Dormancy and dispersal in dimorphic achenes of tansy ragwort, *Senecio jacobaea* L. (Compositae)

Peter B. McEvoy
Department of Entomology, Oregon State University, Corvallis, OR 97331, USA

**Summary.** Marginal and central florets of the capitula of tansy ragwort *Senecio jacobaea* yield different kinds of fruit. The central (“disk”) achenes are lighter ($\bar{x} \pm SE = 199 \pm 5$ g), more numerous ($\bar{x} \pm SE = 58 \pm 0.6$ achenes per head), and are equipped with a pappus aiding wind transport and rows of trichomes aiding animal transport. The marginal (“ray”) achenes are heavier ($\bar{x} \pm SE = 286 \pm 7$ g), less numerous (virtually invariant at 13 achenes per head), and lack dispersal structures. Whereas disk achenes are released shortly after they mature, ray achenes are retained by the parent for a period of months following maturity.

Germination at constant temperature (20°C) and with alternating light (12 h light: 12 h dark) demonstrated that disk and ray achenes exhibit different germination syndromes. Germination percentage increases linearly with achene fresh weight in both types; for a given weight, disk achenes have a higher germination percentage than ray achenes. Germination time decreases with increasing achene weight in disk achenes, but increases with achene weight in ray achenes.

The germination percentages and germination times for disk and ray achenes diverge progressively with increasing achene weight. The divergence in behavior is a result of diverging patterns of dry matter allocation in the two achene types. Increase in the size of disk achenes favors the embryo fraction, thereby speeding germination while reducing protection. Increase in the size of the ray achenes favors the pericarp fraction, thereby increasing protection while delaying germination.

Reduced germination percentage and germination speed of the ray achenes were shown by experimental manipulation to be caused by physical inhibition by their thicker pericarps.

Dimorphism in ragwort likely spreads germination out in space and time, thereby increasing the number of safe sites an individual parent can exploit in disseminating offspring. The syndrome in other heteromorphic composites resembles that of ragwort, generally combining reduced dispersal-delayed germination in the outer achenes and distance dispersal-quick germination in the central achenes. The outer achenes are generally less numerous and larger. Dispersal traits (large numbers, early release and light weight) are the direct opposite of dormancy traits (small numbers, delayed release and heavier weight). Thus conflicts between the properties determining dormancy and dispersal appear to require separate dormancy and dispersal phenotypes.

**Introduction**

Somatic seed polymorphism refers to the production of seeds of different morphologies and behaviors on different parts of the same individual plant. Examples appear to be restricted to short-lived, fugitive species, particularly weeds, and most examples are found in four families: Compositae, Chenopodiaceae, Graminaceae, and Cruciferae (Harper 1977). In some cases, distinct morphological types have been shown to behave differently in dispersal, germination or both (Becker 1912; Salisbury 1942, 1964; Zohary 1950; Koller and Roth 1964; Stebbins 1974; McDonough 1975; Baskin and Baskin 1976; Flint and Palmblad 1978; Sorensen 1978; Venable 1979; Baker and O’Dowd 1982). Here I employ a laboratory study of the differences in morphology and germination of dimorphic achenes to investigate the interplay among dormancy, dispersal, numbers, and size in achenes of tansy ragwort (*Senecio jacobaea* L.).

The achene serves a wide variety of not obviously related roles (Harper et al. 1970): perennation, multiplication, dispersal, and dormancy. Furthermore, it is also so closely linked to the sexual process that it becomes in effect the means of release of genetic variability to the external environment. Heteromorphic flowers and fruits offer an attractive system to test theories linking breeding, dispersal, and dormancy. One of the goals of this study was to identify constraints that delimit pathways of evolutionary change in this suite of characters.

Ragwort has an extremely heterogeneous life cycle—the ramet behaving as an annual, biennial, or short-lived perennial (Cameron 1935; Poole and Cairns 1940; Harper and Wood 1957; Bornemissza 1966; Schmid 1972; Forbes 1977; van der Meijden and van der Waals-kooi 1979), although the genet may be very long lived because of the vegetative spread by root buds (Poole and Cairns 1940; Harper and Wood 1957). Typically rosettes are biennials, spending the first year as vegetative rosettes and producing flowering stalks in the second year. The capitulum of ragwort is differentiated into peripheral, ligulate, female “ray” florets and central, tubular, perfect “disk” florets. Ray achenes are glabrous and shed their reduced pappus during development; disk achenes bear rows of trichomes and retain their pappus. Harper and Wood (1957) report that disk florets average 57 per capitulum while ray florets average 13 (range from 12-15) per capitulum. The two achene types reach maturity within a few days of each other (Baker 1982), but the ray achenes are delayed in their release. Green (1937) noted that the epappose ray achenes are re-
tained, pressed against the inner surface of the involucre when the pappose disk achenes are blown away leaving the ray achenes in the base of the involucral cup from which they are eventually shaken out.

Earlier studies have recognized morphological differences in disk and ray achenes of ragwort, but germination differences have been overlooked because the two types are typically pooled in bulk samples (Cameron 1935; Poole and Cairns 1940; Bornemissza 1966; Schmidl 1972; van der Meijden and van der Waals-kooi 1979; Grime et al. 1981). Accordingly I sought in laboratory germination trials to determine whether the two achene types obey different germination rules. The specific questions asked in this investigation were:

1. What is the relationship between germination percentage and achene weight?
2. What is the relationship between time to germination and achene weight?
3. Do the relationships between germination and achene weight differ for the two achene types?
4. If so, what features of achene design cause the distinction in achene behavior?

Methods

Achene numbers

Numbers of disk and ray achenes per head were determined by photographing the empty receptacle under 20–32 X and counting the scars left by detachments of the achenes. This method avoided underestimating achene numbers which may have arisen due to a loss of achenes in harvest and handling of heads.

Relationship between germination and weight

Mature achenes were collected from a field population 16 km north of Corvallis, Benton County, Oregon. Five plants were selected at random and all mature heads were systematically harvested on 21 August, 5 September, and 20 September 1980. For each achene sampled, I recorded the harvest date and four measures of location – plant, branch, capitulum, and achene type. Achenes were stored in the laboratory under room conditions for four to five months prior to germination.

Each achene was weighed and measured prior to germination. Measurements taken were of the diameter and fresh weight of the pappus, the fresh weight of the achene, and the dry weight of the pericarp shed after germination. Embryo fresh weight was estimated by subtracting pericarp dry weight from achene weight. The use of a dry weight of the pericarp instead of wet weight exaggerates the embryo fresh weight only slightly since the pericarp of a mature achene is very dry (average water content in a sample of 19 achenes was 7%, with a range of 5–10%).

Achenes were germinated in the laboratory at constant temperature (20° C) and with alternating periods of light and dark (12 h light:12 h dark). Achenes were arranged in moisture-proof boxes on moist filter paper impregnated with Thiram® solution (100 ppm, 65% active ingredient) to deter the growth of fungi. An earlier test had shown that the Thiram treatment did not affect germination at this concentration. Estimates of percent germination and germination time were obtained for weight classes spanning the range in weight of each achene type from samples of 50 achenes per weight class. The protrusion of the radicle was the criterion of germination.

Role of the pericarp in inhibiting germination

A delay in germination was discovered in ray achenes which could be removed by excising the embryo from the pericarp. The pericarp could exert its influence:

1. by containing soluble chemicals which inhibit germination
2. by blocking the diffusion of gasses and the uptake of water
3. by physically impeding germination.

An experiment was performed to determine how the pericarp enforces dormancy in disk and ray achenes. Achenes were collected from a roadside population in Corvallis, Benton County, Oregon on September 11, 1980. Achenes were randomly assigned to treatments that varied the level of inhibition by the pericarp – ranging from full inhibition, to partial inhibition, to no inhibition. Forty achenes were allocated to each of three treatments:

1. Control. Unmanipulated achenes should experience full inhibition by the pericarp.
2. Proximal nick. Removal of the pericarp from the proximal tip of the achene should remove resistance to protrusion of the radicle and allow the exchange of gasses and the uptake of water.
3. Distal nick. Removal of the pericarp from the distal tip of the achene should reduce resistance to protrusion of the cotyledons and allow gas exchange and water uptake.
4. Split. An incision running the length of the achene should reduce resistance to protrusion of both the cotyledons and the radicle and allow gas exchange and water uptake.

A daily record was made of the progress of each achene through five stages of germination: (1) radicle protruded, (2) root hairs spread, (3) cotyledons green, (4) cotyledons free of the pericarp, and (5) cotyledons spread. Smaller numbers of achenes were allocated to each of the treatments below:

1. Ten excised embryos were placed in contact with their pericarps to test whether soluble chemicals leaching from the pericarp inhibited germination.
2. Eleven embryos without pericarps were used as controls.

Germination in excised embryos is indicated when growth starts or the embryo remains white and firm at the end of the test (Colbry et al. 1961).

Photomicrography

Achenes were coated with gold/paladium for examination with a scanning electron microscope. Fresh (unfixed) material was sectioned with a freezing microtome at 12 μ and mounted in Hoyer’s medium for examination with a light microscope.

Results

Achene numbers

In a sample of 45 heads, the number of disk achenes per head ranged from 48 to 65 with a mean and standard error