ECOLOGICAL CONSEQUENCES OF DIFFERENCES IN LIFE HISTORY CHARACTERISTICS AMONG FOUR "BIENNIAL" PLANT SPECIES

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The affect of differences in the life history characteristics of plants with a biennial life cycle were investigated in relation to their relative colonizing ability and the range of environments in which they can successfully establish and regenerate. Situations under which biennials can occur were examined first in the context of current theoretical models for the evolution of life history types. Several assumptions implicit in these models are discussed and the effect of incorporating a 1 year time lag to reproductive maturity for organisms with a perennial life history examined.

Field studies were conducted with four biennial plant species, *Verbascum thapsus*, *Oenothera biennis*, *Daucus carota*, and *Tragopogon dubius*. These four species exhibit striking differences in seed size, seed number, and dispersal ability. Although all four are capable of completing their life cycle within two years, a minimum size must be achieved before flowering can be induced. Above this threshold, the probability of flowering increases directly with rosette size and the probability of dying decreases.

Differences in colonizing ability were determined by monitoring the fate of introduced seeds of all four species from April 1978 to October

1979 in three old-fields of different successional ages. Within each field the proportion of the total area in six distinct vegetational patches was determined. Seedlings were marked upon emergence and the number emerging and establishing in each patch type recorded. Differences in emergence and establishment of all four species were determined in relation to the availability of three patch categories (BARE GROUND, TRANSITIONAL, AND VEGETATED) in the 1 and 15 year old-fields.

Seedling emergence and survival were directly correlated with seed size in these species and were highest for all four in BARE GROUND patches. _Verbascum_ and _Oenothera_, the small-seeded species, survived only in these patches. Consequently, populations of these two species established only in the 1 year old-field where BARE GROUND was abundant. _Daucus_ and _Tragopogon_, which produce significantly larger seeds survived in all three patch categories and populations established in both fields. Seedling growth and reproductive success in the second year was higher for both these species in the 1 year old-field.

Verbascum and _Oenothera_ were both able to establish in the 15 year old-field when sown onto artificially-created open patches. Seedling emergence was highest in small openings, but survival was highest in large patches. Differences in the dispersal capabilities of these four species are important in determining their relative probability of colonizing open sites. Both _Verbascum_ and _Oenothera_ seeds can remain viable in the seed pool for decades and are likely to be present in the soil when an opening is created. _Daucus_ and _Tragopogon_ seeds are dispersed broadly in space, but do not survive in the soil for more than 1-2 years. Consequently, they are not generally among the initial colonists after a disturbance occurs. These differences in colonizing ability provide a mechanism for explaining the temporal pattern in which these four species generally occur in early successional old-fields. Implications of these results for theoretical and empirical studies of the evolution of life history strategies and the maintenance of diverse assemblages of species in terrestrial plant communities are discussed.

To my parents and Gary -

for always believing I could and would.

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CHAPTER 1

INTRODUCTION

Although the entire suite of life history characteristics an organism possesses ultimately plays a role in determining when and where an organism will occur (c.f. Stearns 1976, 1977), it is possible to identify those characteristics which are likely to be the most important in determining the ability of a species to successfully establish and reproduce within a particular environment. For plants there is a growing body of evidence which indicates that the regenerative stages (seed, seedling, and juvenile) of the life history are the most important in determining the local success of a species (c.f. Harper 1977; Werner 1979). It is during this stage of the life history that most of the mortality occurs in plants (c.f. Harper 1967a,b; Hett and Loucks 1971; Sharitz and McCormick 1973; Sarukhan and Harper 1973; Werner and Caswell 1977); furthermore, established plants generally have a high and constant probability of survival until senescence. Although interactions among adult plants are important in determining the growth and reproductive output of an individual, ultimately the successful establishment of a species depends upon its ability to produce and disperse propagules there and, once established, to continually recolonize the site.

For plants which are monocarpic, the regenerative stage of the life history is especially important. Although all plant species are eventually doomed to local extinction if they fail to reproduce within a local area, monocarpic species persist both locally and globally only if they are able to continually re-establish in an area or disperse their propagules to new sites and establish there. Consequently, differences among monocarpic species for those life history characteristics which effect colonization and regeneration are likely to be extremely important both in determining their local success and the range of environments in which they are able to successfully colonize.

Plants which have a biennial life history are particularly interesting in this regard, because like perennials they persist for more than one growing season, but like annuals they are monocarpic. Moreover, although the term biennial implies these species reproduce in the second year of growth, for a number of so-called biennial species the length of the rosette stage is variable and flowering is determined by the size of a plant rather than by its age (c.f. Harper and Ogden 1970; Werner 1975; Harper 1977; Baskin and Baskin 1979a,b). Consequently, the success of a plant with a "biennial" life history is dependent upon its ability to persist in an area until it reaches the size at which it can reproduce and, once it reproduces, to produce enough propagules to recolonize the area in which it currently exists or to disperse to and establish individuals in a new site.

Most of the theoretical models for the evolution of plant life histories have focused mainly on the annual/monocarpic and perennial/polycarpic life history strategies (e.g. Charnov and Schaffer 1973; Schaffer and Gadgil 1975; Hastings and Caswell 1979). These models have for the most part ignored any type of intermediate life history (e.g. biennial), tending to view these only in the context of variations of the annual and perennial strategy, rather than as unique life history types (c.f. Schaffer and Gadgil 1975). Moreover, although the past decade has produced a vast body of literature pertaining to the life history of plants (see Stearns 1976 and Solbrig et al. 1979 for reviews), only a few of these studies have considered plants with a "biennial" life history (e.g. Holt 1972; P. Werner 1977; Baskin and Baskin 1979a,b). Consequently, it is difficult to make generalizations about when and where plants with a "biennial" life cycle are likely to be successful. An examination of several plant species which are classified as having a biennial life history, but which have different suites of life history characteristics, would provide both a better framework of empirical evidence for the development of theoretical models of the evolution of plant life history strategies and provide further insights into the relative costs and benefits of various life history characteristics and how these differences effect the distribution and abundance of species in terrestrial plant communities.

Thesis Organization

This thesis has been written as a series of separate chapters each of which deals with a different aspect of the life history of plants with a "biennial" life cycle. The intent of this chapter is to provide a general introduction to the questions pursued in the later chapters and to provide more detailed descriptions of the four species of "biennial" plants used in the experimental field studies and the sites in which those experiments were conducted. Chapter 2 examines the adequacy of current models of the evolution of life histories to predict the types of environmental conditions (typified by different juvenile and adult survival probabilities) under which organisms with a biennial life cycle will be successful (in terms of population growth rate) relative to those with an annual or perennial life cycle. The effect of several implicit assumptions of the previous models with regard to the frequency and timing of reproductive events for organisms with a perennial life cycle are discussed. In Chapter 3, the efficacy of the size of a rosette relative to its age in determining the fate of an individual the following year is examined for four species of plants classified as having a biennial life cycle. Chapter 4 presents and discusses the results of experimental field studies using these same four species of "biennials". Examined is the effect of differences in particular life history characteristics among these four species on their relative colonizing ability and the consequences of these differences in terms of their relative distributions and abundances over a range of environments. Chapter 5 summarizes the general results and conclusions of the previous chapters and discusses their implications for future theoretical and empirical studies of the evolution of life history strategies and the maintenance of diverse assemblages of species in terrestrial plant communities.

Species Descriptions

The four species selected for study all are similar in that all are classified as having a biennial life cycle, all are monocarpic, and have no vegetative reproduction. Censussing of populations of all four species is relatively simple because individuals are easily recognized at all stages of the life cycle (seed, seedling, rosette, and flowering).

The life history characteristics of these four species as well as differences in juvenile and adult morphology are described in detail below and summarized in Table 1-1. Vascular plant nomenclature follows

Table 1-1: Life History Characteristics of Four Species of "Biennials".

Species	Seeds* per plant	Seed wt.	Dispersal Ability (Morphological Adaptations)	Juvenile and Adult Morphological Characteristics	References
Verbascum thapsus L. (Scrophulariaceae)	180,000	0.064	Passive: to 11m; median 1m Dormancy: to 40 yrs in Duvel exp't.	Low, broad, basal rosette to 60 cm in diam.; leaves densely wooly with branched hairs. Adults 0.25 to 2.3 m tall; inflor. a spiral-like dense raceme; flowers emphemeral; protandrous, but able to self-fertilize. Flowers 2nd yr.	Gleason and Cronquist 1963 Toole and Brown 1946 Gross and Werner 1978
Oenothera biennis L. (Onagraceae)	10,000	0.20	Passive: to 4m; median < 1m Dormancy: to 80 yrs in Beal exp't.	Broad, spreading basal rosette of crinkley-wavey, thin leaves with sparse pubesence. Rosettes to 30 cm in diam. Adults to 85 cm tall; flowers alternate to whorled in terminal raceme, heterogamous and self-pollinating. Generally flowers in second year.	Gleason and Cronquist 1963 Kivilaan and Bandurski 1973 Platt 1975 Gross, unpubl.
Daucus carota spp. carota L. (Umbelliferae)	2,000	0.79	Passive (wind): to 15m Animal: ?. attaches to fur of some mammals. (Barbed fruit)	Rosette erect, to 20 cm tall. Flowering plants 0.1 to 1.2 m tall; produce axillary, flowering stalks terminating in a cmpd. umbel. Flowers protandrous; mainly out-crossed, though plant is self-fertile. Flowers 1st yr., 2nd yr., or later	Ridley 1930 Gleason and Cronquist 1963 Holt 1969 Dale 1974 Lacey 1978 Gross, unpubl.
Tragopogon dubius Scop. (Compositae)	200	6.6	Wind: greater than 250m (Broad, flat pappus)	Rosette erect, to 15 cm, with grass-like leaves, alternate and clasping. adult plants $\overline{x}$ ht. 65 cm. Heads solitary at ends of branches, all perfect, ray flowers. Flowers 2nd yr. or later.	Ridley 1930 Fernald 1950 Gleason and Cronquist 1963 Gross, unpubl.

*Seed used here for simplicity; botanically a diaspore.

Gleason and Cronquist (1963). Voucher specimens of the four species have been deposited in the herbarium at the W. K. Kellogg Biological Station.

Verbascum thapsus L. (Scrophulariaceae), the "Common Mullein", was introduced to North America from Eurasia and is found in dense, but widely-spaced patches in pastures, early successional old-fields, and roadsides throughout southern Canada and the continental United States (Gross and Werner 1978). Verbascum seeds are born in a two-celled capsule and typically plants produce large numbers (50,000 - 250,000) of very small seeds (0.064 ± 0.002 mg; $\bar{x} \pm 1$ S. E.; n=100). Verbascum seeds are dispersed in the fall and having no specialized morphological adaptations to aid in dispersal, generally fall within several meters of the parent plant (McLean and Ivimey-Cook 1956; Gross and Werner 1978). The seeds are able to remain viable, although dormant, for extended periods of time (up to 35 years in the Beal buried seed experiment, see Kivilaan and Bandurski 1973; and 40 years in the Duvel experiment, see Toole and Brown 1946). In Denmark, viable seeds of V. thapsus have been collected from soil samples archeologically dated from 1300 A.D. (Ødum 1965).

No cold treatment or after-ripening period is required for germination (Gardner 1921) and although the seeds typically germinate in the spring, seeds germinate throughout the summer following heavy rains and a fall germination pulse is not uncommon in open areas. In Michigan, however, later emerging cohorts of seedlings have a low probability of surviving over-winter. Recruitment to the following year is generally restricted to the early spring emerging cohorts of seedlings (Gross 1980). Seedlings form rosettes which have a broad, flat habit and may grow up to 60 cm in diameter (Gross and Werner 1978). Vernalization is required to induce flowering (Glier and Caruso 1973, 1974) and rosettes which overwinter and survive may produce a stout, flowering stem 0.3 - 2.0 meters high in a subsequent summer and then die after seeds are formed (Gross and Werner 1978). Although the length of the rosette phase is variable (see Chapter 3), populations in Michigan which delay flowering beyond the second summer generally do not successfully set seed (Gross and Werner 1978; Gross 1980).

Oenothera biennis L. (Onagraceae), the "Evening Primrose", is a native species distributed mainly east of the Missouri River, ranging south as far as northern Florida and north through the upper peninsula of Michigan (Cleland 1972). Populations of *Oe. biennis* in Michigan are found in early successional old-fields, along roadsides and railroad tracks, and other open areas. In Iowa, this species is one of a guild of fugitive species which occur only on badger mounds in a tall-grass prairie (Platt 1975).

Seeds of *Oenothera* are dispersed late in the fall within a few meters of the parent plant (Platt 1975). *Oenothera* seeds are capable of remaining viable, yet dormant, in the soil for extended periods of time (up to 80 years in the Beal buried seeds experiment, see Kivilaan and Bandurski 1973). Typically, *Oenothera* plants growing in early-successional old-fields produce 5,000 - 50,000 seeds which weight 0.20 ± 0.008 mg ($\bar{x} \pm 1$ S.E.; n=100). No cold treatment is required for germination, though stratification increases the percentage of seeds germinating (Blake 1935). Seedlings form a broad, flat, basal rosette of crinkley-wavy, thin leaves which may grow to 30 cm in diameter (Cleland 1972). The length of the rosette phase is variable and the probability of flowering in any year is dependent upon the size of an individual at the end of the previous season (see Chapter 3). Flowering plants of *Oenothera* are 0.5 - 1.5 meters tall and die after seeds are formed. In Michigan, individuals flower in their second or third growing season.

Daucus *carota* ssp. *carota* L. (Umbelliferae), commonly "Queen Anne's Lace" or "Wild Carrot", was introduced to North America from Eurasia and is now a common weed of disturbed habitats (Dale 1974; Lacey 1978). The dispersal unit of *Daucus*, a mericarp containing a single seed, has broad, flat barbs which can attach to the fur of animals (Ridley 1930) and may also aid in its dispersal by wind (Lacey 1978). Wind dispersed seeds may travel greater than 15 meters from the parent plant over the crusted surface of the snow (Lacey 1978). In Michigan, as in southern Ontario, *Daucus* seeds are typically dispersed from late August throughout the winter (Dale 1974; Lacey 1978). Although seeds of *Daucus* are reported to be able to remain viable in the soil (c.f. Dale 1974), typically seeds do not survive in the soil for more than 1 or 2 years (Lacey 1978; Gross unpubl.). In Michigan, plants typically produce over 1,000 seeds with an average weight of 1.04 $\pm$ 0.045 mg ($\bar{x}$ $\pm$ S.E.; n=50).

Daucus seeds have a 3 to 6 month after-ripening period after maturation (Dale and Harrison 1966) and generally germinate in the field the spring and following fall after their production, although a few seeds germinate throughout the summer months (Lacey 1978; Gross in prep.). The relative success of spring and fall emerging cohorts of seedlings varies from year to year and is dependent upon the frequency and abundance of rainfall following seedling emergence (Lacey 1978). Seedlings form an erect to semi-erect rosette of highly dissected leaves which can grow up to 20-30 cm tall. Flowering plants generally emerge from an overwintered rosette and range in height from 0.1 to 2.0 meters. The length of the rosette phase is variable (see Chapter 3). Occasionally, rosettes bolt and form a flowering stalk in the first growing season (Holt 1972; Dale 1974); however, the seed production of these annuals is significantly less than that of later flowering individuals (Rempel 1970). Non-flowering *Daucus* rosettes can persist in the vegetation for 3-5 years before flowering (Holt 1972; Chapter 3).

Tragopogon dubius Scop. (=*T. major* Jacq.; Compositae), the "Goat's Beard", is also introduced to North America from Europe (Gleason and Cronquist 1963; Frankton and Mulligan 1970). Populations of *Tragopogon* are generally found in mid- and late-successional old-fields, roadsides, pastures, and meadows. Individual *Tragopogon* seeds are borne in an achene, equipped with a broad, flat pappus (2.5-3.0 cm in diameter). In Michigan populations, individuals typically produce 100 - 250 achenes per plant which weigh 5.45 ± 0.164 mg ($\bar{x} \pm 1$ S.E.; n=50).

In Michigan and northern Iowa (S. Hermann, pers. comm.), seeds are dispersed from late June through mid-July. Dispersal is almost entirely by wind (Ridley 1930) and although 65 - 90% of the seeds fall within 5 meters of the parent plant, seeds which are caught in upward gusts of wind can disperse greater than 250 meters from their release point (Gross unpubl.). Mature seeds of *Tragopogon* do not germinate immediately after maturation, but have a 60 day after-ripening period.

Seedlings of *Tragopogon* emerge in the fall of the year they are produced or the following year in the spring and fall. Generally, seeds do not survive for more than 1 year in the field (Chepil 1946). *Tragopogon* seedlings form an erect rosette of thin, grass-like leaves which can grow up to 30 cm in height. Rosettes which overwinter and survive may produce a flowering stalk 0.4 to 0.8 meters tall in a subsequent summer and die after seeds are formed. Flowering is a function of the size of a rosette the previous year (Chapter 3), and though capable of flowering in the second year, rosettes may persist in the vegetation for 5-10 years before flowering (c.f. Chapter 3).

Field Sites

Three old-fields, all located with 2 km of the W. K. Kellogg Biological Station, Kalamazoo, Co., Michigan, were selected for the study of natural populations of these four "biennial" plant species and for monitoring the success of introduced seeds of each species. All three fields had similar soil (well-drained sandy loam) and topography and had been under similar agricultural production (mainly cereal crops) up to the time they were abandoned. The fields differed in the length of time (number of years) each had been abandoned from agricultural production and provided a gradient of habitat types representing a temporal sequence of successional development. The locations of these three fields at the Kellogg Biological Station are indicated in Figure 1-1 and a detailed description of each field follows below. For simplicity, the fields are referred to throughout by their "age" when the experiments were initiated in 1978.

The 1 year old-field was a 20 x 30 meter strip located along the southern edge of a set of experimental fields used for research on the biological control of the Cereal Leaf Beetle (*Oelema melanopus* Linn.). Prior to 1978, the field had been planted in an annual rotation of winter and spring cereal crops (H. Webster, pers. comm.). In late March, 1978, the field was roto-tilled and then abandoned. In April

Figure 1-1: Locations of the Three Successional Old-fields used for Species Introductions. Fields located at the W. K. Kellogg Biological Station, Kalamazoo County, Michigan. Fields indicated by their age at the onset of the experiments in 1978. Scale: 230 m to the cm.

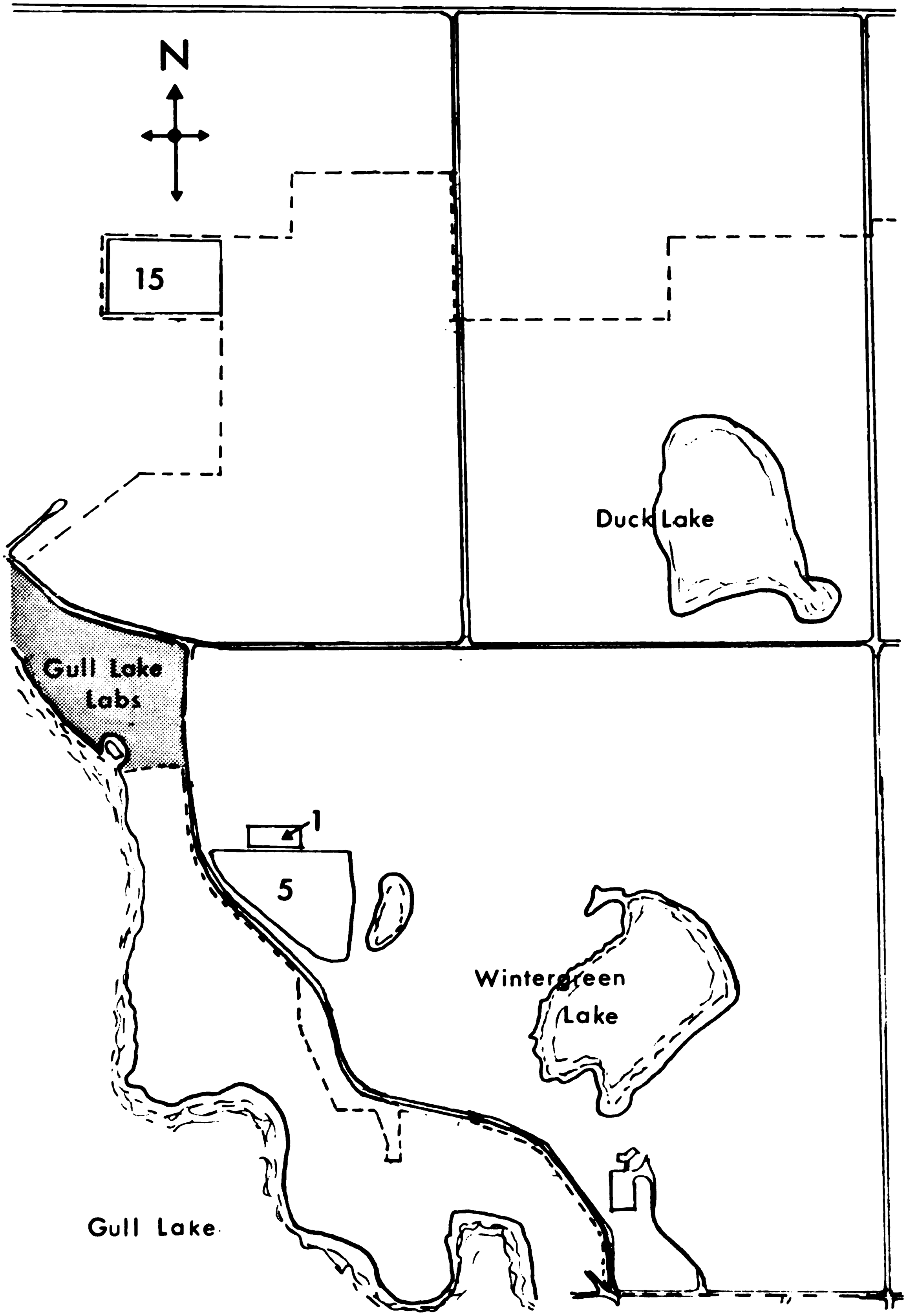

FIGURE 1

this section of the field was completely bare ground, but by May the percent cover of grasses and dicots was 6.3% and 28.1%, respectively, with 66% of the total area still bare ground. Dominant species during the 1978 growing season were mainly spring annuals, including *Amaranthus retroflexus*, *Chenopodium album*, *Ambrosia artemisifolia*, *Erigeron canadensis*, and *Polygonum persicaria*. Other herbaceous annuals and perennials which were less common included *Silene alba*, *S. noctiflora*, *Potentilla recta*, *Rumex acetosella*, *Trifolium repens*, and *Agropyron repens*.

The *5 year old-field* (McKay Field) was a 7 ha field located south of the 1 year old-field. The north and south ends of this field have a gentle slope, with the central portion being relatively flat. The slope at the south end of the field creates a gradient of soil moisture from dry, rocky soils at the top extending down to low, wet areas at the base. The field was under frequent cultivation until abandoned in 1973 (last crop, barley) with a rotation of corn and oats. A small strip of land at the top of the ridge was planted in sorghum in 1975 and then abandoned. In 1978 the percent cover by various life forms was: moss 3%, grass 10%, herbaceous dicots 30%, litter 85%, with only 10% of the ground bare soil. The dominant plant species in 1978 were mainly short-lived perennials and included: *Oenothera biennis*, *Silene alba*, *Rumex crispus*, *R. obtusifolius*, *Medicago sativa*, *Solidago canadensis*, *S. missouriensis*, *Potentilla recta*, *Agropyron repens*, *Phleum pratense*, and *Poa* spp. Along the south ridge (planted in sorghum in 1975) winter annuals and biennials dominated the vegetation cover and included: *Daucus carota*, *Lactuca* spp., *Tragopogon dubius*, *Erigeron strigosus*, and dead flowering stalks of *Verbascum thapsus*.

The *15 year old-field* was a 5 ha field located approximately 2 km north of the 1 and 5 year old-fields. The field is bordered by woodlots on the north and south, by agricultural fields to the east, and by agricultural fields, pastures, and residences to the west and north west. The topography of this field includes a series of gentle-rising (about 5°) east-facing slopes, separated by 'plateaus' 50 to 60 meters wide. The field was last cultivated around 1967. (Aerial photos taken in 1963 show the area under cultivation, but it was abandoned 1-2 years later (H. Webster, pers. comm.).) In 1978, the field was dominated by herbaceous perennial dicots; however, shrubs and trees (particularly *Prunus* spp.) had begun to invade from the adjacent woodlots. Litter accumulation was 3-5 cm in some portions of the field; although, broad patches of mosses and lichens occurred on the slopes. In 1978, the percent cover of the following life forms was: moss 3%, lichen 1%, grass 11%, herbaceous dicots 45%, shrubs 1%, litter 93%, with less than 1% of the total area bare soil. Dominant plant species included: *Hieracium aurantiacum*, *H. floribundum*, *Antennaria* spp., *Achillea millifolium*, *Solidago canadensis*, *S. missouriensis*, *S. nemoralis*, *S. speciosa*, *Potentilla recta*, *Aster* spp., *Daucus carota*, *Tragopogon dubius*, *Centaurea maculosa*, *Bromis inermis*, *Phleum pratense*, *Poa* spp., and *Agropyron repens*.

CHAPTER 2

A MODEL FOR THE EVOLUTION OF BIENNIALITY IN PLANTS

The question of the relative advantage of the perennial versus the annual life history raised by Cole (1954) laid the groundwork for the development of life history theory. Gadgil and Bossert (1970) and Charnov and Schaffer (1973) predicted that the relative mortality schedules on the juvenile and adult stages determined whether the perennial or annual strategy would be most successful. The relative selective advantage of annual, perennial, and biennial life histories were discussed by Schaffer and Gadgil (1975). Hart (1977) expanded these ideas and predicted the types of environments (based on juvenile and adult survivorship rates) where each life history might be expected to occur.

The models of Charnov and Schaffer (1973), Schaffer and Gadgil (1975) and Hart (1977), predict that the perennial habit will result when survivorship of adults is high and survivorship of juveniles is low. In these models, however, the annual habit is never favored over the perennial, even under the opposite conditions of extremely low adult survivorship and high juvenile survivorship. Furthermore, the biennial habit is never favored over either the annual or perennial (although it does come close over a narrow range of values: see Hart 1977 and Figure 2-1).

The limits of the models stem from an inherent assumption about the timing of perennial reproduction which is biologically unrealistic and

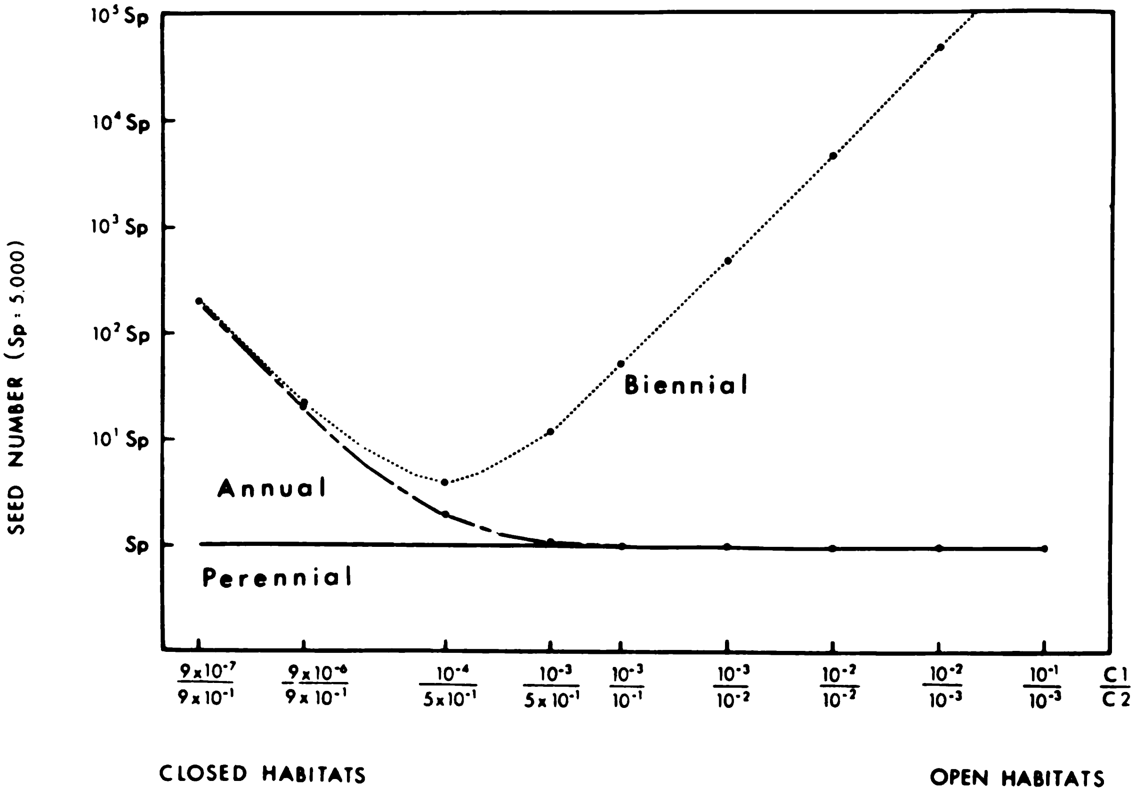

Figure 2-1: Seed Production Required for Annual or Biennial to Equal Growth Rate of Perennial over a Range of Juvenile and Adult Survival Values. Perennial seed production (Sp = 5,000) is assumed to be constant. The range of c_1/c_2 values typifies a continuum of habitats from closed to open. (After Hart 1977.)

which biases in favor of the perennial strategy. The problem is easily rectified. A minor change results in a much stronger model which can mathematically predict conditions in which the annual habit is favored over the perennial.

Using λ, the per capita rate of increase, as a measure of fitness for each of the three life histories, Schaffer and Gadgil (1975) and Hart (1977) define:

$$\lambda a = c_1 S_a \text{ for annuals} \tag{1}$$

$$\lambda b = (c_1 c_2 S_b) \quad \text{for biennials} \tag{2}$$

$$\lambda p = c_2 + c_1 S_p \text{ for perennials} \tag{3}$$

where c_1 is the proportion of propagules surviving the first year (juvenile or seedling survivorship) and c_2 is the proportion of the population (> 1 year old) which survive each succeeding season (annual adult survivorship). c_1 and c_2 are constant for all individuals within a particular habitat. S_a, S_b, and S_p are the number of propagules (seeds) produced by the annual, biennial, and perennial forms respectively.

In relatively stable, closed environments where c_1 is probably very low, c_2 makes a significant contribution to the growth rate, and the perennial form is favored (cf. Figure 2-1). As c_2 decreases, relative to c_1, the annual form is increasingly favored (Schaffer and Gadgil 1975; Hart 1977). However, even for very low values of c_2, annuals and perennials producing the same number of seeds will have equivalent population growth rates (Hart 1977).

In these models, the 'best' the annual can do is match the population growth rate of the perennial, because for $c_2 = 0$, the growth rate of the perennial becomes $\lambda p = c_1Sp$, which for $Sp = Sa$, gives $\lambda p = \lambda a$. If this were true, in open highly disturbed habitats where adult survivorship (c_2) is low, annuals and perennials would be expected to be equally represented. Much data suggest that this is not the case. Annuals may constitute more than 90% of the species in open habitats, whereas perennials are rare or nonexistant (cf. Salisbury 1942; Tramer 1975).

All the previous models assume that perennials reach reproductive maturity in the first year. But, in reality, this is almost never the case. (See current work on the life history of perennials, e.g. Harper and White 1974; Ogden 1974; Stiles 1975; vanAndel 1975; Platt 1976; Davidson and Barbour 1977; McLeod and Murphy 1977.) Even highly opportunistic short-lived herbaceous perennials such as fugitive species in a climax prairie community (Platt 1975, 1976) do not reproduce in the field until their second year of growth. Only 2 out of 152 (1.3%) of the weedy perennial species in Michigan are also listed as annuals (P. A. Werner, unpublished data).

A more biologically realistic but equally general model would incorporate a one year time lag to reproductive maturity for the perennial life history. Using the same parameters as above, a simple 2 x 2 Leslie matrix can be constructed

$$\begin{bmatrix} 0 & c_2S_p \\ c_1 & c_2 \end{bmatrix}$$

which consists of two age classes, or stages, (juveniles and adults).

c_1 is the probability a juvenile will survive the first year. (They do not reproduce that year.) c_2 is the probability an adult will survive; each adult produces c_2Sp seeds. Adult survivorship (c_2) is assumed to be a constant and independent of age; a pattern which is generally true for perennials (cf. Harper and White 1974; Grubb 1977; Werner 1979).

The analytical expression of the dominant eigenvalue for this matrix,

$$\lambda p = \frac{c_2 + \sqrt{c_2^2 + 4c_1c_2Sp}}{2} \qquad (4)$$

is the annual per capita rate of increase for the perennial life history. The reproductive output necessary for a biennial or annual form to achieve a growth rate equal to λp is

$$S_b = \frac{\lambda p^2}{c_1c_2} \quad \text{for the biennials}$$

and

$$S_a = \frac{\lambda p}{c_1} \quad \text{for the annuals.}$$

Figure 2-2 is a graphical representation of the results of this model. Where c_2 is high and c_1 low (closed habitats), the perennial will be favored, a result which is similar to that of the previous models (Schaffer and Gadgil 1975; Hart 1977; see Figure 2-1). But, as c_2 decreases and c_1 increases (open habitats), the advantage shifts to the annual habit. In fact, there is a definite cutoff point, where

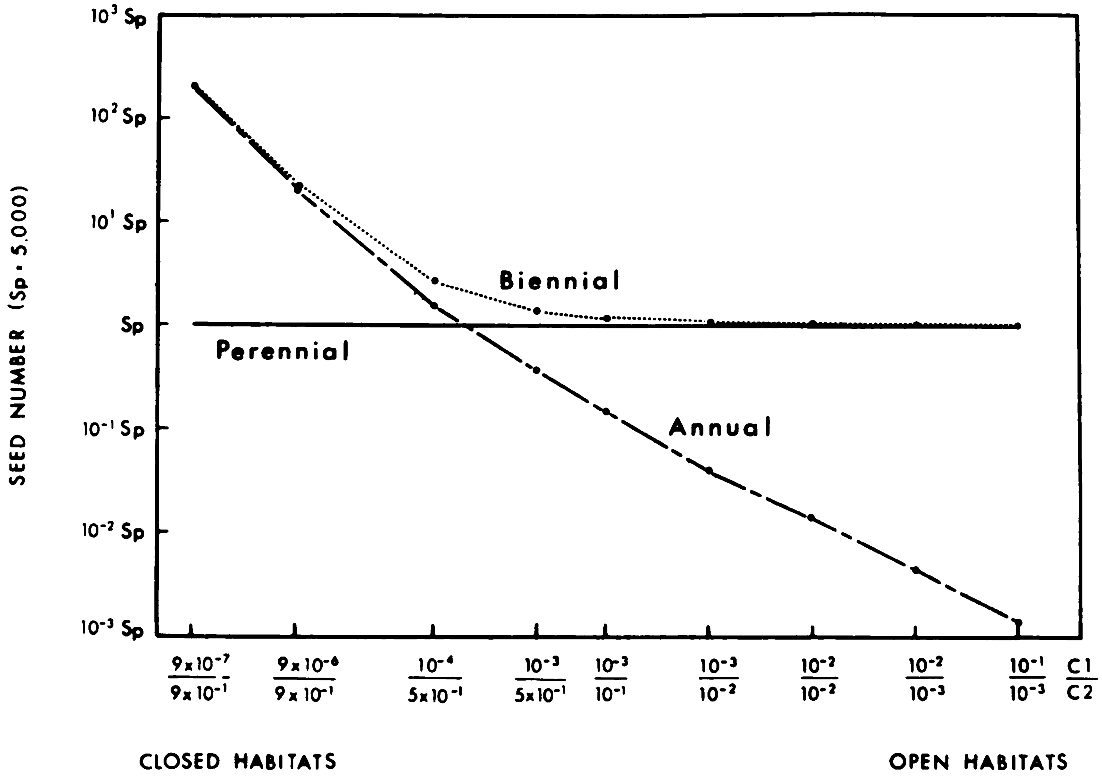

Figure 2-2: Seed Production Required for Annual or Biennial to Equal Growth Rate of Perennial Assuming a 1 Year Time Lag for Perennial Reproduction. Parameter values the same as in Figure 2-1. Decreasing Sp from 5,000 shifts the point where Sp = Sa to the right.

$S_a = S_p$ gives $\lambda_a = \lambda_p$, to the right of which the annual habit will be selected over the perennial and to the left of which selection will be for a perennial habit.

In open habitats, biennials and perennials are nearly equivalent life histories (perhaps because they both incur the cost of second year mortality before reproducing), a result which strongly differs with the predictions of Hart (1977). In closed habitats, the annual and biennial strategies are equivalently disadvantaged, because recruitment of seedlings (c_1) is very low. At no point is the biennial favored over the annual or perennial forms (similar to the predictions of Hart 1977). In the field, however, biennials are quite successful in certain habitats. This inconsistency between the model predictions and the field may be due partially to another assumption in the models, that the perennials achieve their maximal or mean seed production (Sp) the first year they reproduce (cf. Hart 1977). In fact, seed production by perennials does not reach these levels until after several years of growth (e.g. Rabotnov 1950; Harper and White 1974; Davidson and Barbour 1977; Platt, in prep.). Incorporation of a gradually increasing rate of seed production for the perennial (which is possible, but cumbersome mathematically), may allow the models to predict the c_1/c_2 conditions where a biennial life history will be selected over an annual or perennial habit.

Little is known about the actual range of c_1/c_2 values that occur within and between various habitats. In those habitats where annuals predominate, survivorship appears to be controlled mainly by abiotic factors; whereas, in habitats where perennials predominate, biotic factors appear to be more important. The conditions where a biennial habit will be the most successful life history may occur only rarely and may not persist for extended periods of time.

The range of c_1/c_2 values shown in Figures 2-1 and 2-2 can be viewed not only as representing a range of habitat types or patches occurring over a spatial scale, but also as changes occurring within a habitat on a temporal scale. The process of secondary succession on abandoned agricultural land is representative of the latter. The pattern of colonization and dominance of these three life history types that occur over several years in an old field may be the result (and/or the cause) of changes in the c_1/c_2 conditions within that field. Essentially, the environment is shifting from one which is open favoring the annual life history to a more closed environment where the perennial form is favored. At some point along this transition, conditions are such that the biennials are able to temporarily become the dominant form in the vegetation. Such a pattern is commonly observed (cf. Tramer 1975 and Figure 2-3).

The inclusion of a biologically more realistic assumption for the timing of perennial reproduction has enhanced the models of Schaffer and Gadgil (1975) and Hart (1977) allowing them to predict conditions where the annual and perennial forms are each best adapted. The biennial strategy is still never favored in these models; however, it is at less of a disadvantage than Hart (1977) had predicted.

The ability of plants with a biennial life cycle to establish and dominate the landscape (cf. Figure 2-3) presents a striking paradox to the conclusions of these models. Clearly, before more realistic models for the evolution of various life history strategies can be developed the ecological situations in which biennials are favored need to be

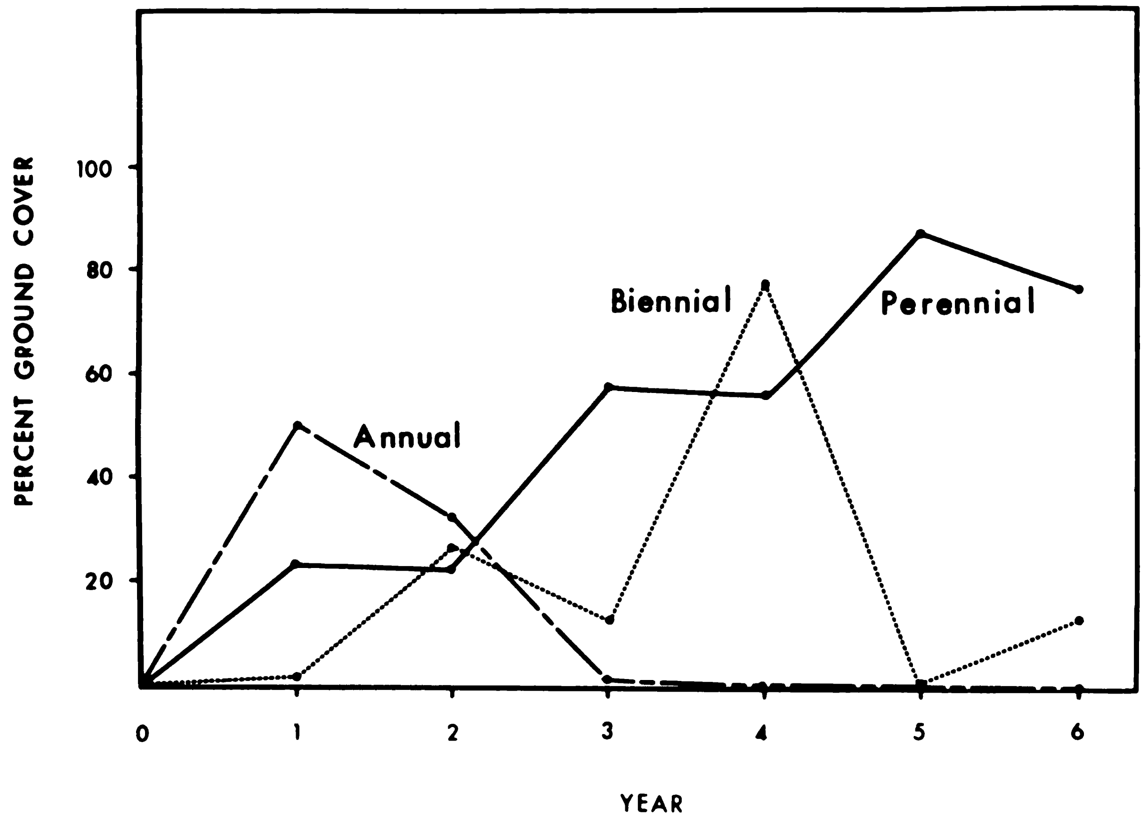

Figure 2-3: Shifts in the Percent Cover of Three Life History Types over Time on Abandoned Agricultural Land. Each point represents a mean of thirty permanently marked plots (0.25 m^2) of a field abandoned from cultivation in 1964 (year 0). Unpublished data of J. E. Cantlon used by permission.

examined more carefully. The following chapters (3 and 4) present the results of empirical studies with four species of plants classified as biennials which indicate that the success of a biennial plant species in a given habit (in terms of colonization and persistence) is dependent upon the particular suite of life history characteristics it possesses. These data provide a framework upon which future modeling efforts of the evolution of life history types can be based.

CHAPTER 3

PREDICTIONS OF FATE BASED ON ROSETTE SIZE

INTRODUCTION

Among plant ecologists there is a growing consensus that the size of an individual is more important in determining its behavior (e.g. whether it flowers, dies, or remains vegetative) than its chronological age (Werner 1975; Werner and Caswell 1977; Baskin and Baskin 1979a,b; see also Harper 1977). Plants with a biennial life history are particularly interesting in this regard because like many perennials they remain vegetative for more than one growing season yet, like annuals, they flower only once. Variation in the length of the vegetative growing period has been observed in several biennial species (e.g. Holt 1972; Oxley *fide* Harper and White 1974; Werner 1975; and Baskin and Baskin 1979a,b); however, only rarely has the relationship between plant size and age to the fate of an individual been directly quantified (Werner 1975; Meijden and Waals-Kooi 1979).

In this chapter the relationship of both plant size and age to the fate of a rosette will be examined in four plant species, *Verbascum thapsus* L. (Common Mullein), *Oenothera biennis* L. (Evening Primrose), *Daucus carota* L. (Queen Anne's Lace), and *Tragopogon dubius* Scop. (Goat's Beard). All four species are classified as biennials (cf. Gleason and Cronquist 1963), are monocarpic and do not propagate vegetatively. Populations of all four species are common along roadsides, in abandoned old-fields, in pastures, and in other disturbed areas throughout North America.

MATERIALS AND METHODS

Field Studies

Several populations of each of these four species were studied in fields of different successional ages (years since abandonment from agriculture) located at the W. K. Kellogg Biological Station (KBS) in Kalamazoo County, Michigan, USA. Individuals in each population were marked and followed for 2 or 3 years. The plants followed included individuals of known age (followed from seedling emergence) and unknown age (marked as rosettes).

In the spring of 1978, 100 0.25m^2 plots were established in three old-fields (1,5, and 15 years since abandoned from cultivation) at KBS. Seedlings of each species were marked with colored plastic picks as they emerged in these plots and monitored for survivorship throughout the growing season. Previously established rosettes of each species occurring in these experimental plots were marked with numbered flags in April, 1978, and their survival monitored throughout the following two growing seasons. In addition, in September 1978, ten 0.25m^2 plots were set up in another area of the 5 year old-field in which Daucus carota rosettes and fall emerging seedlings were marked. In mid-late October, 1978, final measures of all individuals were made of the plant size characteristic which had been determined to give the best prediction of total dry weight for each species (see below). All plants were monitored at regular intervals throughout the 1979 growing season and the fate of individuals determined in relation to their size the previous fall.

Also included in these analyses are data from separate studies on Verbascum thapsus conducted from 1976-1979 in a 4 yr. old-field at KBS.

Three populations of V. thapsus were examined and in all cases the size of marked individuals was determined in late October. The growth, survivorship and reproductive output of individuals in these three populations was monitored until the death of all marked plants.

The observations of fate reported here were determined from all these naturally growing populations and are based on data from over 2800 individuals.

Plant Size and Biomass

In order to determine the measure of plant size most appropriate to use as an indicator of the fate of a rosette the following year, a non-destructive measure of plant size highly correlated with rosette dry weight was determined for each species. In October, 1978, 25-40 rosettes of each species were selected at random from at least three populations. Several characteristics of plant size easily determined in the field were measured for each species including rosette diameter, rosette height, root crown diameter, and number of leaves. The plants were then dug up, taken to the laboratory, and oven dried for 48 hours at 100°C. For each species, the characteristic of plant size most highly correlated with total dry weight was determined by regression analysis, method of least squares.

RESULTS

For Verbascum thapsus and Oenothera biennis, both of which produce a broad, flat vegetative rosette, rosette diameter was the measure of plant size most highly correlated with rosette weight. This relationship was highly significant in both species ($r = 0.946$, $p < 0.001$ and $r = 0.914$, $p < 0.001$, respectively). Daucus carota and Tragopogon dubius both produce an upright rosette of thin, highly dissected (Daucus) or grass-like leaves (Tragopogon). In these species, rosette root crown diameter was most highly correlated with dry weight and again was highly significant ($r = 0.914$, $p < 0.001$ and $r = 0.973$, $p < 0.001$, respectively). The relationship between total rosette dry weight and the appropriate measure of plant size for each species is shown in Figure 3-1.

Table 3-1 lists, for all four species, the composite probabilities (for plants of all ages) of dying, remaining vegetative, or flowering as a function of rosette size at the end of the previous growing season. For all four species the probability of dying decreases and the probability of flowering increases with increasing rosette size (Figure 3-2).

For Verbascum thapsus, rosettes less than 9 cm in diameter do not flower. The probability of flowering increases steadily with rosette size (>9cm) and all rosettes with a diameter greater than 41 cm flower the subsequent year. Oenothera biennis rosettes less than 3 cm in diameter do not flower the following year and the probability of flowering increases directly with rosette size above this threshold. All rosettes with a diameter greater than 14 cm at the end of a growing season flower the following year. In Daucus carota, the minimum size for flowering corresponds to a root crown diameter of 0.10 cm the previous fall. Here again, the probability of flowering increases directly with plant size, and all plants with a root crown diameter greater than 0.36 cm flower the subsequent year. For Tragopogon, the minimum size for flowering corresponds to a rosette root crown diameter of 0.11 cm the previous year. The probability of flowering for Tragopogon rosettes increases with size to a maximum probability of 0.87

Figure 3-1: Linear Regressions of the Relationships Between Rosette Size and Biomass in Four "Biennials". Size for *Verbascum* and and *Oenothera* based on rosette diameter and for *Daucus* and *Tragopogon* on rosette root crown diameter determined in October. The regression equations for each species are: $Y = 0.001\ (X^{2.56})$ for *Verbascum*; $Y = 0.00075\ (X^{2.70})$ for *Oenothera*; $Y = 4.081\ (X^{2.41})$ for *Daucus*; and $Y = 1.683\ (X^{2.62})$ for *Tragopogon*.

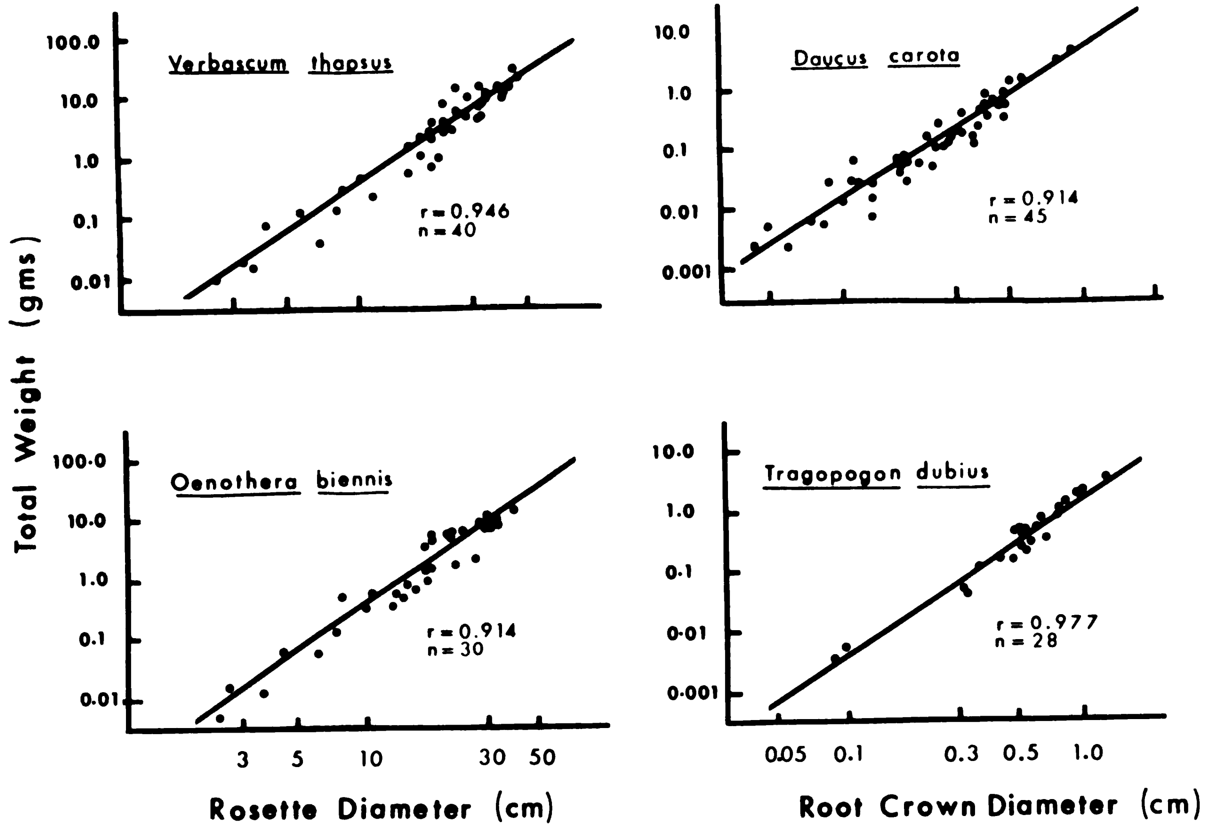
Total Weight (gms)
Verbascum thapsus
r = 0.946
n = 40
100.0
10.0
1.0
0.1
0.01
Daucus carota
r = 0.914
n = 45
10.0
1.0
0.1
0.01
0.001
Oenothera biennis
r = 0.914
n = 30
100.0
10.0
1.0
0.1
0.01
3
5
10
30
50
Rosette Diameter (cm)
Tragopogon dubius
r = 0.977
n = 28
10.0
1.0
0.1
0.01
0.001
0.05
0.1
0.3
0.5
1.0
Root Crown Diameter (cm)

FIGURE 3-1

Table 3-1: Rosette Fate in Relation to Size in Four "Biennials". The probability of a plant dying, remaining vegetative, or flowering as a function of its size at the end of the previous growing season. Measurements of rosette size determined for all species in late October. N = number of observations.

	Rosette Diameter(cm)	Dying	Remaining Vegetative	Flowering	N
Verbascum thapsus	$\leq$ 5.4 cm	0.97	0.03	0	661
	5.5-15.4	0.64	0.24	0.12	175
	15.5-25.4	0.27	0.08	0.65	100
	25.5-35.4	0.20	0	0.80	44
	35.5-45.4	0.06	0	0.94	17
	$\geq$ 45.5	0	0	1.00	9
					1006
Oenothera biennis	$\leq$ 2.4	0.46	0.54	0	11
	2.5- 5.4	0.43	0.43	0.13	30
	5.5-10.4	0.55	0.05	0.40	60
	10.5-14.4	0.16	0	0.84	63
	$\geq$ 14.5	0	0	1.00	39
					203
	Root Crown Diameter(cm)				
Daucus carota	$\leq$ 0.05	0.75	0.25	0	578
	0.06-0.20	0.24	0.63	0.13	229
	0.21-0.30	0.08	0.39	0.54	37
	0.31-0.40	0.07	0.07	0.86	14
	$\geq$ 0.41	0	0	1.00	8
					866
Tragopogon dubius	$\leq$ 0.1	0.48	0.52	0	545
	0.11-0.30	0.16	0.65	0.19	110
	0.31-0.50	0.10	0.59	0.31	49
	0.51-0.60	0.00	0.25	0.75	20
	0.61-0.70	0.13	0.00	0.87	15
	$\geq$ 0.71	0.10	0.20	0.70	10
					650

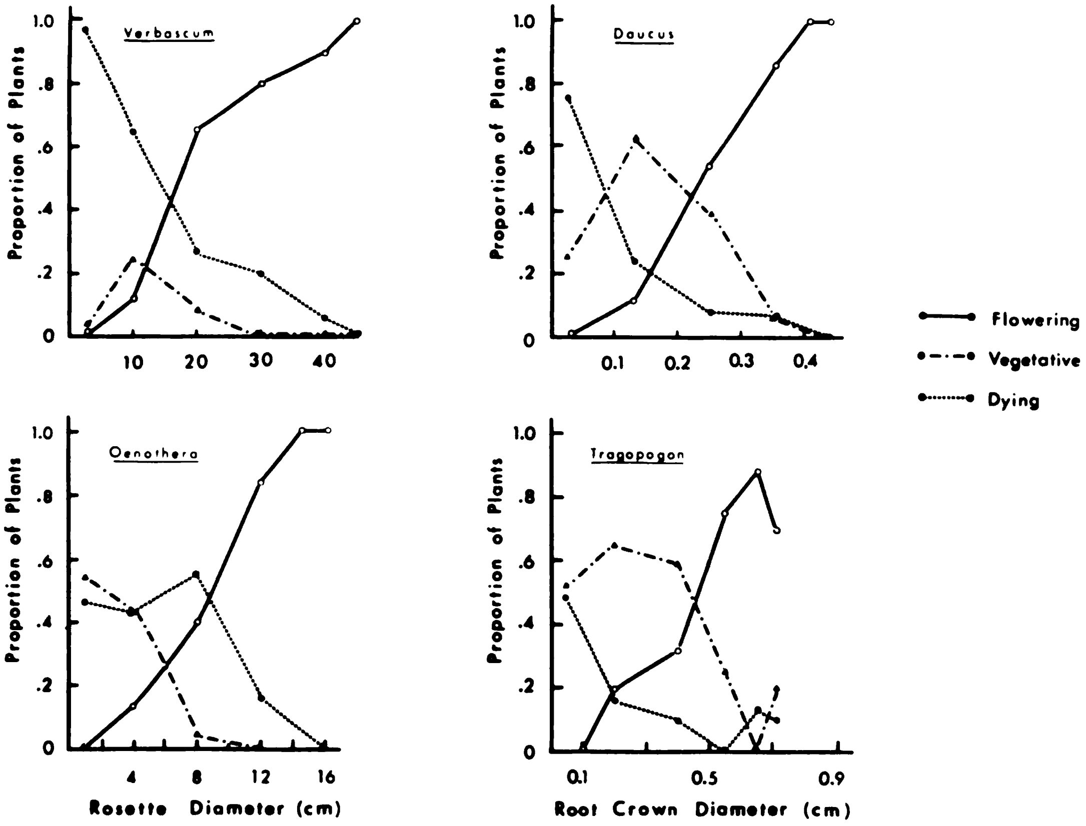

Figure 3-2: Relationships Between Rosette and Fate the Following Year in Four Species of "Biennials". For each species the probability of flowering, remaining vegetative, or dying is graphed at the class mark of the size classes shown in Table 3-1.

at a root crown diameter of 0.70 cm; however, above this size the probability of flowering appears to decline.

Some indication of the influence of age of a rosette on its probability of dying, remaining vegetative or flowering can be determined by computing separate probabilities for plants of known age and by assigning a minimum age of 3 years in 1979 to individuals marked as rosettes at the onset of the experiment in April of 1978. These data are tabulated in Table 3-2.

For Verbascum the probability of dying, remaining vegetative, or flowering within any size class does not change appreciably with age. Only a very small proportion of these plants remain vegetative to a third year (4/1006). Oenothera biennis rosettes $\geq$ 3 years of age have a higher probability of dying than 2 year old plants of the same size. No plants 3 years of age remained vegetative; that is, in the third year, the plants either flowered or died.

For Daucus, the probability of death within any size class does not change appreciably with age. The probability of remaining vegetative within any given size class tends to increase in the older rosettes. For Tragopogon, all rosettes $\geq$ 3 years of age had root crown diameters greater than 0.31 cm and the probability of death for any plant of this size is very low. The probability of flowering for plants between 0.31 and 0.70 cm root crown diameter was higher for plants $\geq$ 3 years of age than for 2 year old plants in the same size range. However, even among plants $\geq$ 3 years old, the probability of remaining vegetative remained high in all size classes.

Table 3-2: Rosette Fate in Relation to Size and Age in Four "Biennials". The probability of dying, remaining vegetative, or flowering the following year for rosettes of various ages within the size classes. "-" signifies there were no plants in that size and age category. Number of observations the same as in Table 3-1.

	Probability of:					
Verbascum thapsus	Dying		Remaining Vegetative		Flowering	
Rosette Diameter (cm)	Year2	Year3	Year2	Year3	Year2	Year3
≤ 5.4	0.97	1.00	0.03	0	0	0
5.5-15.4	0.63	0.71	0.26	0.13	0.11	0.17
15.5-25.4	0.23	0.42	0.09	0.05	0.68	0.53
25.5-35.4	0.21	0.20	0	0	0.79	0.80
35-5-45.4	0	1.00	0	0	1.00	0
>46	0	-	0	-	1.00	-

	Probability of:					
Oenothera biennis	Dying		Remaining Vegetative		Flowering	
Rosette Diameter (cm)	Year2	≥Year3	Year2	≥Year3	Year2	≥Year3
≤ 2.4	0.25	1.00	0.75	0	0	0
2.5-5.4	0.11	0.92	0.72	0	0.17	0.08
5.5-10.4	0.38	0.58	0.38	0	0.25	0.42
10.5-14.4	-	0.16	-	0	-	0.84
>14.5	-	0	-	0	-	1.00

				Probability of:					
Daucus carota	Dying			Remaining Vegetative			Flowering		
Root Crown Diameter (cm)	Year2	≥Year2	≥Year3	Year2	≥Year2	≥Year3	Year2	≥Year2	≥Year3
≤ 0.05	0.76	0.33	-	0.24	0.67	-	0	0	-
0.06-0.20	0.24	0.22	0.30	0.59	0.73	0.70	0.17	0.05	0
0.21-0.30	0	0.08	0.18	0.15	0.31	0.73	0.85	0.62	0.09
0.31-0.40	0	0.11	0	0	0	0.33	1.00	0.89	0.67
≥ 0.41	-	0	0	-	0	0	-	1.00	1.00

	Probability of:					
Tragopogon dubius	Dying		Remaining Vegetative		Flowering	
Root Crown Diameter (cm)	Year2	≥Year3	Year2	≥Year3	Year2	≥Year3
≤ 0.10	0.48	-	0.52	-	0	-
0.11-0.30	0.16	-	0.65	-	0.19	-
0.31-0.50	0.13	0.05	0.66	0.50	0.21	0.45
0.51-0.60	0	0	0.67	0.18	0.33	0.82
0.61-0.70	0	0.15	0	0	1.00	0.85
≥ 0.71	0	.11	0	0.22	1.00	0.67

DISCUSSION

Rosette size in all four of these species gives a reliable estimate of an individual's fate the following year. In all four species a minimum size must be reached before a plant is capable of flowering and above that minimum the probability of flowering increases directly with rosette size (Table 3-1). Conversely, the probability of death decreases with increasing rosette size. The few studies to date with other 'biennial' plant species have demonstrated similar relationships between plant size and the fate of individuals the following year (Werner 1975; Meijden and Waals-Kooi 1979; see also Thomson 1978; Baskin and Baskin 1979a,b). Consequently, the term 'biennial' appears to be a misnomer for these species, since the *age* at which an individual flowers is dependent upon the number of growing seasons it takes to reach a critical *size* for flowering.

Although none of the four species examined in this study adhere to an obligate two year (biennial) life cycle, *Verbascum* and *Oenothera* appear to be the shortest lived. For these two species, the probability of death remains relatively high in size classes above the minimum size for flowering (see Table 3-1) and as a result very few *Verbascum* rosettes survive for more than two years. In neither species did rosettes survive for more than three years in the populations studied. In contrast, for *Daucus* and *Tragpogon* rosettes the probability of death is greatly reduced in size classes above the minimum size for flowering (Table 3-1). After their second year of growth most *Daucus* and *Tragopogon* rosettes are in size classes in which the probability of death is very low. In addition, the low probability of death within any size class does not appear to change appreciably with age (see Table

3-2). As a result, rosettes of these two species may be able to persist for a number of years within the vegetation of an old field community before flowering. Holt (1972) estimated that rosettes from a seedling cohort of *Daucus carota* which emerged in a five year old-field could delay flowering for 4-5 years. Similar estimates were determined for the *Daucus* populations observed in this study. *Tragopogon* rosettes have even higher survival probabilities than similar-sized *Daucus* rosettes (see Table 3-1) and, as a result, rosettes of this species may be able to survive for 8-10 years before flowering, depending upon individual plant growth rate.

Undoubtedly, the type of environment in which an individual is growing will affect the length of time (number of growing seasons) spent in reaching the critical size for flowering. Holt (1972) found that *Daucus carota* rosettes growing in a young fallow field had a higher probability of flowering in their second summer than did rosettes of the same age growing in an older field. In populations of *Dipsacus sylvestris* flowering was delayed to the third or fourth year of growth when rosettes were growing in association with other herbaceous dicots and/or shaded by sumac (*Rhus typhina*) (Werner 1975, 1977).

In this study, rosettes of all four species growing in the 1 year old-field were larger at the end of the first year and hence had a higher probability of flowering in the second year than did populations in the 5 and 15 year old-fields. In the 1 year old-field the percent cover of herbaceous vegetation and litter was only 35% compared to 85% and 95% in the 5 and 15 year old-fields respectively. Ross and Harper (1972) demonstrated that in *Dactylis glomerata*, the space available (size of the opening) affected plant size; individuals growing in larger openings grew larger than those growing in smaller openings. Similarly, Mead (1966) found that in cultivated stands of carrot (Daucus carota) where the plants were grown in rows, a significant proportion (20%) of the variation in plant size could be accounted for by differences in the area available to individual rosettes (based on distances to nearest neighbors). In the 1 year old-field in this study the larger proportion of open area (65%, compared to 15% and 5% in the 5 and 15 year old-fields), and presumably reduced interspecific competition, apparently allowed the plants to grow larger in a single growing season. As a result, a larger proportion of the plants in this population reached or surpassed the critical size for flowering in a single growing season.

Seasonal emergence time may also be an important determinant of the size an individual reaches at the end of a single growing season (cf. Ross and Harper 1972). For Verbascum thapsus, Gross (1980) showed that cohorts of seedlings emerging earlier in the growing season were larger, and had a higher probability of flowering in their second year of growth than did later-emerging cohorts. Similarly, Weaver and Cavers (1979) found that for Rumex crispus and R. obtusifolia (both short-lived perennial species) plants emerging in the earlier cohorts of several germination pulses were generally larger and had higher survival probabilities than did later-emerging cohorts.

A number of factors undoubtedly serve as mechanisms in determining when an individual flowers once it reaches the critical size for flowering. Vernalization is required to induce flowering in Verbascum thapsus (Gleir and Caruso 1973, 1974) and has been found to be a requirement in several other species of monocarpic perennials including

Dipsacus sylvestris (Teasel) (Werner 1975), Pastinaca sativa (Baskin and Baskin 1979a), and Gindelia lanceolata (Baskin and Baskin 1979b). Werner (1975) speculated that a certain amount of reserve food had to be accumulated by an individual Teasel rosette before it could be successfully vernalized. Evidence from studies with Verbascum thapsus by Gleir and Caruso (1973, 1974) indicate that after a rosette reaches a minimum size, low temperatures cause the induction of a starch degrading enzyme which converts stored starch into soluble sugars. This conversion may be necessary for the induction of bolting and subsequently for flower and seed production.

Daylength may also act as an environmental cue to induce flowering in these species. Among a set of greenhouse grown, non-vernalized rosettes of the four species in this study, Oenothera rosettes with diameters greater than or equal to 12 cm bolted and flowered in the greenhouse in mid-April. This corresponds remarkably well to the rosette size at which all plants flowered in field populations (Table 3-1). Thus, for Oenothera rosettes, increasing daylength may provide the environmental cue which induces flowering. However, in Michigan, populations of Oenothera biennis do not bolt until early June indicating that low temperatures may provide an additional environmental constraint on flowering in this species. Of the other three species, only a single Daucus carota rosette and none of the Verbascum and Tragopogon rosettes bolted in the greenhouse, although nearly all were above the critical size for flowering observed in the field populations. This suggests that vernalization (or some exposure to low temperatures) may also be necessary to induce flowering in Daucus carota and Tragopogon dubius. Baskin and Baskin (1979a) found that for Pastinaca sativa long days were not required for flowering; however, vernalized rosettes exposed to long days flowered faster than those exposed to short days. Undoubtedly these environmental cues may to some extent act in tandem, and as a result determine the flowering phenology of these species. Whatever the environmental stimulus (e.g. vernalization or daylength) required to induce flowering, a rosette must reach a critical size before flowering can be successfully induced.

Regardless of the mechanism involved, for these four species of plants, rosette size is clearly highly correlated with the fate of an individual. Moreover, plant size appears to be a more reliable predictor of the fate of an individual than estimates based only on the age of the plant although, clearly the age of a plant influences its behavior to some extent.

A significant relationship between plant size and fate is particularly useful for field studies of the population dynamics and demography of plants. For most herbaceous plants it is difficult to determine the age structure of a population of established plants. Since most demographic models are based on determining age-specific estimates of mortality and fecundity, applying such models to plant populations is exceedingly difficult and time consuming. The adequacy of size as a predictor of the fate of an individual circumvents this problem, because size distributions of plant populations are fairly readily determined. In addition, size specific estimates of mortality and fecundity may provide a more accurate estimate of the future growth and behavior of a plant population than estimates based solely on its age structure (cf. Harper and White 1974; Harper 1977; Werner 1975; and Werner and Caswell 1977).

CHAPTER 4

COMPARATIVE COLONIZING ABILITIES IN 'PATCHY' ENVIRONMENTS: EXPERIMENTAL FIELD STUDIES

INTRODUCTION

Differences in the relative colonizing abilities of plant species (in terms of reaching a site, successfully establishing, and persisting there) are likely to be important in determining the patterns of distribution and abundance observed in plant communities. For plants, most of the hypotheses postulated to explain the existence and persistence of species within a local area have had only limited success, in large part because they have dealt primarily with the adult phase of the life history and have ignored those aspects of the life history affecting colonization and regeneration. Although interactions among adult plants may be important in determining the reproductive capacity of individuals (cf. Harper 1977; Mack and Harper 1977), most of the mortality in plant populations occurs at the regenerative (seed, seedling, and juvenile) stage of the life history (e.g. Harper 1967a,b; Hett and Loucks 1971; Antonovics 1972; Sharitz and McCormick 1973; Sarukhan and Harper 1973; Hawthorn and Cavers 1978; Werner and Caswell 1977; Baskin and Baskin 1974; Leverich and Levin 1979). In fact, it is a growing consensus among plant population biologists that many of the patterns in plants communities are the result of events which occur when the plants became established (cf. Grubb 1977; Harper 1977; Grime 1979; Werner 1979; Hamrick 1979).

The life history characteristics exhibited by a plant species reflect evolutionary processes and in general the evolution of a suite of life history characteristic involves a series of ecologically important trade-offs (Stearns 1976). That is, characteristics which benefit an organism under one set of conditions may be a detriment somewhere else. For example, producing large seeds may increase the probability of individual seedlings successfully establishing; however, since a finite amount of resources are available to reproduction and growth, increasing seed size generally results in a decrease in the number of seeds produced (cf. Werner and Platt 1976; Werner 1979; Cook 1979). By examining the consequences of particular life history characteristics across a range of environments, it should be possible to determine when and where a particular characteristic (or set of characteristics) will be advantageous and to reveal the proximal factors determining the distribution and abundance of a species with a given suite of life history characteristics.

Four plant species, *Verbascum thapsus*, *Oenothera biennis*, *Daucus carota*, and *Tragopogon dubius*, all with a "biennial" (or more correctly, a monocarpic perennial) life history, were selected to examine the affect on colonizing ability of differences in particular life history characteristics. Among these four species there exists a wide range of variability in those life history characteristics that are important determinants of colonizing ability: seed size, seed number, and dispersal ability. These characteristics, as well as differences in juvenile and adult morphology are summarized for each species in Chapter 1, Table 1-1.

Briefly, *Verbascum thapsus* and *Oenothera biennis* produce large numbers of very small seeds (with *Verbascum* producing significantly smaller seeds in larger numbers than *Oenothera*). Seeds of these two species have no specialized morphological adaptions for dispersal and thus are not widely dispersed upon release from the parent (c.f. Platt 1975; Gross and Werner 1978). However, seeds of *Verbascum* and *Oenothera* are capable of remaining viable in the seed bank for long periods of time (35 years for *Verbascum* and up to 80 years for *Oenothera*, see Kivilaan and Bandurski 1973). In contrast, *Daucus* and *Tragopogon* produce fewer, but significantly larger seeds (with those of *Tragopogon* being largest and fewest in number). Seeds of both *Daucus* and *Tragopogon* have specialized morphological adaptions which promote long distance dispersal. *Daucus* seeds are barbed which promotes dispersal by animals (Ridley 1930) and which may aid in wind dispersal as well (Lacey 1978). Seeds of *Tragopogon* have a large, broad, flat pappus and are capable of being dispersed long distances by wind (greater than 250 m from the parent plant, Gross unpubl.). Interestingly, seeds of these species do not appear to be able to remain viable in the soil for more than 1 or 2 years.

The broad range of life history characteristics exhibited by these four species of "biennials" makes them an ideal model system with which to explore the affect of differences in these life history characteristics on colonizing ability. Moreover, although all four species occur in early successional old-fields in Southwestern Michigan, they differ in the time at which they are each locally abundant. *Verbascum* and *Oenothera* are generally abundant in early successional fields (1-4 years after abandonment), followed by *Daucus*, which is commonly abundant in fields 4-7 years after abandonment, and finally by

Tragopogon which usually is not found in fields until later in the successional sere, but which can persist in fields that have been abandoned for 15-40 years.

Two sets of questions were examined with these four species. The first considered the relative cost and benefits of particular suites of life history characteristics in terms of the affect on colonizing ability; the second, examined how these differences in life history characteristics influence the relative abundances of these species over a range of fields at different stages of successional development.

METHODS

Species Introductions and Field Sites

Seeds of the four "biennial" species were collected in September or October 1977 from naturally occurring populations in and around the W. K. Kellogg Biological Station, Kalamazoo Co., in Southwestern Michigan. After collection, the seeds were stored in a dry, dark cupboard in paper sacks at room temperature (20–23° C).

Three old-fields located within 2 km of the W. K. Kellogg Biological Station were selected for study. All three were alike in soil and general topography and had been under similar agricultural production until their abandonment. The three fields differed in the length of time they had been abandoned at the onset of the experiment and represented three stages of successional development: (1) initial abandonment (1 year old-field), (2) early successional (5 year old-field), and (3) mid-successional (15 year old-field). (For a more detailed description of these sites, see Chapter 1.)

Within the 1, 5, and 15 year old-fields selected for study 100 one-half by one-half meter quadrats were established and permanently marked with wooden stakes. In the 5 and 15 year old-fields, the plots were laid out in a 10x10 grid with one-half meter buffer zones between each row and column of plots. In the 1 year old-field, the arrangement of plots was adjusted to avoid shading by a black walnut tree and were arranged in one row of 9 plots and 8 rows of 13 plots, again with one-half meter buffer zones between plots. In each field, twenty plots were randomly selected to receive a known number of seeds of each of the four "biennials" with the remaining twenty plots serving as controls.

Seeds of each species were sown into the quadrats in mid-April

1978. The seeds had previously been divided into lots in the laboratory and put into sealed paper envelopes (Daucus and Tragopogon) or glass vials (Verbascum and Oenothera). The precounted packets were opened in the field and broadcast by hand to simulate a pattern of natural dispersal.

The number of seeds of each species sown per plot is shown in Table 4-1. Species differences in the number of seeds sown reflect the magnitude of the differences in the number of seeds produced by individuals of each species as well as adjustments made for laboratory estimates of germination rates (see below). Seeds of Verbascum and Oenothera, the small-seeded species, were weighed and the number sown per plot estimated on the basis of the average weight of a single seed (see Table 1-1). Seeds of Daucus and Tragopogon, being larger and consequently easier to handle, were counted into lots. The broad pappus on the Tragopogon seeds was removed before sowing to prevent the introduced seeds from being blown out of the plots.

Estimates of potential first year germination of each species were determined from laboratory germination trials both on soil and on moist blotters in covered petri plates. Each treatment was replicated three to five times and the number of seeds per trial varied for each species. Seeds of all four species had a high viability (minimum 63-97%). They germinated earlier and at a higher rate in petri plates than on soil; with the soil treatment generally reflecting a 30% reduction in germination (even higher in Oenothera) compared to the petri plate estimates (Table 4-2).

Table 4-1: Number of Seeds Introduced into Treatment Plots. Each species sown alone into 20 0.25 m^2 plots in the 1, 5, and 15 year old-fields.

	Number/Plot ($\bar{x} \pm 1$ S. E.)
Verbascum thapsus	2500 ± 20
Oenothera biennis	2500 ± 12
Daucus carota	250 ± 0
Tragopogon dubius	30 ± 0

Table 4-2: Seed Germination Trials of Four "Biennials" from Seed Lots used in Experimental Introductions. Petri plate trials run in greenhouse (April 1978) on Whatman #4 filter paper wetted with distilled H_2O. Soil trials run in Scherer-Gillete environmental chamber with a 15 hr/9 hr, 30°/10°C light/dark cycle on Vitahume potting soil watered with distilled H_2O (March 1978). N = number of replicates.

PETRI PLATE TRIALS

Species	Time to First Emergence	% Germination ($\bar{x}$ ± 1 S. E.)	Seeds per Plate	N
Verbascum thapsus	4 days	97.3 ± 2.67	25	3
Oenothera biennis	3 days	76.7 ± 13.50	25	3
Daucus carota	6 days	62.8 ± 8.96	50	5
Tragopogon dubius	6 days	93.3 ± 4.09	10	5

SOIL TRIALS

Species	Time to first Emergence	% Germination ($\bar{x}$ ± 1 S. E.)	Seeds per Tray	N
Verbascum thapsus	7 days	28.0 ± 10.58	50	3
Oenothera biennis	14 days	14.0 ± 13.0	50	3
Daucus carota	7 days	44.7 ± 5.70	50	3
Tragopogon dubius	7 days	66.7 ± 3.33	20	3

Resource Availability within Fields

An old-field is not a homogeneous habitat, but rather a changing mosiac of patches of different types of vegetation. Since these vegetation patches undoubtedly represent different types of environments for seedling establishment, the abundance of various vegetation patch types can be used as an independent measure of the relative 'resource availability' within a field.

Six distinct vegetation patch types within these fields were defined on the basis of ground cover: bare ground, mosses, lichens, grasses, herbaceous dicots, and litter. The abundance of these six patch types within each of the three experimental fields was determined from visual estimates of the percent cover of each patch type within the 100 0.25m^2 experimental plots in each field. Cover estimates were determined at approximately monthly intervals throughout the 1978 growing season on or about 28 April, 29 May, 21 June, 7 July, and 8 October. These data are reported for all three fields in Appendix 1.

Monitoring of Introduced Populations

During the spring germination pulse from 1 May to 28 June, treatment and control plots were monitored for seed germination and seedling survival at weekly intervals. Seedlings were marked with plastic picks as they emerged and the patch type in which they emerged recorded. Monitoring of seedling survival continued on a biweekly basis throughout the 1978 growing season. In October of 1978, all surviving rosettes were marked with numbered flags, the size of each rosette determined, and the patch type in which it was growing recorded. These marked plants were monitored for survival, growth, and reproductive output through the 1979 growing season. Seeds of plants which flowered in the second year (1979) were removed and collected as the seeds matured.

Affect of Patch Size

A second experiment was conducted to investigate the affect of the size of an opening on the establishment success of two of the "biennials", Verbascum and Oenothera. In the 15 year old-field, open patches of bare ground of three sizes ($0.0225m^2$, $0.25m^2$ and $0.50m^2$) were created by turning the soil over with a spade. The soil was allowed to "rest" for 3 to 4 days before seeds of each species were sown on it. The density of seeds sown per patch was adjusted for differences in patch size, such that equal numbers of seeds were sown per unit area. Here again the seeds were weighed into lots and the number of seeds sown was 100,000 per m^2 for Verbascum and 16,000 per m^2 for Oenothera.

Three replicates of each size of open patch were established for each species with an additional three replicates serving as controls, to which no seeds were added, to monitor naturally occurring levels of germination in these patches. In addition, nine 0.0225 m^2 areas of undisturbed vegetation were marked out and seeds of each species sown in three of these plots as well. The germination and establishment patterns within these undisturbed patches was compared to the pattern in the open patches of various sizes.

RESULTS

Germination and Emergence

Seedlings of all four species emerged within the experimental plots in all three fields. The number of seedlings of each species ($\bar{x} \pm 1$ S.E.) which emerged in the treatment plots in the three experimental fields is shown in Table 4-3. Seedlings of these four species also emerged in some of the control plots in these fields (Table 4-4). Therefore, in order to compare the number of individuals emerging from the introduced seeds in each field the number of seedlings emerging in the treatment plots was adjusted for the background levels of seedling emergence from naturally occurring seed populations measured in the control plots. The low levels of emergence in all these plots (maximum density 0.03 seedlings per cm^2) implied that there were no density effects on germination <u>per se</u>.

The number of seedlings emerging from the introduced seeds in these plots can be estimated from the difference in the mean number of seedlings in the treatment (TRT) and control (CON) plots. That is: $\bar{x}_{TRT} - \bar{x}_{CON} = \bar{x}_{TRT-CON}$, where $\bar{x}_{TRT-CON}$ is an estimate of the number of seedlings emerging per plot from the introduced seeds. Assuming there is no covariance between these two sets of plots, the variance about this mean can be estimated from the sum of the variances of the treatment and control means (Gill 1978). The standard error of the mean ($\bar{x}_{TRT-CON}$) can therefore be determined from the following equation:

$$SE_{\bar{x}_{TRT-CON}} = 2MS_e/n; \text{ where } MS_e = \frac{SS_1+SS_2}{n_1+n_2-2} \text{ and } SS_i = X_i - \frac{(X_i)^2}{n_i} \; .$$

The number of seedlings ($\bar{x} \pm 1$ S.E.) of each species which emerged in the treatment plots from the introduced seeds in the three fields are presented in Table 4-5.

Table 4-3: Seedling Emergence in Treatment Plots. Shown are mean number of seedlings (± 1 S.E.) of four "biennials" emerging per treatment plot (0.25 m^2, n=20) in three successional old-fields in the Spring of 1978. Means and standard errors uncorrected for emergence in control plots.

	1 Year Field	5 Year Field	15 Year Field
Verbascum thapsus	21.4 ± 4.08	7.2 ± 2.36	3.0 ± 1.07
Oenothera biennis	1.6 ± 0.37	0.4 ± 0.112	0.05 ± 0.05
Daucus carota	27.6 ± 2.17	5.85 ± 1.22	68.5 ± 6.88
Tragopogon dubius	9.4 ± 0.81	10.5 ± 0.76	14.8 ± 1.33

Table 4-4: Seedling Emergence in Control Plots. Shown are mean number of seedlings (± 1 S.E.) of four "biennials" emerging per control plot (0.25m^2; n=20) in three successional old-fields in the Spring of 1978.

	1 Year Field	5 Year Field	15 Year Field
Verbascum thapsus	0.4 ± 0.22	0.9 ± 0.38	0.25 ± 0.16
Oenothera biennis	0	0.1 ± 0.07	0
Daucus carota	0.15 ± 0.11	0	35.95 ± 6.79
Tragopogon dubius	0	0	4.25 ± 0.75

Table 4-5: Corrected Seedling Emergence in Treatment Plots. Means shown are differences between treatment and control plots; error terms adjusted accordingly (see text for details). For each species, means in each row followed by the same letter are not significantly different at $p = 0.05$. Percent emergence from the introduced seeds indicated in parentheses.

	1 Year Field	5 Year Field	15 Year Field
Verbascum thapsus	20.85 ± 4.07^{a} (0.83%)	6.3 ± 2.32^{b} (0.25%)	2.75 ± 1.06^{b} (0.11%)
Oenothera biennis	1.6 ± 0.37^{a} (0.06%)	0.3 ± 0.09^{b} (0.012%)	0.05 ± 0.05^{b} (0.002%)
Daucus carota	27.4 ± 2.17^{a} (10.96%)	5.85 ± 1.22^{b} (2.34%)	32.5 ± 1.06^{a} 13.00%)
Tragopogon dubius	9.4 ± 0.81^{a} (31.33%)	10.5 ± 0.76^{a} (35.00%)	10.5 ± 1.10^{a} (35.00%)

Analysis of these data revealed differences in the emergence pattern of the four biennials. Since the variances were not homogeneous across fields (F_{max} test), differences between fields were tested using a modified t-test for multiple comparisons of means developed by Gill (1977). For Verbascum and Oenothera, the small-seeded species, the number of seedlings emerging per plot decreased with the age of the field. Significantly more seedlings emerged in the 1 year old-field ($p<0.05$) than did in the 5 and 15 year old-fields (Table 4-5). In contrast, seedling emergence of Daucus and Tragopogon was not affected by the age of the field. Although fewer Daucus seedlings emerged in the 5 year old-field, the number emerging in the 1 and 15 year old-field did not differ ($p>0.05$, see Table 4-5). Emergence of Tragopogon seedlings was also not affected by the age of the field; with nearly equal numbers of seedlings emerging from the introduced seeds in all three fields (Table 4-5).

These differences between fields can be explained by examining the species emergence patterns on a smaller scale, that is, in the various patch types within each field. Across these three fields, the relative abundance of the six patch types differed and the vegetation composition (percent cover of each patch type) of these three fields reflected their relative 'age' and successional development. The percentage of the area of each field in each of the six patch types ($\bar{x} \pm 1$ S. E.) at the time of the peak germination pulse (May, 1978) is given in Table 4-6.

Since the behavior of the plants in some patch types was similar, the six patch types were regrouped into three categories for analysis: BARE GROUND, TRANSITIONAL (which included moss and lichen patches), and VEGETATED (which included grass, dicot, and litter patches). Although

Table 4-6: Percent Cover of Six Patch Types in Three Successional Fields, May, 1978. Values presented are $\bar{x} \pm 1$ S.E. calculated from n=100 0.25 m^2 plots per field. "-" signifies patch type did not occur in this field.

Patch Type	1 Year Field	5 Year Field	15 Year Field
Bare Ground	66.5 ± 1.06	10.8 ± 0.91	0.8 ± 0.09
Moss	-----	2.8 ± 0.30	3.2 ± 1.08
Lichen	-----	-----	0.2 ± 0.04
Herbaceous dicots	28.1 ± 1.10	28.3 ± 1.90	45.2 ± 1.72
Grass	6.3 ± 0.78	10.0 ± 0.84	10.9 ± 0.73
Litter	-----	85.7 ± 1.08	92.8 ± 1.4

strictly speaking moss and lichen patches are vegetated, their growth form and morphology creates little or no reduction in light or moisture to an emerging seedling. The first two categories (BARE GROUND and TRANSITIONAL), thus represent two different types of openings for seedling establishment.

The proportion of the total ground area of the three experimental fields in each of these three patch categories is shown in Figure 4-1. As would be expected, the proportion of the total area which is BARE GROUND in an old-field rapidly decreases over time. The proportion of the area in the BARE GROUND patch category decreased from 66% in the 1 year old-field to 11% in the 5 year old-field and to 1% in the 15 year old-field. The TRANSITIONAL patch category (moss and lichen patches) occurred only in the 5 and 15 year old-fields and was equally abundant in both of these fields (4% of the total area). Even when these two types of openings are combined the pattern of rapidly decreasing open area with the age of a field is still evident: 66% in the 1 year old-field, 14% in the 5 year old-field, and 5% in the 15 year old-field.

The proportion of the total seedlings which emerged in each of these patch categories in each field can be compared to the expected distributions of those seedlings in each field based on the relative proportion of the total area in each patch category. These data for seedlings the 1 and 15 year old-fields are shown for _Verbascum_ and _Oenothera_ in Figure 4-2 and for _Daucus_ and _Tragopogon_ in Figure 4-3. The observed and expected number of seedlings in each patch category in these fields and the corresponding Chi-Square statistic are reported in Table 4-7.

Seedlings of all four species in both the 1 and 15 year old-fields

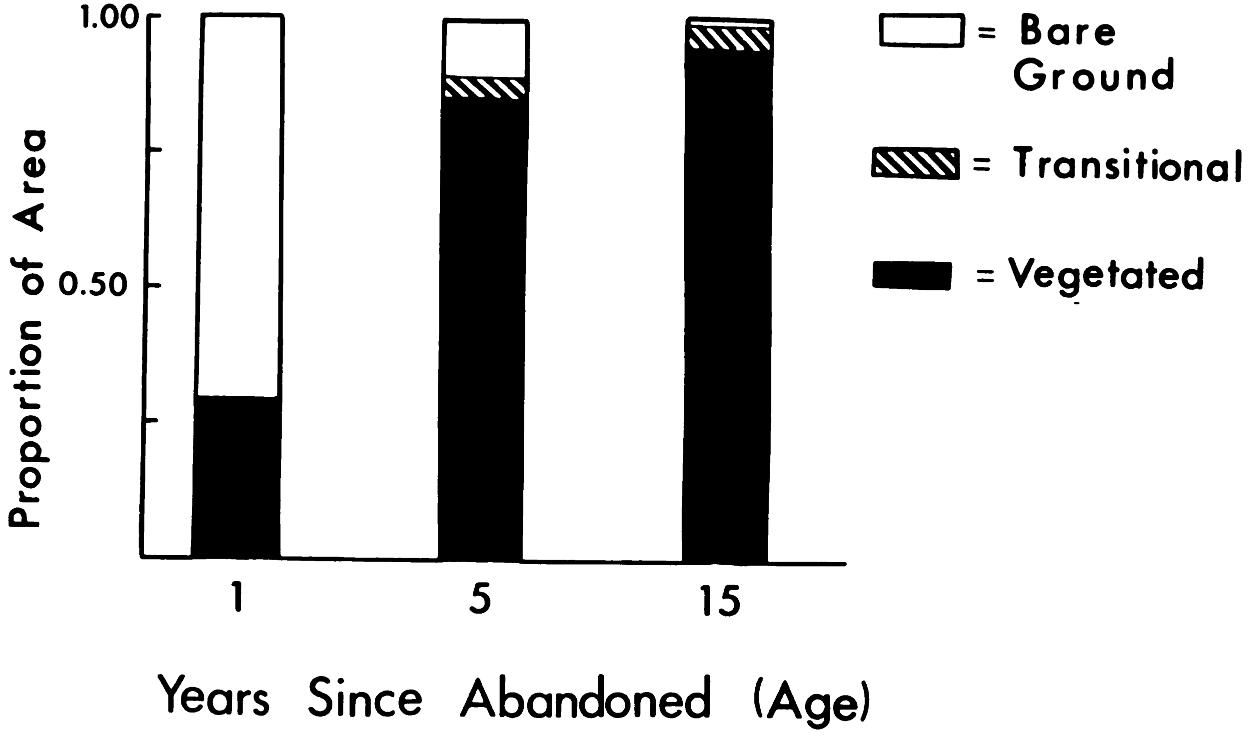

Figure 4-1: Vegetation Composition of Three Experimental Old-fields used for Species Introductions. Shown are means of percent ground cover estimates of three patch categories taken in May 1978 from 100 0.25 m^2 permanent plots in each field.

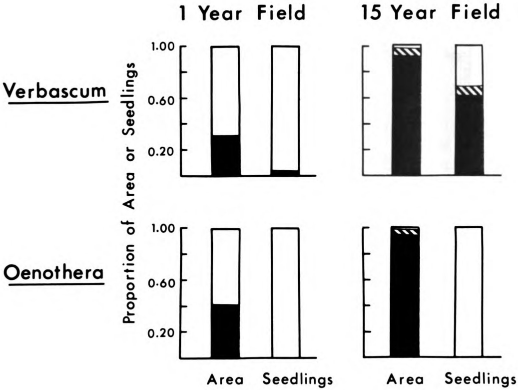

Figure 4-2: Distributions of Seedlings of Verbascum thapsus and Oenothera biennis in Three Patch Categories in the 1 and 15 Year Old-fields, May 1978. Shown are the mean proportion of the total area of the treatment plots (n=20) for each species in each patch category and the proportion of the total seedlings which emerged in each patch category.

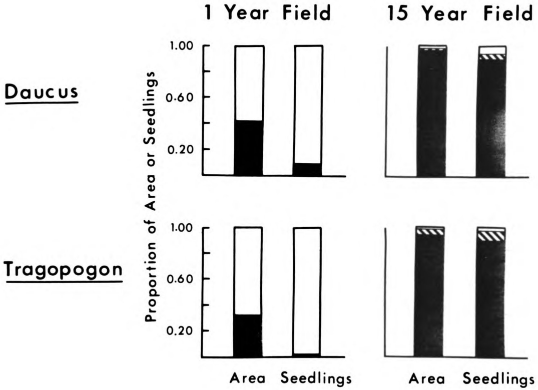

Figure 4-3: Distributions of Seedlings of Daucus carota and Tragopogon dubius in Three Patch Categories in the 1 and 15 Year Old-fields, May 1978. Shown are the mean proportion of the total area of the treatment plots (n=20) for each species in each patch category and the proportion of the total seedlings which emerged in each patch category.

Table 4-7: Chi-Square Analyses of Seedling Emergence Pattern within Patches in the 1 and 15 Year Old-fields. (*** $p<0.005$; NA = not applicable.)

1 Year Old-field

		BARE GROUND	VEGETATED	X^2
Verbascum	Observed:	411	16	
	Expected:	290	136	156.4***
Oenothera	Observed:	32	0	
	Expected:	22	10	14.55***
Daucus	Observed:	501	50	
	Expected:	317	234	251.4***
Tragopogon	Observed:	185	3	
	Expected	129	59	77.46***

15 Year Old-field

		BARE GROUND	TRANSITIONAL	VEGETATED	X^2
Verbascum	Observed:	19	4	37	
	Expected:	0.5	3.3	56.2	103.57***[1]
Oenothera	Observed:	1	0	0	
	Expected:	--	--	--	NA
Daucus	Observed:	82	64	1223	
	Expected	14	14	1341	519.2***
Tragopogon	Observed:	6	23	266	
	Expected:	2	10	283	25.10***[1]

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[1] X^2 calculated on basis of combined values for BARE GROUND and TRANSITIONAL patches to correct for low expected values in BARE GROUND patch category.

emerged more frequently in the two types of open patches than they did in the VEGETATED patches. The pattern was especially striking for the small-seeded species, Verbascum and Oenothera, whose seedlings emerged almost entirely in patches of BARE GROUND. In the 1 year old-field, 96.5% of the Verbascum seedlings emerged in patches of BARE GROUND which made up 68% of the area in these plots. This pattern was even more striking in the 15 year old-field, where 32% of the Verbascum seedlings emerged in patches of BARE GROUND and less than 1% of the total area was in this patch type. In both fields, the emergence of Verbascum seedlings was significantly different from what would be expected from a random pattern of emergence ($X^2 = 156.4$ and 103.57, both with $p<<0.005$). Oenothera seedlings emerged only in patches of BARE GROUND in both the 1 and 15 year old-fields. In the 1 year old-field this distribution was also significantly different from random ($X^2 = 14.54$, $p< 0.005$). In the 15 year old-field only one seedling emerged, but it emerged in an open patch of BARE GROUND.

Seedlings of Daucus and Tragopogon also occurred more frequently in openings than would be expected from a random emergence pattern (see Table 4-7). In the 1 year old-field over 90% of the Daucus and Tragopogon seedlings emerged on BARE GROUND, although the percent of the area in this patch type in these treatments plots was 58% and 69%, respectively. Again, a Chi-Square analysis showed these patterns to be significantly different from random ($X^2 = 251.4$ and $X^2 = 77.46$, respectively $p<<0.005$). In the 15 year old-field, seedlings of these two species emerged more frequently than expected in both types of openings (BARE GROUND and TRANSITIONAL). For Daucus, over 10% of the seedlings emerging in the treatment plots emerged in these two patch categories which together made up less than 2% of the area in these plots ($X^2 = 519.2$, $p<<0.005$). In the Tragopogon plots, 10% of the seedlings emerged in the two open patch categories which in these plots made up approximately 4% of the area ($X^2 = 25.10$, $p<0.005$).

From these analyses it is apparent that the reduced emergence of Verbascum and Oenothera seedlings in the 15 year old-field is the result of the higher emergence of seedlings of these two species in patches of BARE GROUND and the reduction of this patch category in this field. Seedlings of Daucus and Tragopogon also "prefer" openings for emergence, however, a fairly large proportion of the seedlings of these two large-seeded species also emerged in VEGETATED patches (see Figure 4-3). As a result, the total number of seedlings of these two species emerging per plot from the introduced seeds did not significantly differ in the 1 and 15 year old-fields (see Table 4-5).

Seedling Survival and Establishment

The life cycle of these plants can be divided into three distinct phases corresponding to (1) the seedling establishment phase, (2) the established phase, and (3) the reproductive phase. The seedling establishment phase is the period of time from emergence up to the end of the first growing season (which for these species is twenty weeks after emergence). It is during this phase of the life cycle that most of the mortality occurs. Plants which survive to this point can be considered to be established, since the survival curves for all four species level off at this point and the probability of survival from this point in time onward is fairly constant for non-flowering plants (c.f. Figure 4-4). Since all four species are monocarpic, plants which produce flowers subsequently die. Thus, during the reproductive phase

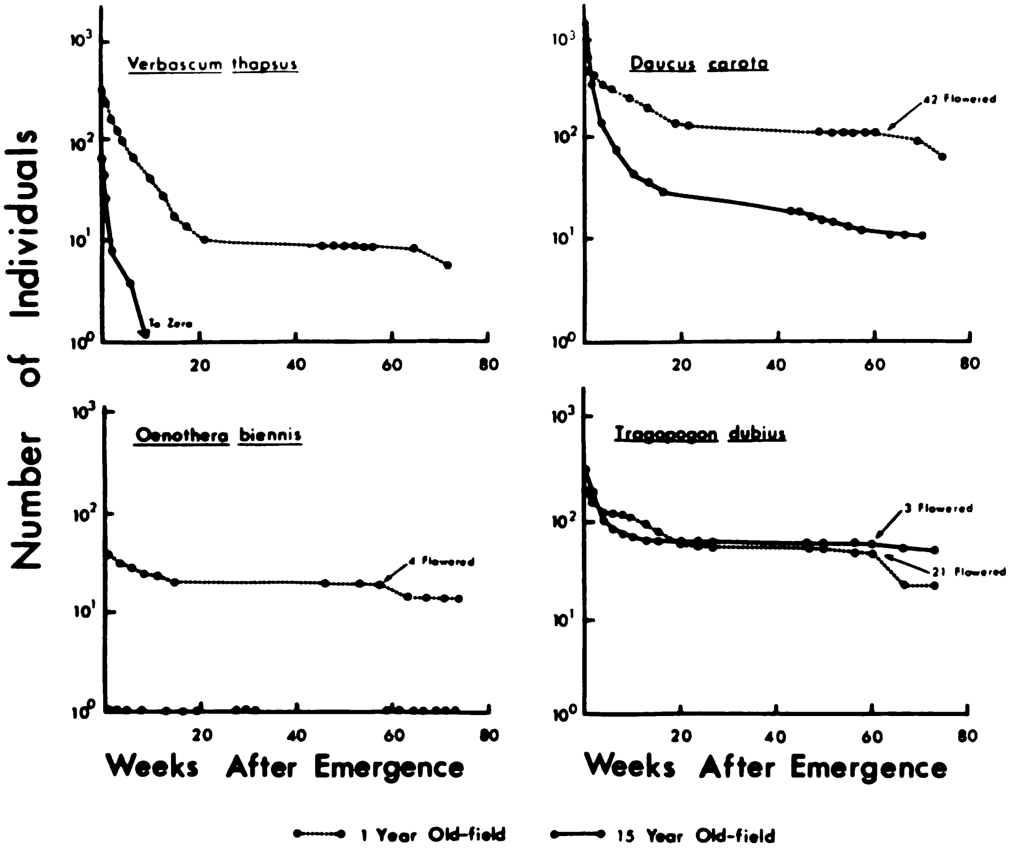

Figure 4-4: Survivorship Curves for Four "Biennial" Species in the 1 and 15 Year Old-fields. Shown are the number of individuals surviving in each field from emergence (May 1978) to the end of the second growing season (October 1979). Number of individuals which flowered in the second year indicated for each species.

of the life cycle, the survivorship curves show a corresponding drop followed by a leveling off, which repeats until all plants in the population have flowered and/or died. The survivorship curves for these four "biennials" in the 1 and 15 year old-fields over two growing seasons (1978-1979) are presented in Figure 4-4.

Seedling survivorship of the four "biennials" differed in these two fields, in general being higher in the 1 year old-field than in the 15 year old-field (Table 4-8 and Figure 4-4). Moreover, the seedling survivorship probabilities of these species in both fields was generally correlated with seed size, being lowest in the smallest-seeded species (Verbascum) and generally increasing with increasing seed size (see Table 4-8).

The survival curve for Verbascum in both the 1 and 15 year old-fields shows an extremely sharp drop in the number of individuals present in these fields during the first 10-12 weeks after emergence. Fewer individuals emerged in the 15 year old-field and, as a result, the Verbascum population in this field was locally extinct ten weeks after emergence (see Figure 4-4).

All of the Oenothera seedlings emerged in openings of BARE GROUND in both the 1 and 15 year old-fields (see Figures 4-2 and 4-3) and the survival probability of these seedlings was relatively high. In both the 1 and 15 year old-fields the total number of seedlings which emerged was low; however, once a seedling emerged it had a high probability of becoming established (Table 4-8). Consequently, a population of Oenothera seedlings established in the 1 year old-field, and even though only a single seedling emerged in the 15 year old-field, this individual successfully established there.

Table 4-8: Seedling Survival Probabilities of the Four "Biennials" in the 1 and 15 Year Old-fields. Seedling survival calculated from emergence to end of establishment phase (20 weeks after emergence). Values shown are $\bar{x} \pm$ S.E. of n=20 plots.

	1 Year Field	15 Year Field
Verbascum thapsus	0.043 ± 0.016	0
Oenothera biennis	0.54 + 0.107[1]	1.00[2]
Daucus carota	0.22 ± 0.033	0.02 ± 0.004
Tragopogon dubius	0.24 ± 0.0372	0.17 ± 0.034

[1] Probability calculated for n=15 plots in which seedlings emerged.

[2] A single *Oenothera* seedling emerged and survived in this field.

Seedlings of *Daucus* and *Tragopogon*, the two large-seeded species, had nearly equivalent probabilities of successfully establishing in the 1 year old-field ($t = 0.54$, $p>0.05$; see Table 4-8). In the 15 year old-field, however, *Daucus* seedling survival was significantly reduced from that in the 1 year old-field ($t = 5.71$, $p<0.01$), whereas, *Tragopogon* seedling survival was not significantly reduced in the older field ($t = 1.35$, $p>0.05$). In fact, the number of *Tragopogon* seedlings recruited in the 1 and 15 year old-fields (20 weeks after emergence) was not significantly different ($t=0.258$; $p>0.05$; see Figure 4-4).

Differences in seedling survival of these species in the 1 and 15 year old-fields compounded the differences in emergence in these fields. As a result, populations of all four "biennials" became established in the 1 year old-field, whereas only *Tragopogon* and *Daucus* established in the 15 year old-field and *Oenothera* was represented by only a single individual. Here again, differences in the establishment pattern of these four species in these two fields can be attributed to differences in the proportion of each field in the three patch categories (BARE GROUND, TRANSITIONAL, and VEGETATED) and to differences in the seedling survival probabilities of these species in these patch categories.

The proportion of rosettes of each species and the proportion of the total area of the 1 and 15 year old-field in the three patch categories at the end of the establishment phase (October, 1978) is shown in Figures 4-5 and 4-6. Seedlings of *Verbascum* and *Oenothera* successfully established only in patches of BARE GROUND. In contrast, seedlings of *Daucus* and *Tragopogon* (the larger-seeded species) were able to become established in all three patch categories.

The number of plants which established in a particular patch

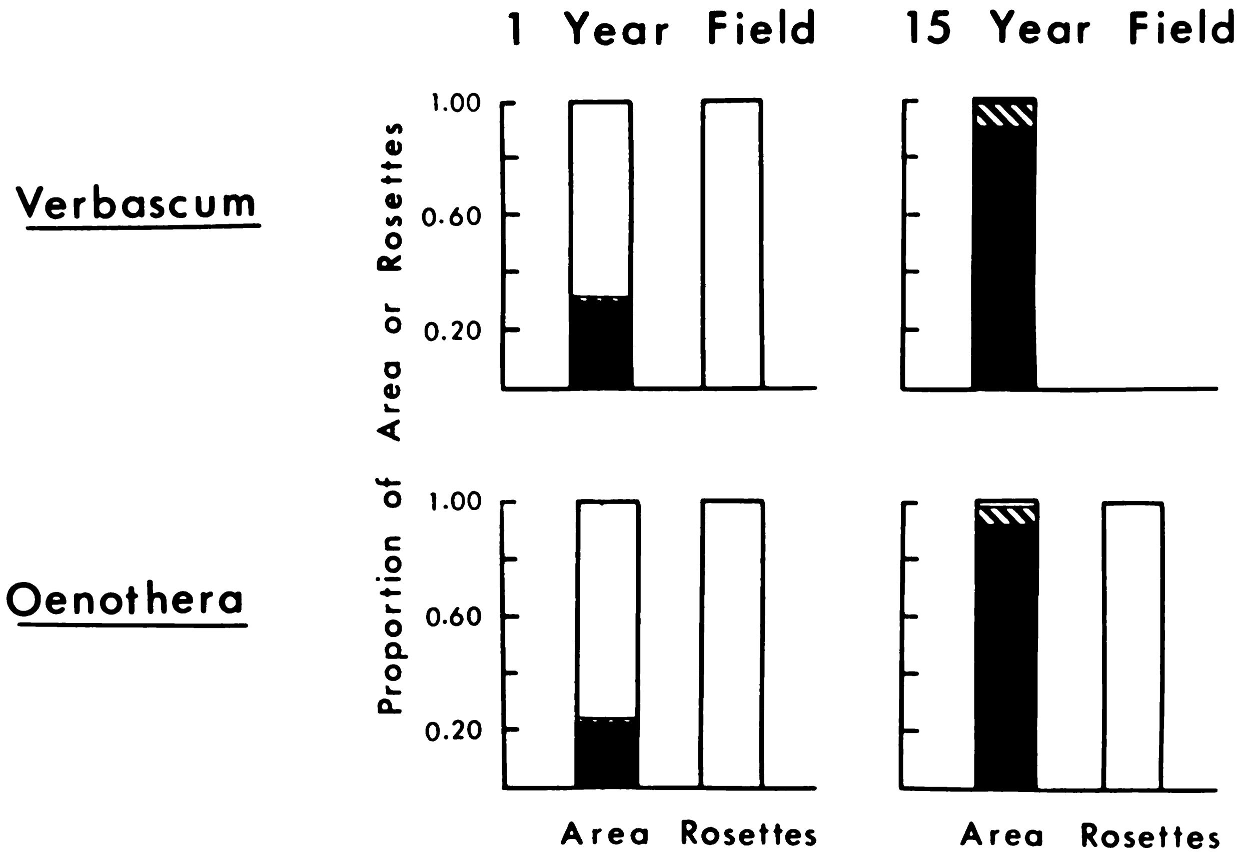

Figure 4-5: Distributions of Rosettes of *Verbascum thapsus* and *Oenothera biennis* in Three Patch Categories in the 1 and 15 Year Old-fields, October 1978. Shown are the mean proportion of the area of the treatment plots (n=20) for each species in each patch category and the proportion of the total rosettes which established in each patch.

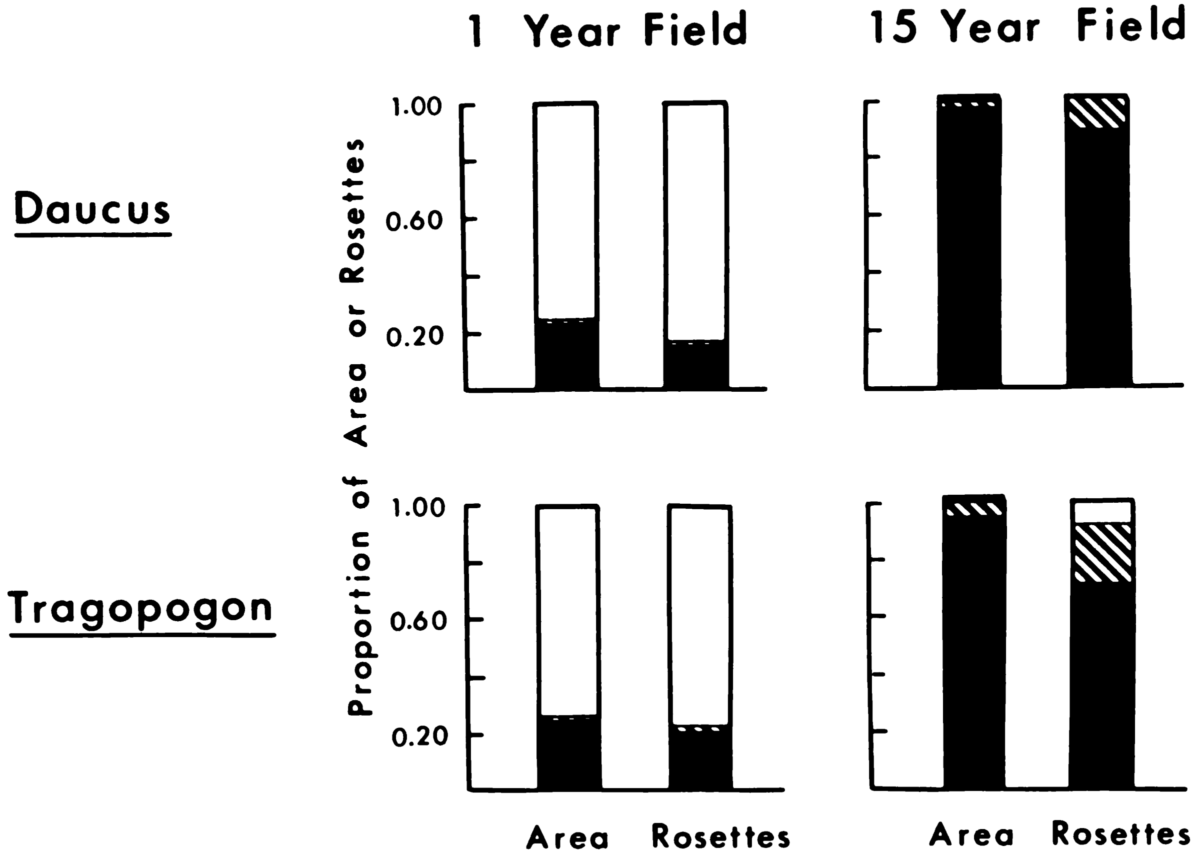

Figure 4-6: Distributions of Rosettes of *Daucus carota* and *Tragopogon dubius* in Three Patch Categories in the 1 and 15 Year Old-fields, October 1978. Shown are the mean proportion of the total area of the treatment plots (n=20) for each species in each patch category and the proportion of the total rosettes which established in each patch.

category can again be compared to the number expected in that patch based on its relative abundance in each field. Because fewer individuals remained at this point in time, the expected values calculated for those patch categories that were rare were too low to permit a legitimate Chi-Sqare test. Therefore, the data for the two open patch categories (BARE GROUND and TRANSITIONAL) were combined into one category (OPEN) for these analyses. Although the expected values were small for some categories, a Chi-Square test is appropriate as long as the expected numbers in each class exceed 5p, where p is the proportion of classes with expected values less than 5 (Yarnold 1970). For these two-way comparisons (OPEN vs. VEGETATED), the minimum acceptable expected value when one cell has an expected value less than 5 is 2.5 (5 x 0.5). The observed and expected values and Chi-Square statistic for each comparison are shown in Table 4-9.

Populations of Verbscum and Oenothera established only in the 1 year old-field; within this field, seedlings established only in open patches of BARE GROUND (see Figure 4-5). For both of these species, this pattern was significantly different from the expected random distribution ($X^2 = 4.28$ and 6.56, respectively; $p<0.05$). Seedlings of Daucus and Tragopogon established in OPEN and VEGETATED patches in both the 1 and 15 year old-fields. Daucus seedlings in the 1 year old-field occurred more frequently in OPEN patches than would be expected from a random distribution ($X^2 = 5.10$; $p<0.05$); whereas, Tragopogon seedlings showed no preference in this field. In the 15 year old-field, Daucus seedlings again occurred more frequently in OPEN patches than expected (Table 4-9), however, the expected value in this category was less than the minimum required for a legitimate Chi-Square test (Yarnold 1979).

Table 4-9: Chi-Square Analyses of Establishment Pattern within Patches in the 1 and 15 Year Old-fields. (*p<0.05; ***p<0.005; NA = not applicable).

1 Year Old-field

		OPEN	VEGETATED	X^2
Verbascum	Observed:	10	0	4.28*
	Expected:	7	3	
Oenothera	Observed:	21	0	6.56*
	Expected:	16	5	
Daucus	Observed:	112	20	5.10*
	Expected:	101	31	
Tragopogon	Observed:	39	10	0.44
	Expected:	37	12	

15 Year Old-field

		OPEN	VEGETATED	X^2
Daucus	Observed:	3	24	NA
	Expected:	1	26	
Tragopogon	Observed:	15	37	50.94***
	Expected:	3	49	

Tragopogon seedling establishment in the 15 year old-field was, however, significantly higher in OPEN patches than expected ($X^2=50.94$; $p<0.005$; see Table 4-9).

The probability of survival for a seedling of Daucus and Tragopogon within the three patch categories in the 15 year old-field corroborate this pattern of establishment (Table 4-10). Note that for Tragopogn, seedling survival probabilities in the two open patch categories (BARE GROUND and TRANSITIONAL) were three to five times higher than those observed in the VEGETATED patch category. Similarly, for Daucus, seedling survival in the OPEN patches was higher than that in the VEGETATED patches.

Although seedling survival was higher in open patches for all four species, it was only in the open patches of BARE GROUND that seedlings of Verbascum and Oenothera successfully established. Consequently, populations of these two species became established only in the 1 year old-field where a high proportion of the total area was in the BARE GROUND patch category. In contrast, seedings of Daucus and Tragopogon were able to successfully establish in both open (BARE GROUND and TRANSITIONAL) and VEGETATED patches. Consequently, populations of these two species successfully colonized both the 1 and 15 year old-fields.

For all four species, survival probabilities following the establishment phase were relatively constant (see Figure 4-4), indicating that individuals which survive to the end of the first growing season are likely to be able to persist. However, whether the populations of these four species can persist in an area is a function of the next stage of the life cycle, flowering and seed production.

Table 4-10: Seedling Survivorship of Daucus and Tragopogon in Different Patches in the 15 Year Old-field. Survival probability from emergence to the end of the establishment phase (May-October 1978).

	BARE GROUND	TRANSITIONAL	VEGETATED
Tragopogon	0.67	0.47	0.14
Daucus	—	0.05	0.02

Persistence and Regeneration

For all four of these "biennial" species, the fate of an individual in any year can be predicted from the size of the plant at the end of the previous growing season (see Chapter 3; Figure 3-2). In particular, for all four of these species, there is a critical size a plant must reach before it will flower. Above this minimum size, the probability of flowering increases directly with rosette size. In addition, the probability of dying in a given year is inversely related to plant size at the end of the previous growing season; large rosettes have a higher probability of survival than small rosettes.

In general plants growing in the 1 year old-field were larger at the end of the first growing season than those plants which established in the 15 year old-field (Figures 4-7 and 4-8). Consequently, the populations growing in the 1 year old-field had a higher probability of surviving to the second growing season and a greater proportion of the plants growing in this field flowered in the second summer (Table 4-11).

None of the Verbascum rosettes growing in the 1 year old-field exceeded the minimum size for flowering (rosette diameter $\geq$ 5.5) at the end of the first growing season (Figure 4-7); consequently, none of these plants flowered in the second year. By the end of the second growing season, however, 83% of the Verbascum rosettes in the 1 year old-field had reached or exceeded the minimum size for flowering.

Fifty percent of the Oenothera rosettes growing in the 1 year old-field were above the minimum size for flowering (3 cm) at the end of the first growing season and of these, 40% flowered in the second year. By the end of the second growing season all of the surviving rosettes in the 1 year old-field equalled or exceeded the size at which all plants

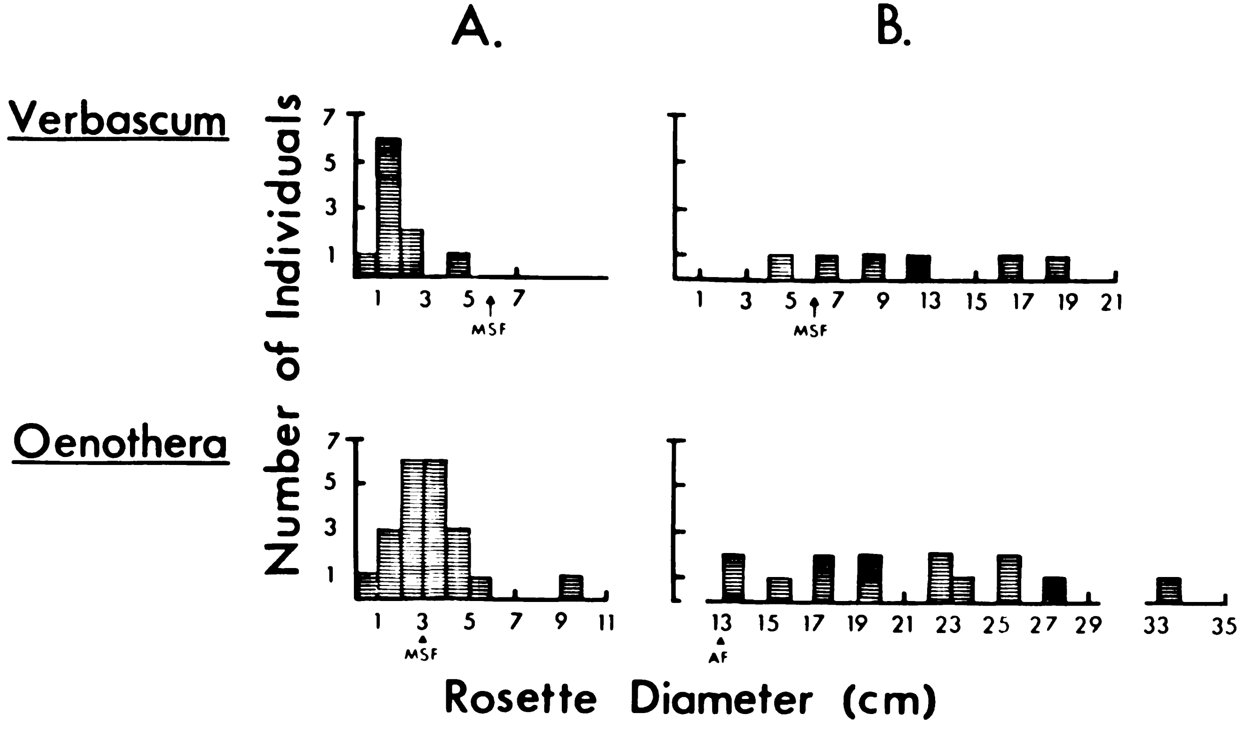

Figure 4-7: Size Frequency Distributions of *Verbascum thapsus* and *Oenothera biennis* Rosettes in the 1 Year Old-field. Distributions are shown for rosettes alive at the end of the first (A) and second (B) growing seasons. The rosette diameter (cm) which an individual must achieve before its probability of flowering is greater than zero (MSF) and above which all plants flower (AF) are indicated for each species.

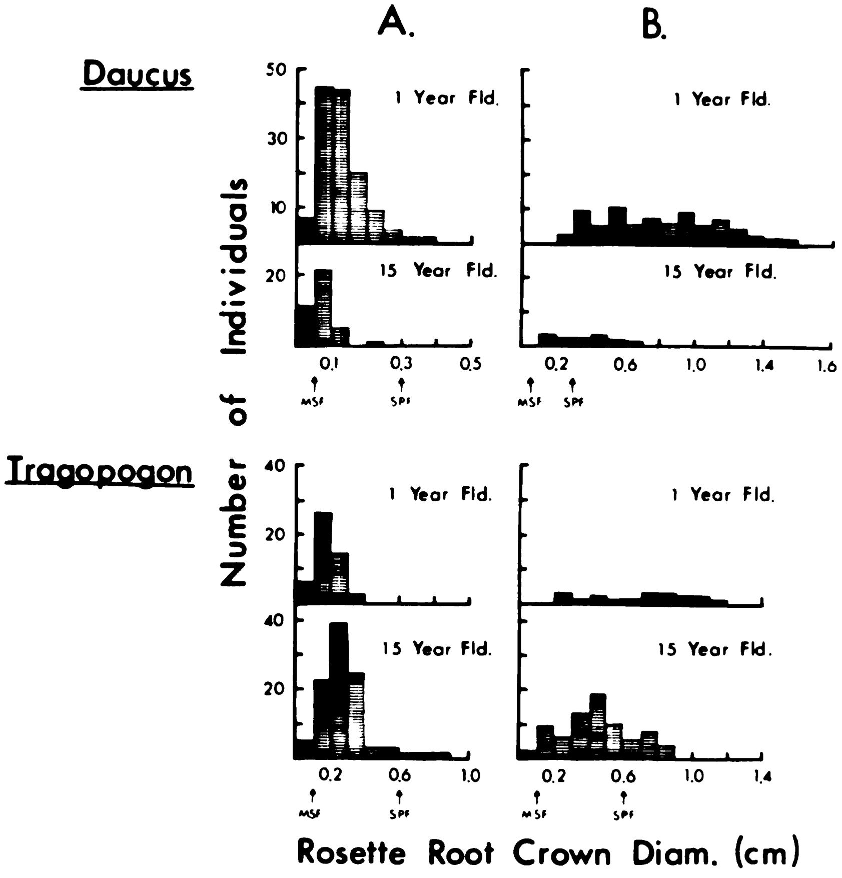

Figure 4-8: Size Frequency Distributions of *Daucus carota* and *Tragopogon dubius* Rosettes in the 1 and 15 Year Old-fields. Distributions are shown for rosettes alive at the end of the first (A) and second (B) growing seasons. The root crown diameter an individual must reach before it can flower (MSF) and above which the probability of flowering is ≥ 0.8 (SPF) are indicated for each species.

Table 4-11: Reproductive Success in the Second Growing Season. The proportion of plants alive in the second year which flowered and the seed production ($\bar{x} \pm$ S.E.) of these flowering plants for the four species of "biennials" growing in the 1 and 15 year old-fields.

1 Year Old-Field

	Proportion Flowering	Seed Production
Verbascum	0	----
Oenothera	0.19	4,178 ± 1796
Daucus	0.35	2,070 ± 260
Tragopogon	0.46	127 ± 14

15 Year Old-field

	Proportion Flowering	Seed Production
Daucus	0	----
Tragopogon	0.06	73.4 ± 13.2

flower the following year (13 cm). Although the single Oenothera seedling growing in the 15 year old-field exceeded the minimum size for flowering at the end of the first year (5.4 cm), it did not flower. By the end of the second summer, this rosette had grown to a diameter (23.5 cm) which exceeded the size at which all plants flower.

The Daucus carota rosettes growing in the 1 year old-field were significantly larger than those rosettes growing in the 15 year old-field at the end of the first growing season (see Figure 4-8A; $t=6.68$, $p<0.001$). Although 75% of the rosettes in the 15 year old-field exceeded the minimum size for flowering, none of the plants growing in this field flowered in the second year. In contrast, 92% of the seedlings growing in the 1 year old-field exceeded the minimum size for flowering at the end of the first growing season and 17 of these plants (13%) reached or exceeded the size at which the probability of flowering was greater than 0.80. In total, 33% of the plants growing in the 1 year old-field flowered in the second year (Table 4-11).

Differences in the size of the non-flowering Daucus rosettes in the 1 and 15 year old-field at the end of the second growing season were again significant; with rosettes in the 1 year old-field being more than twice as large as those plants in the 15 year old-field (see Figure 4-8B). Throughout the second growing season, the non-flowering Daucus rosettes in the 1 year old-field were consistently taller than those in the 15 year old-field (see Figure 4-9). The growth curves for these two populations parallelled each other throughout the second growing season with both showing a steady increase in height up to mid-July, after which the growth of plants in both populations leveled off. Over the entire growing season, the growth rates of individuals in these two

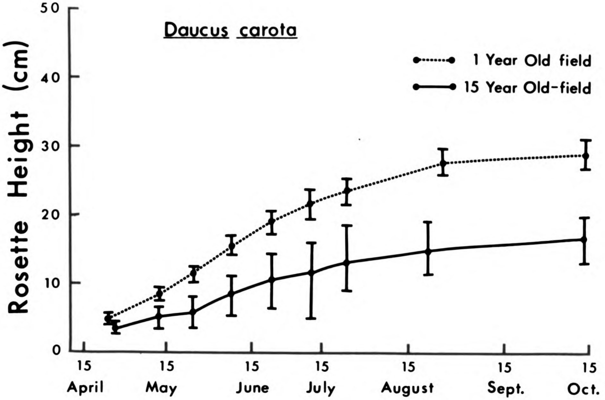

Figure 4-9: Growth of Non-flowering *Daucus carota* Plants in the 1 and 15 Year Old-fields over the Second Growing Season. Plotted are the mean ± 95% C.I. of shoot height (cm) of all plants alive on each date. Sample size in the 1 year old-field ranged from n=78 to n=71 and in the 15 year old-field from n=18 to n=11.

populations differed significantly from each other ($p<0.01$) with plants in the younger field having an average growth rate of 0.15 cm/day and plants in the 15 year old-field growing at about half that rate (0.08 cm/day). These growth rate differences during the second summer accentuated the initial differences in plant size and by the end of the second growing season, plants growing in the 1 year old-field were again significantly larger (both taller and heavier) than those plants growing in the 15 year old-field (Table 4-12).

Over 90% of the Tragopogon rosettes growing in both the 1 and 15 year old-fields reached or exceeded the minimum size for flowering (root crown diameter = 0.11 cm) by the end of the first growing season. Yet, only in the 1 year old-field did plants with a root crown diameter less than 0.51 cm flower in the second summer. Despite the fact that plants in the 1 year old-field were on average smaller than those in the 15 year old-field, a greater proportion of the plants growing in the 1 year old-field flowered in the second summer. Plants which flowered in this field also produced a greater number of seeds than those flowering in the 15 year old-field (Table 4-11).

Non-flowering Tragopogon rosettes in both fields significantly increased in size during the second growing season, with plants in the 1 year old-field showing an average increase of 4 times the size of the previous year. In contrast, plants in the 15 year old-field increased by only a factor of 1.7. The growth rate (based on plant height) of these two populations over the second growing season also differed significantly ($p<0.001$). Plants in the 1 year old-field increased in height an average of 0.11 cm/day and those in the 15 year old-field growing in height only 0.023 cm/day. Interestingly, these differences

Table 4-12: Daucus carota Rosette Sizes. Size comparisons ($\bar{x} \pm$ S.E.) of rosettes of D. carota growing in the 1 and 15 year old-fields at the end of the first and second growing season.

Year 1	1 Year Old-field (n = 128)	15 Year Old-field (n = 29)
Root Crown Diameter (cm)	0.136 ± 0.0053	0.075 ± 0.0051
*Total Dry Weight (g)	0.0416 ± 0.0047	0.0097 ± 0.0016

Year 2	1 Year Old-field (n = 72)	15 Year Old-field (n = 11)
Root Crown Diameter (cm)	0.803 ± 0.0414	0.368 ± 0.0485
*Total Dry Weight (g)	3.168 ± 0.372	0.475 ± 0.125
Plant Height (cm)	29.1 ± 1.01	16.4 ± 1.47

*Calculated from regression equations based on root crown diameter: $y = 4.081\ (x^{2.41})$; where y = rosette dry wt. (g) and x = root crown diameter (cm); r = 0.914, n = 45 (see Chapter 3; Figure 3-1).

in height were not expressed until the latter half of the second growing season (see Figure 4-10). From late April through mid-late July there was no significant difference in the mean height of these two groups of plants and the average growth rates were similar (0.26 cm/day in the 1 year old-field; 0.23 cm/day in the 15 year old-field). The growth rates of individuals in these two populations sharply diverged in the later part of the growing season however, with plants in the 1 year old-field growing at 17 times the rate of those growing in the 15 year old-field (0.10cm/day vs. 0.006 cm/day; respectively). Consequently, at the end of the second growing season, Tragopogon rosettes in the 1 year old-field were both taller ($t = 5.23$; $p<0.001$) and larger ($t = 4.39$; $p<0.005$) than those in the 15 year old field (Table 4-13).

Although at this point in the life cycle, there are detectable differences in reproduction and growth of these species between fields, any pattern of differences among patches within a field are obscured. Daucus and Tragopogon populations established in both OPEN and VEGETATED patches in both the 1 and 15 year old-fields. However, there was no significant difference in the size of plants growing in these two patch categories in either field (see Table 4-14). For Daucus, plants growing in the 1 year old-field were significantly larger than those growing in the 15 year old-field at the end of both the first and second growing seasons ($t=4.59$ and 3.96, respectively; $p<0.01$). However, in neither year was there a significant difference in the size of plants growing in OPEN and VEGETATED patches within these fields (Table 4-14). Similarly, for Tragopogon rosettes, neither at the end of the first nor second growing season was there a significant difference in the size of plants growing in different patch categories within these two fields (see Table

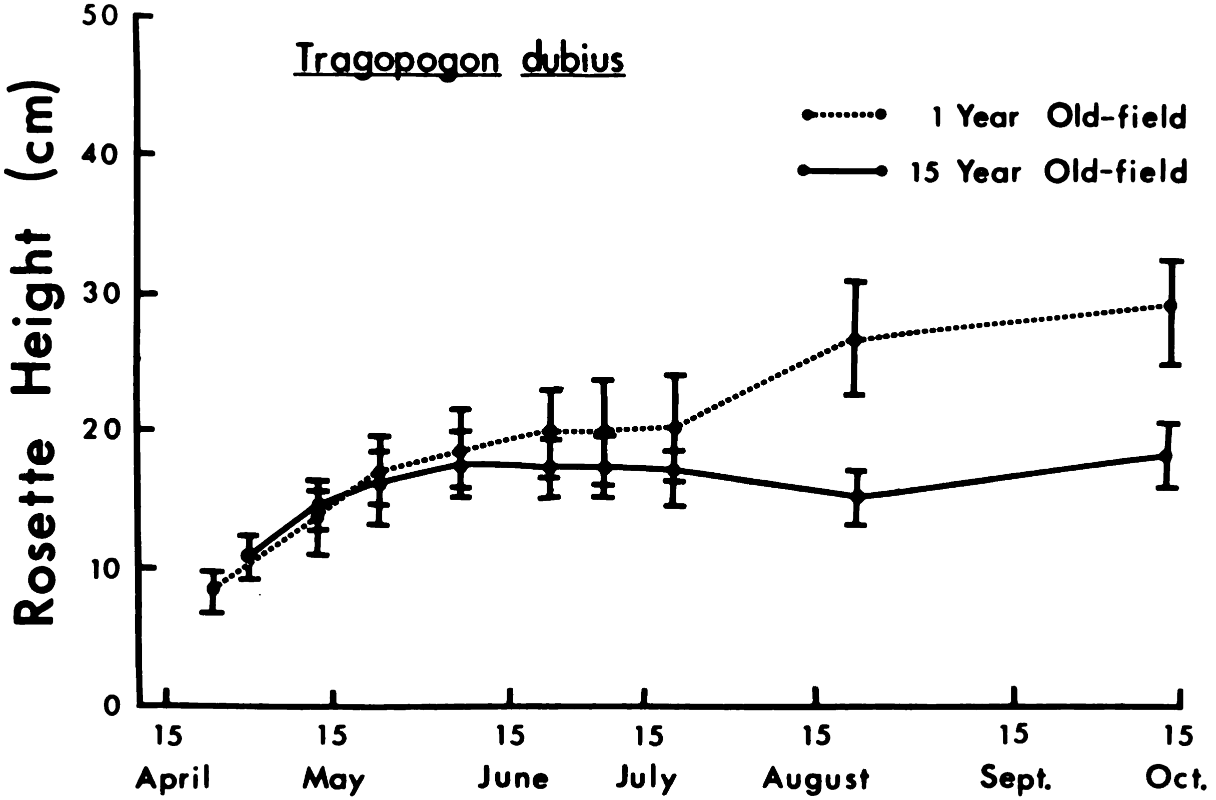

Figure 4-10: Growth of Non-flowering Tragopogon dubius Plants in the 1 and 15 Year old-fields over the Second Growing Season. Plotted are the means ± 95% C.I. of shoot height (cm) of all plants alive on each date. Sample sizes in the 1 year old-field ranged from n=25 to n=19 and in the 15 year old-field from n=48 to n=43.

Table 4-13: Tragopogon dubius Rosette Sizes. Size comparisons ($\bar{x} \pm$ S.E.) of rosettes of T. dubius growing in the 1 and 15 year old-fields at the end of the first and second growing seasons.

Year 1	1 Year Old-field (n = 49)	15 Year Old-field (n = 52)
Root Crown Diameter (cm)	0.180 ± 0.0085	0.248 ± 0.0148
*Total Dry Weight (g)	0.0231 ± 0.0029	0.061 ± 0.0093

Year 2	1 Year Old-field (n = 19)	15 Year Old-field (n = 43)
Root Crown Diameter (cm)	0.712 ± 0.0650	0.435 ± 0.0330
*Total Dry Weight (g)	0.906 ± 0.1661	0.292 ± 0.0531
Plant Height (cm)	29.1 ± 1.74	18.0 ± 1.18

*Calculated from regression equations based on root crown diameter: $y = 1.683 (x^{2.62})$, where y = rossett dry wt. (g) and x = root crown diameter (cm); r = 0.977, n = 28 (see Chapter 3; Figure 3-1).

Table 4-14: Size Comparisons of *Daucus* and *Tragopogon* Rosettes Growing in Different Patches. Measurement of rosette size based on root crown diameter (cm) determined in October of each year. BG = BARE GROUND; TR = TRANSITIONAL; V = VEGETATED.)

1 Year Old-field

	Year 1			Year 2		
Daucus carota	BG	TR	V	BG	TR	V
n	110	1	17	63	1	8
$\bar{x}$	0.135	0.04	0.138	0.817	0.31	0.765
S. E.	0.0061	--	0.0147	0.0445	--	0.0931
Tragopogon dubius						
n	38	1	10	15	1	3
$\bar{x}$	0.187	0.10	0.160	0.711	0.690	0.727
S. E.	0.0099	--	0.0145	0.0729	--	0.2399

15 Year Old-field

Daucus carota	Year 1			Year 2		
	BG	TR	V	BG	TR	V
n	0	3	26	0	2	9
$\bar{x}$	--	0.087	0.074	--	0.34	0.37
S. E.	--	0.0145	0.0055	--	0.1600	0.0534
Tragopogon dubius						
n	4	11	37	3	10	31
$\bar{x}$	0.163	0.256	0.255	0.323	0.322	0.464
S. E.	0.0419	0.0311	0.0178	0.0610	0.0644	0.0403

4-14). Consequently, patch type *per se* is not sufficient to explain differences in the growth and reproductive behavior of these species between fields.

It is important to note, however, that the relative abundances of particular patch types in a field was sufficient to explain differences in both the pattern of seedling emergence and establishment of these four species in these two fields. Moreover, the relative abundances of these four species in these two fields appears to be a direct consequence of the relative abundance of the patch types required for seedling establishment by each species. In particular, the failure of the small-seeded species, *Verbascum* and *Oenothera*, to establish in the 15 year old-field can be explained on the basis of the reduction in the relative availability of openings of BARE GROUND that both require for establishment.

The inadequacy of patch type alone to explain the differences in the behavior of these populations later in their life cycle (i.e. growth and reproduction) indicates that at this point in the life cycle other characteristics of these patches need also be considered; of these, patch size appears to be the most important.

Affect of Patch Size

To test the hypothesis that it was indeed the reduction of BARE GROUND patches in the 15 year old-field which prevented the successful establishment of *Verbascum* and *Oenothera* in this field, a second set of experiments were conducted with these two species in which seeds of each species were introduced onto artificially-created open patches of bare ground in the 15 year old-field. To determine if the absolute size of the area open affected seedling emergence and survival, patches of three sizes were created: small (0.0225 m^2), medium (0.25 m^2), and large (0.50 m^2). (For details of this experimental design, see Methods p. 49.)

The pattern of seedling emergence and establishment in these artificially-created open patches mimicked the patterns observed in the 1 year old-field in the seeding-in experiment begun in the previous year. Verbascum seedlings again emerged both in the open patches and in the undisturbed plots. Three times as many seedlings emerged in the open areas as did in the undisturbed areas; however, this difference was not statistically significant ($t= 1.82$; $p>0.05$). It was only in the openings however, that Verbascum seedlings successfully established (Table 4-15). Oenothera seedlings emerged only in the open patches and were able to successfully establish there (Table 4-15).

The size of the opening created effected both the probabilities of seedling emergence and survival. For both species, seedling emergence (number/unit area) was highest in the small openings (0.0225 m^2) and decreased with patch size. There was, however, no significant difference in the number of seedling which emerged per unit area in the medium and large openings (Table 4-16). Seedling survival showed the opposite pattern and was higher in the large and medium openings than in the small openings. Here again, there was no significant difference in the survival probability for seedlings growing in the medium and large openings (see Table 4-16).

From these experiments it is clear that for both Verbascum and Oenothera the failure of seedlings to establish in the 15 year old-field was due to the lack of open patches of BARE GROUND in this field, since seedlings of both species were able to successfully establish in the artificially-created open patches in this field. Moreover, the size of

Table 4-15: Emergence and Establishment of Verbascum and Oenothera Seedlings in Artificially-created Openings. Shown are number of seedlings ($\bar{x} \pm$ S.E.) in open and undisturbed plots (0.0225 m^2; n=3 plots) in the 15 year old-field. Number established determined in October, 1979.

	Number Emerged	Number Established
Verbascum thapsus		
Open	285.7 ± 88.77	2.0 ± 1.25
Undisturbed	5.3 ± 66.41	0
Oenothera biennis		
Open	3.0 ± 1.4	1.67 ± 0.98
Undisturbed	0	---

Table 4-16: Affect of Patch Size on Emergence, Establishment, and Growth of *Verbascum* and *Oenothera* Seedlings. Percent seedling emergence and establishment ($\bar{x} \pm$ S.E.) determined from three replicates of three patch sizes: small (S) = 0.0225 m^2, medium (M) = 0.25 m^2, and large (L) = 0.50 m^2. Mean (± S.E.) rosette diameter (cm) and range in each patch size determined at end of first growing season (October, 1979). Means in each column followed by the same letter are not significantly different at $p=0.05$ level.

Verbascum thapsus

Patch Size	Seeds Sown	Percent Emergence	Percent Established	Number Established	Rosette Diameter (Range)
S	2,250	12.7 ± 3.0^a	0.6 ± 0.5^a	6	5.13 ± 1.49^a (1.4-11.5)
M	25,000	0.35 ± 0.06^b	5.0 ± 3.0^b	16	5.30 ± 2.69^a (1.8-16.0)
L	50,000	0.33 ± 0.01^b	8.6 ± 0.4^b	28	6.73 ± 1.63^a (1.2-16.8)

Oenothera biennis

Patch Size	Seeds Sown	Percent Emergence	Percent Established	Number Established	Rosette Diameter (Range)
S	360	8.3 ± 0.40^a	50.0 ± 17.0^a	5	7.6 ± 3.47^a (2.0-20.0)
M	4,000	1.4 ± 0.01^b	76.0 ± 12.0^b	13	14.8 ± 1.07^a (9.0-20.5)
L	8,000	0.13 ± 0.05^b	86.0 ± 7.0^b	28	9.23 ± 1.52^a (1.6-25.0)

the opening created effected both the probability of seedling emergence and establishment, with emergence being enhanced in small openings but survival being higher in larger openings. Interestingly, for both species there was no difference in the response (either in terms of emergence or survival) in patches above 0.25 m^2 in diameter, probably because this size is near the limit of the immediate environment influencing the individual plant.

Rosettes of both species reached or exceeded the minimum size for flowering in all three sizes of openings in a single growing season. For Verbascum rosettes, there was no significant difference in the mean size of rosettes at the end of growing season in these three sizes of openings (Table 4-16). However, only in the medium and large openings did some individual rosettes reach a diameter in which the probability of flowering the following year was greater than 0.50. The average rosette size in these plots was affected by inclusion of a late summer (August) cohort of seedlings which survived only in these larger open patches.

The mean size of Oenothera rosettes at the end of the first growing season increased directly with patch size (Table 4-16). Although these differences were not statistically significant ($p>0.05$), here again a greater proportion of the plants growing in the medium and large open patches reached or exceeded the rosette size at which the probability of flowering the following year was greater than 0.50. In addition, it was only in the medium and large openings that a fall cohort of seedlings emerged.

DISCUSSION

Summary of Results

The differences in life history characteristics exhibited by these four "biennial" plant species do in fact affect their relative colonizing abilities. Of these characteristics, differences in seed size appear to be particularly important in determining the type of patch (ground cover type) which consititues a 'safe site' (sensu Harper 1967a) for seedling establishment.

Verbascum and Oenothera, both of which produce small seeds (see Table 1-1) require open patches of bare ground for seedling establishment. Although seedlings of Verbascum emerge in other patch types, seedling survivorship is low. Consequently, seedlings successfully establish only in open patches of bare ground. Oenothera seedlings emerge and establish only in open patches of BARE GROUND. In contrast, Daucus and Tragopogon, which produce significantly larger seeds, are able to establish in a broader range of patch types. Seedlings of these two species emerge more frequently and have higher survival probabilities in openings than in other patch types; however, they are able to successfully establish in all three patch types (BARE GROUND, TRANSITIONAL, and VEGETATED). As a result, populations of Daucus and Tragopogon became established in both the 1 and 15 year old-fields. Interestingly, the number of Tragopogon seedlings recruited in the 1 and 15 year old-fields was the same, even though the patch array in these two fields was very different (see Figure 4-4).

Ecological Tradeoffs in Life Histories

For these four "biennials" seed size is directly correlated with both seedling emergence rate (proportion of seedlings emerging from the introduced seeds) and survival during the establishment phase of the life cycle. Seed size has been shown to be an important determinant of early size differences (Black 1956), seedling vigor (Twamley 1967; Stebbins 1976; Haskins and Gorz 1975), and emergence time (Harper and Obeid 1967) in a number of plant species. In addition, seed size is often directly correlated with juvenile and adult plant size (c.f. Black 1959; Harper, Lovell, and Moore 1970; Anderson 1971; Gross and Soule, in prep.).

A low probability of emergence and survival may be offset in part by an increase in the number of seeds produced per individual. Although *Verbascum* seedlings had both the lowest emergence rate and survival probability of these four species, it produces several orders of magnitude more seeds on average than does *Tragopogon* (see Table 1-1), which had the highest emergence and survival probability (Table 4-5 and 4-8). Consequently, the differences in seed size and seed number exhibited by these four species may represent equivalent strategies, and are thus reflective of the type of tradeoffs that occur during the evolution of a suite of life history characteristics (c.f. Stearns 1976). A similar pattern of differences in seed size and number has been observed by Werner (1979) for several species of goldenrods (*Solidago* spp.) and within a single species, *S. canadensis*.

If the tradeoffs observed in seed size and number for these four species of plants are real, the life history characteristics exhibited by *Daucus* and *Tragopogon* would seem to be more successful in the long term than those of *Oenothera* and *Verbascum*, because these latter two species are limited to a particular patch type for establishment. Consequently, *Daucus* and *Tragopogon* would be expected to be common in a wide range of environments (e.g. old-fields at all stages of successional development); whereas, *Verabscum* and *Oenothera* would be limited to those habitats where a large proportion of the area was open and would be less common in these habitats than *Daucus* and *Tragopogon*. On an evolutionary time scale, it would seem most probable that species with a suite of life history characteristics like those exhibited by *Verbascum* and *Oenothera* would, at best, be limited in distribution.

This conclusion, however, is not supported by field data on the distribution and abundance of these two small-seeded species. Not only are *Verbascum* and *Oenothera* widespread globally (c.f. Gross and Werner 1978; Cleland 1972); but, within the habitats where they occur, they are generally locally abundant. In early successional old-fields in southwestern Michigan, populations of these two species are frequently found growing at densities of 1-3 plants per m^2. Salisbury (1942) reports that in coppiced woodlands in England, population densities of *Verabscum thapsus* frequently exceed 5.2 flowering plants per m^2 (see also Gross and Werner 1978). In the 5 year old-field used in this study, *Oenothera* rosettes from a population that established before the onset of these experiments grew at an average density of 10 plants per m^2 and densities of 50-60 rosettes per m^2 were not uncommon. Similar densities and distributions of *Oe. biennis* have been observed in disturbed areas in north-western New York (S. Kinsmann, pers. comm.). Moreover, in fields where *Verbascum* and *Oenothera* are locally abundant, populations of *Daucus* and *Tragopogon* are rare or non-existant.

Differences in the dispersal ability of these four species appear to account for this discrepancy between the predicted and observed patterns of their distribution and local abundance. Seeds of both

Verbascum and *Oenothera* are extremely long-lived (see Table 1-1), and therefore capable of remaining dormant, yet viable in the seed pool for decades (c.f. Kivilaan and Bandurski 1973; Toole and Brown 1946). Consequently, these dormant seeds are often already present in the soil when an opening is created (dispersal in time). In contrast, seeds of *Daucus* and *Tragopogon* are not long-lived and thus depend entirely upon the annual spatial dispersal of their propagules (by wind or animals) to reach new sites. As a result, these latter two species are less likely to be among the initial colonists at a newly created opening. However, because of their ability to colonize a variety of patch types, these large-seeded species are able to persist for a number of years within the extant vegetation of an old-field community. In contrast, *Verbascum* and *Oenothera* may be ephemeral in the vegetation, but able to persist for long periods of time in the seed pool.

That there should be species having many, dormant seeds or a few, broadly-dispersed seeds has been theoretically postulated (Cohen 1967, 1968; Levins 1969; MacArthur 1972), but this has never been empirically documented nor have the ecological implications been examined in such detail in an experimental field study. Although the evolutionary mechanisms which determine these differences in life history characteristics cannot be precisely determined, it is possible to determine the potential ecological tradeoffs and morphological constraints involved.

The production of large seeds which are capable of establishing in a wide variety of habitats, may preclude the evolution of seed dormancy as a dispersal mechanism. MacArthur (1972) predicted that for seed dormancy to be an effective dispersal mechanism, large numbers of seeds must be produced. Since organisms are limited in the amount of energy they can devote to reproduction (c.f. Cody 1966; Harper and Ogden 1970; Gadgil and Solbrig 1972) species which produce large propagules, are limited in the number they can produce (Werner 1979). Moreover, large seeds are more likely to be vulnerable to post-dispersal predation, which would further decrease their likelihood of being present in the soil for extended periods of time.

Conversely, the production of small seeds may limit the type of environments in which seedlings can successfully establish, but the concomitant increase in number produced increases the likelihood of seed dormancy being an effective dispersal mechanism. These smaller seeds are less likely to be removed by post-dispersal seed predators and frequently are small enough that they rapidly sift beneath the soil surface, which increases their likelihood of being present in the seed pool when a disturbance occurs.

The association of these seed characteristics is probably not random, but rather is indicative of the tradeoffs that occur in the evolution of a successful suite of life history characteristics (c.f. Stearns 1976).

Patterns of Species Abundance in Successional Systems

Classically, the process of secondary succesion has been viewed as an orderly, uni-directional process of species replacements which is community controlled (Clements 1916; Odum 1969; Whittaker 1970). Recently, however, ecologists have challenged this view (see Drury and Nisbet 1973 for an extensive review of the empirical evidence) and have begun to analyze succession in the context of adaptations of individual species and their life histories (Connell 1972; Drury and Nisbet 1971, 1973; Horn 1974, 1975; Werner 1976, 1979). Differences in dispersal ability, and hence arrival time, have not for the most part, been considered in these models (Horn 1974; Pickett 1976; but see Connell and Slatyer 1977).

Differences in dispersal ability, and hence arrival time, are probably the major factor, overriding even adult competitive ability, in determining the pattern of species turnover in secondary successional systems (Connell and Slayter 1977; Harper 1977; Werner 1979). Colonization is a two-step process. First the propagules must reach a site (a function of dispersal ability) and then they must successfully establish there (a function of propagule size and the number that arrive). The interaction between the seed/seedling characteristics of a species and the relative distribution and abundance of safe sites for seedling establishment is a crucial factor in determining whether or not a particular species is able to establish within a given area and, consequently, in determining the pattern of species abundance and distribution in sucessional systems.

The open patches of BARE GROUND that are required for the successful establishment of Verbascum and Oenothera are ephemeral in an old-field community. In the three old-fields used in this study, the proportion of the total area in the open patch types decreased rapidly with the age of the fields, from 66% in the newly abandoned field to 5% in the 15 year old-field (see Figure 4-1). As a result, the seedling recruitment of Verbascum and Oenothera was highest in the 1 year old-field and was reduced in the 15 year old-field to one seedling for Oenothera and none for Verbascum. However, when the patch type these two small-seeded species require for establishment (BARE GROUND) was created in the 15 year old-field, seedlings were able to colonize (Table 4-15).

The range of environments in which *Verbascum* and *Oenothera* will be successful is limited by their requirement for open patches of BARE GROUND for seedling establishment. However, because seeds of these species are able to remain dormant, yet viable, in the soil for long periods of time they are likely to be among the initial colonists of a newly disturbed area. If their seeds are not present in the soil when a disturbance occurs, then the limited spatial dispersal abilities of these two species (see Table 1-1) is probably not sufficient to ensure the arrival of seeds at the field rapidly enough for a population to become established there. Consequently, both *Verbascum* and *Oenothera* have only a narrow "window in time" during which they can successfully colonize an area after a disturbance.

Moreover, populations of these two species are likely to be locally ephemeral, once they have established in an area. Because these species are monocarpic, their persistence within an area depends upon their ability to continually recolonize an area, and thus upon the distribution and abundance of safe sites therein. For *Verbascum* populations the rapid reduction in safe sites within an early successional field can result in only a single generation being successful on a site (Gross and Werner 1978; Gross 1980). Populations of *Oenothera* may also be limited to only 1 or 2 generations on a site. In the 5 year old-field used in this study, population densities of *Oenothera* rosettes decreased from 7.6 per m^2 in 1978 to 0.02 per m^2 in 1979 (Gross, unpubl. data). Similar rapid decreases in density have been noted for *Oe. biennis* populations in early successional old-fields

(5 to 11 years old) in New York (S. Kinsmann, pers. comm.).

It is important to note here, that it is not competition between established (adults) plants that causes the rapid local extinction of these two species, but rather the failure of their seedlings to emerge and/or establish. Once a seedling establishes, it generally can persist in an area (e.g. the single Oenothera seedling which emerged and survived in the 15 year old-field). However, competition with adults of other species may decrease the growth rate and reproductive output of an individual once it successfully establishes.

Daucus and Tragopogon are less likely to be among the initial colonists on a newly created disturbance, simply because their seeds are not likely to be present in the seed pool and their arrival depends entirely upon the spatial dispersal of propagules to the area from nearby source populations. Consequently, these species generally appear later in the successional development of an old-field. Because their seedlings are able to establish in a broad range of patch types, Daucus and Tragopogon are able to successfully colonize several years after a disturbance occurs or agricultural field is abandoned. It is important to note however, that these two later-arriving species are able to establish in younger fields if their propagules arrive (or are introduced) there. In fact, individuals of these species grow faster, have higher survival probabilities, reproduce earlier, and produce more seeds when they are among the early colonists on a site (see Tables 4-8, 4-11, and 4-12).

Additionally, multiple generations of these two large-seeded species are likely to establish and reproduce within a community. The earlier the species arrive, the longer the length of time they can persist there. Both of these species, however, are eventually doomed to local extinction. For Daucus, seedling survival and growth was significantly decreased in the older field (Tables 4-8 and 4-12). In addition, the density of flowering plants in this field (from previously established cohorts of seedlings) decreased from 0.64/m^2 in 1978 to 0.28/m^2 in 1979. Similar decreases in density of flowering plants in response to the age of a field have been observed for Daucus by Holt (1972) and Lacey (1978). Although Tragopogon seedlings show little or no reduction in emergence or survival in the 15 year old-field (Tables 4-5 and 4-8), the reduced growth rate of individual plants in an older field delays the onset of reproduction and the average number of seeds produced by individuals (Table 4-11). Consequently, the population growth rate of Tragopogon will decrease with time and the population will eventually become locally extinct.

Implications for Plant Community Structure

Ecologists have long been interested in the processes determining the structure of communities. The most recent advances, in this area both theoretically and empirically, have focused primarily on differences in resource utilization and habitat selection of co-occurring species and have centered around the niche concept and such constructs as the principle of limiting similarity (c.f. MacArthur and Levins 1967; Whittaker 1969, 1972; Roughgarden 1972; Schoener 1974; Werner and Hall 1976; E. Werner 1977). Werner (1979) has pointed out that most of the empirical work upon which the current theory has been developed has been with mobile animals and has as an underlying assumption a life history that best fits this type of organism. Consequently, most of these models do not work well for sessile organisms (like plants) in which space is frequently the limiting resource (but see, Schaeffer and Leigh 1976).

Additionally, most of this theory has assumed (for mathematical tractability) the environment to be homogeneous and has abstracted temporal and spatial heterogeniety out of the system entirely. The importance of considering such heterogeneity in these models, however, has been pointed out by a number of authors (c.f. Hutchison 1951; Skellam 1951; Smith 1972). The importance of both spatial and temporal heterogeneity in maintaining high species diversity within a community has been documented in empirical studies in several different types of communities: the rocky intertidal (e.g. Paine 1966, 1969, 1974; Dayton 1971; Connell 1961, 1970; Sousa, 1979); tropical coral reefs (e.g. Lang 1973; Porter 1972, 1974; Abele 1976); and several terrestrial plant communities (e.g. Watt 1974; Platt 1975; Grubb 1976; King 1977). The heterogeneity within all these systems involves the formation of localized disturbances (patches) which prevent the species with the competitive advantage from totally monopolizing the limiting resource (in all these cases, space) by interrupting the natural successional sequence.

Mathematical models have been developed which incorporate differences in the ability of organisms to colonize open patches which occur in a matrix of non-colonizable space (c.f. Horn and MacArthur 1972; Levin and Paine 1974; Slatkin 1974). Although this approach would intuitively appear to be useful in attempting to define the mechanisms which determine coexistence and competition in plants communities, it has not yet been developed to a level of sophistication which can deal with absolute abundance data and the spatial patterning of patches <u>per</u>

se (see Werner 1979).

Grubb (1977) presents a conceptual model based on differences in the regenerative capabilities of plants and their 'safe site' requirements which he proposes determines both the number and type of plant species which co-occur in a community. The mechanism by which diverse assemblages of species can coexist in plant communities is labeled the "regeneration niche".

The regeneration niche as defined by Grubb consists of several different axes and divergence between species can occur at any one of them. These stages are:(1) seed production, (2) dispersal of propagules, (3) germination, (4) establishment, and (5) development of the immature (juvenile) plant. The literature of the past decade is replete with examples demonstrating varying degrees of divergence among co-occurring species for such life history characteristics as size and number of propagules produced (e.g. Baker 1972; Werner and Platt 1976; Rabinowitz 1978 a, b), relative dispersal abilities (both in time and space) (e.g. Platt 1975; Marks 1974; Rabinowitz 1978 c), time of germination (e.g. Baskin and Baskin 1974; Raynal and Bazzaz 1975; Watkinson 1978), resource allocation (allocation to sexual vs asexual propagules or ramets) (e.g. Sarukhan and Harper 1973; Sarukhan 1974; Keeley and Zedler 1978), and relative competitive abilities (e.g. Watt 1947; Raynal and Bazzaz 1975). All of these examples may be taken as support of Grubb's hypothesis, and may increase our intuitive feeling that the regenerative stage is extremely important in determining the structure of plant communities. These examples, however, do not constitute a test of this hypothesis since the degree to which these differences in life history characteristics actually effect the local distribution of a species has not been determined. Only rarely has it been determined how differences in regenerative capabilities are related to the distribution and abundance of safe sites within a plant community and ultimately to the pattern of adult distribution within that community (e.g. the work on a guild of fugitive plants in a prairie community by Platt 1975; Platt and Weis 1977).

The major difficulty in testing this model comes in determining exactly what constitutes a safe site for a particular species and in determining its availability (e.g., distribution and abundance) within the dispersal range of the adult population. Such demonstrations are made somewhat easier when the safe site utilized is a discrete patch such as bare ground created by animals, e.g. badgers digging for ground squirrels (Platt 1975; Platt and Weis 1977) or ant mounds (cf. King 1977) or mole hills (cf. Jalloq 1975). Although the importance of an opening to seedling establishment and juvenile survival has been demonstrated for a number of species (cf. Marks 1974; Werner 1975; Platt 1975; Jalloq 1975; Raynal and Bazzaz 1975; Forcier 1975; Grubb 1977; Fox 1977; King 1977; Johnson and Thomas 1978), such openings occur only rarely in most plant communities.

A plant community is a mosaic of patches, whose relative abundances vary both in time and space. Although open patches of bare ground may provide the necessary safe site for some species within a community (e.g. Verbascum and Oenothera in these experiments; see also Platt 1975; Thomas and Dale 1976), the co-occurence of large number of species within most plant communities suggests that not all species are limited to openings for successful establishment. Indeed, the results of the experiments reported here demonstrated differences in the ability of species to colonize other patch types. In addition, differences in dispersal capabilities are important in determining the probability of reaching a particular type of patch and thus which species arrives first.

In this study, differences in life history characteristics of the four "biennial" plant species did affect their relative colonizing abilities, and consequently the range of environments in which each was able to successfully colonize. The results of this study are significant, because they allow one to predict, based only on the proportion of an area in three simple patch categories, whether or not each of these species will be able to establish there (given that the seeds are dispersed or introduced there). However, in order to predict whether or not the population, once established, will be able to persist and regenerate in an area, the growth rates of individual plants and regenerative capabilities of these species in different patches must also be considered. To do this, we need to know more about the characteristics of the patches which occur within a local area. Of these characteristics, patch size appears to be extremely important.

As a seedling grows, the scale at which it responds to its environment becomes increasingly larger. As a result, the size of the patch in which an individual is growing becomes increasingly important in determining the growth and development of a plant (c.f. Ross and Harper 1972). Several studies have shown that the area available to each individual seedling can account for a significant proportion of the variation in plant weight in a population (Yoda et al. 1957; Mead 1966; Ross and Harper 1972; Mack and Harper 1977). The percent cover technique used in this study estimates the proportion of the total area (or plot) in particular patch categories, but reveals little information about the size and distribution of individual patches.

The size of a particular opening may be important even earlier in the life cycle in determining whether or not it actually represents a safesite for a particular species. For example, recall that although Verbascum seedlings emerged in openings of BARE GROUND in the 15 year old-field, none of these seedlings survived (see Figures 4-2 and 4-5). However, in artificially created open patches (≥ 0.0225 m^2), seedlings of both Verbascum and Oenothera established in this field. Furthermore, the size of the opening effected both the probability of emergence and survival within a particular patch. In general, the probability of emergence decreased with increasing patch size, while the probability of survival increased with increasing patch size (see Table 4-16). Similar patterns of emergence and survival in response to differences in patch size have been noted for other plant species (Caruso 1963; Miles 1974; Weaver 1978). Although there was no significant difference in the mean size of the Verbascum and Oenothera plants growing in the three patch size categories in these experiments, only plants growing in the medium and large patches reached a rosette size at which the probability of flowering the following year was significant (greater than 0.5).

Several interesting patterns of plant response to patchy environments were revealed in these experiments which have implications for both empirical and theoretical studies of plant community structure. Although seedlings of all four species emerged more frequently in openings than in other patch categories, the large-seeded species, Daucus and Tragopogon, were able to establish in a broader range of patches than the small-seeded species, Verbascum and Oenothera, which were restricted to openings of a particular type. Moreover, the size of an opening effected not only the probability of a seedling emerging and surviving, but also the plant's probability of flowering the following year. These results point out the importance of considering both the proportion of the total area in particular patch categories and the size and frequency of occurrence of these patches (both in time and space) in order to predict the distribution and abundance of these four "biennial" plant species in an old-field community. The approach used in these experiments is not specific to the species and system involved, but rather can be generalized to other systems and groups of plants (or animals) with similar suites of life history characteristics.

CHAPTER 5

GENERAL CONCLUSIONS AND SUMMARY

The data and analyses presented in the preceeding chapters lend several insights into the biology of plant species which have a "biennial" life history. Although all four species used in these studies are capable of flowering within a two year cycle, for all four the probability of flowering in any year is a function of the size of the rosette at the end of the previous growing season. Moreover, the fate of an individual in any year (i.e. whether it dies, remains vegetative, or flowers) is better predicted from its size at the end of the previous year than its age.

Previous to the initiation of these studies very little was known about the range of variation in life history characteristics which occur within the biennial life history type. In general, species with such a life history were assumed to be highly opportunistic and therefore limited both in space and time to a narrow range of habitat types. While this indeed appears to be the case for some species (e.g. Verbascum and Oenothera in these studies) other species of "biennials" (e.g. Daucus and Tragopogon) are able to establish in a wide range of environments and, more importantly, are able to persist in these habitats for a number of generations. These differences in colonizing ability and the ability to regenerate within a habitat appear to be primarily a function of their particular life history characteristics (i.e. the size and number of propagules they produce and their relative dispersal capabilities).

The failure of current models of life history evolution to predict the success of species with an intermediate life history, lies in part with the failure of these models to incorporate biologically realistic and evolutionarily important constraints on the survival and reproductive behavior of plant species. Future models must incorporate such features as varying survival and fecundity schedules with age and/or size. These models would be enhanced even further, if they could incorporate to some degree differences in particular characteristics within a life history type. This would allow comparisons of the success of particular suites of characteristics over a range of environmental conditions which would provide field-testable hypotheses.

Differences in the relative colonizing abilities of these four species and the type of patch which constitutes a safe site for seedling establishment, not only accounts for their distribution and abundance across the three fields used in these studies, but also appears to be the mechanism determining the time at which they appear during succession on abandoned agricultural fields. Verbascum and Oenothera which are found only in very young fields, are limited to these initial stages because the safe sites their seedlings require are rare in older fields. The ability of seeds of these two species to remain viable in the soil for extended periods of time, however, provides an effective mechanism of dispersal which enhances their probability of being at a site when a disturbance occurrs. Daucus and Tragopogon, in contrast, generally arrive later in the successional sequence, because their seeds are not likely to be present in the seed pool. The ability of seedlings of these two species to establish in a wide range of patch types allows them to successfully colonize later (when propagules arrive) and to persist within a local area for several generations.

Plants, because they are sessile, depend upon the production and dispersal of propagules to persist within a site and to colonize new sites. Consequently, the relative colonizing ability of a plant species is an important determinant of its distribution and abundance. The results of the experiments reported here have clearly demonstrated the importance of differences in life history characteristics, particularly seed size and dispersal ability, in determining the range of environments in which a species is able to successfully establish. Differences between co-occurring species in their regenerative capabilities and the type of patches which constitute a safe site for seedling establishment can provide a mechanism for explaining the maintenance of diverse assemblages of species in terrestial plant communities. However, it will be important to incorporate the dynamics of the patches themselves (e.g. the frequency of disturbance, change in patch size) before we can predict the actual distribution and abundance of species in a community.

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APPENDICES

APPENDIX 1

SEASONAL PATTERN IN THE PERCENT COVER IN THREE EARLY SUCCESSIONAL OLD-FIELDS IN MICHIGAN

Table A-1: Percent Cover ($\bar{x} \pm 1$ S.E.) of Six Patch Types in the 1 Year Old-field over the 1978 Growing Season. Estimates are determined from 100 0.25 m^2 permanent plots.

Patch Type	28 April	29 May	21 June	7 July	8 October
Bare Ground	100 ± 0.00	66.5 ± 1.06	51.1 ± 1.09	73.4 ± 0.91	72.4 ± 1.56
Moss	---	---	---	---	0.1 ± 0.03
Lichen	---	---	---	---	---
Dicots	---	28.1 ± 1.10	51.9 ± 1.13	51.4 ± 0.82	17.4 ± 1.42
Grass	---	6.6 ± 0.78	8.9 ± 0.66	9.0 ± 0.61	9.0 ± 0.77
Litter	---	---	---	---	10.8 ± 0.87

Table A-2: Percent Cover ($\bar{x} \pm 1$ S.E.) of Six Patch Types in the 1 Year Old-field over the 1978 Growing Season. Estimates are determined from 100 0.25 m^2 permanent plots.

Patch Type	2 May	30 May	5 July	7 October
Bare Ground	12.7 ± 1.46	10.8 ± 0.91	9.2 ± 0.97	7.2 ± 0.97
Moss	3.4 ± 0.40	2.8 ± 0.30	3.2 ± 0.37	2.5 ± 0.31
Lichen	---	---	---	trace
Dicots	19.1 ± 1.14	28.3 ± 1.90	42.9 ± 2.05	37.6 ± 2.39
Grass	11.3 ± 0.83	10.0 ± 0.84	7.3 ± 0.67	24.9 ± 2.45
Litter	75.8 ± 2.20	85.7 ± 1.08	85.7 ± 1.42	87.6 ± 1.25

Table A-3: Percent Cover ($\bar{x} \pm 1$ S.E.) of Six Patch Types in the 15 Year Old-field over the 1978 Growing Season. Estimates are determined from 100 0.25 m^2 permanent plots.

Patch Type	25 April	31 May	6 July	2 October
Bare Ground	2.6 ± 0.26	0.8 ± 0.09	0.8 ± 0.16	0.8 ± 0.13
Moss	3.7 ± 1.02	3.2 ± 1.08	4.2 ± 1.32	4.3 ± 1.39
Lichen	0.2 ± 0.07	0.2 ± 0.04	0.2 ± 0.04	0.9 ± 0.23
Dicots	30.3 ± 1.57	45.2 ± 1.72	47.3 ± 1.58	43.5 ± 1.85
Grass	32.3 ± 1.66	10.9 ± 0.73	8.6 ± 0.72	18.8 ± 1.62
Litter	87.4 ± 2.03	92.8 ± 1.14	91.5 ± 1.75	87.5 ± 2.22