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THE ECOLOGICAL AND EVOLUTIONARY SIGNIFICANCE OF
INTRASPECIFIC DIFFERENCES IN SEED SIZE: AN
EXPERIMENTAL ANALYSIS OF PRUNELLA VULGARIS

presented by

Alice Anne Winn

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Patricia Werner
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THE ECOLOGICAL AND EVOLUTIONARY SIGNIFICANCE OF INTRASPECIFIC DIFFERENCES IN SEED SIZE: AN EXPERIMENTAL ANALYSIS OF PRUNELLA VULGARIS

By

Alice Anne Winn

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ABSTRACT

THE ECOLOGICAL AND EVOLUTIONARY SIGNIFICANCE OF INTRASPECIFIC DIFFERENCES IN SEED SIZE: AN EXPERIMENTAL ANALYSIS OF PRUNELLA VULGARIS

By

Alice Anne Winn

The effect of seed size on seedling establishment and the relative fitnesses of individuals that produce seeds of particular sizes were determined for the short-lived, perennial herb, *Prunella vulgaris*. Demographic data from four populations suggested that the seed and seedling stages were critical phases of the life cycle for this species. The effects of seed size on the probability of seedling emergence and establishment were determined by monitoring the fates of seeds of known sizes sown into two woodland and two old-field habitats. The relative fitnesses of individuals that produced particular sizes of seeds were determined using a cost/benetfit analysis where the benefit was the probability that a seed of a given size would produce a successful seedling and the cost was the weight of the seed.

Larger seeds had a greater probability of germination and produced seedlings that were more likely to survive to the end of the first growing season in all habitats. One year after seedling emergence, the effect of seed size on seedling size could no longer be detected. Within a habitat, the availability of microsites favorable for seedling emergence and the mean and range of seed sizes sown determined the magnitude of the effects of seed size.

Cost/benefit analysis indicated significant selection on seed size in two of the four habitats. However, the phenotypes observed in natural populations did not correspond to the optima predicted from the cost/benefit analysis.

Reciprocal transplants of rosettes between a woodland and an old-field habitat and analysis of the relationships among components of seed yield were used to examine the constraints on the response to selection for seed size. The reciprocal transplants indicated that differences in the size of seeds produced were due to phenotypic plasticity rather than genetic differences among individuals and populations. Yield component analysis suggested that components of seed yield vary independently for the most part. However, the number of flowers produced in an inflorescence tended to be negatively related to mean seed weight. As a result, changes in seed size are constrained indirectly by factors that determine the number of flowers produced per inflorescence.

The large non-genetic component of variation in seed size and the negative relationship between the number of flowers produced per inflorencence and seed size could account for the lack of correspondence between predicted optimum seed sizes and the actual distribution of phenotypes.

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CHAPTER 1

INTRODUCTION

Among plant species, the size of seeds produced has been identified as an important factor in determining patterns of distribution and abundance (Salisbury 1942, McWilliams et al. 1968, Baker 1972, Rabinowitz 1978, Gross and Werner 1982). Within species however, differences in the sizes of seeds produced are often overlooked because other characteristics such as total plant size and the number of seeds produced are generally much more variable than seed size. As a result, the ecological and evolutionary significance of intraspecific differences in seed size have not been examined closely.

Although evidence from a number of studies suggests that, within species, larger seeds are more likely to produce successful seedlings (eg. Black 1958, Schaal 1980, Gross 1984, Stanton 1984), no studies have determined whether individuals that produce larger seeds have higher fitness than those that produce smaller seeds. Assuming a trade-off between the size and number of seeds that can be produced, the production of large seeds will increase parental fitness only if the benefits of producing large seeds are sufficient to offset the cost of the accompanying reduction in the number of seeds produced. Thus, comparison of the relative costs and benefits of producing seeds of particular sizes could be used to identify the seed size that maximizes parental fitness or the number of successful offspring produced.

A population may be constrained in several ways in its ability to respond to selection for some optimum phenotype with respect to the size

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of seeds produced. These constraints include genetic and/or developmental relationships between seed size and other traits that contribute positively to fitness, a high degree of phenotypic plasticity of seed size, and gene flow between populations with different optima for genetically-determined phenotypes.

Thus, empirical demonstration of significant selection on the size of seeds produced requires measurement of both the costs and benefits associated with the production of seeds of particular sizes. Determination of whether there will be response to selection requires consideration of developmental and genetic constraints on changes in seed size and examination of the extent to which the size of seeds produced is genetically determined.

Thesis Organization:

This thesis deals with the ecological and evolutionary consequences of differences in seed size in the short-lived perennial, *Prunella vulgaris*. It is divided into six chapters. This first chapter provides a general introduction to the questions of interest, and describes the species and the study sites at which the research was conducted. Chapter 2 presents the results of three years of demographic observations of seeds, seedlings, and adults in four populations of *P. vulgaris*. Attention is focused on the critical importance of the seed and seedling stages of the life cycle. In Chapter 3, the results of field experiments to determine the effects of seed size and microsite characteristics on seedling emergence are presented. In Chapter 4, the relationship between seed size and the probability of producing an established seedling is used to construct a cost/benefit analysis for the production of seeds of

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particular sizes. The optimum phenotype predicted by the cost/benefit analysis is compared with the actual distribution of the sizes of seeds produced in the field, and the genetic basis for the determination of seed size is examined using reciprocal transplants. Chapter 5 focuses on characteristics of seed production and examines the possibility that seed size is negatively related to other components of seed production. Chapter 6 summarizes the conclusions of the preceding chapters and discusses their implications for further study of the ecological and evolutionary consequences of intraspecific differences in seed size.

Species Description: *Prunella vulgaris* L. is a short-lived perennial herb of the mint family (Labiatae). Two subspecies of *P. vulgaris* are recognized in the United States; *P. vulgaris* subsp. *vulgaris*, introduced from Europe and *P. vulgaris* subsp. *lanceolata*, which is believed to be native to North America (Fernald 1913). These two subspecies are completely interfertile (Nelson 1963) and are only distinguished by a difference in the shape and hairiness of the cauline leaves (Fernald 1913).

World-wide, *P. vulgaris* has a nearly cosmopolitan distribution (Bocher 1940). Locally it is found in abandoned fields and pastures, along paths and roads, and in woodland clearings. Extensive populations may also be found in lawns and meadows (Warwick and Briggs 1979).

The common name for *P. vulgaris*, self-heal, derives from an old belief that the crushed leaves of this species could be used to soothe a sore throat (Crockett 1977). The name *Prunella* is a misspelling of the original name *Brunella* coming from the German word *braune* which means a type of sore throat. Most modern herbal encyclopedias agree that the heal

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healing powers of *P. vulgaris* are mythical (Coon 1963).

Prunella vulgaris is a summer-flowering herb which produces pale blue to purple tubular flowers in a compact spike from late July to late October. An individual may produce from one to several flowering stems, each consisting of one terminal inflorescence (bearing from six to more than fifty flowers) and up to six, usually paired, axial inflorescences. Within an inflorescence, the lowermost flowers open several days before the uppermost flowers. Within a flowering stem, flowers in the terminal spike open first followed roughly in order of decreasing height by axial inflorescences. A single individual may bear open flowers for more than a month.

In the field, flowers are visited by bumblebees, butterflies, and moths. Rates of outcrossing in *P. vulgaris* have not been measured. However, the flowers are self-compatible and will set abundant seed when pollinators are excluded (Mulligan and Findlay 1970 and personal observation). Each flower can produce up to four one-seeded nutlets (seeds) which are enclosed in a persistent calyx. The seeds possess no specialized structures to aid in dispersal and most seeds probably do not disperse further than 50 cm from their maternal parent. Seeds are dispersed from September to April and seedlings emerge from the end of April through June. Freshly collected seeds exhibit no dormancy and there is no persistent seed bank in the field.

When mowed, a population of *P. vulgaris* may form a dense mat through vegetative reproduction (Warwick and Briggs 1979). However, in undisturbed populations, I have found lateral spreading only when normally erect flowering stems are knocked down to the ground and then root at the nodes. New rosettes produced in this way remain connected to the

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the parent rosette by visible, above-ground connections for at least three years (personal observation).

Field Site Descriptions: The demography, seedling establishment, and the reproductive characteristics of adult P. vulgaris were examined in detail at four sites located within five km of the W.K. Kellogg Biological Station, Kalamazoo County, Michigan. Two sites were located in the Kellogg Experimental Forest and the other two sites in Louden Field, a 40 year-old abandoned agricultural field.

The Kellogg Experimental Forest (KEF) was established in 1931 on abandoned farmland for the purpose of demonstrating techniques of woodlot management. The 602 acres of land that make up the forest are divided into 30 compartments in which different species of trees have been planted and various management regimes have been implemented. One of the field sites, designated the WOODLAND DECIDUOUS SITE, was located in an unmanaged stand of a mature second-growth forest (Compartment 10 of KEF). A large, sparse population of P. vulgaris was located on a steep hillside at this site. The understory was sparse consisting mainly of P. vulgaris and Viola spp.. Total percent herbaceous cover was estimated to be 3%. The overhead canopy (80%) was made up of Fagus americana and Quercus spp.. Patches of deciduous leaf litter and bare ground made up the forest floor.

The second forest site, designated the WOODLAND CONIFEROUS SITE, was located in a 30 year-old stand of Pinus rubra (Compartment 15 of KEF). A dense population of P. vulgaris was located at the edge of the stand where the canopy cover was 20%. The understory composed of P. vulgaris, Rumex sp., and Ribes sp. made up 10% cover. A continuous layer of coni

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coniferous leaf litter was present.

Louden Field is an 8.5 hectare field which was abandoned from agriculture approximately 40 years ago. The vegetation which includes approximately 112 species of angiosperms (Stergios 1970) is dominated by species of Poa, Agropyron, Solidago, Hieracium, and Rubus. The study site designated the OLD-FIELD CENTER SITE was located near the center of Louden Field. There was no overhead canopy at this site, but herbaceous cover was estimated to be 75%. The vegetation was dominated by Hieracium spp., Erigeron spp., Solidago canadensis, Chrysanthemum leucanthemum, and Trifolium pratense.

The fourth site, designated the OLD-FIELD EDGE SITE, was located on the eastern edge of Louden Field about 100 m distant from the old-field center site on the border between the field and encroaching deciduous woodlands. Several red maples (Acer rubrum), formed a canopy of 20% cover. Herbaceous cover comprising mostly Rubus spp. was 30%.

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CHAPTER TWO

THE DEMOGRAPHY OF PRUNELLA VULGARIS

Advances in our knowledge of population dynamics and natural selection often arise from demographic observations. For example, Darwin's proposal of natural selection as the mechanism for evolution was based on demographic observations made by Malthus. In spite of their potential value, there are few demographic studies of perennial plant species. This dearth is understandable as a number of common logistical problems encumber the study of birth and death rates of perennial plants: It is difficult, if not impossible, to age herbaceous plants, therefore it is necessary to follow individuals from birth to death (cohort analysis) in order to obtain age-specific probabilities of survival and reproduction directly. However, the longevity of many perennials makes this sort of direct measurement prohibitive. Further, many perennials are clonal so that it may be difficult to distinguish individual growth or survival from reproduction (Harper 1977, Abrahamson 1980). Sexual reproduction may be rare and seedlings may appear in sites remote in time and space from adult populations (see examples in Cook 1980). Thus seedlings may be difficult to find. In addition, perennials often experience very high mortality early in the life cycle so that cohort analyses must include a large number of seedlings to insure that at least some will complete the life cycle. A final problem, which is common to demographic studies of annual plants as well, is that of determining the fates of seeds from the time of dispersal until the time of seedling emergence.

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A number of techniques have been devised to deal with some of the problems listed above. These include measuring demographic parameters as a function of size rather than age (eg. Werner 1975, Gross 1981), sowing known numbers of seeds in a limited area to generate large samples of seedlings (Cavers and Harper 1967, Hawthorn and Cavers 1976, Gross 1980), and the measuring of demographic behavior of different life cycle stages (seed, seedling, juvenile,and adult) separately rather than following a single cohort through time (eg. Solbrig 1981).

Reported here is a demographic analysis of a short-lived, perennial herb, Prunella vulgaris L. The study combines the techniques listed above to estimate probabilities of survival through each stage of the life cycle of the plant. In addition, the influence of plant size on subsequent survival and reproduction is examined to determine whether size is a good predictor of future demographic behavior for this polycarpic species as has been shown for a number of monocarpic species (Werner 1975, Thompson 1978, van der Miejden and van der Waals-Kooi 1979, Gross 1981).

MATERIALS AND METHODS

The life cycle of P. vulgaris can be divided into four phases; a dispersal phase between the time seeds are dispersed and seedlings emerge, an establishment phase between seedling emergence and seedling establishment (defined as survival to the end of the first growing season), a juvenile phase between seedling establishment and reproduction, and a predispersal phase between the time seeds are produced and the time they are dispersed (Figure 2.1). Each phase lasts

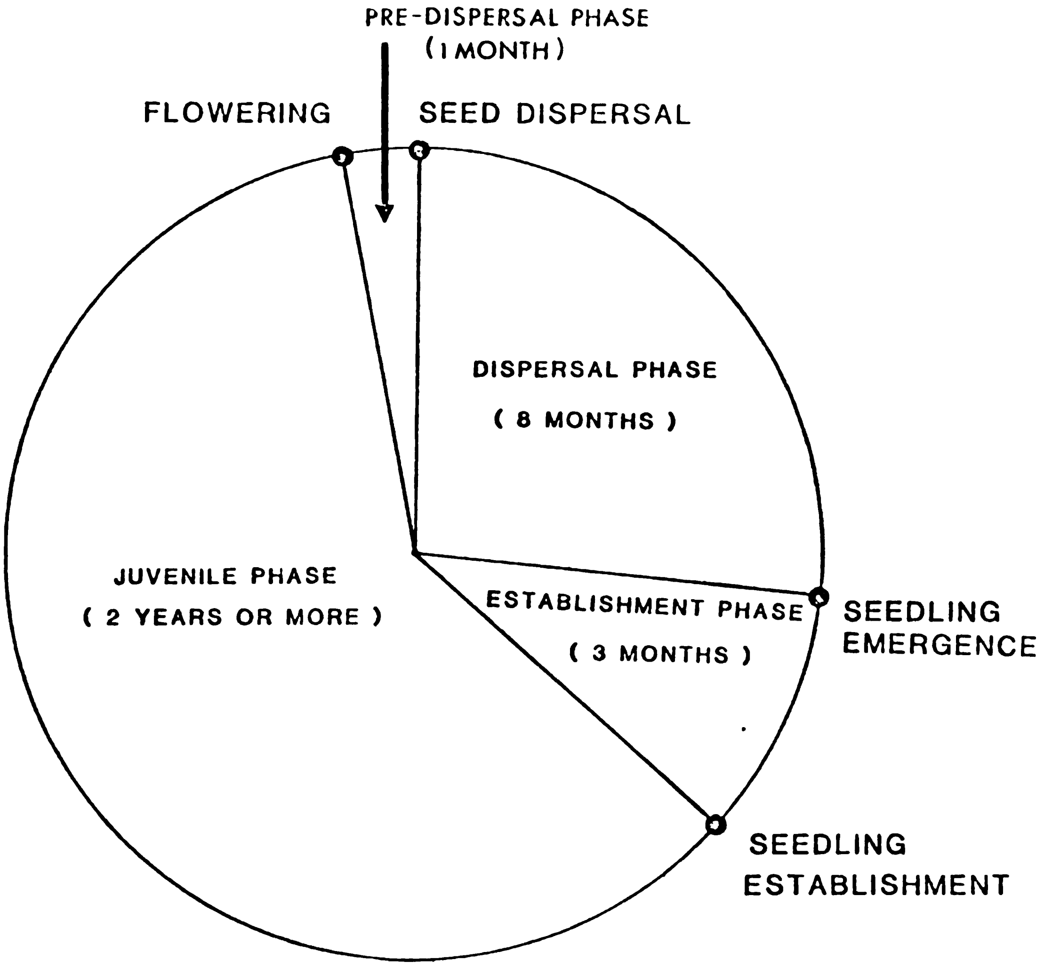

Figure 2.1. The life cycle of Prunella vulgaris

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for a different (and sometimes variable) length of time ranging from one month (predispersal phase) to two or more years (juvenile phase) (Figure 2.1).

Survival and reproduction were measured separately for individual adults, juveniles, seedlings, mature undispersed seeds, and dispersed seeds in four populations of P. vulgaris over a period of three years. Two populations were located in the Kellogg Experimental Forest and the other two were located in Louden Field at the Kellogg Biological Station in southwestern Michigan. These four habitats were all within five km of one another but differed considerably in such factors as canopy cover, percent herbaceous cover, and litter distribution and composition (Table 2.1).

Overhead canopy cover at the four study sites ranged from 80% in the deciduous woodland habitat to none in the old-field center habitat. Conversely, herbaceous cover was most abundant (75%) in the old-field center habitat and least abundant (3%) in the deciduous woodland habitat. The density of P. vulgaris ranged from less than $1/m^2$ at the deciduous woodland site to $17/m^2$ at the old-field edge habitat.

Seeds:

The probability of survival of seeds from the time of dispersal in late Autumn to the time of seedling emergence in the following Spring was measured in each habitat by sowing 6000 seeds into marked plots from which naturally dispersing seed had been excluded. Plots were sown in November, 1982 (Year 1) and seedling emergence was monitored in the Spring of 1983 (Year 2). Because there is no seed pool, seedling emergence is a good estimator of the survival of seeds through the

Table 3.1 Characteristics of the

Table 2.1. Characteristics of the four field sites and the populations of *Pruenlla vulgaris* at each site.

				Prunella vulgaris		
Site	Overhead Canopy Cover (%)	Herbaceous Cover (%)	Litter Distribution and Composition	Population Density (m^{-2})	Mean Size of Seeds Produced (mg)	Mean Number of Seeds Produced
Deciduous Woodland	80	3	Discontinuous Tree leaf	0.8	.772	148
Coniferous Woodland	20	10	Continuous Conifer needles	15	.517	201
Old-field Edge	20	30	Discontinuous Herbaceous	17	.295	231
Old-field Center	0	75	Discontinuous Herbaceous	9	.453	348

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dispersal phase. Subsequent survival of seedlings has been monitored through June 1984 (Year 3).

Seedlings:

The growth, survivorship and reproduction of seedlings emerging in Year 1 in each habitat were monitored until June, Year 3. As seedlings emerged, they were marked with individually numbered stakes. In both old-field habitats, all seedlings which emerged in Year 1 were included in the study. Because large numbers of seedlings emerged in the forest habitats, random subsamples of at least 150 individuals in each habitat were marked and included in the study. The length of the longest leaf of each surviving seedling was measured at monthly intervals from May to September in Year 1, in June and September of Year 2 and in June of Year 3. The length of the longest leaf is significantly correlated with seedling weight (r^2=.85, $p<.01$) and thus provides a good estimate of size.

Adults:

In the Spring of Year 1 in each habitat, all adult P. vulgaris within a defined area containing at least 100 individuals were marked with numbered stakes. The length of the longest leaf and the total number of leaves of each individual were measured in May. Seeds were collected and weighed as they were produced throughout the late Summer and Autumn, Year 1. The following Spring (Year 2), all marked individuals were measured again and seeds produced in Year 2 were collected and weighed. All inflorescences were examined during seed collection for damage by a seed predator (an unidentified beetle larva) which generally consumed all of the seeds in a single inflorescence before pupating. A final census of marked adults in each habitat was conducted in the Spring of Year 3.

From these measurements, the following demographic data were obtained for adults in each habitat in each year; 1) the proportion of individuals that survived from the previous year, 2) the proportion that flowered, and 3) the total weight of seeds (reproductive yield) produced by each individual. In addition, a regression equation relating the length of longest leaf and total number of leaves to total plant weight was used to estimate individual plant weights. Using these estimates, the relationship between weight in two consecutive years, between weight and reproductive yield within each year, between reproductive yield in two consecutive years, and between reproductive yield in one year and weight in the following year were determined. A rough approximation of population mean reproductive effort was calculated by dividing the mean reproductive yield in Year 1 by the mean estimated weight in Year 1 for each population. In addition, the proportion of inflorescences which were attacked by seed predators was calculated.

RESULTS

Seedlings and seeds:

In all four populations, survivorship curves based on naturally occurring seedlings suggest a roughly constant rate of mortality from the time of emergence until three years later (Figure 2.2A). The survivorship curves based on observations in the artificially sown plots show that there is a much higher rate of mortality during the time

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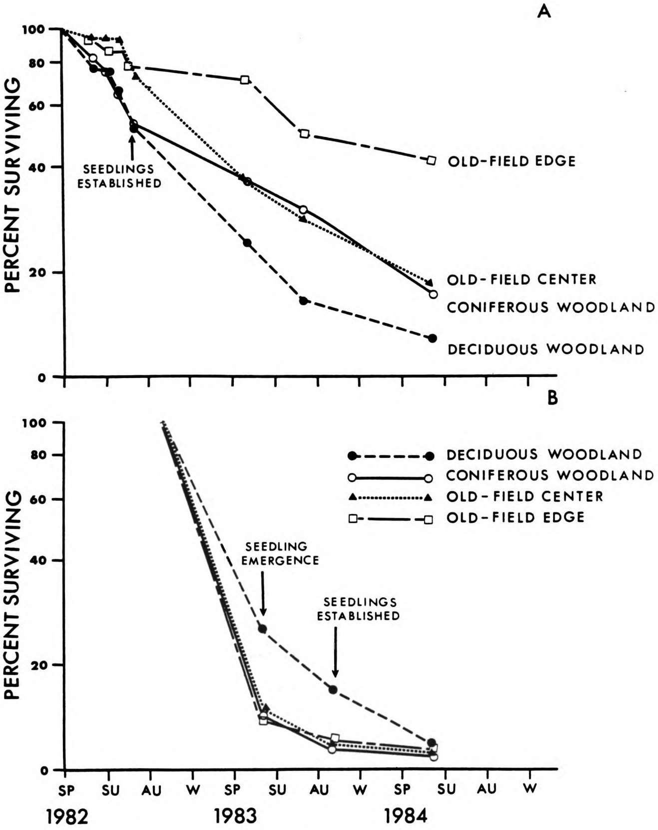

Figure 2.2 Percent of seedlings surviving over time (A) for naturally occurring seedlings and (B) for sown seeds in each habitat.

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between seed dispersal and seedling emergence than after emergence (Figure 2.2B). Seedling survivorship subsequent to emergence in the sown plots was similar to that of naturally occurring seedlings in that the probability of mortality has remained fairly constant over the first two growing seasons.

Size appeared to be important in determining whether a seedling would survive from one year to the next. Within each habitat, seedlings that survived from one year to the next had generally been significantly larger than seedlings that did not survive (Table 2.3).

Individuals marked as seedlings first flowered in their third growing season (1984). Between 6 and 42% of the original cohort of naturally emerging seedlings survived to the third growing season and between 13 and 87% of these survivors flowered (Table 2.4). Individuals that flowered in Year 3 tended on average to be those that had been larger in Year 2 (Table 2.5).

Adults:

Population density and mean plant weight and reproductive effort of adults differed among the four populations studied (Table 2.2). Mean plant weight was greater and population density and reproductive effort much lower in the deciduous forest than in the other three populations. In the old-field edge population, mean plant weight was less than in the remaining two populations.

Adult survival also differed among populations (Figure 2.3). Adults in the deciduous forest site had the highest probability of survival through Year 3. By June of Year 3, a maximum of 12% of the individuals originally marked in Year 1 were still alive in the other three habitats

Table 2.2. Descriptions of populations of *P. vulgaris* in each of the four habitats.

Population	Number of Adults Marked	Number of Seedlings Marked	Mean Adult Weight* (mg)	Estimated Reproductive Effort@ (%)
Deciduous Woodland	124	189	.360	32
Coniferous Woodland	138	150	.187	59
Old-field Edge	158	34	.081	85
Old-field Center	199	93	.198	83

* n for Mean Adult Weight = Number of Adults Marked

@ Estimated reproductive effort = population mean reproductive yield/ population mean weight for Year 1 data.

Table 2.3. Mean weights (mg) of seedlings that did and did not survive from Year 1 to Year 2 and from Year 2 to Year 3. Standard errors are given in parentheses. Probabilities refer to the results of t-tests.

	Deciduous Woodland	Coniferous Woodland	Old-field Edge	Old-field Center
Year 2				
Survived	2.19 (.12)	1.97 (.14)	1.77 (.12)	1.58 (.08)
Died	1.46 (.14)	1.20 (.12)	2.45 (.65)	1.35 (.11)
p	<.01	<.01	ns*	ns
Year 3				
Survived	7.26 (.52)	2.96 (.57)	3.43 (.29)	6.34 (.65)
Died	4.86 (.74)	2.00 (.32)	1.3 (.00)	3.19 (.67)
p	<.02	ns	<.01@	<.01

* Only 2 of 24 seedlings died.

@ Only one of 14 seedlings died.

Table 2.4. Seedling survival and percent flowering: Percent survival from Year 1 to Year 3 and percent flowering in Year 3 calculated for seedlings that survived to Year 3.

	Deciduous Woodland	Coniferous Woodland	Old-field Edge	Old-field Center
% Survival to Year 3	15	6	42	17
% Flowering in Year 3	52	13	29	87

Table 2.5. Mean Year 2 weights of seedlings that did and did not flower in Year 3. Standard errors are given in parentheses. Probabilities refer to the results of t-tests.

	Deciduous Woodland	Coniferous Woodland	Old-field Edge	Old-field Center
Flowering in Year 3	8.09 (.58)	5.30 (.00)	3.70 (.35)	6.64 (.56)
Not Flowering in Year 3	6.44 (.82)	2.63 (.53)	3.31 (.40)	4.70 (3.5)
p	<.12	<.01*	<.48	<.68@

* Only 1 of 8 surviving seedlings flowered.
@ Only 2 of 13 surviving seedlings did not flower.

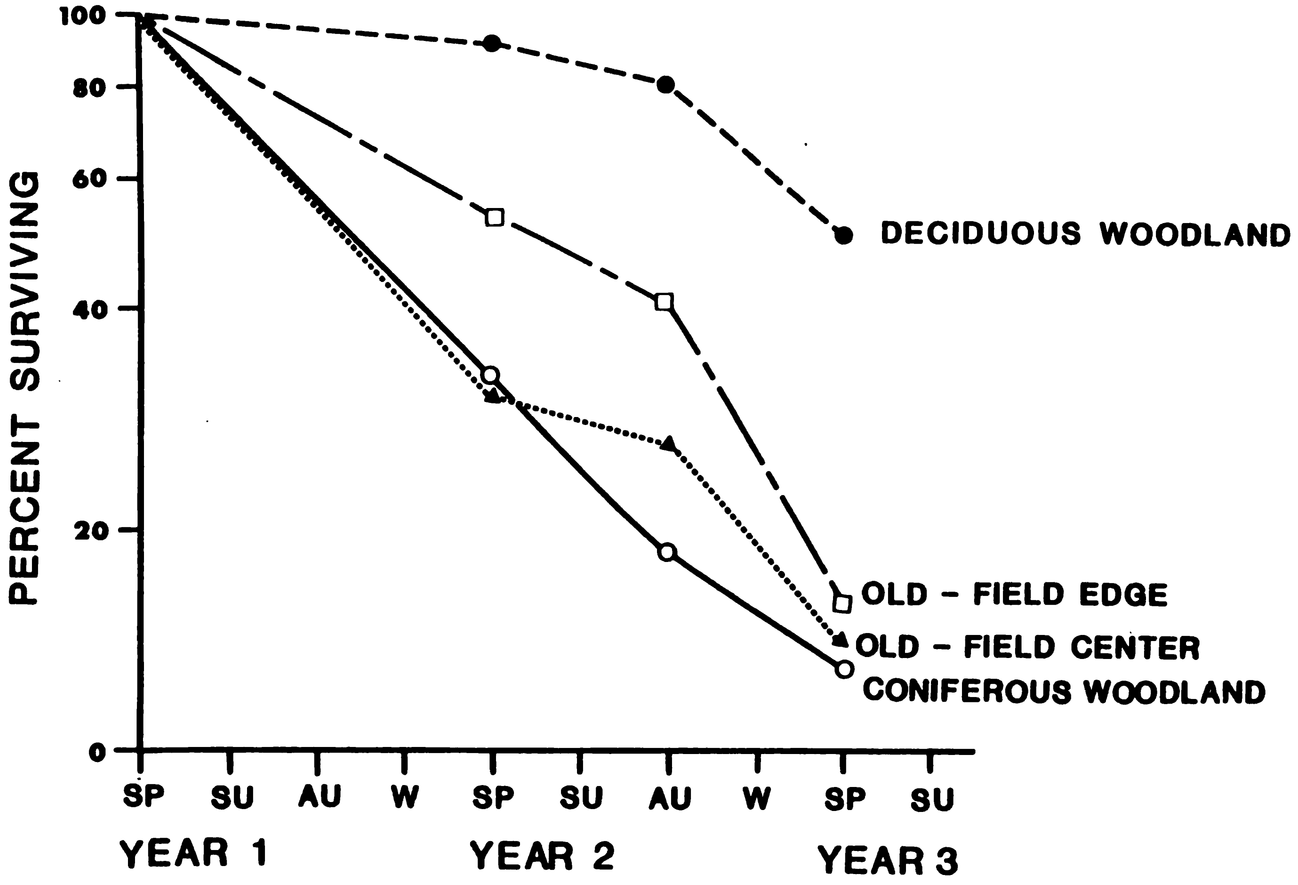

Figure 2.3. Survivorship curves for adults in each habitat.

(Figure 2.3).

The probability of flowering differed among populations by less than 10% in Year 1 (Table 2.6). However, in Year 2, the probability of flowering differed more among populations and tended to increase with increasing Year 1 population mean weight (Table 2.2, Table 2.6).

Among adult plants, weight in Year 1 did not appear to determine the likelihood of survival to Year 2. Within each habitat, there were no significant differences between the mean Year 1 weights of adults that did and did not survive to Year 2 (Table 2.7). Thus, in contrast to the pattern observed for seedlings, larger individuals were not more likely to survive.

Within each of the two forest habitats, the probability of survival from Year 1 to Year 2 was similar for individuals that had and had not flowered in Year 1 (Table 2.8). However, in both old-field populations, plants that flowered in Year 1 were less than half as likely to survive to Year 2 than were plants which did not flower in Year 1.

Although plant weight did not appear to influence the probability that an individual would survive from one year to the next, it did influence whether an individual flowered within a season. Within each population in Year 1, the mean weight in the Spring of individuals which subsequently flowered (in Year 1) was significantly greater than the mean weight of individuals which did not flower (Table 2.9). Thus larger individuals were more likely to flower. Further, in two populations, individual weight also influenced the amount of reproduction. In the deciduous forest and the old-field center populations, there was a significant relationship between individual weight and reproductive yield (the total weight of seeds produced) in both Year 1 and Year 2 (Table

Table 2.6. Proportion of individuals flowering at each site in Year 1 and Year 2.

Population	Proportion Flowering in Year 1	Proportion Flowering in Year 2
Deciduous Woodland	.42	.74
Coniferous Woodland	.37	.33
Old-field Edge	.33	.26
Old-field Center	.39	.49

Table 2.7. Mean estimated Year 1 weights (mg) of adults that did and did not survive to Year 2. Standard errors are given in parentheses. Probabilities refer to results of t-tests.

	Deciduous Woodland	Coniferous Woodland	Old-field Edge	Old-field Center
Survived	.116 (.045)	.356 (.038)	.073 (.011)	.148 (.040)
Died	.198 (.028)	.358 (.069)	.095 (.012)	.207 (.016)
p	>.05	>.05	>.05	>.05

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Table 2.8. Probability of survival (%) to Year 2 for adults that did and did not flower in Year 1.

	Deciduous Woodland	Coniferous Woodland	Old-field Edge	Old-field Center
Did Flower	80	22	20	14
Did Not Flower	79	16	52	35
n	119	121	148	185

Table 2.9. Mean estimated Year 1 weights (mg) of adults that did and did not flower in Year 1. Standard errors are given in parentheses. Probabilities refer to the results of t-tests.

	Deciduous Woodland	Coniferous Woodland	Old-field Edge	Old-field Center
Did Flower	.564 (.04)	.432 (.05)	.158 (.02)	.302 (.02)
Did not Flower	.200 (.02)	.092 (.02)	.057 (.01)	.08 (.01)
P	<.01	<.01	<.01	<.01

2.10). There were also significant relationships between individual weight in Year 1 and weight in Year 2 in these two populations (Table 2.10). Small sample sizes in the other two populations may have made it difficult to detect these relationships. There were no significant relationships between reproductive yield in Year 1 and reproductive yield in Year 2 or between reproductive yield in Year 1 and weight in Year 2 in any of the four populations.

In the one population (deciduous forest) for which the sample size (n=53) was adequate for comparison, the probability of flowering in Year 2 for plants that flowered in Year 1 was somewhat greater than for individuals which had not flowered in Year 1 (51% for plants flowering in Year 1 and 41% for those not flowering in Year 1).

The proportion of inflorescences attacked by the seed predator was 10% or less in Year 1, In Year 2, none of the inflorescences examined were attacked.

Life cycle:

From these data, the probability of survival through each phase of the life cycle in each of the four populations can be determined (Figure 2.4). The probability of survival from the time of seed dispersal to seedling emergence was estimated as the proportion of sown seeds that germinated in each habitat. The probabilities of seedling establishment and subsequent survival through the juvenile phase were measured directly by monitoring naturally occurring seedlings for three growing seasons. Two years was the minimum length of the juvenile period so the reported values are actually underestimates of the probability of survival from establishment to seed production. Pre-dispersal mortality of seeds was

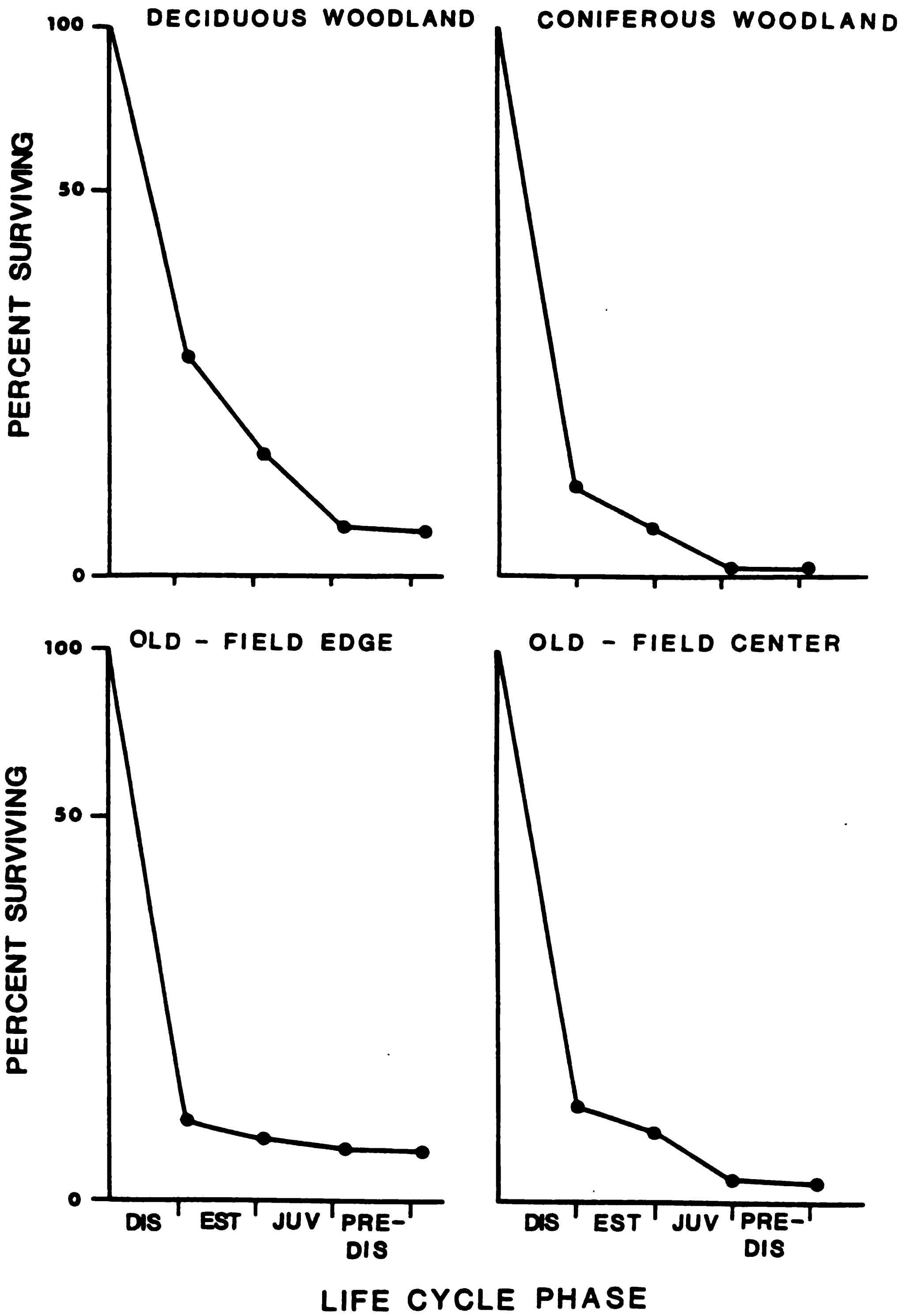

Figure 2.4. Survivorship through the life cycle in each habitat. DIS= dispersal phase, EST=establishment phase, JUV=juvenile phase, PRE-DIS= pre-dispersal phase.

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Table 2.10. Relationships between individual adult weight and reproductive yield within and between years. Values are coefficients of determination (r^2), sample sizes are given in parentheses.

	Deciduous Woodland	Coniferous Woodland	Old-field Edge	Old-field Center
Weight Year 1 x Yield Year 1	$.24^{*}$ (44)	.04 (28)	.10 (26)	$.24^{*}$ (68)
Weight Year 2 x Yield Year 2	$.60^{*}$ (52)	$74^{@}$ (4)	.21 (12)	$.41^{*}$ (22)
Weight Year 1 x Weight Year 2	$.12^{*}$ (57)	.07 (13)	.12 (20)	$.51^{*}$ (24)
Yield Year 1 x Yield Year 2	.00 (39)	.21 (6)	.53 (3)	.41 (8)
Yield Year 1 x Weight Year 2	.03 (25)	.36 (18)	.05 (9)	.53 (8)

* $p<.01$

@ only four individuals produced seeds in year 2.

estimated as the proportion of all inflorescences collected which were attacked by the beetle larvae in Year 1. Reported here is the probability of survival (1-probability of mortality) to the time of dispersal for seeds still attached to the parent plant.

DISCUSSION

Relationship between plant size and demographic behavior:

Among a number of monocarpic perennial species, there is a strong positive relationship between individual size in one growing season and the probability of surviving to the following growing season (Werner 1975, Thomson 1978, van der Meijden and van der Waals-Kooi 1979, Gross 1981). In *P. vulgaris*, a poylcarpic species, adult mortality appeared to be independent of size (Table 2.7). Analyses of the relationship between size and probability of survival in other non-cloning or weakly-cloning polycarpic species show mixed results. Solbrig (1981) found that in *Viola sororia* the probability of mortality decreased with as the number of leaves increased. However, in *Plantago cordata*, probability of survival was unrelated to size (Meagher et al. 1978). In a demographic study of a dioecious perennial *Valeriana edulis*, Soule (1981) observed that among males, the smallest individuals had the lowest probability of survival, but among females, the largest individuals had the lowest probability of survival. In another dioecious perennial, *Chamaelirium luteum*, females were observed to be significantly larger than males but experienced rates of survival equal to or less than those of males (Meagher and Antonovics 1983).

The contrast between patterns of mortality in relation to size in monocarpic perennials (which do not survive after they reproduce) and polycarpic perennials (which may survive to reproduce again) is not wholly unexpected. Differences in size among individuals within a population of monocarpic perennials will result from differences in age, microsite favorability, and/or intrinsic growth rates. In a population of polycarpic perennials, individuals may also differ due to differences in energetic and/or biochemical costs incurred by past reproduction.

In the present study, estimated weight was a good predictor of individual behavior within a growing season. In all populations, the larger plants were those that subsequently flowered (Table 2.9) and, in the deciduous woods and the center of the old-field, there was a significant relationship between individual size and reproductive weight within a season (Table 2.10). However,in some populations, individuals incurred a survival cost by reproducing (Table 2.8).

Rosettes were measured in the early Summer. Individuals that were large at that time might have been less likely to survive to the next Summer because they were more likely to incur the energetic cost of flowering. This explanation is consistent with the observation that although size was not a good predictor of probability of survival among individuals that were first marked as adults, it was a better predictor among individuals which had never flowered (i.e. those first marked as seedlings (Table 2.3).

Meagher and Antonovics (1983) suggest that the higher mortality rates exhibited by females of <u>Chamaelirium</u> <u>luteum</u> are the result of higher reproductive efforts (RE) and therefore greater energetic costs of reproduction as compared with males. Thus the generally higher RE's in the old-field habitat (Table 2.2) might explain why flowering increased the probability of mortality in the old-field populations but had no such effect in the woodland habitats (Table 2.8).

In summary, in Prunella vulgaris, adult size determines whether or not an individual will flower and, in some instances, how much seed it will produce. However, high reproductive effort may increase the probability that an individual will not survive to the next growing season regardless of its size. Therefore, size in one growing season is a poor predictor of probability of survival to the next season for adults of P. vulgaris and perhaps for polycarpic perennials in general.

Demographic Patterns:

The observed differences among habitats in patterns of seedling emergence, seedling and adult survival and adult reproduction may be due to differences among habitats in environmental conditions, population age, population history, and/or genetic composition of populations. It is interesting to note that populations from either forest or old-field habitat types did not behave more similarly than populations from different habitat types. For example, the population in the deciduous woodland habitat had the highest rate of survival from Year 1 to Year 2 but the population at the coniferous woodland habitat had the lowest survival rate (Figure 2.3). Assuming that environmental conditions are likely to be more similar within than between habitat types, this suggests that differences among habitats in environmental factors are not sufficient to explain differences in demographic behavior among populations.

Population mean individual size (weight) was not necessarily a good predictor of demographic behavior either. For example, mean size was similar in the coniferous woodland and old-field center populations (Table 2.2) but the probability of survival from Year 1 to Year 2 and from Year 2 to Year 3 was considerably lower in the coniferous woodland population (Figure 2.3).

In spite of the considerable variation among populations in patterns of survival, in all four populations of *P. vulgaris*, the lowest probability of survival is associated with the period between seed dispersal and seedling emergence (Figure 2.4). It is reasonable to predict, therefore, that any characteristic of a seed that increases its probability of surviving through this critical period (without greatly reducing either the probability of survival at another stage of the life cycle or the number of seeds produced) would be strongly favored by natural selection. Similarly, any characteristic which increases seedling size, and therefore the probability of survival through the juvenile period, will also be favored (with the same qualifications).

Among a number of species which show intraspecific variation in seed size, it has been shown that larger seeds have a higher percent germination (Werner 1979, Weis 1982, Pitelka et al. 1983, Gross 1984) and produce seedlings which are larger and/or more likely to survive than the seedlings from smaller seeds (Black 1958, Weis 1982). Further, Stanton (1984) and Hendrix (1984) have shown that the presence and magnitude of the effects of seed size on seed germination and seedling size may depend on environmental conditions. Therefore, it may be of interest to investigate the effects of seed size on seedling emergence and survival and what characteristics of the environment influence these effects in P. *vulgaris*.

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CHAPTER THREE

THE EFFECTS OF SEED SIZE AND MICROSITE ON SEEDLING EMERGENCE OF PRUNELLA VULGARIS IN FOUR HABITATS

Harper et al. (1961) and Grubb (1977) have suggested that small scale heterogeneity of physical and biotic factors divide a habitat into a mosaic of microsites, only some of which are suitable for germination of the seeds of a particular species. Seeds of different species are expected to require different quantities and qualities of light, moisture, mechanical disturbance of the soil etc. in order to germinate. Although data on the optimal conditions for seed germination in controlled environments are available (cf. references in Harper 1977), there is little information concerning what types of microsites are adequate for seed germination in the field.

One seed characteristic that may dictate some safe-site requirements is size (Grubb 1977). It has been hypothesized that only relatively large seeds possess sufficient stored energy reserves to survive until they reach high enough into the canopy that they can support themselves photosynthetically (Salisbury 1942, Black 1958, Harper, Lovell, & Moore 1970, Fenner 1980). In field experiments using four biennial species, Gross & Werner (1982) demonstrated that two species which required bare ground in order to establish had smaller mean seed sizes (_Verbascum thapsus,_ mean seed size=.064 mg; _Oenothera biennis,_ mean seed size=0.2 mg) than two species which could germinate and survive in both bare ground and established vegetation (_Daucus carota,_ mean seed size=1.0 mg; _Tragopogon dubius,_ mean seed size=6.8 mg). Further, the availability of a particular microsite type (bare ground) in a habitat determined whether either of the former two species could invade or persist. In greenhouse experiments, Gross (1984) found that intraspecific seed size classes of O. biennnis and D. carota showed differences in percent emergence depending on what microhabitat they were sown into. To date, there have been no field studies of the effects of intraspecific differences in seed size on safe-site requirements.

This paper describes field experiments and observations concerning the safe-site requirements of different-sized seeds of an herbaceous perennial, Prunella vulgaris L. (Labiatae). Prunella vulgaris is a widespread weed which reproduces almost exclusively by seed in the habitats examined in this study. Seed size can vary six-fold within a habitat. The effects of seed size and microsite type on seedling emergence were investigated in four habitats.

Two main questions were addressed; (i) Do seeds germinate differentially with respect to microsite type? (ii) Do different sized seeds of the same species have different safe-site requirements?

MATERIALS AND METHODS

This study was conducted at the W.K. Kellogg Biological Station and the W.K. Kellogg Experimental Forest in Kalamazoo County in southwestern Michigan, USA. Prunella vulgaris is commonly found in abandoned fields and pastures, along roads and paths, and in woodland clearings in this area. Populations of P. vulgaris were examined at four sites; two sites were located in an abandoned agricultural field and two in woodland clearings. These four sites differed considerably in the amount of overhead (tree) and herbaceous cover, the quantity and quality of litter present, the density of P. vulgaris, and the mean size and number of seeds produced by P. vulgaris (Table 2.1). Further description of these sites can be found in Chapter One.

Seeds of P. vulgaris are dispersed beginning in October and continuing through the Winter. In the lab, 80% of fresh collected seed will germinate within two weeks when placed on wet filter paper and exposed to light. However, in the field germination does not occur until late April. Seeds do not survive more than one winter in the soil (Winn, unpublished data).

In October 1982, seeds were collected within a marked area at each of the four study sites. Because mature seeds are retained in a persistent calyx, these collections contained seeds that matured at various times throughout the fruiting season. Seeds collected from different sites were kept separate. Few large seeds were produced by plants in the field. However, plants grown in pots and watered daily in the greenhouse produced larger seeds than plants grown in the field ($\bar{X}$ field=0.505 mg, $\bar{X}$ greenhouse=0.977 mg). Therefore, in order to provide a sufficient number of large seeds, some seeds from plants collected as rosettes from the appropriate field sites and grown to maturity in the greenhouse were added to each seed collection. Each collection was divided into six size classes of approximately equal numbers of seeds using a South Dakota seed cleaner (E.L. Erickson Products, Brookings, South Dakota). Within each population the range of seed sizes determined the size class divisions (Table 3.1).

A random sample of fifty seeds from each size class from each collection site were tested for percent germination and viability in the

Table 3.1. Mean seed weight (mg) for seed size classes in each population. Standard errors are given in parentheses.

	Seed Size Class					
Site	1	2	3	4	5	6
Deciduous Woodland	.65 (.03)	.80 (.02)	.86 (.03)	.94 (.02)	.96 (.02)	1.0 (.02)
Coniferous Woodland	.29 (.01)	.53 (.01)	.69 (.02)	.91 (.02)	.97 (.02)	1.0 (.02)
Old-field Edge	.19 (.01)	.30 (.02)	.36 (.01)	.50 (.03)	.87 (.02)	.98 (.02)
Old-field Center	.28 (.01)	.41 (.01)	.50 (.01)	.61 (.02)	.87 (.03)	1.1 (.02)

lab. Seeds were placed on filter paper moistened with distilled water and exposed to light for sixteen hours/day. Germination percent for each seed size class was determined after two weeks. All seeds that did not germinate were judged to be non-viable using a standard tetrazolium chloride test (Bonner 1974).

Within each field area, seventy 0.25m x 0.25m quadrats were permanently marked out and seeds were sown back into their home sites (where they had been collected) as follows. At each site there were ten replicate quadrats for each of the six seed size classes and ten control quadrats which received no seed input. The control quadrats were established to monitor background seedling emergence which was negligible. The quadrats were assigned to seed size treatments at random. One hundred seeds of the appropriate size were hand sown evenly across each quadrat from a height of 2 cm. Seeds were sown in early November when nearly all herbaceous vegetation had senesced. Thus, seeds were not prevented from reaching some microsites by the presence of standing vegetation. At the deciduous woodland site, large pieces of litter such as entire tree leaves were removed before seeds were sown and replaced immediately afterwards. At the other sites, the litter was composed of small plant parts and did not appear to prevent seeds from reaching microsites with litter.

During the Spring and Summer following sowing, seedling emergence and survival were monitored in the quadrats. The quadrats were examined every third day for newly emerged seedlings. More than 99% of the seedlings that were marked survived for at least one week. Therefore it is unlikely that many seedlings emerged and died without being recorded. As each seedling emerged it was marked with a plastic toothpick and the characteristics of the microsite type (an area $1 cm^2$ around the seedling) in which it emerged were recorded.

Eight microsite types were distinguished by combinations of two factors; four substrate types and the presence or absence of herbaceous cover. The four substrates were moss, bare ground, litter, and moss and litter together. The choice of factors used to describe microsite types was based on the results of field studies of seedling emergence in Michigan old-fields (Werner 1975, Gross 1980, Gross & Werner 1982). At each site the proportional availability (percent of the total area covered) of the eight microsite types was measured independent of seedling emergence using point cover estimates (Greig-Smith 1964).

RESULTS

(i) Do seeds germinate differentially with respect to microsite type at each site?

The four sites differed considerably in the proportional availability of the eight microsite types defined (Figure 3.1). In particular, the sites differed in the number of different microsite types available and in the total availability of microsites with herbaceous cover present. If it is assumed that seeds were dispersed randomly with respect to microsite type and if seeds can germinate equally well in all microsite types, then the percent of seedlings emerging should be equal to the availability of each microsite type at each study site (see Figure 3.1). Therefore, if the percent of seedlings emerging is significantly greater than the availability of a microsite, then that type of microsite

Figure 3.1. Percent cover (availability) of microsite types and the proportional distribution of seedlings among microsite types at each study site.

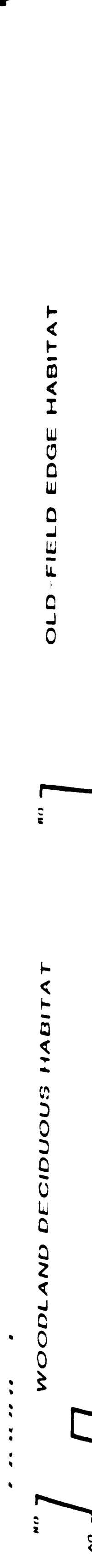
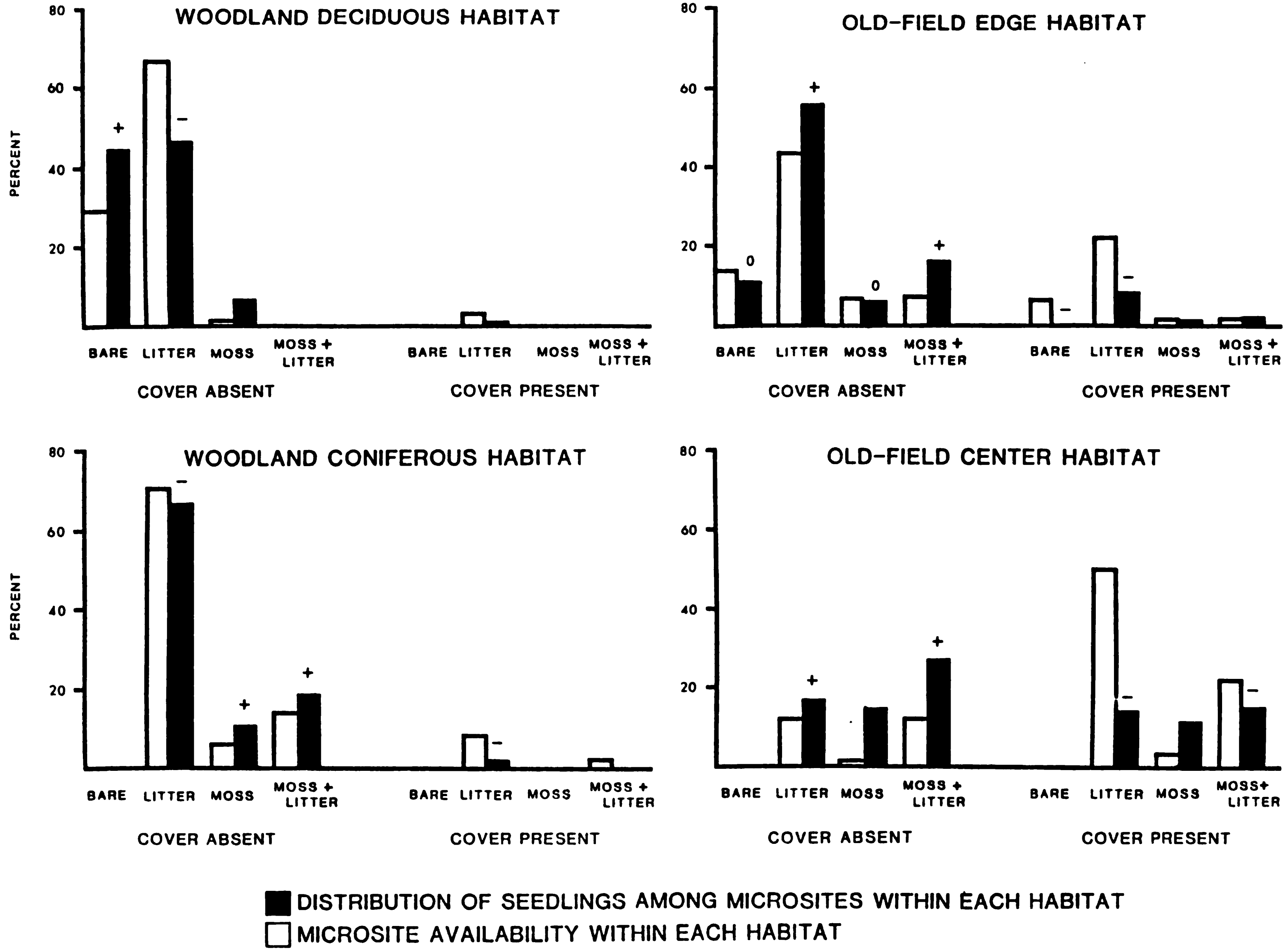


FIGURE 1


WOODLAND DECIDUOUS HABITAT
OLD-FIELD EDGE HABITAT
WOODLAND CONIFEROUS HABITAT
OLD-FIELD CENTER HABITAT
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40
20
+
−
0
BARE
LITTER
MOSS
MOSS + LITTER
COVER ABSENT
COVER PRESENT
■ DISTRIBUTION OF SEEDLINGS AMONG MICROSITES WITHIN EACH HABITAT
□ MICROSITE AVAILABILITY WITHIN EACH HABITAT

is considered favorable for germination.

Seedling emergence and microsite availability were analyzed for each site using a method developed for quantifying the results of selective predation experiments (Manly 1974). The coefficient β has been used to quantify predator selectivity for a prey type with knowledge of its proportional availability in a diet made up of several prey type classes. Here, β was used to quantify the favorability of a microsite type for germination (or the "selectivity" of seedling emergence for a type of microsite given its availability). A restriction of this method is that confidence limits around estimates of selectivity can be computed accurately only if the availability of a microsite is at least 5%. Therefore only those microsite types with at least 5% availability at each site were analyzed (Table 3.2).

DECIDUOUS WOODLAND SITE: In the deciduous woods, only two microsite types, bare ground with no cover and litter with no cover, accounted for at least 5% of total cover (Figure 3.1). Microsites with herbaceous cover present accounted for a combined total of only 3%. There was a high availability of bare ground (29%) in this habitat relative to the other three study sites and the fewest microsite types accounting for at least 5% of total ground cover. Microsites with bare ground and no herbaceous cover promoted seedling emergence and microsites with litter and no herbaceous cover inhibited emergence (Figure 3.1).

CONIFEROUS WOODLAND SITE: Four microsite types accounted for at least 5% total cover in the coniferous forest. In contrast to the deciduous forest, there was no bare ground. Microsites with cover present accounted for a total of 10% cover. Microsites with moss and no cover or moss and litter and no cover promoted seedling emergence and

Table 3.2. Analysis of favorability of microsite types for seedling emergence. Microsites with availability <5% were not included in the analysis (see explanation in text). A "+" in the favorability column indicates that a microsite promotes seedling emergence, "-" indicates inhibition, and "0" denotes a microsite that is neutral with respect to seedling emergence.

Microsite type	Selectivity Coefficient ß ± (se)	Favorability
Deciduous Woodland site:		
bare, no cover	.68 (.03)	+
litter, no cover	.32 (.02)	-
Coniferous Woodland site:		
moss, no cover	.41 (.04)	+
moss and litter, no cover	.32 (.03)	+
litter, no cover	.21 (.02)	-
litter, with cover	.06 (.02)	-
Old-field Edge site:		
moss and litter, no cover	.37 (.03)	+
litter, no cover	.24 (.02)	+
bare, no cover	.15 (.02)	0
moss, no cover	.14 (.03)	0
litter, with cover	.07 (.01)	-
bare, with cover	.02 (.01)	-
Old-field Center site:		
moss and litter, no cover	.50 (.03)	+
litter, no cover	.32 (.03)	+
moss and litter, with cover	.13 (.02)	-
litter, with cover	.05 (.01)	-

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microsites with litter with or without cover inhibited emergence.

OLD-FIELD EDGE SITE: The edge between the old-field and the woods had the largest number (six) of microsites accounting for at least 5% of total cover. The total availability of microsites with cover was 30%. Microsites with litter or moss and litter and no cover promoted seedling emergence, bare microsites and microsites with moss and no cover were neutral, and microsites with cover inhibited emergence.

OLD-FIELD CENTER SITE: In the center of the old-field, four microsites accounted for at least 5% of total cover. Microsites with cover present accounted for 75% of total ground cover. This was the highest total among the four study sites. Microsites without cover promoted emergence and microsites with cover inhibited emergence.

In summary, the availability of microsite types (percent cover) varied considerably from site to site. At each site there were some microsites that promoted and some that inhibited seedling emergence. Microsites with herbaceous cover always had a negative effect on seedling emergence, that is, fewer seedlings emerged than would be expected if emergence were independent of microsite type. Beyond this, there was no clear pattern across sites of the effect of microsite on germination.

(ii) Do seeds of different sizes emerge differentially with respect to microsite type?

Within each habitat, percent emergence tended to increase with increasing seed size (Table 3.3). The results of lab germination trials suggest that this result may be due, in part, to differences in the

Table 3.3. Percent emergence in the field and percent viability determined in the lab for six seed size classes of each population. Mean seed weights for each size class are given in Table 3.1.

	DECIDUOUS WOODLAND		CONIFEROUS WOODLAND		OLD-FIELD EDGE		OLD-FIELD CENTER	
Size Class	Emergence (%)	Viability (%)	Emergence (%)	Viability (%)	Emergence (%)	Viability (%)	Emergence (%)	Viability (%)
1	20	86	0.3	36	0.7	<2	1.1	4
2	23	96	5.2	100	0.4	<2	1.4	2
3	23	80	9.9	100	0.6	<2	1.1	4
4	24	74	10	96	4.6	10	2.9	6
5	31	86	11	100	19	100	20	80
6	31	100	10	100	18	100	30	100

viability of seeds of different sizes, especially at the old-field sites (Table 3.3). Viability was high for most seed size classes at both woodland sites. However, viability was 10% or less for the four smallest size classes at both old-field sites (Table 3.3). This contrast between woodland and old-field sites may be due largely to the fact that seeds in the first four size classes at the old-field sites were smaller than those in the first four size classes at the woodland sites (Table 3.1). In general, size classes with mean weights of at least 0.65 mg had greater than 70% viability at all sites. Non-viable seeds were not different in external appearance from viable seeds, but when non-viable seeds were dissected, no embryos were found.

Not all seed size classes were able to germinate in all microsite types (Table 3.4). In general, small seeds tended not to emerge in microsites with herbaceous cover present. At some sites, there was an interaction between the effects of seed size and microsite type on seedling emergence (Table 3.5).

DECIDUOUS WOODLAND SITE: In the deciduous forest, there was no effect of seed size on percent seedling emergence and no interaction between seed size and microsite type (Table 3.5). The significance of microsite type was due to the favorability of bare ground for seedling emergence (Table 3.2).

CONIFEROUS WOODLAND SITE: The effects of seed size and microsite type and the interaction between them were all significant at the coniferous forest site (Table 3.5). Percent emergence increased with seed size such that three groups of seed size classes with significantly different percent emergence could be distinguished (Table 3.4). The first group contained the smallest seed size class, the second group

Table 3.4. The relationship between seed size and ability to emerge in different microsite types. An "X" indicates that at least one seedling emerged from a seed of the corresponding size class in a particular microsite type. Lines under seed size classes denote groups of size classes within which there are no significant differences in percent emergence. Seed size classes of different sites are not directly comparable (see explanation in methods section).

<table>
<tr><th>Habitat</th><th>Microsite type</th><th colspan="6">Seed Size Class</th></tr>
<tr><td colspan="8">Deciduous Woodland site:</td></tr>
<tr><td></td><td>moss, no cover</td><td>X</td><td>X</td><td>X</td><td>X</td><td>X</td><td>X</td></tr>
<tr><td></td><td>bare, no cover</td><td>X</td><td>X</td><td>X</td><td>X</td><td>X</td><td>X</td></tr>
<tr><td></td><td>litter, no cover</td><td>X</td><td>X</td><td>X</td><td>X</td><td>X</td><td>X</td></tr>
<tr><td></td><td>bare, with cover</td><td></td><td></td><td>X</td><td>X</td><td>X</td><td>X</td></tr>
<tr><td></td><td></td><td>1</td><td>2</td><td>3</td><td>4</td><td>5</td><td>6</td></tr>
<tr><td></td><td></td><td colspan="6">————————</td></tr>
<tr><td colspan="8">Coniferous Woodland site:</td></tr>
<tr><td></td><td>moss, no cover</td><td>X</td><td>X</td><td>X</td><td>X</td><td>X</td><td>X</td></tr>
<tr><td></td><td>litter, no cover</td><td></td><td>X</td><td>X</td><td>X</td><td>X</td><td>X</td></tr>
<tr><td></td><td>moss and litter, no cover</td><td></td><td></td><td></td><td></td><td>X</td><td>X</td></tr>
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<tr><td colspan="8">Old-field Edge site:</td></tr>
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<tr><td></td><td>bare, no cover</td><td></td><td></td><td>X</td><td>X</td><td>X</td><td>X</td></tr>
<tr><td></td><td>litter, no cover</td><td></td><td></td><td></td><td>X</td><td>X</td><td>X</td></tr>
<tr><td></td><td>moss and litter, no cover</td><td></td><td></td><td></td><td></td><td>X</td><td>X</td></tr>
<tr><td></td><td>moss, with cover</td><td></td><td></td><td></td><td></td><td>X</td><td>X</td></tr>
<tr><td></td><td>bare, with cover</td><td></td><td></td><td></td><td></td><td></td><td>X</td></tr>
<tr><td></td><td></td><td>1</td><td>2</td><td>3</td><td>4</td><td>5</td><td>6</td></tr>
<tr><td></td><td></td><td colspan="3">————————</td><td>—</td><td colspan="2">————</td></tr>
<tr><td colspan="8">Old-field Center site:</td></tr>
<tr><td></td><td>moss, no cover</td><td>X</td><td>X</td><td>X</td><td>X</td><td>X</td><td>X</td></tr>
<tr><td></td><td>litter, no cover</td><td>X</td><td>X</td><td>X</td><td>X</td><td>X</td><td>X</td></tr>
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<tr><td></td><td>litter, with cover</td><td></td><td></td><td></td><td>X</td><td>X</td><td>X</td></tr>
<tr><td></td><td>moss and litter, with cover</td><td></td><td></td><td></td><td>X</td><td>X</td><td>X</td></tr>
<tr><td></td><td></td><td>1</td><td>2</td><td>3</td><td>4</td><td>5</td><td>6</td></tr>
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Table 3.5. Summaries of two-way ANOVA's for the effects of seed size and microsite type on percent seedling emergence at each site.

Source of Variation	Degrees of freedom	F-value	Probability
Deciduous Woodland site:			
Seed size	5	.25	.93
Microsite type	4	94.7	<.01
Seed size x microsite type	20	.27	.99
Coniferous Woodland site:			
Seed size	5	4.51	<.01
Microsite type	4	67.9	<.01
Seed size x microsite type	20	4.47	<.01
Old-field Edge site:			
Seed Size	3	7.1	<.01
Microsite type	7	7.0	<.01
Seed size x microsite type	21	1.4	.14
Old-field Center site:			
Seed size	5	10.5	<.01
Microsite type	5	41.5	<.01
Seed size x microsite type	25	4.0	<.01

contained the second size class, and the third group contained size classes 3-6. The first percent emergence group (the smallest seed size class) emerged only in one microsite type, the second in only two microsite types and the third in an average of 2.5 microsite types.

OLD-FIELD EDGE SITE: At the old-field edge, only the main effects had a significant effect on percent emergence (Table 3.5). The effect of seed size on emergence generated 3 seed size groups, the first containing the first three seed size classes, the second containing size class 4, and the third containing size classes 5 and 6 (Table 3.4). Seeds from the first group emerged in 2 microsite types. Seeds of the second group emerged in three types and seeds of the fourth group emerged in an average of 5.5 microsite types. Only seeds in the fourth group (the largest seeds) emerged in microsites with herbaceous cover present.

OLD-FIELD CENTER SITE: Both of the main effects and the interaction between them were significant in the center of the old-field (Table 3.5). Four seed size groups were formed on the basis of percent emergence (Table 3.4). The first contained seed size classes 1-3, each other group consisted of one of the larger seed size classes. Seeds from the first group emerged in an average of 2.3 microsite types, and the seeds of the larger three groups emerged in 6 microsite types. Only seeds from the three largest groups (seed size classes 4-6) emerged in microsites with herbaceous cover present.

In summary, microsite type had a significant effect on percent emergence at all sites. Seed size had a significant effect at three of the four sites, and there was a significant interaction between seed size and microsite type at the coniferous forest site and the center old-field site. At all sites, large seeds emerged in a greater number of microsite type

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DISCUSSION

The seeds of P. vulgaris emerge differentially with respect to the microsite types defined in this study (Table 3.2). In general, litter and herbaceous cover inhibit emergence at the woodland sites and herbaceous cover also inhibits seedling emergence at the old-field sites. Differential emergence with respect to microsite type could also be explained by differential dispersal into the eight microsite types. However, precautions such as sowing seeds after the senescence of most herbaceous vegetation and the removal and replacement of litter at the deciduous woodland site were taken to insure that seeds did reach the different microsites at random. In addition, microsite type was not actually determined until the Spring since the quantity and distribution of litter and herbaceous cover changed considerably between the time of sowing (November 1982) and the time that seedlings began to emerge (April 1983).

It should be noted that microsites with the same description at different study sites are not entirely similar. The fact that litter tends to promote emergence at the old-field sites and inhibits emergence at the woodland sites is probably due to differences in the quantity and quality of the litter present at the different sites. At the woodland sites, there are relatively thick layers of tree leaf litter that could inhibit germination by blocking out light or by physically preventing emergence. At the old-field sites, litter is sparse and consists of relatively small plant parts. This type of litter may prevent microsites from drying out as quickly as microsites with no litter while not inhibiting seedling emergence.

The fact that at all sites, larger seeds were able to emerge in a greater number of microsite types than small seeds and only the largest seeds emerged in microsites with cover present (Table 3.4), suggests that small seeds are inhibited more by herbaceous cover than large seeds are, and therefore that the safe-site requirements of small seeds are more restrictive than those for larger seeds of the same species. Further, when all seeds produced at a site are relatively large (eg. deciduous woodland site), differences in seed size have little effect on percent emergence (Table 3.5). But when mean seed size produced is smaller, differences in seed size are more important in determining percent emergence. These results are consistent with those of Gross (1984) which showed that among species with relatively large mean seed size, differences in seed size within a species did not influence seedling emergence, but among species with intermediate mean seed sizes, intraspecific differences in seed size had significant effects on seedling emergence.

At the population level, the effects of seed size on emergence may be influenced by two factors; population mean seed size and the total availability of microsites favorable for germination in a habitat. Large population mean seed size tends to decrease the importance of seed size possibly because all seeds are large enough to emerge in most microsite types. A high availability of favorable microsites may also decrease the importance of seed size if seeds of any size could emerge in a large proportion of the available microsites. Among the four sites examined in this study there is a rough positive correlation between population mean seed size and the availability of microsites favorable for seedling emergence (that is without herbaceous cover) (Table 2.1). Therefore, the potential effects of these two factors on the relationship between seed size and seedling emergence cannot be separated. For example, it is not possible to determine whether seed size has no effect on percent emergence at the deciduous woodland site because mean seed size is large or because this habitat has a high availability of bare ground (Figure 3.1) which is favorable for emergence of seeds of all sizes.

A possible explanation for the correlation between the mean size of seeds produced and the total availability of microsites with herbaceous cover present is suggested by the results of a reciprocal transplant-replant experiment involving the exchange of rosettes between the deciduous woodland habitat and the old-field center habitat. The mean size of seeds produced in the deciduous woods was 0.772 mg and the total availability of herbaceous cover was 3%. In the center of the old-field, mean seed size was 0.453 mg and the availability of herbaceous cover was 75% (Table 2.1). In both transplant habitats, there were no significant differences in mean seed weight between individuals transplanted from a foreign habitat and individuals replanted in their home habitat (Table 3.6). Mean seed size remained significantly greater for all plants at the deciduous woodland site (despite a fungal infection which afflicted all plants at this site). These results suggest that seed size is a phenotypically plastic characteristic. Further, individuals may respond to a habitat with a high percent herbaceous cover by decreasing mean seed size and to a habitat with a low percent herbaceous cover by increasing seed size.

The plasticity of seed size in response to environmental conditions

Table 3.6. Mean seed weight (mg) for reciprocal transplants between the Deciduous Woodland site and the Old-field Center site. Standard errors are in parentheses. Means followed by the same superscript are not significantly different from one another.

	Transplanted to:	
Transplanted From:	Deciduous Woodland	Old-field Center
Deciduous Woodland	$.503^{a}$	$.342^{b}$
	(.05)	(.01)
Old-field Center	$.426^{a}$	$.335^{b}$
	(.09)	(.01)

may be of advantage to a weedy species such as *P. vulgaris*. It is generally believed that there is a trade-off between the number and size of offspring an individual can produce (Smith & Fretwell 1974, Wilbur 1977, Werner 1979). There is some suggestion that this is true among the four populations of *P. vulgaris* described in this study (Table 2.1). In a habitat with few sites favorable for germination (a site with high percent cover), the larger the number of seeds produced, the more seeds will be likely to be dispersed into the few favorable sites. When sites favorable for germination are plentiful, the advantages of producing a large number of seeds may be outweighed by the higher probability of emergence associated with larger seeds. Thus, the correlation between the number and sizes of seeds produced and the total availability of herbaceous cover in a habitat may permit *P. vulgaris* to invade and persist in a variety of habitats which differ considerably in the amount of herbaceous cover.

CHAPTER FOUR

ECOLOGICAL AND EVOLUTIONARY CONSEQUENCES OF SEED SIZE IN PRUNELLA VULGARIS

Differences in seed size have been used to explain patterns of distribution and abundance of species. Small seeded species have been associated with early successional communities (Salisbury 1942, Baker 1972, Gross and Werner 1982) and/or more mesic environments (Baker 1972), high latitudes (McWilliams et al. 1968), and with the presence of high levels of seed predation (Janzen 1969). It is generally held that large seeded species are better able to invade and persist in established vegetation and that small seeded species are less competitive and therefore restricted to colonizing disturbed sites.

Within species, the ecological and evolutionary consequences of differences in seed size have not been closely examined. This may be because within species, seed size shows less variability than the number of seeds produced or total plant size (Harper et al. 1970) and is therefore considered to be fairly constant. However, wide ranges of intraspecific variation in seed size have been described, even at the level of differences among individuals within populations (Table 4.1). Such differences, some as much as five-fold, raise the question of whether there are important ecological and/or evolutionary consequences of intraspecific differences in seed size.

A number of studies have shown that seed size can significantly affect percent germination (Cavers and Harper 1966, Werner 1979, Weis

Table 4.1. Examples of differences in the mean size of seeds produced by individuals within a population.

Species	Maximum difference in seed size	Reference
Lupinus texensis	5X	Schaal 1980
Silene dioica	2X	Thompson 1981
Mirabilis hirsuta	3X	Weis 1982
Aster acuminatus	2X	Pitelka et al. 1983

1982, Pitelka et al. 1983, Gross 1984), the rate of germination (Schaal 1980, Weis 1982, Hendrix 1984), seedling size (Weis 1982, Schaal 1980, Pitelka et al. 1983, Gross 1984, Stanton 1984) and/or competitive ability (Black 1958, Gross 1984), and dispersal distance (Howe and Richter 1982). However, the results of these studies may not reflect natural patterns of seedling emergence and survival because most have been conducted under artificial conditions. Greenhouse and lab environments often exclude numerous, possibly size-specific, factors such as the presence of established vegetation, predators, and severe weather conditions, which can affect seedling emergence and survival. This problem has been illustrated by Stanton (1984) who found that in the greenhouse different sized seeds of Raphinus raphanistrum produced adult plants of similar size, but in the field, initial seed size significantly affected adult size and the number of flowers produced. Thus, to get an accurate picture of the ecological consequences of seed size, it is necessary to examine the effects of seed size under natural conditions in the field.

The absolute amount of energy available for seed production may limit reproduction and consequently, plants may show a trade-off between the size and number of seeds produced (Smith and Fretwell 1974, Wilbur 1977, Werner 1979). Therefore, even if large seeds are more likely to produce successful adults than small seeds, the production of large seeds will increase parental fitness only if the benefits derived from producing large seeds outweigh the cost of producing them, in terms of the reduction in seed number. In order to evaluate the advantages of producing seeds of a particular size, then, both the amount of resources invested per seed (cost) and the probability that a seed of that size will successfully establish (benefit) must be measured.

A comparison of the relative costs and benefits of producing seeds of particular sizes may be used to identify the optimum seed size (maximum benefit/cost ratio), that which will maximize fitness or the number of successful offspring produced (cf Wilbur 1977). In the absence of constraints on the response to selection, the mean phenotype in a population would be expected to approach the optimum predicted by the benefit/cost analysis.

The present study examines the effect of seed size on seedling emergence and survival and the cost/benefit ratios for producing seeds of different sizes for *Prunella vulgaris*, a short-lived, herbaceous perennial plant. Because the benefits of producing seeds of a given size may vary with habitat, the costs and benefits of producing seeds of particular sizes and the frequency distributions of the mean seed size produced were measured in four habitats. Four specific questions with respect to intraspecific differences in seed size are addressed: 1) Do intraspecific differences in seed size of the magnitude observed within a population have ecological consequences in the field? 2) Do the consequences of seed size differ among habitats? 3) What are the benefit/cost ratios for the production of seeds of different sizes? and 4) Do the sizes of seeds produced in each habitat correspond to the optimum size predicted by benefit/cost ratios?

MATERIALS AND METHODS

This study was conducted at the W.K. Kellogg Biological Station and the W.K. Kellogg Experimental Forest in Kalamazoo County, Michigan. *Prunella vulgaris* is a widespread weed which, in unmowed habitats, reproduces almost exclusively by seed (personal observation). In southwest Michigan, populations of *P. vulgaris* not subjected to mowing can be found in abandoned agricultural fields, along roads and paths, and in woodland clearings. In the present study, populations at four sites were used; two populations were located in an abandoned agricultural field (designated old-field center and old-field edge) and two in woodland clearings (designated deciduous woodland and coniferous woodland). These four sites represent contrasting habitats in which different mean sizes and numbers of seeds were produced (Table 2.1).

Seeds of *P. vulgaris* are dispersed beginning in October and continuing through the Winter. In the lab, 80% of fresh-collected seed will germinate within two weeks when placed on wet filter paper and exposed to light. In the field, germination does not occur until late April. Seeds do not remain dormant in the soil for more than one Winter.

Field and Laboratory Methods: In October, 1982, seeds were collected separately from each of the four study sites. Only a few large seeds were produced by plants in the field. Therefore in order to provide sufficient numbers of large seeds, some seeds from plants collected as rosettes from the appropriate field sites and maintained in the greenhouse were added to each seed collection. Plants collected from the field as rosettes, grown in pots and regularly watered in the greenhouse produced more large seeds than plants grown in the field ($\bar{X}$ field =0.505 mg, $\bar{X}$ greenhouse =0.977 mg).

Each seed collection, consisting of seeds collected from a single field site and seeds from plants collected as rosettes from that site and grown in the greenhouse, was then divided into six size classes of app

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approximately equal numbers of seeds using a South Dakota seed cleaner. The mean seed weight for each size class at each site was estimated by weighing fifty randomly selected seeds from each size class. Within each seed collection, the range of seed sizes produced at the site at which the seeds were collected determined the divisions between size classes. In general the range of sizes was from 0.25 to 1.0 mg but, in the deciduous woodland site, the smallest seeds produced weighed more than 0.6 mg. As a result, the smaller size classes at the deciduous woodland site had greater mean sizes than the smaller size classes for the other sites (Table 4.2).

A random sample of fifty seeds from each size class from each seed collection was tested for percent germination and viability in the laboratory. Seeds were placed on filter paper moistened with distilled water, maintained at room temperature and exposed to 16 hr incandescent light each day. Germination percent was determined after two weeks. All seeds that did not germinate were judged to be non-viable using a standard tetrazolium chloride test (Bonner 1974).

Within each field area, seventy 0.25m x 0.25m quadrats were permanently marked out and seeds were sown into their home sites (where they had been collected) as follows. Ten replicate quadrats were assigned to each seed size treatment at random. In November of 1982, one hundred seeds of the appropriate size were hand sown evenly across each quadrat from a height of 2 cm. In addition, ten control quadrats which received no seed input were used to monitor background seedling emergence, which was negligible.

During the following Spring (1983), the quadrats were examined every third day for newly emerged seedlings. Because, more than 99% of the

TABLE 4.2. Mean seed weight and percent viability determined in the lab for six seed size classes of each population.

	DECIDUOUS WOODLAND		CONIFEROUS WOODLAND		OLD-FIELD CENTER		OLD-FIELD EDGE	
Size Class	Weight (mg)	Viability (%)	Weight (mg)	Viability (%)	Weight (mg)	Viability (%)	Weight (mg)	Viability (%)
1	.65	86	.29	36	.28	4	.19	<2
2	.80	96	.53	100	.41	2	.30	<2
3	.86	80	.69	100	.50	4	.36	<2
4	.94	74	.91	96	.61	6	.50	10
5	.96	86	.97	100	.87	80	.87	100
6	1.0	100	1.0	100	1.1	100	.98	100

seedlings that emerged survived for at least one week, it is unlikely that many seedlings emerged and died without being recorded. Seedlings were censused at monthly intervals from June, 1983 to September, 1983 and in June, 1984. In July, 1984, the length of the longest leaf of each surviving seedling was measured.

The effects of differences in seed size on percent germination and post-emergence survival at each site were measured with analyses of variance using the ten quadrats sown with each size class as replicates. Analysis of variance was also used to compare the sizes (length of longest leaf) of seedlings which emerged from seeds of different sizes.

The benefit/cost ratios for producing seeds of particular sizes were calculated as follows; The benefit, or the probability of producing a successful seedling, was determined by multiplying the probability of seedling emergence by the probability of a seedling surviving to the end of the first growing season for a seed of a particular size. The weight of a seed was considered to be its cost. The ratio of benefit to cost gives the per gram benefit of producing a seed of a particular size and therefore takes into account differences in the numbers of seeds produced. An individual that produces seeds of a size with a higher benefit/cost ratio will produce a larger number of successful offspring per gram invested in seed production (i.e. have a higher fitness) than an individual that produces seeds of a size with a lower benefit/cost ratio. Thus comparison of benefit/cost ratios for seeds of different sizes will permit identification of the seed size that will maximize fitness in a particular habitat. The benefit/cost ratios for seeds of different sizes were compared using a separate analysis of variance for each site.

The extent to which seed size is genetically determined in _P. vulgaris_ was examined using reciprocal transplants of rosettes between the deciduous woodland habitat ($\bar{X}$ seed size = 0.773 mg) and old-field center habitat ($\bar{X}$ seed size = 0.453 mg). At each of these sites, 25 randomly selected rosettes were collected in the Spring of 1982, split into two parts of approximately equal size, and planted in four-inch plastic pots in the greenhouse. These plants were maintained in the greenhouse for four months to reduce carry-over effects due to the influence of their native environments. In October 1982, one rosette from each genetically identical pair was replanted in its native site and the second rosette was transplanted to the other site. The seeds produced in the following year by the transplants and replants were collected and weighed. The sizes of seeds produced by transplants and replants within each transplant site were compared using analysis of variance.

The frequency distributions of the mean seed size produced by individuals at each site were determined by collecting all of the seeds produced by at least 30 individuals and weighing a random subsample of thirty seeds in lots of ten.

RESULTS

Effects of seed size on seedling emergence and survival:

Mean percent germination increased significantly with increasing mean seed size at all four sites (Table 4.3). Percent survival of seedlings from emergence to August of the same year also increased with increasing seed size. Percent germination was highest at the deciduous

Table 4.3. Mean percent germination and survival from emergence to the end of the first growing season for the six seed size classes in each habitat. Means with the same superscript within a column do not differ significantly. Seed size class mean weights are given in Table 4.2.

SEED SIZE CLASS	DECIDUOUS WOODLAND Germination	DECIDUOUS WOODLAND Survival	CONIFEROUS WOODLAND Germination	CONIFEROUS WOODLAND Survival	OLD-FIELD CENTER Germination	OLD-FIELD CENTER Survival	OLD-FIELD EDGE Germination	OLD-FIELD EDGE Survival
1	20^{a}	79^{a}	$.3^{a}$	0^{a}	1.1^{a}	10^{a}	$.7^{a}$	0^{a}
2	23^{a}	81^{a}	5.2^{b}	22^{b}	1.4^{a}	10^{a}	$.4^{a}$	0^{a}
3	23^{a}	65^{a}	9.9^{c}	40^{c}	1.1^{a}	13^{a}	$.6^{a}$	5^{a}
4	$26^{a,b}$	76^{a}	10^{c}	$56^{c,d}$	2.9^{b}	38^{b}	4.6^{b}	36^{b}
5	$26^{a,b}$	76^{a}	11^{c}	$66^{c,d}$	20^{c}	72^{c}	19^{c}	73^{c}
6	31^{b}	80^{a}	10^{c}	$46^{c,d}$	30^{d}	81^{c}	18^{c}	63^{c}

woodland site for all seed size classes. Percent survival of seedlings was also high in the deciduous woods and did not differ among seedlings emerging from seeds of different sizes (Table 4.3). This may be because at this site, even the smallest size class was very large (Table 4.2) so that all seedlings that emerged had a high probability of survival. In the year following emergence (1984), there were no significant differences in the length of the longest leaf of plants that had emerged from seeds of different sizes at any site (Table 4.4). Because the length of the longest leaf is significantly correlated with seedling weight (r^2=.85, p<.01), this suggests that there is no effect of seed size on seedling size beyond the first growing season.

Selection on seed size:

In general, benefit/cost ratios for seeds of different sizes tended to increase with increasing seed size. In only one case (size classes five and six in the old-field edge habitat) was the cost of an increase in seed size significantly greater than the benefit (Figure 4.1).

The relationship between seed size and the probability of producing a successful offspring, defined as an established seedling (i.e. one that survives to August of the first growing season), per gram invested in seeds of a particular size differed among the four sites (Figure 4.1). At the deciduous woodland site, there were no statistically significant differences in benefit/cost ratio among seed size classes. At the coniferous woodland site, there was a threshold seed size (size class 2) above which all seed sizes yielded the same number of successful offspring per gram invested. In the old-field center, the benefit/cost ratio increased steadily with increasing seed size above size class

FIGURE 4.1

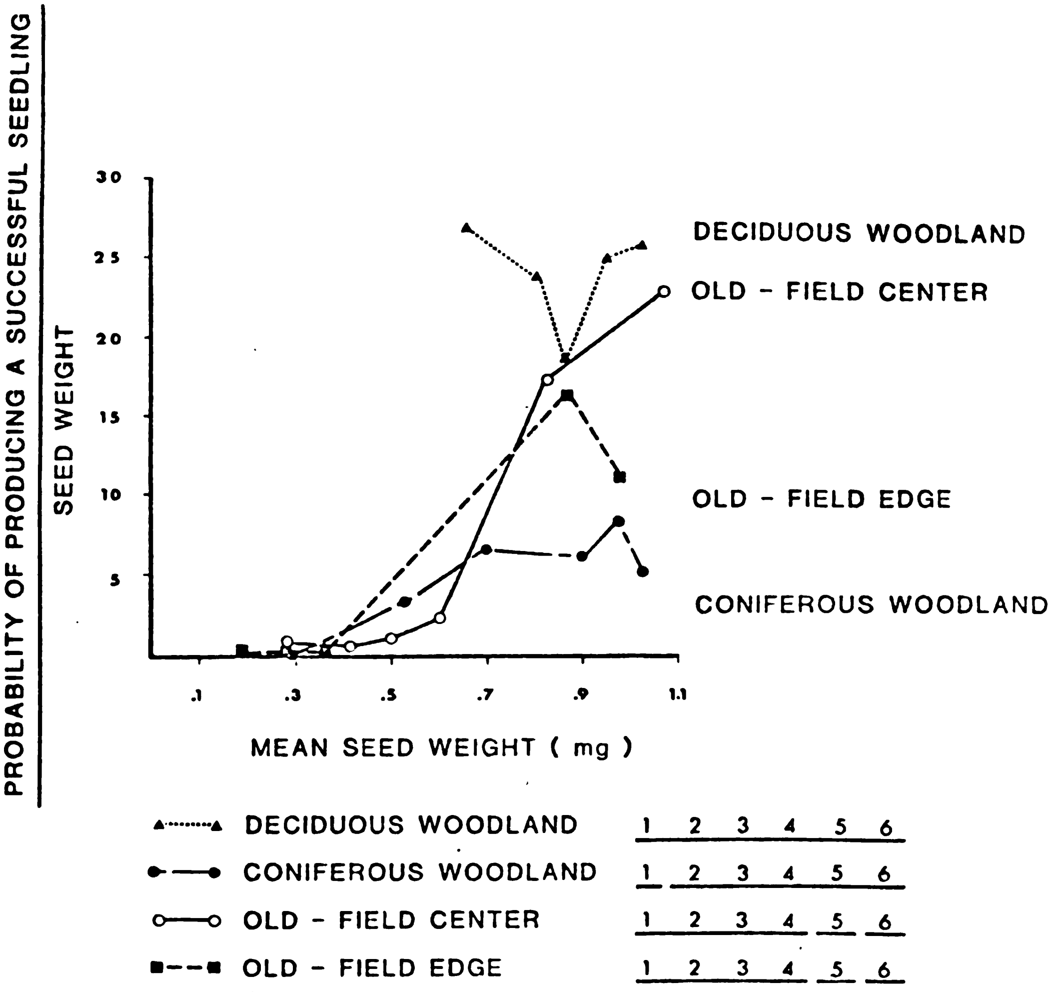

Figure 4.1. Benefit/cost ratios for each seed size class in each habitat. Values for each habitat are connected to show trends. Below the graph are the results of analyses of variance for the effect of seed size class on benefit/cost ratio. Size classes underlined by the same line do not differ significantly in benefit/cost ratio.

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Table 4.4. Mean length of the longest leaf (cm) one year after emergence for seedlings produced by seeds of the six seed size classes at each site. A length of --- indicates that no seedlings survived. P refers to the results of analysis of variance.

SEED SIZE CLASS	DECIDUOUS WOODLAND	CONIFEROUS WOODLAND	OLD-FIELD CENTER	OLD-FIELD EDGE
1	2.88	---	2.00	3.20
2	3.04	2.78	0.00	0.00
3	3.15	3.26	0.00	0.00
4	3.17	2.34	2.47	2.73
5	2.23	3.17	1.71	2.81
6	3.28	3.22	1.86	3.07
	$p<.42$	$p<.24$	$p<.61$	$p<.64$

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three, and at the old-field edge, seed size class five had the highest benefit/cost ratio.

Based on the patterns of benefit/cost ratios described above, the selection regimes for seed size over the range of seed sizes examined differ among sites: At the deciduous woodland site, no selection to produce seeds of a particular size was detected because there were no differences in the fitnesses (numbers of successful offspring produced) of individuals that produced seeds of different sizes. At the coniferous woodland site, there was selection to produce seeds larger than the threshold size. There was selection to maximize seed size at the old-field center site, and there was selection to produce seeds of an optimum size (size class 5) at the old-field edge site. It is important to note here that at the old-field edge site only, the addition of seeds from greenhouse-grown plants increased the range of seed sizes examined. In fact, all of the individuals at this site produced seeds that fell into the first three seed size classes (Figure 4.2, Table 4.2) and among these three size classes, there were no differences in the benefit/cost ratio and therefore no selection (Figure 4.1).

For the sites in which significant selection pressure on seed size was detected, it is of interest to compare the frequency distributions of the mean seed sizes actually produced by individuals at each site with the selection regimes described above (Figure 4.2). At the coniferous woodland site, many individuals produced seeds that were smaller than the threshold above which fitness was significantly increased. At the old-field center site, many individuals produced seeds that fell into the first three seed size classes above which there was a considerable increase in fitness.

Figure 4.2. Frequency distribution of mean weight of seeds produced by individuals growing in each habitat. The arrows mark in b) the mean weight of size class two, in c) the mean weight of size class three, and in d) the mean weight of size class five.

FREQUENCY DISTRIBUTIONS OF THE MEAN SEED SIZES OF INDIVIDUALS

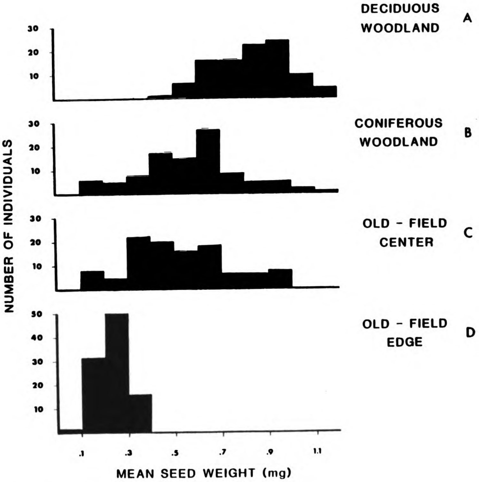

FIGURE 4.2

Within each rosette transplant site, there were no significant differences in the mean size of seeds produced by individuals replanted in their native sites and those transplanted from the opposing site (Table 3.7). There were, however, significant differences in seed size between transplant sites. The estimates of seed size for both transplants and replants at the deciduous woodland site are based on small samples because 80% of these individuals died before they set seed.

DISCUSSION

Effects of seed size on seedling emergence and survival:

In general, differences in initial seed size did lead to differences in percent germination and seedling survival in the field (Table 4.3). Differences in viability among seeds of different sizes are at least partly responsible for the effect of seed size on the probability of germination in the field (Table 4.2). In both old-field habitats, the three smallest size classes have very low viability and this contributes to the extreme difference between the probabilities that small and large seeds will produce successful seedlings in these habitats. It is not clear why so many of the seeds produced in old-field sites were non-viable. It may be that severe environmental conditions (eg. drought) prevent some seeds from developing completely, and that in years during which conditions are more favorable for seed production, more of these seeds would develop completely and be viable (cf. Stephenson 1981).

The differences among habitats in mean percent germination and survival and the relationship between seed size and percent emergence and survival may be due largely to the differences in the mean and range of seed sizes sown in each habitat (Table 4.2). For example, it is probable that there are no significant differences among size classes in seedling survival in the deciduous woodland habitat because all seeds are large enough to produce seedlings that have a high probability of survival or because a smaller range of seed weights was examined in this habitat. Thus the magnitude of the effects of seed size may be reduced if mean seed size is very large or if the range of seed weights examined is small.

Differences among habitats in environmental conditions which affect seedling establishment may also influence the relationship between seed size and percent emergence and survival. In a related study (see Chapter 3), large seeds were better able to emerge under an herbaceous canopy than were small seeds. Thus within a habitat in which a large amount of herbaceous cover is present, the advantages of large initial seed size may be greater than in a habitat in which there is little herbaceous cover.

One year after seedling emergence, no effect of seed size on seedling size could be detected. In fact, the consequences of large initial seed size do not appear to last beyond the establishment phase of the life cycle, as it has been demonstrated that seedling size is a good predictor of future survival and the probability of flowering for _P. vulgaris_ (Chapter 2). In contrast, Stanton (1984) found that differences in initial seed size had significant effects on flower production in the annual _Raphinus raphanistrum_. This differences may be due to the longer juvenile period (at least 2 yr) experienced by _P. vulgaris_ and/or the greater heterogeneity of the habitats in which _P. vulgaris_ was sown. _Raphinus raphanistrum_ was sown in a prepared field and was the first species to emerge in the Spring. Thus there was probably less environmental heterogeneity due to the presence and amount of surrounding vegetation than in the undisturbed plots of established, perennial vegetation into which *P. vulgaris* was sown. The relationship between initial seed size and seedling size and/or performance in *P. vulgaris* may deteriorate over time as differences due to variation in micro-environmental conditions accumulate.

Both the present study and the work of Stanton (1984) demonstrate that intraspecific differences in seed size can have important ecological consequences in the field. However, the presence, strength, and duration of these effects may depend on the habitat to which seeds are dispersed, the range and mean of seed sizes being examined, and the longevity of the plants.

Selection on seed size:

In general, benefit/cost ratios began to increase sharply as seeds reached a weight of approximately 0.6 mg at all sites. However, at the deciduous woodland site, all seeds produced weighed more than 0.6 mg and at the old-field edge site, all seeds produced weighed less than 0.5 mg, and at these two sites, selection did not favor the production of seeds of a particular size. This may be because when mean seed size is large, all seeds produced are large enough to have a high probability of producing established seedlings, and differences among these probabilities are due mainly to chance environmental effects. Similarly, when all seeds are small, so few may become established that there is a large element of chance involved in determining which seeds are successful.

There are several plausible explanations for the lack of correspondence between the optimum seed sizes predicted from the benefit/cost ratios and the actual frequency distributions of the mean seed size produced by individuals in each habitat. One possibility is that the fitness associated with producing seeds of a particular size depends on some aspect of the environment which fluctuates among years. For example large seeds might be favored in a dry year because they can produce a more extensive root system, but smaller seeds could be favored in a wet year because seedlings without an extensive root system also survive and, because they are energetically less costly, more small seeds can be produced with a given amount of resources. Thus the optimum seed size may differ among years depending on the amount and timing of rainfall. Under such circumstances, the selection pressure on seed size may not be consistent or strong enough over time to produce a response.

Even if the selection pressure were consistent between years, seed size might be constrained by developmental and/or genetic relationships with other traits that have not been considered in the present study (cf. Lande and Arnold 1983). For example, an increase in seed size may be linked to a decrease in the number of seeds produced per flower. If a large number of seeds per flower increases fitness more than large seed size, an increase in seed size may not actually increase fitness. If constraints of this sort exist, then the simple trade-off between seed size and number used to define the cost portion of the benefit/cost ratio will not accurately reflect the actual total cost of producing seeds of a particular size.

Gene flow between populations with different genetically determined seed sizes could also hinder the response to selection to produce seeds of a particular size. However the differences in the sizes of seeds produced in the habitats concerned here do not appear to be genetically based (Table 3.7).

Even if selection consistently favored the production of large seeds and seed size was not genetically and/or developmentally constrained, if seed size were strongly affected by environmental conditions, the response to selection would be slow. In fact, the results of the reciprocal transplant between the deciduous woodland habitat and the old-field center habitat suggest that there is environmental influence on seed size that may mask the expression of genetic variation for the size of seeds produced (Table 3.7).

The significant phenotypic plasticity in seed size is surprising in the light of the traditional view that seed size is a relatively non-variable trait (Harper et al. 1970). However, a number of studies report considerable phenotypic plasticity in seed size (Table 4.1) and recent theoretical treatments of life history variation suggest that phenotypic plasticity of life history characteristics, including propagule size, may be advantageous if the environmental conditions (eg. amount and distribution of rainfall) that the propagules must face cannot be predicted at the time of offspring production (Real 1980, Caswell 1983, Lacey et al. 1983, Kaplan and Cooper 1984).

In summary, seed size in _P. vulgaris_ affects the probability of seedling emergence and survival through the first growing season. However, the effect depends on habitat characteristics and the mean and range of seed size examined. Selection to produce seeds of a particular size was present in two of the four habitats examined, but there was little evidence of concurrence with the predicted optimum seed sizes.

This could be due to year to year variation in the direction and intensity of selection, genetic and/or developmental constraints on seed size, and/or a strong environmental influence on seed size.

CHAPTER FIVE

COMPONENTS OF SEED YIELD AND THE RELATIONSHIP BETWEEN YIELD AND FITNESS IN PRUNELLA VULGARIS

Seed yield, or the total weight of seeds produced by a plant, is determined by the product of a number of components. For example, seed yield in peas is determined by the number of pods/plant X the number of seeds/pod X mean weight/seed. Agriculturalists interested in maximizing seed yield in crop species have studied the sources of variation in yield components and how components interact to determine total yield (eg. Dewey and Lu 1959, Olsson 1960, Adams 1967, Rasmussen and Cannell 1970). More recently, population biologists have recognized the parallels between the study of components of seed yield in crop plants and the study of fitness components in natural populations (Primack 1978, Primack and Antonovics 1981, Maddox and Antonovics 1983, Pritts 1984). However, to date, there is little information available concerning variability of yield components, or the relationships among yield components in natural populations. Further, although seed yield is often equated with fitness, the relationship between yield and fitness in natural populations of plants has not been examined.

Variation among individuals in yield components can result in differences in total yield and/or individual fitness. Both genotype and environment may contribute to these differences. Primack and Antonovics (1981) have presented evidence of heritable variation for several yield components in Plantago lanceolata. Others have shown that some yield components exhibit considerable plasticity in response to plant size and environmental conditions, that some components exhibit more variability than others, and that different yield components may respond to different environmental cues (Johnson and Cook 1968, Willson and Price 1980, Primack and Antonovics 1981, Lee and Bazzaz 1982, Stephenson 1984, Pritts 1984). Relationships among yield components, whether or not they have a genetic basis, can affect the potential for changes in total yield (Adams 1967). For example, many crop species exhibit developmentally induced negative relationships among yield components so that a phenotypic increase in one component (eg. the number of seeds per pod) results in a decrease in another component (eg. the mean weight of seeds) and total yield remains unchanged (Adams 1967). Changes in fitness may also be constrained by relationships between yield components (cf. Lande and Arnold 1983).

Individual plant fitness has often been estimated using only the total weight (yield) or number of seeds produced. But seed number alone may not be an adequate predictor of parental fitness because initial seed size can significantly affect seedling size and probability of survival (Harper 1977, Stanton 1984, Chapter 3) and therefore parental fitness. A more accurate estimate of parental fitness might be obtained by incorporating an appropriate measure of the quality as well as the quantity of offspring produced by an individual.

This study examines variation in yield components and the relationships between yield components within and between ten local populations of the perennial weed Prunella vulgaris in field and greenhouse studies. Seed yield in P. vulgaris is the product of five components; (1) the total number of flowering stems, (2) the number of inflorescences per stem, (3) the number of flowers produced per inflorescence, (4) the number of seeds produced per flower, and (5) the mean weight per seed. An estimate of fitness based on both the size and number of seeds produced is compared with total yield.

MATERIALS AND METHODS

Species Description: *Prunella vulgaris* (L) is a weedy, perennial mint (Labiatae) which reproduces mainly by seed in the populations examined in this study. Locally, this species is found in a variety of habitats including abandoned agricultural land, roadsides, lawns, and woodland clearings.

During most of the year, individual plants form compact rosettes up to fifteen cm in diameter. Between July and October, from one to ten or more erect flowering stems may be produced. Each flowering stem bears a terminal inflorescence (spike) and some also bear from one to six, usually paired, axial inflorescences at intervals along the flowering stem. Within a flowering stem, flowers in the terminal inflorescence open first with those in axial inflorescences following roughly in order of decreasing length of the inflorescence pedicel. A single individual may have open flowers for more than a month. The purple, tubular flowers are self-compatible and will set abundant seed without pollinator service (Nelson 1963, Winn unpublished data). Each flower contains one ovary with four ovules. A maximum of four seeds may develop per flower. Mature seeds are enclosed in a persistent calyx which greatly facilitates the collection of seed in the field. There are no specialized means of dispersal and seeds do not survive in the soil for more than one year (A. Winn, personal observation).

Experimental Methods: Components of seed yield were measured for flowering individuals in ten populations of P. vulgaris in southwestern Michigan. Four of these populations were located in woodland habitats and six were located in old-field habitats. In two of the woodland populations and two of the old-field populations, yield components were measured for two consecutive years. These four populations will be referred to as the main populations.

In May 1982 (Year 1), a minimum of 100 individuals within a defined area in each of the four main populations were permanently marked with numbered stakes. At the same time, ten rosettes outside of the defined areas at each site were transplanted to six-inch plastic pots in the greenhouse. From each individual that flowered, inflorescences were collected as they matured in the field and the greenhouse (early August through late October). For each inflorescence, all flowers and the number of filled seeds in each of ten flowers (or all flowers if the total was less than 10) were counted and twenty seeds (or all seeds if the total was less than twenty) were weighed as a group to the nearest .001 mg.

In order to calculate the relationships between each yield component and total plant weight, 25 additional individuals from the old field and 25 from the woods were measured as described above, collected, dried at 60 C for three days and weighed to the nearest .01 g. Regression equations relating plant weight to yield components were derived from these data and used to estimate the total weights of plants that were not harvested.

Twenty-five randomly chosen non-flowering individuals were exhumed from an area adjacent to the marked individuals at one of the main woodland populations (designated W1) and one of the main old-field populations (F1), and were split into two rosettes of approximately equal size. These pairs of genetically identical rosettes were transplanted into four-inch pots and grown in the greenhouse during the Summer of 1982. In October, 1982, the rosettes were replanted according to the following scheme; one from each pair of genetically identical rosettes was replanted in its site of origin (these individuals will be referred to as replants) and the second rosette was transplanted to the other site (these individuals will be referred to as transplants).

In the Summer and Autumn of the next year (Year 2), inflorescences were again collected from marked individuals in each main population, from the six additional local populations, and from transplants and replants. The number of flowers per inflorescence, seeds per flower, and average weight per seed were determined in the lab. Yield was estimated as the number of flowering stems per individual X the mean number of inflorescences per flowering stem X the mean number of flowers per inflorescence X the mean number of seeds per flower X mean weight per seed for each individual in each year in the field and in the greenhouse in Year 1 only.

Analysis of Yield Component Data: Means and coefficients of variation were computed for each yield component within each field population, each greenhouse population, and for transplants and replants. Statistics for field populations were calculated separately for Year 1 and Year 2.

Both path coefficients and correlation coefficients were calculated to determine the relationships between yield components. Correlation coefficients measure the total relationship between two components and thus describe the actual patterns observed. However, the interpretation of simple correlations is complicated if there are interactions among the components. Each correlation between two components is determined by the direct relationship between those two and indirect relationships due to effects mediated through each of these component's relationships with all other components. For example, the number of stems/plant may have no direct effect on seed weight but may be correlated with seed weight because both components are correlated with the number of flowers/inflorescence. Path coefficient analysis (Wright 1921), a partial regression technique, was used to determine the direct relationships between yield components and between each component and total yield. This type of analysis has been used by agricultualists to isolate the direct relationships among yield components (Dewey and Lu 1959, Adams 1967, Duarte and Adams 1972). It involves partitioning a simple correlation coefficient between two components into a direct effect (a standardized partial regression coefficient or path coefficient) and an indirect effect due to relationships of each component with all other components in the system. Thus path coefficient analysis is used to measure the direct relationship between two components eliminating complications due to response to a common third component. When both path coefficients and correlation coefficients are calculated for a set of yield components, the extent to which indirect effects (total - direct) either cause or obscure a relationship between two yield components can be determined.

Correlation coefficients and path coefficients were calculated between yield components for individuals within populations in both years and between means of the ten populations measured in Year 2. All data were normalized using log transformations prior to analysis.

Estimation of Fitness: In order to calculate the relationship between total yield and fitness, the probability of seedling establishment as a function of seed size was measured in the field using a procedure that was described in Chapter Three. Briefly, this procedure involved sowing seeds of known size into separate, permanently-marked field plots from which other seeds of P. vulgaris had been excluded. Six size classes of seeds (1000 seeds/size class) were sown at the site of each main population in the Autumn of Year 1 and seedling emergence and survival were monitored during the following Spring and Summer.

The probability of seedling establishment, defined as the probability of emergence and survival to the end of the first growing season, was determined for each seed size class at each site by dividing the number of seedlings that survived by the number of seeds sown. Analysis of variance was used to determine whether seed size classes differed in the probability of producing established plants at each site.

Estimates of fitness were determined for flowering individuals using the relationship between seed size and probability of establishment in the following equation;

$$\text{Fitness} = \sum_{i=1}^{n} S_i \; E_i$$

where S_i = the total number of seeds produced by inflorescence i

E_i = the probability of seedling establishment corresponding to the mean seed size produced in inflorescence i

n = the total number of inflorescences produced.

Therefore, fitness was estimated as the total expected number of established seedlings per inflorescence summed for all inflorescences produced by an individual. Calculations were done on a per inflorescence basis because in _P_. _vulgaris_ inflorescences borne axially produce seeds that are significantly smaller than those produced by the terminal inflorescence on the same flowering stem (A. Winn, unpublished data) and that seed size affected seedling emergence (Chapter Three). Correlation coefficients between estimated fitness and total yield and path coefficients between estimated fitness and each yield component were calculated for log-transformed data within each main population.

RESULTS

Coefficients of Variation:

Coefficients of variation demonstrate differences in the variability of the five yield components (Table 5.1). The magnitudes of coefficients of variation (c.v.'s) were quite consistent in all populations, in both years, and in the greenhouse were. In all cases, the number of stems/plant and the number of inflorescences/stem had the highest c.v's and, in most cases, seed weight had the lowest c.v's. Coefficients of

Table 5.1. Coefficients of variation (100 X standard deviation/mean) for yield components of P. vulgaris collected from the four main populations in 1982 and 1983 and within groups of individuals collected from these populations and grown in the greenhouse. 'W' = woodland population, 'F' = old-field population.

	Yield Component					
Population	Number of Stems/ Plant	Number of Inflorescences/ Plant	Number of Flowers/ Inflorescence	Number of Seeds/ Flower	Seed Weight	Number of Plants
Year 1 Field-Collected						
W1	71	81	38	41	23	43
W2	65	77	26	36	34	46
F1	64	81	25	27	30	74
F2	72	58	34	40	18	44
Year 2 Field-Collected						
W1	75	30	36	47	26	48
W2	76	51	41	37	29	22
F1	70	61	45	43	20	22
F2	33	95	37	50	21	43
Year 1 Greenhouse						
W1	43	33	33	15	7	9
W2	58	40	12	11	9	10
F1	37	25	14	15	15	10
F2	47	31	23	6	7	10

variation for yield components in the greenhouse were low relative to those in the field (despite the smaller sample sizes in the greenhouse) probably because of reduced environmental heterogeneity in the greenhouse environment.

Means of Yield Components:

Means of yield components differed among populations, between years, and among habitat types (old-field, woodland, and greenhouse) (Table 5.2). Means of all yield components except the number of stems/plant and the number of inflorescences/stem differed significantly among field populations in Year 1. In Year 2, means for all yield components differed among populations. But in the greenhouse, only the number of stems/plant differed significantly among source populations (Table 5.2).

For almost all yield components and for total yield, means were lower in Year 2 than in Year 1 (Table 5.2). A prolonged drought during the 1983 growing season may have been responsible for the decrease in yield. Nevertheless, patterns among populations in the ranking of yield component means were consistent between years for the number of stems/plant, the number of flowers/inflorescence, and seed weight.

In the field, some yield component means were more similar among woodland populations or among old-field populations than between the two habitat types (Table 5.2). Woodland populations tended to produce more stems/plant and larger seeds than old-field populations. Old-field populations generally produced more inflorescences/stem and flowers/inflorescence. There was no consistent pattern for the number of seeds/flower.

Except for the number of flowers/inflorescence, yield components for

Table 5.2. Means of yield components for woodland (W) and old-field (F) populations in Years 1 and 2 and greenhouse populations in Year 1. Standard errors are given in parentheses.

	Yield Component							
Population	#Stems/ Plant	#Inflor./ Stem	#Flowers/ Inflor.	#Seeds/ Flower	Seed Weight (mg)	Yield (mg)	Plant Weight (g)	Number of Plants
Year 1 - Field								
W1	2.0 (.2)	1.9 (.2)	18 (1.0)	1.76 (.11)	.773 (.03)	115 (30)	1.60 (.21)	43
W2	1.8 (.2)	2.5 (.3)	21 (.8)	2.24 (.12)	.523 (.03)	111 (17)	1.70 (.16)	46
F1	1.7 (.1)	2.1 (.2)	35 (1.0)	2.76 (.09)	.453 (.02)	165 (22)	1.41 (.10)	74
F2	1.5 (.2)	2.7 (.2)	22 (1.0)	2.78 (.17)	.296 (.01)	69 (12)	0.75 (.11)	44
Year 2 - Field								
W1	1.9 (.2)	1.1 (.05)	12 (.6)	1.94 (.13)	.736 (.03)	34 (6)	1.11 (.17)	48
W2	1.8 (.3)	1.4 (.15)	12 (1.0)	2.03 (.16)	.665 (.04)	41 (10)	1.13 (.24)	22
W3	1.3 (.1)	1.4 (.20)	15 (1.1)	0.89 (.13)	.763 (.04)	21 (5)	0.73 (.11)	30
W4	1.2 (.1)	1.1 (.03)	14 (1.0)	1.15 (.12)	.378 (.01)	9 (1)	0.58 (.07)	55
F1	1.4 (.2)	3.8 (.50)	22 (2.1)	1.54 (.14)	.376 (.02)	58 (10)	1.03 (.16)	22
F2	1.2 (.1)	1.5 (.22)	17 (1.0)	1.92 (.15)	.276 (.01)	16 (3)	0.25 (.07)	43
F3	1.2 (.1)	1.5 (.19)	17 (1.1)	2.35 (.11)	.492 (.02)	41 (10)	0.38 (.08)	36
F4	1.1 (.1)	2.5 (.49)	17 (1.0)	1.54 (.12)	.379 (.01)	29 (7)	0.39 (.13)	17
F5	1.5 (.3)	2.2 (.31)	21 (1.3)	2.04 (.15)	.412 (.02)	60 (16)	0.79 (.19)	23
F6	3.2 (.4)	1.7 (.68)	16 (1.0)	1.95 (.11)	.339 (.01)	68 (14)	1.60 (.29)	38
Year 1 - Greenhouse								
W1	2.0 (.3)	7.4 (.80)	23 (3.5)	3.70 (.09)	.938 (.04)	1101 (197)	-----	9
W2	1.9 (.4)	8.0 (1.0)	22 (2.5)	3.42 (.12)	1.030 (.03)	1061 (173)	-----	10
F1	3.4 (.4)	6.3 (.50)	23 (1.0)	3.40 (.16)	1.040 (.05)	1162 (288)	-----	10
F2	2.2 (.3)	8.4 (.84)	21 (1.5)	3.67 (.07)	.927 (.02)	1138 (110)	-----	10

greenhouse populations, from which pollinators were excluded, were considerably greater than for field populations (Table 5.2). This suggests that environmental conditions for seed production were less than optimal in the field and seed production in the field was probably resource-limited. Further, patterns of differences among yield component means in the field were not necessarily similar to those observed in the greenhouse. For example, in the field, W1 had the largest mean seed size and F2 had the smallest mean seed size. In the greenhouse, however, there was no significant difference between the mean seed sizes of individuals collected from W1 and F2. In fact, mean seed sizes for individuals collected from W2 and F1 were slightly greater than those for individuals collected from the population (W1) that produced the largest seeds in the field (Table 5.2).

In comparisons between transplants and replants at the old-field planting site, there were no significant differences between the yield component means except in the number of stems/plant and the number of inflorescences/stem which were higher for transplants from the woodland site (Table 5.3). As a result of these differences, total yield also differed significantly between transplants and replants. At the woodland site, no significant differences between transplants and replants were observed but sample sizes were small because 80% of transplants and replants wilted and died after flowering (Table 5.3). There was no visible damage to the plants and the cause of death was undetermined. Between the two transplant sites, there were significant differences for all yield components except the number of seeds/flower. Individuals growing in the woodland habitat produced fewer stems/plant, inflorescences/stem, and flowers/inflorescence but heavier seeds than

Table 5.3. Means of yield components for individuals transplanted reciprocally between a woodland (Wl) and an old-field (Fl) site. Within a column, means with the same superscript are not significantly different from one another.

Yield Component

Source	Site	#Stem/ Plant	#Inflor/ Stem	#Flowers/ Inflor.	#Seeds/ Flower	Seed Weight (mg)	Yield (mg)	N
Wl at	Fl	3.7^a	1.9^a	16^a	2.0^a	$.349^b$	85^a	22
Fl at	Fl	2.6^b	1.4^b	16^a	1.9^a	$.326^b$	43^b	16
Wl at	Wl	1.9^c	1.0^c	6.3^b	2.0^a	$.493^a$	11^c	7
Fl at	Wl	1.4^c	1.0^c	6.5^b	1.5^a	$.395^a$	5^c	5

individuals growing in the old-field habitat regardless of source. This is generally consistent with the pattern of differences observed among all the woodland and old-field populations examined (Table 5.2).

Relationships between Yield Components:

Within populations, correlation coefficients (Table 5.4) and path coefficients (Table 5.5) were similar indicating that indirect relationships (total - direct) among yield components were weak. Therefore, for convenience, only the path coefficients will be discussed here. In all, 140 path coefficients were computed. At the $p<.05$ level of significance, up to 7 relationships may appear to be significant as a result of chance alone. Because it is impossible to distinguish which relationships are significant due to chance, only relationships which were significant for several populations will be discussed in detail. Both positive and negative path coefficients among yield components were observed within field populations in both years (Table 5.5). Although most relationships were weak and not significant, 15 significant positive relationships and five significant negative relationships between yield components were found.

Significant positive relationships between the number of flowers/inflorescence and seed weight were found in six of the fourteen population-year combinations, and these two yield components were positively correlated in all twelve of the fourteen combinations. The number of inflorescences/stem was significantly positively related to seed weight in three cases. Negative relationships between the number of inflorescences/stem and the number of flowers/inflorescence and positive relationships between the number of flowers/inflorescence and the number

Table 5.4. Coefficients of correlation between yield components within populations in Years 1 and 2.

	Relationship										
	#Stems/Plant with;				#Inflor/Stem with;			#Flowers/Inflor. with;		#Seeds/Flower with;	
	#Inflor /Stem	#Flowers /Inflor.	#Seed /Flower	Seed Weight	#Flowers /Inflor.	#Seed /Flower	Seed Weight	#Seed /Flower	Seed Weight	Seed Weight	Number of Plants
Year 1 - Field											
W1	.33*	.21	.13	.30*	-.09	.12	-.02	-.14	.10	.11	43
W2	.07	.08	-.02	-.01	-.02	-.02	.23	.19	.33*	.24	46
F1	.12	-.08	.19	-.12	.07	.05	.28*	.13	.13	.43**	73
F2	.08	.08	-.02	.10	-.33*	.08	-.15	-.03	.45**	-.22	44
Year 2 - Field											
W1	.14	.02	.05	.17	-.08	.09	-.07	-.22	.01	-.31*	48
W2	.29	.18	-.10	-.15	.19	-.09	.15	-.15	.39	-.06	22
W3	-.20	.32	.18	-.10	-.09	.40**	.14	.01	.18	.07	30
W4	.08	-.04	-.23	.03	-.05	-.14	.11	.31*	.20	.14	53
F1	.14	-.12	-.01	-.32	-.56**	.31	-.13	.10	.38	.12	22
F2	-.05	.01	.19	-.06	-.07	.09	.16	.20	.42**	.07	43
F3	.04	.18	-.01	.08	.09	.17	.05	.34*	.54**	.03	36
F4	.15	.17	.24	.15	.12	.25	.28	.27	.58*	-.17	17
F5	-.12	.22	.20	.17	-.20	-.15	.22	.11	.50*	.31	23
F6	.25	-.04	.26	-.12	-.17	.06	.25	.06	.26	.19	38

* Significant at the .05 level
** Significant at the .01 level

Table 5.5. Path Coefficients among yield components within each population in Years 1 and 2.

	Relationship										
	#Stems/Plant with;				#Inflor./Stem with;			#Flowers/Inflor. with;		#Seeds/Flower with;	
	#Inflor /Stem	#Flowers /Inflor.	#Seeds /Inflor.	Seed Weight	#Flowers /Inflor	#Seeds /Flower	Seed Weight	#Seeds /Flower	Seed Weight	Seed Weight	Number of Plants
Year 1 - Field											
W1	.33*	.27	.14	.33	-.17	.06	-.14	-.17	.03	.09	43
W2	.07	.08	-.03	-.05	-.02	-.02	.25	.20	.30*	.19	46
F1	.12	-.10	.20	-.24*	.06	.02	.26**	.15	.06	.45**	73
F2	.08	.11	-.02	.06	-.34*	.08	.01	.01	.45**	-.21	44
Year 2 - Field											
W1	.14	.04	.05	.20	-.09	.06	-.08	-.21	-.07	-.33*	48
W2	.29	.13	-.07	-.27	.16	-.04	.15	-.13	.41	-.01	22
W3	-.20	.32	.28	-.17	-.03	.45*	.11	-.04	.24	.05	30
W4	.08	-.03	-.20	.04	-.05	-.10	.11	.30*	-.18	-.09	53
F1	.14	-.04	-.03	-.29	-.56**	.54*	.14	.41	.43	.03	22
F2	-.05	.01	.20	-.06	-.07	.12	.22	.22	.44**	-.03	43
F3	.04	.09	-.08	-.03	.17	.14	.02	.34*	.60**	-.18	36
F4	.15	.16	.18	.10	.10	.19	.30	.22	.65**	-.44*	17
F5	-.12	.20	.17	.04	-.17	-.13	.38*	.04	.51*	.30	23
F6	.25	.01	.26	-.25	-.17	.01	.36*	.07	.30	.22	38

* Significant, $p < .05$.

** Significant, $p < .01$.

of seeds/flower and between the number of inflorescences/stem and the number of seeds/flower were each observed in two of the fourteen population-year combinations. The relationship between the number of seeds/flower and seed weight was positive in one case and negative in two cases.

Path coefficients and correlation coefficients were also determined for the relationships between population means for yield components using the ten populations analysed in Year 2. Again, path and correlation coefficients were similar and indirect effects were weak (Table 5.6) so only the path coefficients will be described. Although several strong relationships were identified, the only significant positive relationship was between the number of stems/plant and the number of flowers/inflorescence. One trend observed within populations, the positive relationship between the number of flowers/inflorescence and seed weight (Table 5.5), was reversed among population means (Table 5.6). Among populations, the path coefficient between the number of flowers/inflorescence and seed weight was strongly but not significantly negative (the correlation coefficient was significant, however).

The Relationships between Yield Components and Plant Size:

Among the plants harvested for biomass regression, yield components explained 93% (multiple $r=.96$, $p<.01$) of the variation in total plant weight at the woodland site and 91% (multiple $r=.95$, $p<.01$) at the old-field site. The path coefficients between each yield component and plant weight were mostly positive (Table 5.7). This was also true of the path coefficients between means of each population yield component and mean plant weight (Table 5.7). Both within the two sets of harvested

Table 5.6. Correlation coefficients and path coefficients among Year 2 population means for yield components.

	Relationship										
	#Stem/Plant with;				#Inflor/Stem with;			#Flowers/Inflor. with;		#Seeds/Flower with;	
	#Inflor. /Stem	#Flowers /Inflor.	#Seeds /Flower	Seed Weight	#Flowers /Inflor.	#Seeds /Flower	Seed Weight	#Seeds /Flower	Seed Weight	Seed Weight	Number of Populations
CORRELATION COEFFICIENT	-.11	-.11	.31	-.15	$.80^{**}$	-.06	-.36	.06	$-.61^{*}$	-.19	10
PATH COEFFICIENT	-.15	-.11	.34	-.04	$.79^{*}$	.00	.32	.15	-.89	-.14	10

* Significant, $p < .05$.
** Significant, $p < .01$.

Table 5.7. Path coefficients between total plant weight and yield components for plants harvested from the woodland and the old-field in Year 2 and for the means of all populations in Year 2 using estimated plant weights.

	Yield Component				
Field Site	#Stems/ Plant	#Inflor./ Stem	#Flowers/ Inflor.	#Seeds/ Flower	Seed Weight
Woodland	.94**	.24**	.15*	.07	.04
Old-Field	.53**	.79**	.27*	.09	.05
All 1983 Populations	.90**	.34	.05	−.21	.45

* Significant at the .05 level.
** Significant at the .01 level.

Table 5.8. Mean seed weights (mg) and the probability (E_i) of producing an established seedling (E_i) for the six seed size classes in each of the four main populations. Results of ANOVA for the effect of seed size class on E_i in each population are given in the last row.

	Population							
	W1		W2		F1		F2	
Seed Size Class	Weight (mg)	E_i	Weight (mg)	E_i	Weight (mg)	E_i	Weight (mg)	E_i
1	.65	.174	.29	.000	.28	.002	.19	.000
2	.80	.193	.53	.018	.41	.003	.30	.000
3	.86	.156	.69	.145	.50	.005	.36	.001
4	.94	.242	.91	.054	.61	.015	.50	.021
5	.96	.203	.97	.072	.87	.143	.87	.144
6	1.0	.260	1.0	.055	1.1	.243	.98	.113
P	>.35		<.01		<.01		<.01	

plants and among populations means, the relationships between weight and the number of seeds/flower and seed weight were low and non-significant (Table 5.7). Among population means, the relationships between the number of inflorescences/stem and the number of flowers/inflorescence and weight were also not significant (Table 5.7).

The Relationship Between Seed Yield and Fitness:

In general, probability of seedling establishment increased with increasing initial seed size (Table 5.8). Differences in seed size had no effect on probability of seedling establishment at one woodland site (W1) probably because all seeds produced were large. However, at the other woodland site (W2) and at both old-field sites, larger seeds had a significantly greater probability of producing established seedlings than small seeds. The effect of seed size on the probability of seedling establishment differed among populations (Table 5.8) because of differences among sites in the conditions for seedling establishment and in the mean and range of seed sizes produced in each population (see Chapter 3).

Within each year, populations differed in mean fitness per individual calculated as described above. There were also significant differences within populations between years in mean fitness (Table 5.9).

Individual fitness tended to be highly correlated with total seed yield in all populations except one of the old-field populations (F2) in both years (Table 5.10). This population had the lowest mean seed size (Table 5.2) and, in both years, a large proportion of the individuals which flowered produced no seeds that were large enough to produce established seedlings (i.e. estimated fitness was zero). Because so few

Table 5.9. Mean number of established seedlings produced per individual (fitness) in each population in Years 1 and 2.

	Fitness	
Population	Mean	Standard Error
Year 1		
W1	26.7	8.2
W2	6.0	1.2
F1	11.7	2.2
F2	0.8	0.3
Year 2		
W1	9.5	1.7
W2	2.5	0.6
F1	0.5	0.1
F2	0.02	0.01

Table 5.10. Path coefficients between fitness and yield components within each main population in Year 1 and Year 2 and the correlation between total yield and fitness for each population.

	Yield Component Relationship					
Population	#Stem /Plant	#Inflor. /Stem	#Flowers /Inflor.	#Seeds /Flower	Seed Weight	Yield
Year 1						
W1	.46**	.47**	.41**	.40**	.01	.98**
W2	.31**	.54**	.28**	.19*	.28**	.87**
F1	.31**	.50**	.02	.22**	.41**	.86**
F2	.13	.13	.04	.45**	.08	.43**
Year 2						
W1	.55**	.36**	.32**	.59**	-.01	.89**
W2	.24	.49**	.52**	.37**	-.03	.84**
F1	.47**	.69**	.27**	.35**	.33**	.96**
F2	.02	-.42**	.03	.04	-.36*	-.28

* Significant, $p < .05$.
** Significant, $p < .01$.

individuals had fitness greater than zero, the correlation between seed yield and estimated fitness was low for this population in both years, and most yield components were not significantly related to estimated fitness. In the other three populations, path coefficients between each yield component and fitness were mostly positive but were often lower for seed weight than for the other yield components (Table 5.10).

DISCUSSION

Yield Component Variability

Because yield was calculated as the product of all yield components, all components must be positively correlated with total seed yield. However total yield is not equally affected by differences in each yield component. The most variable component will contribute most to variation in total yield unless there are strong relationships between yield components (Primack 1978). Within populations of *P. vulgaris*, there are few significant relationships between yield components (Table 5.5), therefore, the number of stems/plant and the number of inflorescences/stem which have the highest c.v.'s contribute most and seed weight which has the lowest c.v. (Table 5.1) contributes least to differences in total yield. Similarly, Primack (1978) found that within 29 species of the genus *Plantago*, total seed yield was most affected by the number of inflorescences per plant and the number of capsules per inflorescence and least affected by the number of seeds per capsule and seed weight.

Components such as the number of stems/plant and the number of inflorescences/stem are the products of the indeterminate processes of growth therefore one might expect them to be more variable than components such as #seeds/flower and seed weight which are either products of determinate processes or have experienced strong stabilizing selection (Primack and Antonovics 1981). In P. vulgaris, the number of seeds/flower can vary only between zero and four because each flower has only four ovules. Variation in seed size is restricted morphologically by the size of the ovary and evolutionarily by its influence on seedling emergence and survival (Harper et al. 1971, Harper 1977) and the trade-off between seed size and number (Smith and Fretwell 1974, Wilbur 1977).

Year to year differences in population means for yield components and the disparity between means in the field and in the greenhouse (Table 5.2) suggest that, over the range of environments examined, most if not all of the observed variation in yield components, both within and between populations, is due to phenotypic plasticity. This suggestion is strongly supported by the results of the reciprocal transplant experiment. In general, transplants tended to conform to the yield component pattern characteristic of the site to which they were transplanted (Table 5.3).

Yield components may respond plastically to the total availability of resources and/or to specific environmental cues. As the amount of resources available to a plant increases, plant size and total yield will also increase. The relationships between plant size and yield components suggest that within populations, the number of stems/plant, the number of inflorescences/stem and to a lesser extent, the number of flowers/inflorescence respond most to local variation in resource levels (Table 5.7). Among populations, the number of inflorescences/stem, the number of flowers/inflorescence, and the number of seeds/flower were not related to plant size which suggests that these yield components may respond to something other than differences in resource availability between habitats.

Thus in *P. vulgaris*, the yield components which are most closely related to plant size tend to be more variable than those which are constrained more by morphology and/or past selection. Yield component variability is due to plastic responses to differences in resource availability and specific environmental cues.

Relationships Between Yield Components

Two yield components will vary independently if they respond to different independent factors or if they respond to the same factor at different times and the factor shows no autocorrelation. As an example, soil moisture may vary among habitats independent of pollinator availability. If the number of flowers/inflorescence responds to soil moisture and the number of seeds/flower responds to pollinator availability, then over a number of habitats with similar soil moisture but differences in pollinator availability, the number of flowers/inflorescence and the number of seeds/flower will not covary.

In general, the relationships between yield components in *P. vulgaris* were weak and non-significant suggesting that components tend to vary independently. Within populations, some yield components (the number of stems/plant, the number of inflorescences/stem and the number of flowers/inflorescence) are related to size and some (the number of seeds/flower and seed weight) are not (Table 5.7). Because of this, the total number of flowers produced (= number of stems/plant x number of inflorescences/stem x number of flowers/inflorescence) is independent of the number of seeds/flower and seed weight. This independence between yield components would permit the plant to adjust its seed production in response to changes in resource levels between the time flowers are produced and the time seeds are filled. This type of flexibility may permit individuals to react opportunistically to periods of high resource availability (Lloyd 1980, Primack and Antonovics 1981, Lee and Bazzaz 1982, Stephenson 1981, 1984, Pritts 1984). A good example of this is that, in *P. vulgaris*, the number of seeds/flower is rarely greater than one half of its maximum (four) in the field although it approaches the maximum in the greenhouse (Table 5.2). In a season when resources are particularly abundant during the time seeds are being filled, an individual can nearly double its yield by maturing all of its fertilized ovules. On the other hand, if resources are particularly scarce during the time of seed maturation, an individual will not be constrained to divide its resources among a large number of small seeds or to fill all ovules to some minimum size thereby seriously depleting its own resources and possibly jeopardizing its future survival.

In *P. vulgaris*, because the direct relationships among yield components are weak, and the indirect relationships are determined by the products of the coefficients of the direct relationships between the components involved, the indirect relationships are very weak. This lack of strong indirect relationships simplifies the interpretation of relationships among yield components. Direct relationships (measured by path coefficients) between yield components result when two components respond to the same cue or when they respond to different cues that are themselves correlated. Indirect relationships (measured by correlation coefficients) are expected when two components are both directly related to a common third component.

In *P. vulgaris*, yield is determined by the sequential development of the five yield components. Therefore, the directionality of some relationships between components can be established. For example, if there is a negative relationship between the number of stems/plant and the number of seeds/flower, an increase in #stem/plant results in the decrease in the number of seeds/flower. A change in the number of seeds/flower cannot cause a change in component which has already been determined such as #stem/plant. It may not be possible to determine the directionality of relationships between yield components that are directly adjacent in the developmental sequence. For example, seeds may be being filled in the terminal inflorescence while axial inflorescences still have open flowers so that seed weight in the terminal inflorescence can potentially influence the number of seeds/flower in later-developing inflorescences.

Within populations, relationships between yield components are probably principally due to small scale heterogeneity of resource availability. The direction of relationships will depend on the distribution and availability of resources. When resources are abundant and distributed evenly among plants, yield components should not vary therefore there will be no relationships between components. When resources are distributed unevenly, if plants growing in more favorable microsites grow to a large size and have high values for several yield components, positive relationships between yield components will occur (Primack 1979). When resources are limiting individual plants, negative relationships will result when two components compete for resources during their development. For example, Adams (1967) observed that when navy beans (Phaseolus vulgaris) were planted equally spaced at low density, relationships between yield components were low to zero, but at a higher planting density there were significant negative relationships between components.

Field sites may differ in the degree of spatial and temporal heterogeneity and the absolute availability of resources and this could explain why relationships between components are significant in some populations and not significant or even opposite in sign in others (Table 5.5). Primack and Antonovics (1981) also found differences among eight populations of Plantago lanceolata in the direction and magnitude of correlations between yield components. Thus, to some extent, the relationships between yield components depend on characteristics of the environment in which the plants are growing.

In comparisons among populations, relationships between yield components tended to be stronger than the relationships within populations, however indirect effects were again weak. The difference in the strength of relationships between components among all populations relative to within populations is probably due to the greater contrast in resource availability between different habitats than between different microsites within a habitat. Further, differences in specific environmental factors such as light and soil moisture may also be greater among habitats. In fact, differences among habitats in resource availability are indicated by significant differences in mean plant size (Table 5.1) and some relationships between yield component means are likely to be due to the effects of plant size. The number of inflorescences/stem, seed weight and the number of flowers/inflorescence are unrelated to differences among populations in mean plant size (Table 5.7). The greater similarity in the number of flowers/inflorescence among woodland populations and among old-field populations than between the two habitat types (Table 5.2) suggests that the number of flowers/inflorescence may be determined by by some environmental cue (or cues) that is consistent within a habitat type but differs between types. This suggestion is supported by the consistency between years in the ranking of population mean the number of flowers/inflorescence and the fact that in the greenhouse (where resource availability was greatest) all populations converged on an intermediate number of flowers/inflorescence whereas all other yield components increased (Table 5.2).

As a result of the negative relationship between the number of flowers/inflorescence and seed weight between populations, the number of flowers/inflorescence determines mean seed weight. A possible explanation for the negative relationship between the number of flowers/inflorescence and seed weight lies in the morphology and physiology of the flowering stem. Two leaves are produced at each node along a flowering stem. A single inflorescence is produced at the terminal node and one or sometimes two inflorescences are produced at subterminal nodes. If, as has been demonstrated for other species (see references in Stephenson 1983), the resources for filling seeds in an inflorescence come principally from the leaves adjacent to an inflorescence, then an inflorescence which produces more flowers may have to divide the same amount of resources among a larger number of seeds. Thus plants with fewer flowers/inflorescence would produce heavier seeds. This morphology may also explain why axial inflorescences, which are often borne in pairs at a single node, produce smaller seeds than the single terminal inflorescence on the same flowering stem.

It appears that the environmental cue (or cues) which determines the number of flowers/inflorescence is more similar among field sites within a habitat type than between habitat types. As a result, the overall pattern observed is that in woodland populations, individuals produce few flowers/inflorescence and large seeds and in the old-field, individuals produce many flowers/inflorescence and smaller seeds (Table 5.2). This pattern is consistent with theories of life history evolution which predict that a late successional environment (woodland) will select for a larger propagule size than an early successional environment (old-field) (Stearns 1976). However, in this case, the differences between populations in the size of seeds produced are due to phenotypic plasticity rather than genetic differentiation between populations in different habitats. Thus, empirical tests of the predictions of life history theory based on intrapsecific comparisons must examine the possibility that plasticicty rather than evolution is responsible for differences between populations in life history characters.

In summary, yield components in _P. vulgaris_ vary independently for the most part. Within populations, yield components probably vary in response to resource distribution and abundance. In a favorable microsite, an individual may be large and have high values for several yield components. Negative relationships between components are found among components that compete for resources during their development. The magnitude, strength and direction of yield component relationships will depend on resource abundance and distribution in a habitat. Comparing populations, yield component relationships are likely due to both resource availability and distribution and specific responses to environmental cues. In *P. vulgaris*, the number of flowers/inflorescence is particularly sensitive to an unidentified environmental cue and that cue indirectly determines seed weight because there is a strong negative relationship between the number of flowers/inflorescence and seed weight.

The Relationship between Yield and Fitness:

In general, total seed yield is a good predictor of parental fitness except when mean seed size within a population is so low that many of the seeds produced are not large enough to produce established seedlings (Table 5.10). This situation could arise in a population growing in a habitat where particularly small seeds are produced because of environmental conditions or in an environment in which only very large seeds are capable of establishing.

The calculation of fitness using seed number and the relationship between seed size and probability of seed germination and seedling survival to the end of the first growing season will give an over-estimate of fitness because additional mortality of juveniles prior to flowering will certainly occur. Even though absolute fitnesses would be lower, the relative differences in parental fitness due to differences in the size frequency distribution of seeds produced are likely to persist. In fact, demographic observations suggest that in *P. vulgaris*, the effects of seed size do not extend beyond the first growing season (Chapter 2). This estimate of fitness also considers only the female component of reproductive success in only one season and therefore does not take into account the fitness contribution of pollen donation or the potential trade-offs between fecundity and survival. Nevertheless, this method does give a more realistic estimate of fitness than total yield by itself.

The path coefficients between yield components and estimated fitness show the relative strength of selection currently acting on each component; a high path coefficient indicates strong selection (Lande and Arnold 1983). In the four main populations of P. vulgaris for which fitnesses were estimated, there are differences among populations and between years within populations in the components which are subjected to the strongest selection pressure (Table 5.10). In general, these relationships suggest that the components that determine seed number (the number of stems/plant, the number of inflorescences/stem, the number of flowers/inflorescence, the number of seeds/flower) rather than seed size are most important in determining parental fitness and are therefore currently under the strongest selection. This is true even though in some cases offspring fitness is strongly dependent on initial seed size (Table 5.8).

Caution is required in interpreting the path coefficients between yield components and fitness because some of the factors that determine fitness may not have been included in the analysis. It is possible that the inclusion of another factor or factors determining fitness could alter the path coefficients between each component and fitness considerably (Lande and Arnold 1983). Finally, conclusions regarding the course of evolution of yield components would require knowledge of the genetic relationships between components. However, changes in yield (and therefore, in most cases, in fitness) in P. vulgaris will be constrained by the negative phenotypic relationship between the number of flowers/inflorescence and seed weight.

CHAPTER 6

CONCLUSIONS

The results of experiments on the ecological and evolutionary significance of differences in seed size in *Prunella vulgaris* described in the previous chapters yielded a number of conclusions:

1. At all study sites, mortality was highest during the period between seed dispersal and seedling emergence. Post emergence survival was also low suggesting that there would be strong selection for characteristics that increase the probability of survival through the seed and/or seedling stages of the life cycle.

2. In three out of four populations, larger seeds had a significantly greater probability of surviving from the time of dispersal to the time of seedling emergence because larger seeds had higher viability and could establish in a broader range of microsite types in the field. Large seeds produced larger seedlings which had a greater probability of surviving through the first growing season. However, one year after seedling emergence the effects of seed size on seedling size could no longer be detected. Within a population, the presence and magnitude of the effects of seed size on the probability of seedling emergence and survival depended on the mean and range of seed sizes examined and the availability of microsites favorable for germination.

3. In general, the benefits of producing larger seeds were equal to or less than the costs in terms of the reduction in the number of seeds produced. Cost/benefit analysis indicated significant selection on seed

size in two of the four habitats examined. However, the phenotypes observed in natural populations did not correspond to the optima predicted from the cost/benefit analyses.

4. Reciprocal transplants indicated that differences in the sizes of seeds produced were due to phenotypic plasticity rather than genetic differences among individuals or populations. Plants growing in woodland environments produced larger seeds than plants growing in old-field environments. The large non-genetic component of variation in seed size could account for the lack of correspondence between predicted optimum seed sizes and the actual distribution of phenotypes.

5. The size of seeds produced by an individual may be constrained by the observed negative relationship between the number of flowers produced in an inflorescence and seed size. In woodland habitats, few flowers were produced per inflorescence and as a result, mean seed size was large. Conversely, in old-field habitats, a large number of flowers were produced per inflorescence and mean seed size was smaller.

6. In general, the number of seeds produced was more important than the size of seeds produced in determining the fitness of a parent plant.

Prospectus

In the future, a simulation model can be constructed which would permit comparison of the fitnesses of different seed production patterns in a given habitat characterized by the proportional availability of different microsite types. The fitness of a single pattern of seed production in different habitats could also be determined. The data presented in Chapters 2-5 would be used to assign biologically realistic values to parameters in equations which would calculate estimates of individual fitness based on the number and size of seeds produced, the relationship between seed size and the probability of seedling establishment in a number of microsite types, and the proportional availability of the microsite types in a given habitat. This sort of model might be of use in identifying questions for future research on the evolution of seed size.

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