-year

fields on the New Jersey Piedmont (SMALL et al. 1971). These factors indicate that hawkweed may be competitively inferior to rapidly growing annuals, and this may restrict its establishment in recently disturbed fields.

The large number of empty seed coats (which may have been due to germination, decay, and/or predation) indicates that hawkweed seeds are probably not viable in soil for a long period of time. The lack of emergence of seedlings from 2 cm and greater depths, which was also demonstrated in Anoda cristata for depths greater than 10 cm (Solano, SCHRADER, and COBLE 1974), along with the short seed longevity, indicates that in order for hawkweed to become established in an area, fresh seeds must be supplied fairly frequently, and they must be present at or near the soil surface if establishment is to be successful.

In summary, the lack of innate dormancy mechanisms in H. pratense should result in seed germination at most times of the year if enough moisture is available and temperatures are suitable. Thus, germination seems to be synchronized with moisture and temperature conditions advantageous for seedling survival. Germination is restricted by low water availability, which would also be unfavorable for seedling development. Restriction of germination by low fall temperatures might be advantageous since little seedling growth would be expected to occur at these low temperatures, which could result in increased mortality by winter injury. The ability to germinate at low temperatures the following spring (after overwintering) would be expected to coincide with favorable environmental conditions for seedling development. Even though seed and seedling mortality appears to be very high for hawkweed, the establishment of only a small number of rosettes is needed to ensure the success of this species, since it is a perennial and multiplies vegetatively.

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