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Population Ecology Of Panicum Virgatum L And Agropyron Psammophilum Gillett & Senn On The Dune System Along Lake Erie

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POPULATION ECOLOGY OF *PANICUM VIRGATUM* L. AND *AGROPYRON PSAMMOPHILUM* GILLETT & SENN ON THE DUNE SYSTEM ALONG LAKE ERIE

by

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Submitted in partial fulfilment
of the requirements for the degree of
Doctor of Philosophy

Faculty of Graduate Studies
The University of Western Ontario
London, Ontario
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ABSTRACT

Panicum virgatum L. and *Agropyron psammophilum* Gillett & Senn are the two dominant sand-binding grasses on the sand dunes along Lake Erie at Port Burwell Provincial Park. The ecological characteristics of these two species have received little attention. In this thesis, results on some aspects of seed and seedling ecology are presented.

Seeds of *Panicum virgatum* possess innate dormancy. Pretreatment for two weeks at constant or alternating temperatures ranging from 5 to 15 ^{0}C under either dark or light/dark conditions significantly improved seed germination. Injury to the seed embryo also significantly increased seed germination. After ripening of seeds in dry storage at room temperature did not alter their germinability significantly during the first 26 weeks. In contrast seeds of *Agropyron psammophilum* did not exhibit any seed dormancy.

Seed size of *Panicum virgatum* and *Agropyron psammophilum* showed considerable variability. Seed size had significant effect on seedling size at early stages of development in both species. This effect disappeared with time in *P. virgatum*. However, the seedling size fluctuated in *A. psammophilum* because the relative growth rate had a negative correlation with seed size for young seedlings but a positive correlation with seed size for older seedlings.

Greenhouse experiments indicated that seedling size was mainly dependent on weight of the endosperm rather than the embryo size in both species. Removal of a part of the endosperm resulted in seedlings of smaller sizes with more proportion of dry matter allocated to the root and less to the leaf of resulting seedlings in comparison with the control.

The maximum depth of emergence of *Panicum virgatum* and *Agropyron psammophilum* seedlings was 11 and 7 cm in the field and 16 and 8 cm in a greenhouse, respectively. Sand burial stimulated the growth in height of *P. virgatum* seedlings. In *A. psammophilum* burial of seedlings resulted in an increase in height, number of green leaves and tillers, and dry weight. Generally, seedlings of *P. virgatum* that emerged from shallow burial depths had fewer surviving individuals. In contrast, seedlings emerging from deep burial depths had more individuals surviving than random expectation. Seedlings emerging from shallow depths could withstand greater post-emergence sand burial than those emerging from deep sand burial.

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At this stage in my life, I would like to express my sincere acknowledgements to a number of people to whom I owe so much.

First of all, I am especially grateful to my supervisor, Dr. M. A. Maun, for his instructions, encouragement and financial support throughout the project. I enjoyed very much the well maintained and free thinking academic environment provided by him, under which I cut my baby teeth in population ecology and proceeded toward this end. I am also indebted to him for his endless help beyond academic pursuits such as English teacher, driving instructor, etc., that assisted me to adapt to and survive the western life style.

Dr. D. Fashelt deserves special thanks for her help and guidance during the sabbatical year of my supervisor. My advisors, Drs. P. B. Cavers and R. Jancey are also highly appreciated for providing valuable advice that refined my research projects.

Acknowledgements are also extended to the following people: Gino Stroffolino and Teri Cseh for technical assistance; Irene Krajnyk for drawing the figures; Daphne Boyce and Theresa Donworth for providing space in the greenhouse and occasionally looking after the experimental materials; Donna Irwin, Stefani Tichbourne and Tracey Piper for their assistance in the departmental office; my office mates, Peter Baye, Mary Yanful, Mary Ann Hawke, Pam Krannitz and Kevin Gedge for their friendship and concern and Alan Noon for preparing the photographs. I thank the Ministry of Natural Resources for allowing me free access to the study site at Port Burwell Provincial Park. Mr. Henry Valks, park superintendent, was always friendly, helpful and cooperative.

I also would like to thank my parents and elder sister in China for moral and material support. I am indebted to the Kunming Institute of Ecology, Academia Sinica, People's Republic of China for assisting me to overcome the official routine before my departure to Canada.

Finally, the completion of this thesis would not have been possible without the support of my wife, Tao Yuan, and my son, Xiaolei Zhang. I am extremely indebted to them for their patience and understanding while I spent my evenings and weekends in the lab. Their cheers after each successful episode made the whole exhausting research and writing process somehow colourful and enjoyable.

DEDICATION

This thesis is dedicated to my parents, Mrs. Xiaochung Li and Mr. Dadian Zhang, and to my wife, Tao Yuan. Their support made all the difference.

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CHAPTER ONE

GENERAL INTRODUCTION

1.1 HISTORICAL RETROSPECTIVE

The convergence of three heterogeneous media, namely earth, air and water, creates the shoreline habitat that undergoes regular and stochastic changes in time and space. Scientists in various disciplines from all over the world have studied this peculiar system for centuries. For plant biologists the diversity of plant species in dune habitats and the succession of vegetation were of particular interest (Cowles 1899, Warming 1891, Webber 1898). In North America, Cowles' work (1899, 1901) along Lake Michigan was of special significance in the development of the concept of vegetation succession (Kershaw 1973). However, the methodology employed in these studies was basically observational rather than experimental.

Although the later studies covered a broad range of topics (Mclean 1915, Oliver 1913, Oliver and Salisbury 1913, Olsson-Seffer 1909, Thompson 1922, Watson 1918), the biological aspects of dune plants were not examined until about the middle of this century. Several aspects of the morphology, physiology, ecology and evolution of primary dune builders, *Ammophila arenaria* Link and *A. breviligulata* Fernald (Gemmell *et al* 1953, Greig-Smith 1961, Greig-Smith *et al* 1947, Hewett 1970, Hope-simpson and Jefferies 1966, Laing 1954, 1958, 1967, Purer 1942, Seneca and Cooper 1971) were explored.

Recent studies have primarily concentrated on the population biology and demography of annuals, biennials and perennials. For example, a number of researchers have used dune annuals and biennials to test certain ecological principles (Barbour 1970, 1972, Keddy 1980, 1981, Mack 1976, Payne and Maun 1981, 1984, Watkinson 1978, 1982, Watkinson and Harper 1978). Perennial dune species also received considerable attention from ecologists and morphologists (Colosi 1977, 1980, Disraeli 1984, Eldered and Maun 1982, Hester and Mendelssohn 1987, Huiskes 1977, 1979, Huiskes and Harper 1979, Krajnyk and Maun 1981, 1982, Maun 1981, 1984, 1985, Maun and Riach 1981, McLeod 1977, 1982, Wallen 1980, Weller 1980, 1985, Westelaken and Maun 1985a 1985b).

Southwestern Ontario is the home of several dune systems of varying sizes and ages. For instance, the dune system along Lake Huron at Pinery Provincial Park ranges from about six to ten meters in height (Baldwin and Maun 1983) and is several thousand years in age (Morrison and Yarranton 1974) whereas the one at Port Burwell Provincial Park along Lake Erie is less than two meters high and about 60 years old (MacDonald and Beechey 1970). Several studies on the ecology of common sand dune species of the Great Lakes such as *Ammophila breviligulata* Fern., *Calamovilfa longifolia* (Hook.) Scribn., *Cakile edentula* Hook., *Lithospermum caroliniense* (Walt.) McMill. and *Strophostyles helvola* (L.) Ell. have been conducted for a number of years (Maun 1981, 1985, Maun and

Lapierre 1984, 1986, Payne and Maun 1984, Westelaken and Maun 1985a, 1985b, Yanful 1988). However, the two dominant sand-binding grasses, *Panicum virgatum* L. and *Agropyron psammophilum* Gillett & Senn, in the sand dune system along Lake Erie received little attention.

1.2 THE SPECIES AND LITERATURE REVIEW

Panicum virgatum L. (switchgrass) is a warm season (C_4) perennial grass that is widely distributed from Canada (Ontario distribution is shown in Fig. 1.1a) to Central America and from the Atlantic Coast to Nevada in the United States (Fig. 1.1a). In the United States, the species is grown for grazing and soil conservation (Porter 1966, Berg 1971). It was introduced in Ontario via the railroad link to the United States (Dore and McNeill 1980). *Panicum virgatum* has a wide ecological amplitude and is found in the tall grass prairies, open ground, open woods, brackish marshes (Hitchcock and Chase 1950) and sandy foredunes of the Great Lakes (Dore and McNeill 1980). The successful occupation of diverse habitats by this species is associated with a high degree of variability (McMillan 1959). In general, two ecotypes, namely wet lowland and dry upland, are well recognized (Porter 1966, Barnett and Carver 1967). The lowland plants are generally tall, coarse, glabrous and tetraploid ($2n = 36$) whereas the upland plants are shorter, finer and mostly hexaploid ($2n = 54$) (Porter 1966, Barnett and Carver 1967).

Panicum virgatum is a dominant sand-binding grass between the foredune and the slack at Port Burwell Provincial Park along Lake Erie in southwestern Ontario. This population belongs to the wet lowland form and produces large clumps (Plate 1.1a) with many stout tillers about 1 to 2 m in height and numerous short, scaly, sharp-pointed rhizomes. In the field, the plants begin growth in early May and the inflorescences emerge in July. Seeds are produced in large quantities and ripen and disperse in late August. Dispersed seeds usually accumulate in small depressions in the sand surface where they are buried by moving sand. During the winter, the above ground part of both the adult plants and established seedlings die out and the plants survive through the winter by producing dormant buds on rhizomes and tillers below ground.

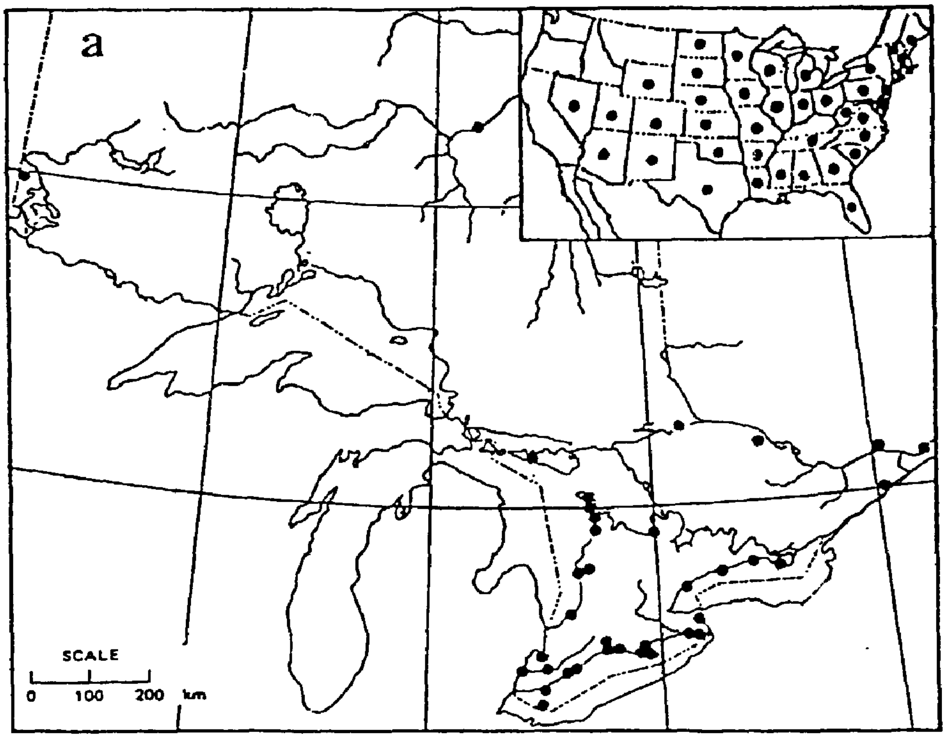
Agropyron psammophilum Gillett & Senn (Great Lakes wheat grass) is a cool season (C_3) perennial grass. It has a somatic chromosome number of 2n = 28 (Bowden 1965). This species has a number of synonyms. Hitchcock and Chase (1950) treated it as *A. dasystachyum* (Hook) Scribn. In 1961, after an extensive comparison among individuals of *A. dasystachyum* from a variety of locations, Gillett and Senn (1961) named populations of Lake Michigan and Lake Huron sand dunes as *A. psammophilum* Gillett & Senn. Subsequently, further changes to the nomenclature have been suggested and names such as *A. dasystachyum* var. *psammophilum* (Gillett & Senn) Voss (Voss 1966) or *Elymus lanceolatus* subsp. *psammophilus* (Gillett &

Senn) Love (Love 1980, Barkworth and Dewey 1985) and *E. dasystachya* subsp. *psammophilum* (Dewey 1983a, 1983b) have been proposed. In this thesis, however, I use *Agropyron psammophilum* Gillett & Senn exclusively.

According to Gillett and Senn (1961) and Dore and McNeill (1980), *Agropyron psammophilum* is mainly found on shoreline sand dunes of Lake Michigan and Lake Huron. The establishment of *A. psammophilum* on the Lake Erie sand dune system at Port Burwell Provincial Park probably occurred by long distance dispersal of rhizome fragments (Gillett and Senn 1961). The updated distribution of *A. psammophilum* along the Great Lakes is shown in Figure 1.1b (Dore and McNeill 1980, Gillett and Senn 1961). At Port Burwell Provincial Park, *A. psammophilum* is more abundant in the low foredune closer to the lakeshore, even though in some sites landward it may be a co-dominant with *Panicum virgatum*. Compared to *P. virgatum*, *A. psammophilum* is shorter (usually less than 1 m high) and has unscaled creeping rhizomes. Once a plant establishes, new individuals are produced from buds on underground rhizomes. The shoots trap mobile sand and small hummocks may be found in the foredune areas (Plate 1.1b).

In the spring, *Agropyron psammophilum* begins to grow earlier than *Panicum virgatum*. Its shoots appear above the sand surface in early April and show luxuriant growth. The inflorescences emerge from the sheath in late May or early June and the seeds ripen in late July or early August. Ripe seeds may either overwinter on the spike or disperse short

Figure 1.1 (a) The natural distribution of *Panicum virgatum* in Ontario. Its distribution in the United States is shown in the box. (b) Distribution of *Agropyron psammophilum* along the shoreline of the Great Lakes (Modified from Hitchcock and Chase 1950 and Dore and McNeill 1980).


a
SCALE
0 100 200 km

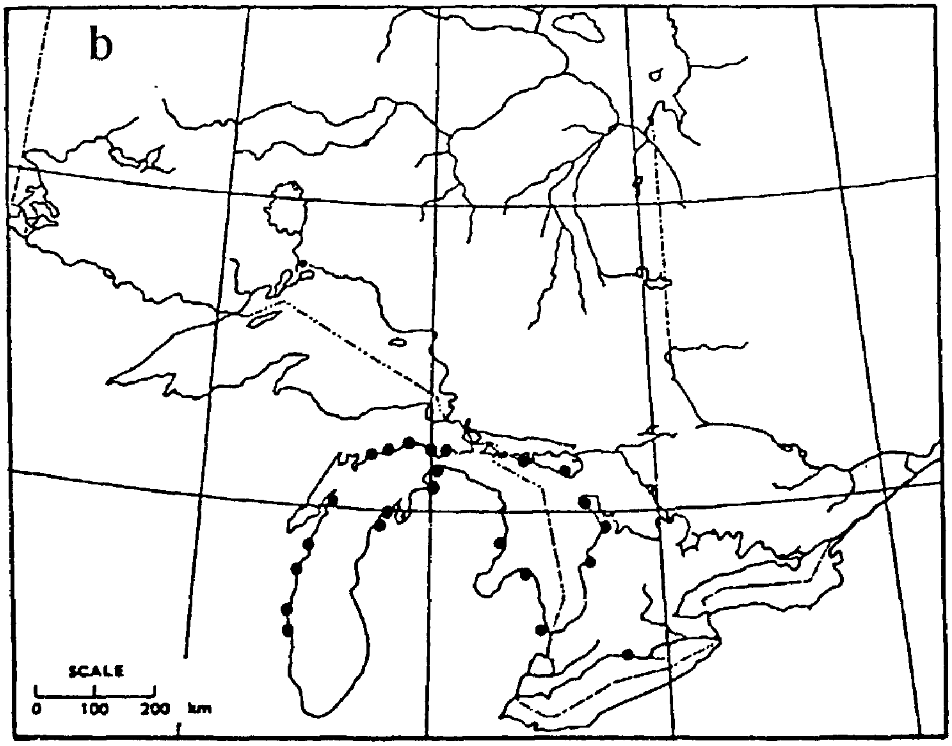
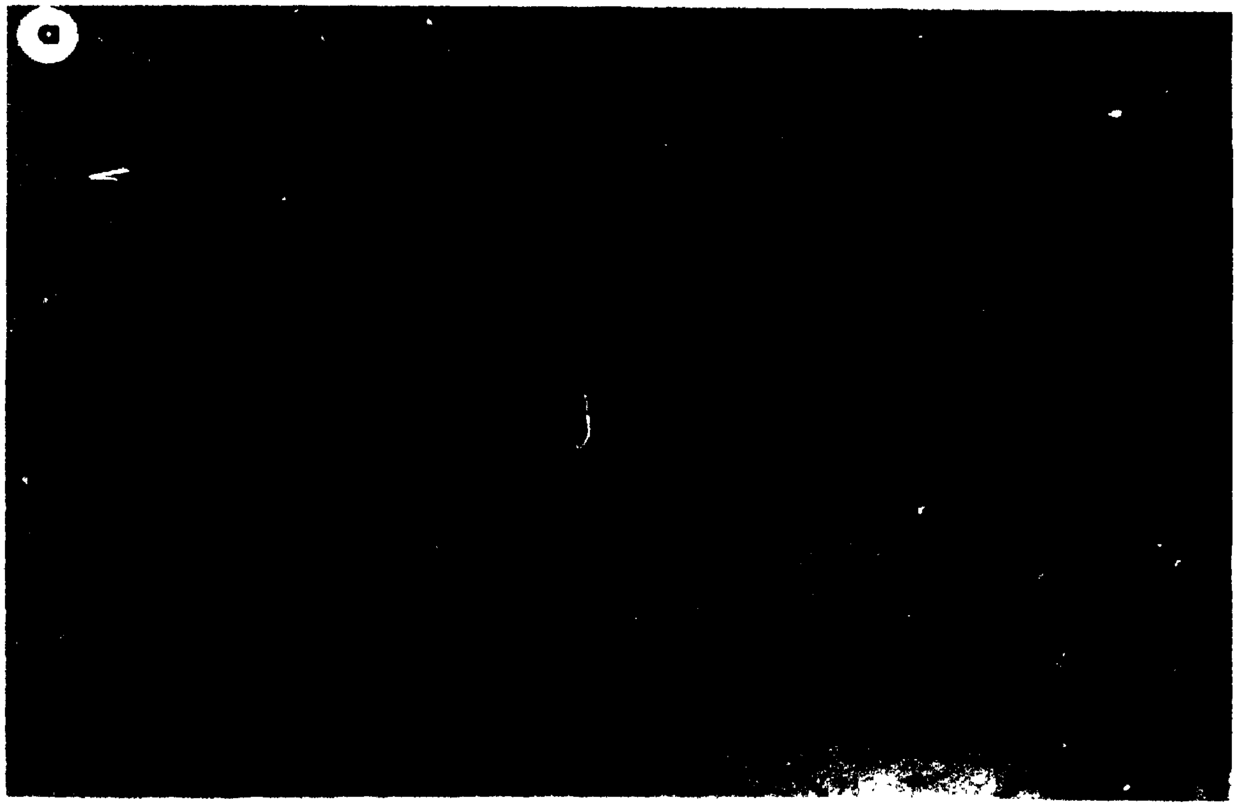

b
SCALE
0 100 200 km

Plate 1.1 Natural populations of *Panicum virgatum* (a) and *Agropyron psammophilum* (b) on the sand dune system at Port Burwell Provincial Park (Summer, 1988).


a


b

distances by the action of wind or animals. The seeds undergo enforced dormancy during severe winter conditions and germinate in early spring. Plants rely heavily on rhizomes to survive through the cold winter.

For *Panicum virgatum*, several studies have been reported on the cytology (Porter 1966, Lewis and Crotty 1977), genetics (Barnett and Carver 1967), seed biology (Blake 1935, Cobb *et al* 1961, Sauter 1962, Porter 1966) and physiology (Balasko and Smith 1971, Berg 1971, Barnett 1972). However, several aspects of the population ecology of this species have not been examined. Fewer studies have been conducted using *Agropyron psammophilum*. Data are available only on the taxonomy (Dewey 1983a, 1983b, Gillett and Senn 1961, Love 1980, Voss 1966), Cytology (Bowden 1965) and distribution (Dore and Mcneill 1980) of this species.

1.3 OBJECTIVE AND THESIS FORMAT

From 1986 to 1989, I conducted a series of experiments under field and greenhouse conditions. The purpose of these investigations was to examine the population ecology of *Panicum virgatum* and *Agropyron psammophilum*.

This thesis is organized according to individual research projects. Chapter two contains some background information on history, location, type of vegetation, climate and edaphic conditions of the study area. In Chapter three, some aspects of seed dormancy of *Panicum virgatum* and *Agropyron psammophilum* are compared. Specifically, mechanisms of dormancy and methods of breaking seed dormancy were explored.

Chapter four addresses questions on seed size variation and its effects on seed germination and seedling growth of the two species. Results of these experiments were analyzed using a growth analysis approach which provided more predictive explanations.

Predation of seeds may destroy part of the embryo, endosperm or both which may have profound effects on germination, seedling emergence and establishment. In one project, attempts were made to examine the relative importance of embryo and endospermic reserves in the determination of seedling size of both species (Chapter five).

In Chapters six and seven, the effects of sand burial on seed germination, seedling emergence, seedling growth and establishment under field or experimental conditions were examined. The purpose was to determine if sand burial was a major factor affecting seedling establishment in the field.

All these data were synthesized and discussed in Chapter eight. Here, the ecological and evolutionary significance of the various population characters of the two species, in relation to their survivorship, growth, reproduction and dispersal, is emphasized.

CHAPTER TWO

THE STUDY SITE

These studies were conducted on a sand dune system situated 65 km southeast of London at Port Burwell (Iroquois Beach) Provincial Park ($42^0$40'N, $80^0$51'W). The park is located on the northern shore of Lake Erie adjacent to the fishing village of Port Burwell at the mouth of Big Otter Creek, Elgin County, Ontario, Canada (Fig. 2.1). This area belongs to the "Carolinian" zone (Fox and Soper 1954) and lies within the Deciduous Forest region of Canada (Rowe 1977). The climate is temperate with an average annual temperature of 8 ^{0}C and a precipitation of 94 cm. A thirty-year record (Fig. 2.2) shows that December, January and February represent the coldest months with a mean temperature of about -5 ^{0}C. The hottest months of the year are June, July and August with mean temperatures around 20 ^{0}C. The average monthly precipitation remains relatively constant throughout the year (Fig. 2.2). The microclimate of the beach strand is modified by the rise and fall of lake levels, wind velocity, wave action and park visitors.

Port Burwell was established as a recreational park in 1968 with an area of 277 hectares and consists of a flat plain about 20 metres above the edge of the lake and a spectacular 2000-metre long sandy shoreline. The beach is a wedge-shaped flat strip that is wider (more than 50 metres) in the southeastern part and narrower (about 20 metres) in

Figure 2.1 Map of southwestern Ontario showing the location of Port Burwell (Iroquois Beach) Provincial Park. Solid triangles indicate nearby Provincial Parks (Modified from Klinkenberg 1984).

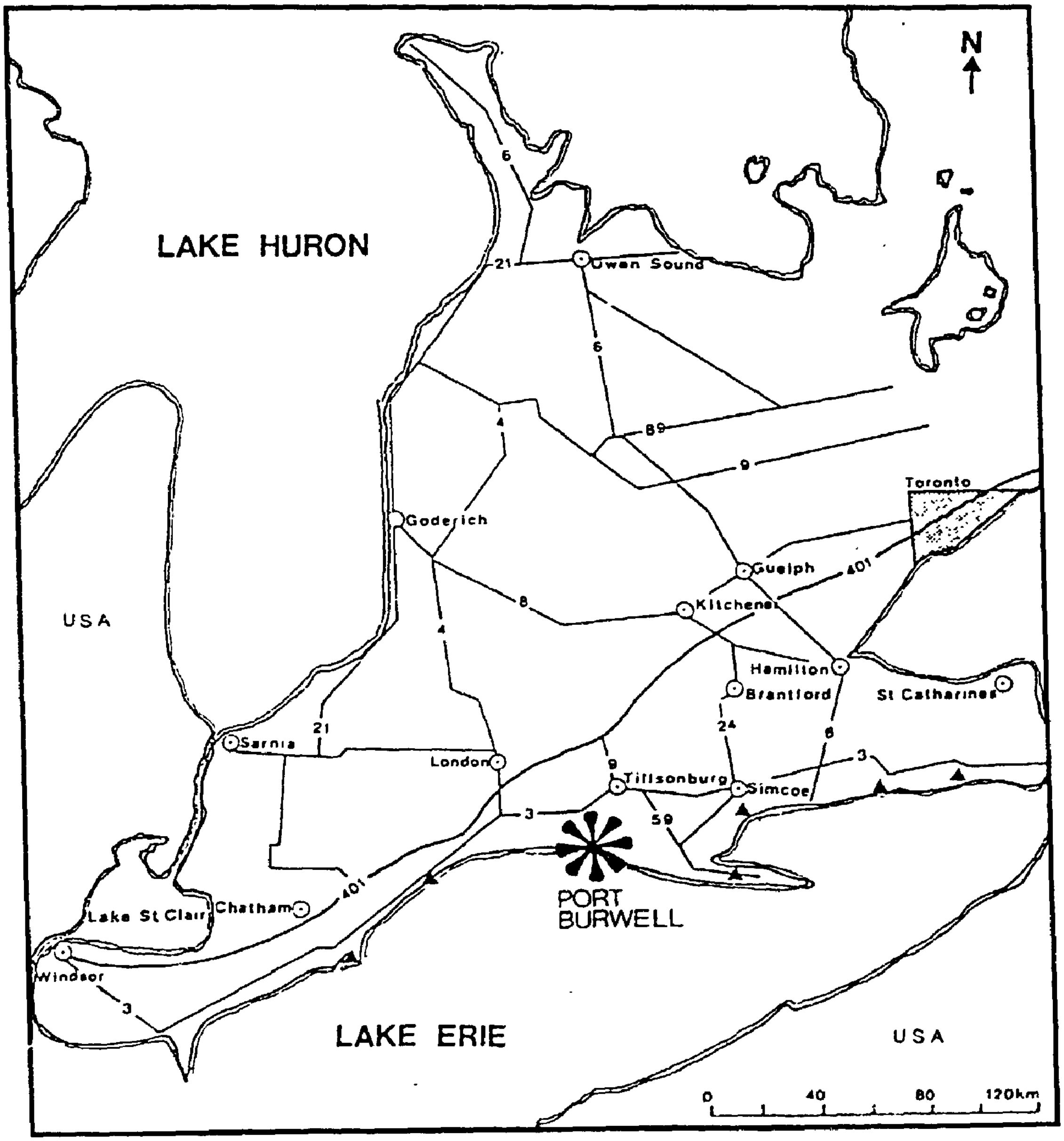
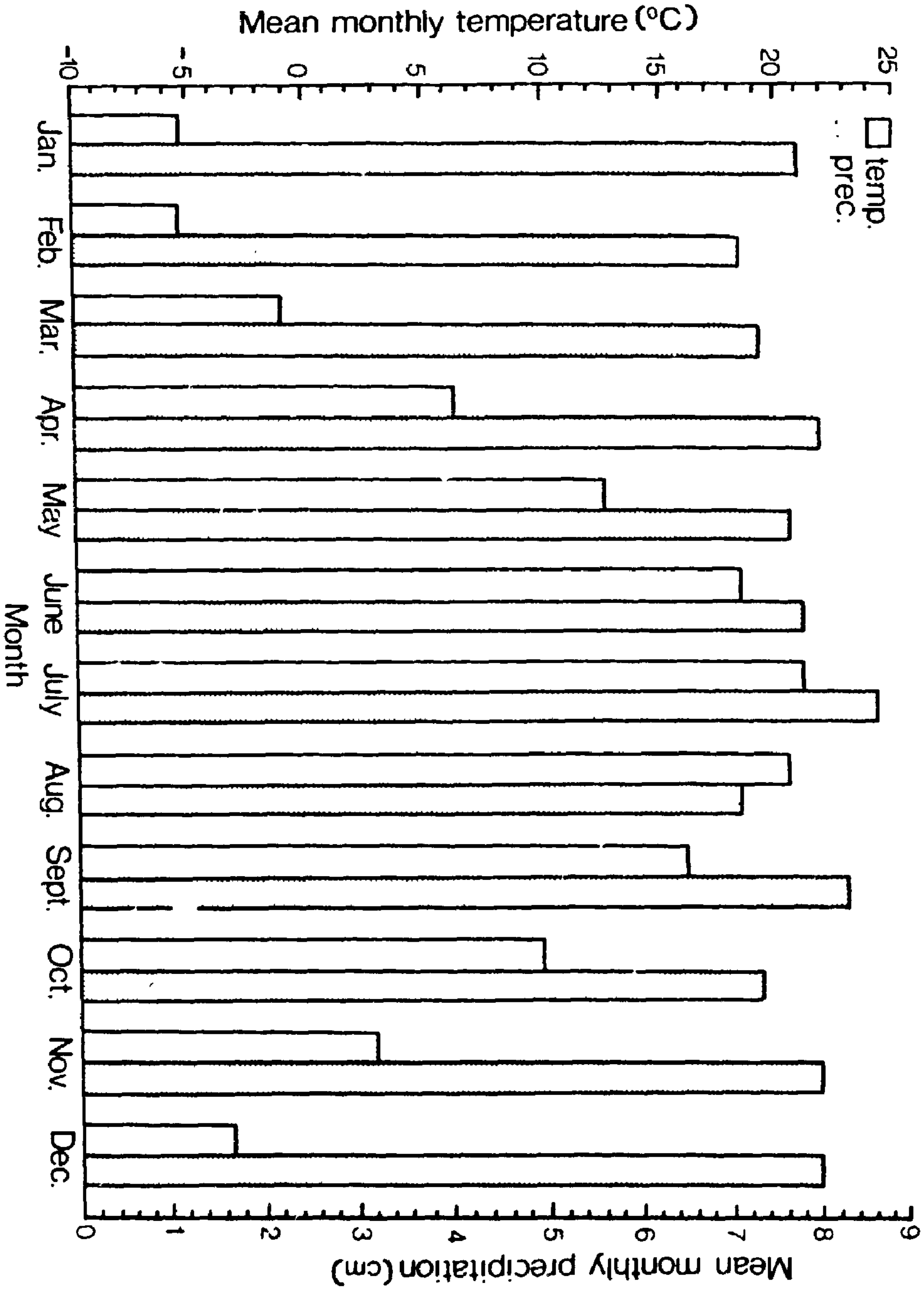

N
LAKE HURON
Owen Sound
21
6
89
9
4
Goderich
Toronto
Guelph
401
Kitchener
8
USA
Hamilton
Brantford
St Catharines
24
6
3
21
Sarnia
London
9
Tillsonburg
Simcoe
3
59
PORT BURWELL
401
Chatham
Lake St Clair
Windsor
3
LAKE ERIE
USA
0
40
80
120km

Figure 2.2 Mean monthly (thirty-year average) temperature and precipitation of the region where Port Burwell Provincial Park is located (data recorded in London Ontario, courtesy of Meteorological Branch, Department of Transport Canada).


Mean monthly temperature (°C)
-10
-5
0
5
10
15
20
25
temp.
prec.
Jan.
Feb.
Mar.
Apr.
May
June
July
Aug.
Sept.
Oct.
Nov.
Dec.
Month
0
1
2
3
4
5
6
7
8
9
Mean monthly precipitation (cm)

the northwestern part. The formation of the beach dune complex is thought to have resulted after the construction of a pier of large boulders in 1927. This pier which juts about 200 m into the lake has altered the direction of the prevailing water currents and forced the accumulation of sand in a wet low land along the edge of the lake (MacDonald and Beechey 1970). Because of its relatively young age, the dune system at Port Burwell does not have tall dune ridges similar to those at Pinery Provincial Park along Lake Huron (Baldwin and Maun 1983). In fact, it is composed of a foredune with a series of indistinct beach ridges that is frequently subjected to flooding mediated by high waves and storms (Plate 2.1).

The study area was selected on the beach in the least disturbed northwestern end of the park (Fig. 2.3) away from the picnickers and visitors to the park. Even on occasions when visitors had access to the study area, the ubiquitous poison ivy (*Rhus radicans*) acted as a deterrent. The plots suffered little human disturbance during this study except one extreme case when one of my experimental plots was destroyed by campers.

All the experimental materials and plant samples used in laboratory and greenhouse experiments were collected from this study area. The vegetation of the beach and sand dune system consists of the so called tall grass prairie complex which extends along the shoreline from the southeastern to the northwestern end of the park (Klinkenberg 1984).

Plate 2.1 A photograph of the beach and sand dune along Lake Erie at Port Burwell Provincial Park (Summer of 1988).

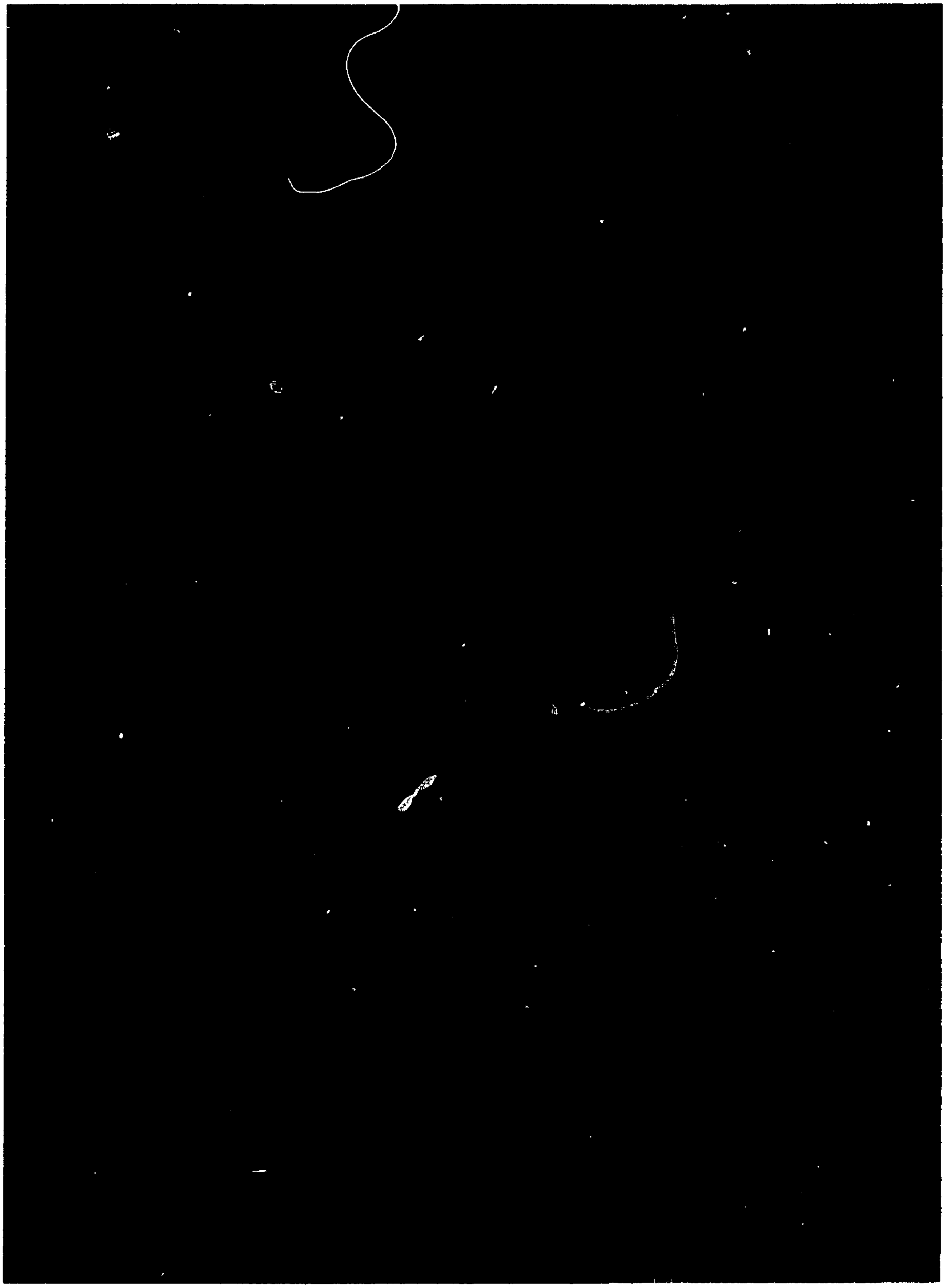
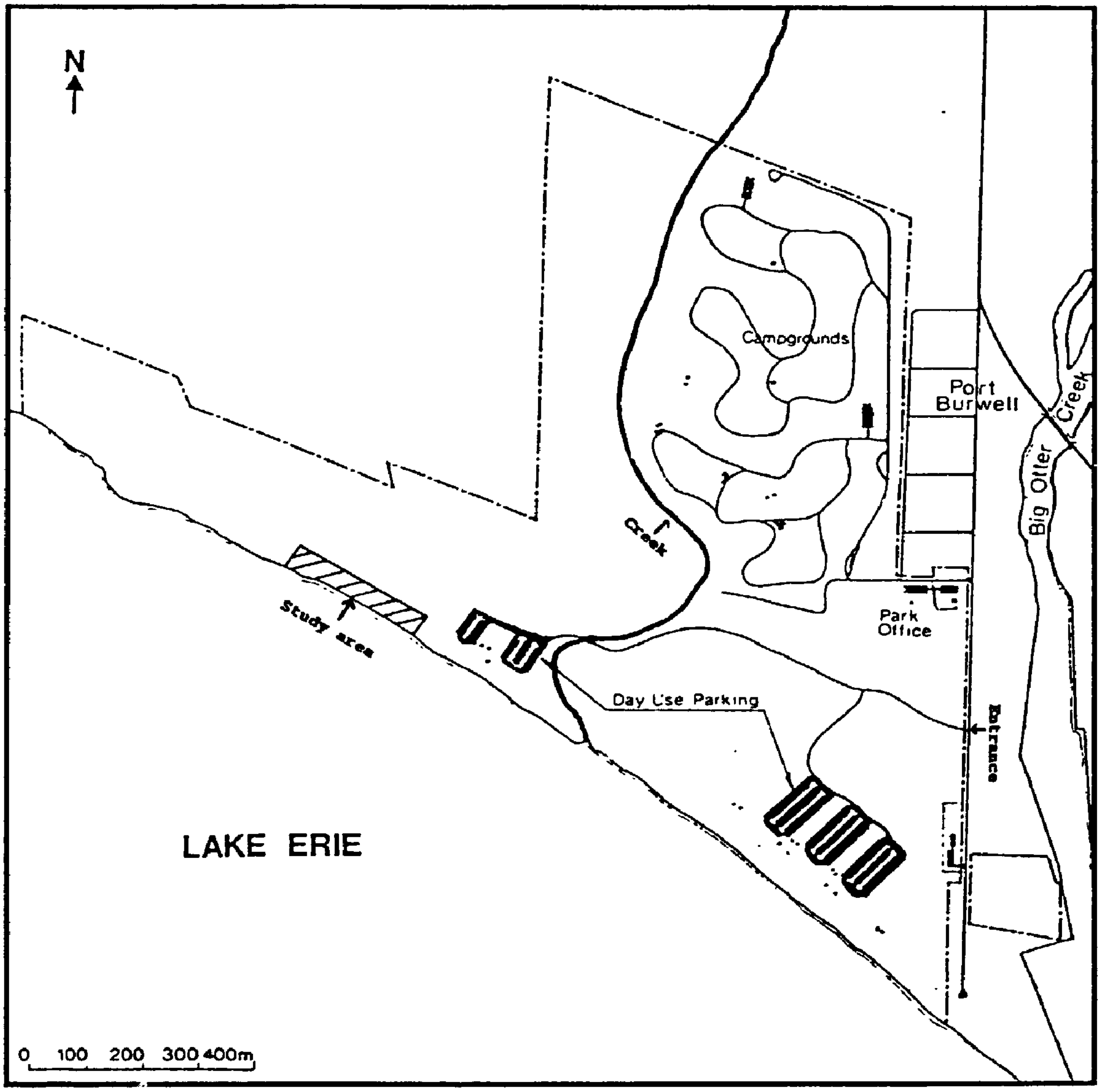


Figure 2.3 Map of Port Burwell Provincial Park showing the location of the study area. Dashed line indicates park boundary (Modified from Klinkenberg 1984).


N
Campgrounds
Port Burwell
Big Otter Creek
Creek
Park Office
Day Use Parking
Entrance
Study area
LAKE ERIE
0 100 200 300 400m

Prominent grasses here are *Panicum virgatum* and *Agropyron psammophilum* with several other dune inhabiting species. During July 1987, I examined the frequency and densities of all the species found within 300 quadrats (0.5 *x* 0.5 m) along 5 randomly laid transect lines (15 to 20 m long) perpendicular to the shoreline. Along each transect line, 0.5 *x* 0.5 m quadrats were laid successively through the vegetation. The frequency of a species was defined as the percentage of quadrats in which the species was found. Densities of species were determined by calculating the number of shoots and seedlings per m^2. The results are shown in Table 2.1. *P. virgatum* and *A. psammophilum* are the most abundant and frequently occurring species with 66 and 17 above ground shoots per m^2 (including seedlings), respectively. The variance : mean ratio (Kershaw 1973) showed that the populations of the two species had significantly ($P < 0.001$) clustered distribution. Other common species found in the quadrats include *Strophostyles helvola* (L.) Ell, *Elymus canadensis* L., *Rhus radicans* L., *Cenchrus tribuloides* L., *Melilotus alba* Desr and several shrubs such as *Salix exigua* Nutt, *Cornus drummondii* Meyer, *Populus deltoides* Marsh. *Tussilago farfara* L. and *Cakile edentula* Hook. are common along the beach.

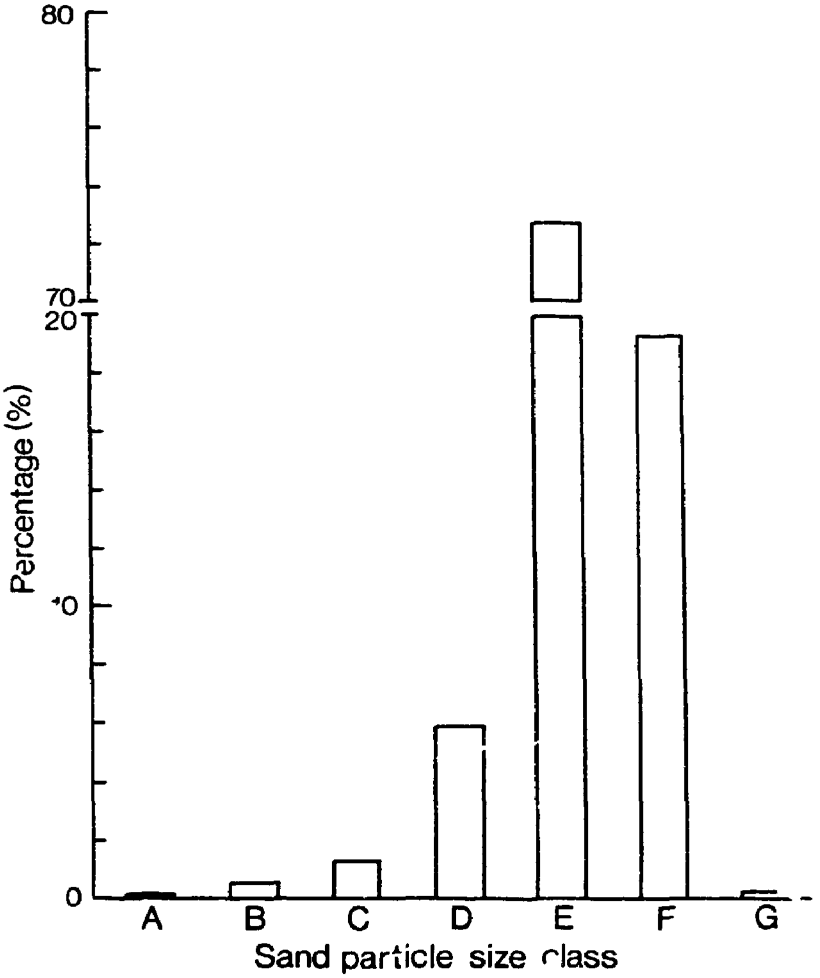
Fifty sand cores were taken from the study site in 1988. The mechanical composition of the sand sample was determined by sifting it through sieves with various sizes of openings. The diameter of sand particles in this area varied from less

Table 2.1 Frequency and mean density of plant species found within 300 quadrats (0.5 x 0.5 m) in the study site.

Name	Frequency (%)	density (shoot/m^2)
Panicum virgatum L.	53.33	65.77
Agropyron psammophilum Gillett & Senn	29.33	17.29
Strophostyles helvola (L.) Ell	15.00	2.08
Rhus radicans L.	10.33	1.96
Elymus canadensis L.	5.67	2.08
Cenchrus tribuloides L.	7.33	1.48
Tussilago farfara L.	6.00	0.72
Melilotus alba Desr.	5.33	0.44
Equisetum arvense L.	3.67	0.16
Solidago sp.	3.33	0.25
Solidago juncea Ait	2.67	0.35
Euphorbia polygonifolia L.	2.33	0.09
Salix exigua Nutt	2.33	0.41
Vitis riparia Michx	2.00	0.17
Xanthium strumarium L.	1.33	0.07
Asclepias syriaca L.	1.33	0.05
Populus deltoides Marsh.	1.33	0.09
Oenothera biennis L.	1.33	0.11
Cakile edentula Hook.	1.00	0.04
Daucus carota L.	1.00	0.05
Potentilla anserina L.	0.67	0.03
Achillea millefolium L.	0.67	0.05
Cornus drummondii Meyer	0.67	0.11
Salix eriocephala Michx.	0.33	0.03
Iris sp.	0.33	0.12
Poa compressa L.	0.33	0.16
Rhus typhina L.	0.33	0.01
Saponaria officinalis L.	0.33	0.01

than 0.053 mm to greater than 2 mm However, particles ranging from 0.2 to 0.5 mm accounted for more than 70% of the total weight (Fig. 2.4).

Figure 2.4 Particle size of the sand collected from the study area in the sand dune at Port Burwell Provincial Park (data from 50 randomly collected cores of 20 cm long and 1.3 cm in diameter). A - > 2 mm, B - 2 to > 1.18 mm, C - 1.18 to > 0.841 mm, D - 0.841 to > 0.5 mm, E - 0.5 to > 0.212 mm, F - 0.212 to > 0.053 mm and G - 0.053 mm or less.


80
70
20
10
0
Percentage (%)
A
B
C
D
E
F
G
Sand particle size class

CHAPTER THREE

SEED DORMANCY

3.1 INTRODUCTION

Seed germination is controlled at two levels. One depends on the operation of environmental factors and is thus called the external control. The other is due entirely to the state of the seed and is referred to as internal control or seed dormancy (Bewley and Black 1985). Seed dormancy refers to the situation when viable seeds fail to germinate under favourable external conditions (Mayer and Poljakoff-Mayber 1963). This property of seed is undesirable since the function of seeds is to produce new individuals. However, it is not always beneficial for the seeds to germinate freely after dispersion under randomly changing environments. Even under environment with regular fluctuations, seedling establishment will be greatly improved if the seeds postpone their germination until certain requirements are fulfilled. Thus, seed dormancy may result in (a) distribution of seed germination in time and space (Bewley and Black 1985), (b) increase in survivorship in seasonal environments (Harper 1977) and (c) the avoidance of extinction by random hazards (Fenner 1985).

In temperate regions, seeds of most fall-ripening plant species are dormant and stay dormant until certain requirements are satisfied. This feature was referred to as innate dormancy by Harper (1977). The control over innate dormancy in seeds is accomplished by various means such as immaturity of seed embryo at dispersion, physical inhibition by seed coat, presence of germination inhibitors and genetic determination (Harper 1977). Release of seeds from innate dormancy can also be achieved artificially through several treatments. According to previous studies, moist chilling (stratification) appears to be a common practice (Bewley and Black 1985, Fenner 1985). However, relatively high constant (Totterdell and Roberts 1979) or alternating temperatures (Totterdell and Roberts 1980), different light regimes (Borthwick *et al* 1954), mechanical injury (Hsiao *et al* 1983, Sung *et al* 1987) and even afterripening (Roberts 1965) induce dormant seeds to germinate as well.

A thorough literature search revealed that only a few studies have examined seed dormancy of *Panicum virgatum* but no studies have been attempted using *Agropyron psammophilum*. For example, Blake (1935) showed that the dormancy of *P. virgatum* seeds could be broken either by moist chilling or dry storage under low temperatures. According to Sautter (1962) external factors such as low temperatures, scarification and even low concentrations of sodium chloride solution improved seed germination in *P. virgatum*. Porter (1966) compared the biological variation between two populations of *P. virgatum* in central Oklahoma and found that the seeds from both the lowland and upland populations exhibited high degree of dormancy but they reacted differently to some chemical solutions.

The objectives of this study are (a) to examine the extent of seed dormancy of *Panicum virgatum* and *Agropyron psammophilum* from populations in the sand dune system along Lake Erie, (b) to determine the effective temperature range for breaking seed dormancy under variable light regimes for different lengths of exposure, (c) to examine the effect of scarification and severing parts of seed on seed dormancy and (d) to monitor over time the variation in total germination of seeds kept in dry storage.

3.2 MATERIALS AND METHODS

3.2.1 Source of seeds

On 14 September 1986 and again on 27 August 1987, panicles of *Panicum virgatum* from more than 100 shoots in the population were collected from six randomly selected 5 *x* 5 m plots in the field. Spikes of *Agropyron psammophilum* were collected on 27 August 1987. After two weeks' drying out at room temperature in a laboratory, the panicles of *P. virgatum* were gently rubbed by hand to remove the seeds from lemma and palea. For *A. psammophilum,* seeds with lemma and palea were manually removed from the spikelets because of the tight adhesion of lemma and palea to the seeds. Clean seeds (caryopsis with or without lemma and palea) of both species were obtained by using a seed blower and then stored in a seed room maintained at 5 ^{0}C and 40% relative humidity until they were used in germination experiments. Seeds of *P. virgatum* used in the experiment on after-ripening were kept in a laboratory under room temperature.

3.2.2 Preliminary tests

Immediately after seed collection in 1986 for *Panicum virgatum* and 1987 for *Agropyron psammophilum*, respectively, lots of 50 seeds (with eight replications) of each species were soaked with 12 ml of distilled water in eight 9-cm glass petri dishes containing two discs of No. 1 Whatman filter paper. The seeds were set to germinate in a growth chamber maintained at 27 ^{0}C under light for 14 h and 17 ^{0}C in dark for 10 h. The chosen germination environment was similar to the actual field conditions in late April and early May when germination occurs. Seed germination was monitored daily for 30 days. During the period of observations, only 1 out of the 400 seeds of *P. virgatum* germinated while 96.24% of the *A. psammophilum* seeds germinated. Germination of newly mature seeds of *A. psammophilum* was also observed during a field observation in early August of 1988. No germination of *P. virgatum* seeds occurred at that time. Since there was no significant innate dormancy in mature seeds of *A. psammophilum*, further experiments on the breakage of seed dormancy were conducted only with *P. virgatum* seeds.

3.2.3 Experiment 1. Effects of pretreatment at different temperatures and light cycles on seed dormancy of P. virgatum

This experiment was designed to determine the effects of a range of temperatures that may be experienced by seeds in the field after dispersion, lengths of exposure to the temperatures and the light regimes on seed dormancy. *Panicum virgatum* seeds of the 1986 collection were used.

In March 1987, 64 lots of 50 seeds each were counted and placed in petri dishes (9-cm diam) containing 2 layers of Whatman filter paper moistened with 12 ml of distilled water. The seeds were then pretreated in growth chambers maintained at three constant (5/5, 15/15, 25/25 ^{0}C) and one alternating temperatures [15 ^{0}C (14 h) and 5 ^{0}C (10 h)] under two photoperiodic regimes (14 h day/10 h night and 24 h darkness). For the dark regime, the petri dishes were sealed in a metal canister before placing them in the same growth chamber as the light/dark regime. This procedure was repeated at 2-week intervals for two months so that at the end, the seeds had been pretreated for 2, 4, 6 and 8 weeks at 5, 15 and 25 ^{0}C constant and 15/5 ^{0}C alternating temperatures under both light/dark and dark conditions. Eight replications were used in each of the above treatments. Following the pretreatment the seeds were set to germinate for 35 days in a growth chamber maintained at 27/17 ^{0}C with 14 h light period at the higher temperature and 10 h dark period at the lower temperature. An additional set (eight replications of 50 seeds each) of seeds that had not been pretreated served as a control.

At the end of the germination tests, ungerminated seeds were examined for viability by gently pressing the seeds with a pair of tweezers. Seeds were considered dead if they were soft. In a preliminary trial, this method showed 95% accuracy as measured by a tetrazolium test (Delouche *et al* 1962). Dead seeds were then excluded from the calculation of germination percentages.

Another experiment with two new temperature pretreatments, 10 and 20 °C constant, and one control was conducted in May 1987 with seeds from the same collection. In this experiment all conditions, except the pretreatment temperature, remained the same. Eight replicates for each treatment were used again.

3.2.4 Experiment 2. Effects of scarification and cutting on seed dormancy of P. virgatum

The purpose of this experiment was to determine if the seed coat or a germination inhibitor is involved in the innate dormancy of *Panicum virgatum* seeds. Seeds collected in 1987 were used for the experiment six weeks after harvest. There were six different treatments:

1. Seed coats were scarified by gently rubbing the seeds between two sheets of sand paper. Injury to the embryo and endosperm was avoided (gentle scarification).
2. Seeds were rubbed relatively hard between two sheets of sand paper to remove the seed (fruit) coat. Embryo and endosperm were visibly injured (hard scarification).
3. Seeds were cut with a surgical knife on the endosperm end of the seeds at about 4/5 of the length of seeds

from the embryo end. The embryo of the seeds was not injured (endosperm cut).

4. Seeds were cut laterally through the embryo and about 15% of the embryo from the radicle end was discarded (embryo cut).
5. Moist seeds were pretreated at 15/5 ^{0}C with 14 h light at the higher temperature and 10 h darkness at the lower temperature for two weeks (pretreated).
6. Control (not pretreated).

All the seeds in the above treatments were soaked with 12 ml of distilled water in 9-cm glass petri dishes with two layers of No. 1 Whatman filter paper and set to germinate at 27/17 ^{0}C with 14 h light period at higher temperature and 10 h dark at lower temperature for 30 days. There were eight replications with 50 seeds each in each treatment. Germination was examined daily. At the end of the experiment, ungerminated seeds were tested for viability by the method used in Experiment 1.

3.2.5 Experiment 3. Decay of seed dormancy over time in *P. virgatum*

This experiment was designed to measure the rate of decay of innate dormancy in *Panicum virgatum*. Seeds were from the 1987 collection and were kept at room temperature. The experiment was started two weeks after seed collection and consisted of two treatments (control and 2-week pretreatment) repeated at 2-week intervals during the first 10 weeks after seed collection and 4-week intervals later on. The control seeds (50 seeds in each of the 8 replications) were soaked with 12 ml distilled water in 9-cm petri dishes and set to germinate in a growth chamber maintained under the same conditions as in Experiments 1 and 2 for 30 days. The second batch of seeds (50 seeds moistened with 12 ml water in each of the 8 replications) were pretreated for two weeks in a growth chamber at 15/5 ^{0}C with 14 h light at the higher temperature and 10 h darkness at the lower temperature before being set to germinate in the same growth chamber as that of control seeds. The experiment lasted for 34 weeks after seed collection and ended in late April when naturally dispersed seeds started germinating in the field.

3.2.6 Statistical analysis

All the germination percentage data were subjected to an arcsin square root transformation for normalization before any statistical analysis. The data shown in graphs and tables are, however, untransformed. One way or multiple analyses of variance (ANOVA) using Scheffe's multiple comparison test (Orloci and Kenkel 1987) were conducted to compare seed germination among treatments.

3.3 RESULTS

3.3.1 Experiment 1. Effects of pretreatment at different temperatures and light cycles on seed dormancy of P. virgatum

The two controls in this experiment were not significantly different by a t-test ($P > 0.3$). Therefore, the controls were pooled (16 replications) and data from the two experiments were analyzed together. Germination of seeds during the pretreatment period was less than 1% and these seeds were included in all the analyses below.

All three factors, temperature, light regimes and duration of pretreatment significantly ($P < 0.01$) affected total germination and all pairwise interaction were significant (Table 3.1). Subsequent one way ANOVAs were conducted to find the pattern of the effects of the temperature regimes on seed dormancy within each light-duration combination.

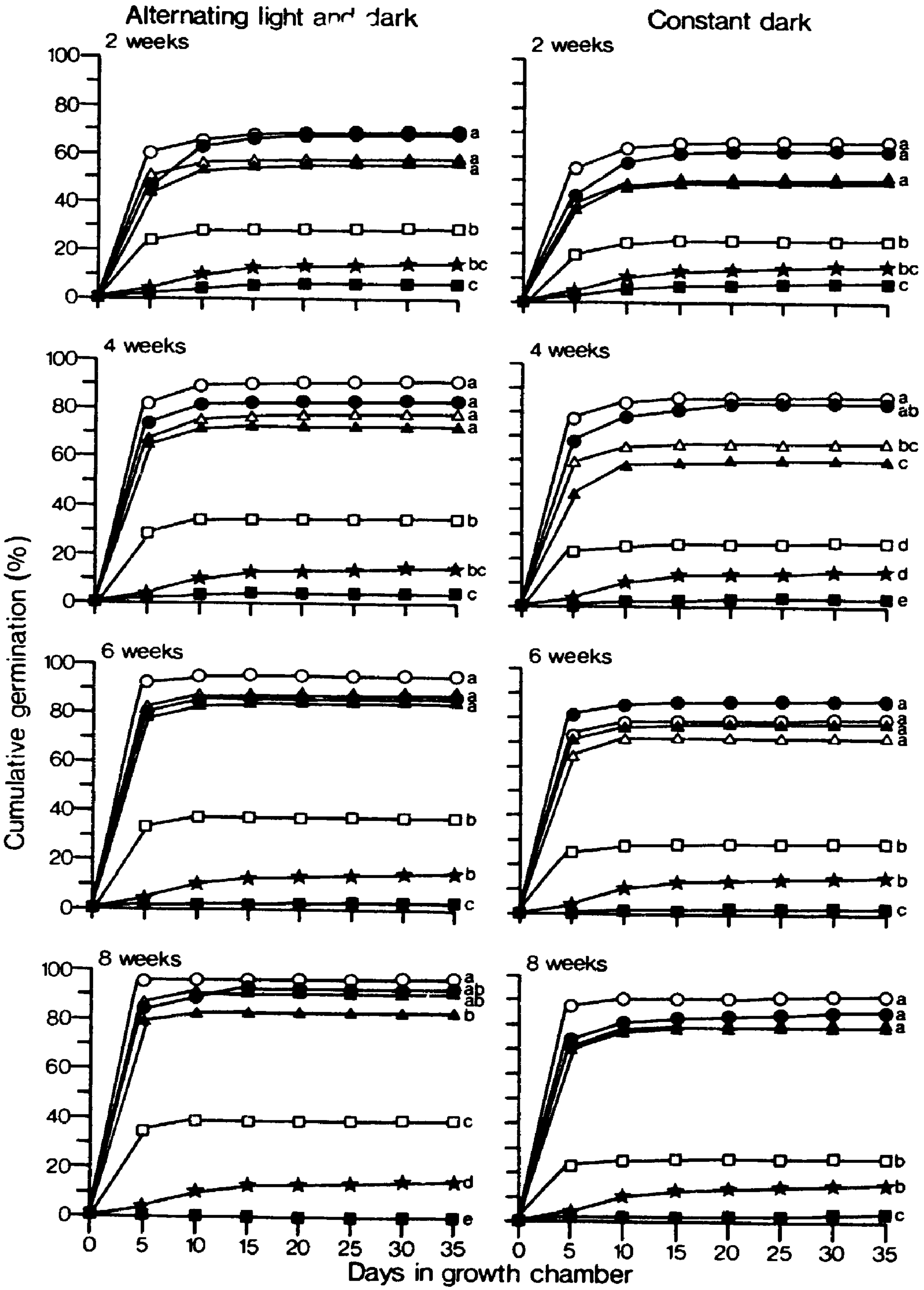
Seed dormancy of *P. virgatum* was broken by pretreatment of seeds at either constant or alternating temperatures ranging from 5 to 15 °C for varying lengths of exposure (Fig. 3.1). Seeds that had been pretreated at these temperatures showed significantly ($P < 0.01$) higher ultimate germination than those of control and 20/20 or 25/25 °C pretreatment. Treatments at temperatures of 15 °C or lower were rarely different from each other. Pretreatment at 25/25 °C was not suitable for breaking seed dormancy; a significantly ($P < 0.01$) lower proportion of seeds germinated relative to the control if they had been kept at this temperature for more than two weeks under dark or four weeks under light/dark conditions, indicating that seeds tended to acquire secondary dormancy at 25/25 °C (Fig. 3.1).

Except for the pretreatment at 25/25 °C, the longer the

Table 3.1 **Analysis of variance table for the germination of *Panicum virgatum* seeds that had been pretreated at various temperatures for different length of time under either light/dark or dark conditions.**

Source of variance	D.F.	Mean square	F	P
Treatment				
Temperature (A)	6	27712.37	613.75	<0.01
Length of time (B)	4	11205.67	248.18	<0.01
Light regime (C)	1	1444.27	31.99	<0.01
A x B	24	2058.85	45.60	<0.01
A x C	6	177.15	3.92	<0.01
B x C	4	181.00	4.01	<0.01
A x B x C	24	52.35	1.16	>0.10
Error	490	45.15		

Figure 3.1 Cumulative germination of *Panicum virgatum* seeds that had been pretreated at various temperatures under either light/dark or dark conditions before being set to germinate at 27/17 ^{0}C. Within a length of exposure the values of final germination for each temperature treatment followed by different letters are significantly ($P < 0.05$) different according to Scheffe's multiple comparison test. Legends: ● 5/5, △ 10/10, ○ 15/5, ▲ 15/15, □ 20/20, ■ 25/25 ^{0}C and ★ control.


Alternating light and dark
Constant dark
2 weeks
4 weeks
6 weeks
8 weeks
Cumulative germination (%)
Days in growth chamber
0
20
40
60
80
100
0
5
10
15
20
25
30
35
a
a
a
b
bc
c
a
a
a
b
bc
c
a
a
a
a
b
bc
c
a
ab
bc
c
d
d
e
a
a
a
b
b
c
a
a
a
a
b
b
c
a
ab
ab
b
c
d
e
a
a
a
b
b
c

exposure to the pretreatment temperatures, the higher was the percent germination (Table 3.2). However, the effects of increasing the duration of pretreatment temperature on seed dormancy depended on the light regimes. For example, the regression equation under light/dark conditions at any temperature had steeper slope than under constant dark conditions (Table 3.2). Within the light/dark regime, the slope for 15/5 ^{0}C pretreatment was significantly higher than those at 15/15, 20/20 and 25/25 ^{0}C. Under dark conditions, all the pretreatments at temperatures lower than 20 ^{0}C had significantly higher slopes than at 20/20 and 25/25 ^{0}C (Table 3.2).

Except under 25/25 ^{0}C, pretreatments under alternating light/dark regime usually produced significantly higher ultimate germination than those under constant dark conditions (Table 3.3). Although 25/25 ^{0}C pretreatment was not good for breaking dormancy, seeds exposed to constant dark for two and eight weeks germinated significantly ($P < 0.05$) more often than those in the light/dark regime (Table 3.3).

3.3.2 Experiment 2. Effects of scarification and cutting on seed dormancy of P. virgatum

All the treatments, except gentle seed-coat scarification, significantly increased ultimate germination over the control (Fig. 3.2). When a small fragment of the embryo was cut or the seeds were hard scarified thus

Table 3.2 Regression equations of the ultimate germination versus the length of time for which seeds of *Panicum virgatum* had been kept at various temperatures under either light/dark or dark conditions. Y is a transformation of the square root of germination percentage. X is the length of time (in weeks) for which seeds had been pretreated at each temperature. Equations followed by different superscripts are significantly differet ($P < 0.05$) in their slopes according to Newman-Keul's multiple comparison test (Zar 1984). Y_L is for light/dark and Y_D for the dark treatment.

Temperature	Regression equations	$r^2 (P<0.05)$
5/5	$Y_L = 28.75 + 49.59 \mathrm{x} \log(1 + X)^{abg}$	0.977
	$Y_D = 23.79 + 46.11 \mathrm{x} \log(1 + X)^{abg}$	0.946
10/10	$Y_L = 23.50 + 53.78 \mathrm{x} \log(1 + X)^{ag}$	0.996
	$Y_D = 24.13 + 41.67 \mathrm{x} \log(1 + X)^{b}$	0.988
15/5	$Y_L = 27.61 + 58.08 \mathrm{x} \log(1 + X)^{hg}$	0.986
	$Y_D = 28.98 + 47.08 \mathrm{x} \log(1 + X)^{abh}$	0.932
15/15	$Y_L = 27.11 + 44.20 \mathrm{x} \log(1 + X)^{ab}$	0.980
	$Y_D = 26.26 + 38.80 \mathrm{x} \log(1 + X)^{b}$	0.984
20/20	$Y_L = 23.52 + 17.28 \mathrm{x} \log(1 + X)^{c}$	0.984
	$Y_D = 24.11 + 8.90 \mathrm{x} \log(1 + X)^{d}$	0.798
25/25	$Y_L = 26.07 - 20.83 \mathrm{x} \log(1 + X)^{e}$	0.972
	$Y_D = 25.83 - 18.58 \mathrm{x} \log(1 + X)^{f}$	0.946

Table 3.3 Differences in percent germination of *Panicum virgatum* seeds in light/dark and dark pretreatment at different temperatures for various lengths of exposure. Each value was derived by subtraction of the mean germination percentage of seeds pretreated under dark (X_D) from those under light/dark (X_L) conditions ($X_L - X_D$).

Pretreatment temperature	Lengt f exposure (weeks)			
(°C)	2	4	6	8
5/5	6.24	-0.70	0.13	7.50**
10/10	6.63**	11.05**	16.55**	12.06**
15/5	2.04	4.95**	16.38**	5.44**
15/15	5.93**	12.49**	8.09*	3.89
20/20	3.74	8.22**	9.73	14.60**
25/25	-2.28*	1.39	1.03	-2.34**

** Significant at $P < 0.01$ according to the t-test.

* Significant at $P < 0.05$ according to the t-test.

resulting in embryo injury, seed germination was rapid and nearly complete within about 10 days. If only the endosperm was cut without injury to the embryos, seed germination continued gradually until the termination of the experiment. Pretreatment at 15/5 ^{0}C for two weeks gave significantly lower ($P < 0.01$) germination than cutting and hard scarification, although it still stimulated a significantly ($P < 0.05$) higher ultimate germination than the control (Fig. 3.2).

Gentle seed-coat scarification did not alter the number of days to first germination or the number of days to 50% germination when compared with the control (Fig. 3.3). In the other four treatments the time taken for the first germination to occur was significantly ($P < 0.01$) reduced. Except for endosperm cutting, these same treatments also took significantly less time to reach 50 % of ultimate germination (Fig. 3.3).

3.3.3 Experiment 3. Decay of seed dormancy over time in *P. virgatum*

Seed germination of *Panicum virgatum* was significantly affected by the pretreatment, age of seeds and the interaction of the two factors according to a two-way ANOVA (Table 3.4). One way ANOVAs were conducted to examine the effect of each of these factors.

Decaying of seed dormancy in *Panicum virgatum* was slow, since dry storage up to 26 weeks did not significantly

Figure 3.2 Cumulative germination, for 30 days in a growth chamber, of *Panicum virgatum* seeds that had been scarified, cut or pretreated at 15/5 ^{0}C. Legends: ▲ control, ■ pretreated at 15/5 ^{0}C for two weeks, □ gentle seed coat scarification, △ endosperm cut, ● hard scarification, and ○ embryo cut. The values of final percent germination with different letters are significantly ($P < 0.05$) different according to Scheffe's multiple comparison test.

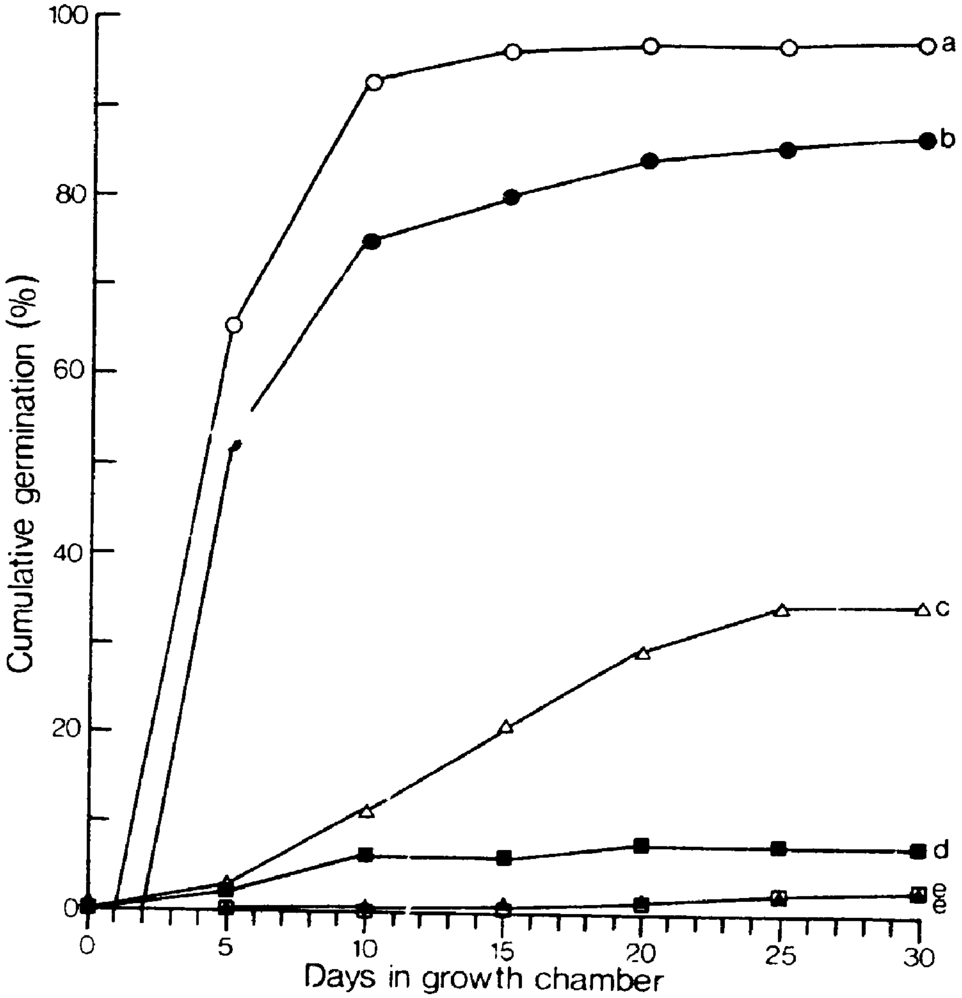

100
80
60
40
20
0
Cumulative germination (%)
0
5
10
15
20
25
30
Days in growth chamber
a
b
c
d
e
e

Figure 3.3 Effects of pretreatment, scarification and cutting on days to first germination (open bars) and days to 50 per cent of the ultimate germination (shaded bars) of *Panicum virgatum* seeds. Vertical lines show the standard errors. Bars with different letters are significantly ($P < 0.01$) different according to Scheffe's multiple comparison test. Treatments: A - control, B - pretreated at 15/5 ^{0}C for two weeks, C - gentle seed coat scarification, D-endosperm cut, E - hard scarification and F-embryo cut.

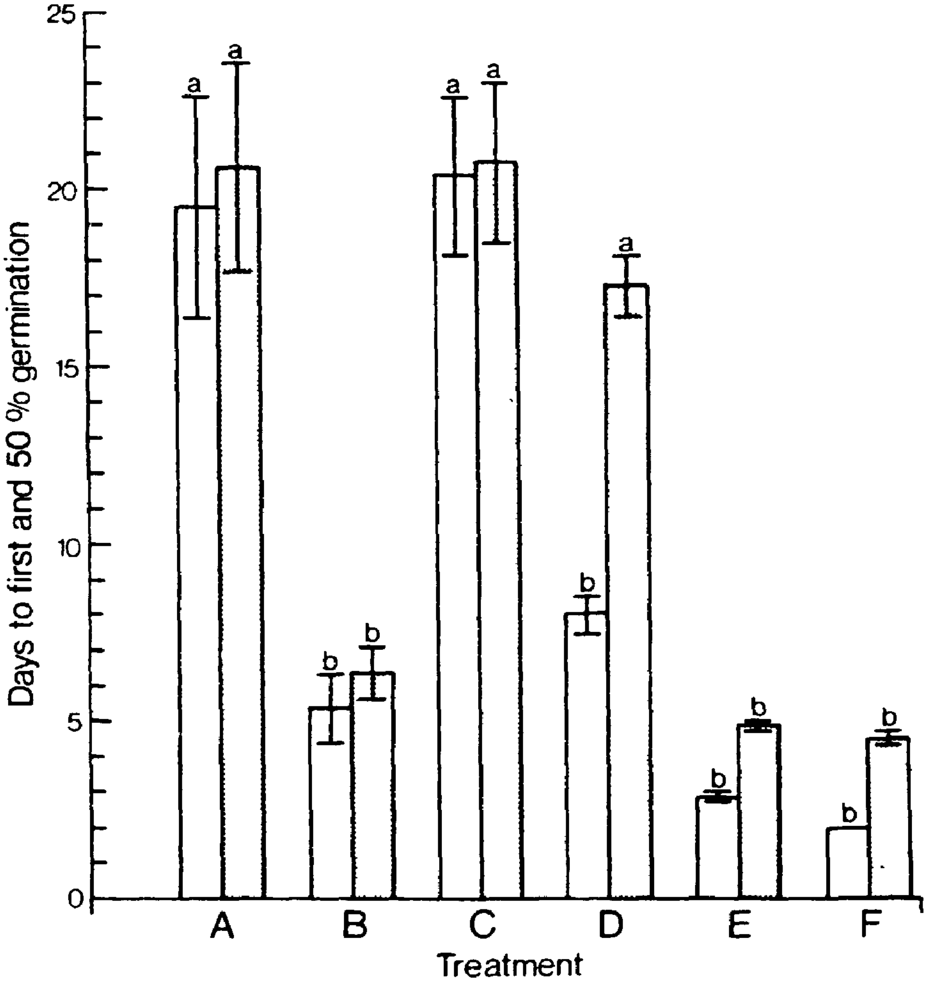

25
20
15
10
5
0
Days to first and 50 % germination
a
a
a
a
a
b
b
b
b
b
b
b
A
B
C
D
E
F
Treatment

Table 3.4. Two-way analysis of variance table for the germination test of *Panicum virgatum* that had been pretreated at 15/5 ^{0}C for two weeks or had been kept at room temperature. Seeds were set to germinate at two or four-week intervals from harvest until 34 weeks after collection.

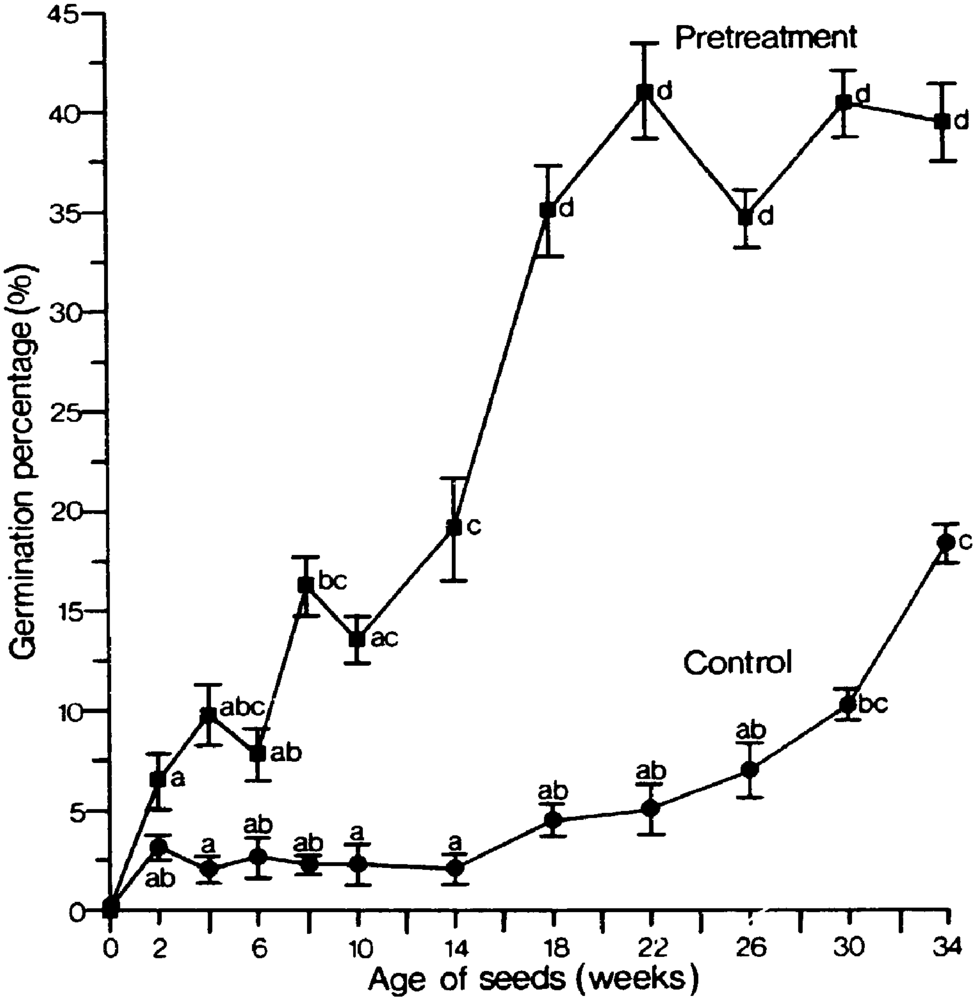
Source of variance	D.F.	Mean square	F	P
Treatment				
Pretreatment	1	12034.50	582.97	<0.01
Age of seeeds	10	911.54	44.16	<0.01
Intreaction	10	209.86	10.17	<0.01
Error	154	20.64		

improve the germinability of control seeds (Fig. 3.4). However, seeds 34 weeks old showed significantly ($P < 0.05$) higher germination than all seeds younger than 30 weeks. For pretreated seeds, there was a gradual increase in the number of germinable seeds with time until a big jump between 14 and 18 weeks after seed collection. Further increase in age did not significantly increase germination (Fig. 3.4). Throughout the experiment, pretreated seeds germinated significantly ($P < 0.01$) better than the control seeds at all the times except for 2-week-old seeds according to a t-test.

3.4 DISCUSSION

Preliminary tests indicated that newly matured seeds of *Agropyron psammophilum* did not possess innate dormancy. In fact, during a field investigation I observed young seedlings soon after the beginning of seed dispersal in early August of 1988 indicating that the seeds germinated in the field before the onset of winter. It seems to be an undesirable feature in terms of ensuing seedling survivorship since the inimical winter may kill those seedlings before establishment. However, these seedlings may also grow and accumulate substantial reserves before the onset of cold weather, and thus survive the winter as rosettes. Under those conditions, germination of *A. psammophilum* seeds would be of some adaptive significance. Further experimental evidence is needed to substantiate this suggestion. My observations also indicated that a substantial quantity of seeds are retained

Figure 3.4 Effects of age on the germination of *Panicum virgatum* seeds in control and pretreated at 15/5 °C for two weeks. Vertical lines show the standard errors. Means within controls or pretreatments followed by different letters are significantly ($P < 0.05$) different according to Scheffe's multiple comparison test.


Pretreatment
Control
Germination percentage (%)
Age of seeds (weeks)
0
5
10
15
20
25
30
35
40
45
0
2
6
10
14
18
22
26
30
34
a
abc
ab
bc
ac
c
d
d
d
d
d
ab
a
ab
ab
a
a
ab
ab
ab
bc
c

on the spike of *A. psammophilum* until late fall and winter and dispersed after the lowering of temperatures to sub-optimal conditions for germination. These seeds would produce seedlings in spring and summer.

My findings that moist chilling breaks innate seed dormancy in *Panicum virgatum* are consistent with previous studies (Blake 1935, Sautter 1962). However, I observed that relatively high constant or alternating temperatures (5 to 15 °C) also break seed dormancy when the seeds are kept in moisture at a temperature within this range for only two weeks. In the field, the seeds of *P. virgatum* ripen and disperse in late August and early September. The mean monthly air temperature of the area is about 20 and 12 °C in September and October, respectively (Maun 1986). It is, therefore, possible that some seeds may receive proper temperature pretreatment and may be released from innate dormancy by late autumn. But in the field, we did not find any seedlings during that time. Most probably the seed microenvironment (temperature, moisture) was not favourable for germination at that time and these seeds underwent enforced dormancy.

At temperatures lower than 25 °C, release of seeds from dormancy was at least partially blocked by constant dark conditions. However, at continuous high temperature (25/25 °C), seeds under constant dark conditions often gave significantly higher germination than those kept under light/dark conditions. In the field, dormant seeds of *Panicum* *virgatum* are buried by sand to various depths during the winter. Some deeply buried seeds may be prevented from breaking dormancy by constant dark and thus remain in the seed bank.

Several mechanisms contribute to innate seed dormancy. In some species seed dormancy may be broken as soon as the immature embryo reaches maturity after seed dispersal. In *Panicum virgatum*, however, immaturity of the embryo is not a likely cause of seed dormancy since seeds germinated soon after the embryo had been cut or injured. Another possible mechanism is the presence of a germination inhibitor in the embryo as shown in *Taxus baccata*, *Prunus domestica*, *Eleagnus angustifolia*, and several other species (Bewley and Black 1985). In these species, if the inhibitor was allowed to diffuse out of the embryo by injuring it, the seeds germinated immediately (Bewley and Black 1985). This also was true in seeds of *P. virgatum*. In my experiment, when the embryos of seeds were cut or injured by hard scarification, seed germination was high. However, the former treatment had even greater effect, suggesting that seed germination of *P. virgatum* is probably blocked by germination inhibitors in the embryo which diffuse out of the seeds when the embryo is injured. The diffusion of the inhibitors may also occur through the endosperm, although it is much slower. For example, endosperm injury significantly improved final seed germination percentage but not germination speed as measured by days to 50 % germination (Fig. 3.3). Physical inhibition by the seed coat might also be responsible for seed dormancy in *P. virgatum*. Sautter (1962) obtained 84% germination by scarifying unhulled seeds of *P. virgatum* with two sheets of emery cloth. In my experiment, however, less than 5% of the seeds germinated when scarification was applied to the seed coat (Fig. 3.2). The divergence was probably caused by the strength used to scarify the seeds. It is probable that in Sautter's experiment the seed coat was adequately scarified or the embryo was injured. Another explanation of the divergent results may be interpopulation variation.

Data on the decay of seed dormancy over time suggested that after-ripening was not the major cause of seed dormancy in *Panicum virgatum*. For example, unpretreated seeds did not increase in germinability up to a period of 26 weeks after collection, but a pretreatment at 15/5 °C for two weeks significantly improved seed germination. However, there might be some internal changes in seeds during 14 and 18 weeks after collection that caused an apparent increase in seed germination in both control and pretreated seeds (Fig. 3.4). The underlying physiological basis for this change is unknown. Again, germination inhibitors may play a role in this process.

In conclusion, innate seed dormancy in *Panicum virgatum* can be removed not only by moist chilling but also by exposing moist seeds to relatively high temperatures. The seed dormancy seems to be controlled by germination inhibitors in the embryo. The germination inhibitors do decay with time after seed dispersion, but it is very slow if there is no other treatment applied to the seeds. The seeds of *Agropyron psammophilum* do not possess any seed dormancy.

CHAPTER FOUR

SEED SIZE EFFECTS ON GERMINATION AND SEEDLING GROWTH

4.1 INTRODUCTION

The effects of intraspecific seed size variation on the growth of seedlings has not been generally examined until recently, for two possible reasons. Firstly, seed size does not vary as widely in magnitude as some other plant characters such as the number of seeds per plant, the weight per plant or height of individual plants within a population. Seed size of some species may vary within very narrow limits or even be constant thus lacking any ecological significance. An extreme example is that of seeds of some species which were used as a standard unit of weight because of their uniformity (Dallman 1933, Puckridge and Donald 1967). Secondly, early practices dealing with seeds were usually concerned with mass of one hundred or thousand seeds rather than the individual seed mass. The seed to seed variations were thus obscured by this relatively stable mean weight (Fenner 1985). However, there is increasing evidence that the seed mass of a species may vary by as much as ten fold or more (Thompson 1984, Mazer 1987, Hawke and Maun 1989). Several factors such as a) competition among individual seeds for limited resources (Maun and Cavers 1971, Stanton 1984a, Wulff 1986a), b) differences in microhabitat (Baker 1972, Payne 1980, Keddy 1982), c) genetic control (Stanton 1984a), d) tradeoff between seed size and seed number (Adams 1967, Werner and Platt 1976) and e) lack of directional selection for a particular seed size (Pitelka *et al* 1983) may contribute to the variation.

Investigations of ecological significance of seed mass indicate that large seeds may have certain biological advantages over small seeds owing to a) differences in seed dormancy (Halloran and Collins 1974), b) higher percent or rate of germination (Wulff 1973, Schaal 1980, Weis 1982, Zimmerman and Weis 1983), c) emergence from deeper burial depths (Harper and Obeid 1967, Wulff 1986b), d) larger seedling biomass (Harper and Obeid 1967, Zimmerman and Weis 1983), e) greater competitive ability and establishment (Black 1958, Gross 1984), f) producing more shade (Grime and Jeffrey 1965) or drought tolerant seedlings (Baker 1972, Schimpf 1977) or g) higher plant yields (Scaife and Jones 1970, Stanton 1984b). In contrast, Maun and Cavers (1971) found that germination of small seeds of *Rumex crispus* was faster than that of large seeds. Several studies also reported no correlation between seed size and seedling weight (Cideciyan and Malloch 1982, Melzack and Watts 1982), survival ability and total yield (Wulff 1986c). In some species the seed mass effects on seedling weight may persist until maturity (Black 1957, Stickler and Wassom 1963, Schaal 1980, Weis 1982); however, in others the seed mass effects may become imperceptible with the passage of time (Harper and Obeid 1967, Howell 1981, Zimmerman and Weis 1983) because seedlings from small seeds have higher relative growth rate than those from large seeds (Black 1957, Stearns 1960, Wulff 1973, Stebbins 1976, Lewis and Garcia 1979, Zimmerman and Weis 1983). If the negative relationship between seed size and relative growth rate of seedlings were to persist, seedlings from small seeds would be expected to become larger than those from large seeds. However, not even a single study shows this to be true. Most studies indicate that the higher relative growth rate of seedlings from small seeds exists only at the early stages of development (Wulff 1973, Zimmerman and Weis 1983). In these studies, however, little effort was made to examine the variation in relative growth rate over time.

In this study, I used a growth analysis approach to examine the effects of seed size on seedling growth of *Panicum virgatum* and *Agropyron psammophilum* and to determine the relationship between seed size and the relative growth rate of seedlings. Data on a) seed size variation b) seed size effects on seed germination and c) seed size effects on seedling growth are presented in this chapter.

4.2 MATERIALS AND METHODS

4.2.1 Seed source

Seeds of *Panicum virgatum* and *Agropyron psammophilum* were collected from 100 randomly chosen plants in the study site on 14 September 1986 and 13 August 1987, respectively, and dried in a laboratory at room temperatures. Clean seeds of *P. virgatum* were obtained by gently rubbing the panicles by hand and then separating the seeds from lemma and palea by using a seed blower. The lemma and palea of *A. psammophilum* seeds were removed manually owing to their tight attachment to the seeds. Clean seeds of both species were then stored in a seed room maintained at 5 °C and 40% relative humidity for later use.

4.2.2 Seed size variation

In April of 1987 and 1988, respectively, the whole samples of clean seeds (caryopsis) of *Panicum virgatum* and *Agropyron psammophilum* were placed on a bench and divided and subdivided until subsamples of 986 seeds for *P. virgatum* and 1017 seeds for *A. psammophilum* were obtained. The selected seeds were then weighed individually with an electronic balance to the nearest 0.1 mg. The cumulative mean seed mass and variance of seeds in the subsamples were calculated by increasing the number of seeds in the sample. As the sample size approached 250 seeds, the mean mass remained close to the sample mean. It may thus be assumed that the numbers of seeds chosen in this study were adequate to reflect the true variations in the seed populations of the two species.

The frequency distribution of seed mass and the mean weight per seed of each species were then calculated and the departure of the distribution from normality was examined using a t-test (Zar 1984). The correlation between the frequency distributions of seed mass of the two species was also examined (Orloci and Kenkel 1987).

Seeds in the subsample were sorted into seven non-overlapping size classes containing seeds weighing < 1.7, 1.7 - 1.8, 1.9 - 2.0, 2.1 - 2.2, 2.3 - 2.4, 2.5 - 2.6 and > 2.6 mg for *Panicum virgatum* and < 1.5, 1.5 - 1.8, 1.9 - 2.1, 2.2 - 2.4, 2.5 - 2.8, 2.9 - 3.2 and > 3.2 mg for *Agropyron psammophilum*. The mean mass of seeds in each of the seven size classes was calculated.

Eight seeds from each of the seven size classes of both species were randomly chosen and weighed with an electronic balance to the nearest 0.01 mg before and after being dried to a constant weight in an oven at 70 ^{0}C. Regressions of the fresh seed mass on dry seed mass were conducted (Orloci and Kenkel 1987). The mean moisture content of seeds in each class was calculated and Tukey's studentized range test (SAS 1985) was used to examine the difference in moisture content among them.

4.2.3 Seed size effects on germination

In the experiments, 13 replicates of ten seeds each from each size class of *Panicum virgatum* and *Agropyron psammophilum* seed samples were placed in 9-cm glass petri dishes containing 2 layers of No. 1 Whatman filter paper. Seeds of *P. virgatum* were then soaked wit '.2 ml of distilled water and pretreated at 15/5 ^{0}C with 14 h light at the higher temperature and 10 h darkness at the lower temperature for eight weeks to break seed dormancy (Zhang and Maun 1989a).

At the end of the pretreatment the petri dishes were placed randomly in a growth chamber maintained at alternating temperatures of 25 and 15 ^{0}C with 14 h illumination at the higher temperature and 10 h darkness at the lower temperature. Seeds of *A. psammophilum* were not pretreated because its seeds did not exhibit seed dormancy in preliminary trials. They were soaked in 12 ml distilled water and placed in the same growth chamber as *P. virgatum*. Germination of seeds in each size class of both species was monitored daily for 30 days. Seeds were considered germinated when coleoptile emerged and then removed from the dish. Water was provided when needed. At the end of the experiment, all of the ungerminated seeds were examined for stainability with tetrazolium chloride. Unstained seeds were considered dead (Delouche *et al* 1962) and excluded from calculations. Seed germination percentage and proportion of dead seeds in each size class were recorded and transformed into arcsin square root values for normalization before analysis of data using the analysis of variance (SAS 1985). The rate of germination was calculated according to Mugnisjah and Nakamura (1986) and can be expressed as follows. The numbers of germinated seeds each day were divided by the number of days at which the germination count was made. All these values were summed and then expressed as percentage of the total number of germinated seeds. The data were then transformed into arcsin square root values and analyzed by using the analysis of variance.

4.2.4 Seed size effects on seedling growth

On 13 June 1987 for *Panicum virgatum* and 12 July 1988 for *Agropyron psammophilum*, 48 seedlings of each species derived from each of the seven seed size classes were selected randomly. They were then grown individually in 12 cm plastic pots filled with 3:1 sand soil mixture. The pots were placed randomly on a bench in an unheated greenhouse with 14 h illumination. At two-week intervals for *P. virgatum* and 10-day intervals for *A. psammophilum*, eight individuals from each size class were harvested and the leaf area, dry weights of leaves, stem and roots were recorded. The measurements were transformed to natural logarithms prior to analysis of variance (SAS 1985). In total, there were six successive harvests for each species. At each harvest, the pots were rotated on the bench to eliminate the effects associated with the positions.

4.2.5 Growth analysis

Data transformed to natural logarithmic values were used. For seedlings from each seed size class, a quadratic model was fitted through polynomial regression (Orloci and Kenkel 1987) with the time of harvest as the independent variable and seedling leaf area or dry weight as the dependent variable. This particular function was recommended because of its simplicity when very advanced stages of growth are not involved (Hunt 1982). A general form of the fitted growth models is

$$f_w(T) = \log_e W = a + b_1 T + b_2 T^2 \qquad (1)$$

where W = the leaf area or seedling weight for a seed size class and T = the time at which the measurement is taken. Constant "a" is the natural logarithm of the initial leaf area or seedling weight. Parameters "b_1" and "b_2" are related to the relative growth rate of the measured seedlings. For example, the first derivative of the fitted function in equation (1)

$$f'_w(T) = dW/dT = b_1 + 2b_2 T \qquad (2)$$

is the relative growth rate (R) of the leaf area or seedling weight. Parameter "b_1" represents the intercept of relative growth rate and parameter "b_2" indicates the slope of the relative growth rate. The former shows the initial relative growth rate and the latter indicates the rate of increase ($+b_2$) or decrease ($-b_2$) in the relative growth rate of leaf area or dry weight of seedlings from a seed size class.

Under experimental conditions, seedlings may achieve their maximum size imposed by the carrying capacity of their environment at certain period of time T_{max} (number of days after emergence). At time T_{max}, the relative growth rate (R) is expected to be zero. According to Equation (2), given $R = 0 = b_1 + 2b_2T$, $T_{max} = -b_1/2b_2$. For seedlings from each seed size class, the time T_{max} can be calculated. When substitute T in equation (1) with T_{max}, the expected maximum size that a seedling can achieve under the experimental conditions is obtained.

4.3 RESULTS

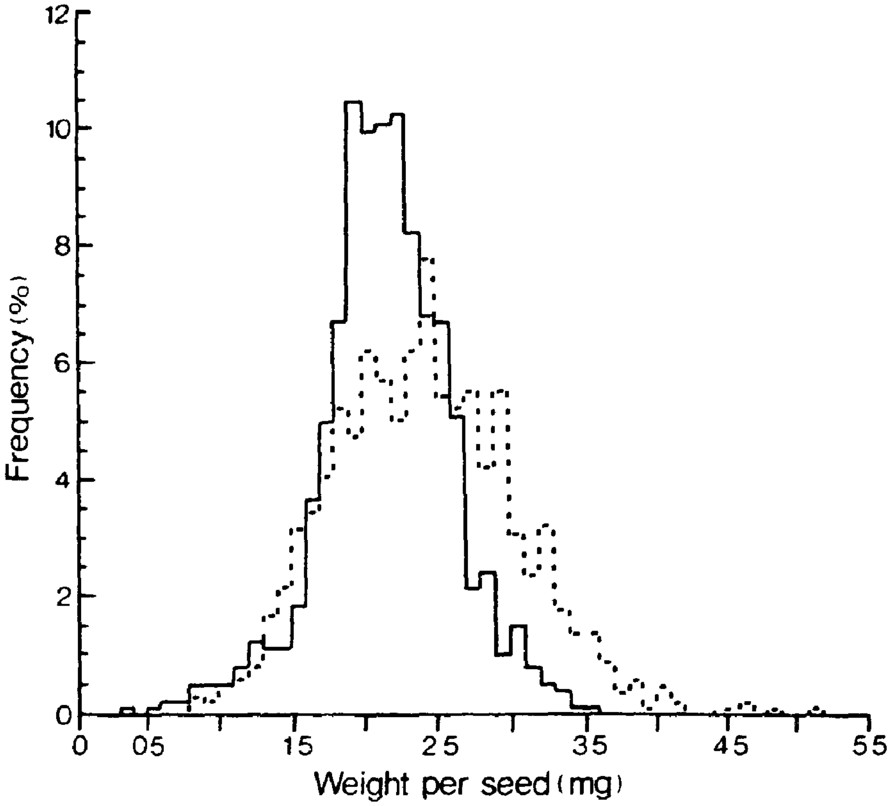
4.3.1 Seed size variation

Seed size varied from 0.3 to 3.5 mg in *Panicum virgatum* and from 0.8 to 5.1 mg in *Agropyron psammophilum*. The mean weight per seed (mean ± standard error) of *P. virgatum* and *A. psammophilum* was 2.1 ± 0.014 and 2.4 ± 0.020 mg, respectively. The latter is significantly larger than the former according to a t-test ($t = 12.270$. $P < 0.01$). The size frequency distribution of *P. virgatum* seeds was significantly ($P < 0.01$) skewed to the left ($g_1 = -0.232$) and leptokurtic ($g_2 = 0.965$) but in *A. psammophilum* it was significantly ($P < 0.01$) skewed to the right ($g_1 = 0.381$. $t = 4.961$) and platykurtic ($g_2 = -2.597$. $t = 16.952$) (Fig. 4.1). Correlation between seed size frequency distribution of the two species is moderately high ($r^2 = 0.6922$. $P < 0.01$).

The mean weights of seed in the seven size classes were 1.3, 1.8, 2.0, 2.2, 2.4, 2.5 and 2.9 mg in *Panicum virgatum* and 1.3, 1.7, 2.0, 2.3, 2.6, 2.9 and 3.4 mg in *Agropyron psammophilum*. In this chapter, these mean weights of seeds were used to symbolize the seven seed size classes of the two species.

The fresh and dry seed weight showed significant ($P < 0.01$) correlations in both species. An increase in the fresh seed weight corresponded with an increase in the dry weight of seeds. The correlation coefficient (r^2) is 0.9901 ($P < 0.01$) for *Panicum virgatum* and 0.9064 ($P < 0.01$) for *Agropyron psammophilum* seeds. No significant difference in

Figure 4.1 Frequency distribution (%) of seed size in *Panicum virgatum* (solid line, N = 986 seeds) and *Agropyron psammophilum* (dashed line, N = 1017 seeds).


12
10
8
6
4
2
0
Frequency (%)
0
0 5
1 5
2 5
3 5
4 5
5 5
Weight per seed (mg)

moisture content was observed among seeds from different size classes in either species (Table 4.1).

4.3.2 Seed size effects on germination

The ultimate germination showed no significant difference among seed size classes in either species (Table 4.2). The number of dead seeds in size class 1.3 mg was significantly ($P < 0.05$) higher than the heavier classes in *Panicum virgatum* (Table 4.2). For *Agropyron psammophilum*, however, the number of dead seeds was independent of seed size since significant differences were observed only between seed size classes 1.3 mg and 1.7 or 2.0 mg (Table 4.2). Germination rate (GR) of seeds in different size classes showed apparent increase with seed size in both species (Table 4.2). Significant linear relationships between seed size (X) and germination rate (GR) were observed for *P. virgatum* [$GR = 31.54 + 7.52 X$ ($r^2 = 0.916$, $P < 0.01$)] and *A. psammophilum* [$GR = 22.44 + 6.55 X$ ($r^2 = 0.920$, $P < 0.01$)].

4.3.3 Seed size effects on seedling growth

Seed size greatly affected the initial seedling size (height and weight) of both species since seedlings from large seeds showed significantly greater values for all the seedling parameters than those from small seeds. Similar pattern of dry matter allocation among leaf, stem and root of seedlings from all seed size classes was maintained throughout the six harvests for both species. Therefore, only

Table 4.1 Moisture content of *Panicum virgatum* and *Agropyron psammophilum* seeds (8 seeds) from each seed size class. Measurements (Mean ± standard error) are not significantly different according to Tukey's studentized range test (SAS 1985).

Panicum virgatum		*Agropyron psammophilum*	
Seed size class (mg)	Moisture (%)	Seed size class (mg)	Moisture (%)
1.3	7.19 ± 1.64	1.3	7.28 ± 1.24
1 8	8.27 ± 1.19	1.7	7.09 ± 1.02
2.0	6.69 ± 0.57	2.0	5.54 ± 1.15
2.2	7.26 ± 0.57	2.3	8.03 ± 1.08
2.4	5.52 ± 0.58	2.6	6.57 ± 1.23
2.5	8.11 ± 0.43	2.9	7.12 ± 0.88
2.9	7.52 ± 0.39	3.4	8.57 ± 0.70
Overall mean	7.22 ± 0.33		7.17 ± 0.40

Table 4.2 Mean percentages of germinated and dead seeds and germination rate of *Panicum virgatum* and *Agropyron psammophilum* in each seed size class at the end of the germination test. Values (mean ± standard error) in each column followed by different letters are significantly (P < 0.05) different according to Tukey's studentized range test (SAS 1985).

Seed size class (mg)	Germinated seeds (%)	Dead seeds (%)	Germination rate (%)
		P. virgatum	
1.3	94.85 ± 1.95^{A}	15.38 ± 4.02^{A}	42.71 ± 1.49^{A}
1.8	96.85 ± 1.40^{A}	0.77 ± 0.77^{B}	42.71 ± 1.54^{AB}
2.0	93.46 ± 2.36^{A}	0.77 ± 0.77^{B}	46.61 ± 1.48^{ABC}
2.2	94.62 ± 1.83^{A}	0.00 ± 0.00^{B}	47.61 ± 1.46^{ABCD}
2.4	96.92 ± 1.33^{A}	0.00 ± 0.00^{B}	49.47 ± 1.59^{BCD}
2.5	96.06 ± 1.44^{A}	0.77 ± 0.77^{B}	51.46 ± 1.66^{DC}
2.9	100.00 ± 0.00^{A}	0.00 ± 0.00^{B}	53.40 ± 1.66^{D}
		A. psammophilum	
1.3	100.00 ± 0.00^{A}	7.69 ± 2.31^{A}	29.54 ± 0.92^{A}
1.7	99.23 ± 0.77^{A}	0.77 ± 0.77^{B}	35.89 ± 0.79^{B}
2.0	99.15 ± 0.85^{A}	0.77 ± 0.77^{B}	36.03 ± 1.27^{B}
2.3	100.00 ± 0.00^{A}	1.54 ± 1.04^{AB}	37.41 ± 0.76^{BC}
2.6	99.23 ± 0.77^{A}	2.31 ± 1.22^{AB}	37.60 ± 1.15^{BC}
2.9	100.00 ± 0.00^{A}	4.62 ± 1.83^{AB}	41.33 ± 1.19^{CD}
3.4	100.00 ± 0.00^{A}	1.54 ± 1.04^{AB}	45.39 ± 1.17^{D}

4.5).

The leaf area ratios of seedlings from all seed size classes were uniform in *Panicum virgatum* according to Tukey's studentized range test (Table 4.3). In *Agropyron psammophilum*, however, significant differences in leaf area ratio were observed in 30 and 40-day old seedlings (Table 4.4). A trend of increasing leaf area ratio with decreasing parental seed size seemed to exist in 40-day old seedlings. However, it contributed little to the variation in seedling size over time.

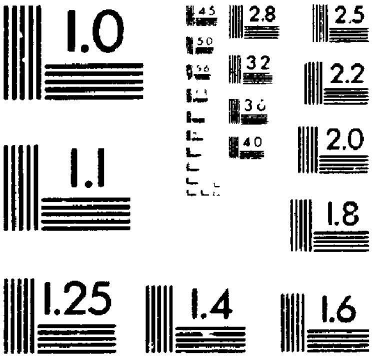
4.3.4 Growth analysis

The fitted quadratic models for leaf area and seedling weight in both species were statistically significant ($P < 0.01$) according to an F-test. The regression coefficients (r^2) ranged from 0.534 to 0.904 (Table 4.5, 4.6).

4.3.4.1 Calculated initial leaf area and seedling weight

The calculated initial leaf area and seedling weight derived from the fitted function, 'a' of these models, showed significantly ($P < 0.01$) positive correlations with seed size in both species (Fig. 4.6). This coincides very well with the data actually obtained. Seed size explained 68 and 93% of the variation in initial leaf area and seedling weight respectively in *Panicum virgatum* and 88 and 95%, respectively, in *Agropyron psammophilum*.

2



MicroD

data on the leaf area and overall seedling weight are presented.

In *Panicum virgatum*, significant differences in leaf area (Fig. 4.2) and overall seedling weight (Fig. 4.3) were observed only at the first three harvests when seedlings were less than 6 weeks old. The initial differences in seedling sizes disappeared completely after the seedlings had been allowed to grow for 8 weeks or longer.

In *Agropyron psammophilum*, the growth of seedlings from different seed size classes fluctuated over time. For example, significant differences in leaf area were observed among seedlings harvested at 10 and 50 days after emergence but not at the other four harvests (Fig. 4.4). Among 10-day old seedlings, those from 2.9 and 3.4 mg seed size classes had significantly ($P < 0.05$) larger leaf area than those from 1.3 and 1.7 mg seed size classes. Similarly, seedlings from 2.6 mg seed size class had significantly larger leaf area than those from 1.3 mg size class. Among 50-day old seedlings, only those from the two extreme seed size classes showed significant ($P < 0.05$) difference in leaf area (Fig. 4.4). Significant differences were observed in absolute dry weight of seedlings in all harvests except those taken at 30 and 40 days after emergence (Fig. 4.5). Within 10, 20, 50 and 60-day old seedlings, significant ($P < 0.05$) differences were observed only between the heaviest and lightest seed size classes. The seedlings from intermediate seed size classes did not differ among themselves and between extremes (Fig.

Figure 4.2 Comparisons in leaf area of *Panicum virgatum* seedlings from different seed size classes over six harvests. Means (solid circles) followed by different letters are significantly ($P < 0.05$) different according to Tukey's studentized range test. Vertical lines indicate the standard errors.

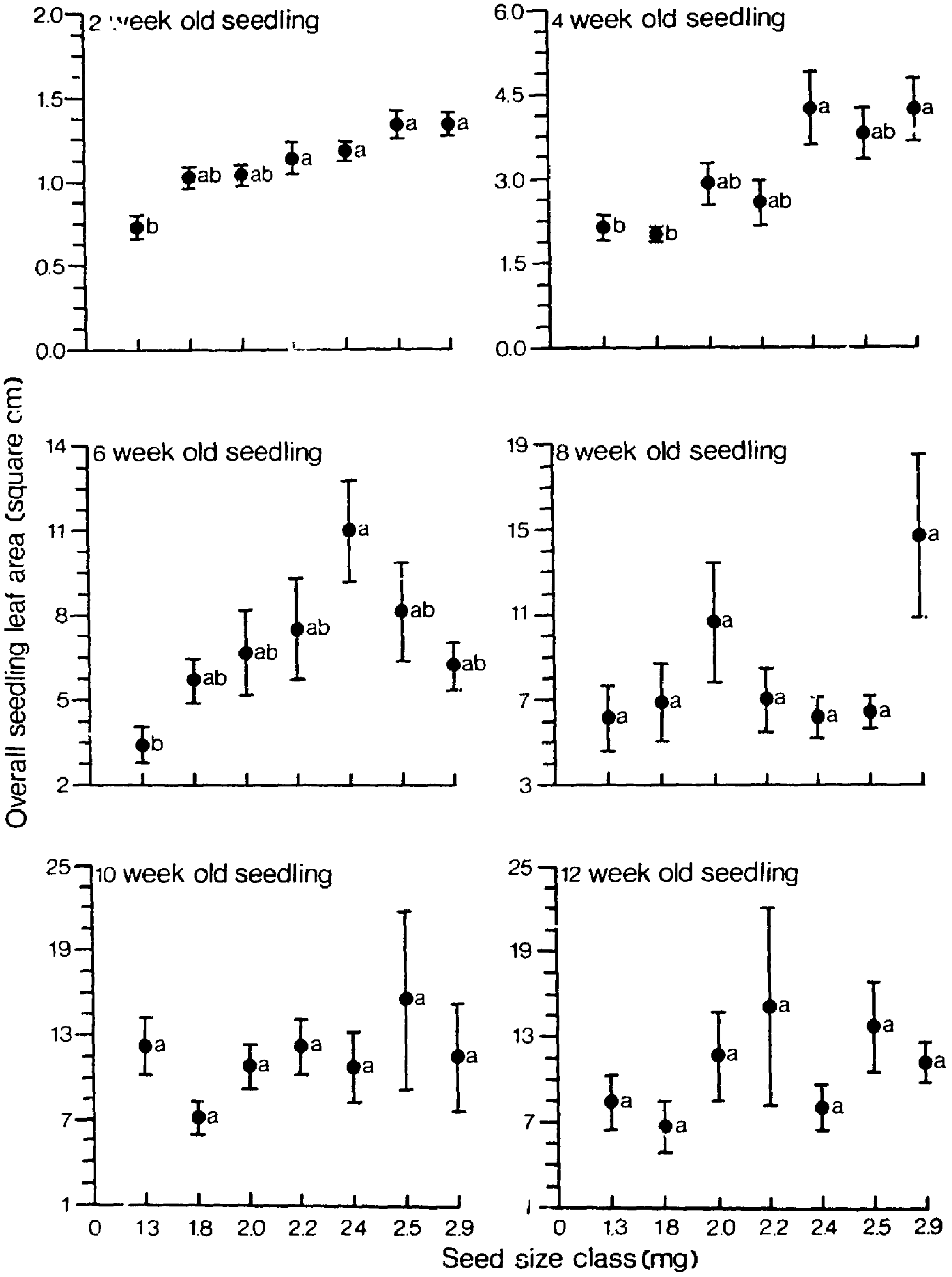

2 week old seedling
4 week old seedling
6 week old seedling
8 week old seedling
10 week old seedling
12 week old seedling
Overall seedling leaf area (square cm)
Seed size class (mg)
0
1.3
1.8
2.0
2.2
2.4
2.5
2.9
0.0
0.5
1.0
1.5
2.0
1.5
3.0
4.5
6.0
2
5
8
11
14
3
7
11
15
19
1
7
13
19
25
a
ab
b

Figure 4.3 Comparisons in dry weight of *Panicum virgatum* seedlings from different seed size classes over six harvests. Means (solid circles) followed by different letters are significantly ($P < 0.05$) different according to Tukey's studentized range test. Vertical lines indicate the standard errors.

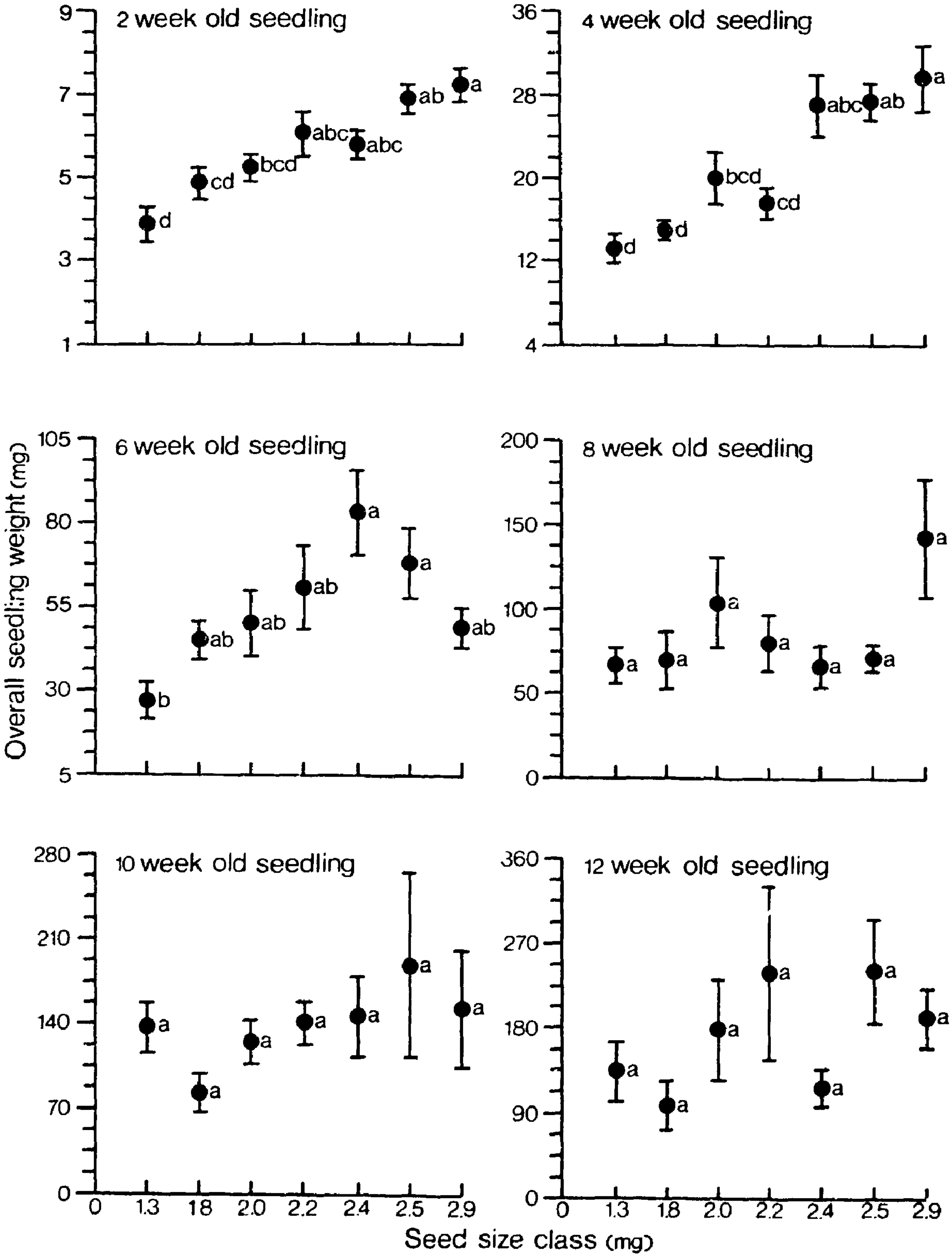
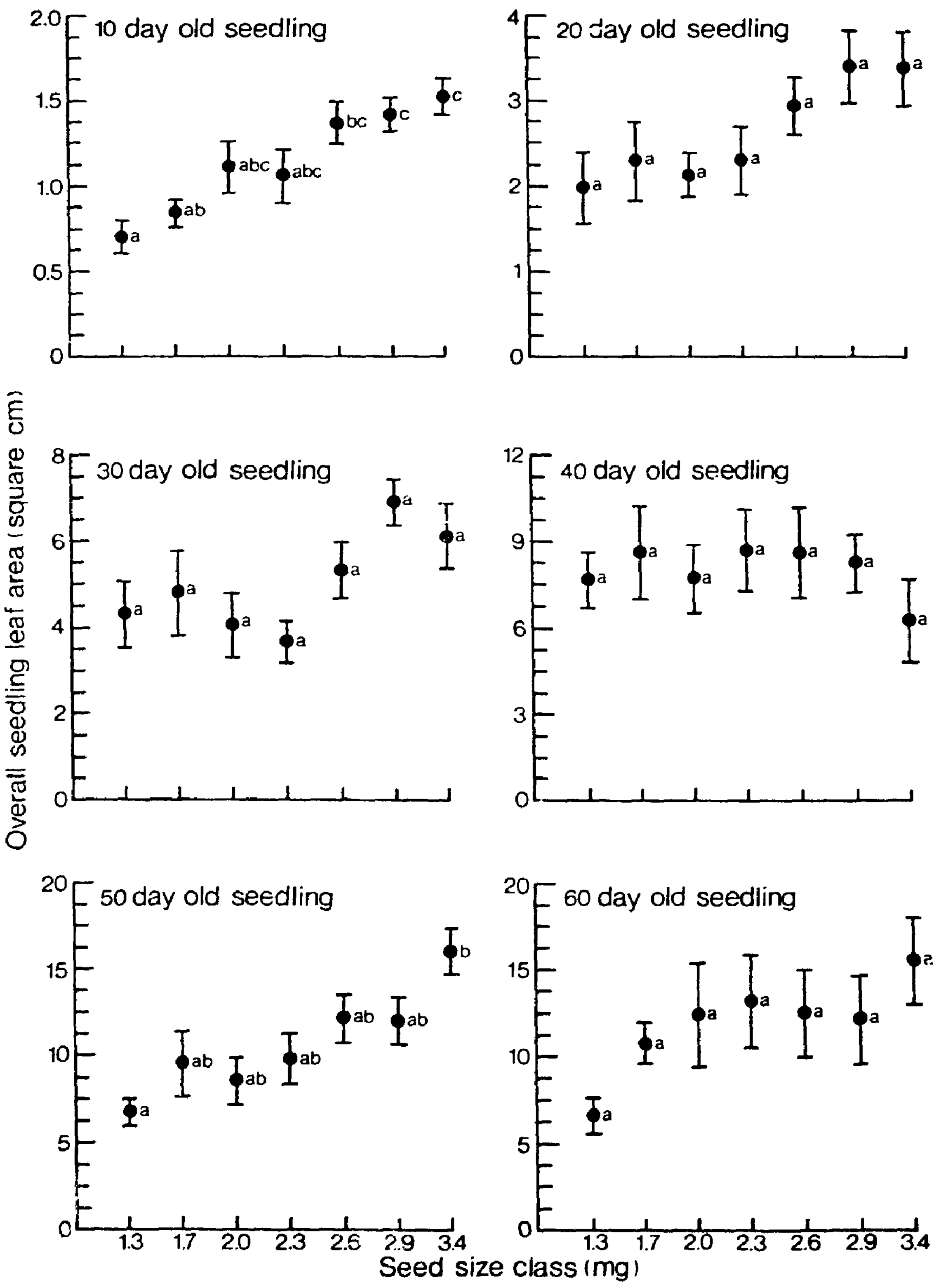

2 week old seedling
9
7
5
3
1
d
cd
bcd
abc
abc
ab
a
4 week old seedling
36
28
20
12
4
d
d
bcd
cd
abc
ab
a
6 week old seedling
105
80
55
30
5
b
ab
ab
ab
a
a
ab
8 week old seedling
200
150
100
50
0
a
a
a
a
a
a
a
10 week old seedling
280
210
140
70
0
a
a
a
a
a
a
a
12 week old seedling
360
270
180
90
0
a
a
a
a
a
a
a
Overall seedling weight (mg)
0
1.3
1.8
2.0
2.2
2.4
2.5
2.9
Seed size class (mg)

Figure 4.4 Comparisons in leaf area of *Agropyron psammophilum* seedlings from different seed size classes over six harvests. Means (solid circles) followed by different letters are significantly ($P < 0.05$) different according to Tukey's studentized range test. Vertical lines indicate the standard errors.


10 day old seedling
20 day old seedling
30 day old seedling
40 day old seedling
50 day old seedling
60 day old seedling
Overall seedling leaf area (square cm)
Seed size class (mg)
1.3
1.7
2.0
2.3
2.6
2.9
3.4
a
ab
abc
bc
c
b

4.5).

The leaf area ratios of seedlings from all seed size classes were uniform in *Panicum virgatum* according to Tukey's studentized range test (Table 4.3). In *Agropyron psammophilum*, however, significant differences in leaf area ratio were observed in 30 and 40-day old seedlings (Table 4.4). A trend of increasing leaf area ratio with decreasing parental seed size seemed to exist in 40-day old seedlings. However, it contributed little to the variation in seedling size over time.

4.3.4 Growth analysis

The fitted quadratic models for leaf area and seedling weight in both species were statistically significant ($P < 0.01$) according to an F-test. The regression coefficients (r^2) ranged from 0.534 to 0.904 (Table 4.5, 4.6).

4.3.4.1 Calculated initial leaf area and seedling weight

The calculated initial leaf area and seedling weight derived from the fitted function, 'a' of these models, showed significantly ($P < 0.01$) positive correlations with seed size in both species (Fig. 4.6). This coincides very well with the data actually obtained. Seed size explained 68 and 93% of the variation in initial leaf area and seedling weight respectively in *Panicum virgatum* and 88 and 95%, respectively, in *Agropyron psammophilum*.

Figure 4.5 **Comparisons of dry weight of *Agropyron psammophilum* seedlings from different seed size classes over six harvests. Means (solid circles) followed by different letters are significantly (P < 0.05) different according to Tukey's studentized range test. Vertical lines indicate the standard errors.**

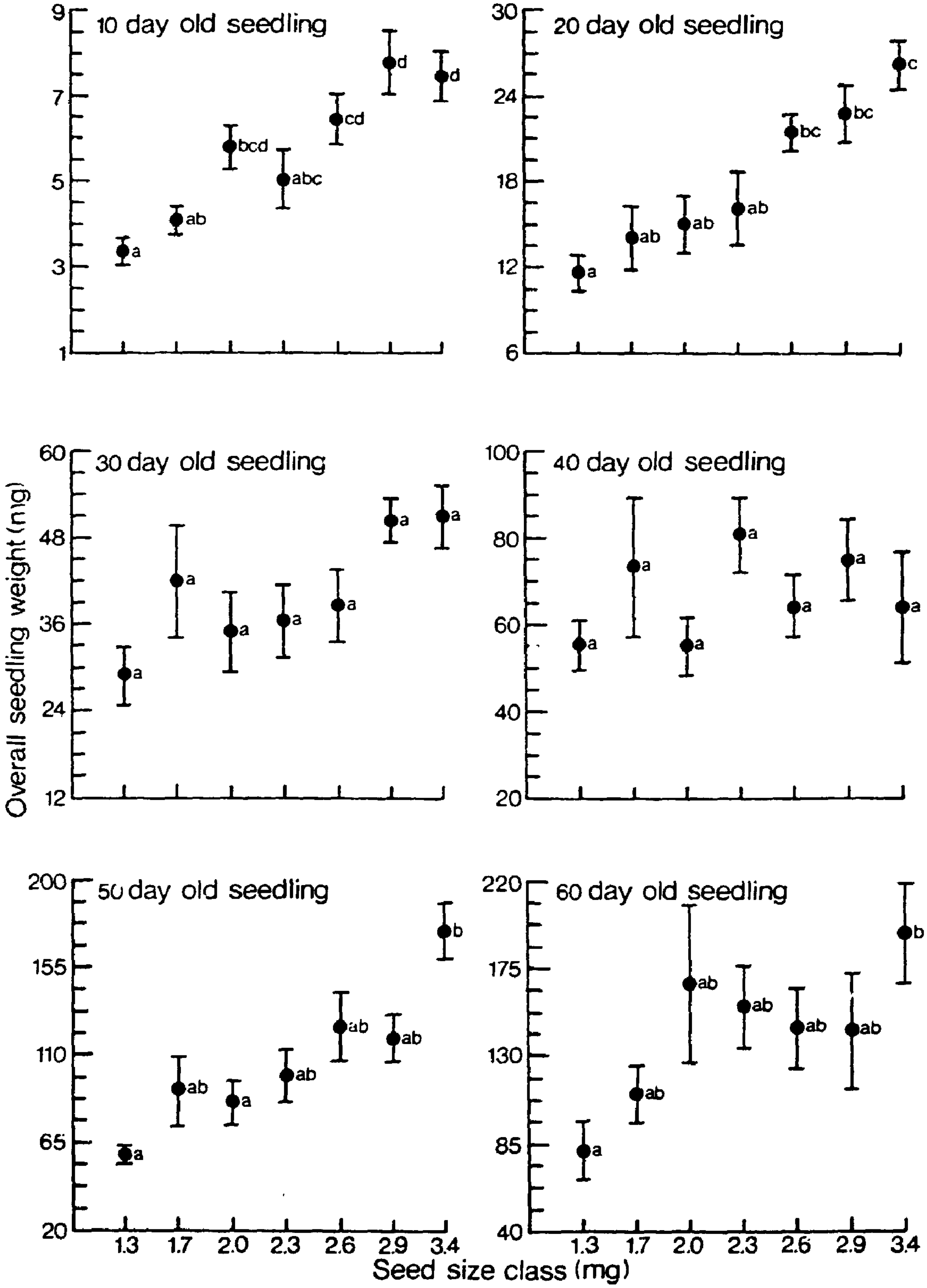

10 day old seedling
9
7
5
3
1
a
ab
bcd
abc
cd
d
d
20 day old seedling
30
24
18
12
6
a
ab
ab
ab
bc
bc
c
30 day old seedling
60
48
36
24
12
a
a
a
a
a
a
a
40 day old seedling
100
80
60
40
20
a
a
a
a
a
a
a
50 day old seedling
200
155
110
65
20
a
ab
a
ab
ab
ab
b
60 day old seedling
220
175
130
85
40
a
ab
ab
ab
ab
ab
b
Overall seedling weight (mg)
1.3
1.7
2.0
2.3
2.6
2.9
3.4
Seed size class (mg)

Table 4.3 Leaf area ratio in cm^2mg^{-1} (leaf area/overall seedling weight) of *Panicum virgatum* seedlings from different seed size classes harvested at 2, 4, 6, 8, 10 and 12 weeks after emergence. Values (mean ± standard error) in each column are not significantly different according to Tukey's studentized range test (SAS 1985).

Seed size class (mg)	Age in weeks					
	2	4	6	8	10	12
			(cm^2mg^{-1})			
1.3	0.200	0.165	0.129	0.090	0.089	0.063
	±0.0'1	±0.014	±0.007	±0.014	±0.008	±0.002
1.8	0.211	0.1351	0.125	0.095	0.086	0.066
	±0.009	±0.006	±0.009	±0.007	±0.007	±0.004
2.0	0.198	0.146	0.132	0.106	0.086	0.067
	±0.006	±0.005	±0.008	±0.007	±0.005	±0.003
2.2	0.191	0.141	0.121	0.087	0.084	0.055
	±0.011	±0.011	±0.005	±0.006	±0.006	±0.004
2.4	0.205	0.155	0.133	0.105	0.072	0.067
	±0.007	±0.012	±0.008	±0.009	±0.005	±0.005
2.5	0.194	0.137	0.115	0.090	0.082	0.057
	±0.011	±0.008	±0.008	±0.003	±0.005	±0.003
2.9	0.185	0.142	0.126	0.105	0.072	0.061
	±0.006	±0.005	±0.007	±0.009	±0.006	±0.004

Table 4.4 Leaf area ratio in cm^2mg^{-1} (leaf area/overall seedling weight) of *Agropyron psammophilum* seedlings from different seed size classes harvested at 10, 20, 30, 40, 50 and 60 days after emergence. Values (mean ± standard error) in each column followed by different letters are significantly ($P < 0.05$) different according to Tukey's studentized range test (SAS 1985).

Seed size class (mg)	Age in days 10	20	30	40	50	60
	(cm^2mg^{-1})					
1.3	0.206	0.162	0.145	0.137	0.114	0.086
	±0.018^{A}	±0.018^{A}	±0.008^{A}	±0.011^{A}	±0.010^{A}	±0.004^{A}
1.7	0.206	0.158	0.112	0.121	0.110	0.102
	±0.014^{A}	±0.022^{A}	±0.005^{AB}	±0.004^{AB}	±0.008^{A}	±0.007^{A}
2.0	0.186	0.146	0.110	0.138	0.098	0.077
	±0.011^{A}	±0.012^{A}	±0.008^{AB}	±0.010^{A}	±0.005^{A}	±0.004^{A}
2.3	0.212	0.145	0.103	0.105	0.099	0.082
	±0.018^{A}	±0.010^{A}	±0.003^{B}	±0.005^{AB}	±0.003^{A}	±0.005^{A}
2.6	0.213	0.135	0.141	0.128	0.103	0.087
	±0.009^{A}	±0.012^{A}	±0.009^{A}	±0.010^{AB}	±0.011^{A}	±0.010^{A}
2.9	0.186	0.148	0.140	0.114	0.102	0.085
	±0.011^{A}	±0.010^{A}	±0.013^{AB}	±0.010^{AB}	±0.005^{A}	±0.001^{A}
3.4	0.206	0.127	0.120	0.095	0.093	0.079
	±0.007^{A}	±0.009^{A}	±0.010^{AB}	±0.005^{B}	±0.004^{A}	±0.007^{A}

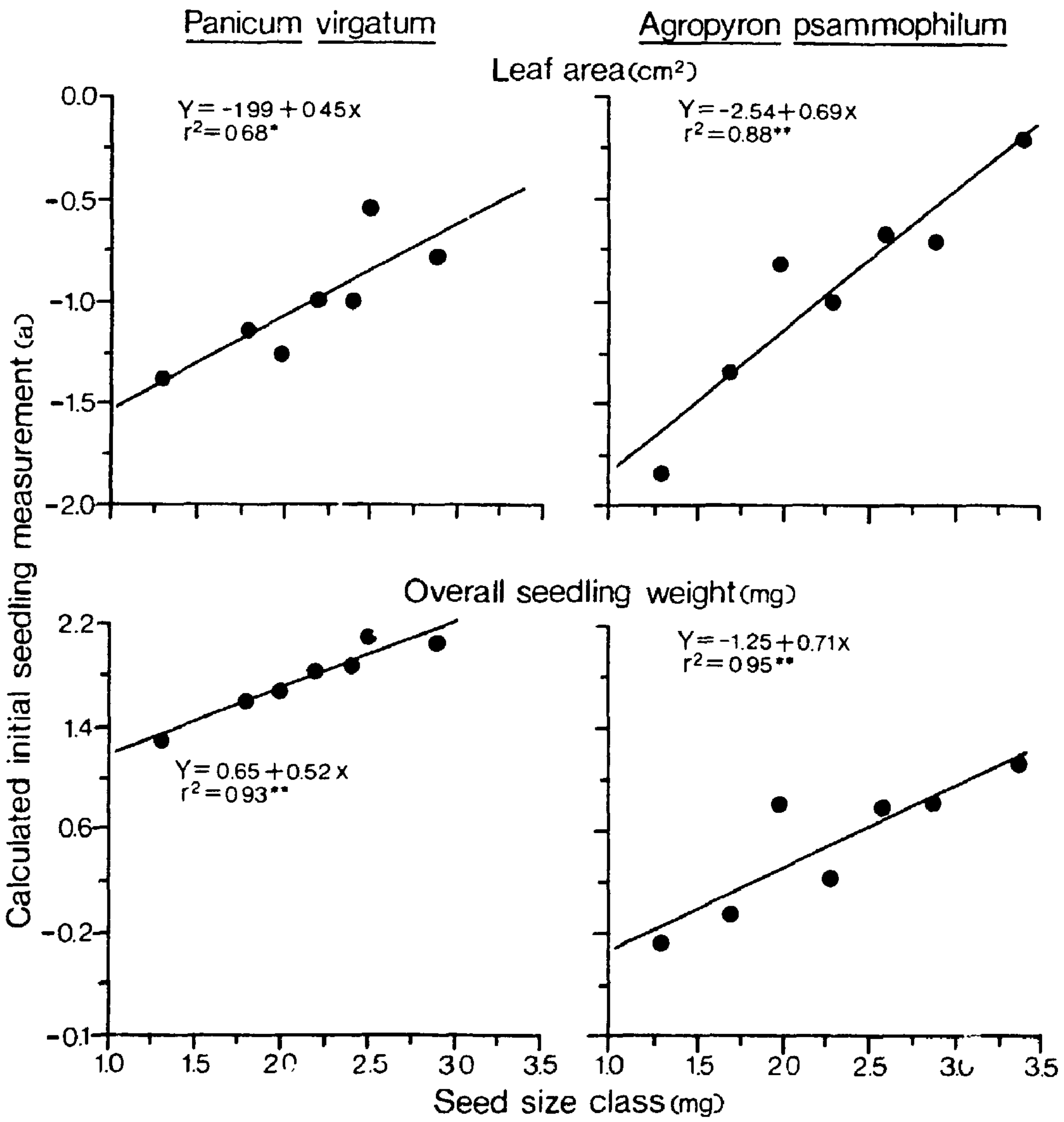
Table 4.5 Polynomial growth models of leaf area and dry weight of *Panicum virgatum* seedlings from each seed size class. Y is the natural logarithm of seedling measurement (leaf area or seedling weight) and T is the time (days after emergence) at which the measurement is taken.

Seed size class(mg)	Regression equations	r^2	P
	Leaf area		
1.3	$Y = -1.3801 + 0.5887T - 0.0249T^2$	0.697	<0.01
1.8	$Y = -1.1334 + 0.6204T - 0.0326T^2$	0.534	<0.01
2.0	$Y = -1.2609 + 0.7092T - 0.0353T^2$	0.695	<0.01
2.2	$Y = -0.9895 + 0.5948T - 0.0272T^2$	0.619	<0.01
2.4	$Y = -0.9941 + 0.7306T - 0.0415T^2$	0.561	<0.01
2.5	$Y = -0.5390 + 0.5130T - 0.0226T^2$	0.626	<0.01
2.9	$Y = -0.7848 + 0.6330T - 0.0317T^2$	0.640	<0.01
	Seedling weight		
1.3	$Y = 1.2905 + 0.6338T - 0.0279T^2$	0.861	<0.01
1.8	$Y = 1.5860 + 0.6455T - 0.0376T^2$	0.786	<0.01
2.0	$Y = 1.6727 + 0.6215T - 0.0299T^2$	0.757	<0.01
2.2	$Y = 1.8352 + 0.5392T - 0.0213T^2$	0.775	<0.01
2.4	$Y = 1.8820 + 0.7044T - 0.0436T^2$	0.786	<0.01
2.5	$Y = 2.0945 + 0.5441T - 0.0234T^2$	0.811	<0.01
2.9	$Y = 2.0550 + 0.6094T - 0.0306T^2$	0.839	<0.01

Table 4.6 Polynomial growth models of leaf area and dry weight of *Agropyron psammophilum* seedlings from each seed size class. Y is the natural logarithm of seedling measurement (leaf area or seedling weight) and T is the time (days after emergence) at which the measurement is taken.

Seed size class(mg)	Regression equations	r^2	P
	Leaf area		
1.3	$Y = -1.8426 + 0.1537T - 0.0016T^2$	0.778	<0.01
1.7	$Y = -1.3457 + 0.1226T - 0.0010T^2$	0.705	<0.01
2.0	$Y = -0.8145 + 0.0877T - 0.0006T^2$	0.651	<0.01
2.3	$Y = -0.9973 + 0.1000T - 0.0007T^2$	0.799	<0.01
2.6	$Y = -0.6689 + 0.1013T - 0.0008T^2$	0.763	<0.01
2.9	$Y = -0.7109 + 0.1163T - 0.0010T^2$	0.812	<0.01
3.4	$Y = -0.1862 + 0.0694T - 0.0004T^2$	0.664	<0.01
	Seedling weight		
1.3	$Y = -0.2821 + 0.1632T - 0.0015T^2$	0.904	<0.01
1.7	$Y = -0.0458 + 0.1588T - 0.0014T^2$	0.797	<0.01
2.0	$Y = 0.8034 + 0.1013T - 0.0006T^2$	0.806	<0.01
2.3	$Y = 0.2284 + 0.1427T - 0.0011T^2$	0.888	<0.01
2.6	$Y = 0.7843 + 0.1214T - 0.0009T^2$	0.879	<0.01
2.9	$Y = 0.8400 + 0.1333T - 0.0011T^2$	0.894	<0.01
3.4	$Y = 1.1054 + 0.1086T - 0.0007T^2$	0.831	<0.01

Figure 4.6 Regressions of the calculated initial measurements of leaf area (cm^2) and overall weight (mg) of *Panicum virgatum* and *Agropyron psammophilum* seedlings derived from the fitted models in different seed size classes.


Panicum virgatum
Agropyron psammophilum
Leaf area(cm²)
Y= -1.99 + 0.45x
r²=0.68*
Y= -2.54+0.69x
r²=0.88**
Overall seedling weight(mg)
Y= 0.65 +0.52 x
r²=0.93**
Y= -1.25+0.71x
r²=0.95**
Calculated initial seedling measurement (a)
0.0
-0.5
-1.0
-1.5
-2.0
2.2
1.4
0.6
-0.2
-0.1
1.0
1.5
2.0
2.5
3.0
3.5
Seed size class(mg)

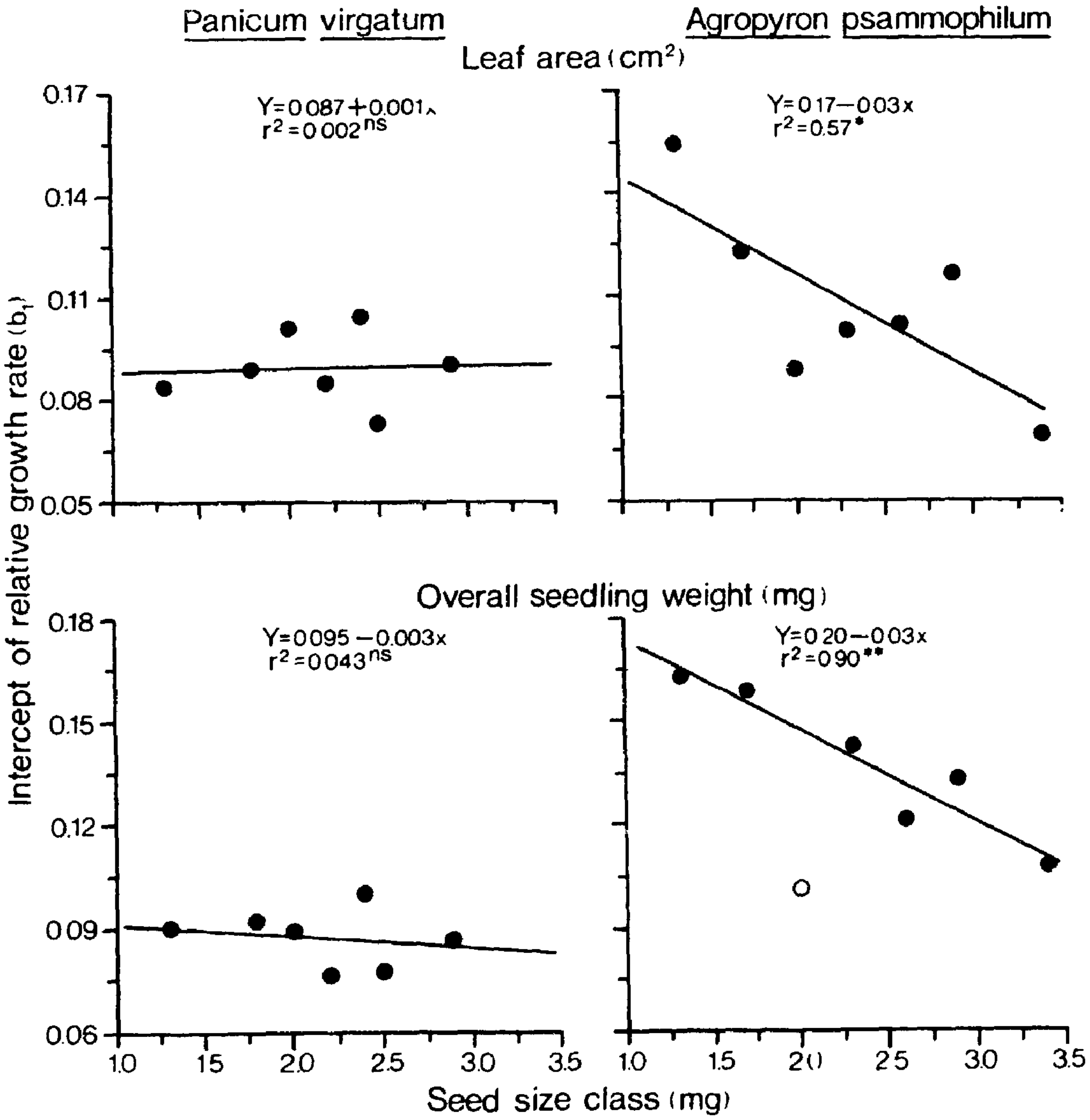
4.3.4.2 Intercept of the relative growth rate

The intercepts of relative growth rate (b_1), which represent the initial relative growth rates, of leaf area and seedling weight showed no significant correlation with seed size in *Panicum virgatum* (Fig. 4.7). However, in *Agropyron psammophilum*, the correlation between leaf area and seed size was marginally significant at $P = 0.05$. The seed size and seedling weight correlation was significant ($P < 0.01$) only when an unusual datum point was deleted from the calculation (Fig. 4.7). About 57 and 90% of the variation in initial relative growth rate of leaf area and seedling weight, respectively, was explained by seed size in *A. psammophilum*.

4.3.4.3 Slope of the relative growth rate

The slopes of the relative growth rate (b_2) for leaf area and seedling weight were not correlated with seed size in *Panicum virgatum* (Fig. 4.8). Similarly, in *Agropyron psammophilum* the slopes of the relative growth rate for leaf area were not significantly related to seed size owing to a nonlinear relationship between b_2 and seed size of seedlings from mid-size (2.0 - 2.6 mg) classes (Fig. 4.8). However, the slopes of relative growth rate for seedling weight were significantly ($P < 0.05$) related to seed size in this species when an unusual datum point was omitted. In general, seedlings from large seeds had smaller absolute b_2 values than seedlings from small seeds. Thus, the rate of decrease in relative growth rate of seedlings from small seeds was

Figure 4.7 Regressions of the intercepts of relative growth rate of leaf area and overall weight of *Panicum virgatum* and *Agropyron psammophilum* seedlings derived from the fitted models in different seed size classes. The unusual datum point is indicated by an open circle.


Panicum virgatum
Agropyron psammophilum
Leaf area (cm²)
Y=0.087+0.001x
r²=0.002ns
Y=0.17−0.03x
r²=0.57*
Overall seedling weight (mg)
Y=0.095−0.003x
r²=0.043ns
Y=0.20−0.03x
r²=0.90**
Intercept of relative growth rate (b1)
0.17
0.14
0.11
0.08
0.05
0.18
0.15
0.12
0.09
0.06
1.0
1.5
2.0
2.5
3.0
3.5
Seed size class (mg)

greater than that of seedlings from large seeds in *A. psammophilum* (Fig. 4.8). This trend is shown clearly by the calculated relative growth rate of leaf area and seedling weight at each harvest (Table 4.7). Higher relative growth rate of seedlings from small seeds was maintained during the first 30 days after emergence. Thereafter, the opposite became true.

4.3.4.4 Days after emergence when R = 0

Seed size showed no significant effects on the length of time taken by the relative growth rate of leaf area and seedling weight to approach zero in either species (Fig. 4.9). However, seedlings of *Agropyron psammophilum* derived from large seeds tended to have greater values than those from small seeds. For example, the relative growth rate of seedlings from 1.3 and 1.7 mg size classes approached zero 48 and 56 days after emergence in leaf area and 54 and 57 days in seedling weight. However, it took 71, 63 and 87 days, respectively, for seedlings from 2.3, 2.6 and 3.4 mg to show zero relative growth rate in leaf area and 65, 67 and 78 days to do so in absolute dry weight of seedlings (Fig. 4.9).

4.3.4.5 Expected maximum seedling measurement

Figure 4.10 shows the expected maximum leaf area and seedling weight (calculated by substituting T with T_{max} in Equation 1) of seedlings from each seed size class of both species. The expected maximum sizes of both leaf area and

Figure 4.8 Regressions of the slopes of the relative growth rate of leaf area and overall weight of *Panicum virgatum* and *Agropyron psammophilum* seedlings derived from the fitted models in different seed size classes. The unusual datum points are indicated by open circles.

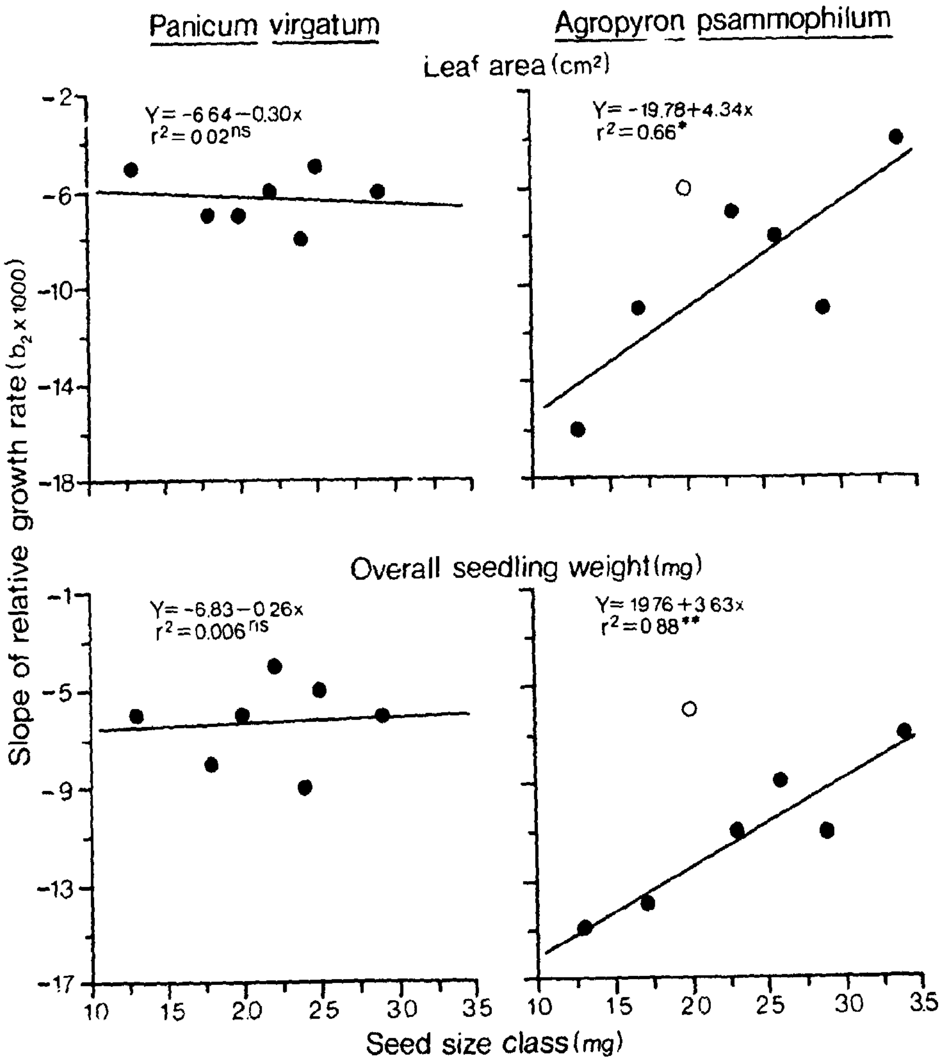

Panicum virgatum
Agropyron psammophilum
Leaf area (cm²)
Y= -6 64 - 0.30x
r² = 0 02ns
Y= -19.78+4.34x
r² = 0.66*
-2
-6
-10
-14
-18
Slope of relative growth rate (b₂ x 1000)
Overall seedling weight (mg)
Y= -6.83 - 0 26x
r² = 0.006ns
Y= 19 76 + 3 63x
r² = 0 88**
-1
-5
-9
-13
-17
10
15
20
25
30
35
10
15
20
25
30
35
Seed size class (mg)

Table 4.7 Calculated relative growth rates of leaf area and seedling weight of *Agropyron psammophilum* at each harvest. Values were obtained by using the equation $R = b_1 + 2b_2T$.

Seed size	Days after emergence					
class(mg)	10	20	30	40	50	60
			Leaf area			
1.3	0.122	0.090	0.058	0.026	-0.006	-0.038
1.7	0.103	0.083	0.063	0.043	0.023	0.003
2.0	0.076	0.064	0.052	0.040	0.028	0.016
2.3	0.086	0.072	0.042	0.044	0.030	0.016
2.6	0.085	0.069	0.053	0.037	0.021	0.005
2.9	0.096	0.076	0.056	0.036	0.016	-0.004
3.4	0.061	0.053	0.045	0.037	0.029	0.021
			Seedling weight			
1.3	0.133	0.103	0.073	0.043	0.013	-0.017
1.7	0.131	0.103	0.075	0.047	0.019	-0.009
2.0	0.089	0.077	0.065	0.053	0.041	0.029
2.3	0.121	0.099	0.077	0.055	0.033	0.011
2.6	0.103	0.085	0.067	0.049	0.031	0.013
2.9	0.111	0.089	0.067	0.045	0.023	0.001
3.4	0.095	0.081	0.067	0.053	0.039	0.025

Figure 4.9 Regressions of the calculated time (T_{Max}) when the relative growth rate of leaf area and overall weight of *Panicum virgatum* and *Agropyron psammophilum* seedlings approached zero in different seed size classes. The unusual datum point is indicated by an open circle.

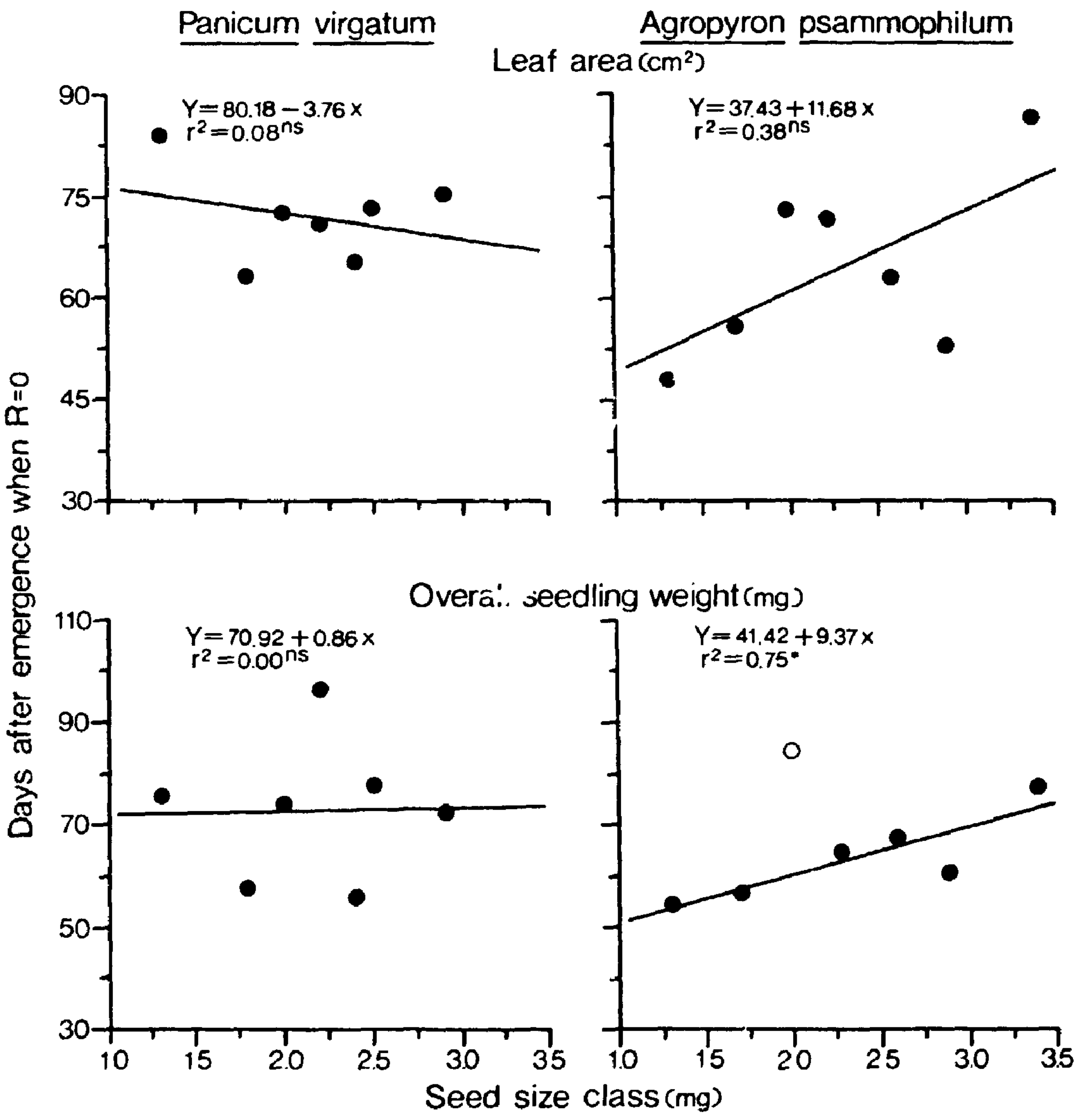
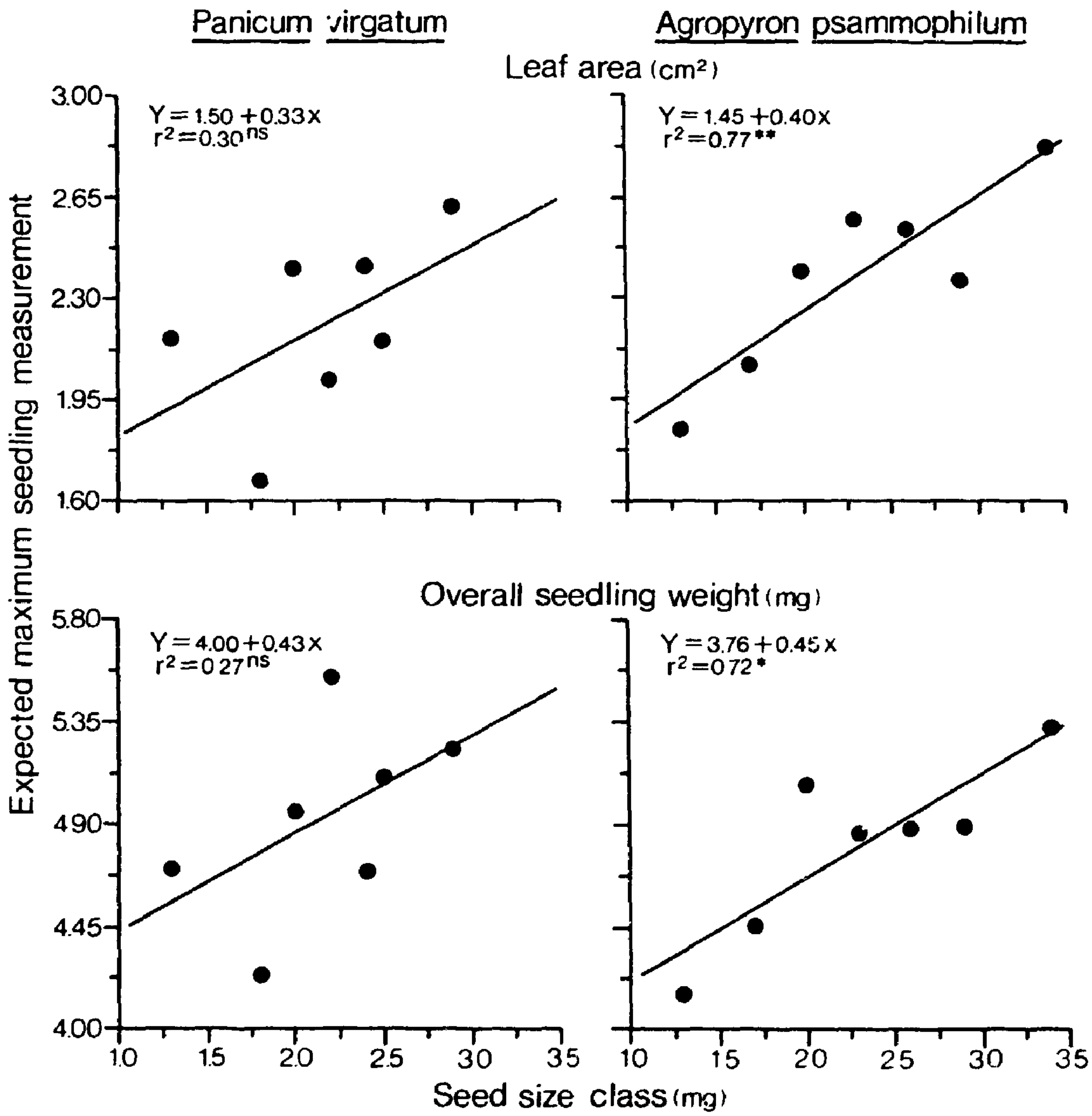

Panicum virgatum
Agropyron psammophilum
Leaf area (cm²)
Y=80.18 − 3.76 x
r²=0.08ns
Y=37.43 + 11.68 x
r²=0.38ns
Overall seedling weight (mg)
Y=70.92 + 0.86 x
r²=0.00ns
Y=41.42 + 9.37 x
r²=0.75*
Days after emergence when R=0
90
75
60
45
30
110
90
70
50
30
1.0
1.5
2.0
2.5
3.0
3.5
Seed size class (mg)

Figure 4.10 Regressions of the expected maximum leaf area and overall weight of *Panicum virgatum* and *Agropyron psammophilum* seedlings in different seed size classes.


Panicum virgatum
Agropyron psammophilum
Leaf area (cm²)
Y = 1.50 + 0.33x
r² = 0.30 ns
Y = 1.45 + 0.40x
r² = 0.77**
3.00
2.65
2.30
1.95
1.60
Expected maximum seedling measurement
Overall seedling weight (mg)
Y = 4.00 + 0.43x
r² = 0.27 ns
Y = 3.76 + 0.45x
r² = 0.72*
5.80
5.35
4.90
4.45
4.00
1.0
1.5
2.0
2.5
3.0
3.5
1.0
1.5
2.0
2.5
3.0
3.5
Seed size class (mg)

seedling weight appeared to be related to seed size. However, the relationship was not significant in *Panicum virgatum*. In *Agropyron psammophilum*, it was significant and seed size explained 77 and 72% of the variation in leaf area and seedling weight, respectively.

4.4 DISCUSSION

Individual seed mass variation of up to 12 fold in *Panicum virgatum* seeds and 6 fold in *Agropyron psammophilum* seeds was observed in this study. Similar observations were also reported with other species by Hawke and Maun (1989), Mazer (1987) and Thompson (1984). Among the various factors affecting seed mass, competition among maturing seeds on a spike for limited resources may be occurring in *Agropyron psammophilum*. In this species, each spikelet usually bears 4 to 8 florets (Gillett and Senn 1961). But I found that only one to three, and rarely four, of those developed into seeds. If a spikelet contained only one seed, it was usually large (greater than 2.1 mg) in size. However, if a spikelet contained more than one seed, the distal one or two seeds were large and the proximal ones were small (less than 2.1 mg). The number of seeds in each spikelet were related to their position on the spike. Generally, spikelets in the middle or upper part of the spike contained more than one seed. The control mechanism in *P. virgatum* is not clear. Possibly there is a tradeoff between seed size and number. In the field, it is common to find individuals with large or relatively small number of seeds. Plants producing large quantities of seeds may have less mean seed mass than those producing a small amount. It is also plausible that other factors such as the age of plants, nutrition and moisture of the microhabitat contributed to the seed size variation.

In *Panicum virgatum*, a left skewed and leptokurtic seed size frequency distribution indicates that in the seed population the number of seeds larger than the mean exceed those smaller than the mean and more seeds are distributed around the mean compared to a normal distribution. Furthermore, results from germination test showed that significantly more seeds in size class 1.3 mg were dead seeds. The skewness is thus stronger when taking the viability of seeds into consideration. In *Agropyron psammophilum*, a significantly right skewed and platykurtic seed size frequency distribution was obtained. It implies that the seed population is composed of more seeds weighing less than the mean than those greater than the mean as compared to a normal distribution. According to previous studies (Obeid *et al* 1967, Turner and Rabinowitz 1983), the size distribution of individuals in a stand of plants changes from a nearly normal shape to a right skewed one with time. Since the seedling size of the two species is significantly related to seed size, we would expect a right skewed size distribution even at the seedling stage in *A. psammophilum*. The size distribution of *P. virgatum* seedlings will probably follow the model presented by Turner and Rabinowitz (1983).

When seedling of both species grow in pure stands, different regulating mechanisms may be operating.

Variation in seed size of a species may be of ecological significance in a number of ways. For example, large seeds (i) may produce higher percentage germination, (ii) may have higher rate of germination, (iii) may produce higher absolute leaf area and seedling weight and (iv) may result in low relative growth rate of seedlings. I tested each of these hypotheses in this study.

More than 90% viable seeds in each size class of the two species germinated in this study suggesting that percent germination was not affected by seed size. However, the germination rate of large seeds was significantly higher than that of small seeds. Several studies (Ross and Harper 1972, Weaver and Cavers 1978, Howell 1981, Stanton 1984b) have suggested that early emergents have higher competitive ability than later emergents because they have first priority in occupying the available space and utilizing the limited resources. In the sand dune environment, the supply of moisture and nutrients is limited (Baldwin and Maun 1983, Hawke and Maun 1988) and early emerging seedlings would probably have better chances of growth and establishment.

It is generally agreed that large seeds produce larger seedlings than small seeds. However, two patterns of absolute growth rate of the subsequent seedlings have been reported; (i) a consistently greater absolute growth of seedlings from large seeds is maintained until maturity (Black 1957, Henson and Tayman 1961, Stickler and Wassom 1963, Schaal 1980) and (ii) the initial size advantage of seedlings from large seeds may disappear with the passage of time because of higher relative growth rate of seedlings from small seeds (Harper and Obeid 1967, Wulff 1973, Lewis and Garcia 1979, Zimmerman and Weis 1983). Seedlings of *Panicum virgatum* followed the second pattern whereas seedlings of *Agropyron psammophilum* did not follow either of these patterns. Instead, the absolute seedling growth fluctuated with time. For example, seedlings from large seeds were significantly larger than those from small seeds until they were 20 days old. The differences disappeared in 30 and 40-day old seedlings but reappeared in 50 and 60-day old seedlings. Data on *A. psammophilum* suggests that the choice of number and dates of harvests may have significant implications on the outcome. For instance, if four harvests (at 10, 20, 50 and 60 days) had been taken, seed size would have had a consistent positive effect on seedling growth. However, if the four harvests had been conducted at 10, 20, 30 and 40 days after emergence, the conclusion would have been the opposite. Stanton (1984b) drew attention to this problem but dit not provide any experimental evidence.

A number of studies (Black 1957, Stearns 1960, Wulff 1973, Stebbins 1976, Lewis and Garcia 1979, Zimmerman and Weis 1983) indicate that soon after emergence seedlings from small seeds exhibit greater relative growth rate than those from large seeds. Thus, the initial size advantage of large seeds compared with small ones is short lived. *Panicum virgatum* seedlings seemed to follow this pattern according to the ANOVA results. However, growth analysis indicated no relationship between the relative growth rate of seedlings and their parental seed size and the initial seedling size differences were not maintained throughout the experiment. Possibly, the carrying capacity of the experimental conditions may have imposed an upper limit on seedling size and resulted in an uniform final size for seedlings from various size classes as suggested by Harper and Obeid (1967). Secondly, the large intra-class variation in seedling size may have masked the differences due to seed size. Thus, seed size effects in *P. virgatum* may be apparent only in the early stages of seedling growth but greatly obscured by other environmental factors as the seedlings age.

The seedlings of *Agropyron psammophilum* followed the aforementioned trend until 40 days after emergence and then, the trend reversed gradually. The major change occurred in the rate of decrease in relative growth rate. For example, the relative growth rate of seedlings from all seed size classes decreased. However, the rate of decrease was lower in seedlings from large as compared to small seeds. Thus, seedlings from large seeds regained their size superiority at later stages of development.

Another important parameter is the length of time required by a seedling to reach zero relative growth rate ($R = 0$). The seedlings of *A. psammophilum* exhibited a clear but non-significant trend. Before the end of 60 days after emergence the seedlings from small seeds had already shown a zero relative growth rate but the seedlings from large seeds still required more time to reach that point suggesting that seedlings from large seeds continue their positive growth for relatively longer period of time. Thus, seedlings from small seeds grew faster after emergence, reached their maximum size earlier and had smaller final sizes. The reverse was true for seedlings from large seeds. Further study is necessary to examine the ecological significance of these two strategies under field conditions.

Under the same experimental conditions, both *Panicum virgatum* and *Agropyron psammophilum* seedlings from large seeds had larger expected maximum size than those from small ones. Since large size is a good predictor of the establishment (Black 1958), seeds of large size may be of adaptive significance in establishment and maintenance of *P. virgatum* and *A. psammophilum* populations.

CHAPTER FIVE

EFFECT OF PARTIAL REMOVAL OF ENDOSPERM ON SEEDLING SIZES

5.1 INTRODUCTION

Predation of seeds by frugivores is one of the factors affecting the spatial pattern of recruitment in plant populations (Platt 1976, De Steven and Putz 1984, Webb and Willson 1985). Frugivores may act as seed consumers and dispersal agents thus reducing seed populations and altering the distribution pattern of seeds. However, in some cases seeds may also be partially consumed and left over in the seed population. For example, I observed partial consumption of seeds in the population of *Panicum virgatum* and *Agropyron psammophilum* in the field. Seeds of these two species contain a large volume of apical endosperm with the small embryo located at the other end. Predators such as insect larvae and ants usually consume part of the endosperm, embryo or both.

The most obvious effects of pre-dispersal predation are direct killing of seeds (Janzen 1971, Oliver and Chapin 1984, Ellison and Thompson 1987), reduction of seed mass without seed mortality (Janzen 1976, Ellison and Thompson 1987, Zhang and Maun 1989a), decrease in seed germination (Bentley *et al* 1980, Oliver and Chapin 1987) and acceleration of the onset of germination (Bremner *et al* 1963, Hsiao *et al* 1983, Bewley and Black 1985, Sung *et al* 1987, Zhang and Maun 1989a). When seeds of *Panicum virgatum* and *Agropyron psammophilum* germinate in the spring, both seeds with partial endosperm injury and intact seeds contribute to the seedling population. Since seed mass of both species affects seedling growth (Chapter 4), seed predation would affect the size specific demography of seedling population. In particular, the survival of seedlings from damaged seeds may be lowered. Janzen (1976) showed a conspicuous decline in seedling fitness of *Mucuna andreana* with an increase in the amount of removal of seed mass. However, for endospermic species, the growth of emerging seedlings may depend on embryo size, endosperm size or both. A better understanding of the effect of seed predation on seedling growth can be obtained by examining the relative importance of embryo and endosperm in the determination of seedling size.

In this study, the endosperm of *Panicum virgatum* and *Agropyron psammophilum* seeds was partially removed to determine its effect on seedling sizes. The objectives were i) to examine the function of seed embryo and endosperm in the determination of seedling size and ii) to determine the effect of injury to seed endosperm on the size of various components of the resulting seedlings.

5.2 MATERIALS AND METHODS

5.2.1 Source of experimental materials

Spikes and panicles of *Agropyron psammophilum* and *Panicum virgatum* were collected from randomly chosen plants in the study site on 13 and 27 August 1987, respectively. The samples were dried at room temperatures and the seeds (caryopses) with lemma and palea were removed from the spikes or panicles manually. Two weeks later, they were stored in a seed room at 5 °C and 40% relative humidity until used.

On 29 July 1988, seeds of the two species were husked manually by removing the lemma and palea and weighed individually to the nearest 0.1 mg with an electronic balance. Husked seeds of *Panicum virgatum* weighing 1.6, 2.8 and 3.0 mg per seed and *Agropyron psammophilum* weighing 1.9, 2.3 and 2.7 mg per seed were used in the two experiments in this study.

The sand used in these experiments was taken from the study site from which the seeds had been collected and sifted before use to remove the contained seeds and debris.

5.2.2 Experiment 1. Effects of partial removal of endosperm on seedling size

Within a species, embryos of seeds of the same shape and size may vary within narrow limits (Bremner *et al* 1963). Surgical removal of part of the endosperm of seeds of the same shape and size would produce seeds with similar embryo size but different endosperm reserves.

In this experiment, 0, 20, 40, 60 and 80% of the endosperm of husked seeds of *Panicum virgatum* weighing 2.8 mg, and *Agropyron psammophilum* weighing 2.3 mg, was removed surgically by cutting off the seeds with a scalpel under a dissecting microscope. To break innate dormancy, the seeds of *P. virgatum* were pretreated in a growth chamber set at

15/5 ^{0}C with 14 h light at the higher temperature and 10 h dark at the lower temperature for 20 days (Zhang and Maun 1989a). *Agropyron psammophilum* did not require any pretreatment for germination. Carefully prepared seeds of both species from each cutting treatment were sown separately at 0.5 cm depth in a 8 x 21 x 40 cm wooden flat filled with sand in an unheated greenhouse. Seven replications were used. A fine spray of water was provided daily. Seedlings were harvested three days after emergence to avoid independent growth that may obscure the effects of embryo and endosperm size on seedling growth. The height, area and dry weight of the leaf, length and dry weight of the primary root of the subsequent seedlings were measured.

5.2.3 Experiment 2. Comparisons of seedlings from small, large and surgically altered seeds

The purpose of this experiment was to see if predation of seeds only reduces stored reserves without affecting the vigour of the resulting seedlings. Husked seeds weighing 1.6 and 3.0 mg of *Panicum virgatum* and 1.9 and 2.7 mg of *Agropyron psammophilum* were considered small and large seeds, respectively for each species. In this experiment, the endosperms of large seeds of each species were surgically removed to reduce their weight to 1.6 mg for *P. virgatum* and 1.9 mg for *A. psammophilum*. Thus, the treatments consisted of intact small (control), intact large (control) and surgically altered (treated) seeds of both species. The controls and treated seeds were sown separately in rows in a 8 x 24 x 26 cm wooden flat filled with sand in an unheated greenhouse. Eleven replications were used. Before planting, the *P. virgatum* seeds were pretreated to remove innate dormancy under the same conditions as in Experiment 1. Similarly, the experimental conditions and the measured parameters of the emerging seedlings were identical to Experiment 1.

5.2.4 Statistical analysis

The means of seedling variables (Y) (Height, leaf area, leaf weight, root length and weight, seedling weight) were regressed on the percentage of endosperm removed (X) by using a program created by Orloci and Kenkel (1987). Nonparametric analysis of variance was used for comparisons between treatments of both experiments because of unequal variances among treatments. Kruskall-Wallis test (Zar 1984) was conducted first and if there were significant differences, further comparisons were made by using Dunn's Q test (Zar 1984).

Because of the difficulty in obtaining seeds of desired weight, sample size was small in this study. Three replications were obtained in two treatments, four in one treatment and more than five in the others. Throughout the experiments, randomization rocedures were followed to assign seeds to each treatment. The results thus obtained were still statistically valid.

5.3 RESULTS

5.3.1 General observations

Seedling emergence was achieved by all the germinated seeds of both species. At the time of harvest, the seedling weight of both species was smaller than the parental seed weight in Experiment 2 indicating that there was little independent seedling growth during the three days after emergence. Therefore, the differences in seedling variables were likely a reflection of the variation in seed embryo and/or endosperm reserve. Seedlings of both species mainly consisted of a fully expanded leaf and the primary root. The stem was not easily distinguishable and hence was considered a part of the leaf.

5.3.2 Experiment 1. Effects of partial removal of endosperm on seedling size

Of the seven *Panicum virgatum* seeds sown in each treatment, three seedlings emerged in the control, six in the 20 and 40% endosperm removal treatment, three in the 60% and none in the 80% endosperm removal treatment. In *Agropyron psammophilum*, six or seven seedlings emerged in all the treatments except the one with 80% of the seed endosperm removed, in which only four seedlings were found.

The mean lengths of time required for the seedlings to emerge from soil were 7, 7, 7 and 10 days after sowing in 0, 20, 40 and 60% endosperm removal treatments, respectively for *Panicum virgatum* and 4, 3, 3, 3, 4 days after sowing in

0, 20, 40, 60 and 80% endosperm removal treatments, respectively for *Agropyron psammophilum*. Nonparametric analysis of variance indicated that there were no significant differences in either species, suggesting that the growth rate of emerging seedlings had not been affected by surgical treatment.

All the measured seedling variables except root length and weight in *Panicum virgatum* showed a significantly ($P < 0.05$) negative linear relationship with the proportion of endosperm removed (Fig. 5.1). For root length (cm) and weight (mg) of *P. virgatum* seedlings, however, drastic decreases occurred when 60% of seed endosperm had been removed. In *Agropyron psammophilum*, significantly ($P < 0.05$) negative correlations between all the seedling parameters and the proportions of endosperm removed were observed (Fig. 5.1).

When 40% or more of the endosperm of *Panicum virgatum* seeds and 80% of the endosperm of *Agropyron psammophilum* seeds were removed, significantly greater amount of dry material was found in the root and significantly less in the leaf of the seedlings as compared to the control (Fig. 5.2).

5.3.3 Experiment 2. Comparisons of seedlings from small, large and surgically altered seeds

Less seedling emergence was observed in large (five out of eleven) and treated seeds (six out of eleven) of *Panicum virgatum* as compared with small seeds (eight out of eleven). In *Agropyron psammophilum*, all the eleven sown seeds emerged.

Figure 5.1 Regressions of seedling measurements of *Panicum virgatum* and *Agropyron psammophilum* on the percentage removal of seed endosperm. * $P < 0.05$. ** $P < 0.01$. ^{ns} Non-significant.

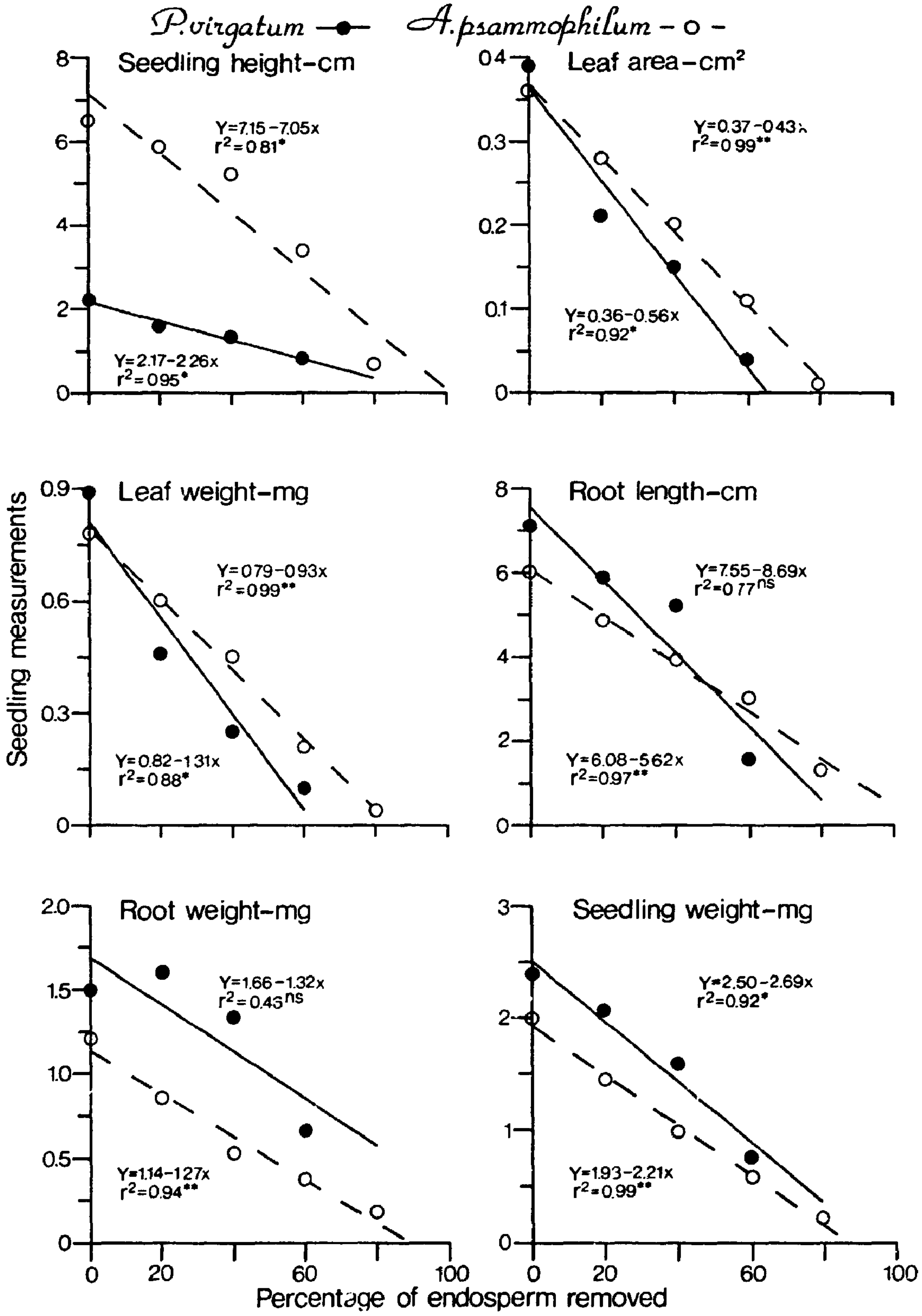
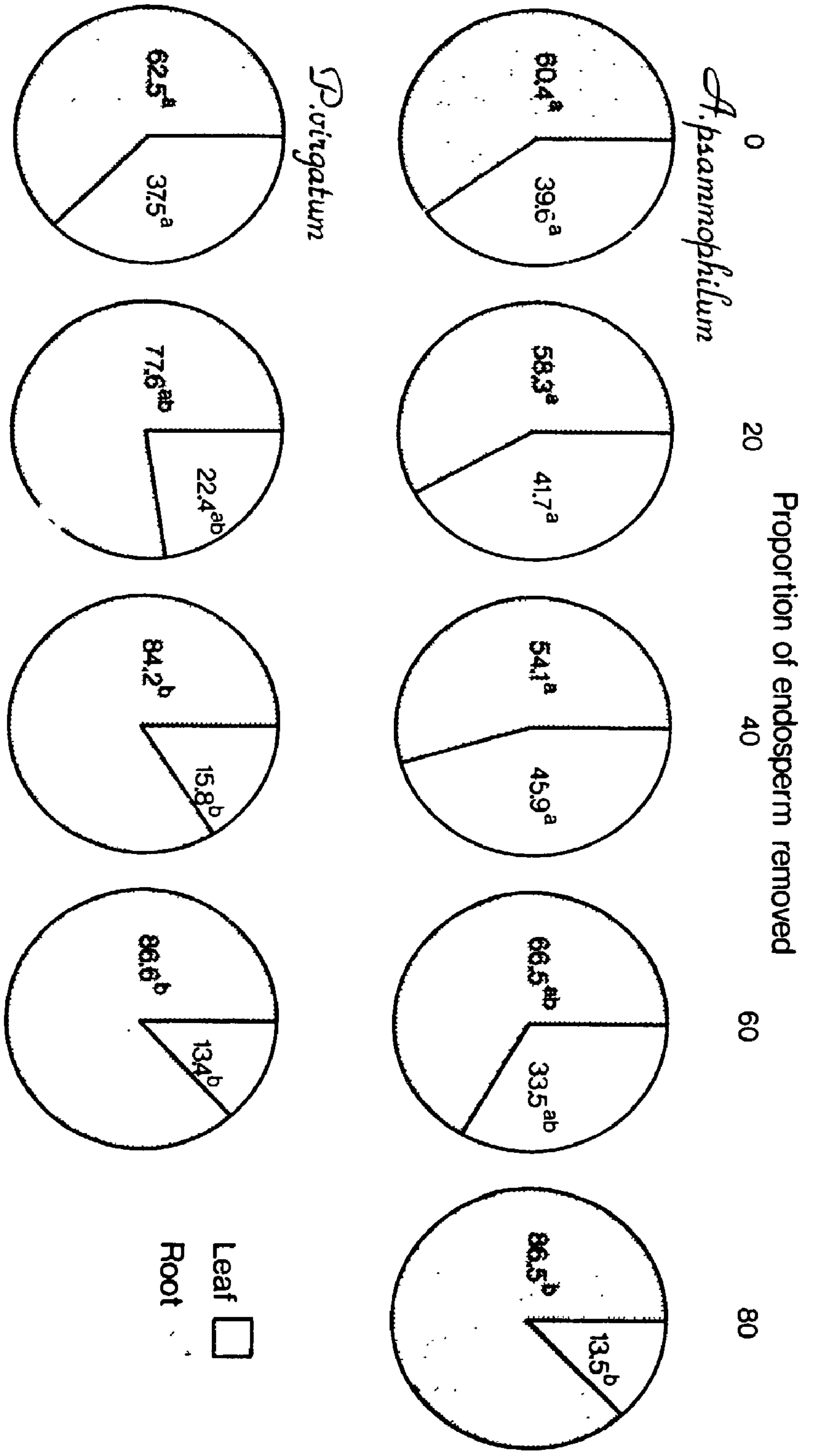

P. virgatum –●–
A. psammophilum – o –
Seedling height-cm
Y=7.15-7.05x
r2=0.81*
Y=2.17-2.26x
r2=0.95*
Leaf area-cm2
Y=0.37-0.43x
r2=0.99**
Y=0.36-0.56x
r2=0.92*
Leaf weight-mg
Y=0.79-0.93x
r2=0.99**
Y=0.82-1.31x
r2=0.88*
Root length-cm
Y=7.55-8.69x
r2=0.77ns
Y=6.08-5.62x
r2=0.97**
Root weight-mg
Y=1.66-1.32x
r2=0.43ns
Y=1.14-1.27x
r2=0.94**
Seedling weight-mg
Y=2.50-2.69x
r2=0.92*
Y=1.93-2.21x
r2=0.99**
Seedling measurements
Percentage of endosperm removed
0
20
60
100
8
6
4
2
0.4
0.3
0.2
0.1
0.9
0.6
0.3
2.0
1.5
1.0
0.5
3
2
1

Figure 5.2 Mean percent allocation of dry matter to leaf and root of *Panicum virgatum* and *Agropyron psammophilum* seedlings from seeds with 0, 20, 40, 60 and 80% endosperm removed. Percentage values of leaf or root of each species followed by different letters are significantly ($P < 0.05$) different according to Dunn's Q test.


Proportion of endosperm removed
0
20
40
60
80
A. psammophilum
60.4^a
39.6^a
58.3^a
41.7^a
54.1^a
45.9^a
66.5^ab
33.5^ab
86.5^b
13.5^b
P. virgatum
62.5^a
37.5^a
77.6^ab
22.4^ab
84.2^b
15.8^b
86.6^b
13.4^b
Leaf
Root

The number of days required for seedlings to emerge were seven or eight for *P. virgatum* and three for *A. psammophilum* showing no significant difference among treatments within each species.

In both species, large seeds produced seedlings with significantly greater measurement in all of the seedling variables than treated seeds (Fig. 5.3). *Panicum virgatum* seedlings from treated seeds did not differ significantly from those of small seeds. However, seedlings from treated seeds of *Agropyron psammophilum* differed significantly in leaf weight (Fig. 5.3c) and overall seedling weight (Fig. 5.3f) from those of small seeds. No significant difference was observed between seedlings from large and small seeds except for root weight (Fig. 5.3e) and overall seedling weight (Fig. 5.3f) in *P. virgatum* and root length (Fig. 5.3d) and root weight (Fig. 5.3e) in *A. psammophilum*.

Seedlings from large and small seeds showed similar patterns of dry material allocation. But seedlings from treated seeds devoted less dry matter to the leaf and more to the root than those from large and small seeds in both species (Fig. 5.4). The differences in dry matter allocation were significant in *Panicum virgatum* but not in *Agropyron psammophilum*.

5.4 DISCUSSION

If any seedling variable depended entirely on the embryo size of its seeds, its measurement in all the treatments in

Figure 5.3 Mean above ground height (a), leaf area (b), dry leaf weight (c), root length (d), root weight (e) and overall seedling weight (f) of *Panicum virgatum* and *Agropyron psammophilum* seedlings from small (S), large (L) and surgically altered (T) seeds. Vertical lines show the standard errors. Bars within each species denoted by different letters are significantly ($P < 0.05$) different according to Dunn's Q test.

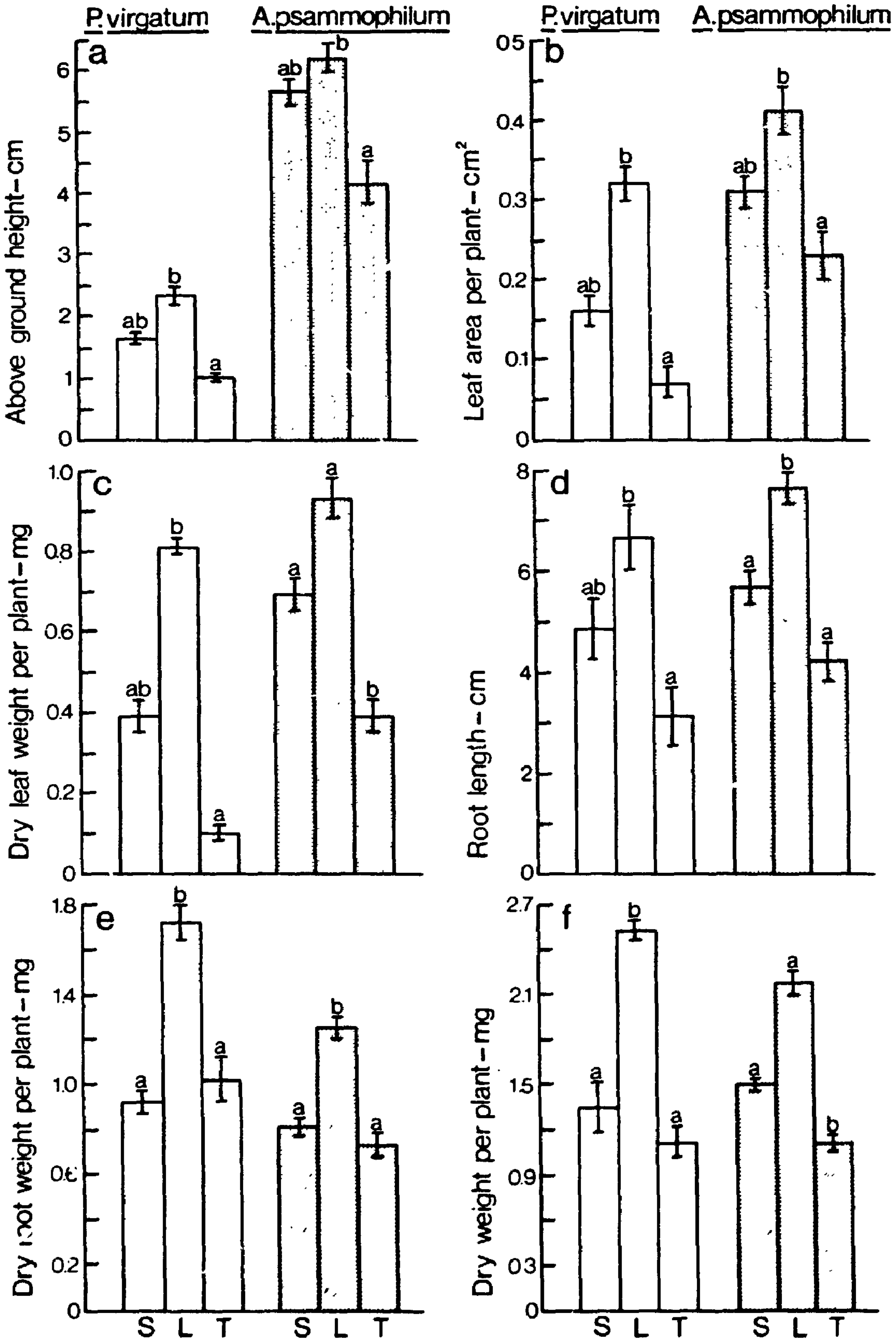
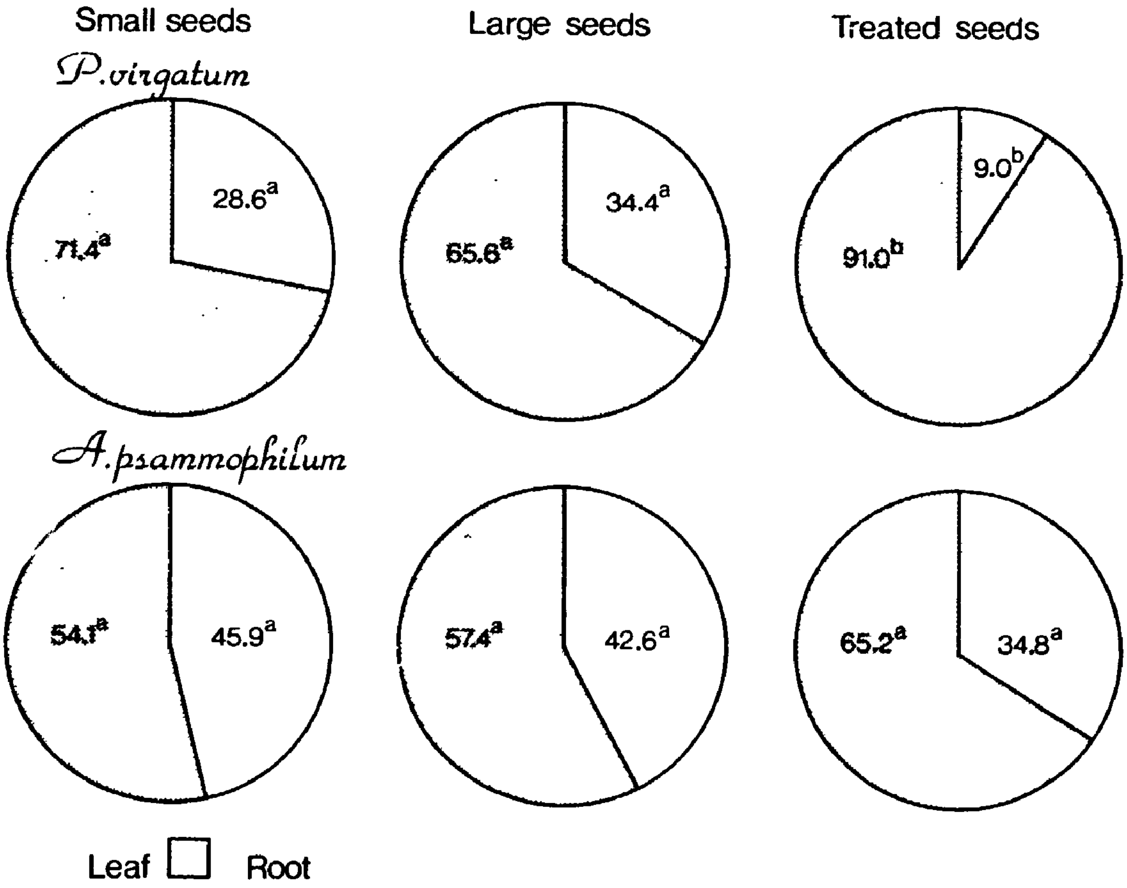

P. virgatum
A. psammophilum
a
Above ground height - cm
0
1
2
3
4
5
6
ab
b
a
ab
b
a
b
Leaf area per plant - cm²
0
0.1
0.2
0.3
0.4
0.5
ab
b
a
ab
b
a
c
Dry leaf weight per plant - mg
0
0.2
0.4
0.6
0.8
1.0
ab
b
a
a
a
b
d
Root length - cm
0
2
4
6
8
ab
b
a
a
b
a
e
Dry root weight per plant - mg
0
0.2
0.6
1.0
1.4
1.8
a
b
a
a
b
a
f
Dry weight per plant - mg
0
0.3
0.9
1.5
2.1
2.7
a
b
a
a
a
b
S L T
S L T

Figure 5.4 Mean percent allocation of dry matter to leaf and root of *Panicum virgatum* and *Agropyron psammophilum* seedlings from small, large and surgically altered (treated) seeds. Percentage values of leaf or root of each species in various treatments followed by different letters are significantly ($P < 0.05$) different according to Dunn's Q test.


Small seeds
Large seeds
Treated seeds
P. virgatum
28.6a
71.4a
34.4a
65.6a
9.0b
91.0b
A. psammophilum
54.1a
45.9a
57.4a
42.6a
65.2a
34.8a
Leaf ☐ Root

Experiment 1 would at least fluctuate within a small range, and both the large and treated seeds in Experiment 2 should produce seedlings with similar measurements in this variable. However, none of the seedling variables manifested this property. On the contrary, when the endosperm was removed in various proportions (Experiment 1), a notable decline in all seedling measurements occurred. Seedlings from surgically altered seeds (Experiment 2) were always significantly smaller than those from large seeds but did not differ significantly from those of small seeds in most cases. It is thus suggested that seedling size of the two species depends heavily on the nutrient reserves in seed endosperm rather than embryo size. A similar conclusion was also reported by Bremner *et al* (1963) who showed that endosperm size of wheat had considerable effect on seedling growth while embryo size had negligible effect.

Several studies indicated that predation of seeds reduced germination (Janzen 1976, Bentley *et al* 1980, Oliver and Chapin 1984, Ellison and Thompson 1987). For the two species used in this study, a reduction in germination and seedling emergence occurred only when the amount of endosperm removed exceeded 80%. Seedling emergence from *Agropyron psammophilum* seeds was not reduced when removed endosperm was 60% or less. In contrast, the removal of 20 and 40% endosperm of *Panicum virgatum* seeds increased seedling emergence probably owing to release of seeds from innate dormancy (Zhang and Maun 1989a).

The surgical removal of seed endosperm had deleterious effect on the growth of seedlings. Surgically reduced seeds usually produced seedlings of smaller size than those from control seeds. Similar reduction in growth of seedlings from insect infested acorns of *Quercus virginina* Miller and larval damaged seeds of *Lomatium grayi* Coult and Rose were reported by Oliver and Chapin (1984) and Ellison and Thompson (1987), respectively. However, the reduction in seedling components of *Panicum virgatum* and *Agropyron psammophilum* was not proportional to the relative amount of injury to the endosperm. For example, in seedlings from treated seeds of both species, greater amount of dry matter was allocated to the root and less to the leaves. Since the radicle of a seedling always begins to elongate first, it may use greater amounts of seed reserves than leaves. According to Bewley and Black (1985), there was a rapid leakage of sugars, organic acids, ions, amino acids and proteins from the seed reserves into the surrounding medium when intact seeds started to imbibe. It was possible that more extensive leakage of the above substances resulted from cutting the endosperm. There may also be greater incidence of bacterial infection following injury to the seeds.

This study showed that when more than 60% of the endosperm of *Panicum virgatum* and 80% of *Agropyron psammophilum* seeds were removed, the seeds did not germinate. Thus, predation would probably alter the spatial pattern of seed distribution as demonstrated in other studies (Platt

1976, De Steven and Putz 1984, Webb and Willson 1985). However, when seeds are partially damaged but not killed, predation would probably change the hierarchical structure of the seedling population by introducing individuals with reduced size.

CHAPTER SIX

SAND BURIAL EFFECTS ON SEED GERMINATION AND SEEDLING EMERGENCE

6.1 INTRODUCTION

On the sand dunes at Port Burwell Provincial Park, seeds of *Panicum virgatum* and *Agropyron psammophilum* ripen and disperse in the fall. The dispersed seeds stay in a state of dormancy (either innate or enforced) until next spring. During the period between seed dispersion and germination, the movement of sand mediated by wind and wave action may bury the seeds to various depths (Maun 1981). In fact the chances for the dispersed seeds to remain unburied are quite low.

According to Harper and Benton (1966), burial of seeds at shallow depths may be beneficial because it maintains a humid environment around the seeds and prevents the seeds from desiccation. However, excessive burial of seeds by sand may have deleterious effects on seed germination and seedling emergence. Maun and Lapierre (1986) in a greenhouse experiment found that seed germination of four dune species was greatly improved by burial at shallow depths as compared to surface sown seeds. However, deep burial reduced germination in some species such as *Ammophila breviligulata*. The maximum depth of sand burial from which seedlings of *Elymus canadensis* L., *Cakile edentula* Hook. and *Corispermum hyssopifolium* L. emerged in the field were ten, ten and six cm, respectively (Maun and Lapierre 1986). Sand burial to six cm also prevented seedlings of *Calamovilfa longifolia* from emerging (Maun 1981). The ability of a seedling to emerge from certain amount of sand burial depended on a) the depth of burial, b) soil type and compaction, c) seed mass (Barbour *et al* 1985) and d) seedling morphology (Maun and Riach 1981).

In this study the effects of sand burial on seed germination and seedling emergence of *Panicum virgatum* and *Agropyron psammophilum* were examined under controlled greenhouse conditions. In addition, observations were made of the depth from which the seedlings had emerged under natural dune conditions at Port Burwell Provincial Park.

6.2 METHODS AND MATERIALS

6.2.1 Source of experimental materials

Seeds were collected from randomly chosen plants in the study site on 14 September 1986 for *Panicum virgatum* and 13 August 1987 for *Agropyron psammophilum*. After collection, seeds were stored in a seed room at 5 ^{0}C and 40% relative humidity until being used. The sand used in the greenhouse experiment was also collected from the same area of seed collection and sifted before use to remove seeds and debris.

6.2.2 Seedling emergence in the field

In May 1987, six transect lines (ranging from 10 to 20 m in length) were drawn perpendicular to the shoreline at randomly selected locations. Seedlings of *Panicum virgatum* within ten cm on both sides of the line were excavated and the depth from which each had emerged was determined by measuring the length from the sand surface to the point of attachment of lemma and palea to the root. In total, 6408 newly emerged seedlings were measured.

On 6 May 1988, six quadrats each measuring about 5 x 5 m were selected to sample *Agropyron psammophilum* seedlings (transect sampling method was not applicable because of the uneven distribution of seedlings). Four of the quadrats were located in the lee of the foredune and the other two in an area facing the lake. The seedlings of *A. psammophilum* contained in these plots were excavated and the emergence depth of seedlings was determined in the same way as in *Panicum virgatum*. In total, 325 emerged seedlings were collected.

For each species, the frequency distribution of the depth of seedling emergence was constructed and the departure from normality of the observed frequency distribution was tested by calculating skewness (g_1) and kurtosis (g_2).

6.2.3 Effects of artificial burial on seed germination and seedling emergence

In march 1987, each of 72 lots (50 seeds each) of *Panicum virgatum* seeds was placed in 9-cm glass petri dishes containing two layers of No. 1 Whatman filter paper. They were then soaked with 12 ml of distilled water and placed in a growth chamber maintained at 15 ^{0}C during day (14 h illumination) and 5 ^{0}C at night (10 h darkness) to break seed dormancy (Zhang and Maun 1989a). Eight weeks later, seeds were removed from petri dishes and evenly spread on the sand surface at different depths in 25 cm diam plastic pots and covered with 0, 2, 4, 6, 8, 10, 12, 14 and 16 cm of sand. There were eight replicates for each depth of sand burial treatment. Pots were then randomly arranged and embedded in sand in a 1 m wide, 3.5 m long and 25 cm deep bench in an unheated greenhouse. Sand inside and outside the pots was kept at the same level and water supply was maintained by a constant water table beneath the bench. Seedling emergence was monitored daily for 30 days after sowing. It was assumed that 30 days was long enough time for the germinated seedlings to emerge even from the deepest burial. At the end of the experiment, sand in each pot was washed through nylon cloth with fine openings to retrieve both the ungerminated seeds and unemerged seedlings. All the ungerminated seeds were tested for stainability with tetrazolium chloride. Unstained seeds were considered (Delouche *et al* 1962) dead and excluded from calculation. Seedling emergence rate was calculated according to Mugnisjah and Nakamura (1986) and can be expressed as follows. The numbers of emerged seedlings each day were divided by the number of days at which the emergence count was made. All the values were then summed and expressed as percentage of the total number of emerged seedlings at the end of 30 days.

On 7 June 1988, the above experiment was conducted using seeds of *Agropyron psammophilum* with sand burial depths ranging from 0 to 14 cm at two cm intervals. The seeds were not pretreated because they did not exhibit any dormancy. All other methods and material were identical to the experiment on *Panicum virgatum*. In this experiment, the temperature at each burial depth was also recorded at 8:30 and 13:30 hrs on several days during the first two weeks of the experiment.

6.2.4 Statistical analysis

All the data on percent germination and seedling emergence were transformed into arcsin square root values before being subjected to the analysis of variance. Comparisons between treatments were made by using Tukey's studentized range test (SAS 1985). The significance of skewness and kurtosis of the frequency distribution of emergence depth of seedlings in the field was determined using a t-test (Zar 1984) and regressions of the seedling emergence and the rate of seedling emergence versus the depth of sand burial were calculated according to Orloci and Kenkel (1987).

6.3 RESULTS

6.3.1 Seedling emergence in the field

In the field, seedlings of *Panicum virgatum* emerged from sand burial depths ranging from 0 to 11 cm. More than 60% of the seedlings emerged from depths ranging from 3 to 6 cm and more than 90% from 1 to 8 cm (Fig. 6.1). The frequency distribution of the emergence depth was significantly ($P < 0.001$) skewed to the right ($g_1 = 0.256$, $t = 8.366$) and significantly ($P < 0.01$) platykurtic ($g_2 = -3.182$, $t = 51.99$) with a mean ± SD of 4.73 ± 1.82 cm.

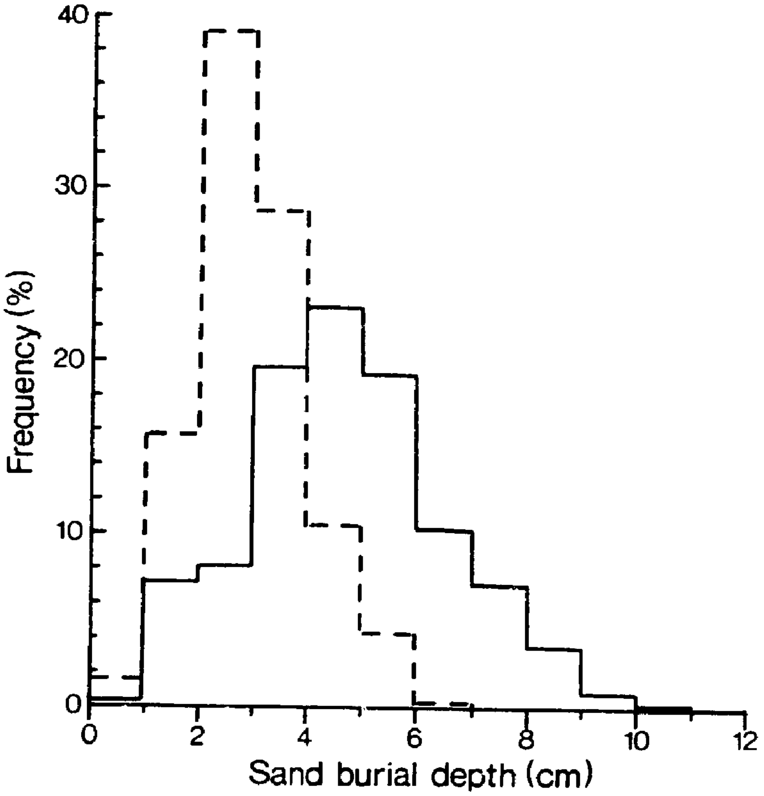
For *Agropyron psammophilum*, seedling emerged from depths ranging from 0 to 7 cm. However, the majority of the seedlings (nearly 70%) had emerged from 2 to 4 cm burial depths (Fig. 6.1). The mean depth of emergence of seedlings was 2.96 ± 1.06 cm SD. The frequency distribution of the depth of seedling emergence was significantly ($P < 0.01$) skewed to the right ($g_1 = 0.5558$, $t = 4.1094$) and platykurtic ($g_2 = -2.9283$, $t = 10.8576$).

The mean emergence depth of seedlings of *Panicum virgatum* was significantly ($P < 0.01$) greater than that of *Agropyron psammophilum* according to a t-test ($t = 17.473$). Correlation between the frequency distribution of the depth of seedling emergence of the two species was rather low ($P > 0.1$, $r^2 = 0.140$) showing very little similarity.

6.3.2 Effects of artificial burial on seed germination and seedling emergence

Seeds at all burial depths germinated significantly ($P < 0.05$) better than unburied (0 cm) seeds in both species. Among the buried seeds, *Panicum virgatum* germinated equally well at all of the burial depths (Table 6.1) but germination of *Agropyron psammophilum* seeds decreased gradually with increasing burial depth. For example,

Figure 6.1 Frequency distribution of the burial depth of naturally emerged seedlings of *Panicum virgatum* (solid line, N = 6408) and *Agropyron psammophilum* (dashed line, N = 325).


40
30
20
10
0
Frequency (%)
0
2
4
6
8
10
12
Sand burial depth (cm)

virtually all *A. psammophilum* seeds planted at 2 and 4 cm germinated. Burial at 6 and 8 cm slightly lowered percent germination but the differences were not significant. However, as the depth of burial increased to 10 and 12 cm, there was a significant ($P < 0.05$) reduction in percent germination as compared to 2 and 4 cm burial treatments (Table 6.2). Significant linear relationship between the germination percentage of buried seeds (Y) and the depth of sand burial (X) was observed in *A. psammophilum* ($Y = 101.79 - 0.73X$. $r^2 = 0.898$).

Sand burial had notable inhibitory effect on seedling emergence (measured as the proportion of seedlings that emerged) of both *Panicum virgatum* and *Agropyron psammophilum*. For example, 30 days after planting, sand burial treatments ranging from 0 to 8 cm did not show any significant effect on the percentage of emerged seedlings of *P. virgatum* (Table 6.1). However, burial of seeds to 10 cm or more significantly ($P < 0.05$) reduced seedling emergence as compared to 4 and 6 cm. The percentages of emerged seedlings in the 12, 14 and 16 cm sand burial treatments were significantly ($P < 0.05$) lower than those in other treatments. About 40% of the germinated seeds emerged from a burial depth of 16 cm (Table 6.1).

For *Agropyron psammophilum*, almost all the germinated seeds at 2 cm burial depth produced seedlings (Table 6.2). But as the burial depth increased, seedling emergence decreased significantly ($P < 0.05$). No seedlings emerged from burial depths greater than 8 cm (Table 6.2).

The rate of seedling emergence was also altered by sand burial. For *Panicum virgatum*, seedling emergence rate decreased gradually with increasing burial depth (Table 6.1). For *Agropyron psammophilum*, the rate of seedling emergence was significantly ($P < 0.05$) higher at 2 and 4 cm burial depths than those at greater depths of burial (Table 6.2).

Figure 6.2 and 6.3 show the cumulative emergence curves of seedlings from different burial depths. Seedlings of *Panicum virgatum* started to emerge only two to three days after sowing and the maximum emergence was usually obtained within five days after sowing when burial depth was 8 cm or less (Fig. 6.2). At sand burial depths of 11 cm or greater, five days or more were required for the first emergence of seedlings and ten days for the completion of emergence. For *Agropyron psammophilum*, seedlings at 0, 2 and 4 cm burial depths began to emerge five to six days after sowing and reached maximum emergence about 11 to 15 days after sowing (Fig. 6.3). As the burial depth of seedlings increased so did the length of time taken by the seedlings to emerge and to reach maximum emergence. Seedlings at 8 cm burial depth began to emerge after 17 days but the total emergence was only 0.28% (Fig. 6.3).

Both percent emergence and emergence rate decreased with an increase in sand burial depth (Fig. 6.4). For *Panicum virgatum* seedlings, percent emergence (Y) showed an exponential response ($P < 0.01$, $r^2 = 0.949$) to the depth (X)

Figure 6.2 Cumulative seedling emergence (emerged seedlings/germinated seeds) of *Panicum virgatum* from seeds buried at various depths in a greenhouse.

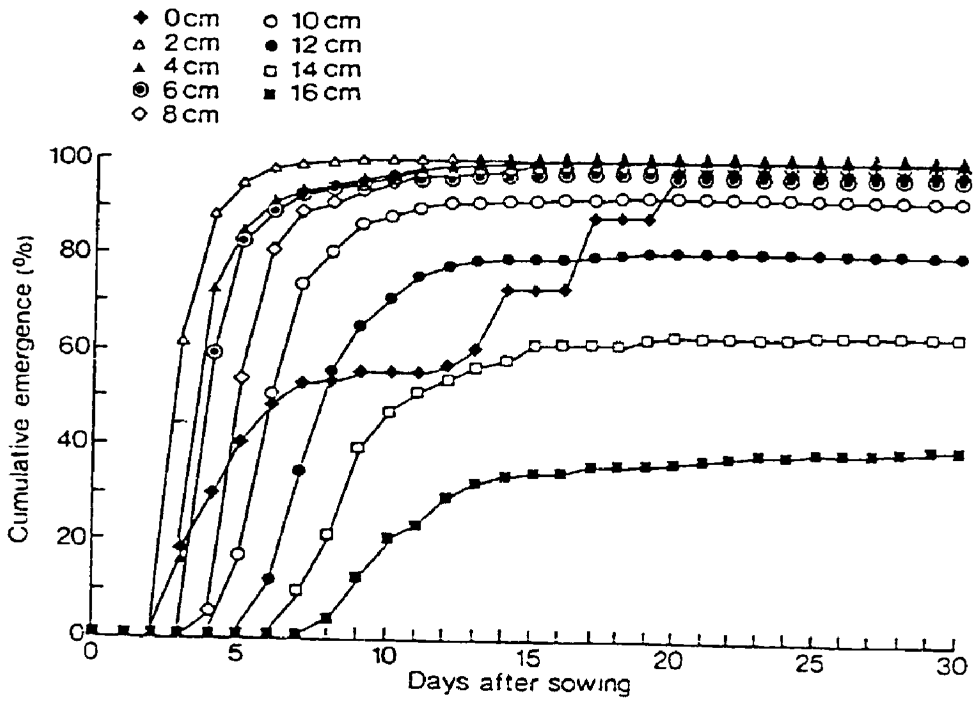
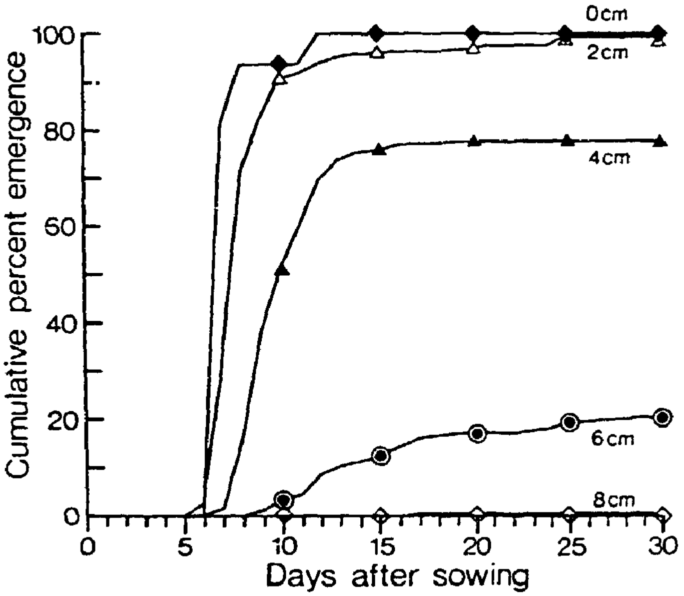

◆ 0cm
△ 2cm
▲ 4cm
◉ 6cm
◇ 8cm
○ 10cm
● 12cm
□ 14cm
■ 16cm
Cumulative emergence (%)
0
20
40
60
80
100
0
5
10
15
20
25
30
Days after sowing

Figure 6.3 Cumulative seedling emergence (emerged seedlings/ germinated seeds) of *Agropyron psammophilum* from seeds buried at various depths in a greenhouse.


0cm
2cm
4cm
6cm
8cm
Cumulative percent emergence
100
80
60
40
20
0
0
5
10
15
20
25
30
Days after sowing

of burial in sand with little variation at shallow depths (8 cm or less) but rapid decrease at sand burial depths exceeding 10 cm. A linear negative response ($P < 0.01$, $r^2 = 0.979$) was found in the rate of seedling emergence with increasing depth of sand burial (Fig. 6.4). For *Agropyron psammophilum* seedlings, linear negative relationships between the depth of sand burial and both percent emergence ($P < 0.01$, $r^2 = 0.867$) and emergence rate ($P < 0.05$, $r^2 = 0.763$) were obtained (Fig. 6.4).

Excessive sand burial adversely affected the survivorship of emerged *Panicum virgatum* seedlings (Table 6.1). During the 30 days after sowing, seedling mortality was observed only among those seedlings that had emerged from burial depths of $\geq$ 10 cm. Burial of seeds to 12 cm or deeper, especially, showed significantly ($P < 0.05$) higher seedling mortality than those at 8 cm or less, in which no seedling mortality was observed. No significant difference in seedling mortality was detectable among 12, 14 and 16 cm burial depths (Table 6.1). Seedling mortality in *Agropyron psammophilum* was significantly ($P < 0.05$) higher at burial depths of 4 and 6 cm (Table 6.2).

Temperatures experienced by seeds of *Agropyron psammophilum* at various depths during the first two weeks of the experiment are shown in Table 6.3. In the morning (8:30), there was little difference in temperature at various depths but in the afternoon (13:30) as the air temperature rose, so did the soil temperature. However, the rise in temperature

Figure 6.4 Regressions of percent seedling emergence (solid square) and rate of seedling emergence (solid circle) versus the sand burial depth from which the seedlings of *Panicum virgatum* and *Agropyron psammophilum* emerged in the greenhouse experiments.

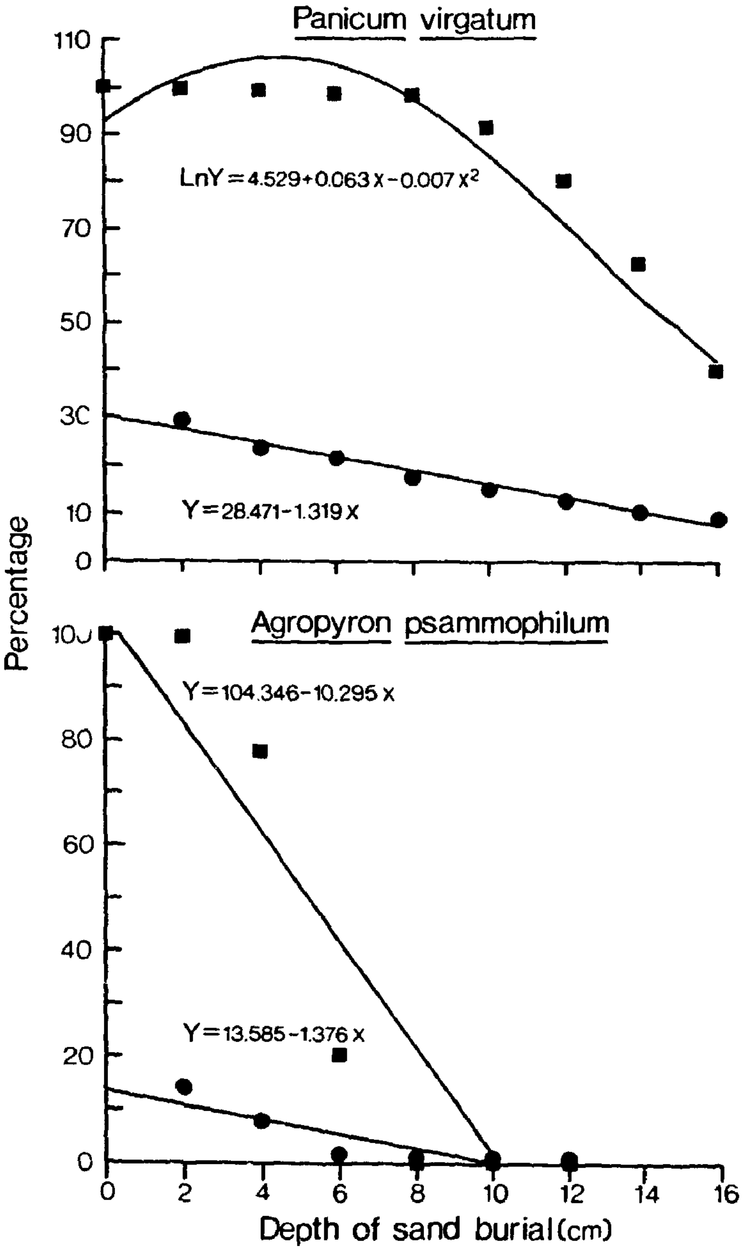

Panicum virgatum
110
90
70
50
30
10
0
LnY=4.529+0.063x-0.007x²
Y=28.471-1.319x
Percentage
Agropyron psammophilum
100
80
60
40
20
0
Y=104.346-10.295x
Y=13.585-1.376x
0
2
4
6
8
10
12
14
16
Depth of sand burial(cm)

Table 6.1 Percentages (mean ± SE) of germinated seeds, seedling emergence, emergence rate and dead seedlings of *Panicum virgatum* under different depths of sand burial in a greenhouse. Values in the same column followed by different letters are significantly different according to Tukey's Studentized test (SAS 1985).

Burial depth (cm)	Germinated seeds (%)	Seedling emergence (%)	Emergence rate (%)	Dead seedling (%)
0	12.33 ± 5.17^{A}	100.0 ± 0.00^{A}	---	0.00 ± 0.00^{A}
2	91.83 ± 2.18^{B}	99.44 ± 0.37^{A}	29.46 ± 0.27^{A}	0.00 ± 0.00^{A}
4	93.65 ± 0.71^{B}	99.46 ± 0.36^{A}	23.98 ± 0.31^{AB}	0.00 ± 0.00^{A}
6	92.67 ± 1.36^{B}	99.09 ± 0.45^{A}	21.90 ± 0.21^{BC}	0.00 ± 0.00^{A}
8	91.55 ± 0.95^{B}	98.66 ± 0.70^{AB}	18.14 ± 0.44^{BCD}	0.00 ± 0.00^{A}
10	86.93 ± 1.74^{B}	91.91 ± 2.79^{B}	15.40 ± 0.38^{CDE}	2.79 ± 0.92^{AB}
12	89.03 ± 1.65^{B}	80.69 ± 2.12^{C}	12.82 ± 0.28^{DEF}	10.59 ± 2.69^{BC}
14	85.73 ± 1.85^{B}	62.88 ± 3.94^{D}	10.44 ± 0.30^{EF}	17.91 ± 4.11^{C}
16	89.65 ± 1.76^{B}	40.30 ± 4.25^{E}	8.89 ± 0.61^{F}	18.00 ± 4.00^{C}

Table 6.2 Percentages (mean ± SE) of germinated seeds, seedling emergence, emergence rate and dead seedlings of *Agropyron psammophilum* at different depths of sand burial in a greenhouse. Values in the same column followed by different letters are significantly different according to Tukey's studentized test (SAS 1985).

Burial depth (cm)	Germinated seeds (%)	Seedling emergence (%)	Emergence rate (%)	Dead seedling (%)
0	1.06 ± 0.58^{A}	100.0 ± 0.00^{A}	---	0.00 ± 0.00^{A}
2	99.72 ± 0.82^{B}	99.46 ± 0.54^{A}	14.19 ± 2.03^{B}	1.90 ± 0.95^{AB}
4	99.15 ± 0.42^{B}	77.87 ± 5.46^{B}	7.99 ± 0.68^{B}	8.32 ± 2.83^{B}
6	97.42 ± 0.75^{BC}	20.43 ± 5.85^{C}	1.48 ± 0.47^{AC}	8.62 ± 6.14^{B}
8	97.04 ± 1.43^{BC}	0.28 ± 0.10^{D}	0.02 ± 0.02^{C}	0.00 ± 0.00^{A}
10	93.94 ± 1.69^{C}	0.00 ± 0.00^{D}	0.00 ± 0.00^{C}	0.00 ± 0.00^{A}
12	92.64 ± 1.75^{C}	0.00 ± 0.00^{D}	0.00 ± 0.00^{C}	0.00 ± 0.00^{A}

was several degrees lower at burial depths of 6, 8, 10 and 12 cm. The range of temperature fluctuation between the morning and afternoon observations declined with increasing burial depth (Table 6.3).

6.4 DISCUSSION

Although the frequency distribution of seedling emergence depth of both species were significantly skewed to the right and platykurtic, they differed significantly from each other in several ways. First, the range of emergence depths of *Panicum virgatum* seedlings (0 to 11 cm) was greater than that of *Agropyron psammophilum* (0 to 7 cm) indicating that the former was able to tolerate relatively greater amount of sand accretion than the latter. Secondly, more than 60% of the *P. virgatum* seedlings emerged from burial depths ranging from 3 to 6 cm. No single burial depth contributed the maximum numbers to the seedling population. For *A. psammophilum*, however, seedlings emerging from 2 cm burial depth alone contributed about 40% to the seedling population and about 70% of the seedlings emerged from burial depths of 2 to 4 cm. Thirdly, the mean depth of seedling emergence of *P. virgatum* was significantly greater than that of *A. psammophilum*. The data suggest that *P. virgatum* seedlings are more flexible than *A. psammophilum* in terms of their ability to withstand burial in sand.

In greenhouse experiments, small amounts of burial in sand improved the germination of seeds of both species.

Table 6.3 Temperature measurements (mean ± standard error) taken at 8:30 in the morning and 1:30 in the afternoon at each burial depth from 0 to 12 cm during the first two weeks of the experiment in a greenhouse.

Burial	Temperature measurements (C)		
depth (cm)	8:30 A.M.	1:30 P.M.	Variation*
0	22.1 ± 1.46	31.7 ± 1.75	11.0 ± 1.34
2	21.1 ± 1.58	30.7 ± 1.61	10.6 ± 1.28
4	20.5 ± 1.52	29.2 ± 1.62	10.2 ± 1.40
6	20.2 ± 1.48	27.9 ± 1.48	8.9 ± 1.15
8	21.1 ± 1.48	27.7 ± 1.32	7.6 ± 1.07
10	21.3 ± 1.51	26.9 ± 1.21	6.4 ± 2.13
12	20.6 ± 1.55	25.1 ± 1.12	5.0 ± 0.75

* Obtained by subtracting the temperature measurement at 8:30 A.M. from that at 1:30 P.M.

Similar results were also obtained by Maun and Lapierre (1986). Seeds placed on the surface usually dried out and were unable to germinate. Among buried seeds, no significant difference in percent germination was observed in *Panicum virgatum*. However, seed germination was significantly inhibited by excessive sand burial in *Agropyron psammophilum*. According to Harper (1977), higher soil moisture, a decrease in soil temperature and poor aeration may be responsible for low germination at greater burial depths. The temperature measurements in this study suggested that a smaller range of variation in temperature at deep burial depths may be responsible for low percent germination of *A. psammophilum* seeds.

The greenhouse experiments indicated that 40% of the emerging seedlings of *Panicum virgatum* have the potential to emerge from a depth of 16 cm under controlled conditions. In contrast, the maximum depth from which the seedlings emerged in the field was 11 cm. The divergence may have been caused by two factors. (i) There was no persistent seed bank at depths greater than 11 cm in the field or (ii) seeds at deep locations were dormant and failed to germinate because of sub-optimal environmental conditions. The first possibility is unlikely because seed germination was previously (July 1987) observed from sand samples taken from more than 15 cm depth in the field which suggests that seeds may be buried at depths greater than 11 cm in the field and would, therefore, contribute to a persistent seed bank.

The second explanation seems more plausible under field conditions. Zhang and Maun (1989a) reported that seed dormancy of *P. virgatum* was significantly reduced by exposing seeds to either constant or alternating temperatures ranging from 5 to 15 ^{0}C under both light/dark and dark conditions for even two weeks. Thus, the deeply buried seeds in the field may stay in a state of enforced dormancy imposed by some environmental limits. A report by Blake (1935) suggested that seed germination of *P. virgatum* was little affected by soil moisture. Therefore, poor aeration at great burial depths was not likely to be the cause. The enforced dormancy of seeds was most probably caused by low soil temperature or temperature fluctuation. Acquiring a dormant state would be ecologically advantageous because ungerminated seeds would be added to the seed bank and would have the potential to produce seedlings in the following years if they are exposed by sand erosion (Pemadmsa and Lovell 1975).

Several studies (Barbour *et al* 1985, Maun and Lapierre 1986, Van der Valk 1974, Wulff 1986b) showed that the heavier the seed size (either between or within species), the greater was the depth from which the seedlings could emerge. Although the mean seed mass of *Panicum virgatum* is only 2.1 ± 0.01 mg (mean ± SE), its seedlings can emerge from deeper locations than *Agropyron psammophilum* (seeds weighing 2.36 ± 0.63 mg) and some other large seeded species. For example, Maun and Lapierre (1986) reported that seeds of *Cakile edentula* Hook., *Elymus canadensis* L. and *Corispermum hyssopifolium* L., respectively, had mean weights of 6.3, 5.2 and 2.8 mg and emerged from a mean burial depth of 3.84, 3.49 and 3.43 cm in the field and maximum depths of 12, 12 and 6 cm under experimental conditions, respectively. The seed mass value of *P. virgatum* is significantly ($P < 0.01$) smaller than these species. Yet, its seeds can emerge from greater depth of burial. Therefore, among different species larger seed size may not always by related to greater depth of seedling emergence. There may be some other features that facilitate seedling emergence in *P. virgatum*. For example, under field conditions, *P. virgatum* seeds accumulate in depressions in the sand surface where they are buried by shifting sand during winter and early spring. In spring, seedlings emerge in clumps, and cumulative force of a number of seedlings would provide stronger force for emergence than a single seedling (Payne 1980). As a result, relatively higher seedling emergence from greater depths may be achieved. Tyndall *et al* (1986) reported that the potential shoot length of emerging seedlings of *Cakile edentula*, as measured by the length of hypocotyl of seedlings grown in the dark, was much greater than the actual depth of emergence of seedlings. For *P. virgatum*, the potential shoot length (measured as epicotyl length) of emerging seedlings is at least as long as 16 cm. Another characteristic of *P. virgatum* is the rate of emergence of seedlings from the sand. In the greenhouse experiment, first seedling emerged seven days after sowing from a burial depth of 16 cm, and the seedling emergence was complete within 15 days after sowing (Fig. 6.2.a). The growth rate of these emerging seedlings was rather high (more than one cm per day).

Sand burial in excess of 12 cm had a deleterious effect on the survivorship of the emerged seedlings of *Panicum virgatum* and caused significantly higher seedling mortality. Possibly, large quantities of seed reserves were consumed in shoot elongation through sand and once the seedlings emerged above the sand surface, they were weak and unable to withstand competition or environmental stress. In the field, a mean seedling density of 851/m^2 with clumped distribution of individuals was recorded (based on forty-five 0.5 x 0.5 m quadrats). Weaver and Cavers (1978) reported that intraspecific competition may eliminate seedlings that emerged from deep burial depths. Because seedlings from shallow burial depths emerged earlier, they probably had better chances of occupying space, utilizing nutrients, and becoming successfully established than those from deeply buried seeds.

In conclusion, *Panicum virgatum* seems to be well adapted to sand burial because its seedlings (i) have a fast growth rate, (ii) possess high potential for epicotyl elongation and (iii) can emerge from a wide range of sand burial depths. *Agropyron psammophilum* appears to be less adapted for seed germination and seedling emergence in the sand dune environment at Port Burwell Provincial Park.

CHAPTER SEVEN

SAND BURIAL EFFECTS ON SEEDLING GROWTH

7.1 INTRODUCTION

The growth and establishment of dune inhabiting plants are limited by several factors such as sand erosion and accretion, low surface soil moisture, extreme soil and air temperature and nutrient deficiency (Baldwin and Maun 1983, Martin 1959, Watkinson 1978). Among them, sand accretion mediated by wind and wave action is one of the most distinct environmental variables. It was reported that the sand accretion per year was 8.7 cm along Lake Huron (Maun 1985), 30 cm along Lake Michigan (Olson 1958) and 30 cm along the Atlantic coast of North Carolina (van der Valk 1974). On the sand dune system along Lake Erie, sand accretion within a week was as high as 20 cm at some locations (Yanful 1988). Dune plants are usually adapted to withstand certain amount of burial in sand and possess the ability to (a) emerge from certain depth of sand burial (Maun and Lapierre 1984, Zhang and Maun 1989b), (b) recover rapidly following exposure from burial (Harris and Davy 1987), (c) produce more tillers following sand accretion (Anderson and Taylor 1979, Huiskes and Harper 1979, Laing 1967), (d) expand leaf area and increase the concentration of leaf chlorophyll (Disraeli 1984) or (e) exhibit increased vigour (measured as dry weight per shoot) following burial (Eldred and Maun 1982, Marshall 1965, Wallen 1980).

A preliminary survey showed that few seedlings of *Agropyron psammophilum* survived through the summer under field conditions. Since sand accretion is a recurrent event on the foredunes of Lake Erie it was hypothesized that excessive burial in sand may be responsible for the mortality. Several studies (Laing 1954, Maun and Lapierre 1986, Ranwell 1958) suggested that plants can withstand only certain amounts of burial in sand and beyond the threshold levels for survival mortality may be rather high. Various factors such as a) the absolute depth of sand burial (Maun and Lapierre 1986), b) the relative depth of burial in relation to plant height (Yanful 1988), c) the initial depth of seedling emergence (Zhang and Maun 1989b) and d) the age or size of plants may play a significant role in survival and growth of plants.

In this chapter, I examined the effects of the aforementioned factors on the growth and survivorship of seedlings of *Panicum virgatum* and *Agropyron psammophilum* under greenhouse and field conditions.

7.2 MATERIALS AND METHODS

7.2.1 Source of experimental materials

Seeds of *Agropyron psammophilum* and *Panicum virgatum* were collected on August 13 and 27, 1987, respectively, from randomly chosen individuals from populations at Port Burwell Provincial Park. The seeds were cleaned and then stored in a seed room at 5 ^{0}C and 40% relative humidity for later use.

The sand used in burial treatments was also collected from the area of seed collection and was sifted before use to remove debris and seeds.

7.2.2 Effects of sand burial on seedling growth in a greenhouse

The purpose of this study was to determine the effects of artificial burial in sand on seedling survival and growth under controlled conditions. On 14 September 1987, seeds of *Panicum virgatum* and *Agropyron psammophilum* were planted individually at 1 cm depth in 20 cm diam plastic pots filled with 5:1 sand and soil mixture. One week after seedling emergence, 48 pots containing one seedling each were selected for each species and randomly sorted into six groups with eight pots each. The height of seedlings was measured and the following burial treatments, 0 (control), burial to 25, 50, 75, 100 and 120% of seedling height, were superimposed on seedlings in each group, respectively (Burial I). Seedlings were kept erect when buried. Another set of seedlings of *A. psammophilum* and *P. virgatum* was given identical treatment two and three weeks after emergence, respectively (Burial II). Table 7.1 shows the mean absolute depth of sand superimposed on seedlings of the two species in each treatment. For burial, 20 cm diam cardboard tubes of desired height were placed on the top and filled carefully with sand to the desired depth of burial. The height, number of green leaves and tillers per plant

Table 7.1 Mean absolute depth (mean ± standard error) of sand (cm) superimposed on seedlings of *Panicum virgatum* and *Agropyron psammophilum* in each treatment of Burial I and Burial II.

Percentage buried	Burial I (cm)	Burial II (cm)
	P. virgatum	
0	0	0
25	0.47 ± 0.04	1.17 ± 0.13
50	0.97 ± 0.10	2.66 ± 0.22
75	1.55 ± 0.15	3.47 ± 0.28
100	2.20 ± 0.14	4.25 ± 0.48
120	2.41 ± 0.14	6.29 ± 0.74
	A. psammophilum	
0	0	0
25	2.80 ± 0.15	5.90 ± 0.38
50	5.52 ± 0.28	11.11 ± 0.84
75	7.93 ± 0.22	19.73 ± 1.13
100	10.59 ± 0.58	22.19 ± 1.68
120	13.37 ± 0.61	30.30 ± 1.18

were monitored weekly until eight (Burial II) and nine (Burial I) weeks after the burial treatment for *A. psammophilum* and 12 (Burial II) and 14 (Burial I) weeks for *P. virgatum*. The experiment was then terminated and the surviving seedlings were washed out of the pots carefully and dried in an oven at 70 ^{0}C to a constant weight. The dry weight of leaves, stems, under ground culm, rhizomes, roots and overall weight of the surviving seedlings were recorded. Natural logarithmic transformation was applied to the collected data and analysis of variance (ANOVA) was used to examine differences between treatments. Tukey's "Honestly Significant Difference" (HSD) of multiple comparisons (Catanzaro 1988) was conducted when the ANOVA showed a significant difference.

7.2.3 Effects of sand burial on seedling survivorship in the field

The effects of original depth from which a seedling emerged and post-emergence sand burial depth on seedling survivorship was investigated under field conditions.

On 7 October 1987, 397 established seedlings of *Panicum virgatum* were collected from 1.5 m wide strips on both sides of six randomly laid transect lines perpendicular to the shoreline. The original depths from which each collected seedling had emerged in the spring was obtained by measuring the length from the point of attachment of lemma and palea to an abrupt thickening at the junction of root and shoot of the seedlings. The data were then grouped into emergence depth classes of established seedlings with one cm intervals from 0 to 12 cm. The amount of sand accretion during summer (after seedling emergence in spring) was then obtained for each seedling by measuring the length from the junction between root and shoot to the actual sand surface. The mean sand accretion depth during summer was calculated for each emergence depth class of established seedlings. No attempt was made to determine the sand erosion that occurred during the summer because all the collected surviving seedlings suffered certain amount of post-emergence sand burial. Seedlings of *Agropyron psammophilum* were not included in this study because of inadequate sample size.

Assuming that survivorship is independent of the depth from which a seedling emerged, the expected number of surviving seedlings in each depth class of seedling emergence was calculated as follows. The sample size of the established seedlings (397) was multiplied by the percentage emergence at each depth class in spring (from Fig. 6.1). The observed frequency distribution of the original emergence depth of established seedlings was then compared with these expected values by using chi-square test to determine whether the departure was significant.

Seedlings were then grouped into four categories, < 2, 2 - 5, 6 - 9 and > 10 cm, on the basis of the original depth at which a seed was located. Within each group, seedlings were sorted into subgroups again according to the depth of post-emergence sand burial that a seedling had been subjected to (Table 7.2). To determine the effects of post-emergence burial on survivorship of seedlings originating from the four emergence depths chi-square test and then analysis of concentration (Feoli and Orloci 1979) were used. The chi-square test examined the correlation between the survivorship of seedlings in the four groups and the depth of post-emergence sand burial. When the correlation was significant, the analysis of concentration was conducted to partition the total chi-square into components (canonical variates) that could be correlated with external environmental variables. Orloci and Kenkel (1987) described the procedure in detail.

7.3 RESULTS

7.3.1 Effects of sand burial on seedling growth in a greenhouse

7.3.1.1 Seedling survivorship

The survivorship of *Panicum virgatum* seedlings was not affected by sand burial of up to 75% of their height. All buried seedlings at 100 and 125% burial treatments died. For *Agropyron psammophilum*, all one week old seedlings buried to 50% of the individual height survived. However, when the burial depth was increased to 75% of their height only one half of the seedlings survived. A further increase in depth of burial to 100 and 120% of plant height killed all the seedlings. For two weeks old seedlings, mortality was 0, 13

Table 7.2 Number of established seedlings of *Panicum virgatum* that emerged from different depths in spring and were subsequently buried to various depths by natural accretion.

Emergence	Post-emergence burial depth (cm)					
depth (cm)	<1	1-2	2-3	3-4	4-5	5-6
Group I						
1	1	1	0	0	0	0
Group II						
2	9	25	10	2	0	0
3	17	28	7	2	3	1
4	24	34	6	3	3	2
5	11	23	10	0	1	0
Group III						
6	13	34	7	0	0	0
7	15	32	12	0	0	0
8	9	24	1	0	0	0
9	3	3	1	0	0	0
Group IV						
10	2	11	0	0	0	0
11	0	1	0	0	0	0

and 75% when burial depth was 25, 50 and 75% of the height of seedlings, respectively. Again, no seedling survived when the whole plant were buried.

One and three weeks old seedlings of *Panicum virgatum* survived absolute post-emergence sand burial of 1.6 and 3.5 cm respectively. In contrast, both one and two-week old seedlings of *Agropyron psammophilum* survived up to 6 cm of sand burial. Seedling mortality occurred when burial depth exceeded 6 cm.

7.3.1.2 Seedling height

Prior to burial the mean height of *Panicum virgatum* and *Agropyron psammophilum* seedlings in all treatments did not differ. However, after the burial treatments the seedlings significantly ($P < 0.05$) differed in their above ground height (Table 7.3).

Small amounts of post-emergence burial increased the vigour of both *Panicum virgatum* and *Agropyron psammophilum* seedlings (Fig. 7.1). For example, *P. virgatum* seedlings buried to 25, 50 and 75% of their height in Burial I were taller than control eight, ten and 12 weeks after burial treatment, respectively. One seedling survived the 100% burial treatment for a very short period of time (Fig. 7.1a). In Burial II, seedlings in 25 and 50% burial treatment were taller than those in control six and nine weeks after burial. The differences were, however, not significant. Seedlings buried to 75% of their height were

Table 7.3 Above ground height (mean ± standard error) of seedlings of *Panicum virgatum* and *Agropyron psammophilum* before and after the burial treatments in Burial I and Burial II. Values in the same column for each species followed by different letters are significantly ($P < 0.05$) different according to Tukey's HSD test (Catanzaro 1988).

Burial treatment (%)	Above ground height (cm)			
	Burial I		Burial II	
	Before	After	Before	After
		P. virgatum		
0	2.11 ± 0.17^{A}	2.11 ± 0.17^{A}	4.81 ± 0.53^{A}	4.81 ± 0.53^{A}
25	1.88 ± 0.15^{A}	1.41 ± 0.11^{B}	4.66 ± 0.53^{A}	3.50 ± 0.40^{B}
50	1.94 ± 0.20^{A}	0.97 ± 0.10^{BC}	5.31 ± 0.44^{A}	2.66 ± 0.22^{B}
75	2.06 ± 0.20^{A}	0.52 ± 0.05^{C}	4.63 ± 0.38^{A}	1.16 ± 0.10^{C}
100	2.20 ± 0.14^{A}	0^{D}	4.25 ± 0.48^{A}	0^{CD}
120	2.01 ± 0.12^{A}	-0.40 ± 0.02^{D}	5.24 ± 0.62^{A}	-1.05 ± 0.12^{D}
		A. psammophilum		
0	11.20 ± 0.54^{A}	11.20 ± 0.54^{A}	20.57 ± 1.77^{A}	20.57 ± 1.77^{A}
25	11.19 ± 0.60^{A}	8.40 ± 0.45^{B}	23.61 ± 1.51^{A}	17.71 ± 1.14^{A}
50	11.04 ± 0.55^{A}	5.52 ± 0.28^{C}	22.21 ± 1.68^{A}	11.11 ± 0.84^{B}
75	10.57 ± 0.30^{A}	2.64 ± 0.07^{D}	26.30 ± 1.51^{A}	6.58 ± 0.38^{B}
100	10.68 ± 0.58^{A}	0^{E}	22.19 ± 1.68^{A}	0^{C}
120	10.69 ± 0.49^{A}	-2.67 ± 0.12^{F}	25.25 ± 0.98^{A}	-5.05 ± 0.20^{C}

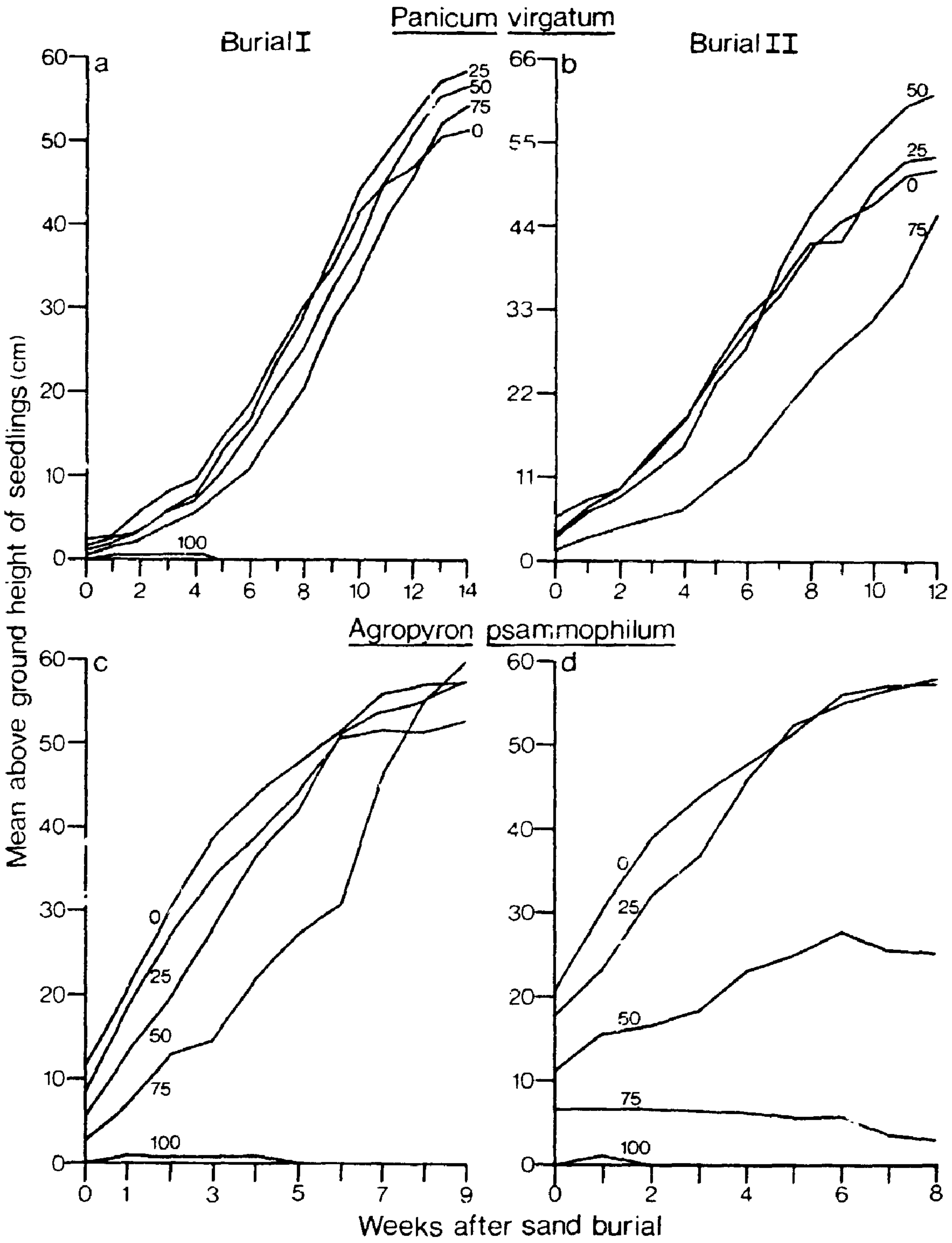
still smaller than control at harvest (12 weeks after burial). However, they had shown a sharp increase in height six weeks after the burial treatment (Fig. 7.1b). If further growth had been allowed, they probably would have surpassed control seedlings.

For *Agropyron psammophilum*, the surviving seedlings at 25, 50 and 75% burial treatments in Burial I showed luxuriant growth so that they caught up in height with control plants six (25 and 50% burial treatment) and eight weeks (75% burial treatment) after the burial treatment. At the end of the experiment, even though seedlings in all but 25% burial treatments were taller than control, the differences were not significant. One seedling emerged from 100% burial treatment. However, it died four weeks later (Fig. 7.1c). In Burial II, only seedlings in the 25% burial treatment showed luxuriant growth in height and caught up with control five weeks after the burial treatment. Seedling growth was significantly impeded by sand burial in 50 and 75% burial treatments. The former maintained slow growth whereas the latter showed reduced vigour. Seedlings in these two treatments were significantly ($P < 0.01$) smaller than those in the control and 25% burial treatment. One seedlings emerged from 100% burial but died two weeks later (Fig. 7.1d).

7.3.1.3 Number of green leaves per plant

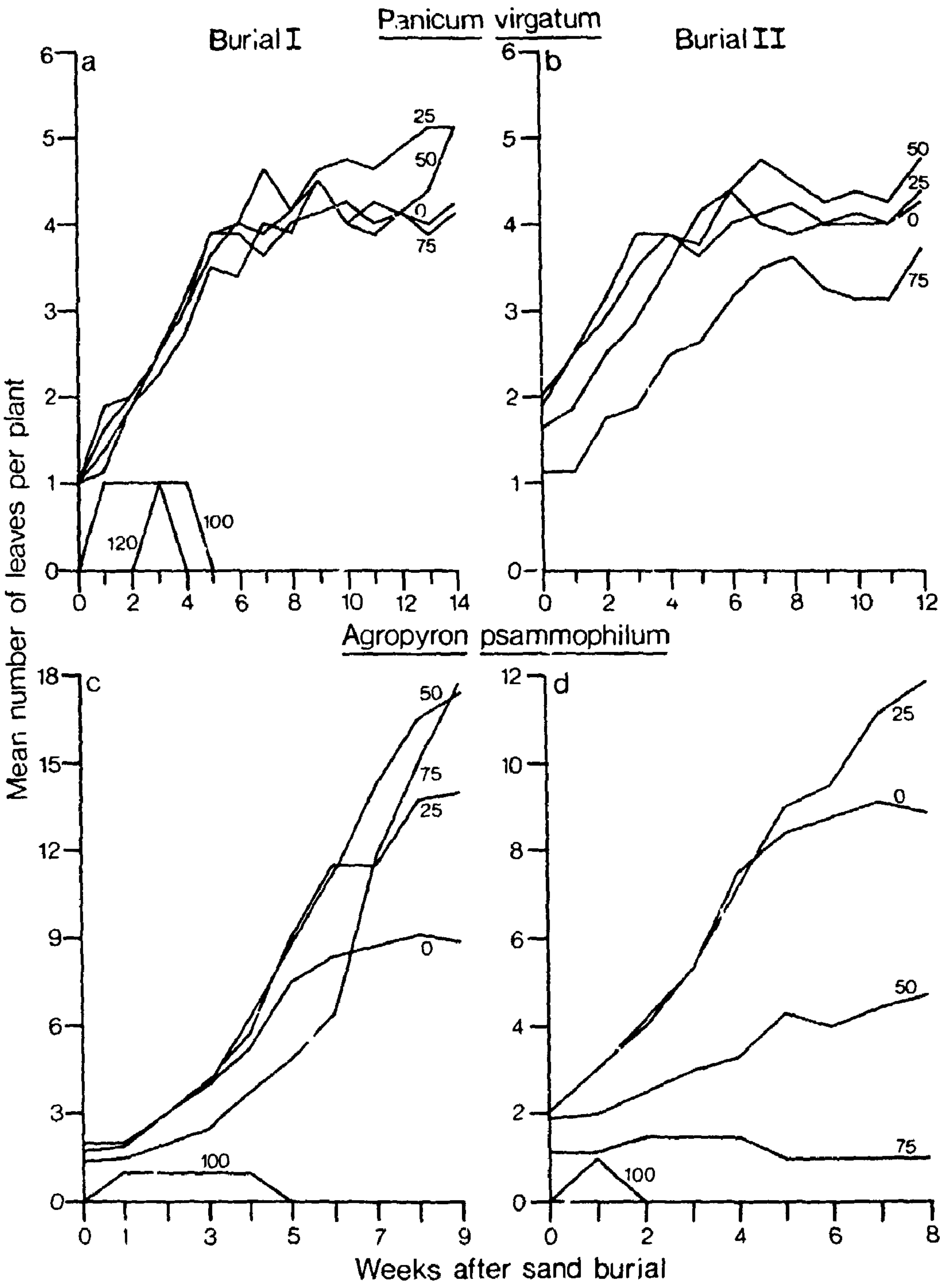
Sand burial did not show any significant effect on the

Figure 7.1 Mean above ground height of *Panicum virgatum* (a, b) and *Agropyron psammophilum* (c, d) seedlings measured at one week intervals after sand burial treatments in Burial I and Burial II. The intercepts of the curves indicate seedling height immediately after the sand burial treatment.


Panicum virgatum
Burial I
Burial II
a
b
60
50
40
30
20
10
0
66
55
44
33
22
11
25
50
75
0
100
0
2
4
6
8
10
12
14
Agropyron psammophilum
c
d
0
25
50
75
100
1
3
5
7
9
Mean above ground height of seedlings (cm)
Weeks after sand burial

number of green leaves per seedling in *Panicum virgatum*. Variations in the number of green leaves produced by buried and unburied seedlings was very low (Fig. 7.2a, b). However, sand burial showed significant effects on the demography of the number of green leaves per seedling in *Agropyron psammophilum* (Fig. 7.2c, d). In Burial I a reduction in the number of green leaves per seedling was observed only in the 75 and 100% burial treatments. After four and seven weeks of growth, seedlings in the 25, 50 and 75% burial treatments produced more green leaves than those in the control (Fig. 7.2c). At harvest (9 weeks after treatment) seedlings buried to 50 and 75% of their height had significantly ($P < 0.01$) greater number of green leaves than control and 25% burial treatment (Fig. 7.2c). A clear but non-significant positive relationship ($Y = 10.00 + 0.12X$. $r^2 = 0.887$, $P = 0.065$) was observed between the number of green leaves of the surviving seedlings (Y) and burial (X). Burial of two-week old seedlings (Burial II) stimulated leaf production only in the 25% burial treatment. However, it took about five weeks for the seedlings to surpass the control in the number of green leaves. Leaf production was impeded in other treatments. In 75% burial treatment, the number of green leaves per plant decreased with time owing to lower leaf production and higher leaf senescence. At the end of the experiment (8 weeks), significant ($P < 0.01$) differences were observed between seedlings buried to 25% and those to 50 and 75% of their height (Fig. 7.2d).

Figure 7.2 Mean number of green leaves per seedling of *Panicum virgatum* (a, b) and *Agropyron psammophilum* (c, d) counted at one week intervals after the sand burial treatments in Burial I and Burial II. The intercepts of the curves indicate mean number of green leaves per seedling immediately after the sand burial treatment.


Panicum virgatum
Burial I
Burial II
a
b
Mean number of leaves per plant
25
50
0
75
120
100
50
25
0
75
Agropyron psammophilum
c
d
50
75
25
0
100
25
0
50
75
100
Weeks after sand burial

7.3.1.4 Number of tillers per plant

Tiller production was poor in both buried (Burial I and II) and unburied seedlings of *Panicum virgatum* and burial in sand did not have any effect (Fig. 7.3a, b). However, in burial I all buried seedlings of *Agropyron psammophilum* produced larger numbers of tiller than the control (Fig. 3c, d). A significantly positive effect of sand burial was maintained on tiller production in Burial I. The deeper the burial depth, the greater were the number of tillers per plant ($Y = 1.077 + 0.035X$. $r^2 = 0.989$, $P < 0.01$). At harvest, significant ($P < 0.05$) differences were observed between seedlings in the 75% burial treatment and control. In Burial II only the 25% burial treatment produced significantly ($P < 0.05$) more tillers than the control after eight weeks of growth (Fig. 7.3d).

7.3.1.5 Dry weight of seedlings

Two-way ANOVAs indicated that the dry weight of all the seedling components of *Panicum virgatum* was not significantly affected by the age at burial, the burial treatments or their interaction. At the end of experiment, seedlings from all treatments in Burial I and Burial II had similar dry weight but those in 25 and 50% burial treatments were usually slightly greater (Fig. 7.4).

For *Agropyron psammophilum*, however, interaction between age at burial and the depth of burial was significant ($P < 0.01$) according to the two-way ANOVAs for

Figure 7.3 Mean number of tillers per seedling of *Panicum virgatum* (a, b) and *Agropyron psammophilum* (c, d) measured at one week intervals after the sand burial treatments in Burial I and Burial II.

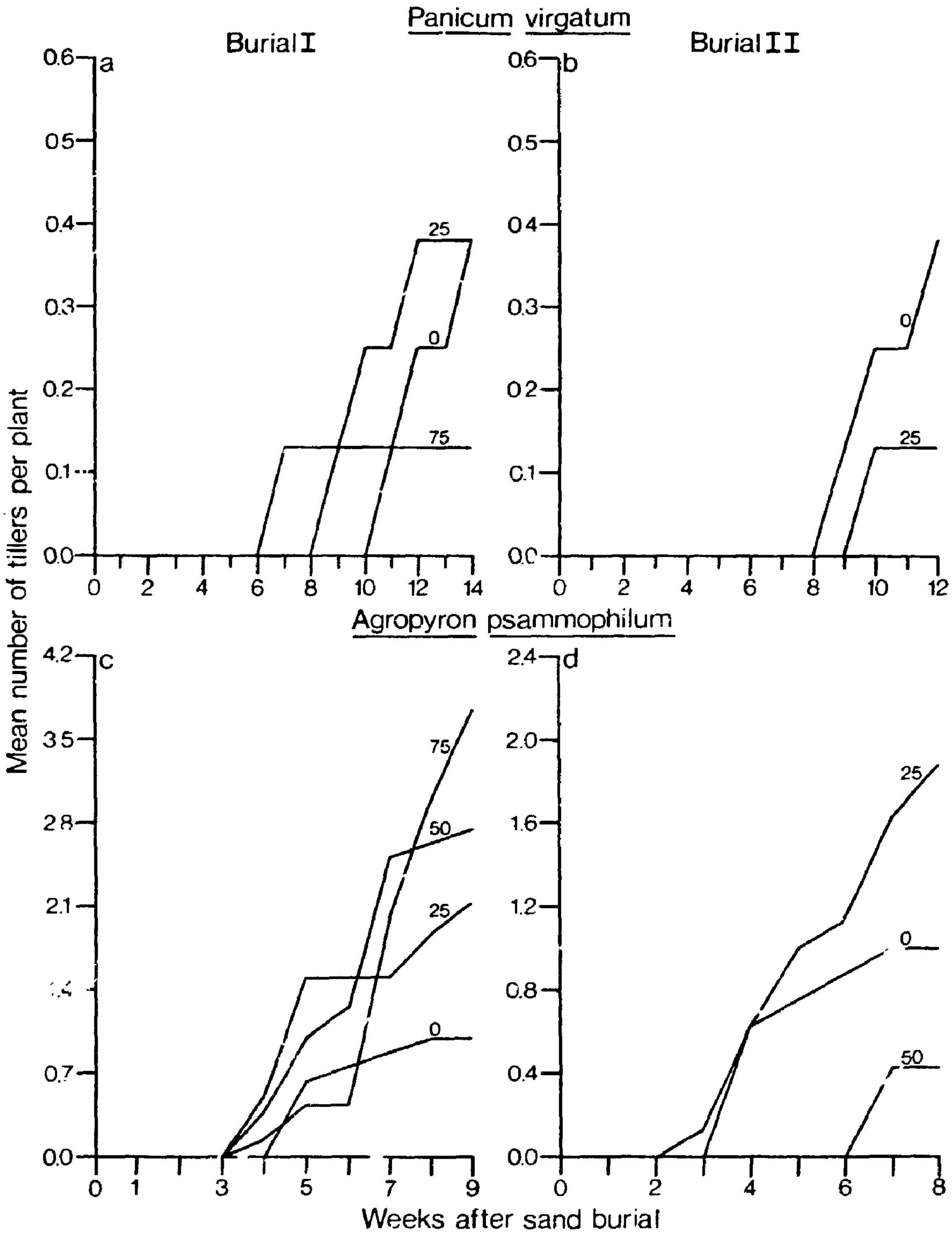
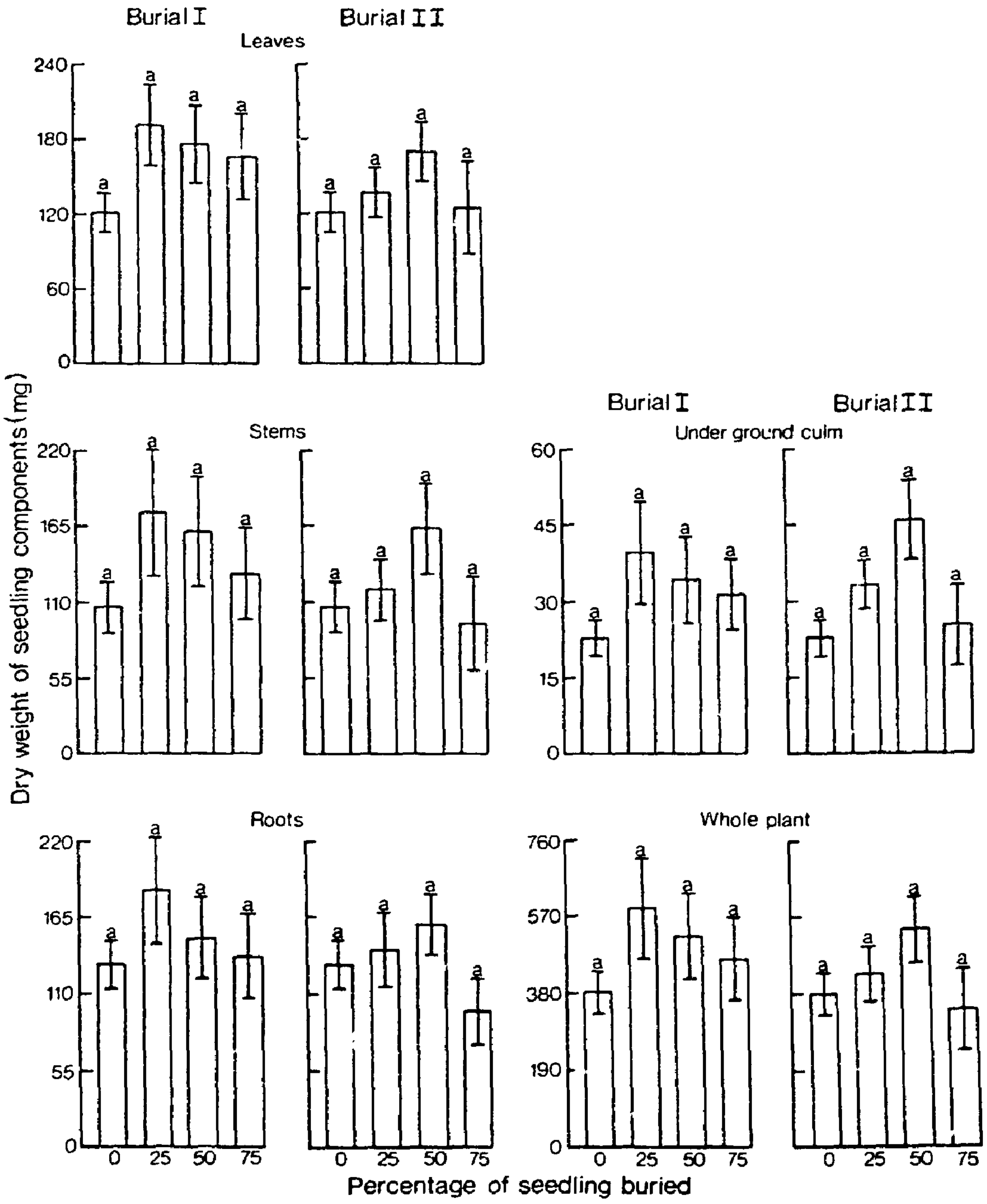
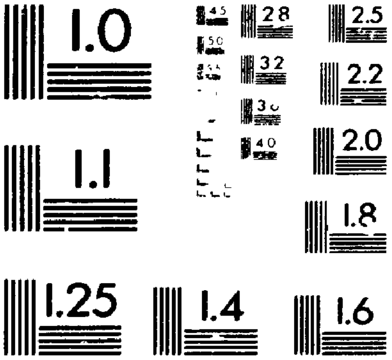
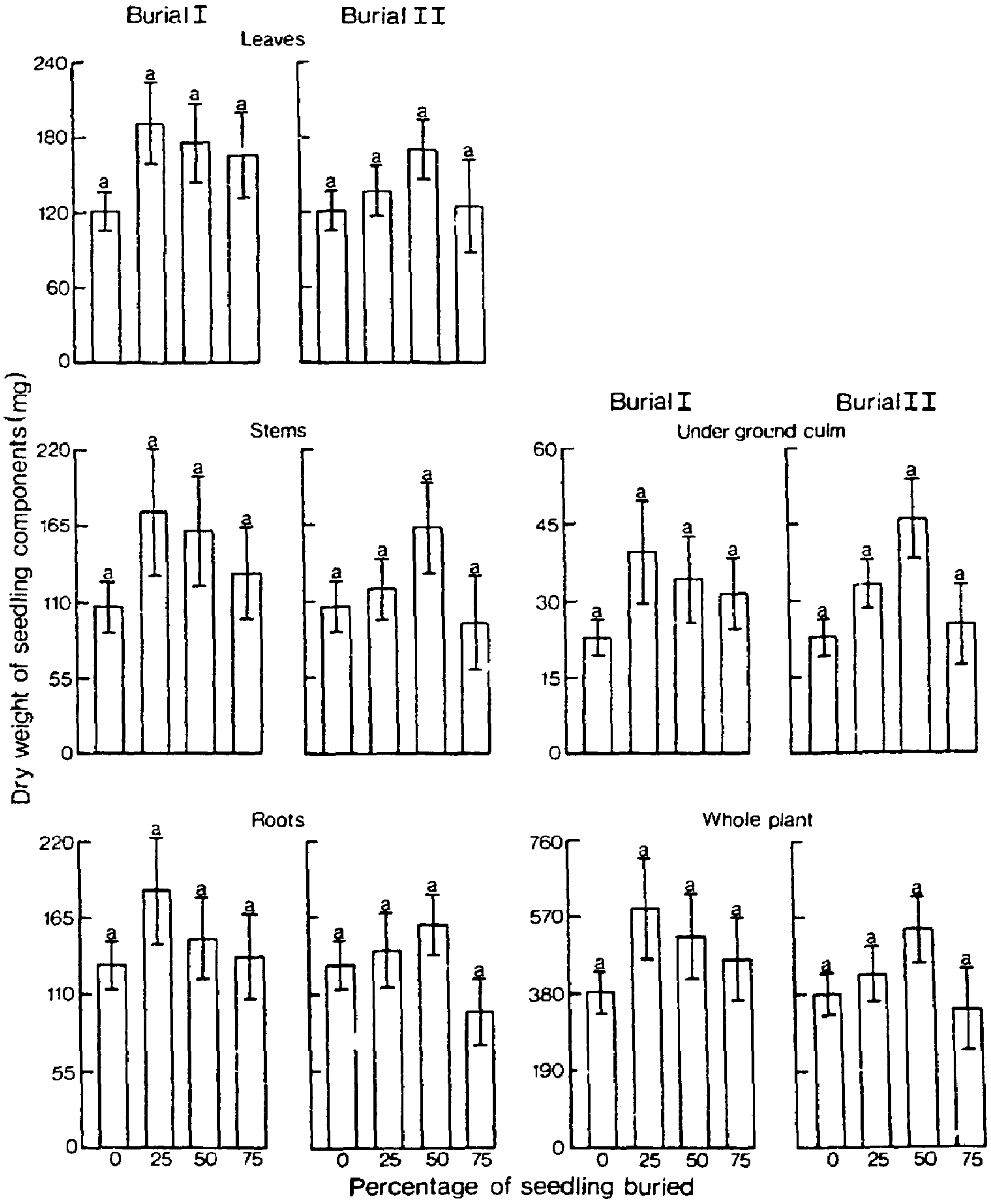

Panicum virgatum
Burial I
Burial II
a
b
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0
2
4
6
8
10
12
14
25
0
75
0
25
Agropyron psammophilum
c
d
4.2
3.5
2.8
2.1
1.4
0.7
0.0
0
1
3
5
7
9
75
50
25
0
2.4
2.0
1.6
1.2
0.8
0.4
0.0
0
2
4
6
8
25
0
50
Mean number of tillers per plant
Weeks after sand burial

Figure 7.4 Mean dry weight per seedling and its components after 14 weeks (Burial I) and 12 weeks of growth (Burial II) after the burial of *Panicum virgatum* seedlings. Vertical lines indicate standard errors. Seedlings within Burial I and Burial II are not significantly different according to Tukey's HSD test (Catanzaro 1988).


Burial I
Burial II
Leaves
Stems
Under ground culm
Roots
Whole plant
Dry weight of seedling components (mg)
Percentage of seedling buried
240
180
120
60
0
220
165
110
55
60
45
30
15
760
570
380
190
25
50
75
a

3 of/de 3




Burial I
Burial II
Leaves
240
180
120
60
0
Dry weight of seedling components (mg)
Stems
220
165
110
55
0
Burial I
Burial II
Under ground culm
60
45
30
15
0
Roots
220
165
110
55
0
Whole plant
760
570
380
190
0
a
0
25
50
75
Percentage of seedling buried

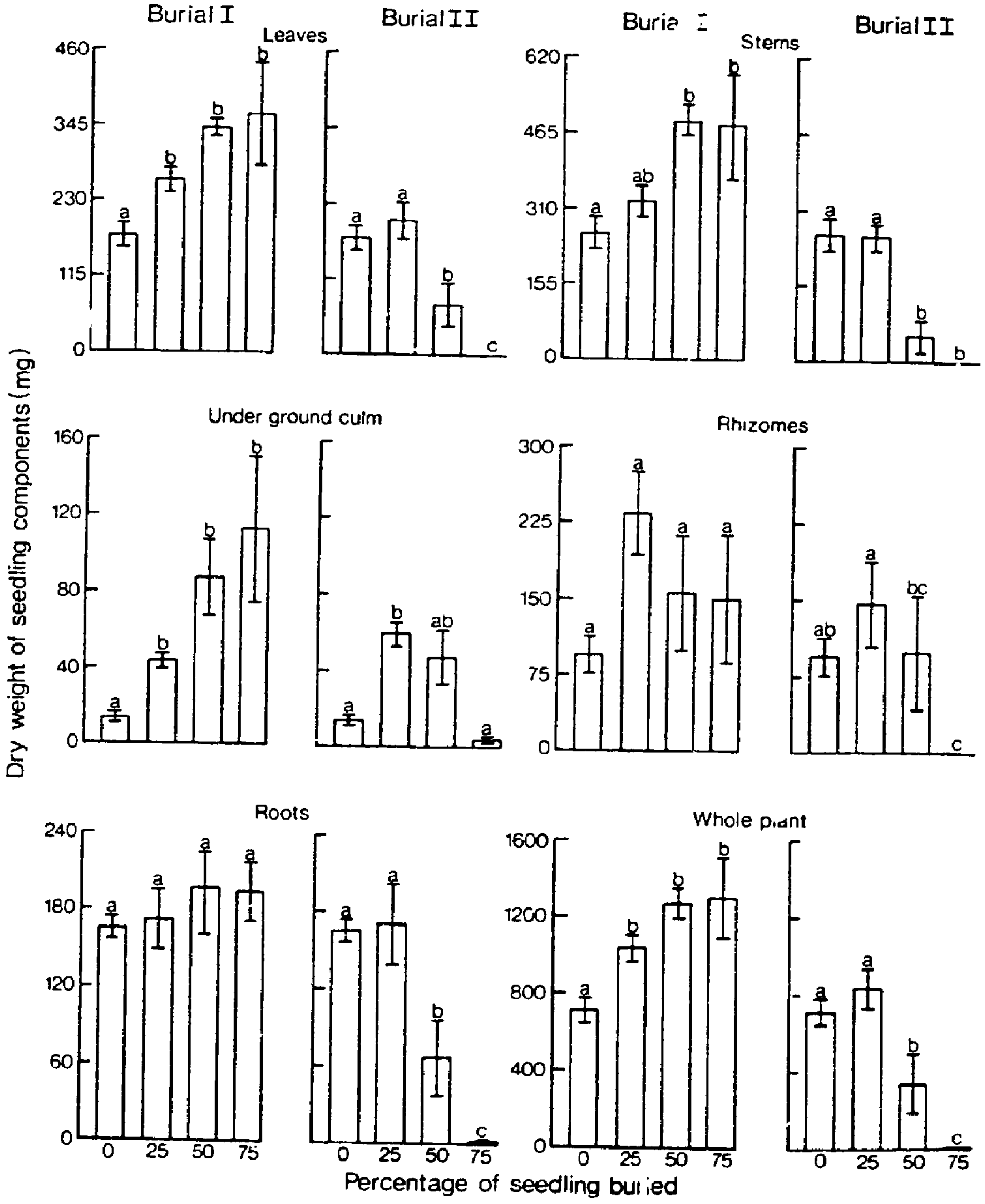
each seedling measurement (ANOVA tables not presented). One way ANOVAs showed that burial had a stimulative effect on the growth of one-week old seedlings (Fig.7.5). For example, dry weights of leaves, stem, under ground culm and overall weights of the surviving seedlings in each burial treatment were significantly ($P < 0.05$) higher than those of control. For Burial II seedlings, 25% burial did not alter the dry weight of the whole plant but burial depths of 50% and 75% significantly ($P < 0.05$) decreased the dry weight per plant than control and the 25% burial treatment (Fig. 7.5).

Sand burial did not significantly alter the dry matter allocation of seedlings of either species. However, seedlings of *Agropyron psammophilum* in the 25% burial treatment in both Burial I and Burial II contributed more dry matter to the rhizomes (data not presented).

7.3.1.6 Dry weight of seedlings in relation to absolute depth of burial and seedling size

Data on dry weight of buried *Panicum virgatum* and *Agropyron psammophilum* seedlings were rearranged according to the absolute depth of sand burial and pre-burial seedling height and are presented as stereo diagrams in Figure 7.6. The absolute depth of sand burial showed the greatest influence on the dry weight of seedlings. For *P. virgatum*, seedlings buried at shallow depths had greater dry weight than control in both Burial I and II (Fig. 7.6a, b). For *A. psammophilum*, seedlings buried at deep depth as a whole were

Figure 7.5 Mean dry weight per seedling and its components at harvest as affected by different burial treatments given to one- (Burial I) and two-week (Burial II) old seedlings of *Agropyron psammophilum*. Vertical lines indicate standard errors. Bars in the same graph with different superscript letters are significantly ($P < 0.05$) different according to Tukey's HSD test (Catanzaro 1988).



Burial I
Leaves
Burial II
Burial I
Stems
Burial II
460
345
230
115
0
620
465
310
155
0
Under ground culm
160
120
80
40
0
Rhizomes
300
225
150
75
0
Roots
240
180
120
60
0
Whole plant
1600
1200
800
400
0
a
b
ab
bc
c
Dry weight of seedling components (mg)
0
25
50
75
Percentage of seedling buried

heavier than those buried at shallow depth in Burial I (Fig. 7.6c). In Burial II, those buried at intermediate depths were heavier (Fig. 7.6d).

For *Panicum virgatum*, pre-burial seedling height did not confer any significant advantage on final seedling weight at shallow burial depths. However, reverse was true for seedlings buried at greater depths (Fig. 7.6a, b). There was no effect of seedling height on the weight of *Agropyron psammophilum* seedlings (Fig. 7.6c, d).

7.3.2 Effects of sand burial on the survivorship of Panicum virgatum seedlings in the field

The mean depth of post-emergence (during summer) sand accretion was similar among the various depth classes from which the seedlings had emerged in spring and it varied only from 1.13 to 1.60 cm (Table 7.4). The survival of a seedling depended on the depth from which it had emerged in spring. The chi-square test showed that the observed frequency of established seedlings in October was significantly ($P < 0.01$) different from the expected. Generally, seedlings that emerged from shallow burial depths (less than six cm) had fewer survivors than expected and those from deep burial depths (greater than six cm) had more survivors than expected (Table 7.4).

The seedlings that emerged from shallow depths could withstand greater depths of post-emergence burial (Table 7.2). As the depth from which a seedling had emerged in

Figure 7.6 Stereo diagrams showing the relationship between seedling dry weight at harvest (vertical axis), absolute depth of post-emergence burial (horizontal axis) and pre-burial seedling height (horizontal vertical axis[illegible].

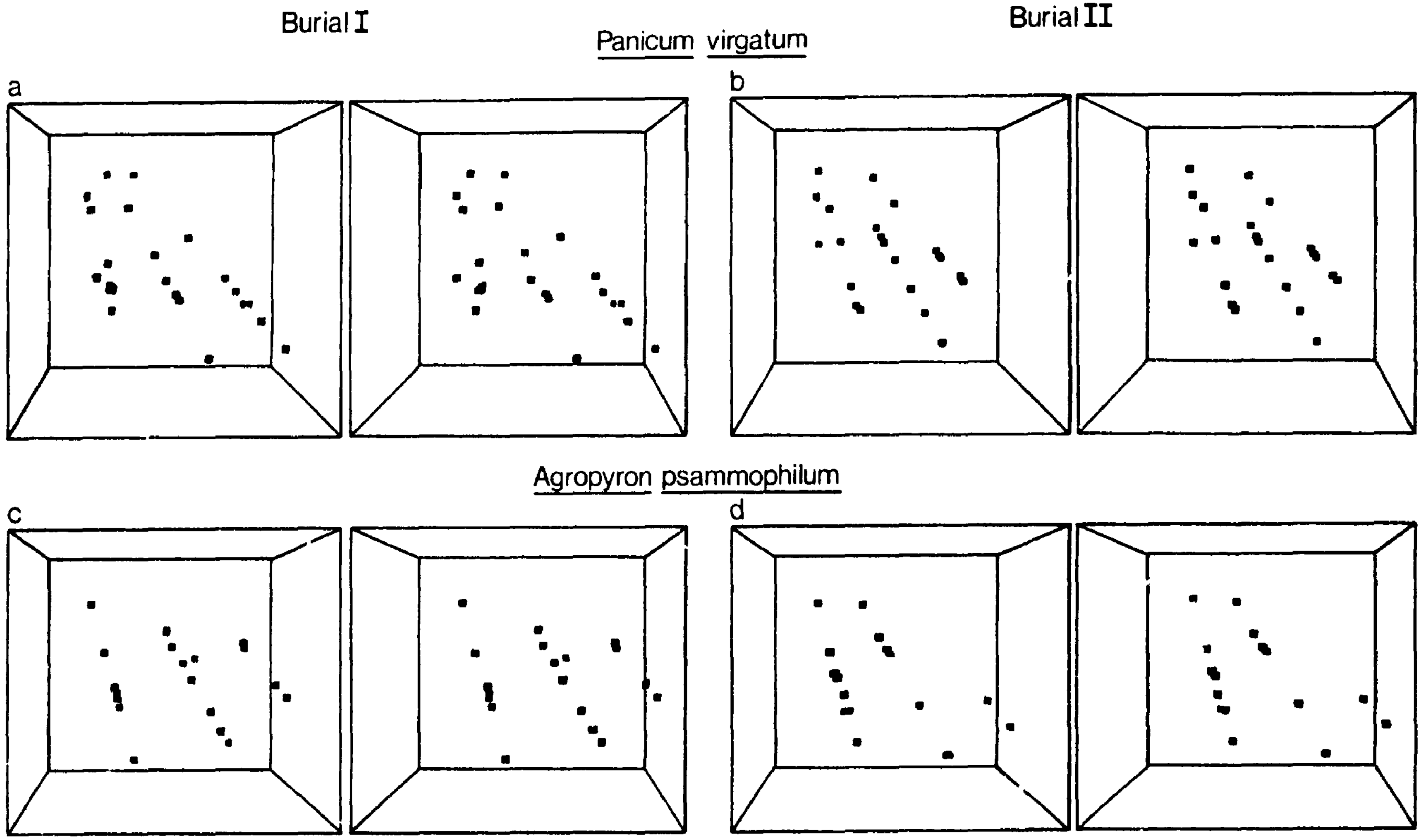

Burial I
Burial II
Panicum virgatum
a
b
Agropyron psammophilum
c
d

Table 7.4 Mean depth of post-emergence sand accretion during summer on established seedlings of *Panicum virgatum* and the observed and expected number of seedlings at each emergence depth in the field.

Depth class (cm)	Post-emergence sand accretion during summer (cm)	Number of seedling	
		Observed	Expected
0 - 1	---	0	1
1 - 2	1.29	2	29
2 - 3	1.53	46	32
3 - 4	1.58	58	78
4 - 5	1.60	72	92
5 - 6	1.44	45	76
6 - 7	1.41	54	41
7 - 8	1.47	65	29
8 - 9	1.23	34	14
9 - 10	1.13	7	4
10-<11	1.32	13	1
11-<12	1.29	1	0
Total		397	397

spring increased, its ability to survive post-emergence burial decreased. For example, seedlings emerging from 3 - 4 cm depths in spring could withstand up to 6 cm of burial. In contrast, seedlings emerging from 10 - 11 cm could survive only 1 - 2 cm of burial. Chi-square test showed that this relationship was significant ($P < 0.05$). Concentration analysis indicated that the total chi-squared could be partitioned into three canonical variates (Table 7.5). Each variate accounted for 76.6, 18.1 and 5.2%, respectively, of the total variation. The first canonical variate increased with increasing post-emergence sand burial and stabilized at greater depths. The second variate fluctuated at shallow depths but stabilized at greater burial depths. The third variate decreased and tended to stabilize with increasing post-emergence burial (Table 7.5). Each of these canonical variates may represent an environmental factor showing the same trend in variation with increasing sand burial depth. Since variation in environmental factors with sand burial depth was not recorded in this study, it was not possible to relate the canonical variates with any environmental factor.

Figure 7.7 shows dispersion profile of seedling survivorship from random expectation at different depths of post-emergence sand burial for each group of seedlings presented in Table 7.2. No explanation was made for seedlings in Group I because of insufficient sample size. The survivorship of seedlings in group II was enhanced by

Table 7.5 Canonical scores for each burial depth of *Panicum virgatum* seedlings and percent variation accounted for by each canonical variate using data presented in Table 7.2.

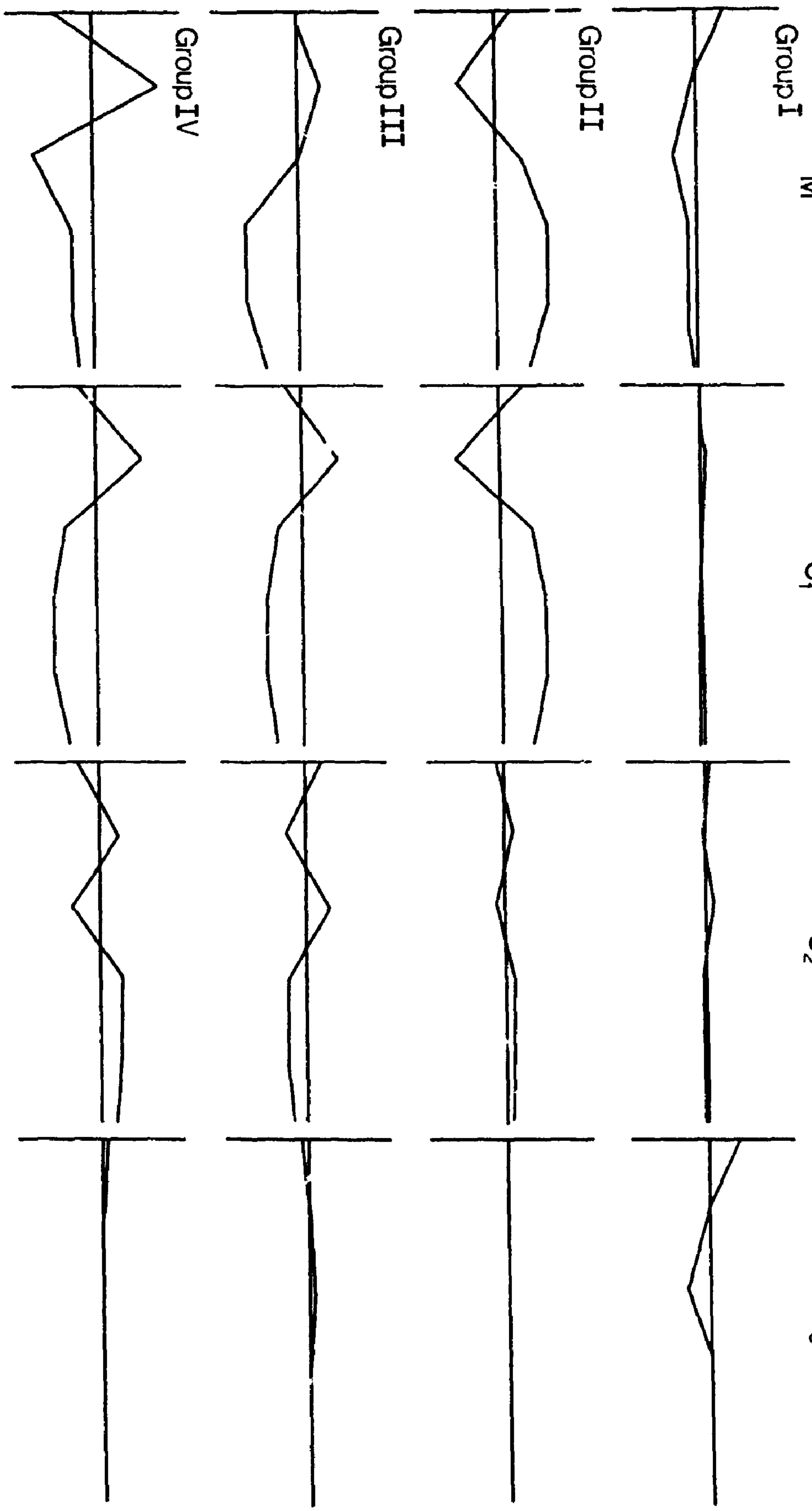
Canonical	Post-emergence burial depth						Correlation
variate	< 1	1-2	2-3	3-4	4-5	5-6	(%)
1	0.41	-0.69	0.93	3.71	3.71	3.71	76.63
2	-0.78	0.50	-1.54	3.03	3.03	3.03	18.13
3	1.42	-0.23	-1.82	-0.10	-0.10	-0.10	5.24

moderate and deep post-emergence burial. Variate C_1 which represents an environmental factor (or factors) shows dominant control over seedling survivorship in this group. In contrast, more seedlings in Group III and IV survived at shallow post-emergence sand burial as compared to a random expectation. Both variates C_1 and C_2 controlled seedling survivorship in these two groups (III and IV). However, seedlings in the two groups responded differently to environmental factors corresponding to canonical variate C_2. Variate C_3 had little effect on seedling survivorship (Fig. 7.7).

7.4 DISCUSSION

A threshold of sand burial depth was evident for the survival of young seedlings of *Panicum virgatum* and *Agropyron psammophilum*. For *P. virgatum*, the depth was about 1.6 cm for one-week old seedlings and 3.5 cm for three-week old seedlings. For *A. psammophilum*, it was around 6 cm for both one and two weeks old seedlings. As the depth of burial exceeded these limits, the seedlings were unable to survive. Under field conditions, sand accretion of up to 20 cm in one week has been recorded at some locations (Yanful 1988). Thus, burial by sand may be a significant causal agent in seedling mortality of both species especially in accreting sites. Since large numbers of *P. virgatum* seedlings are produced each year, the chances of survival and establishment in this unpredictable habitat are still quite

Figure 7.7 Dispersion profiles from random expectation of four groups of *Panicum virgatum* seedlings along post-emergence burial depth gradient. M - general trend. C_1, C_2, C_3 are trends under canonical variates 1, 2 and 3, respectively.


Group I
Group II
Group III
Group IV
M
C_1
C_2
C_3

high. In comparison, the establishment of *A. psammophilum* seedlings is very low. Other limiting factors for seedling establishment of both species are desiccation and sand erosion (Zhang and Maun 1989b).

At depths below the threshold for survival, seedlings of *Panicum virgatum* and *Agropyron psammophilum* showed slightly different responses to sand accretion. In *P. virgatum*, burial at different ages and to various depths did not significantly affect the dry weight of seedlings, although buried seedlings were taller and had more green leaves than control. Seedlings buried to small absolute depths were heavier in dry weight than those buried at greater depths. In *Agropyron psammophilum*, seedlings buried to $\leq$ 6 cm were taller, had more green leaves and tillers and were heavier in weight than control. Thus, seedlings of *P. virgatum* showed smaller threshold for survival and tolerated only small amounts of sand accretion. In contrast, seedlings of *A. psammophilum* exhibited clear increase in vigour in response to sand accretion.

In *Agropyron psammophilum*, the ability to recover from sand burial depended to some extent on the age of seedlings. Although only a small proportion of seedlings survived through 75% burial treatment in Burial I and 50 and 75% in Burial II, the former showed better growth than the latter (7.1c, 7.2c, 7.3c). Older seedlings exhibited slow (50% burial) or reduced (75% burial) growth throughout the experiment (Fig. 7.1d, 7.2d, 7.3d).

Several reports (Anderson and Taylor 1979, Eldred and Maun 1982, Huiskes 1979, Laing 1967, Marshall 1965, Wallen 1980) indicated that burial by sand stimulated tiller production and increased plant vigour (measured as dry weight per shoot) in adult plants of *Ammophila arenaria* and *A. breviligulata*. *Agropyron psammophilum* seedlings showed similar increase in vigour when the burial depth did not exceed six cm. The stimulation in vigour was not clearly evident in *Panicum virgatum* seedlings.

Under field conditions, some *Panicum virgatum* seedlings survived through six cm of post-emergence burial depth. In the greenhouse, however, the maximum depth of burial from which seedlings survived was only 1.55 cm in Burial I and 3.47 cm in Burial II. The burial in the field may have been gradual, and at a stage when plants were least susceptible to injury.

Seedling survivorship of *Panicum virgatum* in the field depended on the original depth from which a seedling had emerged after germination. At sand burial depths of 6 - 12 cm the probability of seedling survival was greater than expected probably because the sand surface during the dry summer months did not dry out to that depth (Baldwin and Maun 1983) and sand erosion from the base of seedlings would not have a deleterious effect. In contrast, seedlings that emerged from shallow (< 6 cm) depths would suffer from desiccation caused by surface drying and even small amounts of sand erosion would expose the root system.

In *Panicum virgatum*, seedlings emerging from different depths responded differently to post-emergence sand burial. When seedlings had emerged from shallow depths, their establishment was improved by sand burial. However, seedlings emerging from greater depths of burial usually did not survive through post-emergence sand burial of greater than three cm. Perhaps, seedlings that emerged from shallow depths suffered from root desiccation owing to the drying out of surface sand. Sand accretion would increase the buffer layer of sand and hence protect the root system. In contrast, for seedlings which emerged from greater depths, post-emergence burial would create poor aeration conditions owing to excessive moisture around the root zone of seedlings.

In conclusion, burial in sand is a major factor that determines the survivorship and spatial distribution of *Panicum virgatum* and *Agropyron psammophilum* seedlings at Port Burwell Provincial Park. Seedling mortality in both species was very high. However, since *P. virgatum* produces large quantities of seedlings each year, survival of even a very small proportion guarantees addition of some new individuals to the population. Seedling establishment of *A. psammophilum* was very limited. Since this species relies heavily on the recruitment of new individuals from vegetative rhizome fragments (Gillett and Senn 1961), seedling establishment may not play a significant role in maintaining its populations.

CHAPTER EIGHT

GENERAL CONCLUSIONS

Along Lake Erie shoreline at Port Burwell Provincial Park two dune-forming grasses, *Panicum virgatum* and *Agropyron psammophilum* are found in abundance. Both species are adapted to withstand sand accretion and form dunes 2 to 5 m in height about 20 to 50 m from the lake shore. A close examination of their relative occurrence reveals that they are separated in space and time. For instance, *A. psammophilum* is mainly found in the low foredune closer to the shoreline while *P. virgatum* is abundant between the foredune and the slack. *A. psammophilum* has a C_3 photosynthetic pathway and starts to grow in early April whereas *P. virgatum* is a C_4 grass and its shoots appear above sand surface about four weeks later. Even though the two species exhibit some similarities, they differ in growth form, mechanism of seed dormancy and some aspects of population ecology.

Panicum virgatum plants exist as individual clumps, which expand laterally by producing short rhizomes on the periphery. Such a growth form has the advantage of consolidating a hold on local patch of resources and resists invasion by other species (Maun 1985). *Agropyron psammophilum* expands into adjacent territory by producing long creeping rhizomes thus forming monospecific stands of varying sizes. Because of its proximity to the shoreline, high waves may break rhizomes into small pieces and transport them to new places. *P. virgatum*, on the other hand, does not fragment and can not disperse through vegetative means. These differences in growth form may partially explain the distribution patterns of the two species in the field.

The seed dormancy mechanism of *Panicum virgatum* may be of adaptive significance in the unpredictable habitat of Lake Erie dunes. For instance, its seeds exhibit innate dormancy which can be broken only after certain requirements are satisfied. The species would thus maintain a persistent seed bank. Either stratification or exposure to a wide range of temperature can break seed dormancy of *P. virgatum*. In the field new individuals of *P. virgatum* establish exclusively from seeds because its clumps or small rhizomes do not fragment. Thus the wide distribution of this species throughout North America and its successful establishment in varied habitats may be partly due to the dispersal of dormant seeds. In contrast, seeds of *Agropyron psammophilum* do not show any innate dormancy, contradicting the common belief that seed dormancy is found in species that occupy unpredictable environments (Fenner 1985). Field observations showed that seedling establishment in this species was rather low. Instead, the species relied heavily on the horizontal expansion of rhizomes and dispersal of rhizome fragments. Thus, reproduction through seeds may be of little importance for local occupancy, but would be essential for dispersal to new locations and an increase in variability of the population. Field observations showed that the species invests considerable amount of resources in seed production each year. These seeds are viable and germinate in late fall, spring and summer when the temperatures are above 15 ^{0}C and moisture supply is adequate. It may be suggested that in years of well distributed rainfall and good weather conditions, the establishment of seedlings may be rather high as seen in some other dune species (Maun 1985). Even a single year of good seedling establishment would insure high genetic variability in its population. Further studies are needed to support this suggestion.

Seed size showed significant effects on seedling size in both species at the time of emergence. Large seeds produced larger seedlings than small seeds. However, the size differences were short-lived in *Panicum virgatum* and fluctuated with time in *Agropyron psammophilum*. For *P. virgatum*, the relative growth rate of seedlings did not show any relationship with seed size. Therefore, the final size of seedlings may be mainly regulated by the carrying capacity of the experimental conditions. Under field conditions, intraspecific competition may be another major regulating factor (Cideciyan and Malloch 1982). For *A. psammophilum*, the relative growth rate of seedlings had significant relationship with seed size and fluctuated over time. The final size of seedlings may be regulated by both the relative growth rate and carrying capacity of experimental conditions. Competition may not be a significant factor under field conditions because seedlings do not normally occur in clumps.

In both species, a large proportion of surgically altered seeds (removal of part of the endosperm) remained viable and produced seedlings when favourable environmental conditions were provided. However, differences in germination of treated seeds were observed. For example, removal of 20 and 40% of the endosperm of *Panicum virgatum* seeds improved germination, suggesting that seeds were released from innate dormancy. In contrast, seed germination of *Agropyron psammophilum* was not influenced by partial removal of endosperm. In both species, seedling size was correlated with seed mass. Removal of a part of the endosperm resulted in smaller seedlings with less proportion of materials allocated to the above ground parts as compared with those from intact seeds. Thus under field conditions, seedlings from predated seeds would be at a competitive disadvantage as compared to seedlings from intact seeds.

Burial by sand had significant effects on seed germination and seedling emergence of both species. However, the adverse effects were stronger in *Agropyron psammophilum* than in *Panicum virgatum*. The reasons for this result can not be explained. Thus deep burial of *A. psammophilum* seeds may eliminate some of the seed population because seeds would germinate (no dormancy) but the seedlings would die before they reach the sand surface. Burial of *Panicum virgatum* seeds would not cause much loss because (i) seeds possess innate dormancy and (ii) if seeds do germinate they can emerge from greater depths than *A. psammophilum*.

The seedlings of the two species exhibited two significantly different strategies in their response to sand burial. A passive response showing no effect to sand burial was manifested by *Panicum virgatum* seedlings and a stimulative response to sand burial through vigorous growth was observed in *Agropyron psammophilum*. According to experimental results, burial by sand was a significant factor in seedling mortality of both species. However, the chances of survival and establishment were still high for *P. virgatum* since large numbers of seedlings of this species are produced each year.

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