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Sand Dune Succession: A Comparison of Plant Life History Characteristics

presented by

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has been accepted towards fulfillment of the requirements for

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SAND DUNE SUCCESSION: A COMPARISON OF PLANT LIFE HISTORY CHARACTERISTICS

Ьу

Mary Lou Marino

A DISSERTATION

Submitted to Michigan State University in partial fulfillment of the requirements for the degree of

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ABSTRACT

SAND DUNE SUCCESSION: A COMPARISON OF PLANT LIFE HISTORY CHARACTERISTICS

By

Mary Lou Marino

This study compares life history characteristics along a successional gradient on the sand dunes of Lake Michigan. Three life history features were examined: reproductive effort, seed characteristics (weight, number, caloric content), and mortality by age-stage class.

Data on seed characteristics, reproductive phenology, and biomass allocation were collected for all reproducing herb and shrub species in the study areas (foredune, slack, dune forest). An energy allocation study was conducted for six species (forest-<u>Solidago caesia</u>, <u>Smilicina racemosa</u>, <u>Polygonatum pubescens</u>; slack-<u>Monarda punctata</u>; foredune-<u>Solidago spathulata</u>, <u>Artemisia campestris</u>). Demographic data were collected for three species (forest-<u>S</u>. <u>caesia</u>; slack-<u>M</u>. <u>punctata</u>; foredune-<u>A</u>. <u>campestris</u>).

The reproductive effort studies showed a pattern of energy allocation like that predicted by 'r' and 'K' selection models. Results depended, however, on the measures used, if species of differing morphology were compared. Measures which incorporate more than the current year's allocation of energy may better represent reproductive effort in such comparisons.

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Intermediate rather than early successional species had the smallest average seed size (.85 mg) and highest average seed number (70 seeds/g biomass). Forest and foredune means did not differ significantly. Consideration of seed caloric content did not change the observed patterns. The dune's xeric and unstable substrate gives large seeds an advantage on the foredune. The slack's topography, vegetation, and greater soil maturity create more favorable microsites for establishment of smaller seeded species. Large seed numbers improve the chances that seeds will reach these microsites.

The pattern of seed specific caloric content was opposite to that normally predicted for succession (5.9 kcal/g foredune, 4.4 kcal/g forest). It is hypothesized that in early stages of dune succession, dispersal features and abiotic influences relative to imbibition rates must be balanced against energy requirements for seedling establishment.

Demographic studies showed that forest species had the lowest juvenile and adult mortality rates (37%, 19%). Reproduction followed establishment of a root-rhizome system. This vegetative structure likely allows the individual to compete effectively as well as survive herbivory. Both factors are likely major causes of death in the forest.

The time of first reproduction can be delayed in both foredune and slack species depending on growing conditions. Such a delay may allow storage of required nutrients and keep individuals in less vulnerable age classes. The small seeded slack species had the highest first year mortality (84%). To my best and most loved field crew: Jack, Grace, and of course Stephen.

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INTRODUCTION

The sand dunes along the eastern shore of Lake Michigan provide an ideal area to examine the life history characteristics of plants within a context of primary succession. The seral sequence for this area is well established (Cowles, 1899, Olson, 1958). The seral stages are in proximity to one another, and it is assumed, therefore, that the overall differences observed in life history characteristics between plants from different seral stages should be primarily due to selective factors inherent in dune succession.

Few comparative life history studies have been done for primary successional systems. Most research has dealt with secondary succession, in particular old field, prairie, and grassland succession. Some examples are: Blake, 1935; Keever, 1950; Gadgil and Bossert, 1972; Abrahamson and Gadgil, 1973; Gaines et al., 1974; Rabotnov, 1975; Platt, 1975; Werner and Platt, 1976; Newell and Tramer, 1978. Several studies have focused on individual dune species or groups of species with some emphasis on life history factors (Hicks, 1938; Laing, 1958; Van Asdall and Olmstead, 1963; Pemadosa and Lovell, 1974a and b, 1975; Hansen, 1976; McLeod and Murphy, 1977a and b; Watkinson, 1978; Watkinson and Harper, 1978; Van der Meijden and Van der Waals-Kooi, 1979). None, however, have made a comparison between seral stages.

An additional reason for undertaking this study relates to some of the current life history models, the most frequently cited of which

is 'r' and 'K' selection. In this model, the levels of density dependent and independent mortality are the prime selective factors in life histories (MacArthur, 1962; MacArthur and Wilson, 1967; Pianka, 1970, 1972; extended to plants - Gadgil and Bossert, 1970, reviewed by Stearns, 1976). This model predicts that in environments where mortality is primarily density independent, species will tend to allocate more resources to reproduction, have larger clutch sizes and smaller offspring, and wait a shorter period before beginning reproduction. These are referred to as 'r' selected species. Those species found in environments where mortality is commonly density dependent are referred to as 'K' selected and are predicted to have characteristics opposite to those of the 'r' selected species. These sets of traits are often placed within a successional context by associating 'r' selection with early seral stages and 'K' selection with the later stages (0dum, 1969; Harper, Lovell, and Moore, 1970; Gadgil and Bossert, 1972).

Grime (1974, 1977) recently suggested that stress as well as levels of density independent and dependent mortality can act as a prime selective factor. It is often inferred from the 'r' and 'K' model that, in environments where density independent mortality is high, resources are not limiting because competitive levels are low. However, this is not always true; some environments are naturally low in one or more important resources, making growth difficult. Thus, Grime feels there are three primary life history strategies which have evolved for plant species.¹

¹Note that this does not necessarily imply there are only three strategies. Many species are exposed to differing levels of stress and/ or competition resulting in a gradation between the three strategies much like that suggested for 'r' and 'K' selection by Pianka (1970).

His ruderal and competitive strategies have characteristics similar to the 'r' and 'K' selected species mentioned earlier. The third type, stress selected, evolves in situations where primary production is difficult. The traits evolved will include an even lower level of reproductive effort than those of competitively selected species, a perennial habit, and a slow growth rate. He makes no comment on progeny size, and gives as examples species from arctic and alpine tundras, deserts, resource depleted soils, and forest floors.

Factors other than stress and levels of density independent and dependent mortality have also been suggested as important in the selection of life history traits. Such factors have been used in the recent literature to explain discrepancies between observed life history characteristics and predictions of 'r' and 'K' selection. Examples of such factors are soil moisture levels relative to seed size (Baker, 1972; Werner and Platt, 1975), foraging strategies relative to clutch mass (Vitt and Congdon, 1978), and levels of physical stress relative to clutch size (Menge, 1974). Wilbur, Tingle and Collins (1974) have suggested that close scrutiny of the selective factors (e.g. density of a population relative to its resources, the trophic and successional position of a population, and the predictability of mortality patterns) acting on organism is more important than an assumed model such as 'r' and 'K' selection which takes into account only one factor.

Grubb (1977) and Werner (1979) have recently emphasized the importance of studying the entire life cycle of a plant to the understanding of life history characteristics. Of particular significance are the seedling and juvenile stages. Pelton (1953, 1951), Curtis

(1952), Stevens and Rock (1952), Glendining (1941), Shrive (1917), and Ganong (1907) have expressed similar ideas. However, Grubb and Werner approach the life cycle from a highly developed framework of niche and evolutionary theory. Particularly emphasized by Werner is the use of plant demography.

Sand dune succession fits well within the framework of 'r' and 'K' selection since density independent mortality likely drops and density dependent mortality likely increases as the soil matures and the vegetation becomes more dense, diverse, and structured. However, nutrients are very low in the initial stages suggesting the stress selection of Grime (1974, 1976). In addition, soil moisture can be limiting especially in the seedling stage. Thus, an array of factors more inclusive than those of 'r' and 'K' selection may have to be considered to explain the life history patterns observed.

Three aspects of life histories were examined in this study. The first was the relationship of reproductive effort to successional age. The ideas of Gadgil and Bossert (1970), Harper and Ogden (1970), Ogden (1968, 1972) and Gadgil and Solbrig (1972) were examined as to their applicability to sand dune succession. The second aspect investigated trends in seed characteristics (seed size, number, and caloric content) relative to successional age. The observed patterns were compared to the ideas of Salisbury (1942); Johnson and Cook (1968); Harper, Lovell, and Moore (1970); Levin (1974); MacNaughton (1979); and Werner and Platt (1976).

To help explain the patterns observed in the first two studies, a demographic study was conducted for one representative species from each

of the successional stages examined. It was hoped that the observed patterns of mortality by life stage would give clues to the type of selective factors acting on dune plants and, as suggested by Grubb (1977) and Werner (1979), help explain why species with certain characteristics are found in particular successional stages.

This dissertation is organized into five chapters. In the first, the sites chosen for study are described and their environments compared. In the next three chapters, each of the three aspects (reproductive effort, seed characteristics, and demography) of life histories considered are examined in detail. Each chapter contains methods, results, and discussion sections. The final chapter is an overall discussion of the findings.

CHAPTER I

DESCRIPTION OF STUDY SITES

Location and Floristic Features

The study was conducted on private property near Saugatuck, Michigan (Allegan County, Range 16 west, Townships 3 north and 4 north), immediately north of where the Kalamazoo River empties into Lake Michigan. The study area is the large tract of land, approximately 405 ha, outlined in black in Figure 1. Due to its relative inaccessibility to the public, this area is fairly undisturbed. Three study sites were selected to represent a sequence of early, middle, and late dune succession based on the botanical and physical descriptions of Cowles (1899) and Olson (1958). These sites were studied for three years (1976-1978).

The foredune area (site 1, Figure 1) represents the earliest seral stage and was located adjacent to Lake Michigan. Figure 2 is a cross section through the area, indicating east and west boundaries relative to vegetative and topographic features. The west border was placed near <u>Ammophila breviligulata</u>'s lakeside edge of colonization. Beyond this edge, there were few plants in 1976. The eastern boundary was placed 10 meters beyond the crest of the first dune ridge, where leeward windspeeds were similar to the windward side's. The study site had an area of 1.2 ha with a north to south distance of 234 m.

Figure 1. <u>Aerial photograph of study area</u>. The private property the study was conducted on is outlined in black. Location of the foredune (1), slack (2), and dune forest (3) sites are shown.





Cross section through foredune site. The distance between the east and west boundaries is approximately 60 meters. Figure 2.

Floristically the foredune is dominated by <u>A</u>. <u>breviligulata</u>. Perennial herbs such as <u>Artemisia campestris</u>, <u>Asclepias syriaca</u>, <u>Solidago spathulata</u>, and <u>Lithospermum caroliniense</u> are less common, but become prevalent near the east boundary. <u>Calamovilfa longifolia</u> is found on the windward face and top of the dune ridge. The annuals <u>Cakile edentula</u> and <u>Euphorbia polygonifolia</u> are more abundant along the western boundary and in the several blow out areas found within the study site. Woody plants are found mostly along the dune ridge. <u>Prunus pumila</u> is the most prevalent followed by <u>Cornus stolonifera</u>, <u>Populus</u> <u>tremuloides</u>, and <u>Ptelea trifoliata</u>. Table Al of the Appendix lists importance values for these species.

The slack area (site 2, Figure 1) represents an intermediate stage of dune succession. However, in appearance it is more similar to the foredune than to the climax situation because it is mainly covered by an herbaceous layer and there has as yet been little soil development. The study area was 0.5 ha in size.

The slack contains most of the species found on the foredune with the exceptions of the two annuals <u>Cakile edentula</u> and <u>Euphorbia poly-</u> <u>gonifolia</u>. The perennial grass, <u>A</u>. <u>breviligulata</u>, is much less dominant, being replaced by <u>Calamovilfa longifolia</u>, <u>Panicum virgatum</u>, and <u>Andropogon scroparius</u>. Additional species not found in the foredune site are <u>Monarda punctata</u>, <u>Arabis lyrata</u>, <u>Hypericum kalmianum</u>, and <u>Oenothera biennis</u>. Both <u>Salix glaucophylloides</u> and <u>Salix syrticola</u> are found along the wet pannes which border the study site. Several <u>Quercus velutina</u> seedlings and saplings were found in the area indicating the advance of subsequent seral stages. Table Al of the Appendix lists the importance values for these species.

The dune forest site (site 3, Figure 1) represents the oldest successional stage studied. The 0.73 ha site was dominated by a mixture of <u>Acer saccharum</u> and <u>Quercus rubra</u>. Other tree species found in the area include <u>Prunus serotina</u>, <u>Fagus grandifolia</u>, <u>Tilia americana</u>, <u>Quercus ellipsoides</u>, <u>Ostrya virginiana</u>, and <u>Tsuga canadensis</u>. A list of the forest floor species and their importance values is given in Table Al of the Appendix. Among the most prevalent were <u>Smilax</u> <u>rotundifolia</u>, <u>Polygonatum pubescens</u>, <u>Viola papilionacea</u>, <u>Mitchella</u> <u>repens</u>, <u>Hepatica americana</u>, <u>Viburnum acerifolium</u>, <u>Solidago caesia</u>, <u>Oryzopsis racemosa</u>, and several species of <u>Lycopodium</u>.

Environmental Comparison

Methods

Environmental data were collected for each of the study areas so that the sites could be characterized and compared quantitatively. The differences between the slack and foredune areas are important since these areas appear physically similar, but have several floristic differences. Environmental factors of particular interest were air temperature, relative humidity, wind speed, sand movement, and soil moisture because these all have bearing on seedling survival.

Monthly hygrothermograph (Belfort, Model 5-594) readings were taken in each area from July 1977 to July 1978, excluding December

through March. The instruments were placed on the ground², near the center of the study site, and ventilated A-frame shelters were used to eliminate radiation error.

The curves obtained from the hygrothermographs were integrated over time so that data for a given interval could be reported and compared as one number. The area under the curves was used rather than an average because it was felt that this better represented the temperature and relative humidity experienced by a plant during the indicated interval. For the integration of temperature curves, $32^{\circ}F$ was used as a lower boundary because most plant metabolic processes stop at or very near this temperature. Thus, temperature data (degree-hours) represent the amount of heat above the threshold temperature which occurred during the indicated interval. The choice of a threshold for relative humidity was more arbitrary; thirty percent was chosen because it was a multiple of ten and was slightly less than the lowest humidity reading recorded. Thus, humidity data (percent-hours) indicate the total amount of relative humidity above 30 percent for the indicated time interval.

Sand movement was measured by placing 10-ounce styrofoam cups in the soil so that their rims were even with the soil surface to allow deposition of wind blown sand. The amount accumulated in the cup approximated the quantity of material deposited on a surface equal in size to the mouth of the cup for the period of time the cup was left out. A grid system was used to place the cups in each study site with

 $^{^{2}}$ These readings represent air temperature at 0-10 cm from the ground surface.

nine cups in the woods, eleven in the slack, and twelve in the foredune. Collections were made once a month during the growing seasons of 1977 and 1978.

A hot-wire anemometer (Hastings airmeter, Model RB1) was used to measure wind speed. Readings were taken during the growing season of 1977 and 1978 in each area at marked stations set up along a transect. In the foredune site, the transect ran perpendicular to the beach, with four stations: one on the dune plain (see Figure 2), one on the side of the ridge, one at the ridge crest, and one near the east boundary. In the slack and forest sites, the transect ran through the center from the east to the west boundary with three stations placed equidistant from one another.

Twenty readings were taken at each station at five second intervals to allow for the variability of wind speed. Readings were taken at 1 cm and 30 cm heights to approximate seedling³ and adult heights, respectively. Because there is a diurnal variation in wind speed, the readings for each study area were taken as close together in time as possible within the period of 0900 to 1700. An average wind speed was obtained for each area by combining all data from all the stations in each area.

Soil moisture information was collected in 1978 at two week intervals, using simple gravimetric measurements. Sample cores (4.5 cm deep by 6 cm diameter) were taken at the stations used for wind speed. At each station three samples (termed Level I samples) were collected from

³Data on seedlings were taken only in 1978.

the top 4.5 cm of soil using six ounce soil cans. Three more samples (termed Level II samples) were taken from the 4.5 cm of soil directly beneath the first three. Samples were collected only to this depth because information on moisture at the seedling level was desired.⁴

Due to the drastic difference in soil texture between the forest and the other sites, moisture content was expressed as grams of water per volume of soil as suggested by Salisbury (1952) and L. R. Stone (pers. comm.). Averages for each study site at each soil depth were calculated.

Data on soil nutrients (nitrate, total potassium, and total phosphorus) and pH were obtained from 20 random six inch soil cores taken at each of the three study sites. The analysis was performed by the Soil Testing Laboratory of Michigan State University.

Results and Discussion

In the analysis, the data for all sampling dates for a given environmental factor were taken as a group for each study area and a comparison was made. Where strong periodicity led to overlapping values for different sites, a pairwise comparison (Fisher Distribution Free Sign Test described on page 39 of Hollander and Wolfe, 1973) which took date into account was used. Otherwise, the Wilcoxon Rank Sum test sufficed. Table 1 summarizes the results of these comparisons. The

⁴The sampling design was set up through the help of L. R. Stone of the Evapotranspiration Laboratory of the Department of Agronomy, Kansas State University.

Environmental characteristic f	Foredune-Slack ¹	Foredune-Forest	Slack-Forest	Test
Temperature (degree-hours)	>,0.05	>,0.01	>,0.01	Paired replicates ²
Relative humidity (percent-hours)	<,0.05	<,0.01	<,0.01	Paired replicates
Wind speed (m/sec)				
30 cm	8	>,0.01	>,0.01	Paired replicates
1 cm	>,0.05	>,0.01	>,0.05	Paired replicates
Sand movement (g/cm ² /day)	>,0.05	>,0.05	>,0.05	Wilcoxon Rank Sum ³
Soil moisture (g/cm ³)				
Level	<,0.05	<,0.05	<,0.05	Wilcoxon Rank Sum
Level 11	11	<,0.05	<,0.05	Wilcoxon Rank Sum

Column headings amond the three study sites romaricon Summary of the environmental TABLE 1

when taken as a group were significantly greater (less) than those of the other site on the heading. An entry of > (<) implies that the area listed first in the column heading had measurements which An equal sign means there was no significant difference. Numbers indicate significance level.

²From page 39 of Hollander and Wolfe, 1973.

³From page 68 of Hollander and Wolfe, 1973.

actual data compared may be found in Tables A2-A6 and Figures A1 and A2 of the Appendix.

As can be seen from Table 1, the foredune most frequently has the highest temperatures (P<0.05, 0.01 by paired replicates) and lowest humidity levels (P<0.05, 0.01 by paired replicates) of the three areas. The forest exhibits just the opposite pattern, as might be expected, due to the enclosure and shading of the tree canopy.

Windspeed levels⁵ are the lowest for the forest for both the 30 cm and 1 cm heights (P<0.05, Wilcoxon Rank Sum). There is little difference between the slack and foredune at the 30 cm height. However, at the seedling or 1 cm height, there is a significant difference (P<0.05, paired comparisons).

Sand movement data indicate that the foredune has the least stable substrate of the three areas, since sand deposition in the sand traps was highest (P<0.05, Wilcoxon Rank Sum) in this area. The slack was next highest, and the forest was last, with little or no sand movement.

The forest had the highest (P < 0.05, Wilcoxon Rank Sum) levels of soil moisture in both Levels I and II samples. This is expected due to this area's greater soil maturity and to the shading of the tree canopy.

⁵In the pairwise comparison, foredune values were regrouped because the topography of this area guarantees that a portion of the sampling stations will be sheltered no matter which direction the wind is blowing (see Figure 2 for reference). Thus, measurements taken east of the dune ridge ('back', Table A4) were separated from the remaining foredune data ('front', Table A4), and averaged as described in the Methods. In the pairwise comparison, the larger of those two averages was compared with the corresponding slack or foredune value.

For the deeper, or Level II, samples there was no significant difference between the slack and foredune areas. However, in the first few centimeters of sand (Level I), the foredune (overall) had significantly less (P<0.05, Wilcoxon Rank Sum) moisture than the slack.

Table 2 shows soil nutrient and pH characteristics. Soil acidity increases in the slack and forest areas reinforcing similar observations by Olson (1958). The data for all areas indicate very infertile soil. All sites have similar nitrate levels, with the slack and foredune lowest in phosphorus and potassium. Though similar in potassium, the foredune has less phosphorus than the slack. It has been suggested by Olson (1958) that phosphorus may be a serious limiting factor on very young alkaline dunes.

	Foredune	Slack	Forest
рН	7.4	6.8	5.4
Phosphorus (kg/ha)	2.24	5.6	6.72
Potassium (kg/ha)	34.7	34.7	58.2
Nitrate (ppm)	4.1	3.9	3.8

TABLE 2. Soil nutrient and pH characteristics of the study areas.

The foredune exhibits the lowest levels of nutrients, soil moisture, and humidity as well as the highest temperatures and windspeeds. The forest is at the opposite extreme. Examination of the absolute values of the abiotic characteristics indicates that the slack more closely resembles the foredune, as is expected. However, there are differences. Of particular interest is the foredune's lower soil moisture in the upper centimeters of sand. This combined with the other abiotic differences between the slack and foredune probably places some constraints on seedling survivorship, and likely plays a major role in determining the seed and seedling characteristics of species able to establish populations on the foredune. This will be looked at in more depth in the chapter on seed characteristics.

CHAPTER II

REPRODUCTIVE EFFORT

Methods

Six species were chosen for detailed study of reproductive effort: <u>Artemisia campestris</u> and <u>Solidago spathulata</u> (foredune); <u>Monarda punctata</u> (slack); and <u>Solidago caesia</u>, <u>Smilicina racemosa</u>, and <u>Polygonatum</u> <u>pubescens</u> (forest). These species were chosen because they were among the more prevalent herbaceous perennials in the areas they represented, and it was possible to determine the annual increment of growth for each species. Time constraints prevented the study of more than six species.

Figure 3 shows a schematic of the methods used to estimate reproductive effort. First, forty healthy and reproducing plants per species were marked in spring of 1977. Twenty plants per species were excavated in the early spring of 1978. Each plant was dried for 18 hours (65-70C), weighed, and its caloric content determined⁶ (via a Parr Adiabatic Bomb Calorimeter), using the methods of Leith (1968).⁷ The twenty values per

⁶Both weighing and caloric content determinations were done by plant part (leaves, roots, stem, and reproductive parts) to assure greater accuracy. This procedure was followed for all aspects of the reproductive effort estimations.

⁷Due to equipment failure, some material was dried at 105-110C rather than the 68C set on the controls. Several individuals (N. Good, P. G. Murphy, and S. N. Stephenson) were consulted and all agreed that caloric content would not be affected. Comparison of caloric content of materials dried at the two temperatures support this. However, dry weight was affected because the temperature differential was high enough

Figure 3. Schematic of methods used to determine reproductive effort.



species were then averaged to determine \overline{Q} (Figure 3), the mean energy accumulated per plant previous to the spring of 1978.

The exception to this procedure was the monocarp <u>A</u>. <u>campestris</u>. At the end of the 1978 growing season, 20 juveniles (rosettes) were harvested according to a predetermined size distribution. This distribution was calculated from 1977 demographic data for rosettes which flowered during the 1978 growing season. An average energy accumulation per plant was determined as described previously. A correction was made for biomass which would be lost during the winter by subtracting an average percentage of leaf loss determined from demographic data. It was assumed that no biomass was lost from roots during the winter period and energy content per gram of biomass did not change.

In the spring of 1978, screen cages were placed around plants marked the previous fall (except <u>A</u>. <u>campestris</u>) to collect dead matter falling from the plants. For <u>A</u>. <u>campestris</u>, newly bolting rosettes were used. The top of these cages was left open to allow access by pollinators and to limit shading by the screen. Material was removed from the cages every two weeks, for the entire growing season. This material was sorted, dried, weighed, and its caloric content determined. When a plant died or failed to flower or fruit, its cage was moved to the nearest plant of similar size and phenologic state. At the end of the growing season, the average dead matter lost per plant (\overline{D} , in Figure 3) was determined for each species.

to drive off more tightly held water molecules. A correction factor was determined from the weight differential of plant material dried at the two different temperatures.
Loss to herbivory was conspicuous only in <u>S</u>. <u>racemosa</u> and <u>P</u>. <u>pubescens</u>. The amount of biomass removed was estimated by measuring the damaged area and converting this measurement to grams using the weight to area ratio of the undamaged portion of the leaf.

Caged plants were harvested at the end of the growing season. This was late September for <u>S</u>. <u>racemosa</u> and <u>P</u>. <u>pubescens</u> and mid-October for the other four species. All roots and rhizomes within 15 cm of the plants were collected. The plants were sorted, dried, weighed, and their caloric content determined as described earlier.

The vegetative data for each plant were then averaged by species to yield the mean vegetative energy present at harvest (\overline{T} , Figure 3).

During periods of flower and fruit loss, caged plants were visited to collect dropped fruit or flowers.⁸ Reproductive material was also gathered during dried matter collection. This combined with the appropropriate harvest information was used to determine, by species, the average amount of energy per plant devoted to reproduction (\overline{L} , Figure 2).

Ratios to express reproductive effort were constructed as shown in Figure 3. The annual accumulation ratio (hereafter referred to as AAR) expresses the current year's energy to reproduction (\overline{L}) relative to the current year's energy accumulation $\int (\overline{T}+\overline{D}+\overline{L})-\overline{Q} \int \overline{J}$. The total accumulation ratio (hereafter referred to as TAR) expresses the current year's energy to reproduction relative to energy accumulation at time of harvest $(\overline{L}/(\overline{T}+\overline{L}))$.

⁸The three composites retained their flowers until time of fruit dispersal; thus, these were collected at time of plant harvest.

A less detailed study of reproductive effort was also carried out on several other herbaceous species from each area (seven species from the foredune, 14 from the slack, and 16 from the forest). The number of species sampled in each study site was determined by the number of species which reproduced during the 1978 growing season. A species list is given in the Appendix (Table A7). Only reproductive and vegetative data at time of harvest were collected, thus only TAR values were calculated. Biomass rather than energy was used.⁹

Plants were excavated near time of fruit maturity. When possible, ten plants were collected. If the species was fairly rare, a lesser number was gathered. All material (stems, leaves, roots, rhizomes, etc.) within 15 cm of the main stem was excavated to avoid problems caused by the great variability in morphology among species (e.g., cloning versus noncloning). All noncloning and many cloning plants were smaller than this. For those that were not, it was felt a good estimate of allocation could be obtained from this section of the clone. A similar method of defining the individual was used by Stevens (1937) in his study of seed numbers of weedy species. The weight of fruit already dispersed at time of harvest was estimated from data collected on fruit and seed characteristics during the previous year.

Results

Table 3 contains the AAR percentages for the six species examined in detail. Looking at only the first four species of the table,

⁹In comparing TAR and AAR for species studied in detail, patterns were little changed whether biomass or energy was used. This agrees with the results of Hickman and Pitelka (1975).

<u>Artemisia campestris</u> which appears earliest in the sere has the highest level of reproductive effort (29.6 percent). <u>Solidago spathulata</u> appears next in the sere and its value (17.5 percent) is similar to that of <u>Monarda punctata</u> (16.8 percent), a species which appears only in areas where some stabilization has occurred (Cowles, 1899; Olson, 1958). <u>Solidago caesia</u>, a late successional species, has a value (6.4 percent) significantly lower (P<0.05) than the other species. These four species show the same pattern whether AAR or TAR percentages are used (compare Tables 3 and 4).

TABLE 3. Reproductive effort estimates for six dune species using annual accumulation (AAR) percentages.

Areas	Species	AAR in percent ¹	95 percent confidence interval
Foredune	<u>Artemisia</u> campestris	29.6	15.8 - 32.2
Foredune	<u>Solidago</u> <u>spathulata</u>	17.5	10.9 - 27.6
Slack	Monarda punctata	16.8	13.1 - 21.9
Forest	<u>Solidago</u> caesia	6.4	4.0 - 9.9
Forest	<u>Smilicina</u> racemosa	29.4	20.4 - 39.4
Forest	Polygonatum pubescens	22.6	19.9 - 27.5

'[(Current year's energy to reproduction)/(current year's energy accumulation)_7 x 100.

The dune forest species, <u>Smilicina racemosa</u> and <u>Polygonatum</u> <u>pubescens</u>, do not follow the predicted pattern when AAR percentages are used. These percentages (29.4 and 22.6 percent, respectively) are

TABLE 4.	Reproductive effort estimates	for six dune species	using total accumula	tion (TAR) percentages.
Areas	Species	TAR in percent	TAR as a percent reduction from AAR	Percent of total energy added in current year
Foredune	<u>Artemisia</u> campestris	26.2 (14.3 - 30.5) ²	11.5	11.8 (6.7 - 28.0) ²
Foredune	Solidago spathulata	14.5 (12.3 - 16.5)	17.1	3.3 (2.1 - 6.9)
Slack	<u>Monarda</u> punctata	13.9 (10.8 - 16.7)	17.3	5.0 (3.6 - 7.5)
Forest	Solidago caesia	4.4 (2.8 - 6.2)	31.3	2.0 (1.4 - 2.8)
Forest	Smilicina racemosa	11.8 (8.2 - 15.2)	59.9	1.3 (0.9 - 1.9)
Forest	Polygonatum pubescens	11.9 (8.9 - 15.1)	47.4	0.7 (0.5 - 1.0)

 \sqrt{C} (Current year's energy to reproduction)/(total accumulated energy) \sqrt{X} x 100. 2 The 95 percent confidence interval for all percentages are parenthesized.

almost as high as that for <u>A</u>. <u>campestris</u>. However, when TAR percentages are used, the order of the magnitudes is now as reported in other studies (Table 4) with all woods species' percentages less than those of the earlier seral species.

The difference in the pattern given by these two ratios may result because of differences in morphology. Both <u>S</u>. racemosa and <u>P</u>. <u>pubescens</u> have large underground rhizomes. <u>S</u>. caesia and <u>S</u>. <u>spathulata</u> have rhizomes as well but they are smaller. Column 3 of Table 4 illustrates this. As can be seen, all four rhizomaceous species have the lowest percentages of annual energy accumulation; however, <u>S</u>. <u>racemosa</u> and <u>P</u>. <u>pubescens</u> are lowest at 1 percent. This is significantly lower than any of the early successional species. Thus, when calculating the TAR percentages, a significantly larger number was divided into reproductive allocation for <u>S</u>. <u>racemosa</u> and <u>P</u>. <u>pubescens</u> resulting in a much different pattern from that of the AAR percentages. The bearing which these two different patterns have on life history characteristics is discussed in the next section of this chapter.

The TAR values obtained when the dominant herbaceous species from each area were included are shown in Table 5. There is a definite trend among the means with the forest's (9.8 percent) less than that of the slack (14.3 percent) or foredune (21.4 percent).

In looking at values for individual species (column one of Appendix Tables A4, A5, and A6), the highest are found for semelparous species (grouped separately, Table 6). This was expected since these species have only one chance to reproduce and must devote a

proportionately larger amount to accomplish what the perennial has several years to accomplish (Williams, 1966; Gadgil and Bossert, 1970; Hart, 1977).

	Mean TAR	Standard
Areas	percentage	error
Foredune	21.4	6.0
Slack	14.3	3.1
Forest	9.8	2.1

TABLE 5. Mean total accumulation (TAR) percentages for the three study sites.

The lowest values are for species which can reproduce vegetatively such as members of the Gramineae or species such as <u>Hudsonia</u> <u>tomentosa</u> and <u>Mitchella</u> <u>repens</u>.

Discussion

Gadgil and Solbrig (1972) associated the ideas of 'r' and 'K' selection with reproductive effort along a successional gradient. Given the influence of abiotic factors in the early stages of sand dune succession and the increased amount of vegetation and structural diversity with seral age, one would expect reproductive effort for this system to follow the predictions of this model. In this study where the reproductive effort of many herbaceous species was examined, these expectations are supported since species from later stages of dune succession appear to allocate lesser amounts of resources to sexual reproduction

	TAR	
Species	percent	Longevity
Foredune		
<u>Cakile</u> edentula	54,62	Annua l
Euphorbia polygonifolia	34.71	Annua I
<u>Artemisia</u> <u>campestris</u>	25.87	Semelparous perennial
Slack		
Arabis lyrata	20,72	Winter annual
Polygonella articulata	26,42	Annua 1
<u>Oenothera</u> <u>biennis</u>	37.25	Biennial
Artemisia campestris	29,48	Semelparous perennial
Forest		
Arabis drummondii	30,24	Biennial
<u>Osmorhiza</u> <u>claytoni</u>	20,92	Biennial

TABLE 6. Total accumulation (TAR) percentages for semelparous species.

than do species from earlier stages. This follows observations on both old field and prairie succession (Gadgil and Solbrig, 1972; Abrahamson and Gadgil, 1973; Gaines et al., 1974; Newell and Tramer, 1978). However, the detailed study of six representative species indicates that the pattern observed is dependent on the ratio used.

Two different ratios (converted to percentages) were examined in the study of the six representative species. The seeming contradiction resulting from the use of both can be resolved if the aspect of allocation measured by each is closely examined. The AAR percentage¹⁰ considers only the allocation of one year's energy between sexual reproduction and vegetative growth. That is, it looks at one year's energy allocation to flower and fruit production relative to that year's production of stems, leaves, root, and rhizome tissue. This is almost the same ratio used by Gadgil and Solbrig (1972) and Abrahamson and Gadgil (1973). A slight difference results because they did not include allocation to new root and rhizome tissue due to the difficulties associated with sampling underground tissue and estimating the annual growth of these types of tissue. However, they acknowledge that this tissue should be included in reproductive effort ratios (Abrahamson and Gadgil, 1973; W. G. Abrahamson, pers. comm.). The sampling for the six representative dune species was designed as an improvement over these previous studies of reproductive effort.

The AAR percentages of some species (<u>S</u>. <u>racemosa</u> and <u>P</u>. <u>pubescens</u>) do not follow the prediction of Gadgil and Solbrig (1972). This

^{10 (}The current year's energy allocation to sexual reproduction)/ (the current year's energy accumulation) x 100.

results not from the inclusion of the current year's root and rhizome tissue, but rather from the failure of the AAR percentage to incorporate respiration. Thus, to permit the comparison of reproductive effort between different species, two assumptions must be made: (1) that respiration requirements for producing a unit of biomass is similar for all species examined and (2) that respiration levels needed to maintain the various plants are similar. There has been little research into the truth of the first assumption, perhaps due to the difficulties of measuring the respiration of different plant parts in the field. Thus, this assumption may or may not be true. However, it is a common, if unstated, assumption used in studies of reproductive efforts (Gadgil and Bossert, 1972; Abrahamson and Gadgil, 1973; Gaines et al., 1974; Newell and Tramer, 1978).

The second assumption may result in problems for this study. It was demonstrated that the later successional species, in particular <u>S. racemosa</u> and <u>P. pubescens</u>, have a higher level of biomass accumulated from previous years. Thus, the relative amount of energy needed to maintain these plants is probably higher than for the early successional species. Since most of the tissue was accumulated previously, this represents a drain of this year's energy to the maintenance of vegetative tissue not even included in the AAR percentages. Also, if energy required for the maintenance of reproductive and vegetative tissue had been included, as it ideally should be, the AAR percentages might have followed the predicted pattern. Likely Gadgil and Bossert (1972) and Abrahamson and Gadgil (1973) may not have encountered this difficulty

because when examining a few species in detail, these species were of the same genus and/or of similar morphological structure. When many different species are examined, averages over all species could well have concealed differences due to morphology in the variance.

Age at first reproduction is another factor which must be considered when evaluating reproductive effort. It is often predicted that age of first reproduction will be greater for later successional species than for early successional species (Odum, 1969; Pianka, 1970; Stearns, 1976). In plants this pre-reproductive period is often spent producing structures which will help assure survival of the adult. Demographic data indicate this is true for S. caesia, since plants of this species do not reproduce until the root-rhizome is well established (4 or more years). Comparison of reproducing and nonreproducing S. racemosa and P. pubescens indicate that this is perhaps the case for these species as well. When these species do commence reproduction, their manner of energy allocation is not only a function of the energy available at that time, but is also likely to be affected by these preestablished vegetative structures as well. Thus, it is conceivable that plants which spend several years building an extensive root rhizome system before beginning reproduction could allocate more to reproduction in a given year than those which build this system while reproducing. With the system already established, the plant merely has to maintain it and replace dead tissue.

This may be the case for <u>S</u>. <u>racemosa</u> and <u>P</u>. <u>pubescens</u>. The rhizome for these species is a linear series of nodes. Each year a new node is

added at one end, and the oldest node (located at the other end of the rhizome) dies. Thus, a certain number of nodes (6-8 <u>S</u>. <u>racemosa</u>; 5-6 <u>P</u>. <u>pubescens</u>) appear to be maintained alive at all times. Plants with less than this number were never observed to reproduce. The AAR percentages for these species were almost as high as <u>A</u>. <u>campestris</u> which is a semelparous early successional species. However, because this percentage only considers the latest year's allocation, the influence of the previously established root rhizome system is ignored. TAR percentages do not ignore this aspect of the life history since they express allocation to reproduction relative to the plant's total energy reserve. ¹¹ When these percentages are used, the reproductive allocation of <u>S</u>. <u>racemosa</u> and <u>P</u>. <u>pubescens</u>, though larger than that of <u>S</u>. <u>caesia</u>, is less than the reproductive allocation of both the slack and foredune species. Thus, the pattern follows the predictions and observations of Gadgil and Solbrig (1972).

Ratios similar to the TAR percentages have been used in more recent reproductive effort studies (Gaines et al., 1974; Newell and Tramer, 1978). However, the relationship between this ratio and those used in early allocation studies was not mentioned.

It is the TAR percentages which were used in the overall examination of many herbs. Given the nature of this percentage, the results of this study and the data on the six representative species, it appears that plants from later stages of dune succession are much more conservative in their allocation to reproduction than are species from

¹¹⁽The current year's allocation to reproduction)/(the total energy at time of harvest) x 100.

earlier seral stages. Later stage plants always maintain a much higher vegetative base relative to that allocated to reproduction. This supports the prediction that plants in more highly competitive situations will allocate more energy to structures which will help assure the survival of the adult (MacArthur and Wilson, 1967; Pianka, 1970; Gadgil and Bossert, 1970; Gadgil and Solbrig, 1972; Schaffer and Gadgil, 1975). This allocation may take place largely before the plant begins reproduction (<u>S. racemosa</u>, <u>P. pubescens</u>) or continue throughout the life of the plant (<u>S. caesia</u>).

Newell and Tramer (1978) suggest that allocations to root-rhizome systems for herbs in deciduous forests help in competition with nearby plants. However, they may also be defenses against predation as well. Herbivory was observed for all three forest species studied in detail. Large underground reserves would aid in overcoming losses in energy due to foliage lost to predation. The above-ground tissue of several <u>S. caesia</u> plants in the demographic studies was partially or totally eaten. However, most of the plants reappeared the next year, because the root rhizome system remained alive.

In early stages of dune succession, allocation to vegetative structures probably does not provide as much defense against causes of death as they do in the dune forests, since abiotic factors are more often critical. A good root system is of importance, but studies have shown that below 25 to 30 cm (Salisbury, 1952; McLeod and Murphy, 1977 a and b) the sand remains permanently wet. Thus, allocation to vegetative structures would be of less importance, as both overall and detailed reproductive effort studies seem to indicate. Also, as will

be demonstrated in the demographic studies, the survivorship of adults from early stages of dune succession appears to be much less than that of species from the dune forest; thus, early successional adults have less time to reproduce themselves (especially <u>A</u>. <u>campestris</u>). Therefore, reproduction is at a higher premium when it occurs. This is particularly true since demographic studies also indicate that survivorship of seedlings and juveniles is less.

CHAPTER III

SEED CHARACTER ISTICS

Methods

Three major seed characteristics (numbers, weight, and caloric content) were examined for all herbaceous and shrubby species reproducing in the study areas (11 foredune species, 17 slack species, and 16 forest species). Voucher specimens were deposited in the Kellogg Biological Station Herbarium of Michigan State University at Hickory Corners, Michigan.

Seed number per plant was estimated by first determining the average number of fruiting heads per plant, the average number of fruits per fruiting head, and the average number of seeds per fruit. Sampling was continued for each mean until the standard error was ten percent or less of the mean. These means were then multiplied by one another to yield the number of seeds per individual for each species. Average seed numbers were divided by average plant weight to adjust for size and morphological differences. Thus, numbers for a species were expressed as numbers of seeds produced per gram of accumulated biomass.

To obtain seed weights, all ovary tissue (fruit) was removed from seeds.¹² The seeds were then dried for 48 hours at 65-70 C in a forced

¹² In seed studies, this is not always done (Stevens, 1932; Salisbury, 1942; Baker, 1972) due to the difficulty in removing ovary tissue. However, most theories dealing with seed size refer to the amount of endosperm available to the newly emerged seedling. Thus, it was felt this procedure was necessary.

air oven, and placed in a desiccator for 12 hours. Seeds were weighed individually on a Cahn microbalance (Model 4700). Weighing was continued until the standard error was less than five percent of the mean.¹³ To obtain weight distributions for analysis, 20 seed weights were randomly selected from the seed data for each species and combined by study area (foredune, slack, forest).

Seed caloric content was obtained using a Parr Adiabatic Bomb Calorimeter. Whole seeds were embedded in a pellet of starch of known weight (and, therefore, of known caloric content) and bombed. Seed caloric content was determined by subtraction.¹⁴ The techniques of Leith (1968) were not used because of their tendency to allow seed oil to be lost during pellet preparation.

Ash free weights were not used in this portion of the study because of the small seed size of many species. The difficulty in removing seeds from ovary tissue made prohibitive the number of seeds required for ash weight determination.

Results

Frequency distributions of herbaceous seed weights for each of the study areas are given in Figure 4. The distributions were normalized using a log₁₀ transformation so that parametric statistical techniques could be used (Tables A8-A10 of the Appendix give untransformed data).

¹³For some of the more variable species (e.g., <u>A</u>. <u>campestris</u> and <u>Galium circaezens</u> seven percent was used.

¹⁴This technique was developed through the help of Dr. Kwen Pao Ku from the Department of Animal Husbandry, Michigan State University.

Figure 4. <u>Seed weight (a) and energy per seed (b) fre-</u> <u>quency distributions for herbaceous species from</u> <u>each study site</u>. A log₁₀ transformation was used to normalize the distributions. Thus, parameters given with the distributions have been transformed. The means are shown, and the bars to either side indicate the standard error.



The mean seed weight for the slack area is significantly less than the means of the forest and the foredune. The averages of the earliest and the latest seed stage cannot be distinguished from one another $(t^* = -.195)$.¹⁵

This same pattern emerges when mean kilocalories per seed are examined (Figure 4). Again, the slack mean is significantly smaller $(P < 0.01)^{15}$ than the means of both the forest and the foredune. The foredune and forest averages still cannot be distinguished statistically. However, the difference between the two means is larger because the median level of kilocalories per gram (Figure 5) of seed tissue is significantly less (P < 0.05)¹⁶ for the forest than for the foredune. The forest's median kilocalories per gram of seed tissue is also significantly less (P < 0.10)¹⁶ than the slack median.

The reason for the differences in median kilocalories per gram of seed tissue for the areas is found by comparing each of the area's frequency distribution for this characteristic (Figure 5). The slack and foredune distributions are significantly different from that of the forest (P < 0.01).¹⁷ Only 12 percent of the forest sample was greater than 4.6 kilocalories per gram whereas the slack and foredune had 63 percent and 77 percent, respectively.

Returning to the slack and foredune distributions of seed weight and kilocalories per gram of seed tissue (Figure 4), it can be seen that

¹⁵The Behrans-Fisher Test was used to compensate for nonhomogeneous variances.

¹⁶The Wilcoxon Rank Sum Test was used.

¹⁷The Kolmogorov-Smirmov Test was used.

Figure 5. Energy per gram of seed tissue frequency distributions for the herbaceous species from each study site. The medians are indicated by the arrows.



the slack distributions are more skewed toward small seed weight and caloric content than are the foredune's. Also, the foredune has a grouping of large seeds (1.0-1.2) that the slack does not have. By the Kolmogorov-Smirnov test, the foredune distributions are significantly different (P < 0.05) from those of the slack. To help explain this difference, the samples for each area were divided into those species common to both areas (overlap species) and those species which are found far more frequently in one of the areas than the other (non-overlap species).

The foredune nonoverlap group includes those species which colonize the most stressful portions of the dune system (foredune, blowouts), but are less frequently found in more stabilized areas such as the slack (<u>Cakile edentula</u>, <u>Ammophila breviligulata</u>¹⁸, and <u>Euphorbia</u> <u>polygonifolia</u>). The overlap grouping contains species which can establish sizable populations in both types of situations (<u>Artemisia</u> <u>campestris</u>, <u>Calamovilfa longifolia</u>, <u>Lithospermum caroliniense</u>, and <u>Solidago spathulata</u>). In the slack nonoverlap grouping are those species which have difficulty establishing in areas such as the foredune, but are quite prevalent in the slack (<u>Hudsonia tomentosa</u>, <u>Monarda</u> <u>punctata</u>, <u>Polygonelia articulata</u>, <u>Oenothera biennis</u>¹⁹, <u>Arabis lyrata</u>, <u>Panicum viragatum</u>, and <u>Andropogon scoparius</u>). This categorization was

 $¹⁸_{\underline{A}}$. <u>breviligulata</u> was present in the slack area. However, the population was small and produced only three flowering heads both in 1977 and 1978.

¹⁹This species is sometimes characteristic of older portions of the foredune (Cowles, 1899). However, only two plants were found in the study area. These were in protected areas beyond the hillcrest.

based on personal observations as well as on the accounts of Cowles (1899) and Olson (1958).

Means of transformed (\log_{10}) seed weight and energy per seed were calculated for the foredune and slack overlap and nonoverlap species. These are shown in the top two graphs of Figure 6 (untransformed numerical values are given in Table All). The pattern for both seed characteristics is similar. The foredune non-overlap species have the highest (P < 0.01) mean seed weight and mean energy per seed, whereas the slack nonoverlap means are the smallest (P < 0.05). The means for the overlap groupings are intermediate in value and are significantly different (P < 0.05) from the nonoverlap groups.

This pattern becomes even more interesting when seed numbers are examined. The distributions for adjusted²⁰ seed numbers for each of the study sites are given in Figure 7. The slack area's mean seed number is significantly higher (P < 0.05) than both the foredune and forest means. Though the foredune mean is larger than the forest's, the two means do not differ statistically.

Using the Kolmogorov-Smirnov Test, the foredune and slack seed number distributions are significantly different (P < 0.05) from one another. This results because the foredune's distribution is skewed to the left whereas that of the slack is skewed to the right. This is exactly the opposite of what was observed for seed weight and energy per seed

²⁰As was explained in the Methods, these are termed 'adjusted' because average number of seeds per plant was divided by average plant weight to allow a comparison of plants of different sizes.

Figure 6. Averages of seed characteristics for foredune and slack overlap and non-overlap species. The x-axis is an ordinal scale indicating the relative age of site where the species of the indicated grouping are most frequently found. The seed characteristics are given on the y axes. The standard errors are indicated by the bars on either side of the means. All data were transformed using a log₁₀ transformation.



Figure 7. Adjusted seed number distributions for herbaceous species from each study site. A log₁₀ transformation was used to normalize the distributions. Thus, the parameters given with the distributions have been transformed. The mean for each distribution is shown and the bars to either side indicate the standard error.



distributions. Again, the data were separated into the overlap and nonoverlap groupings described earlier. The slack nonoverlap species' average seed number is significantly larger (P < 0.01)²¹ than the foredune nonoverlap group's average seed number as well as that of both overlap groupings (bottom, Figure 6). (Table All shows actual numbers and statistical comparisons.). Though the foredune nonoverlap group has the smallest mean, this mean is not significantly different from the averages of the two overlap groupings.

Combining the information on seed weight (or energy) with that of seed numbers, it would appear from Figure 6 that dune species (foredune nonoverlap) frequently colonizing the most environmentally stressful and least stable portions of the dune system tend to have a smaller number of large seeds whereas those species (slack nonoverlap) found most frequently in the more stable and less stressful slack area tend to have a large number of small seeds. Those species found in both types of areas appear to exhibit seed characteristics intermediate between these extremes.

Up to this point we have examined only the foredune and slack distributions of seed characteristics in detail. Examination of the forest's distributions is also enlightening. Returning to Figure 4, it can be seen that though the slack and foredune distribution of seed weight and energy per seed are skewed, the forest's distributions encompass the entire range of values exhibited by both of these earlier

²¹The Behrans-Fisher Test was used.

seral stages. Use of the Kolmogorov-Smirnov Test shows a significant difference (P < 0.05) between the forest's distribution and those of the slack and foredune. For seed numbers (Figure 7), the forest's distribution primarily encompasses a smaller range of values than do the slack and foredune distributions. Thus, it would appear that though forest species exhibit seed weights and energy per seed values which, on the average, are larger than those of the slack and equal to those of the foredune, the individual species exhibit a wider range for these seed characteristics. This is less true for seed number.

Distributions of $(\log_{10} \text{ transformed})$ seed weight and caloric content per seed for shrubs species are shown in Figure 8. As was the case for herbs, the slack averages are smallest, and the foredune and forest means are similar in size both for seed weight and for energy per seed. However, it could not be determined whether these differences were statistically significant due to the trimodal distribution exhibited by slack species for these characteristics. However, comparison of the distributions themselves is enlightening. All are significantly different from one another (P < .001).²² The foredune distributions are not as variable as the slack's, but are more so than the forest. The largest seeds of the foredune belong to <u>Prunus pumila</u>, which is the most abundant shrub of the foredune area. It is found on the foredune crest as well as the dune plain, and can establish on blowing sand (Cowles, 1899). Of middle seed size is the far less

²²The Kolmogorov-Smirnov Test was used.

Figure 8. Seed weight (a) and energy (b) per seed frequency distributions for shrub species from each of the study sites. All data were transformed using a log₁₀ transformation. The transformed means are indicated on the distributions as are the standard errors.



abundant <u>Ptelea</u> <u>trifoliata</u> which is able to colonize bare sand, but at a high rate of mortality (McLeod and Murphy, 1977b). It establishes best in thickets of more stabilized areas. The smallest seed belongs to <u>Cornus stolonifera</u>. The two thickets present in the study are both in protected areas just beyond the crest of the first dune ridge. Though a good dune former, its seedlings most frequently establish in moist protected areas (Cowles, 1899).

The slack area, with its trimodal distribution, has species which have three different site requirements for germination. The largest seeds (<u>Prunus pumila</u>) can colonize open sandy areas. The smallest (<u>Hypericum kalmianum and Salix glaucophylloides</u>) are dune swamp species and need moist protected areas for their seedlings to survive (Cowles, 1899). Species of middle seed size (<u>Arctostphylous uvi-ursi</u> and <u>Vitis</u> <u>riparia</u>) invade only areas which have been stabilized by other species (Cowles, 1899; Olson, 1958).

The forest shows the least variability of the three areas in seed size since only two species are represented (<u>Viburnum acerifolium</u> and <u>Euonomus obovatus</u>). Both must develop woody tissue in shaded closed communities, thus, selection on seed size may leave little room for variability.

Figure 9 contains the distributions of adjusted seed numbers for shrub species. The forest mean (0.599) is significantly smaller (P < 0.05) than both the foredune and slack area means.²³ The latter two means cannot be distinguished from one another (1.828 and 1.820, respectively).

²³The Kolmogorov-Smirnov Test was used.

Figure 9. Adjusted seed number frequency distributions for shrub species from each of the study areas. Data were transformed using a log₁₀ transformation. Transformed means and standard errors are indicated on the distributions.



The distributions for the slack and foredune areas are not significant by the Kolmogorov-Smirnov Test. Both are spread over a range from 0.6 to 2.8 with the smallest seeded plants having the largest seed numbers. However, for the slack, the largest seeded species have intermediate numbers.

The forest distribution for adjusted seed numbers is more variable than it was for seed size. However, it is much less spread than the other areas. It appears that the forest species have large seeds, but few of them.

Median²⁴ kilocalories per gram of seed tissue for shrubs are: 5.734 kcal/g for the foredune, 5.189 kcal/g for the slack, and 5.713 kcal/g for the forest. None are significantly different from one another since the ranges are so large (4.476-5.937 kcal/g for the foredune, 4.862-5.941 kcal/g for the slack, and 5.171-6.320 kcal/g for the forest). Shrub and herbaceous medians are similar for both the slack and foredune areas (foredune--5.734 kcal/g for shrubs versus 5.68 kcal/g for herbs; slack--5.184 kcal/g for shrubs versus 5.281 kcal/g for herbs) whereas those of the forest are significantly different (5.713 kcal/g for shrubs versus 4.411 kcal/g for herbs, P < 0.05 by Wilcoxon Rank Sum).

²⁴Medians are shown because the Wilcoxon Rank Sum Test was used, and this test compares medians rather than means.

Discussion

Unlike other studies which have shown that seed size increases with successional age (Salisbury, 1942; Harper, Lovell, and Moore, 1970; MacNaughton, 1975; Werner and Platt, 1976; Newell and Tramer, 1978), this study found that in dune systems seed size is similar for the earliest and latest seral stages. It is in intermediate seral stage that the smallest average seed size is observed. The pattern for seed numbers was exactly the reverse of this with the largest numbers occurring in the intermediate stage and the smallest in the earliest and latest seral stages. Again, this contradicts the findings of other studies (Salisbury, 1942; Cody, 1966; Johnson and Cook, 1968; MacNaughton, 1975; Werner and Platt, 1976; Newell and Tramer, 1978). These apparent contradictions can be explained, however, if the selective pressures acting in the different seral stages are examined.

The early stages of sand dune succession are edaphic deserts (Salisbury, 1952). The low moisture holding capacity of the sand, drying effects of the wind, and high soil temperatures (sometimes > $50^{\circ}C$) result in moisture levels in the first few centimeters of sand being less than 0.05 percent of field capacity (Salisbury, 1952; McLeod and Murphy, 1977b). As indicated by the environmental data, the soil moisture in the first 4.5 cm of the foredune sand can fall below 0.002 g of water per cm³. This, combined with the high air temperatures, wind speed, and soil temperatures, result in a poor environment for seedling establishment. However, soil moisture increases with depth and at approximately 25 cm is permanently wet (Salisbury, 1952; McLeod

and Murphy, 1977b). The closer a seedling roots are to this area of permanent wetness, the greater the seedling's chances of survival (McLeod and Murphy, 1977b). Soil nutrients are also low, especially on the foredune, making root growth difficult. However, a large seed would allow the development of an extensive root system in the face of these low nutrients much as it would in the competitive situation. Also, due to the instability of the dune substrate, the chances are high that a seed will become buried. A large seed would provide reserves for stem growth to the sand surface, and a deep root system would provide anchorage if sand is blown from around the seedling. Evidence for the importance of large seed size in xeric systems also comes from Baker's (1972) study of the California flora and Went's (1955) study of desert perennials.

The environmental section demonstrated that there were differences in windspeed, air temperature, humidity, soil moisture, and sand movement between the foredune and slack areas. With the combination of these differences, the foredune becomes the least hospitable for seedling establishment. However, xeric and low nutrient conditions exist in the slack area as well. The question arises as to why there is such a difference in average seed size and number between these two areas. The answer lies in the comparison of overlap and nonoverlap species.

As was discussed in the Results section, those species found primarily on the foredune, on the average, have the largest seeds and the lowest seed numbers, whereas those found only in the slack are just the reverse. Those which overlapped were intermediate in size and numbers.
It is possible that the combined effects of reductions in the stress factors mentioned earlier allow enough favorable microsites so that smaller seeded species can establish. Of particular importance would be the higher soil moisture and nutrient levels as well as protection provided by topographic relief and vegetative cover. The importance of the microsite in the establishment of seedlings has been demonstrated by Harper et al. (1965), Sheldon (1974), and Oomes and Elberse (1976). Even on the foredune, some of these smaller seeded species can infrequently be found; however, these have usually established in protected areas behind the crest or in shaded and more vegetated areas. Since most foredune or slack species are wind dispersed, the higher seed number of small seeds found in slack nonoverlap species would allow greater dispersal distance and would increase the probability that enough suitable microsites will be found for replacement and/or population increase. The large numbers of seeds would also be important, because the mortality of seedlings established from these small seeds is likely high, due to xeric conditions of the slack area and to the random location of favorable microsites. The larger seeds of the overlap group allow establishment in either area.

Of interest in the overlap group are the two species which have the smallest seeds (<u>Artemisia campestris</u> and <u>Solidago spathulata</u>). In both size and numbers, they are similar to the slack nonoverlap group yet they have been able to establish sizable populations on the foredune, apparently contradicting what was said earlier. However, both have adaptions to compensate for their small seed size. The fruit of

<u>A. campestris</u> is an achene which when wet provides a mucilagenous seed cover. Mucilage allows a much faster uptake of water and can make germination levels less sensitive to water supply (Harper and Benton, 1966; Oomes and Elberse, 1976). In addition, the dispersal unit is far from spherical²⁵, increasing the surface area and imbibition rate (Harper and Benton, 1966). The specific energy content of the seed is among the highest of any species found in the three study areas. The high imbibition rate and lower moisture requirement for germination could allow for fast germination and root system establishment. The high caloric content allows for an adequate food reserve.

The seeds of the other small seeded overlap species, <u>Solidago</u> <u>spathulata</u>, appear to germinate on the foredune only infrequently, and if they do, the seedling may survive only a short time. <u>S</u>. <u>spathulata</u> seedlings were looked for when <u>A</u>. <u>campestris</u> and <u>M</u>. <u>punctata</u> seedlings were surveyed at two week intervals. Though several were found in the slack area, none were found in the foredune. This species can, however, reproduce vegetatively by budding from its roots. Once the ramet is large enough and its own root system is well established, the connection with the parent plant degenerates. The distribution of this species is highly clumped on the foredune and in many cases radiates from behind the dune crest and/or from more highly vegetated areas. Thus, it would appear that seedlings can infrequently establish in protected areas, and further colonization slowly radiates from these

 $^{^{25}}$ The length is more than two times the width and the width is 1.75 times the depth.

points through vegetative propagation and very rare seedling establishment.

Though a large seed can be advantageous in a xeric environment, there are concomitant disadvantages as well. These are listed in Table 7 along with the advantages discussed to this point. (The same is done for small seeds.) These disadvantages may place constraints on how large a seed may become. Though average foredune seed size was larger than the forest's, there were several forest species of much larger seed size than any foredune species. A possible constraint is imbibition rate. Imbibition takes longer in larger seeds because of their low surface to volume ratio (Harper and Benton, 1966; Harper, 1977). In the foredune and slack areas, periods favorable for germination are short. If a seed germinates too slowly, conditions may become too harsh to allow establishment of a root system. Thus, the advantages of a large seed size would be lost. Imbibition rates are even slower if the seed is on the soil surface because water is more easily lost from the seed to the surrounding atmosphere than if the seed were surrounded by soil (Harper and Benton, 1966). The probability is higher that a seed would be buried on the foredune than on the slack, due to the greater instability of the foredune's substrate. It is possible that seeds of equal size may more frequently have imbibition difficulties in the slack than they would on the foredune. Thus, the slack areas may have even greater constraints on large seed size than the foredune does. This may help explain why larger seeded species are

	Large s	seeds			Small	seeds
	Advantages		Disadvantages		Advantages	Disadvantages
-	Rapid root development	-	Poorer wind dis-	_	Improved wind	. Fewer resources
	ditions		persar		lispersal	available tor rapid root
		Ċ	-	•		development
	A. Promotes survivor-		LOWER IMDIDITION	2.	Higher imbibi-	A. Complicates
	snip through		rates may delay cermination		tion rates	survivorship
	alought				reauing to more rapid germination	under drought
	B. Improves anchor-	ы.	Fewer seeds pro-			COND I LIONS
	age in blowing		duced for a	س	More seeds produced	D 1 imite anchor.
	sand		given reproductive		for a given repro-	age in blow-
			allocation		ductive allocation	ing sand
2.	Shoot can more easily					
	penetrate to surface				~	More difficult
	if seed is buried by				1	for short to
	sand					reach surface if
						seed is buried
						by sand

TABLE 7. Selective advantages and disadvantages of large and small seed sizes in the early stages of dune succession.

not found in the slack area when a large seed size would seem advantageous. This may also help explain why overlap species have "intermediate" seed characteristics.

Most dune species are wind dispersed and this may also result in selection against large seeds. Since most species do not have special mechanisms to aid in wind dispersal, the distance traveled is highly dependent on seed size. Thus, the size a seed attains must be balanced against the probability of the seed being dispersed to a favorable germination site (Salisbury, 1975).

Increases in seed size are accompanied in this study and have been noted in others (Harper, Lovell, and Moore, 1970; Stebbins, 1971; Werner and Platt, 1976; Werner, 1980) by reductions in seed numbers and thus of potential offspring. Beyond a certain point, these reductions can more than offset the survivorship gains due to large seeds (Werner, 1980). This is particularly true given the low survivorship for all life stages observed in the demographic studies²⁶ of <u>A. campestris</u> and <u>M. punctata</u>.

The pattern of specific caloric content of seeds for the three study sites reflects these constraints on seed size. This pattern is exactly the opposite of that usually predicted for a successional sere (Levins, 1974; Harper, Lovell, and Moore, 1970). However, increasing the specific caloric content of a seed would be a way of

²⁶See Chapter IV for presentation of data.

balancing the energy requirements for seedling survival with the needs of dispersability, numbers, and fast imbibition rates. In the forest, such a balancing would not be as necessary. Seeds are primarily animal dispersed and soil moisture is high. Those few forest species which are wind dispersed have the smallest seeds and the highest specific caloric content. The trade off between seed size and number probably occurs in the forest as well. However, given the lack of a dispersability constraint for the animal dispersed seeds, the survivorship and competitive gains from very large seeds likely more than offsets the loss of potential offspring due to decreased seed numbers. This is particularly true in light of the high survivorship of all life stages observed in the demographic study²⁷ of <u>S</u>. <u>caesia</u>.

Thus far, seed characteristics have only been considered within the dune system. Table 8 allows a comparison with other systems. This table contains information on seed size for species and/or genera common to both dune systems and old field or prairie environments. Data were taken from Stevens (1932), Werner and Platt (1976), and K. Gross (unpublished data). In each case where a species is common to the dune environment and another system, the dune population always has the largest seed. In most cases this is true of overlapping genera as well. Of interest is <u>Oenothera biennis</u> which is present in both old fields and the tall grass prairie of lowa as well as sand dunes. Although seed size of the prairie population is

²⁷See Chapter IV for presentation of data.

	<u>Mean weight</u>	per seed (mg)
Species	Sand dune	or prairie
<u>Cakile</u> edentula	10,23	6,35
Euphorbia esula Euphorbia nutans Euphorbia seryphyllifolia Euphorbia humestrata	1 10	3.5 .56 .30 .24
<u>Cirsium aryense</u> <u>Cirsium megacephalum</u> <u>Cirsium pitcheri</u>	5.79	1.575 8.45
Artemisia <u>biennis</u> Artemisia campestris (caudata)	.336(F) ² .342(S) ³	.075 .100
Ascleplias syriaca	7.98(F) 9.18(S)	4,20
4 Solidago <u>nemoralies</u> Old field Prairie Solidago missouriensis		.0267 .104
Old field Prairie Solidago <u>speciosa</u>		.0176 .0393
Old field Prairie Solidago canadensis		.0195
Old field Prairie <u>Solidago giganta</u> (Prairie) Solidago graminifolia (Old field)		.0273 .0583 .0508 .0245
<u>Solidago</u> <u>caesia</u> (Dune forest) <u>Solidago</u> <u>spathulata</u> Foredune	.234 .489	
Slack Panicum virgatum	1,625	1.25
<u>Monarda</u> fistulosa Monarda punctata	.375	.320

TABLE 8. Intersystem comparison of seed sizes.

TABLE 8 (cont'd).

	Mean	weight	per seed	(mg)
			01d fie	ld
Species	Sand	dune	or prai	rie
<u>Oenothera</u> <u>biennis</u> 5				
Old field			. 198	
Prairie		-	.307	
Dune slack	.72	28		

¹Unless otherwise noted, all data not from the sand dunes were taken from Stevens (1932).

 2 An 'F' in parentheses stands for foredune,

3An 'S' in parentheses stands for slack.

⁴All data on Solidago species not found on the sand dunes were taken from Werner and Platt (1976).

⁵Data for old field and prairie were taken from Gross (unpublished data).

greater than that of the old field, the sand dune population's is even greater. A similar situation exists for the <u>Solidago</u> species, with the species found in the slack and foredune areas having larger seeds than any species found in the slack and foredune areas having larger seeds than any species population from either old field or prairie. Werner and Platt (1976) have demonstrated that the competitive levels in the prairie are higher than in the old field, and feel that this factor accounts for seed size differences observed for species common to both areas. Due to the sparsity of vegetation, competitive levels are probably low in slack and foredune communities; thus, xeric conditions appear to have selected for large seed size just as competitive factors have in more mature systems. It would appear that, although average seed size is less in slack species than foredune species, relative to species from other systems, slack seeds are large as well.

The distribution of seed numbers and size for the forest species was more variable (Figure 6) than either that found in the slack or foredune. The forest contains the species with very large seeds as well as those with very small seeds. The same is true for seed numbers. The reduction of abiotic stress factors such as blowing sand and low soil moisture as well as soil development allow the establishment of a much more diversified vegetation with a wide variety of traits. Here competitive factors become very important. Small differences in microtopography, soil moisture, and soil type can give one species an

advantage over another at a certain place in the environment. The role which these factors play in the distribution of forest herbs has been discussed by others (Struick and Curtis, 1962; Bell, 1974; Bratton, 1979).

Reproductive traits must be finely tuned to the existence of favorable microsites for seedling germination. Forest species tend to rely on animal vectors for seed dispersion. Because animals tend to move from one attractive location to another, animals can selectively transport seeds to habitats resembling those occupied by the parent plant (Stebbins, 1971). However, such places are probably highly vegetated and successful seedling establishment will depend on large food reserves in the seed.

Some forest species (<u>Solidago caesia</u> and <u>Arabis</u> <u>drummondii</u>) are wind dispersed. To assure distance dispersal, seeds are small. However, seeds more than likely must land in disturbed and less vegetated areas to aid seedling survival. Demography studies of <u>S</u>. <u>caesia</u> seem to bear this out. Since such areas are scattered and the probability of landing in a favorable site is small, these species tend to have a larger number of seeds than other forest herbs relying on animal vectors.

The diversity of species in the forest also allows the establishment of symbiotic relationships. For example, <u>Chimaphila maculata</u>²⁸ has very small seeds (less than 0.0015 mg) and a high average seed number (4,741).

²⁸The data for this species were not used in the study because the mycorhizal relationship made the selective factors acting on this species much different from those acting on the other species in the study.

The seedlings quickly establish a mycorhizal relationship, allowing the adult to produce minute seeds which can withstand competition. The large seed number assures that seeds will come in contact with the proper fungi (Salisbury, 1942).

The diversity in reproductive traits found in the dune forest has also been observed for the tall grass prairie of lowa which is also a structured community of high species diversity. Platt (1970) found a spectrum of reproductive characteristics which allowed each species to be finely tuned to the availability and type of microsite required for seedling survival. This, as we saw for the dune forest species, required a balancing of dispersal factors and germination requirements.

Data on shrubs reflect a pattern of seed characteristics similar to that of the herbaceous species just discussed. The foredune and forest median seed sizes are similar to each other and larger than that of the slack. The pattern is just the reverse for seed numbers. Due to the paucity of reproducing forest shrubs, these plants do not exhibit the diversity of characteristics which was seen for forest herbs.

Of interest is the slack's trimodal distribution of seed size and numbers, indicating three distinct sets of characteristics. The grouping with the smallest seeds and highest numbers contains <u>Salix glauco-</u> <u>phylloides</u>, and <u>Hypericum kalmianum</u>. Both are swamp species and need moist protected areas for germination (Cowles, 1899; Moss, 1938). The willow has only a short period in the spring when conditions are proper for germination after which seeds do not remain viable (Moss, 1938). Given the paucity of proper microsites in a slack environment, there is likely a high mortality among seeds and seedlings. Thus, both species produce a large number of small seeds which can be dispersed long distances by the wind, increasing the probability that the proper microsite will be found.²⁹

Species of intermediate seed size and smallest numbers are <u>Vitis</u> <u>riparia</u> and <u>Arctostaphylous uvi-ursi</u>. Both invade the slack after it has been stabilized and many other plants are already present (Cowles, 1899; Olson, 1958). Sites of germination are frequently protected by vegetation which reduces the effects of abiotic factors. However, competitive factors likely become more important due to the density of vegetation and the natural scarcity of nutrients. Large seed size may be an advantage under these conditions. Both species rely on animal vectors for seed dispersal. Since animals can selectively transport seeds to areas resembling those occupied by the parent plant, fewer seeds may be needed to assure attainment of a proper germination site than those species such as <u>Salix glaucophylloides</u> and <u>Hypericum</u> <u>kalmianum which are wind dispersed (Stebbins, 1971).</u>

<u>Prunus pumila</u> has the largest seed size and is found both in the slack and foredune areas. It is one of the few shrubs which can establish in open sand (Cowles, 1899). Therefore, xeric factors become very important in the establishment of seedlings and account for the large seed size. Its seed is even significantly larger (P < 0.05) than the dune forest tree species, <u>Prunus serotina</u> (<u>P. pumila</u>: slack 29.89 mg, foredune 36.10 mg versus <u>P. serotina</u> at 24.57 mg).

²⁹Note that the willow's rapid stem elongation and spread allow it to be covered by sand once established (Cowles, 1899). Thus, the site of the adult can become very different from that initially colonized.

<u>P. pumila</u> produces an intermediate number of seeds (less than <u>S. glaucophylloides</u> and <u>H. kalmianum</u>, but more than <u>V. riparia</u> and <u>A. uvi-ursi</u>). This species is animal dispersed, but produces more seeds than either <u>V. riparia</u> and <u>A. uvi-ursi</u>. This may be necessary to compensate for mortality among seedlings due to the greater exposure of <u>P. pumila</u> seedlings to xeric factors. This phenomenon has been observed for <u>Ptelia trifoliata</u> (McLeod and Murphy, 1977a and b) which is also a slack and foredune species. <u>P. trifoliata</u> seedlings establish best in protected and shaded areas. However, the seed is large and can germinate in open sand, but mortality is higher there. Unlike <u>P. pumila</u>, this species does not reproduce vegetatively. McLeod and Murphy (1977b) feel that with a high seedling and juvenile mortality and the species' lack of vegetative reproduction, a high seed production is necessary for <u>P. trifoliata</u> to survive in a dune habitat.

In terms of specific caloric content of seed material, there is little difference between the shrubs from the three study areas. Median caloric content for shrubs and herbs were also similar for slack and foredune species. However, the forest shrub median was much higher than that of the forest herbs. A higher oil content in shrubs than in herbs has been observed by Harper, Lovell, and Moore (1970) and Levins (1974). The establishment of a woody habitat by shrubs is hypothesized as the possible reason for the differential. It is of interest, however, that the specific caloric content of foredune and slack herbs is as high as that of shrub species. This may reflect the balancing in herbaceous species of food reserve requirements with dispersal and imbibition rate requirements, as discussed earlier. To summarize, early sand dune species tend to have a small number of large seeds of high specific caloric content. Xeric and low nutrient factors likely have played a role in selecting these characteristics. As the community matures and vegetative and topographic factors begin to ameliorate abiotic factors, species of small seed size and larger seed numbers begin to move in due to a greater number of sites favorable to the survival of their seedlings. It is in this stage that species come closest to having characteristics often associated with "colonizing" species (Baker and Stebbins, 1965; Harper, Lovell and Moore, 1970). However, xeric factors are still probably important since, in the comparison of seed size of species common to both old fields and sand dune slack areas, the slack population's seed size was larger.

As the community matures further and a more dense and diverse vegetation moves in, competitive factors seem to become more important. Thus, dune forest species have a smaller number of larger seeds. However, due to the diversity of structure and reduction in the constraints of abiotic factors, a greater variety of seed characteristics was observed for this seral stage than was observed in the earlier stages.

CHAPTER IV

DEMOGRAPHIC STUDIES

Methods

Three species were chosen for detailed demographic studies: <u>Artemisia campestris</u> (foredune), <u>Monarda punctata</u> (slack), and <u>Solidago</u> <u>caesia</u> (forest). Each is characteristic of the area it represents, and lives for more than one year.

Permanent, $1 m^2$, plots were set up in each of the study areas in the late summer and fall of 1976; all plants of each of the three species were marked. Because placement was random, some plots were devoid of plants. However, several of these became colonized by the species in question during the study. In total there were 50 foredune plots, 30 slack plots, and 30 forest plots. Because dry conditions in 1977 caused high mortality in <u>A</u>. <u>campestris</u> and <u>M</u>. <u>punctata</u>, eight plots were later added both to the foredune and to the slack areas.

The condition, size, and phenologic state of marked plants were recorded monthly. If a plant appeared dead, it was watched for two months. If it did not recover and appeared to be decomposing, the plant was recorded as being dead at the date of the first observation. Seedlings of the marked species, which appeared in the plots, were also marked and their survivorship followed.

To assure that a large number of seedlings were marked for each of the studied species, seedlings outside the plots were also marked.

During the growing season of 1977, temporary 1 m^2 plots were randomly placed, once a month, in each of the areas (50 in the foredune, 30 in the slack, 30 in the forest). If a seedling was found in a plot, it was marked and rechecked each month on the same date that the permanent plots were checked. A similar procedure was followed in 1978, except that a larger sample (80 in the foredune, 50 in the slack, 50 in the forest) was taken at two-week intervals.

Mortality was high for adults and juveniles of <u>A</u>. <u>campestris</u> during 1977. Thus, additional plants (22 adults and 22 juveniles) were marked and checked at monthly intervals to assure an accurate estimate of mortality in 1978.

Seed viability at dispersal time was examined for each of the species with both germination and tetrazolium tests (Association of Official Seed Analysts, 1970a and b). For each species, 250 seeds were tested. For germination tests, seeds were placed on moistened blotters and covered by a petri dish top. For an unchilled treatment, the seeds were then placed in a germinator (30 C day, 20 C night) and checked at two-week intervals for one month. For a pre-chilled treatment, seeds were kept at 9 C for one week and then placed in the same germinator as the unchilled seeds. All tests were performed at the Seed Laboratory of the Michigan Department of Agriculture.³⁰

To examine spring viability of seeds left in the field, packets of seeds were placed in each of the areas at the end of the growing season

³⁰Seed germination and viability tests were set up with the help of the seed testing personnel of this laboratory.

(November, 1977). Seeds (25 in the foredune, 25 in the slack, 20 in the forest) were placed in a nylon sock and covered with two tablespoons of substrate (sand in the foredune and slack, dune forest soil and leaves in the forest). The socks were knotted, enclosed in aluminum screening, buried (12 in the foredune; 12 in the slack; 10 in the forest, sand; 10 in the forest, leaves) just beneath the ground surface in early November, and retrieved in mid-April, 1978. Seeds were separated from substrate and tetrazolium tests run.

Results

Life Cycles and Survivorship

Following the format of Hubbell and Werner (1979), Figures 10-12 contain pictorial representations of life cycles for <u>A</u>. <u>campestris</u>, <u>M</u>. <u>punctata</u>, and <u>S</u>. <u>caesia</u>. The top illustration in each figure has the life history separated into as many age and morphological classes as could be inferred from the data. The bottom diagram is a condensed form and has the best data base of the two. Because of this, the latter was used in the calculation of rates of increase as described by Hubbell and Werner (1979). Arrows indicate the direction of transition from one phase to another and numbers indicate the probability of transition. The term λ^{-n} is used to symbolize a time requirement of n units and indicates time between phases. In the diagrams, the time units are months. The term represents the finite rate of increase, and as described later, will be used to solve for the intrinsic rate of increase. Figure 10. Artemisia campestris life history. The top portion of this figure shows a detailed life cycle. The bottom cycle is a condensed version of the top cycle. The procedure for making up the cycles follows Hubbell and Werner (1979). All numbers less than one indicate the probability of taking a given pathway. The numbers next to the probabilities indicate the year. The whole numbers on the path "adult to seeds" indicate the number of seeds produced per plant for the indicated year. The superscripts on the lambdas indicate the time period in months. The Roman numeral after 'adult' indicates the year of adulthood the plant is presently in. This symbolism was also used for juveniles. Also, note that a juvenile is a plant which is more than one year old but has not yet flowered.





Figure 11. <u>Monarda punctata life history</u>. For an explanation of this figure, see the caption of Figure 10.

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Figure 12. <u>Solidago caesia life history</u>. See the caption for Figure 10 for a detailed explanation of this figure.





Table 9 contains the probability of survivorship for each of the stages found in Figures 10-12. A separate table was needed to present these because the numbers in Figures 10-12 combine survivorship and the proportion of a given life stage which took a given path to the next life stage.

Comparing Figures 10-12, all three species release seeds in the fall: <u>M. punctata</u> in mid-September, <u>A. campestris</u> in mid to late October, and <u>S. caesia</u> in late October to early November. In 1977, <u>M. punctata</u> had the highest seed viability at dispersal (75 percent, Table 9). <u>A. campestris</u> was next at 61 percent, and <u>S. caesia</u> was lowest at 40 percent. Viability does not appear to be consistent from year to year since 1978 figures for <u>M. punctata</u> (54 percent) and <u>A.</u> <u>campestris</u> (65 percent) are lower than 1977 and <u>S. caesia</u> is almost two times as high. Comparing unchilled and prechilled treatments, all three species do not need a cold treatment to germinate since percentages are similar for both treatments.

Some of the causes of inviability are shown in the second grouping of numbers in Table 10. All of the categories are self explanatory except 'empty fruit'; this represents seeds which developed, but the endosperm had been eaten without any visible outside damage. This was less frequently a cause of inviability in <u>A</u>. <u>campestris</u> and <u>S</u>. <u>caesia</u> (3.79 and 10.40 percent, respectively), but was significant in <u>M</u>. <u>punctata</u> (16.9 percent). A fungus, Coelomycetes (H. Imshaug, pers. comm.), was always present inside these seeds (see Figure 13). However, it could not be determined if the fungus actually caused the death of the seed or if it invaded after a seed became inviable.

	Artemisia	campestris	Monarda	punctata	Solidage	o caesis
Category	1977	1978	1977	1978	1977	1978
Germination: Fall Spring-Summer	0.0 ² 5×10 ⁻⁴	.014 ³ .0023	0.0 ² 5×10-5	.0017 ³ .0073	NA ⁴ .016	NA .02 ⁴
First year: Overwinter (fall germination) Fall germination Spring-Summer germination	ND ⁵ ND .29	.39 ² .20 .21	ND ND .16	.38 ² .057 .157	NA NA 23	NA NA .26
Juvenile: 6 First year Second year Overall	.90 ND 18.	.46 .38 .38	.25 ND .31	.50 ND .43	ON ON ON	.5585 ND .5585
Adult: First year Second year Overall	.04 ND .03	.04 0.0 .03	1.00 ND .83	.70 .43	ND ND 75	UN ND 8.

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and November. The 'spring-summer' category under germination was for the period of April through August. For further information see Figures 10-16 and footnote 31 in text. The time period for all categories except those for germination and first year overwintering are Germination probabilities were calculated as the proportion of seeds germinated relative to the number of seeds produced. The 'fall' category under germination was for the months of October First year overwintering is for the 6-month period of mid-October to mid-April. one year.

²Seed germinated in fall of 1976, but seedling developed in 1977 growing season.

³Seed germinated in fall of 1977, but seedling developed in 1978 growing season.

⁴Does not apply to this species.

⁵No data available.

⁶This is the first year of the juvenile stage; plants are actually in their second year of life.

Category	<u>Artemisia</u> campestris	<u>Monarda</u> punctata	Sol ida	go caesia
Percent viability at dispersal:	(%)	(%)		(%)
1977: Tetrazolium Prechilled germination Unchilled germination	61.0 62.8 60.0	76.0 75.0 73.0		38.0 41.0 42.0
1978: Tetrazolium	54.0	65.0		77.0
Mortality sources at dispersal as a percent of seeds tested (tetrazolium, 1977 seeds): Empty fruit Insect damage Inviable by tetrazolium (viable by tetrazolium)	3.8 0.0 ¹ 35.2 (61.0)	او.9 0.0 ¹ 6.5 (76.0)		10.4 36.0 15.2 (38.0)
Results of overwintering tests (tetrazolium, 1977 seeds): Viable: by tetrazolium germinated by packet recovery	5 9.0 0.04 100	49.5 26.3 23.2	<u>sand</u> 24.0 1.8 22.2	<u>leaf litter</u> 10.00 .9
Inviable: by insect or fungal damage by tetrazolium	41.0 4.0 37.0	50.5 41.4 9.1	76.0 20.2 55.8	90.0 30.3 59.7

TABLE 10. Sources of seed set mortality.

¹None evident on seeds themselves.

Figure 13. Monarda punctata seed with fungal damage. The picture was taken with a scanning electron microscope. A portion of the fruit covering (outer layer) was cut away to show inside. All the endosperm is gone; only the damaged seed coat remains. Hyphal strands permeate both seed coat and fruit. The small white bar at the bottom of the photograph represents 100 micrometers.



For <u>S</u>. <u>caesia</u>, insect damage was the greatest cause of death (36 percent). In these seeds, a hole of entry would be present and endosperm would be eaten. A reduction of this type of damage (25 percent of 1977 levels or 9 percent) is one of the reasons viability for <u>S</u>. <u>caesia</u> was so much higher in 1978.

In <u>A</u>. <u>campestris</u>, the most important cause of death was inviability of the embryo itself. Many embryos were not stained or would only partially stain with tetrazolium, indicating death or imminent death of the embryo. The cause of this mortality is unknown.

During the winter, the viability of <u>A</u>. <u>campestris</u> seeds was not reduced appreciably, dropping from 61.0 percent at dispersal to 59.0 percent at winter's end (Table 9). The reduction for the other species was much higher. For <u>M</u>. <u>punctata</u> the reduction in viability was 25 percent and that for <u>S</u>. <u>caesia</u> was 40 and 75 percent for sand and leaf substrates, respectively. An increase in fungal or insect damage contributed to these increases. These values are much higher than seed predation values reported by Watkinson (1978) for <u>Vulpia fassciculata</u>, an annual on the coastal dunes of England.

Sand is a better substrate than leaf litter for maintaining viability in <u>S</u>. <u>caesia</u> seeds, because two times more seeds remain viable in this substrate. These findings correspond with field observations because seedlings are seldom found in areas covered with leaves, but are frequently found in open sandy areas. Seeds in leaf litter seem more susceptible to insect damage (30 and 20 percent for leaf and sand, respectively) as well as embryo death indicated by tetrazolium (24 and 10 percent for leaf and sand, respectively).

Germination of A. campestris and M. punctata can occur in the fall after seed dispersal or during the following spring and summer (see Figures 10-12) whenever conditions are favorable. For M. punctata the fall germination starts in early to mid-October and runs into November. A. campestris begins later, usually in late October to early November. No seedlings of either species germinated³¹ in the fall of 1976 (Table 9). In M. punctata this likely resulted from the very dry fall of 1976. Many of the wet panne areas around the slack area dried up, and mortality was higher for the later age classes. The lack of proper environmental conditions may have placed the seeds in a state of enforced dormancy (Harper, 1977) since germination and tetrazolium tests indicated no innate dormancy. Germination was also very low during the spring and summer of 1977 with a seed's probability of germinating being 5x10⁻⁵. Likely, dormancy continued during this period. The probability of germination rose to .0017 in the fall (1977) since conditions were favorable. Both recently dormant and newly dispersed seeds likely contributed to this higher level of germination because conditions were just as favorable for fall, 1978, but the probability of germination was only .0012. Dormant seeds from the previous year likely contributed to the high spring-summer (April through August) germination levels of 1978, since the probability of germinating in this period rose to .0073.

³¹Germination probabilities for a given species were obtained by first estimating the number of that species' seedlings which came up in the study area. This number was then divided by the number of total seeds produced by the species in the study area.

A. <u>campestris</u> showed a similar germination pattern with germination probabilities being zero for fall of 1976 and 5×10^{-4} for springsummer of 1977. The germination probability for fall of 1977 rose to .014, and that for spring-summer, 1978 to .0023. Again, dormant seeds from 1976 probably contributed to these levels. No germination occurred in fall, 1978, because fruit dispersal was delayed until the second week of November. Thus, it is not known if the germination pulse of fall, 1977, was normal or an artifact of the dry conditions of the 1976-1977 growing season. However, fall germinated seedlings survive as well as fall <u>M. punctata</u> seedlings, indicating that fall germination may not be a rare occurrence.

<u>S</u>. <u>caesia</u> does not have fall germination because seeds are released so late in the season. Seeds germinate only in late April to early June; however, germination probabilities were higher for this species than for the others both in 1977 (.016) and 1978 (.024). Although levels were reduced in 1977, <u>S</u>. <u>caesia</u> did not show the drastic reduction found in <u>A</u>. <u>campestris</u> and <u>M</u>. <u>punctata</u> indicating that this species was less affected by the dry conditions.

The next category of Table 9 ('First year') includes all plants in their first year of life. This categorization is morphologically based because first year plants look the same as they did when obtaining their second set of leaves. Because survivorship was different, fall and spring-summer germinated plants were separated. These data were pooled for two-year-old plants.

First year <u>A</u>. <u>campestris</u> plants attain an average size of 8.5 cm. They have one stem with a series of finely dissected leaves. At the

end of the growing season, the stem takes on a woody appearance and the plant overwinters as a rosette.

First year plants of <u>M</u>. <u>punctata</u> also have only one stem. In moist years, several small branches may form at the base, and the plant will reach a height of 7.8 cm by late September (1978). At this time, several branches grow out from the base to form a small rosette $(36 \text{ cm}^2 \text{ by growing season's end})$, and, in appearance, the small plant resembles a miniature second year nonflowering plant. The plant overwinters as a rosette.

First year <u>S</u>. <u>caesia</u> plants remain as small rosettes closely appressed to the ground. During the year, several leaves are added and the overall plant grows in diameter to about 2.4 cm. This species also overwinters as a rosette.

Fall germinating first year plants of <u>A</u>. <u>campestris</u> and <u>M</u>. <u>punctata</u> had similar levels of overwinter survivorships³² (Table 9) being .39 and .38, respectively. During the first growing season of these plants, however, <u>M</u>. <u>punctata</u>'s survivorship was much lower than <u>A</u>. <u>campestris</u>'s (.057 and .198, respectively). Comparing fall and spring-summer germinating plants, the fall individuals had lower survivorship rates for both species with a reduction of 7 percent of <u>A</u>. <u>campestris</u> and 63 percent for <u>M</u>. <u>punctata</u>.

³²Survivorship was calculated by dividing the number alive at the end of a given period by the number which were alive at the beginning of the period. The overwintering period was from November to April. Periods for age classes are one year (April to April) unless otherwise noted. See Figures 10-12 and Table 9 for further information. Survivorship (probability) indicates the chances a plant has of surviving the given period.

Comparing the survivorship of spring-summer germinating plants for the three species, <u>S</u>. <u>caesia</u> had the highest survivorship in 1978 followed by <u>A</u>. <u>campestris</u> (.26 and .21, respectively). In 1977, the pattern was just the reverse (.29 for <u>A</u>. <u>campestris</u> and .23 for <u>S</u>. <u>caesia</u>). <u>M</u>. <u>punctata</u> had the lowest survivorship for both years (.16 for both 1977 and 1978). <u>M</u>. <u>punctata</u>'s difference in survivorship for 1977 and 1978 was only 2.5 percent whereas for the other two the differential was much greater (11.54 percent for <u>S</u>. <u>caesia</u>, 26.9 percent for A. campestris).

The cause of death for the first year plants was not examined in depth. However, it is felt that for the two earlier successional species desiccation was a major cause whereas for the forest species predation was important. In early successional species, a plant would usually become brown and dried before dying or disappearing. <u>S. caesia</u> plants would look healthy or have several leaves missing on one sampling date, and on the next would be completely gone.

A juvenile is a plant which is older than one year but has not flowered. Thus, a first year juvenile is a plant in its second year. Again, the distinction is morphological.

A first year <u>M</u>. <u>punctata</u> plant can go into this juvenile phase or change directly into the reproductive (adult) phase in its second year (see Figure 11). The probability³³ of entering the juvenile phase was

³³This is a transition probability and not a survivorship probability. It indicates the probability of first year plants, alive at the end of the winter, becoming juveniles in the next year. If a plant became a juvenile, it was placed in the first year juvenile category as

.44 for 1977 and .80 for 1978. The dry condition of 1977 likely made it difficult for first year plants to store enough resources to allow them to flower in their second year. This is evidenced by the lower growth of 1977 first year plants as compared to those of 1978. The 1977 plants were 3.3 cm high with 4 cm² rosettes whereas the 1978 plants were 7.8 cm high with 36 cm² rosettes. Additionally, a 1978 first year plant reproduced.³⁴ Such plasticity of flowering time has been observed for Dipsacus fullonum (Werner, 1975).

The <u>M. punctata</u> juvenile looks much like the adult plant. It has a basal rosette which will eventually grow into several bolts; however, these bolts do not produce flowers. During the course of the summer, most of the bolt leaves are lost. In mid-September, a basal rosette will begin forming, and by winter will average 8 cm in diameter. The bolts by now have dried up and many have been blown away. The plant overwinters as a rosette.

Transition³⁵ of first year plants to the juvenile phase is 100 percent for <u>A</u>. <u>campestris</u> and <u>S</u>. <u>caesia</u> since both wait at least one more year before flowering (Figures 10 and 12). <u>A</u>. <u>campestris</u> during

³⁵See footnote 33 for explanation of a transition probability.

of April, since all survivorship was calculated on a yearly basis, running from April 1 to April. Plants which flowered in the next year were labeled adults in April. If a plant died before its stage class could be determined, it was called a juvenile.

³⁴Preliminary data from 1979 indicate that the transition probabilities from first year to juvenile was .43. This further supports the hypothesis that dry conditions kept plants from flowering in their second year.
this period remains a rosette; however, the plant becomes much more bushy in appearance. The caudex becomes very woody and by the end of the year these plants average 11.8 cm in size and will overwinter as rosettes.

First year juveniles of <u>S</u>. <u>caesia</u> remain as rosettes closely appressed to the ground. However, more leaves are added and there is growth in diameter to 4.7 cm. At the end of the year, many of the first year plants appeared to add new shoots indicating rhizome growth. These plants also overwinter as rosettes.

The survivorship probabilities (Table 9) for first year juveniles of <u>S</u>. <u>caesia</u> were highest (.69). Those for <u>A</u>. <u>campestris</u> and <u>M</u>. <u>punctata</u> juveniles were lower, but similar in size (.46 and .50, respectively). The 1977 figures for <u>A</u>. <u>campestris</u> and <u>M</u>. <u>punctata</u> juveniles were very different from 1978 levels (.90 and .25, respectively). No S. <u>caesia</u> juveniles were marked in 1977.

<u>A. campestris</u> and <u>M. punctata</u> first year juveniles can either remain as a juvenile in the next year or flower. The probability³⁶ of remaining a juvenile was much higher for <u>A. campestris</u> and is almost two times that of <u>M. punctata</u> (.63 versus .37). Plants remaining as juveniles appear as described earlier.

The period of study was not long enough to allow direct estimation of probabilities of remaining a juvenile beyond a second year. However, some inferences can be made from marked juveniles of unknown age,

 36 See footnote 33 for definition of transition probability.

because these plants were juveniles for at least the period they were marked. For some, this was as long as three years. In general, the probability of remaining a juvenile becomes less as the plants become older (Table 11).

Unlike the other two species, there was not an obvious morphologically distinct middle phase for <u>S</u>. <u>caesia</u>. There are plants which look like adults, but do not flower. Because adults can flower one year and not the next, it is impossible to tell whether these plants are older juveniles or nonreproducing adults. Preliminary data from 1979 indicate that these plants wait at least until their fourth year of life before reproduction begins. However, during the second year of the juvenile phase, growth of an underground rhizome begins. By the end of this period the plants have grown several centimeters in height and are no longer closely appressed to the ground.

In <u>A</u>. <u>campestris</u> and <u>M</u>. <u>punctata</u>, the survivorship of juveniles beyond the second year was inferred from juveniles of unknown age. For the 'overall' category of Table 9 the survivorship of juveniles of all ages was included. Both species had similar survivorship for both years in this category.

The first year <u>A</u>. <u>campestris</u> adult will bolt in late spring and be in full flower by late August. In <u>M</u>. <u>punctata</u> flowers are produced by mid-summer. <u>S</u>. <u>caesia</u> adults flower in mid-September.

<u>Artemisia</u> campestris	<u>Monarda</u> punctata	<u>Solidago</u> <u>caesia</u>
0.0	0.01	0.0
0.0	.38 ²	0.0
.37	ND ⁴	0.0
.32 ³	.63 ⁵	ND
.754	ND	ND
	<u>Artemisia</u> <u>campestris</u> 0.0 0.0 .37 .32 ³ .75 ⁴	$\begin{array}{c c} \underline{\text{Artemisia}} & \underline{\text{Monarda}} \\ \hline \text{punctata} \\ \hline 0.0 & 0.0^1 \\ \hline 0.0 & .38^2 \\ \hline .37 & \text{ND}^4 \\ \hline .32^3 & .63^5 \\ \hline .75^4 & \text{ND} \end{array}$

TABLE 11. Proportion of plants reproducing for the first time, by age class.

¹On rare occasions a first year plant can reproduce. In three years only one was found to do this (1978). Growing conditions were excellent that year. The probability of this happening in a good year is .0019.

²This is the average of 1977 and 1978 probabilities (.56 and .20, respectively).

³This is the average of 1977 and 1978 probabilities (.43 and .20, respectively).

⁴No data.

⁵Data from juveniles of unknown age which had been marked for at least the period indicated.

The two earlier successional species (Table 9) had the lowest 'overall'³⁷ adult survivorship. For 1978, <u>A. campestris</u> was the lowest (.03) because most adults reproduced once and died during the following winter. The survivorship to fruit dispersal was .51 for both 1977 and 1978. In each year **a** very small fraction of the adults (.01) live to reproduce again. These plants are usually very large and robust, and will die during the winter after fruiting the second time.

<u>M. punctata</u> is iteroparous, thus adult survivorship is much higher than for <u>A. campestris</u>. Survivorship levels were high for first year adults both in 1977 and 1978 (1.0 and .88, respectively). Survivorship declines with age because survivorship of the second year adult was .70 and 'overall' adult survivorship was .43 for 1978. <u>M. punctata's</u> 1977 'overall' adult survivorship was much higher than 1978 and was the highest of the three species. During the very dry fall of 1976 many adults died and the winter survivorship was only .30. Likely marginal and older individuals which would have died in the following year died when exposed to the unusually dry conditions. Thus, the adult population of 1977 contained the heartiest and youngest individuals resulting in high survivorship. It is suspected that the 1978 figure better approximates the usual level of survivorship.³⁸

³⁷Calculated by combining data from adults of unknown age with those of known age.

³⁸Preliminary results for 1979 indicate an overall adult survivorship of .32. This is low because there were almost no first year adult plants due to low germination in 1977 and low survivorship for those plants which did germinate in 1977.

S. caesia had the highest adult survivorship in 1978 (.81) and was second highest in 1977 at .75. Most mortality occurred during the winter to plants badly damaged by insects during the previous growing season. Unlike the other species, S. caesia can flower one year and in the next year remain nonreproductive (Figure 12). In 1977 and 1978, the probability that a plant would flower in two consecutive years was .31 and .37, respectively. It is not known if nonreproducing adults can reproduce again, because none of these individuals ever successfully bore fruit. In 1978, 3 percent (0 in 1977) started to reproduce again, but aborted after flower development. These plants were not under physiological stress because the survivorship for nonreproducing adults was higher than reproducing ones (Table 9). It is suspected that these individuals may reproduce again because the percentage of flowering adults has declined from 60 percent in 1976 to 12 percent in 1978. No juveniles became adults during this period. To attain the high 1976 flowering level, new adults and nonreproductive adults must flower. A seven-year flowering cycle has been observed for Frasera speciosa (Taylor, 0., pers. comm.), and such a pattern may be part of the <u>S</u>. <u>caesia</u> cycle.

Overall Comparison of Life Stages and Life Expectancies

Table 12 contains a summary of the life stages for each species. The top portion gives the probability of a plant in a given life stage living for one year (1978 data). The bottom portion shows expected length of life for a plant in each stage, calculated using a method outlined by Pielou (1977).

Age	<u>Artemisia</u> campestris	<u>Monarda</u> punctata	<u>Solidago</u> <u>caesia</u>		
Probability of Surviving to Next Year					
First year	.21	.16	.26		
Juvenile (first year)	.47	.50	.5585		
Juvenile (overall)	.38	.42	ND ²		
Adult (overall)	.03	.43	.81		
Average Expected Length of Life					
First year	3.0 mo.	2.3 mo.	3.5 mo.		
Juvenile	8.9 mo.	6.9 mo.	ND ²		
Adult	6.3 mo.	21.8 mo.	6.9 yr. ³		
Overall	4.2 mo.	4.5 mo.	1.8 yr.		
Reproductive adult - length of time re- maining reproductive	6.3 mo.	21.8 mo.	15.1 mo.		

TABLE 12. Comparison of overall survivorship and life length for the life stages of <u>A</u>. <u>campestris</u>, <u>M</u>. <u>punctata</u> and <u>S</u>. <u>caesia</u>.

¹Takes into account the probability of changing to the next life stage.

²No data.

³Nonflowering clones were included because of their adult morphology.

For <u>M</u>. <u>punctata</u> and <u>S</u>. <u>caesia</u>, the most risky period is the first year (0.16 and 0.26, respectively). The very short life expectancy for these stages (bottom, Table 12) reflects this. The first year survivorship of <u>A</u>. <u>campestris</u> is also low (0.21), but survivorship of the adult is much lower (0.03). However, most adult death occurs in the winter after fruit production. During the growing season, seedling survivorship is much lower (0.24) than for the adult (0.51). Thus, the adults are better able to withstand the rigors of the environment than the seedlings are until the adults begin reproduction.

The adult survivorship for <u>S</u>. <u>caesia</u> is very high (0.81), indicating that once the early stages have passed and the plant is established, conditions are such to allow a high survival. As indicated earlier, most death has a biotic source. This is not true for <u>M</u>. <u>punctata</u>. Though its survivorship is high enough to allow iteroparity, abiotic conditions are harsh enough to keep survivorship levels usually far below that of <u>S</u>. <u>caesia</u>. Differences in life expectancy reflect this. However, it is of interest that though the <u>S</u>. <u>caesia</u> adult lives longest, it remains reproductive for an even shorter period than <u>M</u>. <u>punctata</u> (15.07 mo. versus 21.84 mo., respectively). The ability to become nonreproductive causes this.

The first year juvenile, is the least risky stage for <u>A</u>. <u>campestris</u> and <u>M</u>. <u>punctata</u> (0.47 and 0.50, respectively). It is this stage which has the highest life expectancy for <u>A</u>. <u>campestris</u>. The smaller length of time in the juvenile stage for <u>M</u>. <u>punctata</u> individuals reflects the higher tendency for juveniles to begin reproduction sconer than <u>A</u>. <u>campestris</u> juveniles.

A range was given for <u>S</u>. <u>caesia</u> juveniles because overwintering mortality could not be estimated from previous data. Since the seedling stage has the lowest survivorship, this overwintering mortality was used for the minimum; a zero mortality was assumed for the maximum. The real probability is probably somewhere between because juvenile overwintering mortality is less than seedling mortality in the other species.

The overall expected lifetime for each of the species is enlightening. Though <u>M</u>. <u>punctata</u> and <u>A</u>. <u>campestris</u> individuals have similar expected life spans, the adult of <u>M</u>. <u>punctata</u> lives two times longer. The difference is in the seedling stage; a death here has a greater effect on overall life length than a death in a later stage. Though the difference in seedling mortality is 25 percent, it is enough to make up for the semelparity of <u>A</u>. <u>campestris</u>, resulting in the overall life expectancy of both species being the same.

<u>S. caesia</u> lives the longest, almost two years. The shortness is surprising given the expected life length of the adult. Again, the reason is the higher mortality rate in the early stages.

Survivorship Curves

Figure 14 combines the life histories of the three species into survivorship curves. The curves were constructed based on 1000 hypothetical seedlings which were subjected to the survivorship and transition probabilities used to construct Figures 10-12. As much as possible, mortality by age class was utilized. First year adult

Figure 14.	Survivorship curves for <u>A</u> . <u>campestris</u> ,		
	<u>M. punctata, and S. caesia</u> . The abscissa		
	is time (Ap is April, 0 is October), and		
	the ordinate is the number of survivors		
	in an initial cohort of 1,000 individuals.		



survivorship was used for first year adults. For the next three years overall mortality figures were used. Beyond this, the mortality for adults which were at least three years of age was used.

Survivorship curves reflect what was said in the previous section. The steep decline in the early portions of the curves reflects the high seedling mortality. If seed mortality had been included the decline would have been even steeper. Beyond this, the curves level off and resemble straight lines, indicating the higher survivorship in later stages. The relative steepness of the curves indicates the relative survivorships of the three species. <u>A. campestris</u>'s curve is above <u>M. punctata</u> for the first two years but then drops below indicating <u>A. campestris</u>'s semelparity. Though <u>A. campestris</u> is semelparous, its curve does not drop off sharply after the seedling stage because it takes at least three years before reproduction occurs. For some individuals this period is even longer. <u>S. caesia</u>'s curve is the most shallowly sloped of the three curves because of this species' lower adult mortality.

The survivorship curves resemble Deevey Type 11 curves. Such curves have been observed for meadow herbs (Linkola, 1955 reworked by Harper, 1977) and for early old field species (Yoder et al., 1963 reworked by Harper, 1977). However, the linearity of the later portion of the curves in this study results because very old adults were assumed to have a constant mortality rate. This would have had the greatest effect on <u>S. caesia</u> if the survivorship of these older individuals was much lower than the average. The curve would then more resemble the Deevey Type 1

which is more often associated with later successional species. However, the mortality of adult plants still alive at the end of the study was not higher than adults alive at the beginning.

Finite and Instantaneous Growth Rates

Table 13 contains values for finite and instantaneous rates of increase for <u>A</u>. <u>campestris</u>, <u>M</u>. <u>punctata</u> and <u>S</u>. <u>caesia</u>. These were calculated using the methods of Hubble and Werner (1979).³⁹ As indicated previously, the bottom diagrams of Figures 10-13 were used. An advantage of this method is that a stable age distribution is not assumed as is the case in other estimation methods. Given the variability of the environment in the early stages of succession, it was felt this assumption should not be made.

The rates of increase differed greatly from 1977 to 1978 (Table 13). All 1977 figures are lower, reflecting the dry conditions of this year and the preceding fall. The rates for <u>A</u>. <u>campestris</u> and <u>M</u>. <u>punctata</u> species are startlingly low; however, very low germination rates account for this. For <u>A</u>. <u>campestris</u> the 1977 probability of germination was only 22 percent of rates for 1978, and that of <u>M</u>. <u>punctata</u> was less than one percent of 1978 levels. The effect was as if the population did not reproduce in 1977, because seeds either died or went into dormancy. Adults for both species had a higher survivorship in 1977 than in 1978, but this did not balance the large drop in germination levels.

³⁹After rearranging the polynomial, the Complex Method of Box (1965) was used to solve for the finite rate of increase.

	Finite ¹ rate	l nstantaneous rate
<u>Artemisia</u> <u>campestris</u>		
1977	0,404	-0.292
1978	0,918	-0,086
<u>Monarda</u> punctata		
1977	0,0003	-8,251
1978	1,463	0.380
<u>Solidago</u> <u>caesia</u>		
1977 ²	0, 909	-0, 095
1978	1.057	0, 055

TABLE 13. Finite and instantaneous rates of increase forA. campestris, M. punctata, and S. caesia.

¹These are calculated on a yearly basis.

²To calculate the rates for both years, it was assumed that at four years of age all plants flower. This allows an estimate of the maximum rates possible. Table 14 contains estimates with reproduction first occurring at a later age. The 1977 germination level for forest species was 68 percent of 1978 levels, thus the difference between the 1977 and 1978 growth rates is much less than for the other two species.

In 1978, <u>M. punctata</u> had the highest rate of increase ($\lambda = 1.463$, r = 0.3804) followed by <u>S</u>. <u>caesia</u> ($\lambda = 1.057$, r = 0.055). <u>A</u>. <u>campestris</u> was the lowest and again did not replace itself ($\lambda = 0.918$, r = -0.086). Though germination rates were very good for this species in 1978, the number of seeds produced per individual dropped sharply and were only one third of the 1977 numbers (2252 in 1977, 806 in 1978). Only one third as many seeds were produced per inflorescence.

Rates of increase were recalculated under different conditions for each of the species to examine different aspects of the life cycles (Table 14). If <u>A</u>. <u>campestris</u> had maintained 1977 levels of seed production, it could have more than replaced itself in 1978 (category 'a', number 1, Table 14). The increase from 806 to 2253 seeds represented a 29 percent change from 1978 levels. If seed production is at slack <u>A</u>. <u>campestris</u> levels (3353 seeds), rates of increase still do not equal 1978 <u>M</u>. <u>punctata</u> rates. A 67 percent increase in seed numbers is still not enough to compensate for <u>A</u>. <u>campestris</u>'s delayed reproduction and semelparity.

By switching to a strict biennial cycle (category 'b', Table 14), <u>A. campestris</u> can more than replace itself by producing only 806 seeds and can more than equal <u>M. punctata</u>'s 1978 rate of increase by producing a seed set like that of 1977. However, given the low nutrient

Category		Finite rate	lnstan- taneous rate	Percent change from 1978
Arten	nisia <u>campestris</u>			
Α.	Different levels of reproduction			
	1. 1977 reproduction 1978 mortality	1,180	0,166	+28.56
	2. Slack reproduction 1978 mortality	1,385	0.3256	+50,86
Β.	Two year biennial cycle			
	l. 1978 reproduction 1978 mortality	1,178	0.163	+28,27
	2. 1977 reproduction 1978 mortality	2.335	0.848	+154.37
	3. Slack reproduction 1978 mortality	3.158	1,150	+243.98
Monar	rda punctata			
Α.	<u>A. campestris</u> adult mortality (semelparity) -for rest-1978 mortality and reproduction	1,249	0.222	-14,62
Solic	lago <u>caesia</u>			
Α.	1978 reproduction and mortality; all flower at 6 yrs.	1,027	0.0262	-2,84

TABLE	14.	Hypothetical rates of increase for species studied
		demographically.

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levels of the foredune and the energy requirement for reproduction, the biennial cycle is unlikely for this species.

<u>M. punctata</u>'s rates of increase were recalculated under the assumption of semelparity. Survivorship and transition rates for first year and juvenile stages remained the same. Rates of increase declined by 15 percent (relative to 1978 levels); however, the population was still able to replace itself. Rates were not reduced to <u>A. campestris</u> levels (1.249 and 1.181 for <u>M. punctata</u> and <u>A. campestris</u>, respectively) because <u>M. punctata</u> begins reproduction a year earlier.

The recalculations for <u>S</u>. <u>caesia</u> (Table 14) illustrate the effects of waiting an additional amount of time before first reproduction. Even with waiting until the sixth year, the population is still increasing, reflecting higher survivorship rates for most age classes. The species probably could not wait beyond the sixth year because as 1977 and 1978 rates of increase indicate, seedling survivorship can fluctuate. Thus, to balance in the long run, rates of increase would have to be above replacement part of the time.

Seed Characteristics

Table 15 summarizes seed characteristics for <u>A</u>. <u>campestris</u>, <u>M</u>. <u>punctata</u>, and <u>S</u>. <u>caesia</u>. For seed weight, the pattern is the same as that observed for the study areas as a whole in that the slack species' weight is significantly less than both that of the foredune species and that of the forest species. Seeds of the foredune species have the greatest weight; however, unlike the overall case, seeds of the foredune

Category	<u>Artemisia</u> campestris	<u>Monarda</u> punctata	<u>Solidago</u> <u>caesia</u>
Seed weight (mg)	.336(.0198)	,189(,0122)	.234(.0103)
Specific caloric content (kcal/g)	5.65(.0451) ²	5.38(.196)	6.933(.0026)
Energy per seed (kcal)	1,897(,119)	1.021(.057)	3 1,624(,0714)
Seed number			
per plant			
1977 1978	806(243,9)	2120(269,4) 2363(433,6)	190(26,99) 210(146,7)
Adjusted seed number			
1977	114.61	109,23	83,08
1978	41,01	121.76	92.01
Average life time			
seed production			
1977	1022,86	2670.14	266,29
1978	366,50	3039.30	294, 32
Average	694.39	2823.17	278,90
Reproductive effort (%) (kilocalories)			
AAR	29.66	16,76	6,36
TAR	26.23	13.87	4.38

TABLE 15. Summary of seed characteristics and reproductive effort for <u>A</u>. <u>campestris</u>, <u>M</u>. <u>punctata</u>, and <u>S</u>. <u>caesia</u>.

Unless footnoted all comparisons between species are significant at p > 0.05. Only numbers with standard errors were compared statistically; standard errors are parenthesized.

²The comparison between foredune and slack is not significant.

 3 The comparison between foredune and forest is not significant.

species are significantly larger. This is partly because the <u>Solidago</u> has the smallest (non-parasitic) seed of the forest species examined. If another species had been chosen from the forest, this species could have had the largest seed; however, the slack species would still have had the lowest weight.

The forest species has a significantly greater specific caloric content (P<0.05) than that of the two earlier successional species. 40 The slack and foredune species were not significantly different. 40 This does not follow the overall pattern observed earlier for the three study sites. This is explained by the fact that only for forest species is there a negative correlation between seed size and specific caloric content. Because <u>S</u>. <u>caesia</u> has the smallest seeds of the forest, it has one of the highest specific caloric contents and thus deviates greatly from the average for the area as a whole. If a large seeded species had been studied instead of <u>S</u>. <u>caesia</u>, the seed size pattern would not have been observed but the pattern for specific caloric content would have.

The relationship among the species for energy per seed is similar to that observed for seed size. However, because of the larger specific caloric content for <u>S</u>. <u>caesia</u>, there is no significant difference between <u>A</u>. <u>campestris</u> and <u>S</u>. <u>caesia</u> in seed energy content.

In 1977, <u>A</u>. <u>campestris</u> had the highest seed number followed by <u>M</u>. <u>punctata</u> and then by <u>S</u>. <u>caesia</u>. This pattern still applies when

40The Student t-test was used.

numbers are adjusted by plant size (category 5). This does not reflect the overall pattern for the areas, but does reflect <u>A</u>. <u>campestris</u>'s semelparity. For 1978, <u>A</u>. <u>campestris</u>'s seed numbers were greatly decreased, and, thus, dropped below those of <u>M</u>. <u>punctata</u>. The seed number for both <u>S</u>. <u>caesia</u> and <u>M</u>. <u>punctata</u> increased slightly in 1978.

The expected life time seed production for an adult plant was calculated by using the following summation:

$$\sum_{i=1}^{n} x_{ij} N_{j}$$

x, - probability a plant lives to reproduce in year i
for species j.

 \boldsymbol{N}_{i} - number of seeds produced per year for species j.

i - the number of adult years, 1 to n.

It was assumed that the plant had reached the first year of adulthood. Looked at this way, the slack adult has produced more than two times more seeds in its lifetime than an <u>A</u>. <u>campestris</u> adult (1977 numbers). For 1978 the difference is even higher. However, <u>A</u>. <u>campestris</u> compensates for this by having higher seedling survivorship than <u>M</u>. <u>punctata</u>. <u>A</u>. <u>campestris</u> can more than replace itself in a good year if seed production is at 1977 levels, but it will likely never reach the density on the foredunes which <u>M</u>. <u>punctata</u> achieves in the slack area. The lifetime seed production of the <u>S</u>. <u>caesia</u> adult is much lower than the other two species. Though the adult plant has a long life, reproduction is restricted because in some years the plant may not reproduce. If at some time plants can return to flowering, the number of seeds produced will increase, but for the calculation it was assumed that this did not occur. Even if an adult is unable to resume flowering, this population, as its rates of increase indicate, is more than replacing itself due to the higher survivorship of all life stages.

The last category of Table 15 shows reproductive effort percentages. <u>A. campestris</u> is highest for both the AAR and TAR percentages. It is followed by <u>M. punctata</u> and then <u>S. caesia</u>. This pattern was examined more closely for these species in the chapter on reproductive effort.

Discussion

The results from the demographic studies parallel the findings of the seed characteristics study. The species exhibiting the most 'r' selected traits (shortest generation time, highest rates of increase, smallest seeds, and largest life time seed production) is the slack species, <u>M. punctata</u>, rather than <u>A. campestris</u> which appears earlier in the successional sere. As expected, <u>S. caesia</u> exhibits more 'K' selected traits than the others (largest generation time, lowest lifetime seed production, very high adult survivorship). But even this species exhibits unexpected characteristics such as a seed size smaller and a rate of increase higher than <u>A. campestris</u>'s. However, as was the case with overall seed characteristics, these seeming contraditions may be explained by examining the selective factors likely acting on each of the species.

Of the three species, <u>S</u>. <u>caesia</u> is likely the least affected by changes in environmental factors. This was well demonstrated by the dry conditions of the 1977 growing season. The germination levels of <u>S</u>. <u>caesia</u> dropped only 30 percent whereas those of <u>A</u>. <u>campestris</u> and <u>M</u>. <u>punctata</u> dropped 77 percent and 90 percent, respectively. <u>S</u>. <u>caesia</u> adults showed less signs of water stress than those of the other species, as well.

Biotic causes of death appear to be the most important for <u>S</u>. <u>caesia</u>. Seedlings often showed signs of predation before they died. Frequently, the seedling would completely disappear, whereas <u>A</u>. <u>campestris</u> and <u>M</u>. <u>punctata</u> seedlings would show signs of desiccation before dying or disappearing. Most of the <u>S</u>. <u>caesia</u> adults which died were those which were highly insect damaged in the previous growing season. Competition, though not experimentally demonstrated, likely plays a role as well. Roots, in the dune forest, are densely matted in the thin upper soil layer. Though the forest soil is the most mature of the successional sere, it is still very low in nutrients. Thus, resources are likely limited for the species found there.

<u>S</u>. <u>caesia</u> had the highest germination levels of the three species studied. This is understandable since <u>S</u>. <u>caesia</u> seeds have a more continuously moist environment in which to germinate than do <u>M</u>. <u>punctata</u> and <u>A</u>. <u>campestris</u> seeds. In some years, germination conditions are so

frequently unfavorable in the slack and foredune areas that almost no germination occurs there.

Seedling survivorship levels are likely higher in <u>S</u>. <u>caesia</u> than in <u>M</u>. <u>punctata</u> because the slack species has a small seed and germinates in a xeric environment. The small food reserves make it difficult for a seedling to develop the root system necessary to allow survivorship through low moisture periods. Thus, mortality is high for this stage. However, a small seed size likely contributes to mortality in <u>S</u>. <u>caesia</u> seedlings as well.

<u>S</u>. <u>caesia</u> has one of the smallest (nonparasitic) seeds found in the forest herb flora. Thus, competitive factors may contribute to mortality among these seedlings, and may exclude <u>S</u>. <u>caesia</u> from certain areas of the forest floor. The most frequent germination sites and areas of highest seedling survivorship for this species were places of sparse vegetation and low litter cover. Seed predation likely contributes to this pattern as well because the study of overwintering viability demonstrated that seed predation by insects was higher in leaf litter than in sand.

A small seed size may also place <u>S</u>. <u>caesia</u> seedlings at a disadvantage when fed upon by predators. Without the resources to quickly establish a root rhizome system, any loss of leaf material would be critical in the low light levels of the forest. This may explain why seedlings with predator damage frequently died.

With these disadvantages of a small seed, the question arises as to why <u>S</u>. <u>caesia</u>'s seed is not larger. The answer may well lie in this

species' dispersal mechanism. <u>S</u>. <u>caesia</u> is wind dispersed, as are all other members of the genus <u>Solidago</u>. Wind levels are low in the forest. Thus, seed size must be small to assure that seeds are carried over a large enough area to secure the microsites necessary for the species to reproduce itself. There is evidence, however, that there may have been selection for a larger seed in this species since <u>S</u>. <u>caesia</u>'s seed is among the largest in the genus <u>Solidago</u> (Werner and Platt, 1976).

The seed numbers for <u>S</u>. <u>caesia</u> are among the highest for forest herbs. This probably helps to balance seedling mortality. It also increases the probability that enough seeds will reach favorable microsites to allow survivorship of the species in the forest.

The root rhizome system is likely very important to the survivorship of the <u>S</u>. <u>caesia</u> adult. An <u>S</u>. <u>caesia</u> plant does not reproduce until it is at least in its fourth year. During this period the root rhizome system develops as observations of first year and juvenile plants show. The root rhizome development is probably slow due to the light constraints of the forest floor. As the system develops, the likelihood of plant survivorship increases, and once adulthood is reached, survivorship is 80 percent. The root rhizome system helps the plant establish its place in the forest floor by aiding in competition for limited resources. In addition, if the plant is preyed upon, the root rhizome system is a good reserve source which can make up for the photosynthetic loss. Several of the marked <u>S</u>. <u>caesia</u> plants had most of their above-ground biomass eaten, but were able to survive the following growing season.

The reproductive effort of this species is also low relative to the other species studied. Most of the resources available go to vegetative functions. This supports the prediction of Gadgil and Schaffer (1975) that in environments where mortality of adults tends to be low, energy expenditure for survival of the adult should be high in comparison with energy expenditure for reproduction. There is some indication, as well, that reproduction may slightly reduce the survivorship of adults since mortality was higher for reproductive clones than it was for nonreproductive ones.

Rates of increase indicate that as long as germination levels and adult survivorship remain like those of 1978, <u>S</u>. <u>caesia</u> can maintain its population within the dune forest. This is mostly due to the high levels of adult survivorship, since reproductive allocation is low and first reproduction does not begin before the fourth year. This species is among the most prevalent herbs of the forest floor as the importance values of Table Al indicate.

Life history characteristics of <u>A</u>. <u>campestris</u> reflect the strong abiotic element of the dune system. Of the three species studied demographically, its seeds were the largest. This combined with mucilagenous fruit probably accounts for a higher seedling survivorship than <u>M</u>. <u>punctata</u>'s and levels equal to <u>S</u>. <u>caesia</u>'s. The <u>A</u>. <u>campestris</u> juvenile has the highest chances of survivorship of any life stage of this species. In this stage, the plant has a well developed root system and can withstand the xeric dune conditions. In addition, the resource drain of reproduction is not present.

It takes at least three years before an A. campestris individual will reproduce. For many plants this period is even longer. This is contrary to the characteristics of early successional species predicted by the 'r' and 'K' model. The delay in reproduction likely allows storage of nutrients needed for the seemingly suicidal reproduction of this semelparous species. When reproducing, 30 percent of the A. campestris plant's current year's net energy budget is devoted to reproductive structures. Additionally, tall (up to 100 cm) bolts serving both photosynthetic and reproductive functions also appear to be necessary. Thus, before the plant produces seeds, many of the vegetative structures necessary to assure survival of the adult through reproduction must be already present. This is supported by the fact that most adults died in the winter after reproduction occurred rather than before it. Accumulation of the resources needed is likely slow for this species due to the low nutrient soil and xeric summer conditions of the foredune. The storage of a requisite amount of resources has been observed for other semelparous species: Dipsacus fullonem (Werner, 1975) for species of Agave (Schaffer and Gadgil, 1975) and Scenecio jacobaea in dune systems (Van der Meijen and Van der Vaals-Kooi, 1979). It has also been discussed by Harper (1977).

The examination of alternate life histories indicated that <u>A</u>. <u>campestris's</u> level of increase could be much higher if it were an obligate biennial. However, Mertz (1971a, b) and Van der Meijden and Van der Vaals-Kooi (1979) have suggested that prolonged age at first reproduction is advantageous in declining populations since extinction

can be avoided or postponed. It increases the probability that good conditions will be encountered again and that renewed growth can occur. This is particularly true if the environment is variable and the survivorship of older nonreproductive age classes is high. In <u>A</u>. <u>campestris</u> rates of increase appear to fluctuate widely from one year to the next, and in some instances conditions can become so stressful that greatly lowered germination levels are so low that rates of increase are negative. Such years can be followed by favorable years as was the case in 1977 and 1978. The detrimental effects of an unfavorable year can be minimized if many individuals are in less vulnerable life stages (e.g. juvenile).

The very low levels of seed production in 1978 kept the foredune <u>Artemisia</u> population from replacing itself as the examination of alternative life histories indicated. The reason for the sharp decline in seed numbers between 1977 and 1978 is unknown; however, pollination difficulties due to low density may be a possibility since the foredune population was very small in 1978. The slack <u>A. campestris</u> population maintained a much higher density level and its seed production declined only slightly in 1978.

The life history of <u>M</u>. <u>punctata</u> also reflects the effects of abiotic factors. Harsh conditions can delay time of first reproduction as the comparison of the transition probabilities for juveniles in 1977 and 1978 indicated. However, if conditions are favorable, an individual can reproduce in a period shorter than <u>A</u>. <u>campestris</u>. Less stressful abiotic factors in the slack may contribute to M. punctata's ability

to flower sooner than <u>A</u>. <u>campestris</u>. However, <u>A</u>. <u>campestris</u> is present in the slack and appears to delay reproduction there as well (personal observation).⁴¹ The morphology and vegetative phenology of <u>M</u>. <u>punctata</u> are perhaps the keys. Bolts are present in <u>M</u>. <u>punctata</u> both in reproductive and nonreproductive plants. Those of the reproductive plants are taller and more robust than those of nonreproducing individuals; however, they reach neither the size (31 cm versus 54 cm) nor the woodiness characteristic of <u>A</u>. <u>campestris</u>. There is also little difference in mortality between juveniles and adults in <u>M</u>. <u>punctata</u>. Thus, <u>A</u>. <u>campestris</u> may have a resource drain much like that hypothesized for <u>Agave species</u> (Schaffer and Gadgil, 1975).

In <u>M. punctata</u>, seed number is high and reaches levels similar to the foredune population of <u>A. campestris</u>. This, as well as higher adult survivorship, account for <u>Monarda's higher reproductive rates during</u> good years. However, such rates may be needed to balance unfavorable years, since seedlings are highly vulnerable and seeds do not have mucilage which allows germination under low moisture levels as suggested by the drastic drop in germination levels as well as in rates of increase for 1977. Thus, this species not only had the highest rate of increase for the three species in the favorable year, 1978, but the lowest rate of increase in the very dry year, 1977, as well.

<u>M. punctata's lower allocation to reproduction likely contributes</u> to higher adult survivorship than found in <u>A. campestris</u>. However, the

⁴¹Several <u>A</u>. <u>campestris</u> seedlings and juveniles from the slack area were marked and followed.

more highly stressful abiotic conditions likely keep this survivorship for <u>Monarda</u> well below that of <u>S</u>. <u>caesia</u>.

M. punctata allocates its vegetative resources very efficiently. When fruit is developing, much of the energy stored in leaves is transferred and most leaves are lost. (Energy content drops from 4.55 k.cal./ g for green leaves to 3.93 k.cal./g in dead ones). This occurs during periods of greatest moisture stress (late July and August). By ridding itself of leaves, M. punctata individuals can reduce transporation levels. Some productivity is lost by this process, but this portion of the growing season is probably of lesser importance for growth since processes which reduce water loss also inhibit photosynthesis. Stomata close and, thus, stop the flow of carbon dioxide as well as water (Kramer, 1969). M. punctata forms a basal rosette in the fall, when moisture conditions are again favorable for growth. Overwintering in this form, photosynthesis can begin immediately in the spring when conditions become favorable again. Thus, this species grows during the most favorable periods of the growing season, and then transfers some of the accumulated energy to fruit development during the worst periods.

<u>A. campestris</u> does not show such an efficient vegetation phenology, and this may further contribute to its semelparity. This species loses some leaves during July and August, but most loss occurs during the fall when fruit is developing. Thus, the adult cannot take full advantage of the good growing conditions of this period. In addition, many leaves are present during conditions of greatest moisture stress, and tall flowering bolts place leaves into areas of higher wind speeds

because wind speeds increase with distance from the ground (Ranwell, 1972; Murphy, P. G., unpublished data). Thus, some adults die before fruit is fully developed. This is not as true for <u>M. punctata</u> (0.19 for <u>A. campestris</u> versus 0.08 for <u>M. punctata</u>).

<u>M. punctata</u>, with its high rates of increase during favorable periods and its efficient vegetative phenology, would appear better adapted to the dune environment than <u>A. campestris</u>. However, as the demographic study has shown, the seed and seedling stages of this slack species are the most vulnerable portions of its life cycle. The harsher conditions found on the foredune combined with the smaller seed size of this species likely explain why <u>M. punctata</u> is rarely found close to the lake.

CHAPTER V

SUMMARY

1. Findings from the reproductive effort studies support models based on 'r' and 'K' selection since reproductive effort declined with successional age. High allocation to reproduction probably helps balance the mortality levels for all age classes found in the early successional species studied demographically. This would help to offset the periodically very dry years like that of 1976-77 when the finite rates of increase for <u>A</u>. <u>campestris</u> and <u>M</u>. <u>punctata</u> can be less than one. Reproductive effort was also high for monocarpic species. This was expected since these species have only one chance to reproduce and must devote proportionately greater resources to accomplish what the perennial has several years to do (Williams, 1966; Gadgil and Bossert, 1970; Hart, 1977).

2. Species from the earliest successional stage tend to have a small number of large seeds. Xeric and low nutrient factors have probably played a role in selecting these characteristics. Seedlings must establish in the face of scarce resources just like in competitive situations. In low nutrient sand, a large seed allows rapid development of a deep root system which confers resistance to the low water levels often occurring in the first few centimeters of sand. A large seed also permits the seedling to grow up through several centimeters of sand if the seed becomes buried.

3. As the dune community matures, vegetative and topographic features ameliorate abiotic factors. Species of small seed size and high seed numbers, such as <u>M. punctata</u>, <u>A. lyrata</u>, and <u>P. articulata</u>, begin to appear due to the greater numbers of sites favorable to the survival of their seedlings. It is in the slack area that species come closest to having characteristics often associated with "colonizing" species (Baker and Stebbins, 1965; Harper, Lovell, and Moore, 1970). However, xeric factors are still important since, in the comparison of seed size for species common to both old fields and sand dune slack areas, the slack population had the highest average seed size. Apparently, dryness plays the same role in selecting for large seed size that competition does in more mature systems.

4. As more dense and diverse vegetation enters the dune community, competitive factors become more important. Thus, dune forest species have a small number of large seeds. However, due to the diversity of vegetative structure and corresponding reduction in the constraints imposed by abiotic factors, a greater variety of seed characteristics is observed than is seen in the earlier stages.

5. Though selection appears strong for large seeds in the early stages of dune succession, there appear to be factors present which may constrain seed size. This is evidenced by the pattern of specific caloric content which is opposite to that normally predicted for succession. It is hypothesized that abiotic influences relative to imbibition rates and dispersal factors are balanced against energy requirements for seedling establishment. Large, slowly imbibing seeds may not successfully

germinate in the short favorable periods available or may not be able to reach suitable germination sites. Additionally, since increases in seed size are often accompanied by decreased seed number (Harper, Lovell and Moore, 1970; Stebbins, 1971; Werner and Platt, 1976; Werner, 1980), there may be a point where further reductions in numbers (and thus in potential offspring) may negate survivorship gains due to larger seeds (Werner, 1980). This is particularly true given the low survivorship for all life stages observed in the demographic studies of <u>A. campestris</u> and <u>M. punctata</u>.

6. Demographic studies further illustrate the influence of stress on the early stages of dune succession. Both <u>A. campestris</u> and <u>M. punctata</u> can exhibit delayed first reproduction if conditions are too stressful. In addition, <u>A. campestris</u> is a long lived monocarp, waiting at least until the third year before reproducing. Such delays may be necessary for this species because of low soil nutrients and the large amount of resources this species devotes to structures associated with reproduction. <u>S. caesia</u> waits four or more years before reproducing. However, this is probably to establish vegetative structures necessary for the plant to compete effectively as well as to survive herbivory.

7. Of the three species studied demographically, <u>S</u>. <u>caesia</u> is the least affected by changes in environmental factors. During the dry, 1977 growing season, germination levels for this species dropped by only 30 percent and adults showed little signs of moisture stress. Germination levels for <u>M</u>. <u>punctata</u> and <u>A</u>. campestris dropped by 90 and 70 percent,

respectively. As a result both species, for 1977, had finite rates of increases which were less than one.

8. Survivorship levels for the three species studied demographically reinforce findings of the reproductive effort and seed characteristics studies. Seedling survivorship was lowest for the slack species <u>M. punctata</u> which has the smallest average seed size. Once plants of this slack species develop beyond this vulnerable stage, survivorship levels are higher than those of <u>A. campestris</u>. <u>M. punctata</u>'s lower allocation to reproduction likely contributes to higher adult survivorship than found in <u>A. campestris</u>. However, the more highly stressful abiotic conditions probably keep the survivorship well below that of <u>S. caesia</u>. This latter species had the highest juvenile and adult survivorship; once the root-rhizome system is established, mortality declines suggesting this structure probably helps the plant survive competition and herbivory. Low reproductive effort in the adult may help keep survivorship high for this stage since mortality of reproductive.

9. Throughout this summary the influence of stress and abiotic factors has been emphasized; thus, it would seem this study advocates the adoption of Grime's model. However, it is felt that this model is too simplistic. While it does point out the importance of stress factors, it leaves out such important influences as age specific mortality, the availability of favorable microhabitats and their fluctuation through time, trophic positions, and environmental predictability (Charnov and Schaffer, 1973; Schaffer, 1974; Wilbur, Tinkle, and Collins, 1974; Platt, 1975; Grubb, 1977; Hart, 1977; Werner, 1977; Vitt and Congdon, 1978; Michod, 1979; Werner, 1979; Whittaker and Goodman, 1979; Gross, 1980). It would seem a far better procedure to first isolate the factors of selection likely to be acting on a particular species within a given system or stage of succession. Then, the observed set of life history characteristics should be explained in the context of these factors rather than factors deemed important in other systems (or situations). The process should not stop here, however, experiments should be set up which test these explanations (or hypotheses) and provide more than correlative evidence that certain selective factors are important. Viewed within this context, this study of dune succession becomes only the first or inductive step toward an understanding of dune succession.

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APPENDIX

Figure Al. <u>Level I soil moisture data for the three</u> <u>study areas</u>. Brackets enclose two standard error lengths.



Figure A2. Level II soil moisture data. Brackets enclose two standard error lengths.



Area	Species	Importance ¹ value
Foredune		
Herbaceous	Ammophila breviligulata Artemisia campestris Calamovilfa longifolia Solidago spathulata	284.5 1.1 7.2 7.1
Shrubs	<u>Prunus pumila</u> Open area <u>Ptelea</u> <u>trifoliata</u> ² <u>Cornus</u> <u>stolonifera</u> ²	200.0 100.0 0.0 0.0
Trees	Populus tremuloide ² , ³	0.0
<u>Slack</u>		
Herbaceous Shrubs	Ammophila breviligulata Andropogon scoparius Artemisia campestris Asclepias syriaca Hudsonia tomentosa Lithospermum caroliniense Monarda punctata Panicum vergatum Solidago spathulata Taxicadendron radicans Cryptogams	22.4 3.7 1.2 2.6 48.5 3.8 12.3 24.2 11.6 5.2 75.7 229.6
	Prunus pumila	70.4
Forest		
Herbaceous	Aralia nudicaulis Chimaphila maculata Direa palustris Hepatica americana Mitchella repens Oryzopsis asperfolia Oryzopsis racemosa Osmorhiza claytoni Polygonatum pubescens Smilicina racemosa Solidago caesia Viola papilionacea Viola (unknown)	3.9 0.9 7.7 22.5 63.3 35.3 8.8 1.1 13.9 6.1 10.0 63.8 0.6

TABLE Al. Importance values for species from the three study sites.

TABLE Al (cont'd).

Area	Species	Importance ¹ value
Forest (cont'd)		
Herbaceous (cont'd)	Cryptogams Ferns	48.1 0.6
Shrubs	Amelanchier	1.2
	Euonymus obovatus Hamamelis virginiana	16.8 0.7
	<u>Rubus</u> sp. <u>Smilax rotundifolia</u>	0.4 32.7
	<u>Taxicadendron</u> <u>radicans</u> Viburnum <u>acerifolium</u>	2.5 55.5
Trees ⁴	Acer saccharum	114.5
	<u>Fagus grandifolia</u> Ostrya virginiana	22.7 12.4
	<u>Prunus</u> <u>serotina</u> Quercus borealis	48.2 52.7
	<u>Quercus palustris</u> <u>Tilia americana</u>	22.9 21.9
	<u>Tsuga</u> canadensis	4.5

¹Data were taken from projects performed for Botany 450 of Michigan State University. The Transect Method was used unless otherwise noted.

²This species was present in the study area, but was not sampled in the transects due to its low density and clumped distribution.

³Also present as a shrub.

⁴ Data were collected using the Point-quarter Method.

	C	legree (C ^O)-hours	
Date	Foredune	Slack	Forest
<u>1977</u>			
July 25	67.3	58.1	50.0
August 23	72.2	64.5	55.1
September 28 ¹	50.1	37.8	28.8
October 29	25.3	28.6	23.4
<u>1978</u>			
May 18	54.3	48.4	50.1
June 17	58.0	55.7	49.9
July 20	80.2	63.7	62.5

TABLE A2.	Degree-hour	values	for	the	three	study	areas	The	period
	of measureme	ent is	1030-	-1830	unles	s oth	erwise	stated	

¹Measurement period was 1030-1630.

.

		Percent-hours	
Date	Foredune	Slack	Forest
1977			
June 27	65.6	ND ²	205.2
July 25 ³	136.5	204.7	503.9
August 23	219.5	318.2	501.9
September 28 ⁴	142.8	205.9	365.7
October 29	403.5	379.0	474.4
1978			
1)/0			
May 18	279.1	288.9	291.0
June 17	518.1	551.4	557.4
July 20	237.5	467.1	534.2

TABLE A3. <u>Percent-hour data for the three study areas</u>. The period of measurement was 1030-1830 unless otherwise noted.

¹Time period was 1130-1600.

²No data due to equipment failure.

³The period was 1030-1600.

⁴The period was 1030-1630.

Date	Ove	rall	Fore	idune ront		3ack	Slack	Forest
ly 25	0.8	(0.05)	0.9	(0.05)	0.5	(0.05)	0.9 (0.05)	0.9 (0.05)
gust 13	1.7	(60.0)	2.1	(60.0)	0.7	(0.05)	1.4 (0.09)	0.6 (0.05)
tember 28	1.5	(60.0)	1.8	(60.0)	0.6	(0.02)	1.4 (0.09)	0.5 (0.02)
cober 23	1.3	(0.01)	1.2	(0.23)	0.9	(60°0)	1.3 (0.09)	0.4 (0.02)
just]]	0.4	(0.05)	0.3	(0.02)	0.1	(0.05)	0.3 (0.05)	0.3 (0.02)
just 19	1.4	(60.0)	2.0	(14.0)	0.8	(0.05)	0.8 (0.05)	0.6 (0.05)
just 31	0.7	(0.05)	0.6	(0.05)	1.1	(0.05)	0.8 (0.05)	0.2 (0.02)
tember 3	1.2	(0.05)	1.4	(0.05)	0.7	(0.05)	0.7 (0.05)	0.5 (0.01)
tember 23	0.5	(0.05)	0.5	(0.05)	0.6	(0.05)	0.7 (0.05)	0.5 (0.01)
stember 28	0.6	(0.05)	0.5	(0.05)	1.0	(60°0)	0.6 (0.05)	0.2 (0.01)
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		Foredune			
Date	Overal 1	Front	Back	Slack	Forest
August 14	0.68 (0.018)	0.72 (0.018)	0.59 (0.045)	0.36 (0.045)	0.41 (0.045)
August 31	0.38 (0.018)	0.27 (0.018)	0.68 (0.018)	0.32 (0.018)	0.14 (0.009)
September 3	0.72 (0.045)	0.77 (0.045)	0.59 (0.045)	0.50 (0.045)	0.27 (0.009)
September 23	0.32 (0.014)	0.27 (0.014)	0.41 (0.045)	0.32 (0.018)	0.27 (0.045)
September 28	0.27 (0.014)	0.27 (0.014)	0.18 (0.023)	0.27 (0.045)	0.04 (0.005)
November 4	0.40 (0.045)	0.50 (0.045)	0.18 (0.014)	0.36 (0.014)	0.18 (0.018)

TABLE A6. <u>Sand movem</u> centimeter	ent levels for the t of sand per day and	three study areas. I the standard erro	Units are grams of ors are parenthesize	f sand per ed.
	Fored	dune		
Time period	Overal I	Front	Slack	Forest
<u>1977</u> 11/1 10 - 11/2 10	(2 1) 8 6	2 1/ (2 2)	2 2 (2 2)	0 03 (0 03)
or the - or kind	(/.) 0.7	(() +.((2.2) C.C	0.02 (0.02)
Aug. 10 - Sept. 11	0.05 (0.2)	0.7 (0.2)	0.9 (0.5)	0.03 (0.08)
Sept.]] - Oct.]5	4.2 (2.9)	5.0 (2.7)	2.5 (1.6)	0.01 (0.01)
Oct. 15 - Nov. 4	3.0 (9.1)	3.7 (2.6)	0.1 (0.03)	0.01 (0.0004)
<u>1978</u>				
April 29 - May 27	2.5 (2.7)	3.2 (2.8)	0.8 (0.3)	0.02 (0.01)
May 27 - July 6	1.1 (0.6)	1.2 (0.8)	0.8 (0.3)	0.003 (0.002)
July 6 - Aug. 3	1.8 (1.6)	3.0 (2.6)	0.3 (0.002)	0.02 (0.01)
Aug. 3 - Aug. 31	0.6 (0.4)	0.8 (0.4)	0.5 (0.1)	0.003 (0.001)
Aug. 31 - Sept. 28	1.8 (1.1)	2.0 (1.5)	1.1 (0.2)	0.01 (0.004)
Sept. 28 - Nov. 4	1.5 (0.8)	1.4 (0.5)	0.2 (0.04)	0.002 (0.001)

Herbaceous	Woody
Foredune	<u>e</u>
Calamovilfa longifolia	<u>Prunus</u> pumila
Ammophila breviligulata	<u>Ptelea</u> <u>trifoliata</u>
Cakile edentula	<u>Cornus</u> stolenifera
Euphorbia polygonifolia	
<u>Asclepias syriaca</u>	
Lithospermum caroliniense	
Artemisia campestris	
Solidago spathulata	

Arabis lyrata Lithospermum caroliniense Hudsonia tomentosa² Asclepias syriaca Calamovilfa longifolia <u>Panicum</u> virgatum Ammophila breviligulata Fragaria virginiana² Monarda punctata Solidago spathulata Andropogon scroparius Polygonella articulata Salsola kali <u>Cirsium</u> pitcheri³ <u>Smilicina</u> stellata³

Salix glaucephylloides <u>Vitis riparia</u> Prunus pumila Arctostaphylous uvi-ursi Populus tremuloides²

TABLE A7. A list of the species studied.

TABLE A7. (cont'd)

Herbaceous	Woody

<u>Woods</u>

Hepatica americana¹ Polygonatum pubescens Smilicina racemosa Oryzopsis asperfolia¹ Arabis drummondii Viola papilionacea¹ Aquilegia canadensis¹ Ozmorhiza claytoni Galium circaezans Mitchella repens Carex convoluta¹ Festuca obtusa¹ Oryzopsis racemosa¹ Solidago caesia

<u>Viburnum</u> <u>acerifolium</u> <u>Euonymus</u> <u>obovatus</u>

Resource allocation partially estimated from last year's data.

²Reproductive phenology only.

³No data on reproductive phenology.

4 No data on seed number or resource allocation.

species.						
Species	Repro- ductive ^l effort	Seed weight (mg)	Kilo- calories per seed	Kilo- calories per gram	Seed number	Adjusted seed number
<u>Calamovilfa</u> longifolia	6.01	2.163	171.9	4.240	719.19	34.23
Ammophila breviligulata	10.23	2.856	12.374	4.333	16.51	1.518
<u>Cakile</u> edentula	54.62	10.228	66.368	6.489	210.24	238.64
<u>Euphorbia</u> polygonifolia	34.71	1.192	7.019	6.08	26.22	287.42
<u>Asclepias syriaca</u>	22.45	7.893	11.175	5.217	424.11	9.54
Lithospermum caroliniense	4.346	4.089	23.630	5.779	201.84	3.28
<u>Artemisia</u> <u>campestris</u>	25.41	0.336	1.897	5.645	2252.72	19.411
<u>Solidago spathulata</u>	12.88	0.489	3.032	6.200	8449.16	172.45
<u>Prunus pumila</u>	4.996	36.102	212.13	5.876	40.52	0.0527
<u>Ptelea</u> trifoliata	ŊŊ	10.772	62.230	5.777	QN	QN
<u>Cornus stolonifera</u>	3.685	4.889	24.119	4.933	277.27	2.77

TABLE A8. Untransformed means of reproductive effort and seed characteristics for foredune

l This is expressed as a TAR percentage.

TABLE A9. Untransformed me	ans of repro	oductive effort	and seed o	characteris	tics for :	slack species
	Repro- ,		Kilo-	Kilo-		Adjusted
Species	ductive' effort	Seed weight (mg)	calories per seed	calories per gram	Seed number	seed number
<u>Calamovilfa longifolia</u>	5.01	1.663	6.381	3.837	474.38	19.16
Panicum virgatum	9.20	1.625	7.517	4.626	1865.64	41.26
<u>Andropogon scoparius</u>	3.80	1.621	8.418	5.193	4071.75	26.26
<u>Salsola kali</u>	QN	2.533	10.308	4.069	102.67	ND
<u>Polygonella</u> articulata	26.42	0.586	2.470	4.216	565.33	1426.24
<u>Arabis</u> <u>lyrata</u>	20.72	0.1130	0.729	6.451	1590.73	1230.77
<u>Hudsonia</u> tomentosa	4.97	0.546	2.497	4.573	777.20	155.84
<u>Asclepias syriaca</u>	16.17	9.18	50.613	3.980	388.33	226.42
Lithospermum caroliniense	2.82	2.974	18.809	6.324	439.35	9.23
<u>Monarda</u> punctata	13.72	0.1893	1.022	5.397	2119.73	109.23
<u>Artemisia campestris</u>	29.48	1.663	1.931	5.645	3553.06	155.84
<u>Solidago</u> spathulata	9.78	0.496	3.075	6.260	6174.38	226.42
<u>Oenothera</u> <u>biennis</u>	37.25	0.728	3.784	5.198	2731.16	605.58
Prunus serotina	7.02	29.83	175.03	5.867	172.52	0.265
<u>Vitis riparia</u>	10.47	24.62	121.400	4.931	18.33	0.854
<u>Hypericum kalmianum</u>	3.84	0.0733	0.382	5.214	7027.45	939.31
Arctostaphylous uvi-ursi	5.26	1.23	6.681	5.432	1.77	0.621
<u>Salix glaucophylioides</u>	QN	0.159	ŊŊ	QN	6520.19	24.073

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Species	Repro- _l ductive effort	Seed weight (mg)	Kilo- calories per seed	Kilo- calories per gram	Seed number	Adjusted seed number
Festuca obtusa	5.98	1.007	4.099	4.071	101.41	42.42
<u>Oryzopsis</u> asperfolia	5.05	6.720	28.024	4.171	83.07	5.71
<u>Oryzopsis</u> racemosa	6.77	5.351	18.883	3.529	19.84	9.16
Carex convoluta	2.75	0.712	2.451	3.444	295.32	34.78
Smilicina racemosa	11.58	29.28	110.906	3.788	28.50	20.68
<u>Maianthemum canadense</u>	19.73	13.83	49.234	3.560	4.75	20.83
Polygunatum pubescens	11.81	20.25	88.189	4.355	22.45	9.39
<u>Hepatica</u> <u>americana</u>	10.99	1.387	9.368	6.754	48.57	54.97
<u>Aquilegia</u> canadensis	1.73	1.207	6.819	5.650	16.70	15.34
<u>Osmorhiza claytoni</u>	20.92	5.400	25.302	4.686	38.60	38.43
<u>Viola papilonaceae</u>	3.35	0.722	4.139	5.733	54.58	73.55
<u>Chimaphila maculata</u>	QN	0.0015	QN	QN	4740.71	QN
<u>Galium circaezans</u>	7.28	2.228	10.580	4.749	33.38	44.98
<u>Mitchella</u> repens	5.54	2.642	12.505	4.733	22.24	11.47
Solidago caesia	4.04	0.234	1.624	6.93	189.61	83.08
<u>Arabis drumondii</u>	30.24	0.125	0.583	4.660	2125.00	2014.24
Prunus serotina	QN	24.57	·153.794	6.259	QN	DN
Euonymus obovatus	ŊŊ	16.14	87.182	5.402	3.35	6.73
Viburnum acerifolium	0.74	15.67	97.948	6.251	11.45	0.545

¹This is expressed as a TAR percentage.

Category	Foredune	Slack
Seed weight (mg):		
Overlap species	0.216 (0.0527) ¹	0.135 (0.0543)
Non-overlap species	0.517 (0.0519)	-0.284 (0.0377)
Energy (Kcal) per seed:		
Overlap species	0 .9 46 (0.0511)	0.869 (0.0541)
Non-overlap species	1.257 (0.0560)	0.419 (0.0388)
Adjusted seed numbers:		
Overlap species	1.541 (0.1108)	1.573 (0.0842)
Non-overlap species	1.420 (0.1790)	2.065 (0.0974)

TABLE All. Transformed (log₁₀) seed characteristic means of foredune and slack overlap and non-overlap species.

¹The standard errors are parenthesized.

		For	edune
		overlap	non-overlap
Seed weigh	t (mg):		
clack	overlap	n.s. ¹	P < 0.01
STOCK	non-overlap	P < 0.01	P < 0.01
Energy (Kca slack	al) per seed: <u>overlap</u>	n.s.	P < 0.01
Adjusted so	eed numbers:	P < 0.05	P < 0.01
J			
slack	overlap	n.s.	n.s.
SIDUK	non-overlap	n.s.	P < 0.01

TABLE A12. T-test comparison of transformed (log₁₀) seed characteristic means for foredune and slack overlap and nonoverlap species.

¹Not significant.