ECOLOGY AND EARLY LIFE HISTORY TACTICS OF WILD RICE: SEED BANK DYNAMICS, GERMINATION, AND SUBMERGED LEAF PHENOPHASE GROWTH

by

TREVOR A. ATKINS H.B.Sc.For.

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A thesis submitted to the Faculty of Graduate Studies of the University of Manitoba in partial fulfillment of the requirements of the degree of

DOCTOR OF PHILOSOPHY

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If all is not well with his world, the rooster never admits it... But there is no mistaking the real thing: as the window panes brighten from purple to mauve to white he flaps up on his roof with a slap like a newspaper hitting the porch and gives a crow as if to hoist with his own pure lungs that sleepy fat sun to the zenith of the sky. He never moderates his joy, though I am gradually growing deafer to it. That must be the difference between soulless creatures and human beings: creatures find every dawn as remarkable as the ones previous, whereas the soul grows calluses.

From: Problems and other stories.
John Updike.

ABSTRACT

Overwintering of the seed, germination, and early plant development of wild rice (Zizania palustris L.) all occur underwater prior to the later emergent growth stages. Perhaps for this reason, the ecology of the submersed stages of the wild rice life cycle has remained largely a matter of speculation.

Investigations were undertaken to elucidate: the germination behaviour of wild rice seed using a 100-cell germinator; the dynamics of wild rice in the seed bank through a seed burial experiment; and the growth of the wild rice plant during the submerged leaf phenophase in a controlled environment experiment.

It was found that a suite of life-history traits serves to ensure the survival of a wild rice stand over time:

- A subpopulation of seed which requires more than one winter of afterripening to break primary dormancy and so adds a "fixed" proportion of annual seed production to the seed bank.
- Environmentally induced secondary dormancy which adds a variable proportion of annual seed production to the seed bank.

- Germination beginning very soon after ice-breakup allowing the early starting plants to exploit the environment before their competitors.
- Germination occurring over a protracted period of time which reduces the risk of a catastrophic event decimating the entire population.
- A plastic growth pattern during the submerged leaf phenophase which permits "escape" from adverse growing conditions or, alternatively, growth co-ordinated to increase plant robustness in an amenable environment.

This suite of life-history traits reveals a life-history strategy which is adapted to the exploitation of a temporally unpredictable environment through bet-hedging and buffering of annual "boom-or-bust" seed production.

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I couldn't have done it alone! During the past four years I have met, worked with, and been helped by many people whom I would like to acknowledge here.

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Over the past four years I have been helped immeasurably in the field and in the lab by a small platoon of helpers. It is not possible to do justice to the efforts they have gone to or the troubles we have been through together! Thanks to: Mr. K. Warren, Mr. T. Stevens, Ms. D. Heiman, Ms. C. Heiman, Ms. B. Kindret, Mr. C. Fyfe, and Ms. B. Hiltz.

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Finally, as is tradition to save the best for last, I would like to thank my wife, Ms. J. Hall, for being there. We have literally endured snowstorms, sleet, rain, hail, and even a bit of sunshine together in the pursuit of the mysteries of wild rice. This thesis is as much yours as mine.

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Chapter I

GENERAL INTRODUCTION

1.1 INTRODUCTION

Wild rice (Zizania palustris L) is an annual aquatic grass which grows in the shallow waters of lakes, slow moving rivers, and marshes of northern Minnesota, northern Ontario, Manitoba, Saskatchewan, and Alberta. The range of wild rice is continually expanding through the introduction of wild rice to new areas by man.

The wild rice plant grows best in waters 15-30cm in depth, but can be found in up to 2m of water if sufficient light is available for growth during the submerged leaf phenophase. Rising water levels, especially during May and June, can severely weaken or kill the developing plant (Moyle, 1944; Rogosin, 1958). Deep organic sediments are considered best for wild rice growth but it can be found growing in sediments with high mineral content (Lee, 1979).

Wild rice grows both in pure stands and in mixtures with other species (Moyle, 1944). Co-existing species are known to both reduce growth (Ceratophyllum demersum L. - Atkins, 1984) and to enhance it (Potamogeton robbinsii Oakes - Lee, 1979).

The life cycle of the wild rice plant involves several growth stages, or phenophases, each with well defined anatomical and ecological differences. The phenophases are loosely defined on the basis of leaf morphology and the presence or absence of reproductive structures. Figure 1.1 depicts the stages of the wild rice life cycle.

Growth begins in the spring during late April and May with the germination of seed overwintered in the submerged sediments. The seedlings grow through the water column during the submerged leaf phenophase which may last up to six weeks (Fig. 1.2). Upon reaching the water surface a morphologically distinct floating leaf is produced which grows for approximately two weeks on the water surface during the floating leaf phenophase (Fig. 1.2). The emergent stem and leaves follow in the vegetative aerial leaf phenophase and tillering may occur (Fig. 1.2). During late July and August the panicles emerge and flowering begins. Seeds develop and mature within two weeks following fertilization. Mature seeds either shatter and enter the water or are predated by insects and wildlife or harvested by man for food.

The Native people of North America have a long tradition of using wild rice as a basic food (Hallowell, 1935). In northern Minnesota prehistoric tools associated with the processing of wild rice have been excavated (Johnson, 1969).

Wild rice grown in lakes and processed in the traditional Native ways became a gourmet food item to non-Natives; and today, the wild rice plant is the basis of a modern 11.1

Figure 1.1: Life Cycle of the Wild Rice Plant (Stewart, pers comm, 1986).

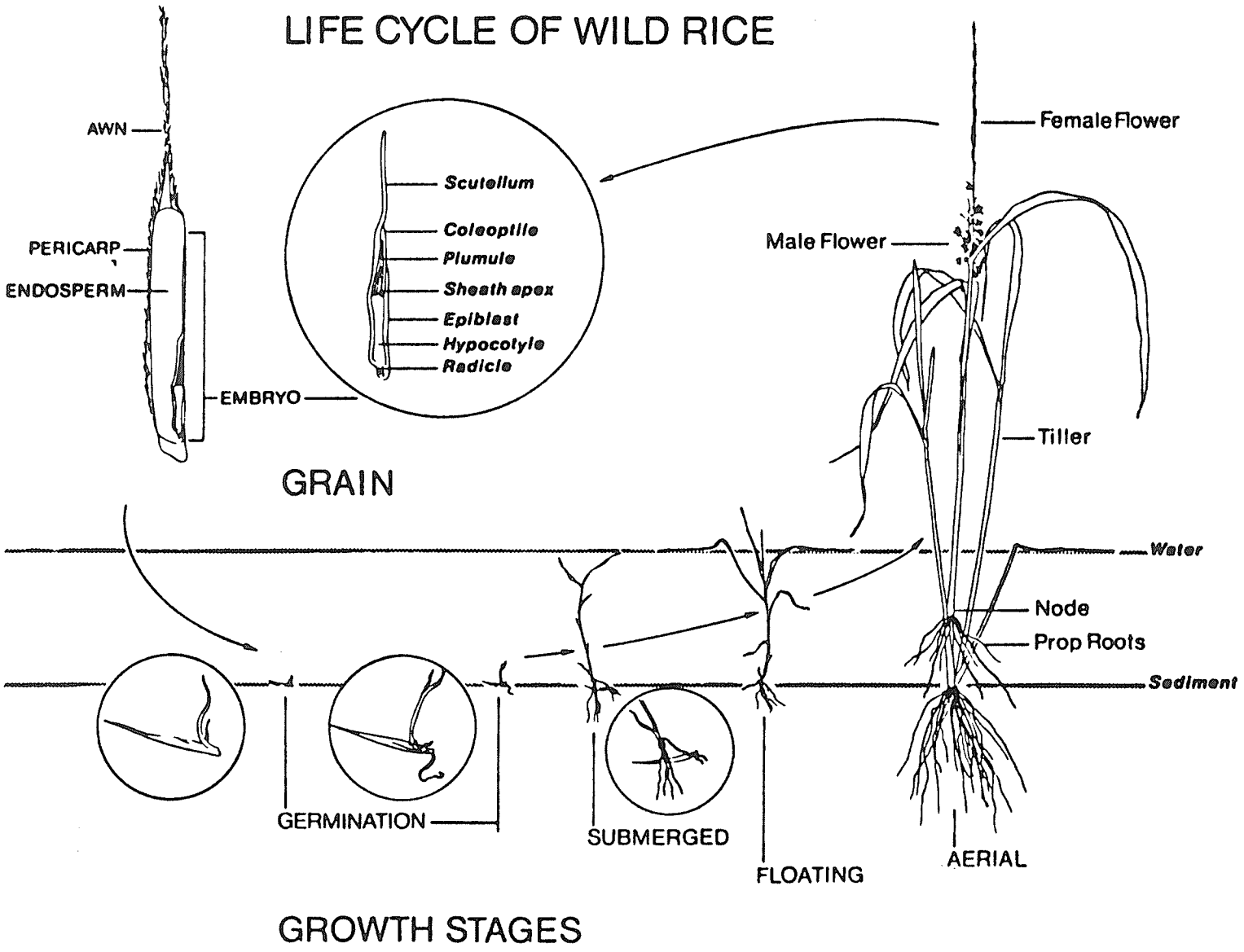

LIFE CYCLE OF WILD RICE
AWN
PERICARP
ENDOSPERM
EMBRYO
Scutellum
Coleoptile
Plumule
Sheath apex
Epiblast
Hypocotyle
Radicle
GRAIN
Female Flower
Male Flower
Tiller
Water
Node
Prop Roots
Sediment
GERMINATION
SUBMERGED
FLOATING
AERIAL
GROWTH STAGES

Figure 1.2: Illustrations of wild rice plants growing in the submerged leaf, floating leaf, and aerial leaf phenophases.

Facing page - submerged leaf phenophase.

Following page - floating and aerial leaf phenophase.


14
5
4

million kg industry (Lee, 1986) with world production and consumption increasing at over 15% per year (Nelson and Dahl, 1985). At the heart of the modern wild rice industry is the domestication of wild rice through paddy culture, primarily in the U.S. The domestication of wild rice has stabilized annual production which had been subject previously to the wide fluctuations of lake production (Winchell and Dahl, 1984).

As a consequence of paddy development, commercial harvesting of wild rice from lakes is in danger of becoming obsolete unless production can be increased and stabilized (Lee, 1985).

Research to this end has been concentrated primarily on the influences of the environment on the emergent phenophases, and the development of allied management techniques. The early developmental stages have received relatively little attention; though early growth is known to affect the productivity of other species.

This thesis reports on investigations into the early developmental stages of wild rice: the effects of afterripening and temperature on germination, the behaviour of wild rice seed in the seed bank of natural stands, and the effects of light and temperature on growth and expression of life-history strategies of the submerged leaf phenophase wild rice plant. The development of a wild rice plant growth model derived from these data is also presented. This model was developed to synthesize the data collected

regarding the early growth stages of wild rice and to highlight areas in which further research is needed. Finally, this thesis draws conclusions regarding the general implications of these investigations in the context of natural wild rice stand ecology and in the context of managing wild rice as a crop in both lakes and paddies.

1.2 LITERATURE REVIEW

1.2.1 Taxonomy

The taxonomy of the genus Zizania has not been fully resolved. Much of the confusion arises from uncertainties regarding the type-specimens used in Linnaeus' original treatment of the North American annuals of this genus (Fassett, 1924). In an attempt to clarify the taxonomy of Zizania, Fassett (1924) listed one species Z. aquatica, with three varieties: vars. brevis, angustifolia, and interior.

Dore (1969) felt that the North American annuals were more properly two species, Z. aquatica with two varieties: aquatica and brevis; and Z. palustris, also with two varieties: palustris and interior. Recent isozyme studies (Warwick and Aiken, 1986) support this concept of two distinct species and, therefore, Dore's (1969) taxonomy will be adopted for this thesis.

The wild rice of Manitoba and northwestern Ontario is the narrow-leaved and shorter northern form Z. palustris L.

1.2.2 Anatomy

The submerged leaf phenophase is characterized by ribbon-like leaves arising as eccentric collars surrounding the vegetative shoot apex (Weir and Dale, 1960). The initial leaves are simple but after the production of 5 internodes can be differentiated into shoot, ligule, and blade. Leaf growth occurs at two intercalary meristems: one at the junction of the sheath and stem and one on the blade just above the ligule (Weir and Dale, 1960).

The submerged leaf has a relatively undifferentiated mid-vein and contains much schizogenous aerenchyma (Weir and Dale, 1960) providing positive buoyancy to the leaf. Lacunae are septate and little lignification of the veins occurs (Weir and Dale, 1960). No stomata are found on the submerged leaf (Weir and Dale, 1960) and its surfaces are relatively free of epicuticular wax until the submerged leaf is approximately 5cm from the water:air interface (Hawthorn, 1968). Hawthorn speculated that epicuticular waxy rods trap oxygen against the upper portions of the submerged leaf and provide a pseudo-aerial environment in which to initiate the morphological changes associated with the floating leaf phenophase.

Normally between 2 and 4 submerged leaves are produced (Weir and Dale, 1960; Hawthorn and Stewart, 1970).

The floating leaf phenophase is transitional between the submerged environment and the aerial environment. Weber and Simpson (1967) speculated that the floating leaf may provide

oxygen to other tissues of the plant for respiration . The floating leaf is characterized by a well developed mid-vein, 10-12 large lateral veins, and a high proportion of aerenchyma (Weir and Dale, 1960).

The upper surface of the floating leaf is covered with cuticle, has depressed stomata, and bulliform cells are present in large numbers (Weir and Dale, 1960). The entire upper leaf surface is associated with wax rods and platelets (Hawthorn and Stewart, 1970) which help keep water from wetting the upper leaf surface (Weir and Dale, 1960; Kaul, 1976).

The lower surface of the floating leaf has an anatomy similar to the submerged leaf being devoid of wax (Hawthorn and Stewart, 1970) and stomata (Weir and Dale, 1960). Kaul (1976), however, noted the presence of stomata on both surfaces of the Zizania sp. specimens which he examined.

The emergent aerial leaf phenophase follows the production of 2 to 3 floating leaves (Weir and Dale, 1960). The anatomy and morphology of the aerial leaf differs greatly from the submerged and floating leaves having more lignified tissues and with the presence of over 50 veins (Weir and Dale, 1960). Aerenchyma is a dominant feature of the leaf midrib which has 4 large septate lacunae. The upper surface of the aerial leaf is characterized by rows of bulliform cells (Weir and Dale, 1960). Both surfaces are covered with wax rods and platelets which are thought to play a role in reducing the abrasive effects of wind and water on the aerial leaf (Hawthorn and Stewart, 1970).

The adventitious root system of the mature wild rice plant does not possess root hairs (Stover, 1927) and the epidermis of the developing root is replaced functionally by the large celled hypodermis at maturity. Much of the cortex tissues consist of aerenchyma. Sclerenchyma 2 to 3 cells deep surrounds the cortex and provides mechanical support (Stover, 1927).

The transition to the production of aerial leaves also marks the transition from a vegetative to a reproductive shoot apex (Weir and Dale, 1960). The apex elongates and floral branch primordia are produced. Meristems on the floral branch primordia produce the spikelet primordia. Therefore, the potential number of seeds which can be produced by a plant is determined well before the emergence of the panicle.

The monoecious panicle emerges in late July and August and flowers shortly after. Cross-pollination is aided through the superior position of the female florets in the panicle and the timing of flowering. Male florets within a panicle generally do not begin to shed pollen until after the stigmas of the female florets are no longer receptive (Weir and Dale, 1960).

The "seed" of wild rice, correctly a fruit termed the caryopsis, develops in the ten days to two weeks following fertilization. Development is typical of the cereals (Weir and Dale, 1960). Shortly after fertilization the abscission layer begins to develop and is completely formed by the end

of embryogenesis (Hanten et al, 1980). At maturity the seed consists of the hulls (palea and lemma) which are removed during processing; the seed coat (pericarp); a protein layer inside the seed coat (aleurone layer); the white starchy endosperm; and the embryo which consists of a seed leaf (scutellum), the first root (radicle) with its covering (coleorhiza), and the shoot (epicotyl) with its covering (coleoptile).

1.2.3 Life History And Ecology

1.2.3.1 Afterripening and seed dormancy

Wild rice seed is dispersed from the parent plant during late August and September. Dispersal distances are generally not great (Lee, 1979), though seed may be moved by ice or currents (Rogosin, 1951; Steeves, 1952) and long distance transport may occur as a result of the activities of man, animals, and birds.

Wild rice seed is dispersed in an innate state of dormancy which inhibits germination until spring. The seed overwinters in the sediments where afterripening conditions of cold temperatures and low oxygen tension reduce dormancy (Simpson, 1966). The increased germinability of wild rice seed with increased period of afterripening has been shown by Simpson (1966), Gutek (1975), and Oelke and Albrecht (1980).

The physiology of wild rice seed dormancy is not well understood. Albrecht et al (1979) found that the concentration of the growth inhibitor abscisic acid (ABA) was reduced

with afterripening and that the reduction was greatest in the pericarp and embryo. It is therefore likely that ABA, and possibly other growth regulating hormones, play a role in wild rice seed dormancy. The reduction in ABA levels observed during afterripening may result from increasing seed water content. Gutek (1975) observed that the water content of wild rice seed slowly increased with afterripening which supports a role for seed coat impermeability in controlling dormancy. Partial removal or disruption of the seed coat through pricking (Simpson, 1966), scraping (Woods and Gutek, 1974), mechanical scarification (Oelke and Albrecht, 1978), or exposure to ultrasonics (Halstead and Vicario, 1969) will result in increased germination. Techniques to enhance the germination of wild rice seed are currently only used in experimental conditions, but may be of use for general seeding applications to reduce the quantity of seed required.

Several workers have noted that the effect of seed coat disruption on germination behaviour changes with the length of afterripening period to which the seed is subjected. Simpson (1966), for example, noted that the effect of seed coat disruption on the percentage of seed germinated was minimal if the seed was afterripened more than 180 days. The rate of germination, however, was greater with scraping of the seed coat even with seed afterripened more than 180 days. These results led Simpson to conclude that wild rice seed dormancy was a function of seed coat impermeability to water and gases and that seed coat permeability increased

with afterripening. Cardwell et al (1978) found that the proximity of pericarp disruption to the embryo became less important as the length of afterripening period increased and postulated that wild rice possesses several dormancy mechanisms. They proposed that the mechanisms of dormancy immediately after harvest are mechanical resistance of the pericarp and the presence of germination inhibitors. In older, fully afterripened seeds, they postulated that pericarp impermeability to gases was the main cause of dormancy. Little evidence was presented, however, to support these specific mechanisms.

The prolonged dormancy of a portion of the wild rice seed population has been noted by several authors. Oelke et al (1983) noted that wild rice seed could remain dormant under flooded conditions for at least six years. In addition to innate primary dormancy, Gutek (1975) hypothesized that secondary dormancy - dormancy induced by environmental conditions - may also occur in wild rice.

Prolonged dormancy serves an important role in the ecology of natural wild rice stands by maintaining viable seed in the seed bank and buffering the impact of low seed production years on subsequent stand establishment. Steeves (1952) noted the establishment of a wild rice stand, following a year in which no seed was produced, from seed in the sediments which was two or more years old.

Harper (1977) developed a general model to describe the fate of seed dispersed from any species of plant. He termed

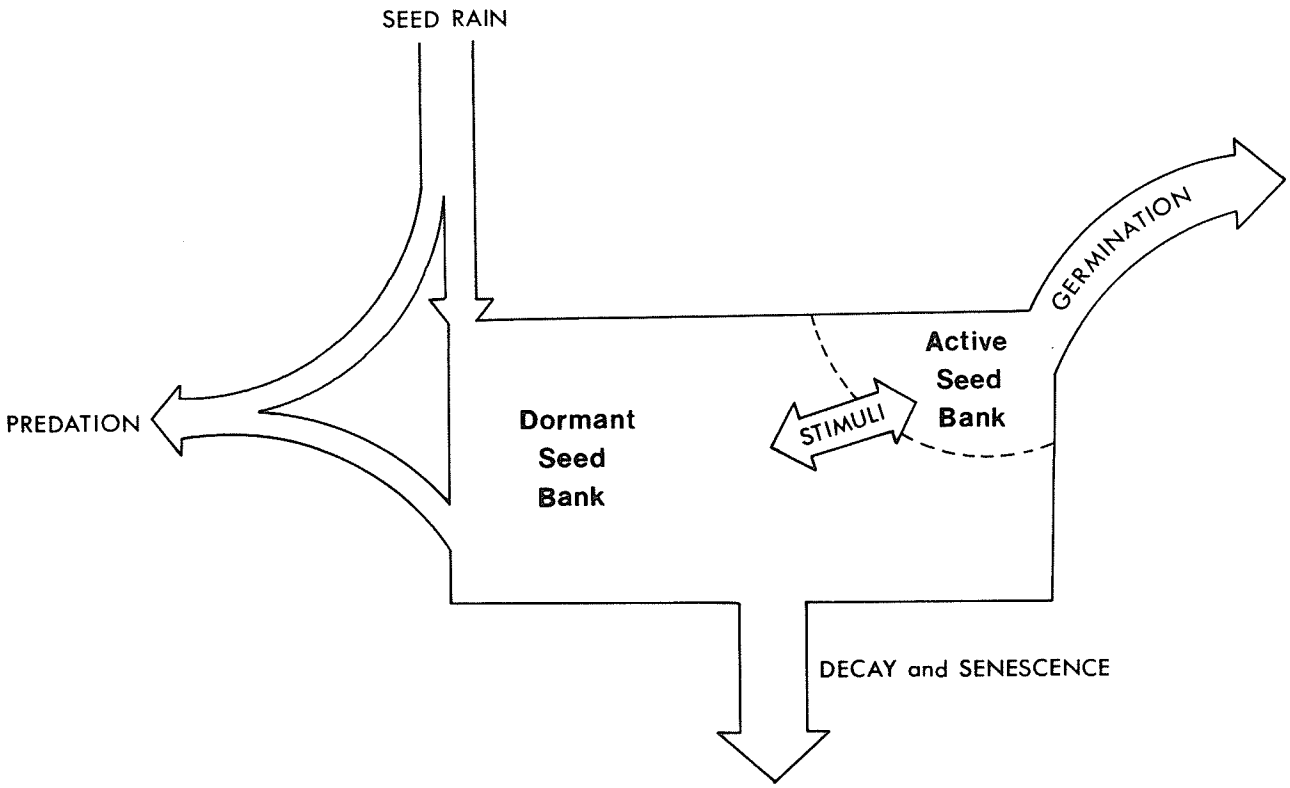
the sum of seeds in the soils or sediments underlying a community the seed bank. Within the seed bank are pools which interact dynamically in response to environmental and biotic influences. The proportions of seed in the various pools, and the environmental cues which cause a flux between pools, are life history characteristics of individual species. Figure 1.3 identifies the pools and illustrates the dynamic nature of the seed bank as hypothesized by Harper (1977). Very little is known regarding the dynamics of wild rice in the seed bank.

1.2.3.2 Germination

The life cycle of the wild rice plant continues in the spring at the time of ice-breakup with the germination of seed which has lost dormancy through afterripening. For the purposes of this thesis, germination is defined as the emergence of the coleoptile through the pericarp. It is important that juvenile events such as early growth of the coleoptile not be confused with germination sensu stricto (Come and Thevenot, 1982) as the environmental requirements and responses to stimuli are quite different between germination of the seed and early growth of the wild rice plant (Svare, 1960).

In laboratory conditions, wild rice germination is optimal at a constant temperature of 20°C and is enhanced by fluctuating temperatures (Simpson, 1966). Simpson tested the percent germination and rate of germination of wild rice seed

Figure 1.3: Conceptual model of the seed bank (after Harper, 1977).


SEED RAIN
GERMINATION
Active
Seed
Bank
STIMULI
PREDATION
Dormant
Seed
Bank
DECAY and SENESCENCE

in three constant temperature regimes: 15, 20, and 30°C; and in one fluctuating temperature regime: 15/30°C. Germination rate was highest in the fluctuating temperature regime followed by 20>15>30°C. Percent germination was also highest in the fluctuating temperature regime but the order of constant temperature treatments differed: 15>20>30°C.

The dissolved oxygen concentration of the water surrounding the seed also influences germination. Svare (1960), found that the percent germination of fully afterripened wild rice seed was inversely related to dissolved oxygen concentration. He considered this to be an adaptation to the anaerobic conditions found in the sediments of most lakes in which wild rice grows. Campiranon and Koukkari (1977), however, found no influence of dissolved oxygen concentration on germination in an experiment involving seed of Zizania aquatica L. which was insufficiently afterripened to germinate without scraping the pericarp from the embryo area. The difference between the results of Campiranon and Koukkari (1977) and the results of Svare (1960) may be due to either a difference in species tested or the dormancy state of the seed tested. Svare's conclusion that wild rice seed germination is adapted to low dissolved oxygen concentration seems likely in light of the natural habitat of wild rice.

Simpson (1966) found no change in the germination behaviour of wild rice seed over a range of water pH from 6.0 to 8.7, nor did he find an effect of gibberellic acid over a

wide range of concentrations. Oelke and Albrecht (1980), however, did find that gibberellic acid enhanced the germination of Zizania aquatica seed from which the seed coat had been partially removed. Again, differences in species or in dormancy states may account for observed differences in germination response.

1.2.3.3 Submerged leaf phenophase

Following germination, the coleoptile emerges at the sediment:water interface and the submerged leaf phenophase begins. The number of submerged leaves produced by an individual plant varies but is usually between one and four with a greater number of leaves being produced in deeper water (Thomas and Stewart, 1969).

Photosynthetically active radiation during the submerged leaf phenophase was identified by Lee and Stewart (1984) as being one of the factors possibly controlling the productivity of a wild rice stand. They found that lakes with a high coefficient of light extinction supported less productive wild rice stands than lakes with more transparent waters.

In contrast to germination, the shoot and root growth of the seedling are impaired by low dissolved oxygen concentrations. At oxygen levels below approximately 5ppm, root and shoot growth are markedly reduced and shoot chlorophyll content lowered (Svare, 1960). Campiranon and Koukkari (1977) showed that the activity of alcohol dehydrogenase, an enzyme active in alcoholic fermentation, increased in young wild

rice plants subjected to anaerobic conditions suggesting that fermentation reactions provide the energy for growth under anaerobic conditions. Sustained anaerobic conditions, however, led to the loss of plant viability.

The data of Campiranon and Koukkari (1977) show that shoot growth is proportionately higher than root growth under conditions of lower oxygen availability. Jenks (1899) and Moyle (1944) both noted an approximate four year periodicity in wild rice production. It is possible that the cyclic nature of wild rice production may, in part, be attributable to the effects of low dissolved oxygen on wild rice plant growth following bumper years in which a large volume of straw is produced. Decomposing straw would greatly increase biological oxygen demand and reduce dissolved oxygen concentrations resulting in weakly rooted submerged leaf plants.

1.2.3.4 Floating leaf phenophase

In a controlled experiment, Rogosin (1958), demonstrated that water depth increases during the submerged leaf and floating leaf phenophases induced stresses that were manifested at maturity in reduced plant weight and reduced seed production.

Thomas and Stewart (1969) showed that the floating leaf phenophase is a period of proportionally high allocation of growth resources to the shoot. During this stage the ratio of photosynthetic leaf area to total plant dry weight is at a peak (Thomas and Stewart, 1969). The allocation of re-

sources between photosynthetic and non-photosynthetic tissues was found by Thomas and Stewart (1969) to be highly susceptible to changes in water depth leading them to conclude that environmental conditions during the floating leaf phenophase have an important bearing on subsequent growth and development.

1.2.3.5 Aerial leaf phenophase

Much of the ecology of wild rice is deduced from observations on the distribution and performance of aerial leaf and flowering phenophase plants in the field. Moyle (1944) assessed the chemical and physical environments of 14 stands of wild rice in Minnesota and drew conclusions regarding the habitat requirements of wild rice. From his study Moyle concluded that wild rice growth was reduced in waters with greater than 10ppm sulphate and that wild rice performance in Minnesota was controlled by water chemistry.

Lee and Stewart (1984) seeded 32 lakes in northwestern Ontario after identifying them as being potentially productive from an aerial survey. By monitoring subsequent wild rice performance and relating performance to the environmental characteristics of each lake they concluded that in the area studied, sediment texture and phosphorous availability played a major role in controlling wild rice plant performance. Garrod (1984) found plant performance to be highly correlated with the sediment phosphorous concentrations of the stands he studied in southern Ontario.

Nitrogen may also be a limiting nutrient in wild rice ecosystems. Sain (1984) found that over 80% of the nitrogen in wild rice straw had not been released by the beginning of the jointing stage of the next years crop. The high nutrient demands of the wild rice plant at this stage of growth have been shown by Grava and Raisanen (1978). The binding of nitrogen by straw may have an influence on the cyclical nature of wild rice production noted by Moyle (1944) since the amount of straw produced in one year would directly influence the availability of nitrogen for wild rice growth the following year.

Sediment micronutrient status has also been shown to be important in controlling the productivity of wild rice stands. Peden (1982) empirically deduced the importance of micronutrients in controlling wild rice productivity in northern Saskatchewan. Sediment micronutrient concentrations were found by Garrod (1984) to be correlated with the productivity of wild rice stands in southern Ontario.

Rogosin (1958) investigated the effects of sediment nutrition and plant density on the performance of wild rice. Increased plant density had inconsistent effects on the survival rate but consistently resulted in reduced individual plant weights and less tillering. Increasing sediment nutrition through fertilization with nitrogen, phosphorous, and potassium increased survivorship, mean plant weight, and tillering.

1.2.3.6 Competition

Wild rice co-exists in mixed stands with many other species. Moyle (1944) lists Najas flexilis (Willd.) Rostk. & Schmidt., Ceratophyllum demersum L., Lemna minor L., Utricularia macrorhiza B., and Potamogeton zosteriformis G., as being the species most commonly found in mixed stands with wild rice in Minnesota. Moyle (1944), however, did not speculate on the influence of interspecific competition in determining wild rice performance.

A large number of species were documented by Atkins (1985) as co-existing with wild rice. These species noted in the order of their abundance were: Nymphaea odorata Ait., Ceratophyllum demersum L., Potamogeton sp, Vallisneria americana Michx., Scirpus sp, Sagittaria sp, Megalodonta beckii (Torr.) Green, Elodea canadensis Michx., Nuphar advena Ait., Utricularia vulgaris L. Atkins (1984) illustrated the competitive exclusion of wild rice from high sediment nutrient sites by Ceratophyllum demersum and interspecific competition was thought by Lee and Stewart (1984) to control the productivity of wild rice in at least one stand they examined, though they do not mention what species were present.

1.2.3.7 Predation and pathology

Much of the early attention given to wild rice was for its use in the management of waterfowl. Stoddard (1950) for example discusses the creation of wild rice habitat to attract waterfowl. Wildlife is also thought to have an effect on

the commercial production of wild rice. Moulton (1979) discusses control measures for blackbirds in wild rice paddies and feels that they are responsible for large losses in these conditions. While blackbirds are known to inhabit areas where the lake production of wild rice occurs their impact is unknown. Coulter (1957) found that wood ducks eat wild rice almost to the exclusion of all other foods when it is available. In a waterfowl survey (Peden, 1977) 93% of the birds were observed in wild rice areas. No estimates of crop loss to waterfowl are available but given the populations involved, potential losses may be substantial. Emerson (1960) also lists muskrat as causing losses in wild rice production. The larvae of the wild rice worm (Apamea) are also known to consume wild rice but no quantitative estimates of loss are available.

The role of pathogens in the loss of seed viability associated with the overwintering of seed is unknown (Percich et al, 1986).

A survey of lakes in Manitoba by McQueen (1981) revealed that five diseases had widespread occurrence in lakes; but, in most cases probably did not seriously reduce the production of seed. McQueen stressed the need for further studies to correlate crop loss with disease incidence and severity.

Chapter II

THE GERMINATION BEHAVIOUR OF WILD RICE SEED IN RESPONSE TO AFTERRIPENING PERIOD AND DIURNAL TEMPERATURE REGIME

2.1 INTRODUCTION

As an annual plant, wild rice depends totally upon seed buried in the sediments for stand re-establishment. The year to year fluctuation in seed production, and hence in seed supply for stand re-establishment, was noted by Jenks (1899) and Moyle (1944). Moyle suggested that even in years of seed crop failure sufficient seed is produced to maintain the continuity of a stand. Steeves (1952), however, noted the re-establishment of a wild rice stand following a year of complete seed crop failure. He concluded that stand establishment had come about through seed which had persisted ungerminated in the sediments for at least 18 months.

The persistence of ungerminated viable seed in the seed bank has been noted in many other species and in many diverse ecosystems (Freedman et al, 1982; Granstrom, 1982; van der Valk and Davis, 1978). An understanding of the behaviour of seeds in the marsh seed bank is considered vital to understanding the dynamics of marsh vegetation (van der Valk and Davis, 1978). This behaviour can include:

1. a requirement for afterripening to break dormancy (Simpson, 1966; Come and Thevenot, 1982),
2. the induction of secondary dormancy (Totterdell and Roberts, 1979),
3. an enhancement of germination through diurnally fluctuating temperatures (Simpson, 1966; Totterdell and Roberts, 1980), and
4. a requirement for, or enhancement by, exposure to light for germination (Thompson and Grime, 1983; Come and Thevenot, 1982).

The germination of seeds in response to environmental factors follows a pattern similar to that of any plant process: A minimum or threshold level of the factor is required before a response is effected; an optimum level of the factor exists beyond which increasing levels of the environmental factor degrade the response; and finally, a maximum level exists above which the response is suppressed completely. Environmental factors known to affect germination include: temperature (Baskin and Baskin, 1979; Totterdell and Roberts, 1980), oxygen (Svare, 1960; Come and Thevenot, 1982), and light (Thompson and Grime, 1983).

Temperature has been shown to be a major controlling factor in the germination of wild rice seed (Simpson, 1966). However, the cardinal temperatures (the minimum, optimum, and maximum) for wild rice germination have not been reported. Neither is it known if the cardinal temperatures change

over time with increased afterripening as has been reported in other species (Karssen, 1982). The role of temperature in the persistence of wild rice in the seed bank is also unknown.

The study reported here was undertaken to: determine the cardinal temperatures of wild rice germination; investigate if the cardinal temperatures change with increased length of afterripening period; and to elucidate the fate of seeds which failed to germinate during the laboratory experiments. It was thought that investigation of those seeds failing to germinate would shed light on the pathways by which wild rice seed persists in the seed bank.

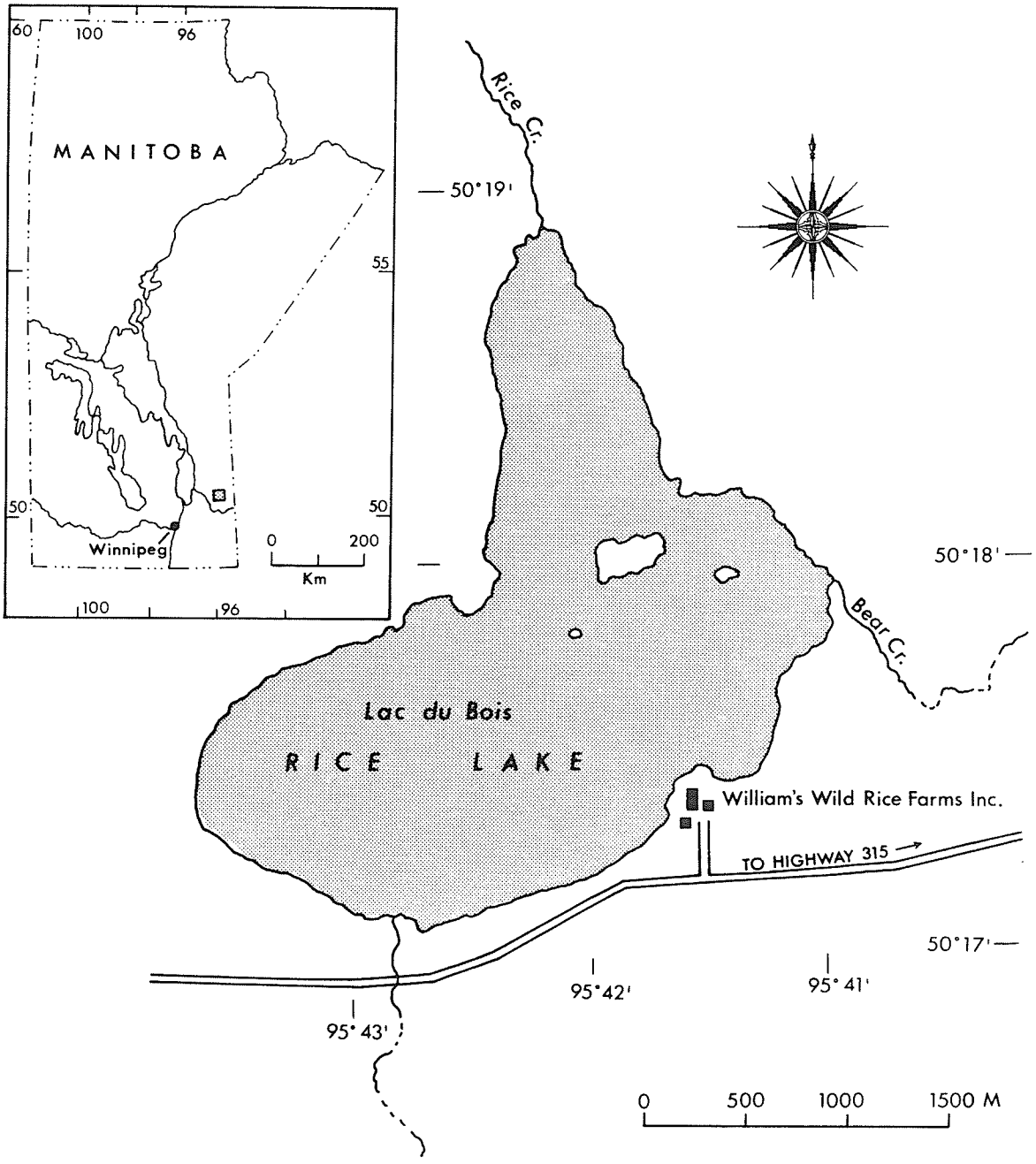
2.2 METHODS

2.2.1 Laboratory Procedures

Wild rice seed was collected from the tray of a mechanical harvester in late August of 1983 at Lac du Bois (50°17'N;95°42'W); 160 km northeast of Winnipeg, Manitoba (Fig. 2.1). Empty hulls were removed through flotation and the seed stored for one week in lake water at ambient room temperature and aerated with 10 psi air forced through an air-stone; then, afterripened in the dark without aeration at 5°C.

Germination behaviour was tested following three periods of afterripening: 5 months, 6 months, and 7½ months. The period from seed dispersal until ice-breakup in the Spring at Lac du Bois is approximately 7½ months. During this

Figure 2.1: Location of Lac du Bois (Rice Lake) in Manitoba.


60
100
96
MANITOBA
55
50
50
Winnipeg
0
200
Km
100
96
Rice Cr.
— 50°19'
50°18' —
Bear Cr.
Lac du Bois
RICE LAKE
William's Wild Rice Farms Inc.
TO HIGHWAY 315
50°17' —
95°42'
95°41'
95°43'
0
500
1000
1500 M

period ice cover persists for about 5 months (Williams, pers comm).

The germination tests were carried out using a 100 cell germinator described by McLaughlin et al (1985) and illustrated in Figure 2.2. The germinator provides 100 independently controlled combinations of 10 peak day and 10 peak night temperatures from 0°C to 45°C in steps of 5°C. A 12 hour light and 12 hour dark photoperiod was used.

Each of the 100 treatments for each afterripening period consisted of a 9 cm glass Petri dish containing 30 seeds and 75ml of distilled water. Germinated seed was counted and removed every two to three days for one month. Germination was defined as the emergence of the coleoptile through the pericarp. Subsequent growth of the coleoptile was excluded from the definition of germination to ensure separation of the effects of environment on germination from effects on early plant growth. The requirements of these two phases have been shown to be distinctly different in wild rice (Svare, 1960).

The causes for non-germination of seed during the one month in the 100 cell germinator were investigated by observing subsequent germination behaviour as follows. All seed which remained ungerminated in the 100 cell germinator was transferred for 1 month to a conventional growth chamber set to 35/15°C (8 hours light/ 16 hours dark) in what were thought to be near-optimal conditions for germination from the preceding experience with the 100 cell germinator. The

Figure 2.2: System used to test germination response to diurnal temperature regime.

Plate - overhead view of a Petri plate with seeds set into a cell of the 100 cell germinator.

Inset - the 100 cell germinator.

100 temperature regimes of the 100 cell germinator can be considered as "pre-treatments". Under a hypothesis that seeds failed to germinate in the "pre-treatments" simply due to sub-optimal conditions (ie too cold), the sum of germination observed in the 100 cell germinator and in the near-optimal conditions should be the same for all "pre-treatments". If the "pre-treatment" influenced the ability of the seeds to subsequently germinate in the near-optimal conditions - either through mortality or the induction of secondary dormancy - then the sum of germination observed in the 100 cell germinator and in the near-optimal conditions will differ with "pre-treatment".

Seed which remained ungerminated following the 1 month in the conventional growth chamber was tested for viability using a .25% tetrazolium solution following the procedure of Simpson (1966). Only seed afterripened 5 and 6 months was tested for viability.

2.2.2 Analysis Procedures

The percent germination data from the 100 cell germinator tests for each of the three afterripening periods were graphed in a 3-dimensional co-ordinate system. Peak day and peak night temperatures formed the base co-ordinates and percent germination the height above the base.

The germination rate of each treatment was determined by graphing the cumulative percentage of seeds germinating over time and estimating the number of days to reach 50% germina-

tion. Germination rate was then expressed as the inverse of time to 50% germination. This measure has the advantage over the simpler time to 50% germination of having a natural zero point and an increasing magnitude with increasing rapidity of germination.

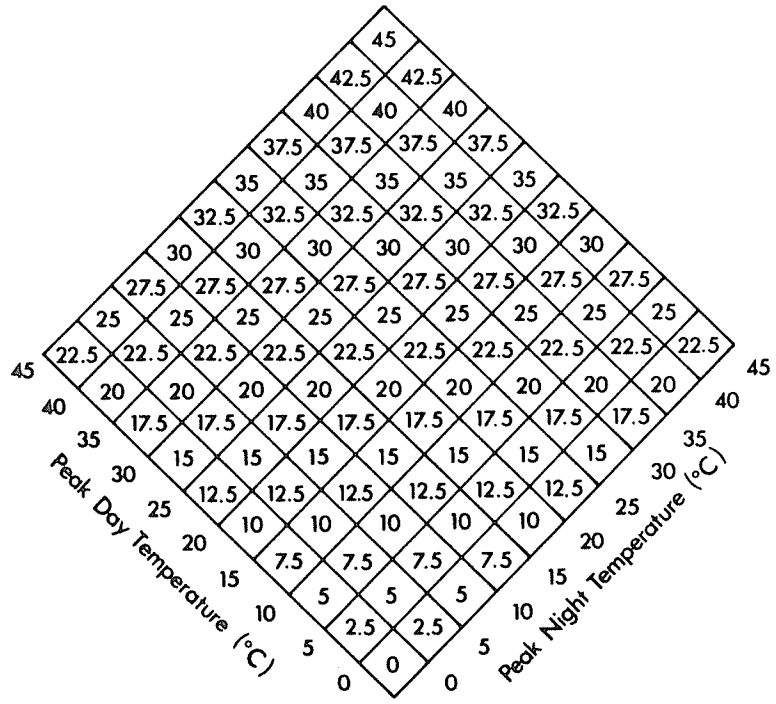
Germination rate was graphed in a co-ordinate system similar to that used for percent germination.

The grid of peak day and peak night temperatures forming the base of the 3-dimensional co-ordinate system has several characteristics of interest. The mean daily temperature of each temperature combination can be calculated by averaging the peak day temperature and the peak night temperature. All temperature combinations in the grid on a common horizontal line have a common mean daily temperature (Fig. 2.3). The mean daily temperature increases from 0°C at the front of the grid to 45°C at the rear.

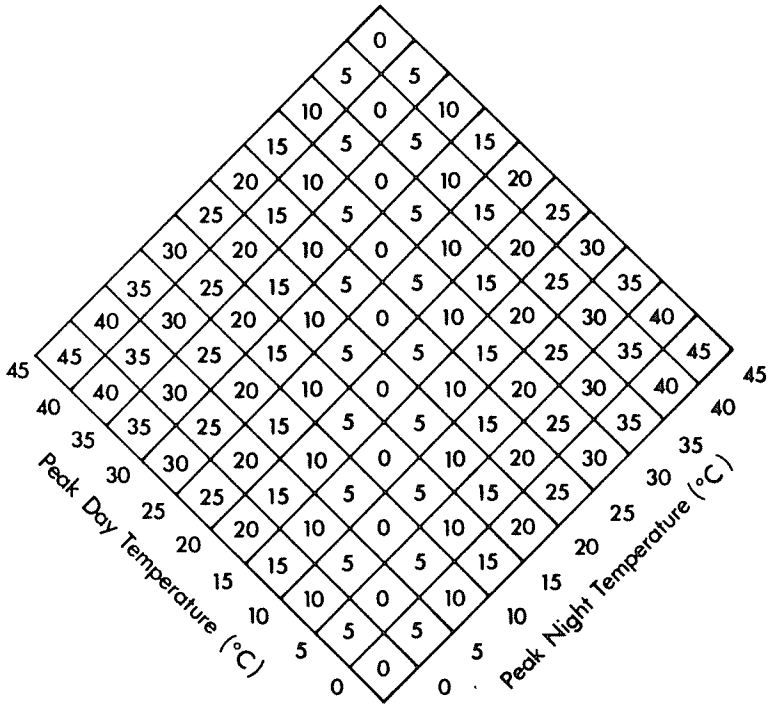
The magnitude of the daily temperature fluctuation of a treatment is calculated as the absolute value of the difference between the peak day and peak night temperatures. Constant temperature treatments (peak day and peak night temperatures equal) lie along the vertical diagonal of the grid which forms the base of the co-ordinate system (Fig. 2.3). Vertical rows of treatments on the grid all have a common daily temperature fluctuation. The magnitude of fluctuation increases with distance from the vertical diagonal to a maximum fluctuation of 45°C at the two outer corners.

Figure 2.3: Spatial relationships of mean daily temperature and magnitude of daily temperature fluctuation on base grid used to present data from 100 cell germinator.

MEAN DAILY TEMPERATURE



DAILY TEMPERATURE FLUCTUATION



As well as the vertical and horizontal relationships described, a symmetry exists in the grid across the vertical diagonal - treatments reflected across the vertical diagonal are "isothermal"; that is, they have the same peak high and peak low temperatures. For example, the 15°C peak day/30°C peak night temperature treatment and the 30°C peak day/15°C peak night temperature treatment are isothermal.

Percent germination and germination rate data were also graphed as a function of mean daily temperature. Because of high temperature suppression of germination, the data from treatments with peak day or night temperatures of 45°C were excluded since they occur only in treatments with mean daily temperature in excess of 20°C and disproportionately "down-weight" the marginal response.

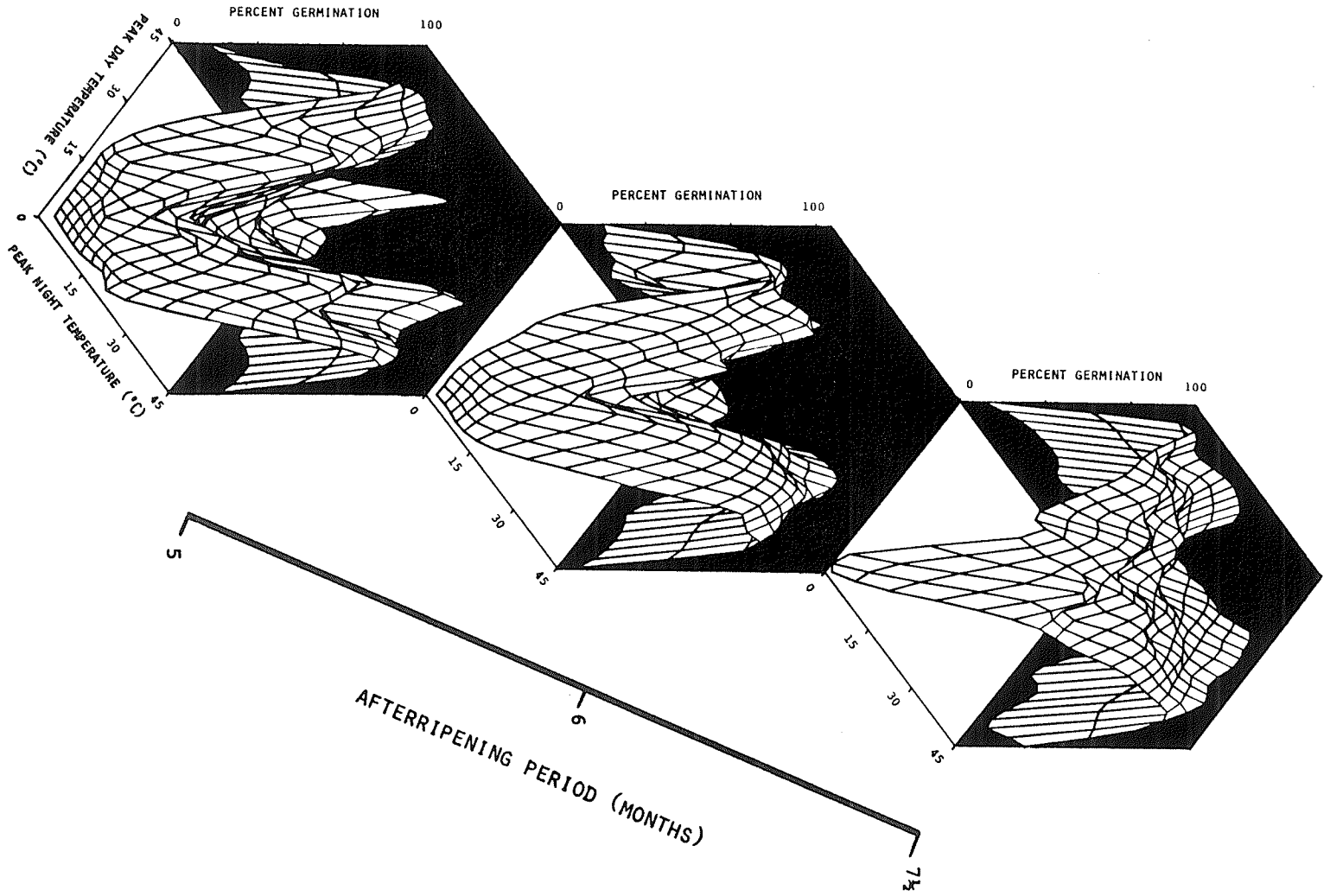
All graphs were produced using the SAS/GRAPH package (SAS Inst., 1981) on the University of Manitoba Amdahl mainframe computer. Procedure G3GRID using spline interpolation was used in conjunction with procedure G3D to produce the 3-dimensional graphs.

2.3 RESULTS

2.3.1 Percent Germination And Germination Rate Of Seed Afterripened 5 Months

The percent germination of wild rice seed afterripened 5 months was a function of the magnitude of daily temperature fluctuation, mean daily temperature, and an intolerance to peak temperatures in excess of 40°C (Fig. 2.4). The symme-

Figure 2.4: Percent germination of wild rice seed afterripened 5, 6, and 7½ months in response to diurnally fluctuating temperatures.


PERCENT GERMINATION
0
100
PEAK DAY TEMPERATURE (°C)
0
15
30
45
PEAK NIGHT TEMPERATURE (°C)
0
15
30
45
PERCENT GERMINATION
0
100
0
15
30
45
PERCENT GERMINATION
0
100
0
15
30
45
5
6
7½
AFTERRIPENING PERIOD (MONTHS)

try of Figure 2.4 (the response surfaces can be reflected across the vertical diagonal of the base grid) also indicates that percent germination is independent of the timing of peak temperatures in relation to the light/dark cycle. A paired t-test of the isothermal treatments confirmed this (mean difference=2.9%; pr(>|t|=.19)).

Virtually no germination occurred with seed subjected to constant temperatures. With a greater magnitude of daily temperature fluctuation the percentage of seeds which germinated increased subject to high peak day or night temperatures (Fig. 2.4). The "shoulders' which are evident in Figure 2.4 result from markedly reduced percent germination when peak temperatures were in excess of 40°C.

Percent germination was also a function of mean daily temperature. Germination was negligible in mean daily temperatures of less than 12.5°C; although, some germination occurred at mean daily temperatures as low as 5°C (Fig. 2.5). Mean daily temperatures of 17.5-22.5°C were optimal for percent germination.

The rate of germination was affected by mean daily temperature, magnitude of daily temperature fluctuation and an intolerance to high temperatures (Fig. 2.6) similar to the response pattern of percent germination (Fig. 2.4). Increased germination rate was associated with a greater magnitude of daily temperature fluctuation up to peak temperatures of 35°C (Fig. 2.6) indicating that germination rate was more sensitive to high temperatures than percent germination.

Figure 2.5: Percent germination of wild rice seed afterripened 5, 6, and 7½ months as a function of mean daily temperature.

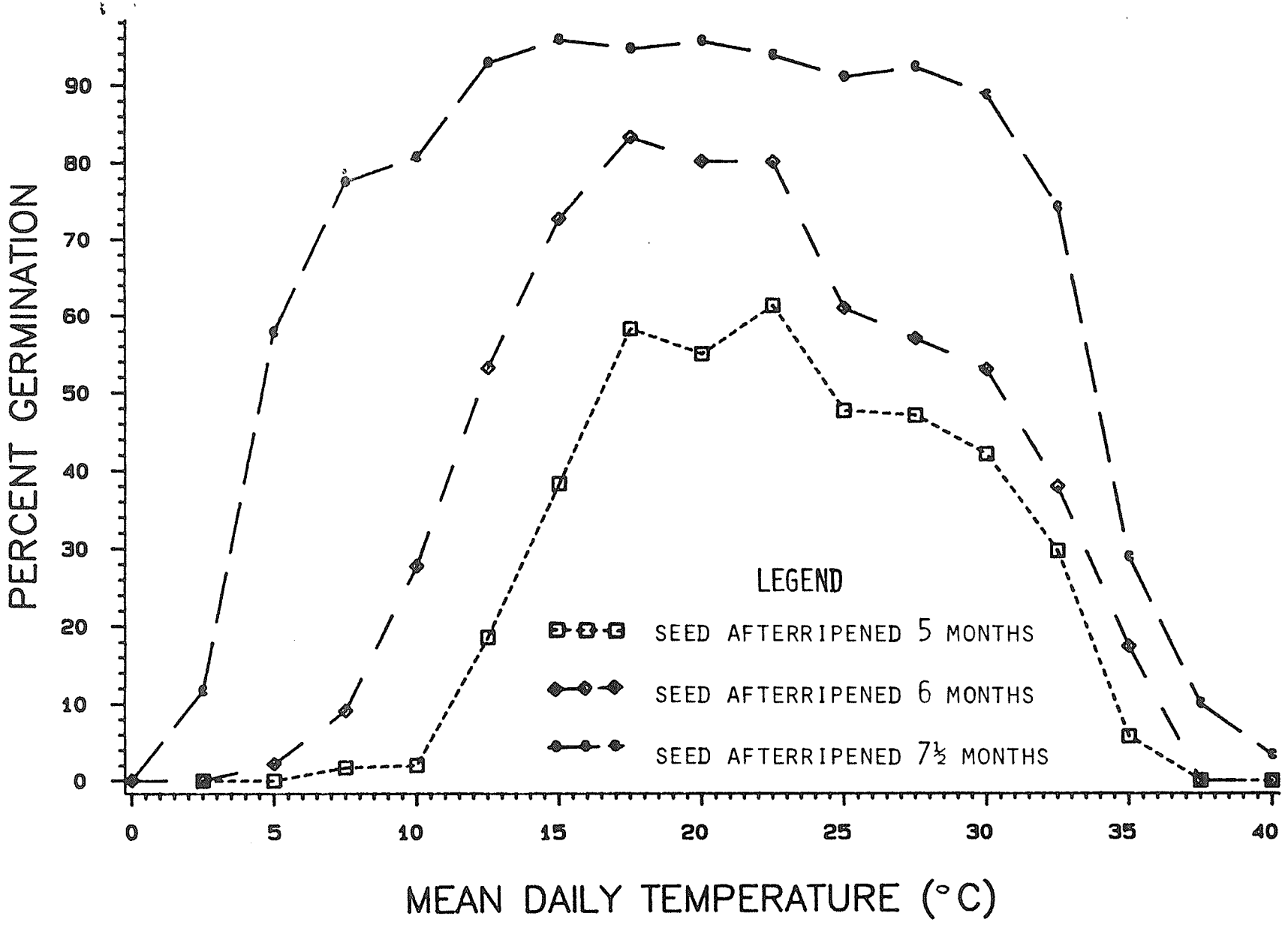
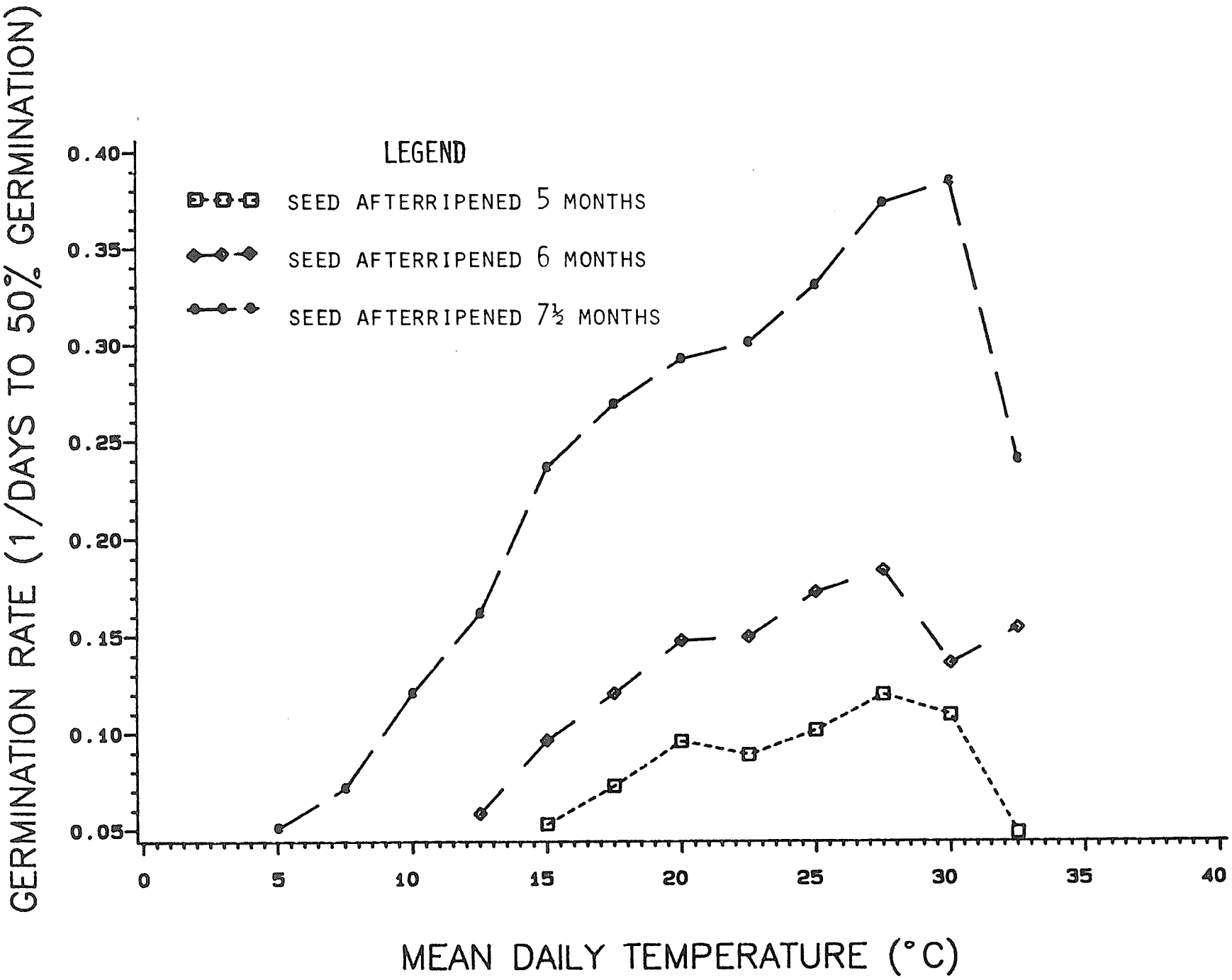
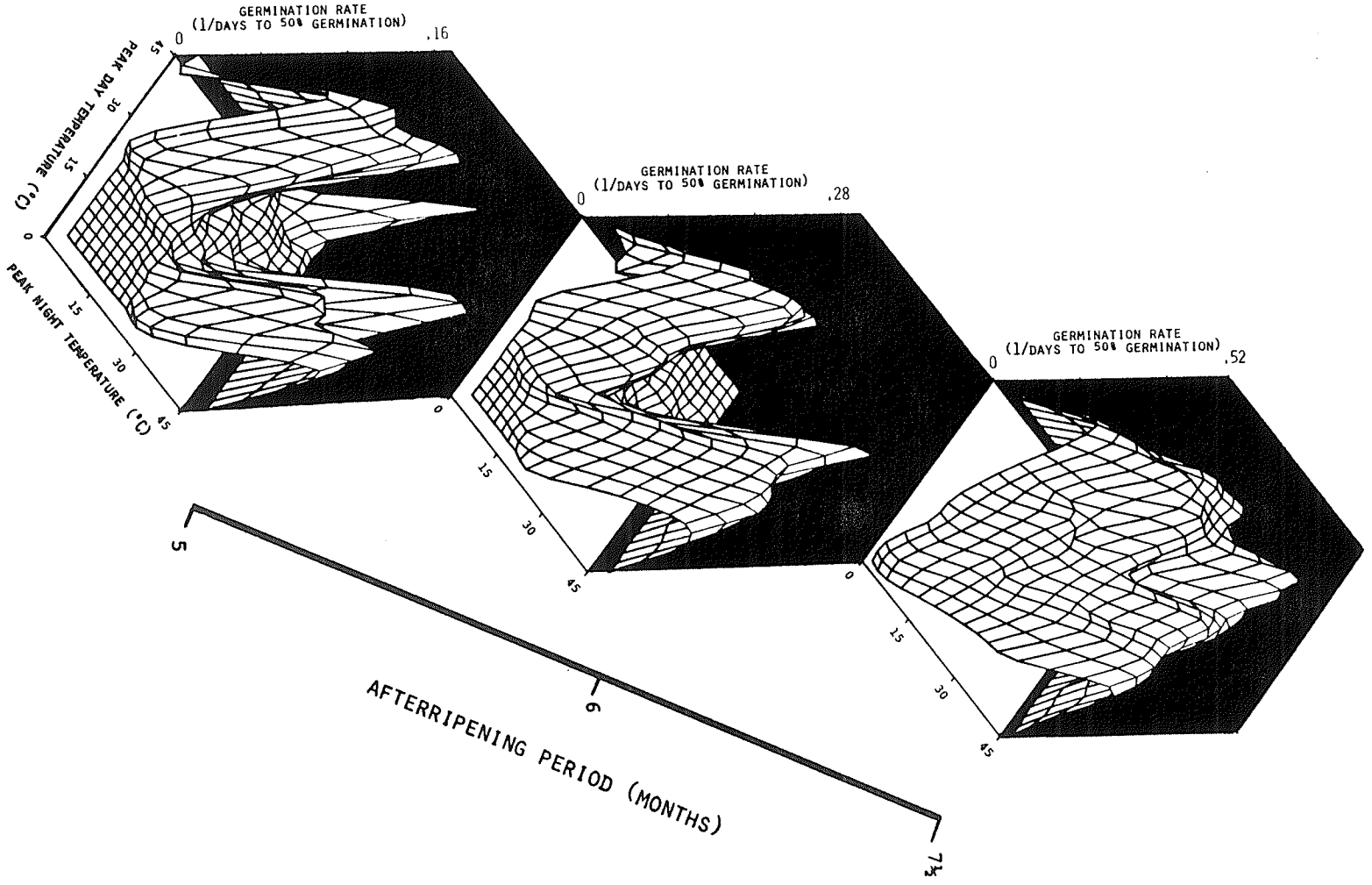

PERCENT GERMINATION
0
10
20
30
40
50
60
70
80
90
0
5
10
15
20
25
30
35
40
MEAN DAILY TEMPERATURE (°C)
LEGEND
SEED AFTERRIPENED 5 MONTHS
SEED AFTERRIPENED 6 MONTHS
SEED AFTERRIPENED 7½ MONTHS

Figure 2.6: The rate of germination of wild rice seed afterripened 5, 6, and 7½ months in response to diurnally fluctuating temperatures.


LEGEND
SEED AFTERRIPENED 5 MONTHS
SEED AFTERRIPENED 6 MONTHS
SEED AFTERRIPENED 7½ MONTHS
GERMINATION RATE (1/DAYS TO 50% GERMINATION)
0.40
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0
5
10
15
20
25
30
35
40
MEAN DAILY TEMPERATURE (°C)

Germination rate was also a function of mean daily temperature (Fig. 2.7). The optimum mean daily temperature for germination rate was 27.5°C at which 50% germination occurred in 8 days. Mean daily temperatures higher than 30°C resulted in a markedly reduced germination rate (Fig 2.7).

Figure 2.7: The germination rate of wild rice seed afterripened 5, 6, and 7½ months as a function of mean daily temperature.


GERMINATION RATE
(1/DAYS TO 50% GERMINATION)
0
.16
PEAK DAY TEMPERATURE (°C)
0
15
30
45
PEAK NIGHT TEMPERATURE (°C)
0
15
30
45
GERMINATION RATE
(1/DAYS TO 50% GERMINATION)
0
.28
0
15
30
45
GERMINATION RATE
(1/DAYS TO 50% GERMINATION)
0
.52
0
15
30
45
5
6
7½
AFTERRIPENING PERIOD (MONTHS)

2.3.2 Percent Germination And Germination Rate Of Seed Afterripened 6 Months

Wild rice seed afterripened for 6 months exhibited a similar pattern of percent germination and germination rate in response to temperature as seed afterripened 5 months (Fig. 2.4). However, the increased afterripening period resulted in a broadening of the germination peaks. Some germination occurred in constant temperature treatments in contrast to the seed afterripened 5 months which showed no germination in constant temperature treatments (Fig 2.4).

A paired t-test of the isothermal treatments showed that germination was on average slightly higher in the treatments that had peak high temperatures at night (mean difference=6.9%; pr(>|t|=.002)).

The minimum mean daily temperature for germination (Fig. 2.5) decreased to 5°C and the range of mean daily temperatures in which at least 50% germination occurred increased to 12.5-30°C. Percent germination was again optimal at mean daily temperatures of 17.5-22.5°C. The maximum mean daily temperature in which germination occurred was again 35°C (Fig. 2.5). Peak day or night temperatures in excess of 40°C markedly reduced percent germination (Fig. 2.4).

The germination rate of seed afterripened 6 months followed the same trends as seed afterripened 5 months (Fig. 2.6). The broader, higher peaks indicate an overall higher germination rate with the extra month of afterripening. The optimum mean daily temperature for germination rate was, again, 27.5°C (Fig. 2.7).

2.3.3 Percent Germination And Germination Rate Of Seed Afterripened 7½ Months

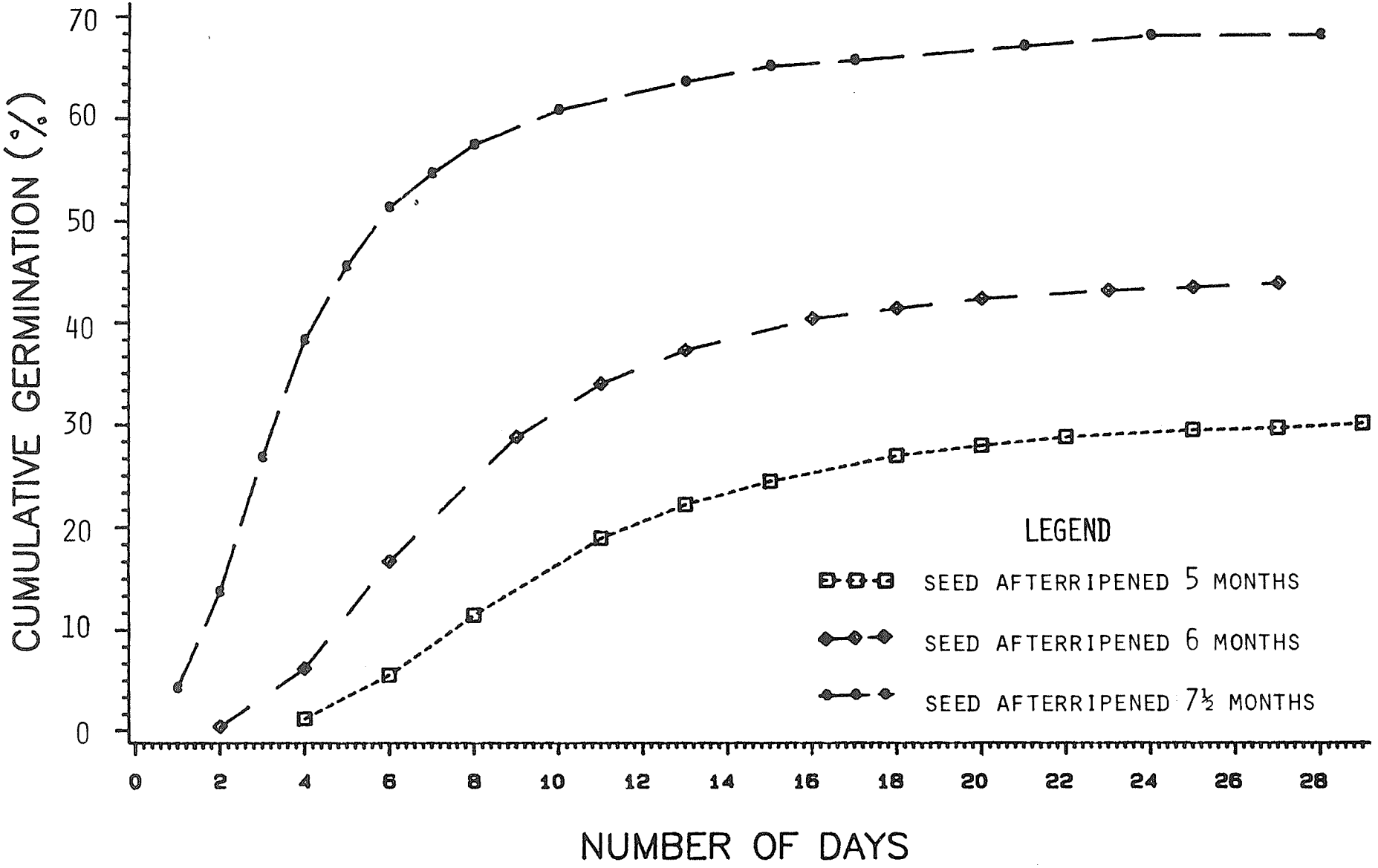
The pattern of percent germination of wild rice seed afterripened for 7½ months was different from that of seed afterripened only 5 or 6 months. Percent germination was mainly a function of mean daily temperature and an intolerance of high peak day or night temperature (Fig. 2.4). The effect of diurnally fluctuating temperatures on percent germination was markedly reduced when the seed had been afterripened for 7½ months (Fig. 2.4). A paired t-test of the isothermal treatments showed no difference in percent germination associated with the timing of the light/dark cycle (mean difference=0.4%; pr(>|t|=.78)).

Germination occurred in mean daily temperatures as low as 2.5°C (Fig. 2.5) with an optimum mean daily temperature for percent germination between 12.5°C and 30°C. The range of mean daily temperatures in which at least 50% germination occurred was 5-32.5°C (Fig. 2.5). The maximum mean daily temperature in which germination occurred was 40°C.

The effect of fluctuating temperature on germination rate was also markedly reduced with seed afterripened 7½ months (Fig. 2.6). Germination rates at all temperatures were greatly increased with the lengthened afterripening period and were a function of mean daily temperature (Figs. 2.6 and 2.7). The optimum mean daily temperature for germination rate was 27.5°C (Fig. 2.7).

The overall increase in percent germination with increased afterripening period is illustrated by plotting the cumulative germination in all of the 100 treatments against time (Fig. 2.8). Percent germination over the 100 treatments increased from 29% with 5 months of afterripening to 42% with 6 months of afterripening, to 66% with 7½ months of afterripening. The steeper initial slope indicates an increased rate of germination with increased afterripening period (Fig. 2.8).

Figure 2.8: The effect of length of afterripening period on cumulative germination in the 100 cell germinator. (Sum of daily germination occurring in the 100 cell germinator).


CUMULATIVE GERMINATION (%)
70
60
50
40
30
20
10
0
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
NUMBER OF DAYS
LEGEND
SEED AFTERRIPENED 5 MONTHS
SEED AFTERRIPENED 6 MONTHS
SEED AFTERRIPENED 7½ MONTHS

2.3.4 Germination Behaviour Of Seed Remaining Ungerminated Following One Month Of Testing In The 100 Cell Germinator

Germination in the conventional growth chamber was a function of the length of afterripening period and of the "pre-treatment" they had received in the 100 cell germinator (Fig. 2.9). Seed which had previously been exposed to mean daily temperatures in excess of 10°C showed little or no further germination when transferred to the conventional growth chamber (Fig. 2.9). The proportion of seed from the cooler pre-treatments (mean daily temperature of 10°C or less) which germinated in the conventional growth chamber increased with increased afterripening period.

Total germination (the sum of germination in the 100 cell germinator and in the conventional growth chamber) as a function of mean daily temperature (Fig. 2.9) increased from 10-30% with 5 months of afterripening, to 38-45% with 6 months of afterripening, and to 80-90% with 7½ months of afterripening.

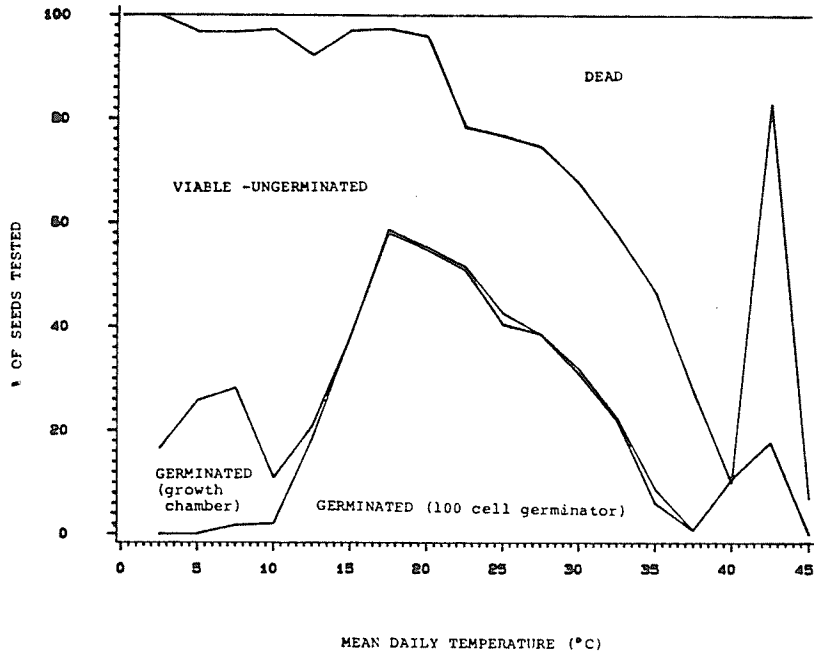
The proportion of the seed afterripened 5 and 6 months which died is shown in Figure 2.9. For both afterripening periods mortality was very similar with a trend of increasing mortality with increasing mean daily temperature (an exception was seed afterripened 5 months and subjected to a mean daily temperature of 42.5°C). With seed previously subjected to mean daily temperatures of 20°C, or less, mortality was generally less than 15%. Mortality increased to 90-95% at 40°C mean daily temperature.

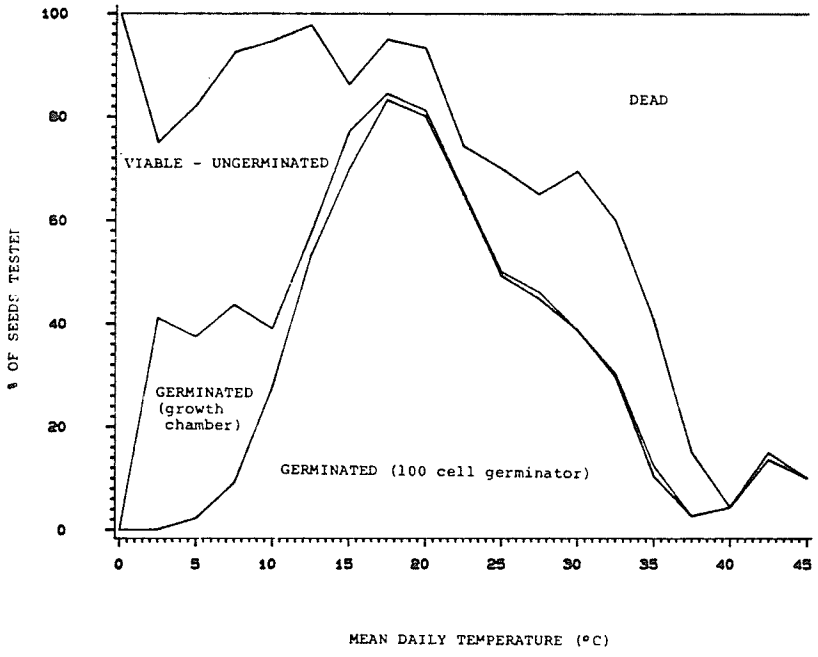
Figure 2.9: The fate of wild rice seed as a function of mean daily temperature and length of afterripening period.

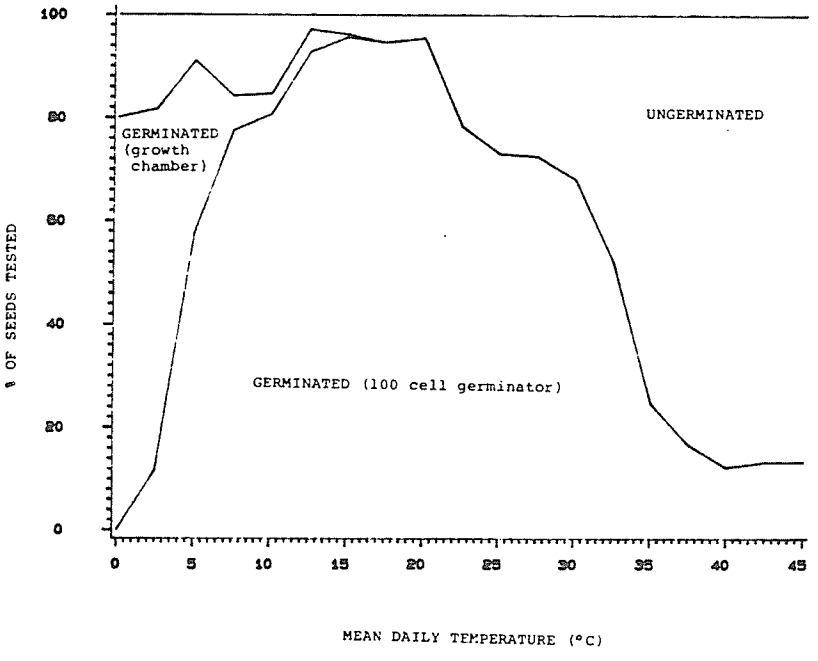
(a) Top - Seed afterripened 5 months.

(b) Middle - Seed afterripened 6 months.

(c) Bottom - Seed afterripened $7\frac{1}{2}$ months.


100
80
60
40
20
0
% OF SEEDS TESTED
DEAD
VIABLE -UNGERMINATED
GERMINATED (growth chamber)
GERMINATED (100 cell germinator)
0
5
10
15
20
25
30
35
40
45
MEAN DAILY TEMPERATURE (°C)


100
80
60
40
20
0
% OF SEEDS TESTED
DEAD
VIABLE - UNGERMINATED
GERMINATED (growth chamber)
GERMINATED (100 cell germinator)
0
5
10
15
20
25
30
35
40
45
MEAN DAILY TEMPERATURE (°C)


100
80
60
40
20
0
% OF SEEDS TESTED
UNGERMINATED
GERMINATED (growth chamber)
GERMINATED (100 cell germinator)
0
5
10
15
20
25
30
35
40
45
MEAN DAILY TEMPERATURE (°C)

The proportion of the seed population which remained viable but did not germinate in either the 100 cell germinator or in the conventional growth chamber ranged from 85% to 0% for both 5 and 6 months of afterripening. The proportion of the seed population which remained viable but ungerminated was a function of both afterripening period and of "pretreatment". This proportion decreased with an increase in afterripening period from 5 to 6 months and was greater at mean daily temperatures of less than 20°C.

2.4 DISCUSSION

The germination behaviour of wild rice changed significantly with increased length of afterripening period. Increased afterripening resulted in higher percent germination for the individual temperature treatments (Figs. 2.4 and 2.5) and an increase in the rate of germination (Figs. 2.6 and 2.7). It was also found that the need for fluctuating temperatures to induce germination was reduced as the length of afterripening period increased (Fig. 2.4). This increased germinability with increased afterripening period is consistent with the observations of Simpson (1966) and Oelke and Albrecht (1980) for wild rice and of Karssen (1982) for species in general with an afterripening requirement.

The enhancement of germination by exposure to fluctuating temperatures has been found in many marsh species by Thompson and Grime (1983) who suggested that fluctuating temperatures evolved as a trigger for germination in response to

the marsh thermal environment during the spring. In the case of wild rice it is more likely that a highly fluctuating temperature regime is a substitute for the usual requirement of afterripening to break primary dormancy (possibly through an effect on seed coat permeability) since the magnitude of temperature fluctuation required to break dormancy is large relative to the temperature fluctuations which occur in the sediments of natural wild rice stands.

For the seed used in this experiment, the cardinal temperatures were shown to be influenced by the length of afterripening period. Increasing the length of afterripening period from 5 to 7½ months reduced the minimum mean daily temperature in which germination occurred from 5°C to 2.5°C. The maximum mean daily temperature at which germination occurred increased with increased afterripening period from 37.5°C to 40°C. As well, the range of mean daily temperatures in which germination was optimal increased with the length of afterripening period from 17.5-22.5 °C to 12.5-32.5°C; but, consistently centred around 20°C. Changes in minimum and maximum temperatures associated with length of afterripening period have been reported in other species and are consistent with the concept that the "germination window" - the range of conditions in which germination occurs - widens with afterripening (Vegis, 1964).

Similarly, germination rate increased with increased afterripening period but the mean daily temperature at which germination rate was maximum remained relatively constant (27.5-32°C; Fig. 2.7).

Simpson (1966) reported the following order of treatments with respect to percent germination of wild rice seed in response to temperature: 15/35>15≥20>30°C; and with respect to germination rate: 15/35>20>15>30°C. The results of the experiment reported here do not differ significantly from those of Simpson except for one discrepancy in the rate of germination: 15/35>30>20>15°C. The seed tested by Simpson (1966) showed high-temperature reduction in germination rate at a lower temperature than the seed lot tested here (Figs. 2.6 and 2.7).

The minimum temperature at which germination occurred indicates that germination in the field may begin very soon after ice-breakup; and that some seeds may actually germinate before ice-breakup. These early plants may have a competitive edge over later developing plants in exploiting the environment.

The percent germination of seed afterripened 7½ months remained partially a function of the magnitude of daily temperature fluctuation as evidenced by the depression in percent germination at constant temperatures (Fig. 2.4). Germination was up to 20% higher in highly fluctuating temperatures than in constant temperatures even at the optimum mean daily temperatures. This would indicate that up to 20% of the seed population tested was insufficiently afterripened after 7½ months to germinate without temperature fluctuations greater than those normally found in natural wild rice stands. These seeds presumably require a second sea-

son of afterripening in order to germinate under natural conditions. Prolonged primary dormancy is one pathway by which wild rice seed could enter and persist in the seed bank.

The results of the conventional growth chamber tests with the seed which failed to germinate in the 100 cell germinator show that mortality was not affected by increased afterripening period from 5 to 6 months (Fig. 2.9). Mortality was negligible at mean daily temperatures of less than 20°C but increased greatly at mean daily temperatures above 20°C.

Total germination (the sum of germination occurring in the 100 cell germinator and in the conventional growth chamber) increased with afterripening period (Fig. 2.9). Since mortality rate was little affected by the length of afterripening period, the decrease in the proportion of seed remaining viable but ungerminated at the end of the tests can be attributed to the increased proportion of seeds which germinated.

Seeds remained ungerminated at the end of the tests either due to the induction of secondary dormancy or because the "near-optimal" conditions for testing were less than optimal and so did not result in the germination of all viable seed. Since no controls were included in the conventional growth chamber tests it is not possible to differentiate these reasons. The somewhat lower total germination at higher temperatures however suggests that secondary dormancy may be induced at temperatures above those optimal for germination.

Field observations on seedling emergence (Lee and Stewart, 1981; Atkins, 1983) indicate that very little or no germination occurs following a burst of germination in the spring, even though the sediments continue warming beyond this period towards those found to be optimal for germination. This suggests that secondary dormancy does occur under field conditions but at temperatures lower than in this laboratory experiment.

In terms of the seed bank, the results of this experiment indicate that wild rice will persist in the seed bank through unbroken primary dormancy and possibly through the induction of secondary dormancy. Under laboratory conditions it was found that approximately 20% of the seed lot tested remained viable and ungerminated due to unbroken primary dormancy even after 7½ months of afterripening. The induction of secondary dormancy would add seed to the seed bank in proportion to the sub-optimality of conditions for germination. The seed bank would buffer the impact of seed production fluctuations on subsequent stand establishment.

Chapter III

THE DYNAMICS OF WILD RICE IN THE SEED BANK

3.1 INTRODUCTION

The annual re-establishment of a wild rice stand occurs from seed in the seed bank. Moyle (1944) suggested that even in years of seed production failure, a minimal amount of seed was produced from which the stand would re-establish the following year. Steeves (1952), however, noted the re-establishment of stands following a year of complete seed production failure and attributed the re-establishment to seed which had persisted in the sediments for more than 18 months. Cardwell et al (1978) attributed the long-term survival of wild rice seed to seed coat impermeability.

The importance of the seed bank to the vegetation dynamics of a marsh has been noted by van der Valk and Davis (1978). Wild rice has not featured prominently in reports of the dynamics of natural seed banks; though, McDonald (1955) mentions an increase in the area and density of a stand of Zizania in response to a colonizing opportunity presented by a marsh die-off. Oelke et al (1983) have demonstrated that wild rice seed can persist in continuously flooded paddy conditions for up to six years.

Laboratory studies have shown that wild rice may persist in the seed bank due to unbroken primary dormancy and, tentatively, due to the induction of secondary dormancy (chapter 2). Primary dormancy is the state of innate dormancy in which all wild rice seed is dispersed in the fall. Secondary dormancy is a state of dormancy induced in some seed, which have broken primary dormancy, in response to environmental conditions adverse to germination.

The production of seed in wild rice stands is known to fluctuate widely from year to year (Jenks, 1899; Moyle, 1944; Steeves, 1952). Both Jenks (1899) and Moyle (1944) noted an approximate four year periodicity in wild rice seed production varying from crop failure to bumper crop. Given the widely fluctuating supply of seed from year to year and the potentially unstable environment in which wild rice grows, the persistence of wild rice seed in the seed bank is important to long term stand survival.

The dynamics of wild rice seed in the seed bank involves five interacting pools. These pools (Fig. 3.1) are defined as follows (after chapter 2):

1. Seeds insufficiently afterripened to break primary dormancy - further afterripening is required to overcome primary dormancy (Primary Dormancy Pool).
2. Seeds germinated. (Germinated Pool).
3. Seeds viable but conditions suboptimal for germination - seeds which if given better environmental con-

ditions are capable of germination (Suboptimal Conditions Pool).

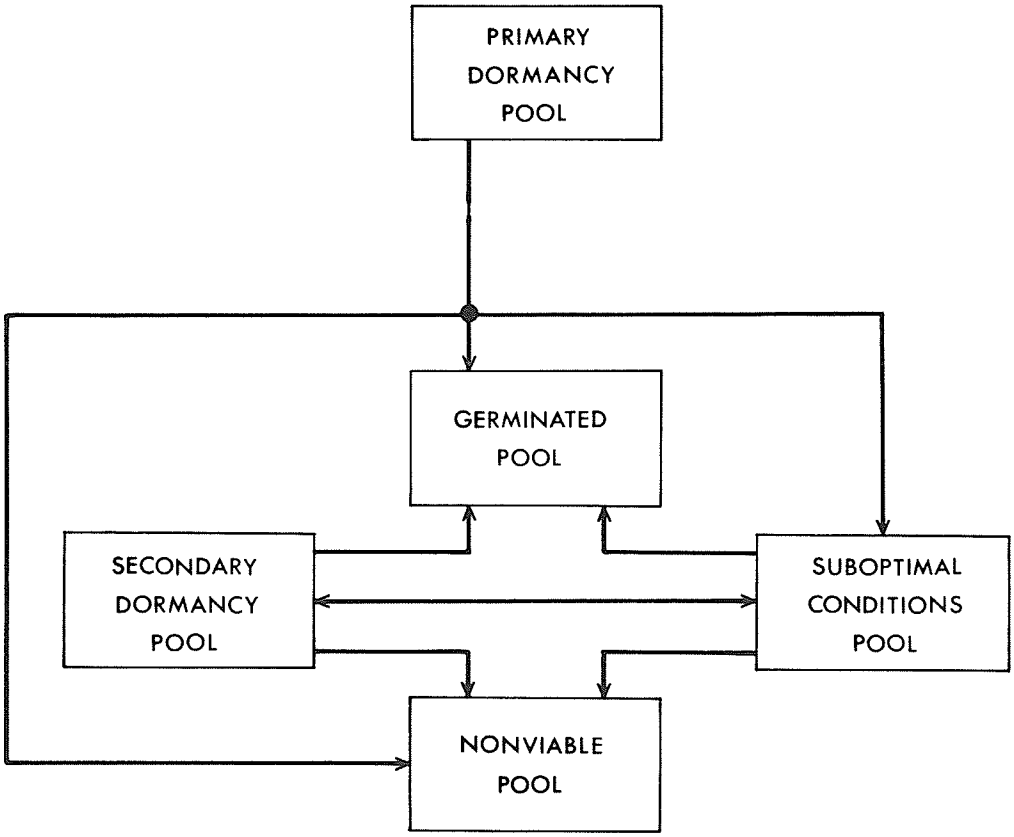
4. Seeds in environmentally induced secondary dormancy (Secondary Dormancy Pool).
5. Seeds not viable due to predation, decay, and senescence (Non-viable Pool).

These five pools collectively account for all wild rice seed in the seed bank. The amount of seed in each pool at any given time constitutes the "seed budget". The flux of seed between the interacting pools over time constitutes the dynamics of wild rice in the seed bank. The influence of environmental factors on these fluxes is unknown, though speculation has been made (Svare, 1960; Simpson, 1960; Cardwell et al, 1978; chapter 2).

The studies reported here were undertaken to investigate the dynamics of wild rice in the seed bank and to elucidate the role of temperature in these dynamics. Specifically, the following hypotheses were examined:

1. Prolonged primary dormancy is the major pathway leading to the persistence of wild rice in the seed bank. It was demonstrated in chapter 2 that under laboratory conditions a subset of the seed population requires more than one winter of afterripening and hypothesized that this was a pathway by which wild rice seed may persist in the seed bank.

Figure 3.1: A conceptual model of the dynamics of wild rice in the seed bank.


PRIMARY
DORMANCY
POOL
GERMINATED
POOL
SECONDARY
DORMANCY
POOL
SUBOPTIMAL
CONDITIONS
POOL
NONVIABLE
POOL

2. Secondary dormancy occurs in wild rice seed and is a pathway leading to the persistence of wild rice in the seed bank. It was postulated in chapter 2 that secondary dormancy can be induced in wild rice; however, it could not conclusively demonstrated.
3. The induction of secondary dormancy is temperature dependent. The induction of secondary dormancy has been shown in other species at temperatures unfavourable for germination (Karsson,1982; Totterdell and Roberts, 1979) and is hypothesized as a life-history strategy at temperatures unfavourable for seedling growth (Caswell, 1983).
4. The behaviour of wild rice seed in the seed bank will change with seed burial depth.
5. Changes in seed behaviour with burial depth are due to both differences in the environment during afterripening and to different environmental conditions with depth at the time of germination.

3.2 METHODS

3.2.1 Seed Source and Storage

All experiments described in this chapter were conducted using seed collected from the tray of a mechanical wild rice harvester at Lac du Bois (50°17'N; 95°42'W), 160km northeast of Winnipeg, Manitoba (Fig. 2.1). Empty hulls were removed by flotation and the seed stored in afterripening conditions of 5°C, unaerated, until required.

3.2.2 Experiment 1. The Dynamics Of Wild Rice Seed In The Seed Banks Of Two Natural Stands

Seed was removed from storage in mid-November and placed into nylon screen bags in batches of 50 seeds by weight. Six bags were stapled to each of 32 posts at predetermined intervals; such that, when the posts were sunk into the sediments though holes cut in the ice of Lac du Bois, the seed bags were buried at depths of 1cm, 5cm, and 10cm in the sediments (Figs. 3.2 and 3.3). Twenty cm of each post was left exposed above the sediments in order to prevent the posts from being displaced by ice and to aid in the collection of seed bags. The accuracy of seed burial depth in the sediments was found to be satisfactory during sampling the following summer. Two grids of 16 posts were set out at two sites in Lac du Bois (Fig. 3.2).

Three days after breakup of the ice in the spring an automatic temperature recorder was set up at each of the two grid sites (Fig. 3.3). Temperatures were recorded hourly by probes located 10cm, 5cm, and 1cm below the sediment:water interface (Fig. 3.3) and 5cm and 50cm above the interface in the water column. Temperatures were recorded at both sites from 3 days after ice-breakup for 15 days until rising water levels resulted in equipment malfunction.

Posts were removed at random from each of the two grids periodically from April 23 (3 days after ice-breakup) until August 20 during the commercial wild rice harvest.

Figure 3.2: Location of the two study sites at Lac du Bois, configuration of the posts at each study site, and illustration of the seed bag positions on individual posts.

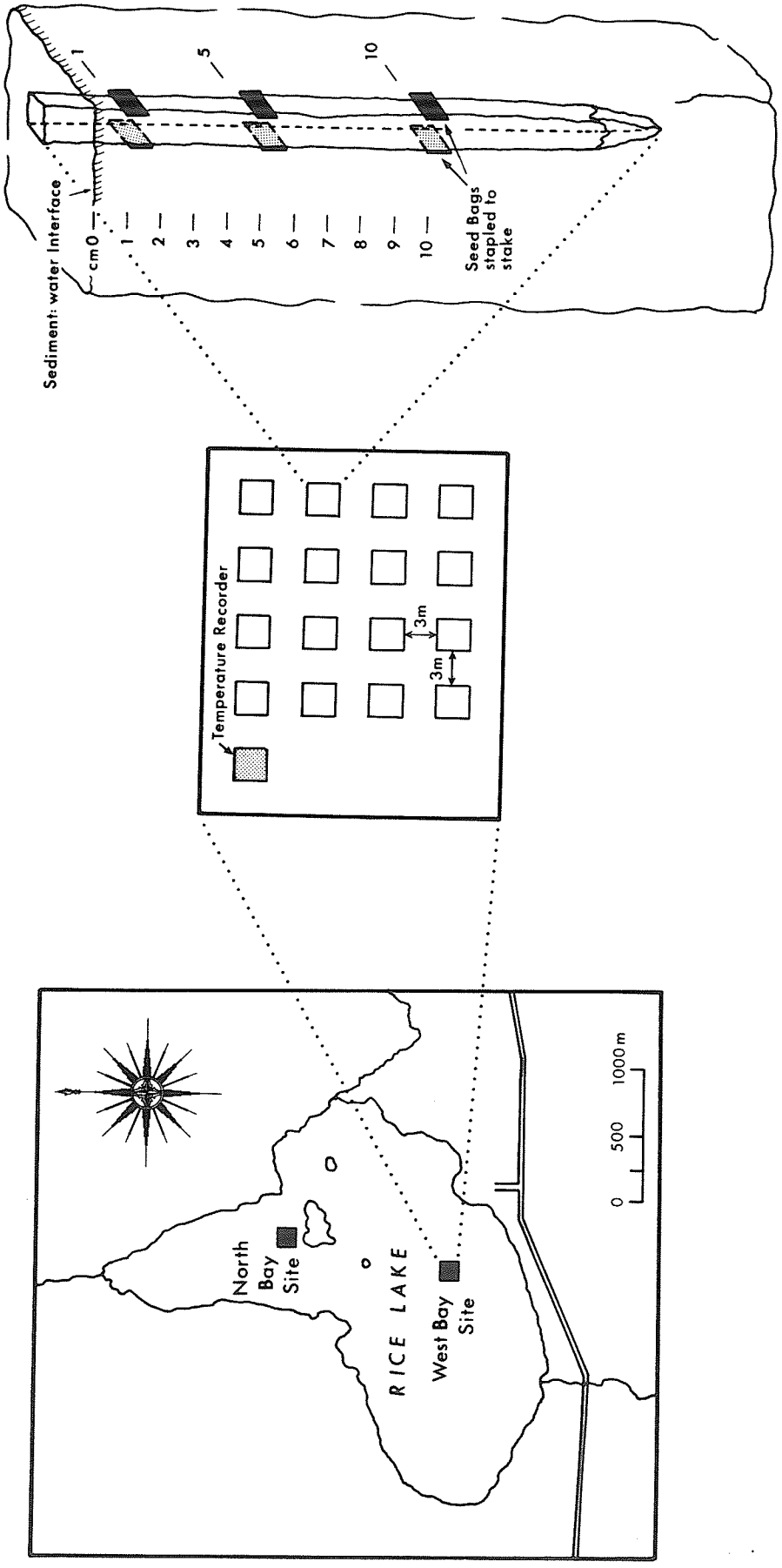
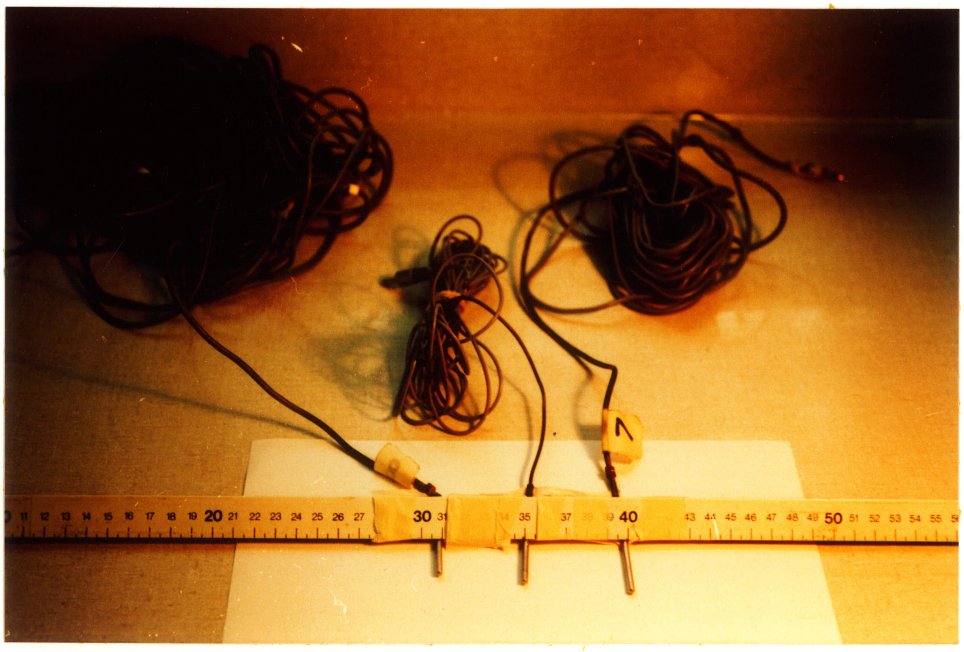

1
5
10
Sediment: water interface
cm 0
1
2
3
4
5
6
7
8
9
10
Seed Bags stapled to stake
Temperature Recorder
3m
3m
North Bay Site
RICE LAKE
West Bay Site
0
500
1000 m

Figure 3.3: Establishment of the seed bank experiment at Lac du Bois.

Top - drilling holes through ice for placement of stakes at West Bay site.

Middle - temperature recorder in place at West Bay site.

Bottom - temperature probes prior to placement in the sediments.


20
30
40
50

The seed bags were removed from the posts and transported in water to the University of Manitoba where they were opened and the seeds sorted into the following groups: germinated, soft or damaged by insects, and ungerminated but firm. The number of seeds in each group was recorded for each of the three seed burial depths.

The ungerminated seed recovered from the field was then incubated at 20°C for one month. Germinated seed was counted and removed periodically. Seed remaining ungerminated was experimentally afterripened five months, then tested again at 20°C for one month. Seed still ungerminated was scraped and retested at 20°C for a further month to test viability.

Seed budgets were constructed to account for the seed at each of the three burial depths within each of the two bays. The five pools within the seed bank were accounted for as follows:

1. Germinated pool - the proportion of the seed population that germinated in the field.
2. Non-viable pool - the proportion of the seed population which became soft during the course of the experiment or which failed to germinate at 20°C after scraping the seed coat.
3. Suboptimal conditions pool - the proportion of the seed population that germinated when transferred from the field to 20°C.

4. Primary dormancy pool. In early spring following ice-breakup the sediments are cool and viable seed remains ungerminated due to either suboptimal temperatures or to a requirement for further afterripening. On the assumption that secondary dormancy does not occur early in the growing season, the proportion of seed requiring further afterripening can be calculated from early season data as the proportion of viable seed which did not germinate in the field or in the growth chamber at 20°C. The proportion of the seed population requiring further afterripening was considered to be constant throughout the growing season since no further afterripening would occur and it was necessary to allow calculation of the secondary dormancy pool.
5. Secondary dormancy pool. Since the five pools account for all seed in the seed bank, the amount of seed in secondary dormancy can be calculated as the difference between the total number of seeds in the seed bank and the number of seeds in the four other pools. Secondary dormancy is assumed not to occur at the beginning of the growing season prior to the sediments warming. This assumption is necessary to allow calculation of the primary dormancy pool.

3.2.3 Experiment 2. Behaviour Of The Pools Of An Artificial Seed Bank In Response To Temperature

A 100 cell germinator (Fig. 2.2), described by McLaughlin et al (1985) and in the Methods section of Chapter 2, was used to investigate the role of temperature in the behaviour of wild rice seed in the seed bank.

Each of the 100 temperature treatments tested consisted of a pyrex dish filled with 450ml of distilled water containing approximately 260 seeds (by weight) which had been afterripened for a period of 7½ months as described earlier.

Germinated seed was removed and discarded during a 3 week period. The seed which remained ungerminated in each dish was counted and transferred to a water filled Petri plate and incubated in a conventional growth chamber under a "near-optimal" temperature regime of 20°C/5°C (16 hours/8 hours). Germination was monitored over a 2 week period to determine if the seeds remained ungerminated in the 100 cell germinator due to suboptimal conditions.

Three groups of seeds were established as controls to test the optimality of the "near-optimal" temperature regime. The controls were similar to the experimental units (a pyrex dish filled with 450ml of de-ionized water and containing 260 seeds by weight) but placed directly into the conventional growth chamber set to the "near-optimal" temperature regime at the time the experimental units were placed in the 100 cell germinator. The controls were used to quantify the percent germination which could be expected if the pre-

treatment of seed in the 100 cell germinator had no effect on subsequent germination.

Following the 2 weeks of near-optimal temperatures, further tests were conducted on the ungerminated seeds to account for the number of seeds which died in each of the 100 temperature treatments and the number which remained viable. Seed which remained ungerminated following one month of near optimal temperatures was experimentally afterripened for a further 5 months, then incubated at 20°C for one month and the number of germinated seed counted. Seed still remaining ungerminated was scraped and incubated for a further month at 20°C to assess viability.

Seed budgets were constructed to account for the fate of seed subjected to the 10 constant temperature treatments in the 100 cell germinator. Only treatments with constant temperature were included in this analysis since fluctuating temperature treatments in the 100 cell germinator confound the germinated seed pool and the primary dormancy pool as defined earlier for the natural seed bank (the effect of fluctuating temperatures is to break primary dormancy in seeds which would normally require further afterripening to germinate (chapter 2). These seeds would then be included in the germinated seed pool rather than in the primary dormancy pool as described below).

The seed budgets were constructed as follows to account for the indicated pools:

1. Germinated pool. Seed which germinated in constant temperatures in the 100 cell germinator.
2. Suboptimal conditions pool and primary dormancy pool. Seed that germinated when transferred to the growth chamber set to 20°C/5°C plus the number of control seeds which did not germinate in the conventional growth chamber. The rationale for this combined pool follows. If the control seed group in the "near-optimal" conditions germinated at 100% then the seed which germinated when transferred from the 100 cell germinator would completely make up the primary dormancy and sub-optimal conditions pool since both these conditions are alleviated under an optimal temperature regime. If the control groups only germinated at, for example, 92% then 8% of the suboptimal conditions and primary dormancy pools would not be accounted for. To correct for this sub-optimality the number of non-germinated control seeds is added.
3. Non-viable seed pool. Seed which became pulpy during the course of the experiment or that did not germinate following scraping and incubating at 20°C.
4. Secondary dormancy pool. Seed unaccounted for by the previous pools.

The calculation of the secondary dormancy pool size is unaffected by the confounding effect of fluctuating temperatures, in contrast to the primary dormancy and sub-optimal

conditions pools, as it is simply the total number of seeds less those which germinated or died. Therefore, the size of the secondary dormancy pool in each temperature treatment can be calculated using the method described above in point 4 and the thermal conditions conducive to the induction of secondary dormancy can be investigated over the entire range of temperature regimes tested.

3.2.4 Experiment 3. The Effect Of Seed Burial Depth On Subsequent Germination Behaviour Under Controlled Temperature Conditions

The effect of the environment in which seed afterripens on the subsequent germination behaviour was investigated as follows. Seed for the experiment was afterripened:

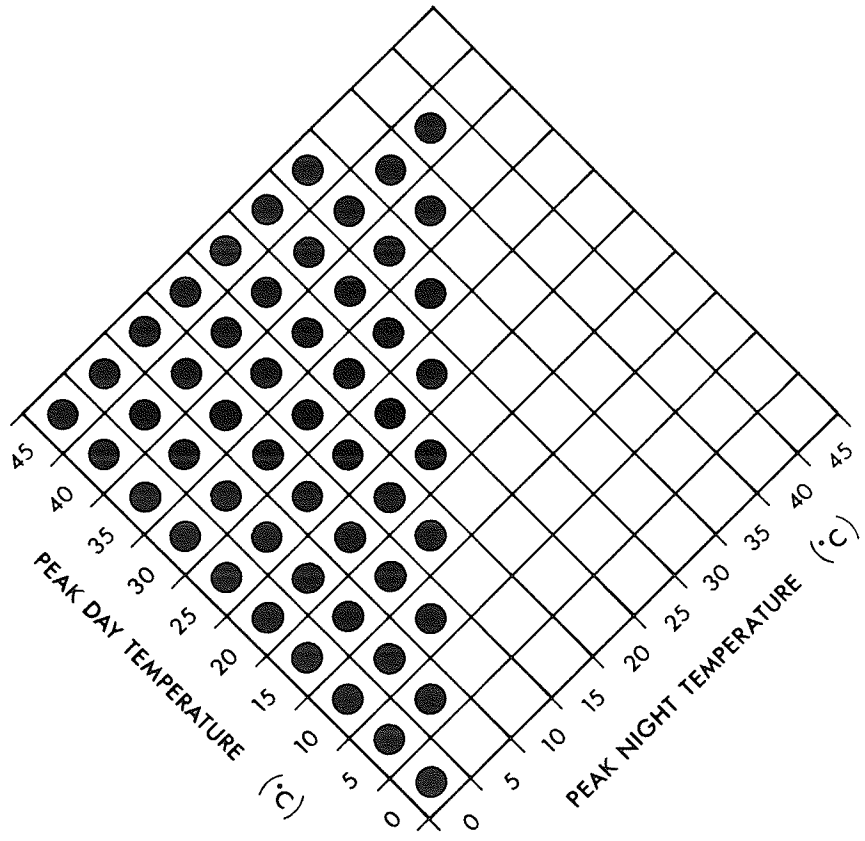
1. at three depths in the sediments of a natural wild rice stand at Lac du Bois, and
2. under laboratory conditions of 5°C, unaerated, in the dark.

The field afterripened seed was afterripened at the West Bay site as a part of the experimental design previously described in Section 2 of this chapter (Fig. 3.1). Ten posts, with attached seed bags, were removed from the sediments. The seed bags were removed, marked as to the depth at which they were buried in the sediments and stored for 16 hours in ice-water prior to being transferred to the 100-cell germinator previously described. For each burial depth, the seed was combined from the ten posts and the bulked seed sample

divided into groups of 10 seeds. Each of the temperature treatments tested in the 100-cell germinator consisted of a petri plate divided into four sections and filled with distilled water. One section contained 10 seeds experimentally afterripened under laboratory conditions to serve as a control. The remaining sections each contained 10 seeds from one of the three afterripening depths tested. Due to difficulties encountered in recovering the seed bags from the field, sufficient seed existed to test only 52 temperature treatments. Those temperature combinations tested are shown in Fig. 3.4.

Germinated seed was counted and removed daily for one month. Following one month in the 100 cell germinator all ungerminated seed was transferred to a growth chamber at near optimal conditions of 35°C and 15°C for 12 hours and 12 hours respectively. Germinated seed was counted and removed periodically for one month. The ungerminated seed was then transferred to experimental afterripening conditions for five months followed by incubation at 20°C for one month. Seed which still remained ungerminated was scraped and incubated for a further month at 20°C to assess viability.

Figure 3.4: The 52 temperature combinations used in testing for the effect of afterripening environment on subsequent germination.


45
40
35
30
25
20
15
10
5
0
PEAK DAY TEMPERATURE (°C)
0
5
10
15
20
25
30
35
40
45
PEAK NIGHT TEMPERATURE (°C)

3.3 RESULTS

3.3.1 Experiment 1. The Dynamics Of Wild Rice Seed In The Seed Bank Of Two Natural Stands

3.3.1.1 West bay site

Considering the average of all three seed burial depths tested (Fig. 3.5 a), 5% germination had occurred in the West Bay site by 3 days following ice-breakup when the first sampling took place. Germination continued until 34 days following ice-breakup after which no further germination was detected (Fig. 3.5 a). Average total germination at the West Bay site was 30%.

Conditions suboptimal for germination accounted for 75% of the seed population remaining ungerminated until 12 days after ice-breakup (Fig. 3.5 a). The proportion of seed which did not germinate due to suboptimal conditions then declined continually to 5% of the seed population by 34 days after ice-breakup. By the end of the growing season virtually no seed remained ungerminated due to suboptimal conditions (Fig. 3.5 a).

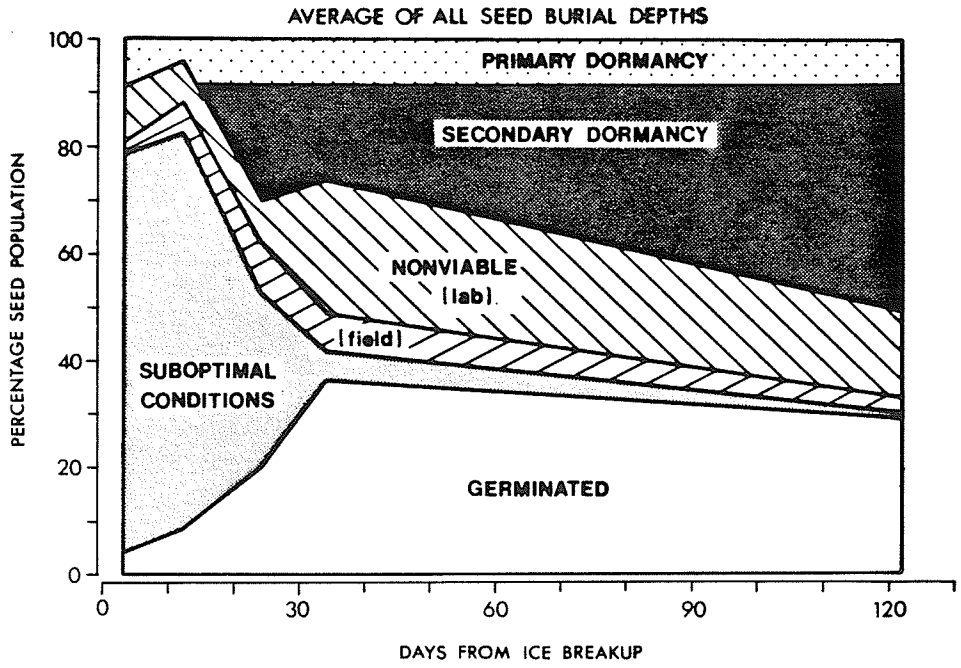
Secondary dormancy became increasingly important in the dynamics of the West Bay seed bank following ice-breakup (Fig. 3.5 a). The proportion of the seed bank in secondary dormancy increased steadily from 12 days until 34 days following ice-breakup when 20% of the seed examined was in secondary dormancy.

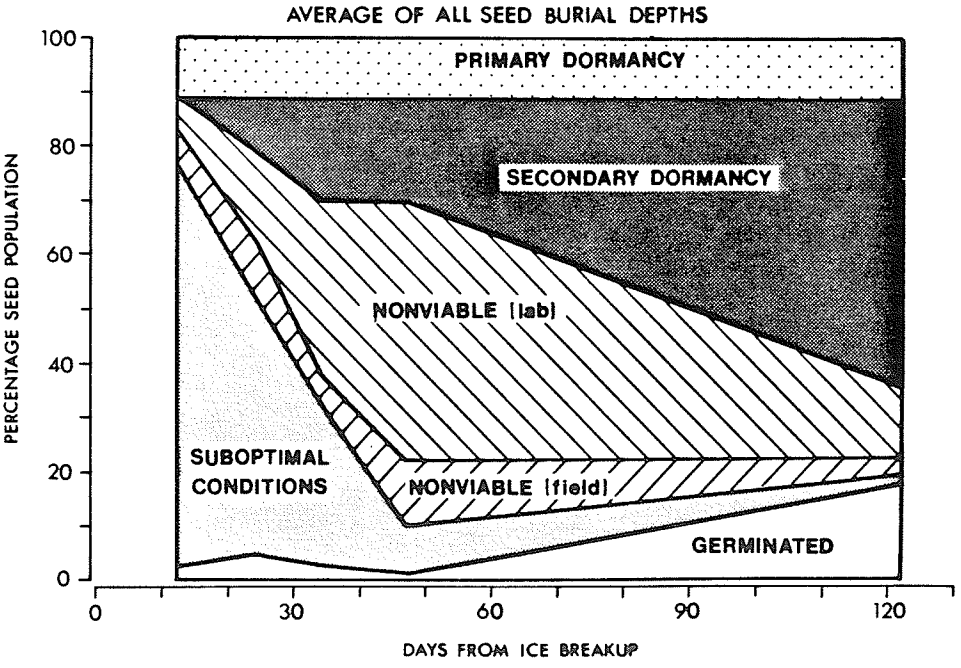
Seed mortality over the course of the growing season was divided into two categories: mortality due to decay and pre-

Figure 3.5: Relative proportions of the seed bank pools in the field over the course of the growing season - average of seed buried at all depths.

(a) Top - West Bay site.

(b) Bottom - North Bay site.


AVERAGE OF ALL SEED BURIAL DEPTHS
PRIMARY DORMANCY
SECONDARY DORMANCY
NONVIABLE (lab)
(field)
SUBOPTIMAL CONDITIONS
GERMINATED
PERCENTAGE SEED POPULATION
100
80
60
40
20
0
0
30
60
90
120
DAYS FROM ICE BREAKUP


AVERAGE OF ALL SEED BURIAL DEPTHS
PRIMARY DORMANCY
SECONDARY DORMANCY
NONVIABLE (lab)
SUBOPTIMAL CONDITIONS
NONVIABLE (field)
GERMINATED
PERCENTAGE SEED POPULATION
100
80
60
40
20
0
0
30
60
90
120
DAYS FROM ICE BREAKUP

dation of the seed while in the sediments and mortality detected during the course of the laboratory tests which included a further 5 months of afterripening. The proportion of seed which died as a result of decay and predation in the West Bay site was less than 10% and relatively constant over the course of the growing season. The proportion of seed mortality detected during the course of the laboratory tests was highly variable and at times accounted for up to 25% of the seed examined (Fig. 3.5 a). Because of the methods used to determine mortality, the non-viable seed pool in the field will be overestimated by including laboratory test-induced mortality. The problem of overestimation of seed bank mortality was investigated at the end of the growing season by testing a subsample of seeds for viability with tetrazolium (Simpson, 1966) and comparing these results with the seed coat scraping test usually used. It was found that the scraping test overestimated seed mortality by 0.3 to 3 times relative to estimates using tetrazolium.

While variability in the data between sampling periods makes precise estimates of the size of the different pools at specific sample times unreliable, overall trends can be discerned. Major changes in the proportions of seed in each pool of the West Bay site seed bank occurred during the first 34 days after ice-breakup. Changes in the relative importance of the pools early in the season were associated with seed moving from the suboptimal conditions pool to either the secondary dormancy pool or germinated seed pool

(Fig. 3.5 a). After approximately 34 days from ice-breakup the seed bank pools had stabilized and little further change was found. At the end of the growing season approximately 30% of the seed had germinated and 40% had entered secondary dormancy or remained in unbroken primary dormancy in the West Bay site (Fig. 3.5 a).

The proportions of seed in the various pools of the West Bay seed bank were different at the three seed burial depths examined (Figs. 3.6 a, b, and c). A higher proportion of the seed buried 1cm in the sediments had germinated by the end of the growing season than seed buried at either 5cm or 10cm in the sediment (50% vs 15-20% respectively).

The dynamics of the West Bay site seed bank, at a burial depth of 1cm, were dominated by germinable and germinated seed shortly after ice-breakup, and primarily by germinated seed later in the growing season (Fig 3.6 a). The seed bank dynamics at burial depths of 5cm and 10cm in the sediments of' the West Bay site (Fig. 3.6 b and c) were similarly dominated by germinable and germinated seed shortly after ice-breakup; but later in the growing season were dominated primarily by secondary dormancy.

3.3.1.2 North bay site

Considering the average of all three seed burial depths tested, less than 5% germination had occurred by the first sampling time at the North Bay site 12 days following ice-breakup (Fig. 3.5 b). Little further germination was de-

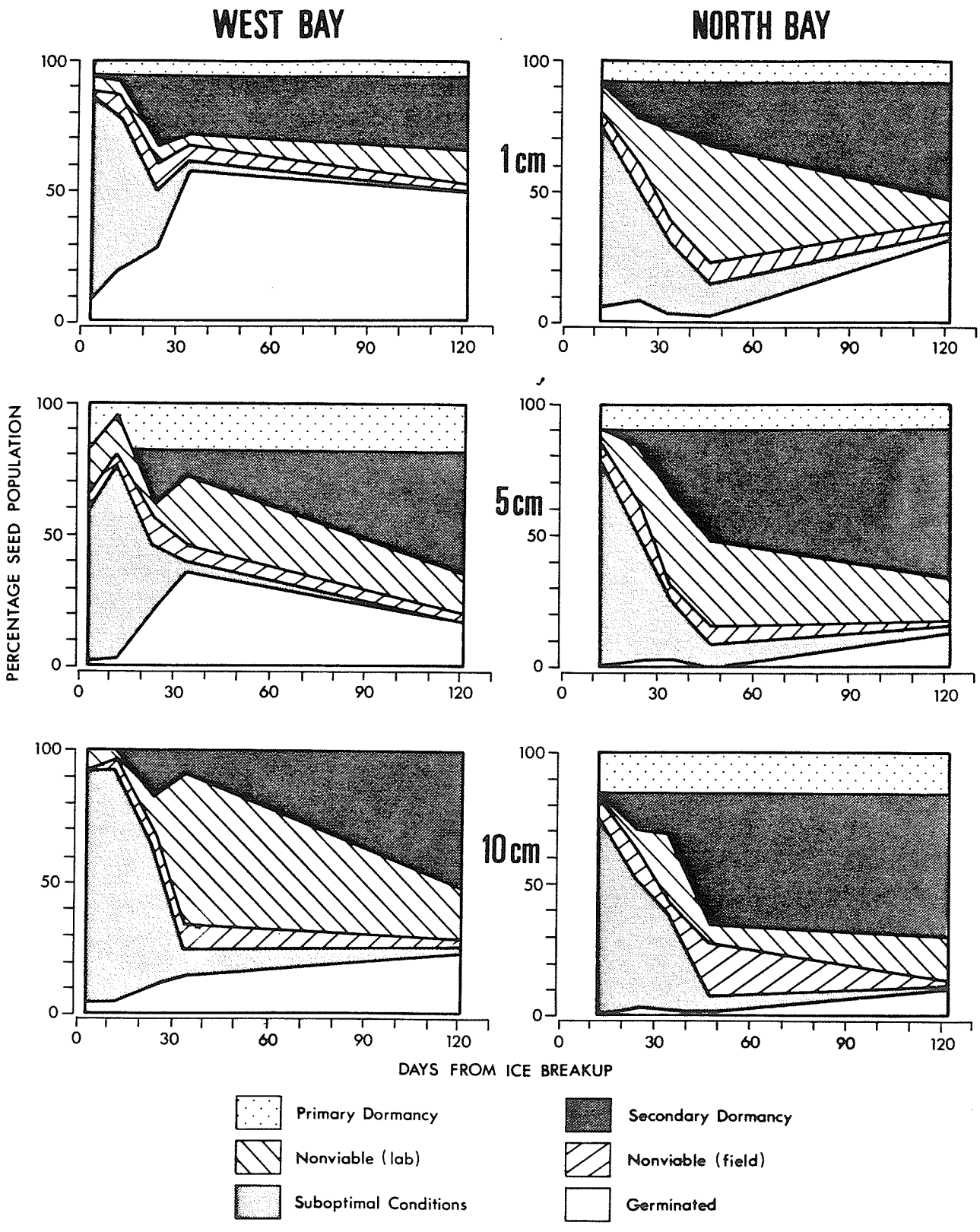
Figure 3.6: Relative proportions of the seed bank pools in the field over the course of the growing season by seed burial depth.

Left column, West Bay site.

(a) Top - seed buried 1 cm in sediments.
(b) Middle - seed buried 5 cm in sediments.
(c) Bottom - seed buried 10 cm in sediments.

Right column, North Bay site.

(d) Top - seed buried 1 cm in sediments.
(e) Middle - seed buried 5 cm in sediments.
(f) Bottom - seed buried 10 cm in sediments.


WEST BAY
NORTH BAY
1cm
5cm
10cm
PERCENTAGE SEED POPULATION
DAYS FROM ICE BREAKUP
Primary Dormancy
Secondary Dormancy
Nonviable (lab)
Nonviable (field)
Suboptimal Conditions
Germinated

tected until the final sampling time when approximately 20% germination was observed. The proportion of seed which did not germinate due to suboptimal conditions declined continuously from 80% of the seed population 12 days after ice-breakup to 10%, 47 days after ice-breakup. At the end of the growing season a small proportion of the North Bay site seed bank (less than 5%) still remained ungerminated due to suboptimal conditions (Fig. 3.5 b).

Secondary dormancy is seen in Figure 3.5 b to be increasingly important during the course of the growing season. The apparent flux of seed into the secondary dormancy pool is from the non-viable seed pool which is not physiologically possible! It is possible that the mid-season mortality is grossly overestimated and that the actual flux between pools occurred early in the growing season but was masked by the mortality over-estimate.

Major changes in the proportions of seed in each pool of the North Bay seed bank occurred during the first 47 days after ice-breakup. The latter part of the growing season was relatively stable, though some germination continued later than 47 days following ice-breakup. Changes early in the season were associated with seed moving from the suboptimal conditions pool to either the secondary dormancy or the germinated pool. The majority of the seed went into secondary dormancy (Fig. 3.5 b). Changes during the latter part of the season were associated with seed moving from the suboptimal conditions pool to the germinated pool, though

this accounted for only 10% of the total seed in the North Bay site seed bank.

The proportions of seed in the various pools of the North Bay seed bank were similar during the early growing season at the three burial depths examined (Figs. 3.6 d-f). During the latter part of the growing season a higher percentage of seed buried 1cm in the sediments had germinated compared with seed buried 5cm or 10cm (30% vs 15-20%). As well, 2-5% of the seed buried 1cm and 5cm in the sediments remained ungerminated due to suboptimal conditions at the end of the growing season. None of the seed buried 10cm in the sediments of the North Bay site remained ungerminated due to suboptimal conditions at the end of the growing season (Figs. 3.6 d-f).

3.3.1.3 Comparison between sites

The dynamics of the West Bay site seed bank were similar in many respects to those of the North Bay site (Figs. 3.5 and 3.6). At the time of ice-breakup most seed was either not germinated due to a requirement for further afterripening (10%) or due to conditions suboptimal for germination (75%). During the early part of the growing season the proportion of seed not germinated due to suboptimal conditions decreased significantly at both sites. At the North Bay site this reduction was predominantly due to the induction of secondary dormancy (Figs. 3.5 b and 3.6 d-f). At the West Bay site both the germination of seed and the induc-

tion of secondary dormancy accounted for the reduction in the proportion of seed not germinated due to suboptimal conditions (Figs. 3.5 a and 3.6 a-c)

The duration of the period of rapid change in the relative sizes of the various pools was longer at the North Bay site than at the West Bay site (47 days vs 34 days respectively). Overall, percent germination during the growing season was higher, and occurred earlier, at the West Bay than the North Bay site. The percentage of the seed population that remained viable and would therefore be subject to afterripening during the next winter was higher in the North Bay site (65%) than in the West Bay site (50%). The difference was primarily due to lower germination and higher induction of secondary dormancy in the North Bay site (Fig. 3.5 a and b).

3.3.1.4 Sediment temperatures

The sediment temperature data for the first 15 days following ice-breakup are summarized in Table 3.1 for the two sites. Mean sediment temperatures were generally .5-1°C higher at the North Bay site than at the West Bay site. This difference approaches the accuracy of the temperature recorder, however. As well, daily sediment temperature fluctuation was .5-1.5°C greater at the North Bay site (Table 3.1). The temperature differences observed were consistent with site differences in water depth. The North Bay site was approximately 60cm shallower than the West Bay site which had a winter water depth of 180cm.

TABLE 3.1

Summary of temperature data collected at Lac du Bois following ice breakup

MEAN DAILY TEMPERATURE

DAYS FROM ICE BREAKUP	SITE					
	WEST BAY			NORTH BAY		
	1cm	5cm	10cm	1cm	5cm	10cm
3	10.0	8.5	3.9	10.7	8.8	4.8
4	8.8	8.0	3.8	10.7	9.4	5.0
5	7.3	7.1	4.5	9.7	9.4	5.8
6	6.1	6.2	4.8	8.0	7.7	5.6
7	7.0	6.4	4.8	8.9	8.1	5.7
8	8.3	7.3	4.8	9.5	8.3	5.6
9	10.8	9.1	4.6	12.0	10.0	5.6
10	11.6	10.6	5.0	12.9	11.4	6.0
11	12.3	11.0	5.2	13.0	11.6	6.5
12	12.1	11.1	6.2	13.3	11.9	6.6
13	12.7	11.4	6.0	14.3	12.4	6.8
14	13.6	12.2	6.8	14.3	13.0	7.0
15	12.9	12.3	7.2	13.6	12.7	7.2

TABLE 3.1 (cont'd).

DAILY TEMPERATURE FLUCTUATION

DAYS FROM ICE BREAKUP	SITE					
	WEST BAY			NORTH BAY		
	1cm	5cm	10cm	1cm	5cm	10cm
3	1.0	0.0	0.5	2.5	1.5	0.5
4	1.5	0.5	0.5	1.5	1.5	1.0
5	1.5	1.0	0.0	2.0	1.0	0.5
6	1.0	0.5	0.5	2.0	1.5	1.0
7	1.0	1.0	0.5	2.0	2.0	1.0
8	3.0	1.5	0.5	3.0	2.0	1.5
9	2.5	2.0	0.5	4.5	3.0	1.0
10	0.5	0.5	0.0	2.0	1.5	2.0
11	1.5	1.0	0.5	1.5	1.0	1.0
12	1.5	0.5	1.0	1.0	1.5	1.0
13	2.0	1.0	0.0	1.5	1.0	1.5
14	1.5	1.0	0.5	1.0	0.5	0.0
15	1.5	1.0	0.5	1.0	1.0	0.5

Sediment temperatures were lower and less fluctuating at greater depths. The disparity in mean daily temperatures between depths became less during the course of the period monitored as the sediments warmed.

3.3.2 Experiment 2. Behaviour Of The Pools Of An Artificial Seed Bank In Response To Temperature

3.3.2.1 Size of the seed pools in constant temperature regimes

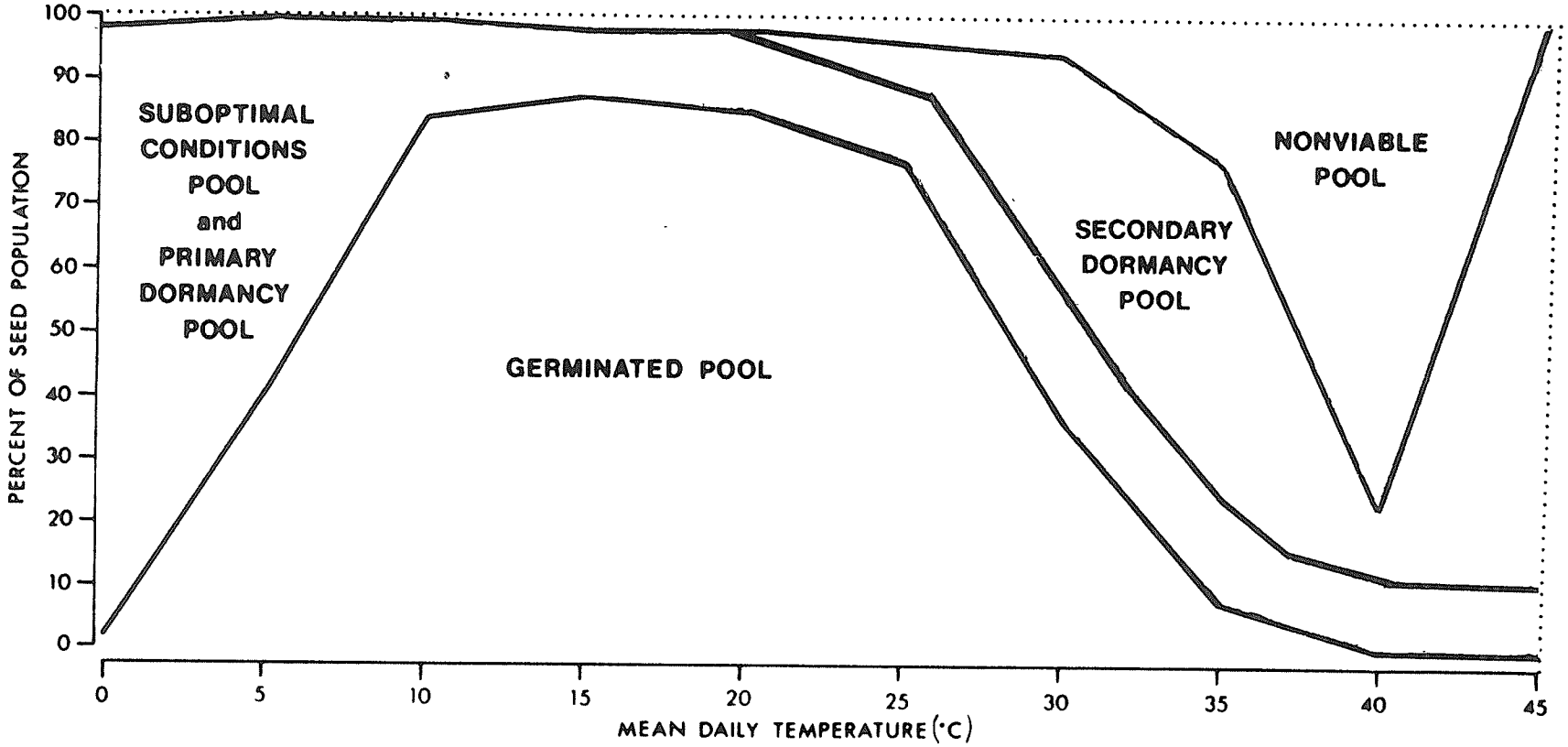
The percent germination of experimentally afterripened seed at constant temperatures observed in this experiment (Fig. 3.7) was similar to that observed in chapter 2 using another seed lot afterripened 7½ months (Fig. 2.4). Virtually no germination occurred with seed incubated at 0°C in the 100-cell germinator and percent germination rose rapidly to over 80% between temperatures of 10 - 20°C (Fig. 3.7).

The size of the seed pools was greatly influenced by the temperature conditions to which the seed was exposed in the 100 cell germinator. The majority of seed incubated in the 100-cell germinator at constant temperatures of less than 10°C did not germinate in the 100 cell germinator due to suboptimal conditions or due to primary dormancy (Fig. 3.7).

Seed mortality was quite low (less than 10%) at constant temperatures of less than 30°C but then rose rapidly to a high of 80% at 40°C (Fig. 3.7).

The induction of secondary dormancy was found at all constant temperatures above 22.5°C (Fig. 3.7). At temperatures above 22.5°C the induction of secondary dormancy increased.

Figure 3.7: Relative proportions of the pools of an artificial seed bank in response to constant temperatures.


SUBOPTIMAL CONDITIONS POOL and PRIMARY DORMANCY POOL
GERMINATED POOL
SECONDARY DORMANCY POOL
NONVIABLE POOL
PERCENT OF SEED POPULATION
MEAN DAILY TEMPERATURE (°C)
0
10
20
30
40
50
60
70
80
90
100
0
5
10
15
20
25
30
35
40
45

At 35°C, 65% of the seed population tested had entered secondary dormancy and at 45°C, 85% entered secondary dormancy. The role of temperature in the induction of secondary is reported more fully in the next section.

To summarize the effect of constant temperature on the size of the seed pools (Fig. 3.7): At temperatures below 20°C mortality was very low and secondary dormancy was not detected. The majority of seeds were either germinated or viable but not germinated due to suboptimal conditions. The proportion of seeds germinated as compared with being in the suboptimal conditions pool increased as the temperature approached 20°C. At temperatures above 20°C the proportion of seed which germinated declined as secondary dormancy and mortality increased. Mortality was highest at 40°C.

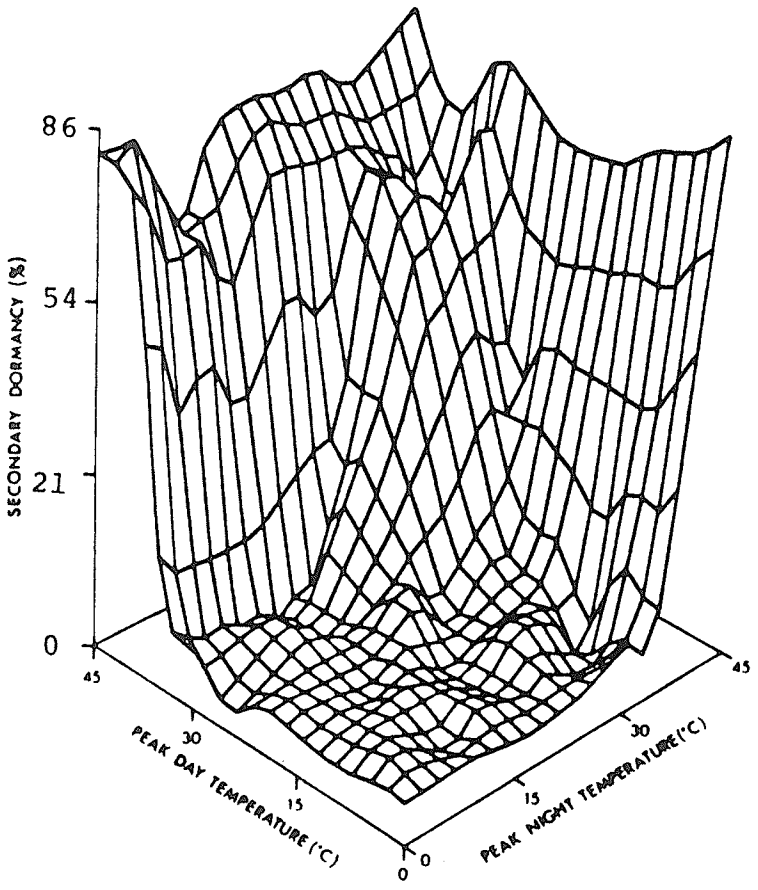
3.3.2.2 Thermal conditions conducive to the induction of secondary dormancy

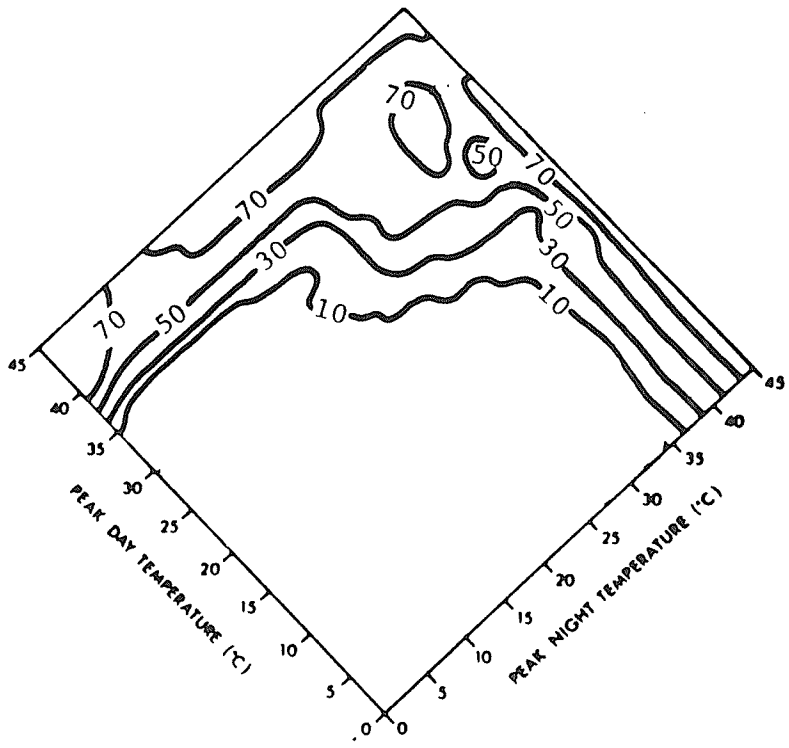
The induction of secondary dormancy over the entire range of conditions tested is illustrated in Figure 3.8. As can be seen in Figure 3.8 peak day or night temperatures of 35°C or higher resulted in the induction of secondary dormancy. Peak temperatures in excess of 40°C resulted in over 70% of the seeds tested entering secondary dormancy. An effect of mean daily temperature is also evident with the induction of secondary dormancy in seed subjected to mean daily temperatures in excess of approximately 22.5°C.

Figure 3.8: The proportion of seed population entering secondary dormancy in response to diurnal temperature regime.

Left - 3 dimensional representation of data.

Right - 2 dimensional representation of data. Isopleths join regions with same induction of secondary dormancy.


86
54
21
0
SECONDARY DORMANCY (%)
45
30
15
0
PEAK DAY TEMPERATURE (°C)
0
15
30
45
PEAK NIGHT TEMPERATURE (°C)

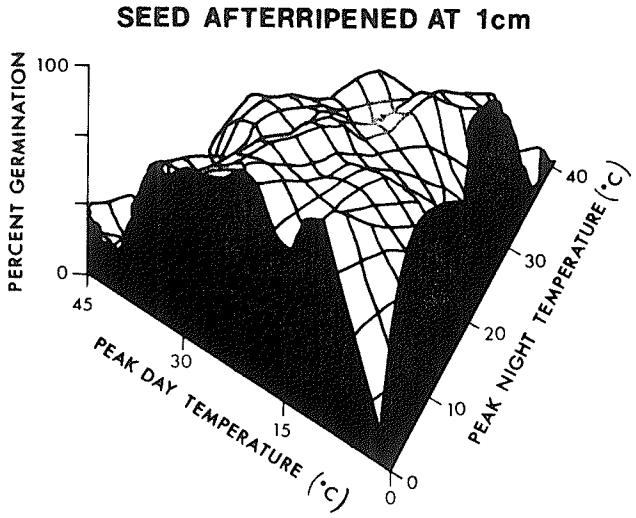

70
50
70
70
50
30
30
10
10
45
40
35
30
25
20
15
10
5
0
PEAK DAY TEMPERATURE (°C)
0
5
10
15
20
25
30
35
40
45
PEAK NIGHT TEMPERATURE (°C)

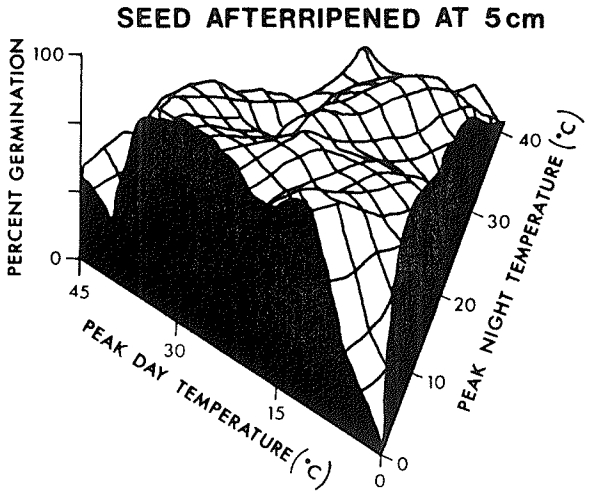
3.3.3 Experiment 3. The Effect Of Seed Burial Depth On Subsequent Germination Behaviour

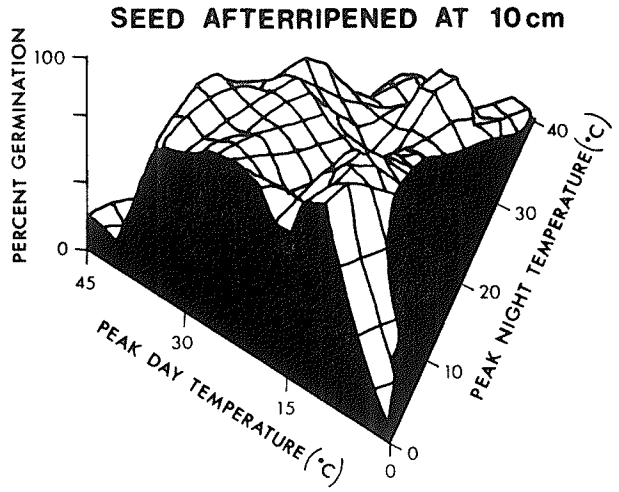
The four response surfaces illustrating the influence of both afterripening environment and temperature on percent germination after one month are found in Figure 3.9. Inspection of the four surfaces indicates that the seeds from all four afterripening environments had the same trends with respect to mean daily temperature, daily temperature fluctuation, and intolerance to peak temperatures in excess of 40°C as those described in chapter 2. All showed very low percent germination at low mean daily temperatures, a wide range of temperatures in which percent germination was quite high, and an intolerance to temperatures in excess of 35°C (Fig. 3.9).

The effect of seed burial depth during afterripening on subsequent germination behaviour over the 52 temperature treatments tested can be illustrated by plotting the cumulative germination summed over the 52 temperature treatments against time (Fig. 3.10). The germination behaviour observed was distinct between the four treatments tested. Seed afterripened experimentally in a growth chamber had the lowest percentage germination (48%) after one month. For seed afterripened in the field, percent germination was inversely related to the depth at which the seed was afterripened. The percentage germination of seed afterripened at depths of 1cm, 5cm, and 10cm was 59%, 54%, and 50% respectively. Analysis of variance using the highest order inter-

Figure 3.9: Percent germination of seed afterripened in four environments as a function of diurnal temperature regime.


SEED AFTERRIPENED AT 1cm
PERCENT GERMINATION
100
0
45
30
15
0
PEAK DAY TEMPERATURE (°C)
0
10
20
30
40
PEAK NIGHT TEMPERATURE (°C)


SEED AFTERRIPENED AT 5cm
PERCENT GERMINATION
100
0
45
30
15
0
PEAK DAY TEMPERATURE (°C)
0
10
20
30
40
PEAK NIGHT TEMPERATURE (°C)


SEED AFTERRIPENED AT 10cm
PERCENT GERMINATION
100
0
45
30
15
0
PEAK DAY TEMPERATURE (°C)
0
10
20
30
40
PEAK NIGHT TEMPERATURE (°C)

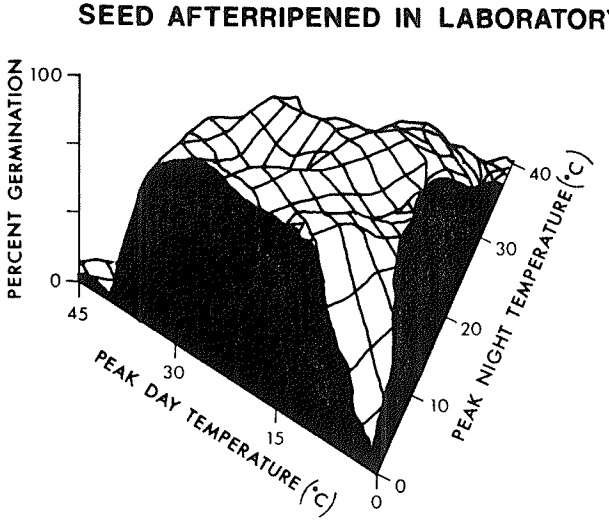
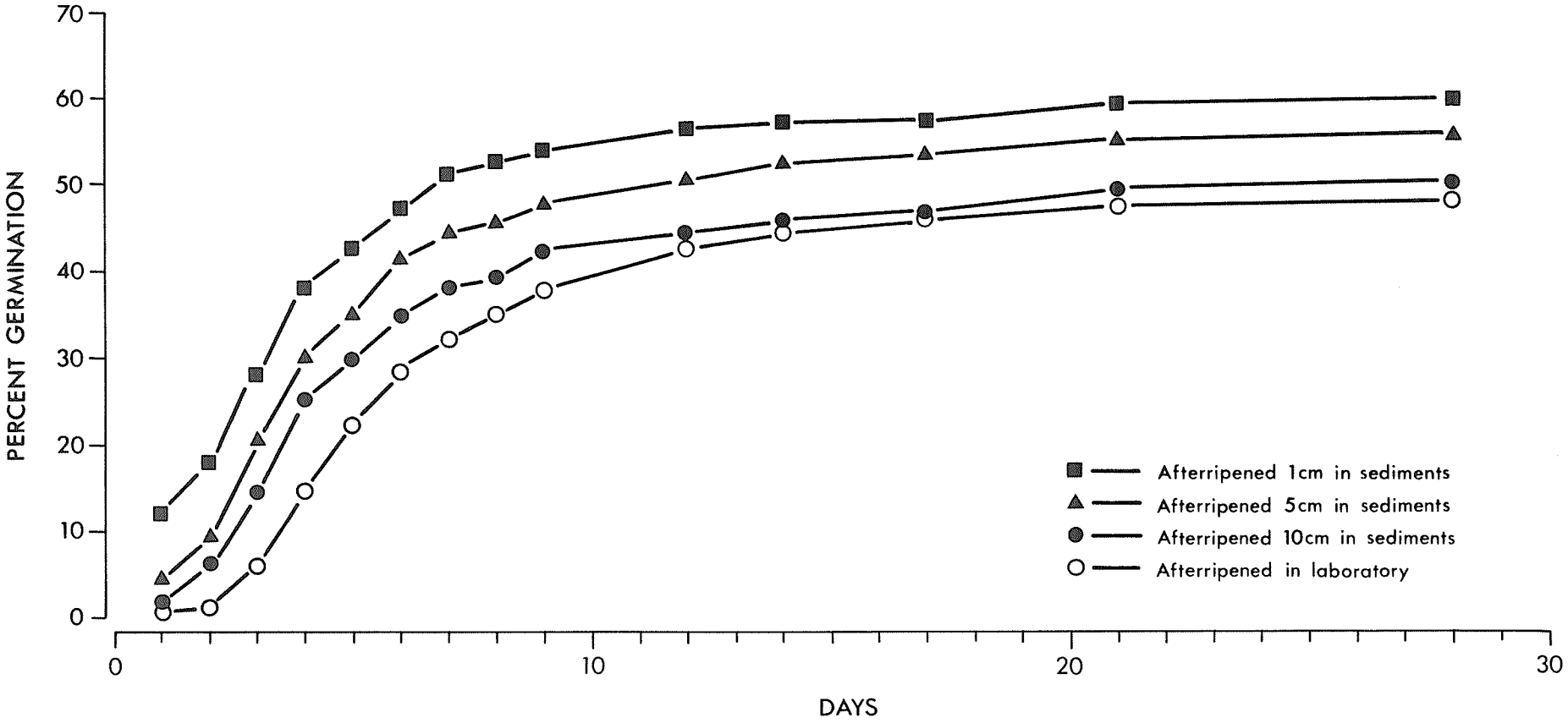

SEED AFTERRIPENED IN LABORATORY
PERCENT GERMINATION
100
0
45
30
15
0
PEAK DAY TEMPERATURE (°C)
0
10
20
30
40
PEAK NIGHT TEMPERATURE (°C)

Figure 3.10: The effect of afterripening environment on subsequent germination (sum of daily germination occurring in the 100 cell germinator).


70
60
50
40
30
20
10
0
PERCENT GERMINATION
0
10
20
30
DAYS
Afterripened 1cm in sediments
Afterripened 5cm in sediments
Afterripened 10cm in sediments
Afterripened in laboratory

action term (peak day temperature * peak night temperature * afterripening treatment) showed that seeds afterripened at 1cm and 5cm in the sediments had significantly (alpha=.05) higher germination than seeds afterripened at 10cm and in the lab.

The difference in percent germination observed between the seed from the four afterripening environments arises from differences in germination during the first two days (Fig. 3.10). Total germination in the 100-cell germinator after two days was 1%, 2%, 4%, and 11% for seed afterripened in the lab, and afterripened at 10cm , 5cm, and 1cm in the sediments respectively. If the differences in germination of the first two days are removed from the results there is no significant difference in the percentage of seeds germinated over the entire experiment due to afterripening environment. The rationale for discounting an effect of environment during afterripening on subsequent germination behaviour is as follows. The order of germination results obtained: seed afterripened at 1cm>5cm>10cm>lab, corresponds to the degree to which the seeds were exposed to temperatures above those for afterripening before being placed in the 100 cell germinator. From Table 3.1 it can be seen that the sediment temperature decreased with depth (as would be expected three days following ice-breakup). On the day the seeds were removed, the sediment temperatures recorded were: 10°C at 1cm; 8.5°C at 5cm; and 3.9°C at 10cm. Therefore, it was concluded that the effect of afterripening environment apparent in

Fig. 3.9 is due not to differences in the environment in which afterripening occurred, but to the differential warming of the sediments immediately following ice-breakup.

3.4 DISCUSSION

The dynamics of wild rice seed in the seed bank at both sites of Lac du Bois were found to be dominated by the induction of secondary dormancy. By the end of the growing season 40-50% of the seed population had entered secondary dormancy (Figs. 3.5 and 3.6). The degree to which secondary dormancy was induced was surprising in light of the data reported in Experiment 2 which found that secondary dormancy was induced in laboratory conditions only at mean daily temperatures above 22.5°C or when the seed was exposed to a peak temperature in excess of 30°C. The known temperature regimes of Lac du Bois (Atkins and Stewart, 1985) suggested that little secondary dormancy would be induced in the field. Possibly the slow rise in temperature experienced by seed in natural conditions alters their germination behaviour relative to seeds transferred directly from afterripening conditions to a germination test treatment. As well, Totterdell and Roberts (1979) found that the induction of secondary dormancy in Rumex was more rapid in the dark. It is unknown if this is the case with wild rice seed but exposure to light is a difference between the natural system and the 100 cell germinator.

If the approximately 10% of the seeds which remained in unbroken primary dormancy is added to the proportion entering secondary dormancy, then 50-60% of the seed population tested would be expected to persist, ungerminated, in the seed bank for more than one growing season. It is possible that the seed thought to be in prolonged primary dormancy at the beginning of the growing season had actually entered secondary dormancy already. Totterdell and Roberts (1979) postulated that afterripening, the induction of secondary dormancy, and germination are concurrent processes with different environmental optima.

Seed mortality (both field and lab - Figs. 3.5 and 3.6) was estimated as accounting for 5-15% of the seed population immediately after ice-breakup. At the end of the growing season mortality still only accounted for 15-20% of the seed population. A much higher seed mortality rate had been anticipated in light of the 99% figure postulated by Whigham and Simpson (1977) based on population studies of Zizania aquatica L. The seeds in this experiment were protected from predation by nylon mesh bags, but it seems unlikely that predation would account for such a large difference in mortality. Either the speculation of Whigham and Simpson is incorrect or the seed bank dynamics of these two species are very different.

The mid-season mortality estimated from the lab procedures appears to be a gross overestimate as evidenced by the apparent flux of seed from the non-viable (lab) pool to the

secondary dormancy pool (ie Fig. 3.5 b, for example). The seeds classified as being in secondary dormancy are known to have been viable since they germinated during the test procedures; therefore, the mid-season mortality must be overestimated. Future seed bank studies of wild rice should test seed mortality on subsamples using destructive tests such as tetrazolium to conclusively separate dead from dormant seed concurrent with testing for suboptimal conditions. The method used here to differentiate dormant from dead seed accumulated error through test-induced mortality.

The much higher percent germination observed over all depths in the West Bay site compared with the North Bay site (Fig. 3.5 a and b) cannot be explained in terms of the temperature data available (Table 3.1). The period of time during which temperature data were recorded was too short, and the temperature differences observed during that time too small to account for the differences in germination. The environmental factor causing the difference in germination between the two sites is unknown, but sediment oxygen concentration is a possibility as oxygen tension is known to have a pronounced effect upon the germination of wild rice seed (Svare, 1960).

The behaviour of wild rice seed in the seed bank changed with the depth at which it was buried in the sediments. Germination was highest (Fig. 3.6) when the seed was buried 1cm (30-50%) and reduced when buried 5-10cm (10-25%). Conversely, the size of the secondary dormancy pool increased

with greater seed burial depth from 25-40% at 1cm to 45-55% at 5-10cm (Fig. 3.6).

The data of Experiment 3 would indicate that the environment in which afterripening occurs does not affect the subsequent germination behaviour of the seed. The changes in behaviour over depth then must arise from differences in the environment at the time of germination. Sediment temperatures differed between the three seed burial depths at both the West Bay and North Bay sites during the time for which data are available (Table 3.1) and may account for much of the variation seen in percent germination and induction of secondary dormancy at the different depths. The data of Atkins (1985) show that sediment temperature differences are maintained over the course of the summer at Lac du Bois.

The five hypotheses presented earlier regarding the behaviour of wild rice seed in the seed bank were:

1. Prolonged primary dormancy is the major pathway leading to the persistence of wild rice in the seed bank.
2. Secondary dormancy occurs in wild rice seed and is a pathway leading to the persistence of wild rice in the seed bank.
3. The induction of secondary dormancy is temperature dependent.
4. The behaviour of wild rice seed in the seed bank will change with seed burial depth.

5. Changes in seed behaviour with burial depth are due to both the environment in which the seed afterripens and to different environmental conditions with depth at the time of germination.

The first hypothesis, that prolonged dormancy is the major pathway leading to the persistence of wild rice seed in the seed bank was rejected using the data collected in Experiment 1. While up to 15% of the seed population was found to be in prolonged primary dormancy (Fig. 3.6 b) it was not the major pathway leading to the persistence of wild rice seed in the seed bank (Figs. 3.5 and 3.6).

The second hypothesis, that secondary dormancy does occur in wild rice seed, and the third hypothesis, that the induction of secondary dormancy is temperature dependent were both shown to be correct. Experiment 2 demonstrated the induction of secondary dormancy in seed exposed to peak temperatures in excess of 30°C or mean day temperatures above 22.5°C. The proportion of the seed population which entered secondary dormancy was found to be a function of both the mean daily temperature and of the peak temperatures which occurred (Fig. 3.8). Experiment 1, the field study, demonstrated that not only did secondary dormancy occur under field conditions, it was the major pathway leading to the persistence of wild rice in the seed bank. 40-50% of the seed population was found to have entered secondary dormancy by the end of the growing season.

The fourth hypothesis, that the behaviour of wild rice seed changes with seed burial depth, was confirmed by Experiment 1 (Fig. 3.5). Germination tended to be reduced with increasing seed burial depth and secondary dormancy increased with burial depth. It should be noted that these trends could not be tested statistically without replication. The results of Experiment 3, which investigated the effect of afterripening environment on subsequent germination, negate the fifth hypothesis that seed burial depth during afterripening influences subsequent germination behaviour. Therefore, it can be concluded that the differences observed in seed behaviour at the different burial depths are attributable to differences in the environment at the time of germination. The role of temperature in controlling germination in the field could not be demonstrated because of the limited temperature data that were collected.

In conclusion, it can be seen that the secondary dormancy pool has a significant role in the dynamics of wild rice in the seed bank. By the end of the growing season secondary dormancy accounted for 40-50% of the seed population. Temperature was found to control the induction of secondary dormancy under laboratory conditions but may not be the only environmental factor controlling the flux of seed into the secondary dormancy pool of the natural seed bank, since it was induced in the field at temperatures lower than those anticipated from laboratory studies. This suggests an interaction with another environmental factor, possibly sediment oxygen concentration.

Unbroken primary dormancy was found to contribute approximately 10% of the seed population tested into the population of seeds that remains ungerminated for more than one year. Unbroken primary dormancy may be a "bet-hedging" mechanism to ensure that at least a minimum proportion of the seed produced in one year will persist in the seed bank.

The addition of seed to the seed bank is at the expense of germination. Percent germination ranged from 10-50% depending on the depth of burial and the site. Germination was greater with seed buried 1cm in the sediments. The period during which germination occurred was variable but appeared to be at least 45 days in many cases. This spreading out of germination over time serves to reduce the risk of catastrophe affecting all germinated seed (van der Vegte, 1978).

The persistence of wild rice in the seed bank through the induction of secondary dormancy and unbroken primary dormancy may play a critical role in the long-term survival of a wild rice stand. Prolonged dormancy both ensures that a seed supply will exist from which a stand can re-establish following years of catastrophe as well as ensuring that the genetic base of a stand is maintained against short-term selection pressures (van der Vegte, 1978).

Chapter IV

THE ROLE OF TEMPERATURE AND LIGHT IN THE SURVIVAL AND LIFE HISTORY STRATEGY OF THE SUBMERGED LEAF PHENOPHASE WILD RICE PLANT

4.1 INTRODUCTION

The mortality of wild rice plants during the submerged leaf phenophase is variable and can be significant. For example, Atkins (1983) found submerged leaf phenophase mortality in excess of 80% based on repeated harvest techniques at Lake of the Woods. Despite its obvious importance to the establishment of individual wild rice plants, the submerged leaf phenophase has not been well studied and its physiology and ecology remain virtually unknown.

As well as affecting the establishment and survival of an individual plant, environmental influences during the submerged leaf phenophase can have an impact upon the productivity of the mature plant. For example, in a series of raft experiments, Rogosin (1958), showed that the stresses induced by increasing water depth during the submerged leaf phenophase reduced both mature plant weight and the seed production of individual plants. Lee and Stewart (1984) found a correlation between water column photosynthetically active radiation (PAR) and mature plant weight leading them to postulate that PAR during the submerged leaf phenophase has a controlling influence on later plant performance.

The observations of Lee and Stewart (1984) and of Rogosin (1958) can be integrated through life-history theory which can be used to predict plant form and timing of events during the life cycle. According to Harper (1977) the life history strategy of an individual represents a "strategic allocation of energy or time to conflicting ends". That is, the favouring of one life-history trait is often at the expense of another life-history trait since finite resources are being divided among competing sinks.

From the observations of Rogosin (1958) and Lee and Stewart(1984) there appears to be a trade-off in the life-history strategy of wild rice between growth and survival during the submerged leaf phenophase and subsequent reproductive capacity. That is, the growth of the submerged leaf plant is at the expense of the subsequent reproductive growth, which, while satisfying conventional life-history theory, would seemingly reduce the individual plant's ecological fitness. Harper (1977, pg. 651), however, convincingly points out that fitness is inextricably linked with vegetative growth:

> "The production of seed is seldom wholly compatible with the vigorous growth of the vegetative plant, yet fitness depends as much on the survival of the plant in the vegetative phase of growth as on its ability to produce seed after it has survived. It will certainly be a fitter strategy to produce few seeds and to reach maturity than to have the potential of producing a vast number of seeds but to fail in a struggle for existence with more vigorous neighbours in an environment of limited resources."

Rose (1983) advances the theory of competition between life history characteristics in what he terms the "variable pleiotropy" theory of life history evolution. In this theory, life history traits interact in function but are under separable genetic control. Rose (1983), uses this theory to predict that early life history traits which favour survivorship, even at the expense of later reproductive growth, will be favoured in natural selection and that these life history traits will be plastic.

The role of phenotypic plasticity in life-history strategy is seemingly at odds with the perceived evolutionary goal of homeostasis (Caswell, 1983). This paradox was solved by Caswell (1983) using a model of life-history strategy developed by Ashby (1956). In this model a life-history trait is considered essential if it can change only within narrow bounds in order for the plant to survive. The essential life-history trait is buffered from changes in the environment by "response variables" which are plastic traits. Such an essential life-history trait might be the transition of the wild rice plant from the submerged leaf to the floating leaf phenophase. If this trait is accepted as being essential, then a suite of plastic traits should exist which buffers the impact of environmental changes upon it. Under conditions adverse for submerged leaf growth; for example, low PAR, high or low temperature, and low dissolved oxygen concentration, the buffering traits would tend to maximize the probability of the submerged leaf growing to the water

surface. Such plastic traits could include changes in the allocation of resources to the shoot versus the roots, changes in shoot morphology, and changes in seed resource utilization. These non-essential traits then should vary with environmental changes in a predictable manner to buffer the impact of the changes upon the essential trait.

The experiment reported here was established to investigate the effects of photosynthetically active radiation (PAR) and temperature on the submerged leaf growth of wild rice. PAR was examined because it was identified by Lee and Stewart (1984) as having a role in growth during the submerged leaf phenophase of wild rice which is manifested in the subsequent reproductive growth of the plant. The effects of temperature were also examined because preliminary experiments (Atkins, unpublished data) indicated a strong interaction effect between temperature and PAR in the growth and development of the submerged leaf wild rice plant. The interactions of PAR and temperature is known to be of importance to the growth of other aquatic macrophytes (Barko et al, 1982).

Specifically the experiment investigated variability in the plastic life-history traits which were thought to buffer the essential transition from submerged leaf to floating leaf phenophase. The following parameters were examined:

1. Parameters reflecting the success of buffering the essential trait.

a) Survival. The number of plants in each treatment which survived the submerged leaf stage was monitored. Plant survival to enter the floating leaf stage is essentially the life-history trait to be buffered.

b) Shoot elongation rate. The rate at which the shoot elongates integrates the amount of resources available for growth in each treatment and the utilization of those resources. It is expected that changes in the plastic traits measured by shoot:root ratio and length per unit of shoot weight will maximize shoot elongation rate under adverse growing conditions.

c) Plant weight. Dry weight can be used as a proxy for energy allocation in plants (Hickman and Pitelka, 1975) and so was used here as an indicator of the success of a plant in exploiting its environment and as an indicator of stress.

2. Plastic response traits.

a) Shoot:root ratio. The proportion of total plant growth occurring in the shoot relative to the root. In unfavourable environments (low PAR and high temperature) it was expected that the allocation of resources to the shoot relative to the root would increase in order to increase shoot growth to "escape" the adverse submersed environment.

b) Shoot morphology. It was expected that under adverse growing conditions the morphology of the shoot would show a plastic response in order to maximize the shoot elongation rate for the given resources. Two possible responses would be to decrease the number of leaves supported by the plant and the width of the leaf relative to its length. Both of these changes in shoot morphology were monitored simultaneously by an index. The length per unit weight of shoot reflects both of these traits.

c) Utilization of seed resources. It was expected that under adverse growing conditions the utilization of seed resources would be increased to supplement the resources provided by photosynthesis for plant growth.

A life-history tactic is a suite of "co-adapted traits, designed by natural selection, to solve particular ecological problems" (Stearns, 1976). In the case of the submerged leaf wild rice plant the problem at hand is survival through "escaping" adverse growing conditions when they occur in the submersed environment by entering the aerial environment. This experiment investigates a suite of plastic traits which may serve to ensure the survival of the submerged leaf plant under varying conditions of PAR and temperature.

4.2 METHODS

Wild rice seed was collected from the tray of a mechanical harvester at Lac du Bois, Manitoba (Fig. 2.1) in early September, 1984, and afterripened in the dark at 5°C until required.

For each of the 5 temperatures investigated (10, 15, 20, 25, and 30°C), six 60-litre aquaria were filled with 7cm of a silty-loam greenhouse potting soil which was then covered to a depth of 30cm with deionized water (Fig. 4.1). Deionized water was used to facilitate replication of the experiment and to control algae. Soils were allowed to equilibrate for a minimum of one week prior to planting. For each temperature investigated, six light levels ranging between 4 to 175 $uE \cdot m^{-2} \cdot s^{-1}$ were randomly allocated to the six aquaria. Light levels were controlled by wrapping the sides of each aquarium with green plastic to exclude lateral light and using nylon shade cloth to control the amount of incident light entering the water (Fig. 4.1). Light levels were determined for the middle of the water column using a Li-Cor 185A light meter with underwater quantum sensor. Daphnia sp was used to maintain the water in an algal-free state.

Ten plants were grown in each aquarium from germinated seed whose individual fresh weights had been determined.

Plant length was monitored daily by measuring the distance from the sediment:water interface to the tip of each plant using a scale mounted on the front of each aquarium. Parallax error was reduced by sighting along a square placed

Figure 4.1: Growth chamber setup used to investigate the effects of temperature and PAR on submerged leaf stage growth.

(a) Top - two of the six aquaria illustrating the use of shade cloths and lateral light exclusion to control PAR levels.

(b) Middle - measuring plant height using parallax reduction unit!

(c) Bottom - illustration of submerged leaf plants growing in aquaria.


12
13
15
16
17
19
20

against the scale (Fig. 4.1 b). Plant length could be measured accurately to the nearest ½ cm using this method. The rate of leaf length growth was calculated by regressing the natural logarithm of plant length against time. The slope of this line is the calculated growth rate (Hunt, 1978) and can be expressed as a percentage (cm of growth per hour per 100cm of existing plant).

Each plant was carefully removed from the sediments when it reached the water surface. It was then divided into roots, shoot, and seed and dried 24 hours in a forced air oven at 85°C. 100% recovery of the root system was possible by carefully removing the soil surrounding the roots and rinsing very gently.

An index of the amount of the seed reserve utilized during the submerged leaf phenophase was developed by taking the difference between seed fresh weight at the beginning of the experiment and seed dry weight at the end of the submerged leaf phenophase. This seed weight depletion index measures the total loss in seed weight over the course of the experiment which includes both the seed reserves utilized and the moisture content of the seed at the beginning of the experiment.

Temperature and incident light (with a photoperiod of 16 hours which approximates the spring photoperiod at the seed source) were controlled in a Conviron "walk-in" growth chamber used to house the 6 aquaria (Fig. 4.1). Five nominal water temperature treatments were tested: 10, 15, 20, 25,

and 30°C, and the sequence of temperatures randomized. Water temperature was controlled by monitoring water temperature with a Fischer digital thermometer and adjusting the air temperature of the growth chamber as required. Since water temperature varied by 1-2°C between individual aquaria, the average of temperatures in the six aquaria was adjusted to give the nominal temperature treatments desired.

The entire experiment required the period of May to September, 1985, to complete.

The results of individual parameter response to PAR and temperature were presented using contour plots to represent the response surfaces. For each parameter, the average response in each PAR and temperature regime was plotted and bi-variate interpolation used to form the isopleths.

The co-action of growth parameters was investigated through canonical correlation using SAS PROC CANCORR (SAS Inst., 1982a).

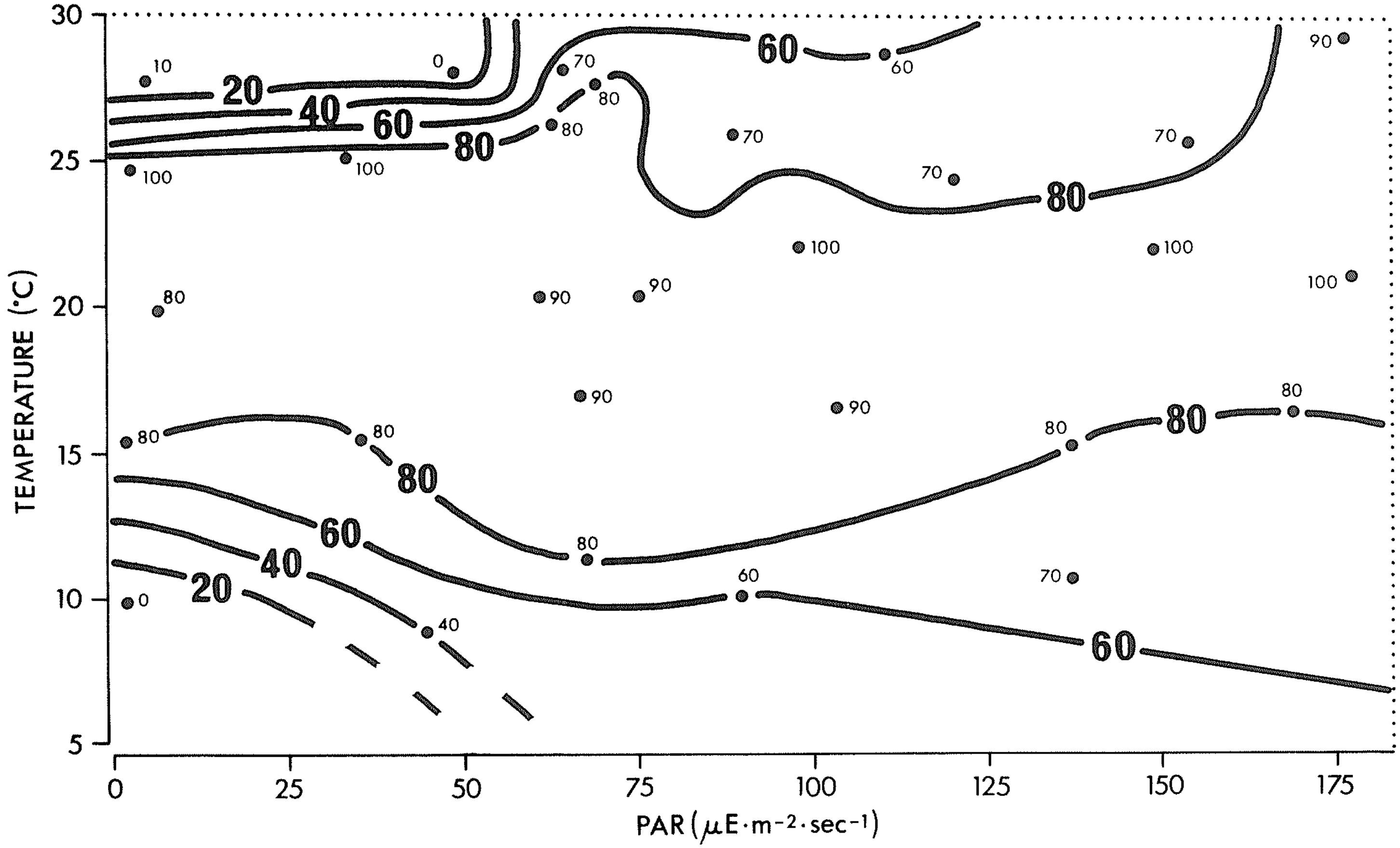
4.3 RESULTS

4.3.1 Plant Survival

The proportion of the plant population which survived to the end of the submerged leaf phenophase is shown as a function of PAR and temperature in Figure 4.2.

In Figure 4.2 the lines which join temperature and PAR treatments with common survivorship (isosurvival lines) generally run parallel to the PAR axis at PAR levels between 75 and 150 $uE \cdot m^{-2} \cdot s^{-1}$. This indicates that PAR is generally

Figure 4.2: Percentage of plants surviving at the end of the submerged leaf phenophase as a function of PAR and temperature.


TEMPERATURE (°C)
PAR (μE·m-2·sec-1)
30
25
20
15
10
5
0
25
50
75
100
125
150
175

not limiting to the survival of the submerged leaf plants at levels between 75 and 150 uE·m^{-2}·s^{-1}. For a given PAR level in this range, survivorship was mainly a function of temperature. For example, plants grown in 100 uE·m^{-2}·s^{-1} of PAR at 10°C had approximately 60% survival; at 22°C 100% of the plants survived; and at 28°C survival was approximately 60%. For a specific temperature, changes in the PAR level between 75 and 150 uE·m^{-2}·s^{-1} resulted in little change in survivorship relative to the changes induced by temperature.

Examining all treatments (Fig. 4.2), it can be seen that survivorship increased with increasing temperature to a maximum at approximately 20-25°C. Survivorship then decreased with increasing temperature. The effects of temperature on survival were most pronounced at low levels of PAR. At PAR levels below approximately 25 uE·m^{-2}·s^{-1}, plant survival rose from 0% at 10°C to 100% at 20°C and then dropped abruptly to 10% at 28°C.

Increasing PAR levels were associated with increased survival at all temperatures. For example, at 20°C survival at 10 uE·m^{-2}·s^{-1} of PAR was 80%; at 75 uE·m^{-2}·s^{-1} survival was 90%; and at 175 uE·m^{-2}·s^{-1} survival was 100%. Of significance is the effect of increased PAR levels on the survival of plants grown at both high and low temperatures. For example, none of the plants grown at 10°C in 4 uE·m^{-2}·s^{-1} of PAR survived the submerged leaf phenophase while plants grown at 10°C in 45 uE·m^{-2}·s^{-1} of PAR had 40% survival; and plants at 130 uE·m^{-2}·s^{-1} of PAR had 70% survival. Similar-

ly, the survival of plants grown at approximately 28°C rose from 0-10% at PAR levels below 50 $uE \cdot m^{-2} \cdot s^{-1}$ to 90% at 175 $uE \cdot m^{-2} \cdot s^{-1}$.

4.3.2 Plant Dry Weight

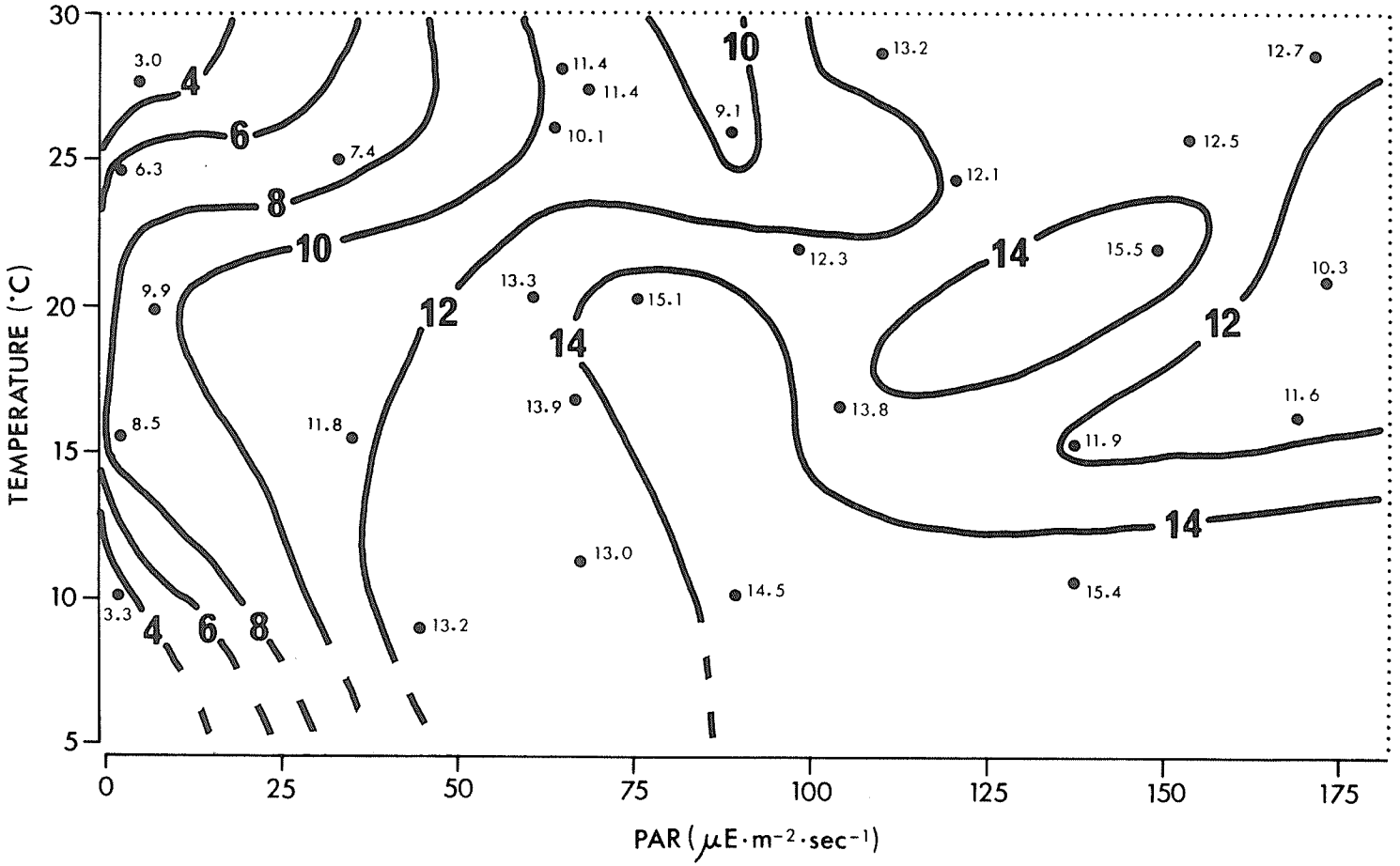
The average dry weight of the plants surviving in each treatment at the end of the submerged leaf phenophase ranged from 3.0-15.5 $mg \cdot plant^{-1}$ (Fig. 4.3).

In general, for a given temperature, the average plant dry weight increased with increasing PAR to a maximum weight at PAR levels of 100-150 $uE \cdot m^{-2} \cdot s^{-1}$. At higher PAR levels plant dry weight either reached a plateau or declined with further increased PAR. Plants grown at temperatures above 15°C showed a reduction in average weight at PAR levels above 150 $uE \cdot m^{-2} \cdot s^{-1}$ while plants grown at temperatures of less than 15°C reached a plateau weight. For example, the maximum average plant dry weight in this experiment was 15.5 $mg \cdot plant^{-1}$ and occurred at 22°C with 150 $uE \cdot m^{-2} \cdot s^{-1}$ of PAR. Plants grown at 22°C at 170 $uE \cdot m^{-2} \cdot s^{-1}$ of PAR had an average weight of only 10.3 $mg \cdot plant^{-1}$ (Fig. 4.3).

For a given PAR level below 100 $uE \cdot m^{-2} \cdot s^{-1}$, the average plant dry weight increased with increasing temperature to a maximum at approximately 15-20°C and then decreased.

For a given PAR level above 100 $uE \cdot m^{-2} \cdot s^{-1}$ the average plant dry weight was highest at temperatures of less than 15°C. At temperatures above 15°C plant dry weight was somewhat erratic in relation to temperature. The trend of plant

Figure 4.3: Plant dry weight ($mg \cdot plant^{-1}$) at the end of submerged leaf phenophase as a function of PAR and temperature.


TEMPERATURE (°C)
PAR (μE·m⁻²·sec⁻¹)
30
25
20
15
10
5
0
25
50
75
100
125
150
175
4
6
8
10
12
14
3.0
6.3
7.4
11.4
11.4
10.1
9.1
13.2
12.7
12.5
12.1
12.3
15.5
10.3
9.9
13.3
15.1
8.5
11.8
13.9
13.8
11.6
11.9
13.0
14.5
15.4
3.3
13.2

dry weight with increased temperature was to decline, then to increase to a local maximum, and then to finally decrease again (Fig. 4.3). The temperature at which the local maximum occurred was higher with increased PAR level. For example, at 125 $uE \cdot m^{-2} \cdot s^{-1}$ of PAR the local maximum occurred at approximately 17°C. At 175 $uE \cdot m^{-2} \cdot s^{-1}$ the local maximum occurred at approximately 28°C (Fig. 4.3).

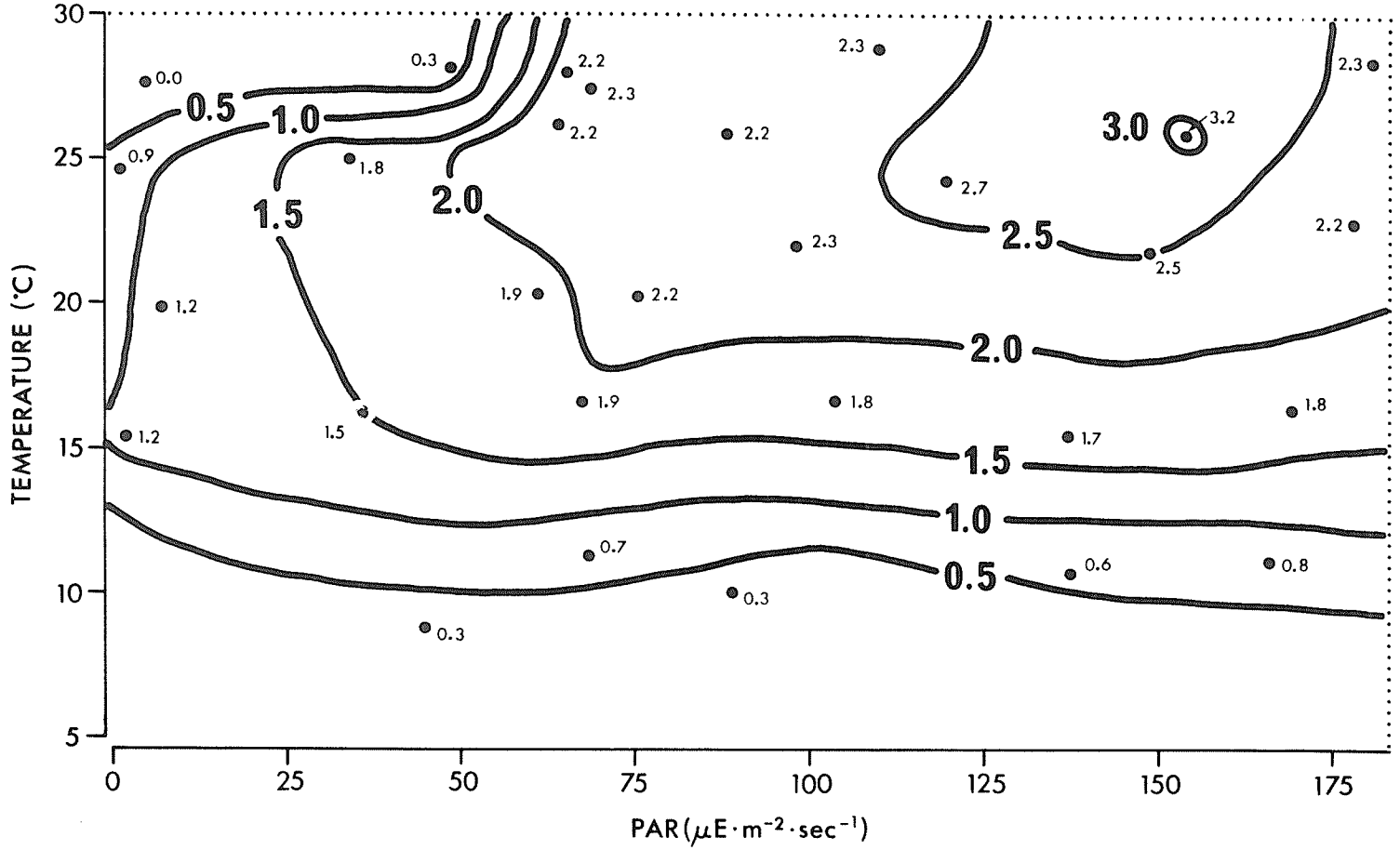
4.3.3 Shoot Elongation Rate

The average rate of shoot elongation of the plants which survived the submerged leaf phenophase varied from a high of $3.2\% \cdot h^{-1}$ to a low of less than $.5\% \cdot h^{-1}$.

At temperatures below 15°C shoot elongation rate was a function of temperature, virtually independent of the level of PAR. The isorate lines which parallel the PAR axis (Fig. 4.4) indicate that shoot elongation rate increased with increasing temperature but remained relatively unchanged by increasing PAR.

At temperatures above 15°C elongation rate was a function of both temperature and PAR (Fig. 4.4). For a given temperature, elongation rate increased with increasing PAR to a plateau level above which no further increase occurred. For example, the shoot elongation rate of plants growing at 20°C increased from $1.2\% \cdot h^{-1}$ at 10 $uE \cdot m^{-2} \cdot s^{-1}$, to $2.2\% \cdot h^{-1}$ at approximately 75 $uE \cdot m^{-2} \cdot s^{-1}$. At PAR levels above 75 $uE \cdot m^{-2} \cdot s^{-1}$ plants which grew at 20°C had the same shoot elongation rate of approximately $2.2\% \cdot h^{-1}$.

Figure 4.4: Rate of shoot elongation ($\%\cdot hr^{-1}$) as a function of PAR and temperature.


TEMPERATURE (°C)
30
25
20
15
10
5
0
25
50
75
100
125
150
175
PAR (μE · m⁻² · sec⁻¹)
0.5
1.0
1.5
2.0
2.5
3.0
0.0
0.3
2.2
2.3
0.9
1.8
2.7
1.2
1.9
1.5
1.7
0.7
0.6
0.8
3.2
2.5

As temperature increased, both the elongation rate at the plateau and the level of PAR at which the plateau began increased. For example, at 15°C the plateau elongation rate of approximately 1.5%·h^{-1} occurred at PAR levels as low as 50 uE·m^{-2}·s^{-1}. At 20°C the plateau elongation rate of approximately 2.2%·h^{-1} occurred at PAR levels above 80 uE·m^{-2}·s^{-1}. Photoinhibition of shoot elongation may have occurred at PAR levels above 150 uE·m^{-2}·s^{-1} when temperatures exceeded 20°C (Fig. 4.4).

At temperatures above 25°C the shoot elongation rate was significantly reduced by PAR levels of less than 70 uE·m^{-2}·s^{-1} as the photo-compensation point was approached. Plants grown at 28°C in 70 uE·m^{-2}·s^{-1} of PAR had an average shoot elongation rate of 2.3%·h^{-1}. Plants grown at the same temperature, but at 50 uE·m^{-2}·s^{-1} of PAR, had a shoot elongation rate of only 0.3%·h^{-1}.

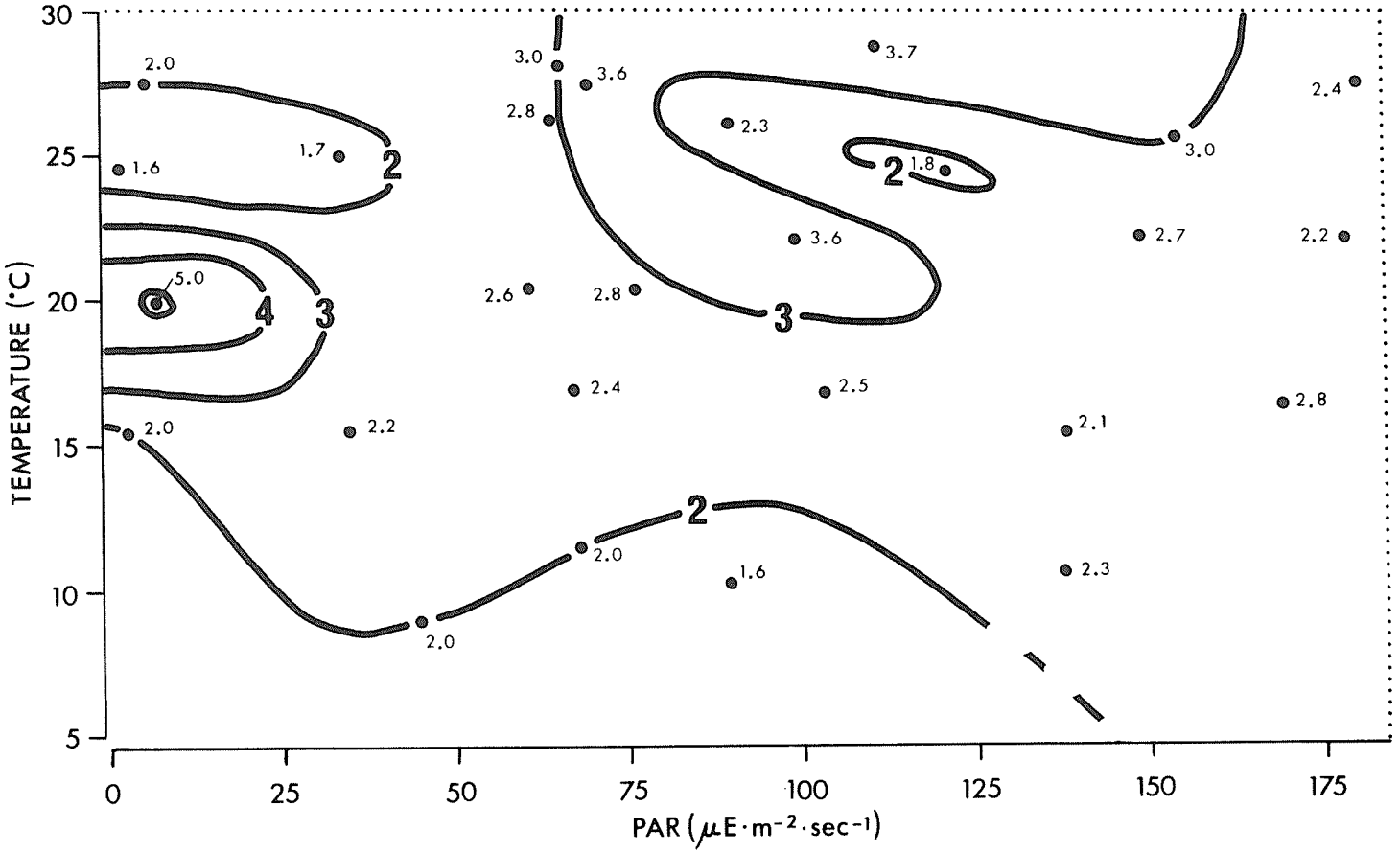
The general pattern of shoot elongation observed in Fig. 4.4 is one of increased shoot elongation rate with increased PAR and temperature. At low temperatures elongation rate was independent of PAR and varied directly with temperature. PAR was limiting to elongation rate at temperatures above 15°C, especially at temperatures above 25°C.

4.3.4 Morphological Indices

4.3.4.1 Shoot:root ratio

The average shoot:root ratio of the plants which survived in each treatment ranged from a low of 1.6 to a high of 5.0

Figure 4.5: Shoot:root ratio of plants at the end of submerged leaf phenophase as a function of PAR and temperature.


30
25
20
15
10
5
TEMPERATURE (°C)
0
25
50
75
100
125
150
175
PAR (μE·m⁻²·sec⁻¹)
2.0
1.6
1.7
2
5.0
4
3
2.2
2.0
2.0
2.0
1.6
2
3.0
3.6
2.8
3.7
2.3
2.4
3.0
1.8
2
3.6
2.7
2.2
2.6
2.8
3
2.4
2.5
2.8
2.1
2.3

(Fig. 4.5). The trend of shoot:root ratio with PAR and temperature was quite variable but a general pattern of increased shoot:root ratio was observed with increasing temperature. The maximum shoot:root ratio tended to occur at higher PAR levels at lower temperatures. For example, the maximum shoot:root ratio of plants grown at 28°C occurred at 75 $uE \cdot m^{-2} \cdot s^{-1}$ of PAR. For plants grown at 15°C the maximum shoot:root ratio occurred at 170 $uE \cdot m^{-2} \cdot s^{-1}$ of PAR.

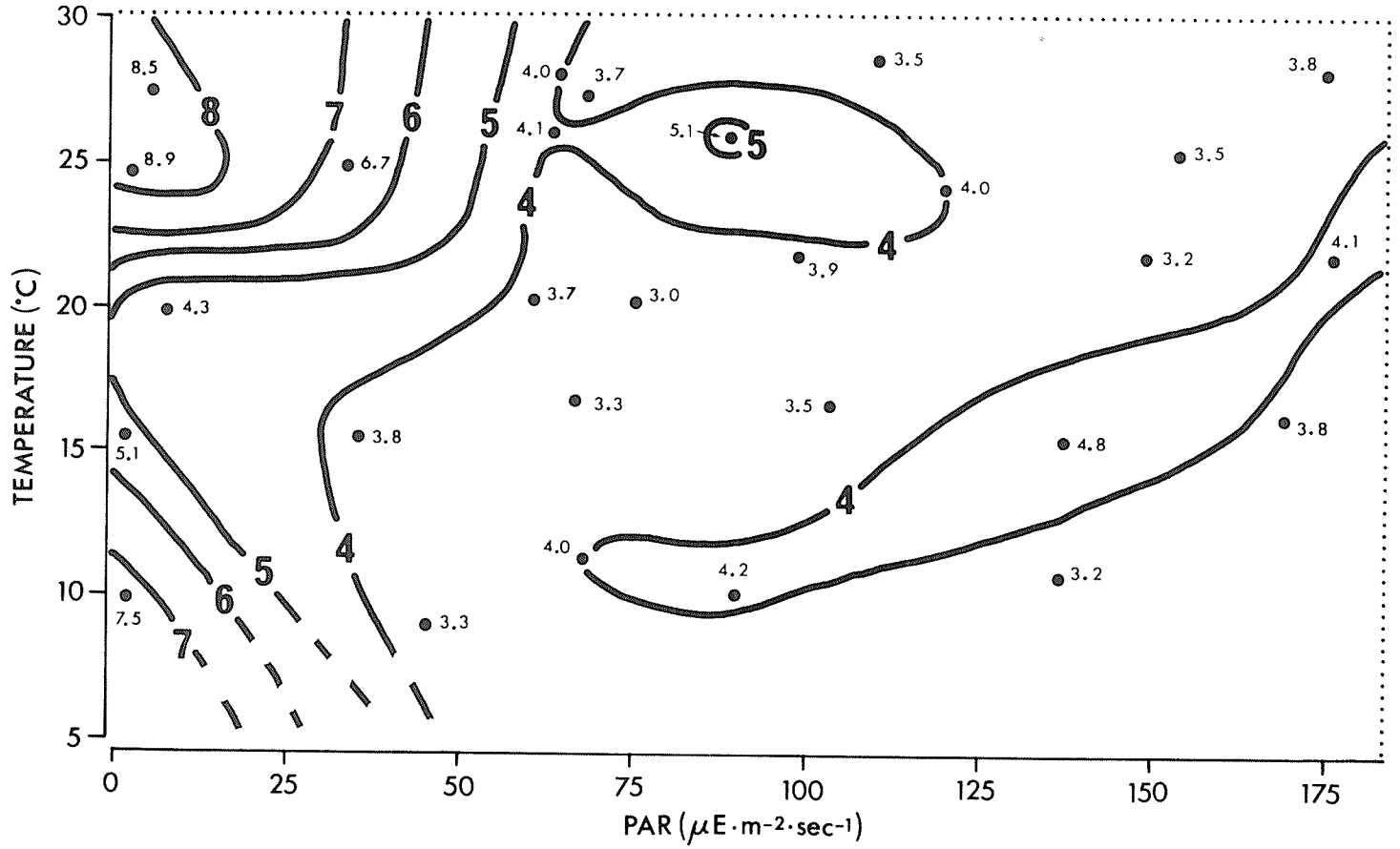
Plants grown at a given PAR level had a higher shoot:root ratio with increased temperature. For example, plants grown at approximately 70 $uE \cdot m^{-2} \cdot s^{-1}$ of PAR had a shoot:root ratio of 2.0 at 12°C; and of 3.0 at 28°C.

The trend of increased shoot:root ratio with increased temperature was more consistent than the trend of increased shoot:root ratio with increased PAR. The trend of shoot:root ratio with PAR may be obscured by the very high value at 20°C which requires further investigation.

4.3.4.2 Length per unit dry weight of shoot

The length per unit dry weight of shoot varied from a low of 3.0 $cm \cdot mg^{-1}$ shoot to a high of 8.9 $cm \cdot mg^{-1}$ shoot (Fig. 4.6). The length per unit dry weight of shoot increased with decreasing PAR, especially at PAR levels of less than 75 $uE \cdot m^{-2} \cdot s^{-1}$. For example, plants grown at 28°C in 170 $uE \cdot m^{-2} \cdot s^{-1}$ of PAR had a length per unit dry weight of shoot of 3.8; at 70 $uE \cdot m^{-2} \cdot s^{-1}$ of 4.0; and at 4 $uE \cdot m^{-2} \cdot s^{-1}$ of 8.5. The increased length per unit dry weight of shoot indicates

Figure 4.6: Length per unit of shoot dry weight ($cm \cdot mg^{-1}$ shoot) as a function PAR and temperature.


TEMPERATURE (°C)
30
25
20
15
10
5
0
25
50
75
100
125
150
175
PAR (μE·m-2·sec-1)
8
7
6
5
4
8.5
8.9
6.7
4.3
4.0
3.7
4.1
5.1
3.5
3.8
3.9
3.0
3.3
3.2
4.1
4.8
5.1
7.5
4.2

that as PAR decreases the shoot becomes narrower and/or less leaves are supported by the plant.

For a given level of PAR, the length per unit dry weight of shoot tended to be a minimum at approximately 20°C. An anomaly in the pattern described is the "ridge" of higher values which occurs from approximately 10°C, 70 $uE \cdot m^{-2} \cdot s^{-1}$ to 22 °C, 175 $uE \cdot m^{-2} \cdot s^{-1}$. This local maximum has values approximately 25% higher than expected based on the patterns already described.

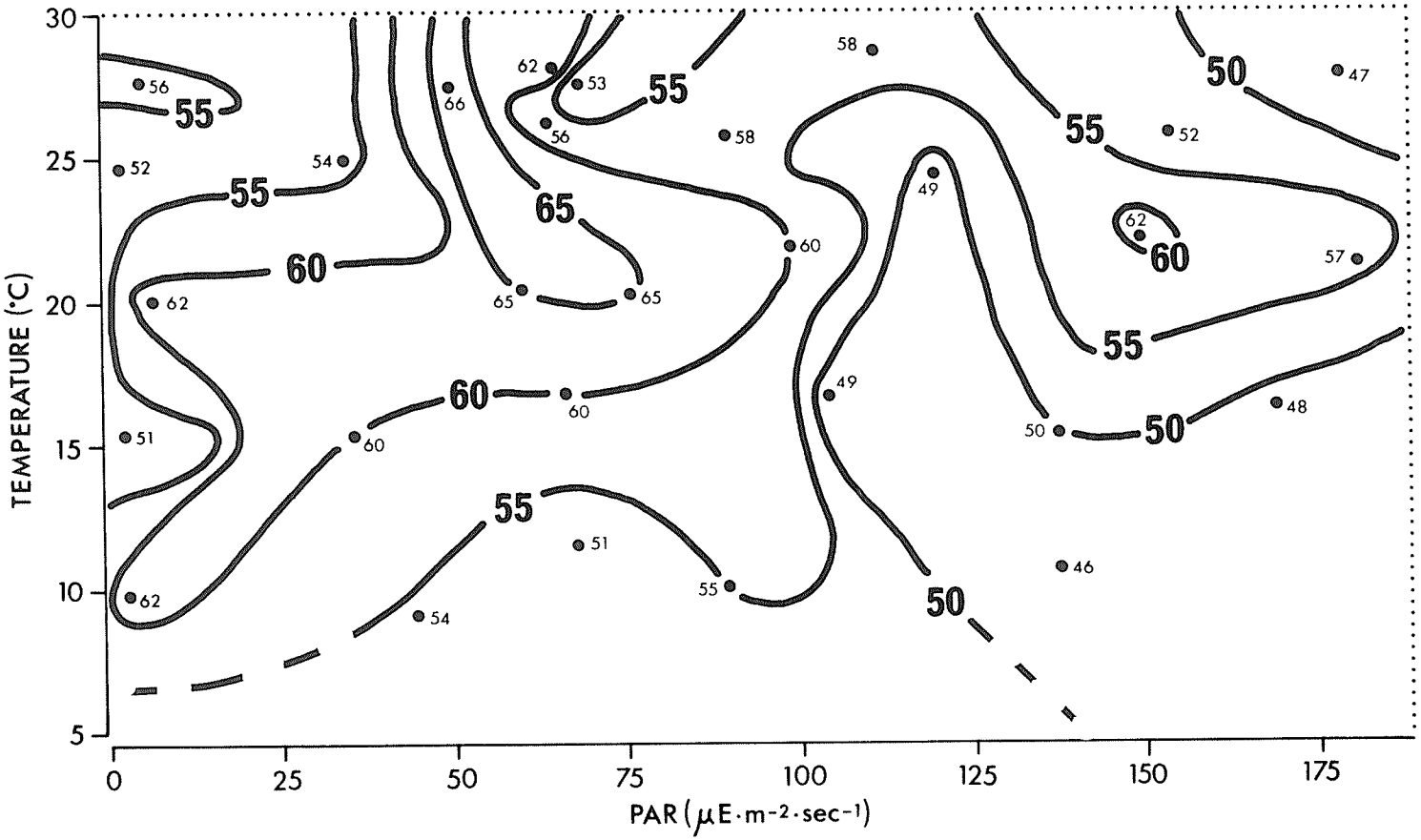
4.3.5 Seed Weight Depletion

Seed weight depletion ranged from a low of 46mg to a high of 66mg (Fig. 4.7).

The pattern of seed weight depletion observed was difficult to relate to PAR and temperature in a detailed manner; however, in general, seed weight depletion tended to be highest at PAR levels of 50-75 $uE \cdot m^{-2} \cdot s^{-1}$, and was greater at higher temperatures (Fig 4.7). For example, seed weight depletion at 15°C rose from 48mg at 140 $uE \cdot m^{-2} \cdot s^{-1}$ of PAR to 60mg at 30 $uE \cdot m^{-2} \cdot s^{-1}$ then dropped to 51mg at 4 $uE \cdot m^{-2} \cdot s^{-1}$. At 20°C seed weight depletion rose from 57mg at 175 $uE \cdot m^{-2} \cdot s^{-1}$ of PAR to 65mg at 60 $uE \cdot m^{-2} \cdot s^{-1}$ then dropped to 62mg at 10 $uE \cdot m^{-2} \cdot s^{-1}$.

The trends described are very general in nature: seed weight depletion did not show highly consistent trends with PAR and temperature (Fig. 4.7). Correlation analysis (Table 4.1) shows that seed weight depletion was weakly corre-

Figure 4.7: Utilization of seed reserves (initial seed fresh weight(mg) - final seed dry weight(mg)) during submerged leaf phenophase growth as a function of PAR and temperature.


TEMPERATURE (°C)
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25
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15
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5
0
25
50
75
100
125
150
175
PAR (μE·m⁻²·sec⁻¹)
55
60
65
50
56
52
54
66
62
53
56
58
58
49
52
47
62
57
65
65
60
62
60
60
49
48
51
50
60
55
51
46
55
62
54
50

lated with temperature and PAR (r=.16 and r=-.35 respectively) indicating that seed weight depletion was virtually independent of temperature and only slightly affected by PAR (within the limits of linear trends). Seed weight depletion was, however, more highly correlated with the shoot:root ratio (r=.43 - Table 4.2) indicating that a cause and effect relationship may exist between seed weight depletion and shoot:root ratio.

TABLE 4.1

Correlation of seed weight depletion with PAR and temperature

		TEMPERATURE	PAR
SEED WEIGHT DEPLETION	r	.16	−.35
	pr(>|r|)	.39	.06

TABLE 4.2

Correlation of seed weight depletion with plant growth parameters

		PLANT DRY WT	ELONG. RATE	ROOT: SHOOT	LENGTH PER UNIT SHOOT DRY WT
SEED WEIGHT DEPLETION	r	−.03	.07	.43	−.05
	pr(>|r|)	.87	.74	.02	.80

4.3.6 Integrated Plant Growth

Canonical correlation analysis was used to examine the variation of the environmental factors PAR and temperature in relation to the simultaneous variation in the plant parameters: plant weight, shoot elongation rate, shoot:root ratio, and length per unit dry weight of shoot. The fifth plant parameter which was monitored - seed weight depletion - was not included in the canonical correlation analysis as it was desired to have a "cause-and-effect" model to relate the environmental forcing variables to the plant response variables. Seed weight depletion is an index of seed resources utilized for growth. As such it occupies a gray area in this cause and effect relationship since seed resource utilization is both a forcing variable in plant growth (provision of growth resources) and a response variable to environment (differing seed resource utilization in varying environments).

The plant growth parameters (plant dry weight, shoot elongation rate, root:shoot ratio, and length per unit dry weight of shoot) were initially examined for normality. Plant dry weight and shoot elongation rate were approximately normally distributed while the two ratio variables, shoot:root ratio and length per unit of shoot dry weight, were both skewed. A square root transformation rendered the two ratio variables approximately normal.

The nature of the relationship between the plant growth parameters and the forcing variables PAR and temperature was

of concern as canonical correlation analysis summarizes only linear trends. Univariate correlations of the response variables with PAR and temperature were markedly improved by expressing PAR and temperature as natural logarithms (Table 4.3), and heteroscedasticity of residuals was reduced. This improvement was expected because of the non linear relationships described in the previous sections.

The model used in the canonical correlation analysis is defined in Table 4.4. Tests of significance of the two canonical variables defined by the canonical correlation analysis (Table 4.5) showed both to be highly significant. A two dimensional solution was therefore accepted (Gittins, 1985).

The meaning of the canonical variables was interpreted through analysis of the canonical structure. Table 4.6 describes the linear relationship between the measured plant parameters and the 2 canonical variables extracted from them. The correlation between individual parameters and the composite variables derived from them generally yields a more stable interpretation of the composite variable than an interpretation of the canonical weights (Gittins, 1985). Shoot elongation rate was highly and positively correlated with the first plant parameter canonical variable (PLANT1) with a correlation coefficient of .78. Plant dry weight was also correlated, but negatively, with PLANT1 (r=-.45). The two morphological variables, shoot:root ratio and length per unit of shoot dry weight, were more weakly associated with PLANT1 (r-.38 and r=.30 respectively). The canonical vari-

TABLE 4.3

Comparison of correlation coefficient improvement with log transformation of PAR and temperature

		PLANT DRY WT	ELONG. RATE	ROOT: SHOOT	LENGTH PER UNIT SHOOT DRY WT
PAR	r	.59	.41	.07	−.60
	pr(>|r|)	.001	.03	.73	.001
temp	r	−.20	.58	.33	.13
	pr(>|r|)	.30	.001	.09	.50

		PLANT DRY WT	ELONG. RATE	ROOT: SHOOT	LENGTH PER UNIT SHOOT DRY WT
ln(PAR)	r	.77	.40	.13	−.76
	pr(>|r|)	.0001	.03	.52	.0001
ln(temp)	r	−.17	.63	.36	.11
	pr(>|r|)	.38	.0002	.06	.59

TABLE 4.4

Canonical correlation analysis model used

PLNT WT, ELNG. RATE, SQRT(SHT:RT), SQRT(LENGTH PER UNIT SHT WT)
=
ln(TEMPERATURE), ln(PAR)

TABLE 4.5

Tests of significance of canonical variables

CANONICAL VARIABLE	CANONICAL CORRELATION	PROB>F	COMMENTS
1	.95	0.0000	reject H_0
2	.82	0.0000	reject H_0

H_0 : the canonical correlation in current row and following are 0

TABLE 4.6

Correlations of plant parameters with the canonical variables extracted from the plant parameters

PLANT PARAMETER	CANONICAL VARIABLE	
	PLANT1	PLANT2
PLANT DRY WEIGHT	−.45	.83
ELONGATION RATE	.78	.61
SHOOT:ROOT RATIO	.38	.17
LENGTH PER UNIT SHOOT WT	.30	−.85

TABLE 4.7

Correlations of environmental factors with the canonical variables extracted from the environmental factors

ENVIRONMENTAL FACTOR	CANONICAL VARIABLE	
	ENV1	ENV2
TEMPERATURE	1.00	−.00
PAR	−.04	1.00

able PLANT1 was interpreted as being a combined index dominated by the speed with which a plant grew and how light it was; and with some indication of plant morphology (slenderness and disproportionate allocation of resources to shoot growth).

The second canonical variable derived from the plant parameters (PLANT2 - Table 4.6) was highly and negatively correlated with the length per unit of shoot dry weight (r=-.85). Plant weight was as strongly correlated with PLANT2 but positively (r=.83). Shoot elongation rate was also correlated with the canonical variable PLANT2 (r=.61). The canonical variable PLANT2 was interpreted as being a measure of a plant's robustness and speed of growth.

The correlation between the environmental factors and the extracted environmental canonical variables ENV1 and ENV2 are found in Table 4.7. The first canonical variable extracted from the environmental factors (ENV1) was dominated by temperature. ENV1 was very highly correlated with temperature (r=1.0) and virtually independent of PAR (r=-.04). The first environmental canonical variable was, therefore, interpreted as being temperature.

The second canonical variable extracted from the environmental factors (ENV2) was dominated by PAR (Table 4.7). ENV2 was highly correlated with PAR (r=.999) and virtually independent of temperature (r=-.002). The second environmental canonical variable was interpreted as being PAR.

The correlation between the environmental factors and the canonical variables extracted from the plant parameters gives insight into the relationship between the environment and plant growth (Gittins, 1985). These correlations (Table 4.8) show that temperature was very highly and positively correlated with the canonical variable PLANT1 which was an index of plant morphology, dry weight, and speed of growth (r=.95). Therefore, higher temperatures were associated with lighter, more slender, and more rapidly elongating plants with higher allocation of resources to the shoot.

PAR was very strongly and positively associated with the canonical variable PLANT2 (r=.82) which is an index of robustness and speed of growth (Table 4.8). This indicates that higher levels of PAR were associated with heavier, more robust, and more rapidly growing plants. Temperature was not correlated with PLANT2 (r=-.002).

Examination of the correlation between the plant parameters and the canonical variables extracted from the environmental factors reveals a similar pattern of plant response to temperature and PAR (Table 4.9). Shoot elongation rate was highly and positively correlated with the first environmental canonical variable ENV1 (r=.74) which was dominated by temperature. Plant dry weight was negatively correlated with ENV1 (r=-.42). These correlations were interpreted as meaning that higher temperatures result in lighter and more rapidly growing plants. The two indices of plant morphology, shoot:root ratio and the length per unit of shoot dry

TABLE 4.8

Correlations of environmental factors with the canonical variables extracted from the plant parameters

ENVIRONMENTAL FACTOR	CANONICAL VARIABLE	
	PLANT1	PLANT2
TEMPERATURE	.95	−.00
PAR	−.04	.82

TABLE 4.9

Correlations of plant parameters with the canonical variables extracted from the environmental parameters

PLANT PARAMETER	CANONICAL VARIABLE	
	ENV1	ENV2
PLANT DRY WEIGHT	−.42	.68
ELONGATION RATE	.74	.51
SHOOT:ROOT RATIO	.36	.14
LENGTH PER UNIT SHOOT WT	.29	−.70

weight, were weakly correlated with ENV1 (r=.36 and r=.29 respectively) indicating that higher temperatures also resulted to some degree in more slender shoots but with higher allocation of resources to the shoot (Table 4.9).

The second canonical variable extracted from the environmental factors (ENV2) was very highly correlated with the length per unit of shoot dry weight (r=-.70) and plant dry weight (r=.68 - Table 4.9). ENV2 was also highly correlated with the shoot elongation rate (r=.51). These correlations were interpreted as meaning that higher levels of PAR result in heavier, more robust, and more rapidly elongating plants. The weak correlation of shoot:root ratio with ENV2 (r=.14) indicates that the allocation of resources between the root and the shoot is not a linear function of light.

The proportion of variation in the individual plant parameters explained by the environmental canonical variables is given by the squared multiple correlation co-efficient (Gittins, 1985). The left-hand column of Table 4.10 is the squared correlation between the individual parameters and the first environmental canonical variable. The right-hand column is the squared multiple correlation between the individual plant parameters and both environmental canonical variables. The squared multiple correlation between the plant parameters and the 2 canonical variables extracted from the environmental factors (Table 4.10) indicates that 80% of the observed variation in shoot elongation rate can be summarized as a linear function of PAR and temperature.

TABLE 4.10

Squared multiple correlations between plant parameters and the 2 environmental canonical variables

	ENVIRONMENTAL CANONICAL VARIABLE	
PLANT PARAMETER	1	2
PLANT DRY WEIGHT	.18	.65
ELONGATION RATE	.55	.81
SHOOT:ROOT RATIO	.13	.15
LENGTH PER UNIT SHOOT WT	.08	.57

TABLE 4.11

Proportion of variation of the plant canonical variables accounted for by environmental canonical variables

		CUMULATIVE PROPORTION OF STANDARDIZED VARIANCE OF PLANT PARAMETERS EXPLAINED BY:	
		PLANT CANONICAL VARIABLES	ENVIRONMENTAL CANONICAL VARIABLES
CAN.	PLANT1	.26	.24
VAR.	PLANT2	.72	.54

Similarly, 65% of the variation in plant dry weight; 57% of the variation in length per unit of shoot dry weight; and 15% of the variation in shoot:root ratio can be summarized as a linear trend with PAR and temperature.

Redundancy is the proportion of variation in one set of canonical variables which is explained by the other set of canonical variables (Gittins, 1985). Table 4.11 shows that 54% of the variation observed simultaneously in the composite plant variables can be accounted for in terms of linear relationships with PAR and temperature.

4.4 DISCUSSION

4.4.1 Indicators Of The Essential Trait

4.4.1.1 Plant Survival

A wide range of survivorship was observed between treatments ranging from 0-100% indicating that the temperature and light conditions ranged from very good for survival to conditions highly adverse to survival. In this wide range of conditions tested it should also be possible to discern the behaviour of the response traits in buffering the essential trait from the wide range of PAR and temperature.

The survival data indicate that environmental stress was lowest at temperatures of 20-25°C since these treatments all had 90-100% survival (Fig. 4.2). Temperatures above and below this resulted in reduced survival, especially when PAR was less than 50 $uE \cdot m^{-2} \cdot s^{-1}$. Water temperatures at Lac du Bois (the seed source) during the period of time when the

wild rice plants were in the submerged leaf phenophase ranged from 13°C to 22°C during the day (Atkins and Stewart, 1985). The optimum temperatures for survival found in this growth chamber experiment seem slightly high in light of this. The survival data from this experiment is probably biased upward relative to field survival as the plants were protected from environmental stresses other than PAR and temperature.

At temperatures above 25°C and PAR levels below 50 $uE \cdot m^{-2} \cdot s^{-1}$ survival was markedly reduced. Plants grown in conditions approaching this threshold should show the largest plasticity in attempting to escape the adverse conditions.

4.4.1.2 Plant Dry Weight

Net primary production is the net accumulation of inorganic carbon resulting from the physiological processes of photosynthesis and respiration: both of which are highly temperature and light sensitive (Ting, 1982). Plant dry weight then should reflect the physiological status of the plant.

The plant dry weight data (Fig. 4.3) followed a pattern similar to that of plant survival (Fig. 4.2) but were more affected by PAR than was survival. Plant dry weight was greatest at temperatures of 20°C and decreased rapidly at PAR levels below 50 $uE \cdot m^{-2} \cdot s^{-1}$. The change in plant dry weight at low levels of PAR was more pronounced that the reduction in plant survival (Fig. 4.2). As well, plant dry

weight declined slightly at levels of PAR above 150 $uE \cdot m^{-2} \cdot s^{-1}$. Plant dry weight may be a better indicator of stressful conditions than plant survival in this case because of the sheltering from other stresses. In an environment not protected from physical stresses the threshold for survival would have been reduced.

The plant dry weight data are indicative of the resources available to the plant for growth. As the resources become more limited (ie higher stress) the response of the plastic traits should become more evident as the only tactic available will be more efficient use of the limited resources to buffer the essential trait of conversion to the floating leaf phenophase.

The optimum temperature for net primary production in this experiment was approximately 20°C which is within the range of temperatures recorded at Lac du Bois, the seed source. The optimum temperature found in this experiment for net primary production appears to be well adapted to the environment of Lac du Bois.

The apparent decrease in net primary production at PAR levels above 150 $uE \cdot m^{-2} \cdot s^{-1}$ was surprising as light levels are commonly above this level at Lac du Bois. The decrease in net primary production observed in this experiment may be an artifact of the experimental design. Under field conditions PAR levels fluctuate widely during the day. In the growth chamber experiments PAR was maintained at a constant level during the day. It has been shown elsewhere that de-

pression of photosynthesis levels occurs under continuous exposure to a single PAR level. Short term ^{14}C experiments may be required to determine if photosynthesis is depressed at high light intensities.

4.4.1.3 Shoot Elongation Rate

Shoot elongation integrates the resources available for growth of the shoot with shoot morphology. The rate of shoot elongation (Fig. 4.4) was a very smooth function of PAR and temperature. In view of the differences observed in plant dry weight (Fig. 4.3) it appears that shoot elongation rate is highly buffered so that it proceeds at a "steady" level in a given set of conditions.

The upturning of the iso-growth rate lines of shoot elongation rate (Fig. 4.4) are indicative of an abrupt change from light to temperature as the factor limiting shoot elongation. Barko et al (1982) mistakenly interpret this pattern as resource switching. Tilman (1982) clearly points out that temperature can not be considered a growth resource in the same sense as PAR, and hence, resource switching is not possible.

4.4.2 Response of Plastic Traits

4.4.2.1 Shoot:root ratio

The shoot:root ratio is an index which measures the amount of growth resources allocated to the shoot relative to the resources allocated to the roots. While this index

does suffer from the shortcoming of not taking into account root turnover it does still give an indication of allocation patterns.

The root:shoot ratio data (Fig. 4.5) show that while more resources were committed to shoot growth in all treatments, no clear trends were displayed with PAR or temperature as was hypothesized. Barko et al (1982) found a very strong correlation between temperature and the preferential allocation of resources to the shoot but at higher PAR levels than were tested here. The general trend in this experiment was an increase in the proportion of growth resources committed to the root at low light levels but many exceptions were found.

It therefore appears that the preferential allocation of resources to the shoot is not one of the hypothesized suite of plastic traits which buffers the essential trait.

The shoot:root ratio, however, is the only plant parameter to correlate significantly with shoot elongation rate which in turn showed a clear trend with PAR and temperature. This suggests that while the shoot:root ratio is not a simple function of temperature or PAR, it does have an effect on growth rate.

4.4.2.2 Length per unit dry weight of shoot

Changes in shoot morphology, which were monitored via length per unit dry weight of shoot, were hypothesized as being a plastic life-history trait of wild rice. Fig. 4.6

illustrates that the length per unit dry weight of shoot was greatly increased at PAR levels below 50 $uE \cdot m^{-2} \cdot s^{-1}$. The large change in length per unit of shoot dry weight from approximately 4 $cm \cdot mg^{-1}$ shoot at 50 $uE \cdot m^{-2} \cdot s^{-1}$ to over 7 $cm \cdot mg^{-1}$ shoot at under 10 $uE \cdot m^{-2} \cdot s^{-1}$ of PAR follows the changes predicted from the plant dry weight quite well. As well a lower length per unit dry weight is seen at temperatures above and below 20°C, especially at low PAR.

The response of shoot morphology to adverse growing conditions is to moderate the influence of changes in available resources on shoot elongation rate. Shoot morphology fits the criteria for being considered a plastic life-history trait.

4.4.3 Seed Weight Depletion

Seed weight depletion is an index of the amount of seed resources utilized by the plant for growth. Seed weight depletion is not a highly accurate index since it incorporates weight loss due to the initial seed moisture content. Since moisture content was not constant among all of the seeds an uncontrolled source of variation was introduced. Importantly though, the average seed weight depletion within each treatment should be unbiased as individual seed moisture content was random.

The general trend of higher seed utilization at lower light levels (Fig. 4.7) lends weak support to the hypothesis that seed resources are preferentially used under lower

light conditions. Seed resource utilization also generally increased with increasing temperature, especially at temperatures above 20°C and at PAR levels below 75 $uE \cdot m^{-2} \cdot s^{-1}$.

The correlations between seed utilization and the parameters considered to reflect the essential life-history trait (shoot elongation rate, plant dry weight, and survival) were all quite low (Table 4.2). A relationship, though, does exist between seed weight depletion and shoot:root ratio leading to speculation that seed resources may be preferentially utilized for shoot growth.

Seed resource utilization while not being strictly controlled by PAR and temperature may play a role in promoting shoot growth.

4.4.4 Integrated Plant Growth

Results of the canonical correlation demonstrated the coaction of the various growth parameters and showed that increasing temperature resulted in plants accumulating less biomass, being more slender, and elongating more rapidly. The effects of increased PAR levels were higher accumulation of biomass, and more robust and rapidly elongating plants.

The canonical correlation analysis separated the effects of PAR and temperature almost completely onto two separate variates, reflecting the experimental design.

The canonical correlation analysis summarized the major trends of plant dry weight, plant robustness, and rapidity of shoot elongation as a linear function of PAR and tempera-

ture. The plastic traits shoot:root ratio and length per unit shoot dry weight played little part in defining plant growth in these conditions. This is not to say that they do not have a role, simply that the linear canonical correlations model did not detect it well, if it exists.

4.4.5 General Discussion

The results of this experiment demonstrate that growth of the wild rice plant is significantly affected by both PAR and temperature over the range of conditions tested. This is consistent with results from studies of other aquatic macrophytes (Barko and Smart, 1982; Tobiessen and Snow, 1982).

PAR levels below 50 $uE \cdot m^{-2} \cdot s^{-1}$ resulted in a marked reduction in plant dry weight, especially at temperatures above 20°C. Dry weight generally plateaued at PAR levels greater than 150 $uE \cdot m^{-2} \cdot s^{-1}$ which is less than 10% of the maximum surface insolation levels found under field conditions and less than PAR levels commonly recorded in the water column at Lac du Bois, the seed source (Atkins and Stewart, 1985).

This adaptation to growing at low light levels has several implications. Optimization of growth under conditions of low light enhances competitive ability in situations of attenuated light such as stained waters or in the shade of competitors (Barko et al, 1982). The adaptation of submerged leaf phenophase wild rice to growth in lower light conditions than those in which it is often found suggests that competition may be an important factor in the evolution

of its life history strategy; although, wild rice is not generally considered a good competitor. The ability to grow efficiently at low light levels also increases the potential number of sites in which wild rice can grow.

Figure 4.3 indicates that photoinhibition of dry weight accumulation occurs at PAR levels above 150 $uE \cdot m^{-2} \cdot s^{-1}$ (Fig. 4.3). However, exposure to constant light regimes, as used in this experiment, has been found elsewhere to cause partial inhibition of photosynthesis; and so, inhibition may be an artifact of the experimental conditions. Further studies are required to investigate this. If photo-inhibition of submerged leaf phenophase growth does occur, then water level management practices for wild rice production should be changed.

The response of the plants to stressful levels of PAR and temperature was altered shoot morphology. Plants grown under conditions thought to be stressful (based on plant dry weight) all showed an increase in length per unit shoot weight proportional to the degree of stress (Fig 4.6). The production of a more slender shoot in response to low PAR and high temperature conditions has been demonstrated in other aquatic macrophytes (Tobiessen and Snow, 1984). Barko et al (1982) consider the plastic response of shoot morphology to PAR and temperature to confer a competitive advantage upon a species since more rapid height growth gives access to higher light levels.

Shoot elongation rate (Fig. 4.4) exhibited a markedly consistent pattern in response to temperature and PAR; thus it appears that it is the interaction of shoot morphology with the resources available for growth (as measured by plant dry weight) which determines shoot elongation rate. The role of other factors which were hypothesized as being involved in the determination of elongation rate (shoot:root ratio, and seed resource utilization) could not be shown conclusively although there was some weak evidence for the preferential use of seed resources for shoot growth. It is possible that the methods used to investigate seed utilization were not sufficiently sensitive to detect differential utilization under most conditions.

The conclusion drawn from these data is that changes in shoot morphology compensate for differences in the amount of resources available for shoot elongation which results in a relatively consistent elongation rate for a given PAR and temperature regime.

The net result of this buffering is to "maximize" the robustness of the plant relative to the stress level of its environment. A high stress environment would evoke a rapid elongation rate and allow an individual to "escape" by a more rapid conversion to the floating leaf phenophase. In a less stressful environment, plant growth would be co-ordinated towards the production of a more vigorous and robust individual preparatory to entering the aerial environment. This increased vigour may translate into better chances for

survival in the aerial environment where the plant is exposed to more physical forces (wind, waves) than it is during the submerged leaf phenophase.

Undoubtedly there are costs associated with both strategies. In the case of the latter strategy the costs are probably associated with competition for space in the developing canopy. With the former, "escape" is at the cost of developing into a less robust individual. Presumably a less robust individual would have reduced chances for survival during later stages in the life cycle in the physically harsher aerial environment and in competition with other plants. This apparent "cost", though, enhances the chances for survival through the floating leaf phenophase. The tradeoff between escape and robustness was found to vary with the stress of the environment.

The plastic traits of shoot morphology and possibly differential seed utilization were found to strongly buffer the rate of shoot elongation over a range of PAR levels and temperatures. Wild rice seems to fit the theory of Caswell (1983) that plastic traits do serve to buffer an essential life history trait.

4.5 GENERAL CONCLUSIONS

The traditional view of wild rice ecology has been of an unbuffered "boom or bust" species living in an unpredictable environment. Life history theory of plants grown in unpredictable environments, however, predicts the evolution of buffering mechanisms (Caswell, 1983).

The studies reported here and in chapters 2 and 3 revealed five buffering mechanisms:

1. A subpopulation of seed which requires more than one winter of afterripening to break primary dormancy and so adds a "fixed" proportion of annual seed production to the seed bank.
2. Environmentally induced secondary dormancy which adds a variable proportion of annual seed production to the seed bank. Much of the seed produced in any year will persist in the seed bank and presumably be available for stand establishment in following years.
3. The initiation of germination immediately following ice-breakup enables the subpopulation of early wild rice plants to fully exploit their environment by maximizing the length of the growing season and enabling development to occur before many competitors.
4. The extended period of time over which germination occurs (>30 days) is a life history strategy of "bet-hedging" against catastrophe. This drawn out germination period reduces the chances of the whole popu-

lation being decimated in the event of catastrophe such as a severe storm.

5. The life history strategy during the submerged leaf phenophase is one of maximizing plant robustness relative to the stress of the environment. In conditions of high PAR and moderate temperature, plant growth is co-ordinated toward the production of a robust plant preparatory to entering the aerial environment. In stressful conditions of low PAR or high temperature, changes in shoot morphology, and possibly the utilization of seed reserves, increase shoot elongation rate for the limited growth resources available. This strategy permits the plant to "escape" to the aerial environment by a more rapid conversion to the floating leaf phenophase.

In summary, the life history strategy of wild rice is one of "bet-hedging" against the unpredictability of its environment.

Chapter V

AN INDIVIDUAL PLANT MODEL FOR THE PRE-FLOATING LEAF PHENOPHASES OF WILD RICE GROWTH

5.0.1 INTRODUCTION

Today's trend towards reductionist Science can lead to very detailed understanding of the individual components of a system. Models can be used to integrate the known behaviour of these components in order to return to the holistic viewpoint (Hall and Day, 1977). The integration of the components of a system often leads to insights about the system that were not obvious from its components (Prasad et al, 1983; Hopkinson and Day, 1977). At a more basic level, models can also be used to formalize what is known about a system and to give insight into the data required to gain further knowledge about it (Hall and Day, 1977).

Early life history events are known to have an impact on growth and development during later stages of the wild rice life cycle (Rogosin, 1958). Thomas and Stewart (1969) used regression models to describe the influence of water depth on the morphology of the submerged leaf wild rice plant; but, no attempts have been made to model the growth of wild rice through its various developmental stages.

This chapter describes the development of a model which integrates the data from the studies of chapters 2,3, and 4

regarding the germination and submerged leaf phenophases of the wild rice life cycle. The model was developed:

1. in response to a perceived need to synthesize the growing body of data regarding the early growth of wild rice.
2. to permit generalization of the database and to gain insight into the processes operating within the system.
3. to determine weaknesses in the database which require further research, and to give insight into methodologies which will provide useful data; and
4. to provide a framework within which to test hypotheses and to integrate new information as it becomes available.

The model developed is an individual plant - stand model similar in concept to "Jabowa" developed by Botkin (1977). The forcing functions (daily total PAR; and mean daily sediment and water temperatures) are used to determine the response of the state variables (growth stage (phenophase) and size ie plant length and dry weight). The data base used to develop the model comes from the data presented in chapters 2, 3, and 4.

5.1 MODEL DEVELOPMENT AND VALIDATION

5.1.1 Overview

The modelling system consists of two parts: the "frontend" program, and the plant-growth model program.

5.1.1.1 "Frontend" program

The "frontend" is an interactive program, written in Mantes[1] which interfaces the user with the model. The "frontend" polls the user for the information required to configure the input data stream and to run the growth model. The question and answer format relieves the user from learning a complex array of keywords or data entry options in order to run the model. The "frontend" program also has the advantage of interfacing interactively with the user, while the growth model itself can be run as a batch job. Batch running of the model was considered essential due to the number of statements which are executed in the running of a typical individual plant-stand growth model.

The data polled by the "frontend" program include:

1. Environmental data. Either user-defined or default datasets may be selected for use in modelling.
2. Stand parameters. The user defines the following parameters: water depth, coefficient of light extinction, number of seeds per square meter at the begin-

[1] MANTES (MANitoba Text Editing System) is the text editing and file handling system in use at the University of Manitoba. Conversion of the "frontend" program to other systems or programming languages should be relatively simple.

ning of the winter, and the proportion of seed not surviving until ice-breakup.

3. Environmental data bias. To facilitate the investigation of the effect of changes in water temperature, sediment temperature, and photosynthetically active radiation on plant growth, the user can systematically bias the data. For example, when investigating the effects of increased sediment temperature during germination on stand development, the user would run the model with successively higher bias factors applied to the sediment temperature data.

5.1.1.2 Plant growth model program

The growth model was written in the Watfiv programming language as implemented at the University of Manitoba. Graphical output is produced by linking the model to a SAS/GRAPH (SAS Inst., 1982b) program.

The system modelled is an area 1m X 1m in a hypothetical pure wild rice stand. Initial plant density is user-defined as are the site characteristics water column depth and transparency. Growth of the individual plants is modelled from seed dispersal in the fall until the end of the submerged leaf phenophase. Plant growth is modelled as a function of daily total PAR and daily mean water and sediment temperatures using the plant growth data of chapters 2-4.

Model output includes population frequency-histograms of plant dry weights at the end of the submerged leaf pheno-

phase, and the number of days from ice-breakup until: germination, emergence from the sediments, and to the end of the submerged leaf phenophase. The frequency distributions arise from developmental differences brought about through germination lag which subjects the individual plants to subtle differences in daily PAR and temperature environments. The model is deterministic in nature.

For individual plants in the population, a series of "events" was recognized. A program module was developed to model each "event". The modular approach facilitated program development, but more importantly, allows updating of the model as more information becomes available.

The data requirements and module linkages of the growth model are illustrated in Figures 5.1 and 5.2.

The modelling strategy for each "event" was a function of the data available as detailed below and in Figure 5.1 and 5.2. One "event" was modelled as a function of conditions during the autumn and winter:

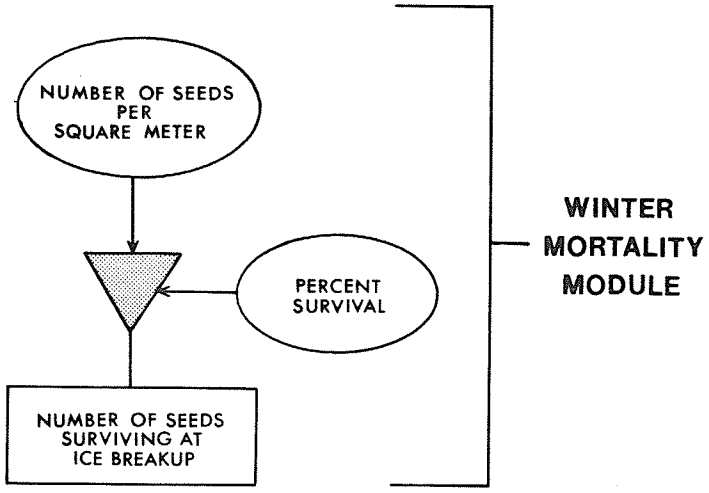
1. Winter mortality of seed: The loss of individual seeds during the period from seed dispersal to ice-breakup for whatever reason (predation, decay, desiccation, etc).

Three "events" were modelled as a function of daily environmental parameters starting with the day of ice-breakup - time 0:

Figure 5.1: Flow of information through the winter mortality and plant dry weight modules.

Top - Winter mortality module. Determination of number of seeds surviving until ice-break-up.

Bottom - Plant dry weight module. Determination of plant dry weight at the end of submerged leaf phenophase.


NUMBER OF SEEDS PER SQUARE METER
PERCENT SURVIVAL
NUMBER OF SEEDS SURVIVING AT ICE BREAKUP
WINTER MORTALITY MODULE

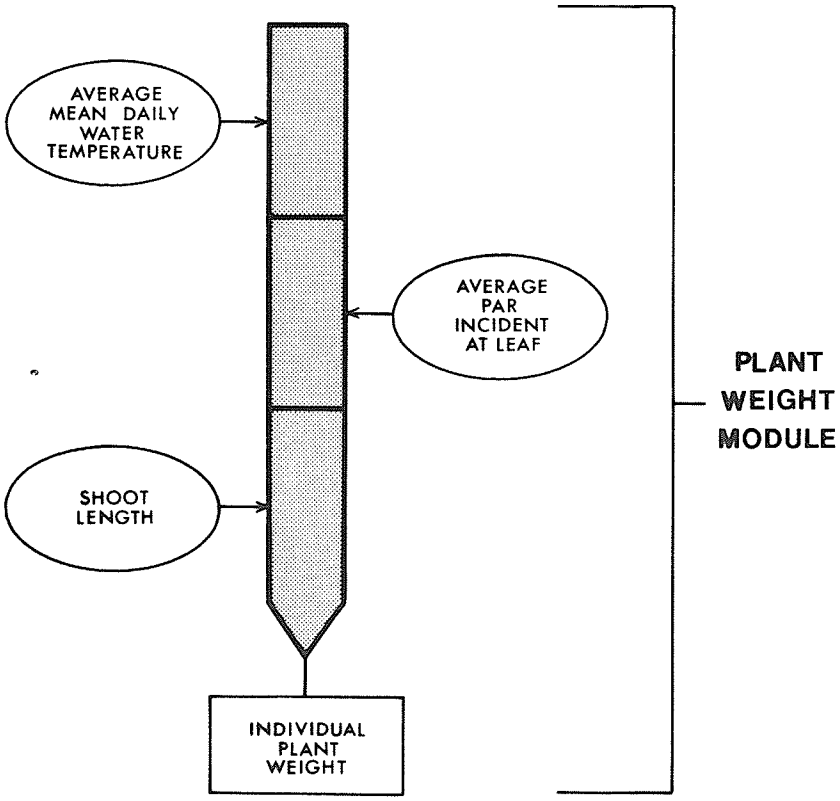
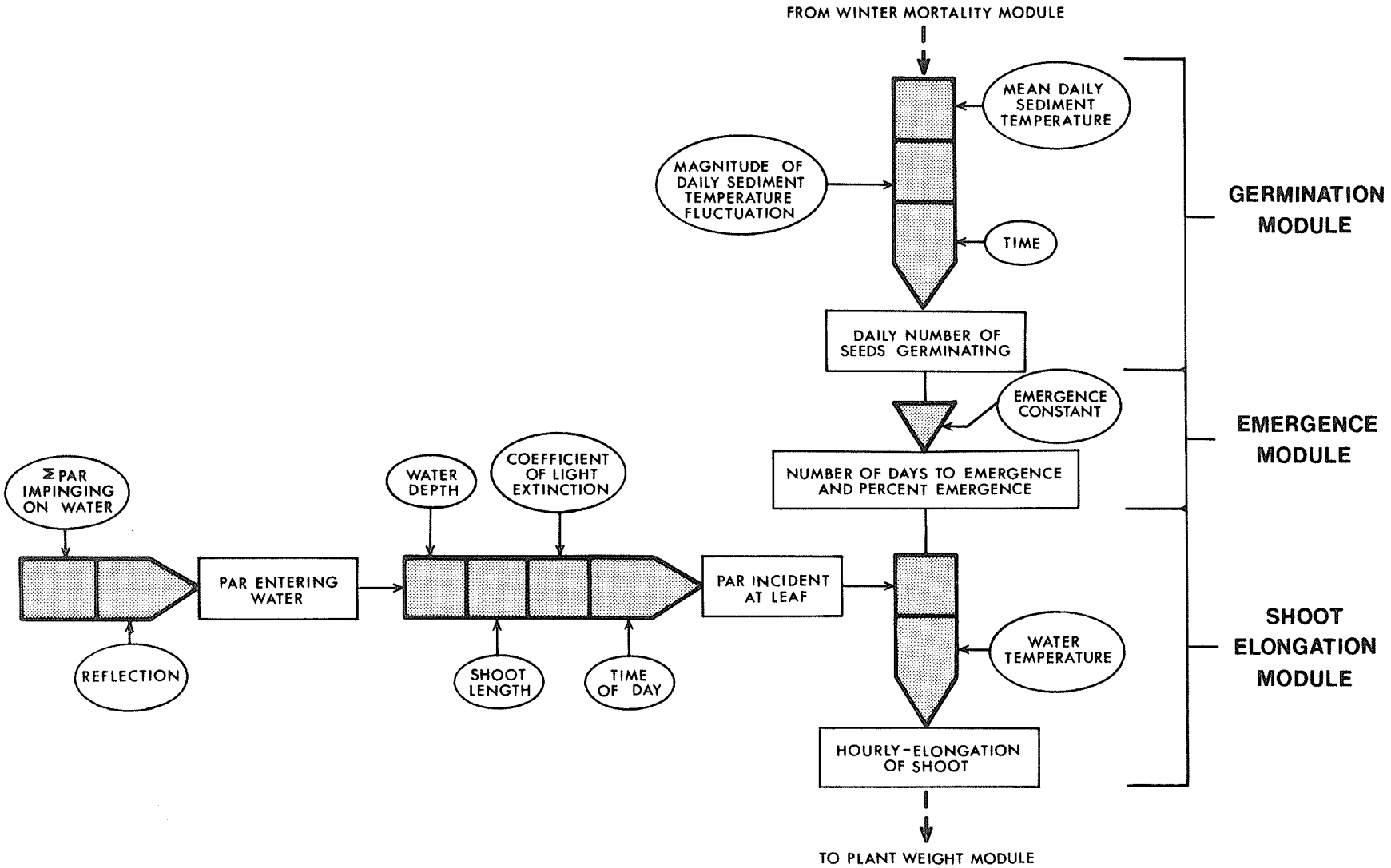

AVERAGE MEAN DAILY WATER TEMPERATURE
AVERAGE PAR INCIDENT AT LEAF
SHOOT LENGTH
INDIVIDUAL PLANT WEIGHT
PLANT WEIGHT MODULE

Figure 5.2: Flow of information through the germination module, emergence module, and shoot elongation module; and linkage of modules in the pre-floating leaf stages growth model. (Winter mortality and plant dry weight modules previously described in Figure 5.1).


FROM WINTER MORTALITY MODULE
MEAN DAILY SEDIMENT TEMPERATURE
MAGNITUDE OF DAILY SEDIMENT TEMPERATURE FLUCTUATION
TIME
DAILY NUMBER OF SEEDS GERMINATING
EMERGENCE CONSTANT
NUMBER OF DAYS TO EMERGENCE AND PERCENT EMERGENCE
ΣPAR IMPINGING ON WATER
WATER DEPTH
COEFFICIENT OF LIGHT EXTINCTION
REFLECTION
PAR ENTERING WATER
SHOOT LENGTH
TIME OF DAY
PAR INCIDENT AT LEAF
WATER TEMPERATURE
HOURLY-ELONGATION OF SHOOT
TO PLANT WEIGHT MODULE
GERMINATION MODULE
EMERGENCE MODULE
SHOOT ELONGATION MODULE

2. Seed germination.
3. Emergence: The elongation of the coleoptile until emergence at the sediment:water interface.
4. Submerged leaf phenophase growth: Elongation of the shoot to the water:air interface.

Finally, one "event" was modelled as a function of the "average" environmental conditions in which submerged leaf growth occurred:

5. Plant weight. Plant weight at the end of the submerged leaf phenophase.

The plant growth model is controlled by a driver which:

1. co-ordinates the growth of individual plants from seed by controlling access of individuals to the various growth "event" modules,
2. controls the flow of data into the model from datasets configured by the "frontend" program, and
3. controls the flow of data out of the model to specified devices.

5.1.2 Model Development and Validation

5.1.2.1 Winter mortality module

Purpose

The winter mortality module controls the number of seeds which die during the period of seed dispersal to ice-breakup and determines the individual seeds that will die.

Methods

A proportion of the seed dispersed in the autumn is known to not survive until ice-breakup in the spring due to predation by wildlife (Coulter, 1957; Peden, 1977), decay (chapter 3), or removal by ice or currents (Rogosin, 1951; Steeves, 1952). The actual proportion of the seed population which will not survive the winter has not been researched. For the purposes of the model it is a constant which is user defined (Figure 5.1).

The absolute number of seeds "killed" is calculated by taking the total number of seeds in the 1m by 1m area (input data) and multiplying by the proportion of the seed population which will die over the winter.

The required number of seeds to be killed is then selected at random from the total seed population and the selected seeds marked as being dead. A matrix called the "status board" is used to keep track of the growth stage of each individual plant in the simulation. Individuals marked as being dead are precluded from further growth!

Results

The program listing for the winter mortality module is found in Appendix I in program segment Remote Block WMORT.

Discussion

Whigham and Simpson (1977) speculated that seed mortality of Zizania aquatica L. from all sources was as high as 99%. In chapter 3 seed mortality of Zizania palustris L. from sources other than wildlife was estimated to be in the range

of 10-15% at Lac du Bois, Manitoba. Obviously, estimates of losses due to wildlife predation and decay are needed before the role of winter seed mortality during afterripening in the dynamics of the seed bank can be properly understood and modelled. At a more refined level, the factors regarding the survivorship of individual seeds need to be considered in relation to factors such as seed size (weight) which are known to affect survivorship in other species.

5.1.2.2 Seed germination module

Purpose

The germination module controls the germination of individual seeds in the stand over time in response to the mean daily sediment temperature and the magnitude of diurnal sediment temperature fluctuation (Fig. 5.2).

Methods

The germination of wild rice seed has been investigated in laboratory conditions over a wide range of temperatures (Simpson, 1966; chapter 2) and in field conditions (chapter 3). It was shown in chapter 2 that the rate of germination, and percent germination are a function of mean daily temperature and magnitude of daily temperature fluctuation in seed which was transferred from afterripening conditions to a time-invariant temperature regime (for example, a temperature regime in which day temperature was always 25°C and night temperature was always 15°C). It was further shown

that secondary dormancy was induced under laboratory conditions in seed subjected to mean daily temperatures in excess of 20°C. The seed bank experiments reported in chapter 3, however, showed that in field conditions, secondary dormancy was induced at much lower temperatures, possibly a result of oxygen deficit, or possibly due to time-varying temperature regimes (ie a thermal environment in which mean daily temperature increases over time).

The following approach was taken to model germination in time-varying temperature regimes as a function of temperature using the laboratory data reported in chapter 2 which involved time-invariant treatments. The assumption was made that as sediment temperature increased from winter afterripening conditions following ice-breakup, germination and the induction of secondary dormancy were competing processes (Totterdell and Roberts, 1979). Therefore, a proportion of the viable seed which remained ungerminated at any given time was subject to the induction of secondary dormancy and that induction was time and temperature dependent. For modelling purposes, an approximate solution to the induction of secondary dormancy was found by calculating (from the time-invariant data) the proportion of seeds which germinated in response to the current temperature conditions occurring in the model on the same number of days from exit from afterripening conditions. In this way germination was modelled as occurring during the early part of the growing season in response to rising temperatures, but over time the rate of

germination declined as secondary dormancy, germination, and mortality reduced the number of seeds available for germination.

The actual process involved in forming the germination module follows. Using the data reported in chapter 2 for seed afterripened 7½ months, a logistic curve was fit to the germination over time data for each of the 100 temperature treatments tested. The logistic curve was used to model germination (Schimpf et al, 1977). An example of one of the germination curves modelled is shown in Figure 5.3 a.

The model:

$$\text{GERMINATION} = \frac{A}{1 + Ce^{B*\text{time}}} \qquad (4)$$

where, time is time (days) from transfer out of afterripening conditions,
e is the base of the natural logs, and
A, B, and C are regression constants.

was fit to the data using SAS PROC SYSNLIN (SAS Inst, 1982b), a least-squares procedure for fitting non-linear models.

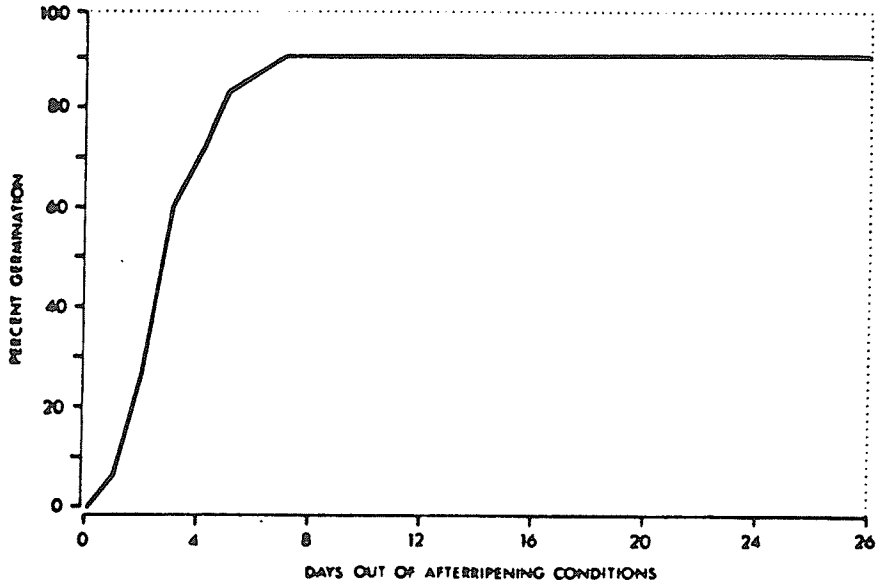
The parameters describing the 100 logistic curves were in turn modelled as a function of mean daily temperature and magnitude of daily temperature fluctuation using linear regression (SAS PROC REG (SAS Inst., 1982a)). These modelled parameters were then substituted back into the equation describing the logistic curve, permitting an estimate to be made of germination in any combination of day and night temperature, and for any time interval.

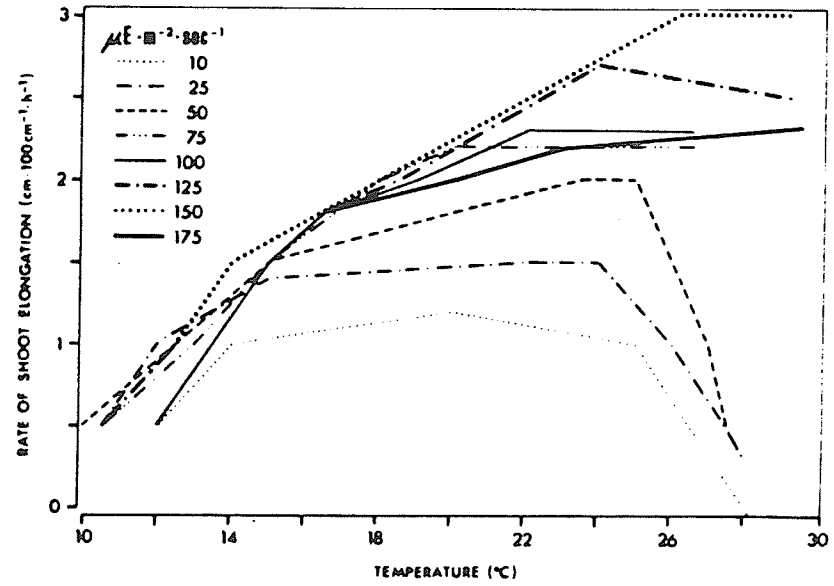
Figure 5.3: Examples of the data curves modelled in the first stage of the modelling process.

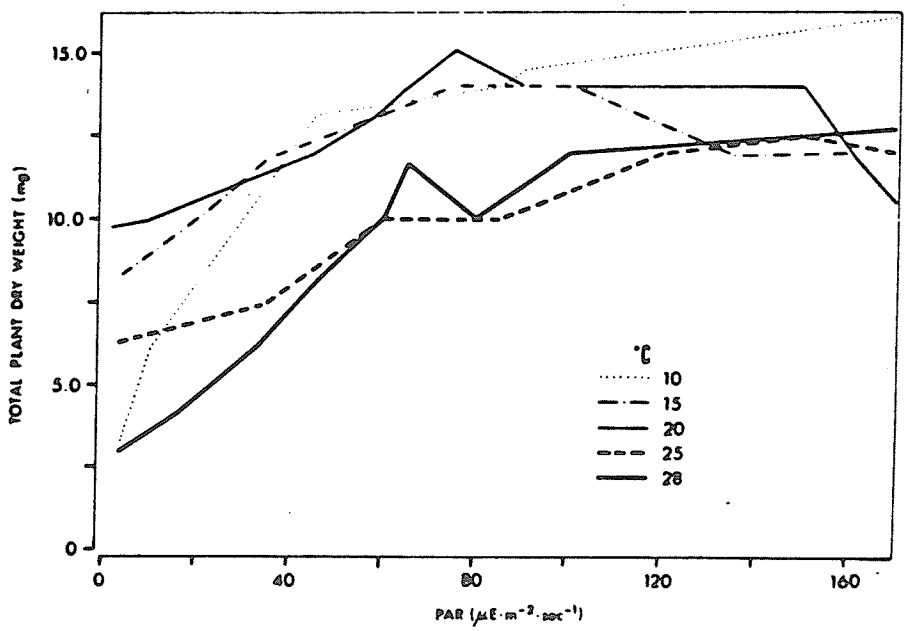
(a) Top - one of the 100 germination curves modelled as a function of time.

(b) Middle - shoot elongation rate as a function of temperature in eight PAR regimes.

(c) Bottom - Plant dry weight as a function of PAR in five temperature regimes.


PERCENT GERMINATION
0
20
40
60
80
100
0
4
8
12
16
20
24
26
DAYS OUT OF AFTERRIPENING CONDITIONS


RATE OF SHOOT ELONGATION (cm·100 cm⁻¹·h⁻¹)
μE·m⁻²·sec⁻¹
10
25
50
75
100
125
150
175
0
1
2
3
10
14
18
22
26
30
TEMPERATURE (°C)


TOTAL PLANT DRY WEIGHT (mg)
0
5.0
10.0
15.0
0
40
80
120
160
PAR (μE·m⁻²·sec⁻¹)
°C
10
15
20
25
28

The "goodness of fit" of the model was examined by plotting the residuals which were then examined for independence and by calculating the proportion of the total variation in the observations explained by the model (Arnason, pers comm).

The germination module uses the germination function developed to estimate the proportion of seeds which will germinate given the number of days from ice-breakup and the current sediment temperature conditions. Ice-breakup was considered to be the equivalent of transferring seeds from afterripening conditions in the laboratory. The proportion of seeds estimated to germinate is then used to calculate the number of seeds which will germinate in the current day of the simulation. This number of seeds is then picked at random from the ungerminated seeds and the "status board" matrix updated to reflect those individuals germinating.

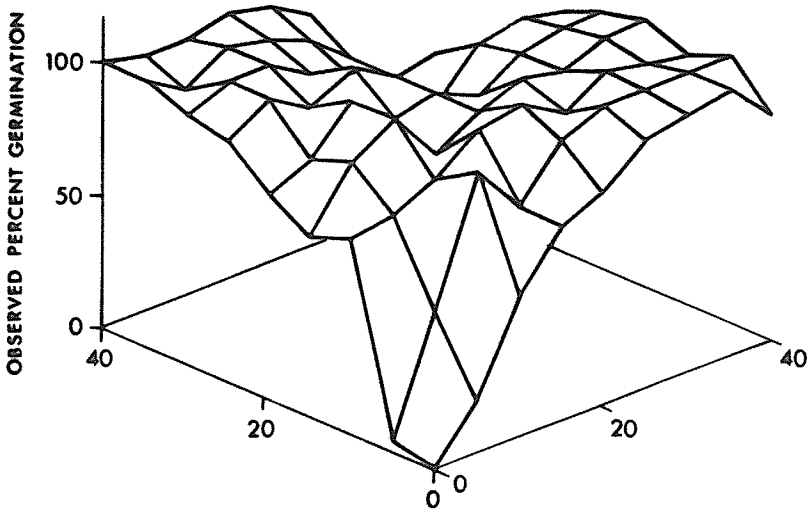
Results

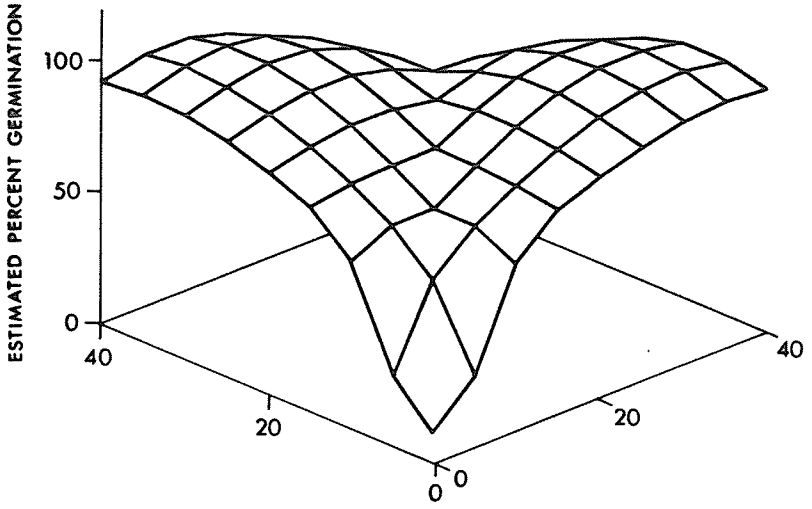
The program listing for the seed germination module is found in Appendix I in program segment Remote Block GERMIN.

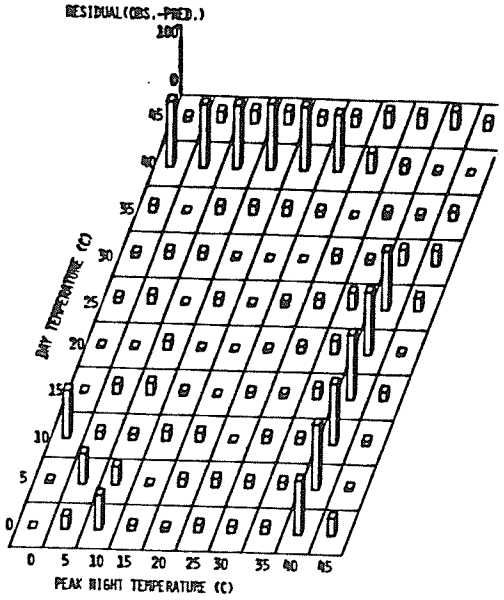
The germination model was developed on the assumption that the germination of wild rice seed follows a logistic curve over time. The model developed from this assumption tends to underestimate initial germination by approximately 5-10% as it does not rise rapidly enough. The model accounts for 50% of the variation in the data from which it was developed and follows the <u>trends</u> found in the germination data of

Figure 5.4: Characteristics of germination model.

(a) Top - data used in model development. This response surface: seed afterripened 7½ months and following 28 days in the 100 cell germinator (chapter 2).
(b) Middle - response surface generated by germination model for 28 days following ice breakup.
(c) Bottom - error of model in predicting real system (residuals).







positive residual

negative residual

chapter 1 as illustrated in Figure 5.4. The plot of residuals for 28 days after ice-breakup (Figure 5.4) shows that the error is structured with regard to treatment. The residuals are predominantly positive (the model has under-estimated germination) but generally less than 10%. The exception are all treatments with a mean daily temperature of 5°C or peak day or night temperature of 40°C which are generally overestimated by 70 to 100%. These large residuals result from the model setting germination percent equal to zero for all peak temperatures above 35°C which was determined as the limits for the model during development.

Discussion

The germination response model describes the germination of wild rice seed in time-invariant temperature regimes as documented in chapter 2. Despite the sometimes poor fit of the logistic curve to the data of individual temperature regimes, the germination model accounts for 50% of the variation in the data set from which it was developed. The seriousness of the lack of fit to some individual temperature regimes depends upon the application for which the germination model is being used. The mix of positive and negative residuals (Fig. 5.4) in constant temperature and low temperature fluctuation treatments indicates that the germination model should produce relatively unbiased estimates when temperature fluctuations are low. The model should provide adequate estimates to compare the relative effects of

treatments since the major data trends are followed (Fig. 5.4). The model is not considered adequate, however, to predict the effects of specific treatments on germination over time.

Other assumptions underlying the applicability of the model to field situations regard the correspondence of laboratory experiment results and germination behaviour in the field. It was assumed that the data of chapter 2 are representative of wild rice seed germination behaviour under laboratory conditions in general. The data of chapter 3, however, illustrate that while the trends remain the same, the magnitude of the germination response to temperature will vary between seed lots. Without knowledge of the factors influencing the germinability of a seed lot, the development of a highly accurate germination model cannot proceed. For this reason, it was decided to use the germination model as developed.

The most sweeping assumption made in the model regards the induction of secondary dormancy which was approximated by allowing time as a parameter in the model to reduce the rate of germination. This does not truly model the induction of secondary dormancy, and so cannot accurately reflect the induction of secondary dormancy in response to specific conditions.

The problem addressed by this modelling process centred on the role of time in the germination behaviour of wild rice seed and the possible effect of a time-varying environment.

It seems from this exercise that the induction of secondary dormancy in the field occurs over time and is induced by some factor other than, or in concert with, temperature. The factors which induce secondary dormancy need to be elucidated and quantified before the induction of secondary dormancy can be modelled.

The model yields predictions which follow the major trends in wild rice germination over time and have given insight into the role of time in the germination behaviour of wild rice. Further work remains to be done to model germination as a process.

5.1.2.3 Emergence module

Purpose

The emergence module models the extension of the coleoptile of germinated seeds through the sediments to the sediment:water interface (Fig. 5.2).

Methods

The emergence process was modelled as having 100% survival and as taking 4 days to attain 50% emergence based on estimates derived from unpublished preliminary work on the subject which can be found in Appendix II.

Results

The program listing for the seedling emergence module is found in Appendix I in program segment Remote Block EMERGE.

Discussion

Emergence was included in the model despite the paucity of data with which to model it to highlight the need for more work in this area. The preliminary data of Appendix II indicates that emergence may have a substantial effect on stand dynamics. It can be hypothesized that success in seedling emergence is a factor in the four year cycles noted in wild rice stand productivity by Moyle (1944) and Jenks (1899).

The effects of sediment temperature, oxygen concentration, and seed burial depth in relation to seedling emergence success and rate need to be investigated. As well, in order to utilize this information, the distribution of seed in the sediments with respect to depth requires elucidation.

5.1.2.4 Shoot elongation module

Purpose

The shoot elongation module models the shoot elongation of the submerged leaf phenophase plant in response to hourly PAR levels and water temperatures (Fig. 5.2).

Methods

In chapter 4 a very strong relationship was found between PAR level, water temperature and shoot elongation rate in a controlled environment. Using the shoot elongation rate data of chapter 2, a response surface was developed to model shoot elongation rate as a function of PAR and temperature. The response surface was modelled by interpolating elonga-

tion rate values across the range of temperatures tested (10-30°C) at a series of PAR levels (10, 25, 50, 75, 100, 125, 150, and 175 $uE \cdot m^{-2} \cdot s^{-1}$). The shoot elongation rate vs temperature curves modelled are shown in Figure 5.3. For each PAR level a curve was fit to the elongation rate data using SAS PROC SYSNLIN (SAS Inst, 1982b). The model fit was:

$$\text{ELONGATION RATE} = X^{a} - e^{bX} \qquad (2)$$

where; ELONGATION RATE is the shoot elongation rate ($\% \cdot h^{-1}$),
e is the base of the natural log,
X = Temperature - 8,
and a & b are regression constants.

The rationale for fitting this model is as follows. The first part of the function:

$$X^{a}$$

was fit to approximate the constantly declining rate of increase observed in shoot elongation rate at temperatures below 20-25°C.

The second part of the equation for the curve:

$$- e^{bX}$$

was included to approximate the decline in rate of shoot elongation observed at high temperatures, probably as a result of increasing respiration costs. The term X (X=temperature-8) was used rather than including a variable

intercept term in the model to force the elongation rate function to approach zero as temperature approaches 8°C. Eight °C was the temperature extrapolated from the data at which elongation rate approached zero. Including this term as a constant rather than as a variable reduced the level of model parameterization required which simplified the next step in the process of modelling the whole response surface.

The next step in modelling the surface was to estimate the model parameters, a and b, as a function of PAR level using linear regression in a manner analogous to that described for the germination module. The resulting parameter estimates were then substituted back into the model describing elongation rate (equation 2). A restriction was then placed on the calculated rate: if calculated rate was less than zero then it was set to zero.

The resulting response surface was examined for goodness of fit by plotting residuals and calculating the proportion of variation explained by the model as described previously in the germination module section.

To model shoot elongation in absolute units (cm), the rate of elongation ($\%\cdot h^{-1}$) was determined for each plant for every hour of the day using the equation developed to describe the elongation rate response surface and PAR and water temperature data.

The input data to the submerged leaf growth module are mean daily water temperature and total PAR impinging on the water surface ($E\cdot day^{-1}$). The data required to drive the

submerged shoot elongation rate function are hourly water temperature and the level of PAR impinging upon the leaf surface. Diurnal temperature was assumed to follow a sine wave with peak amplitude occurring at 4:00pm and calculated using the following function:

$$\text{temperature} = A * \frac{\sin(t+14 * pi)}{12}$$

where; t is the time of day in hours
(+14 centres curve at 4:00pm),
pi is as always, and
A is the amplitude of the sine curve
(assuming 24 thermoperiod).

The calculation of hourly PAR levels at the leaf surface was more complicated. First, the total PAR value for the day was reduced by 40% to allow for reflection from the water surface (Gurney, pers comm). Next, it was assumed that the PAR level at each hour of the day was approximated by a sine curve with period length of 2 times the photoperiod. The amplitude of this sine curve was calculated from the total PAR value for the day (less reflection) as follows:

$$\text{Integral of sine curve 0 to 16 hours} = A * \frac{\sin(t * pi)}{16}$$

(Total PAR for the day less reflection)

$$\text{solving for A:} \quad A = \frac{\text{Total PAR} * pi}{32}$$

where; A is amplitude of sine curve,
pi is as always, and
t is time in hours

Finally, the calculated amplitude was substituted into the following equation which was solved to give the PAR level at each hour of the day.

$$\text{hourly PAR } (uE \cdot m^{-2} \cdot s^{-1}) = A * \sin\left(\frac{t+27 * pi}{16}\right)$$

where; A is the calculated amplitude of curve,
pi is as always, and
t is time of day in hours (+27 to centre the curve at 1:00pm).

Results

The program listing for the shoot elongation module is found in Appendix I in program segment Remote Block SUBMRG.

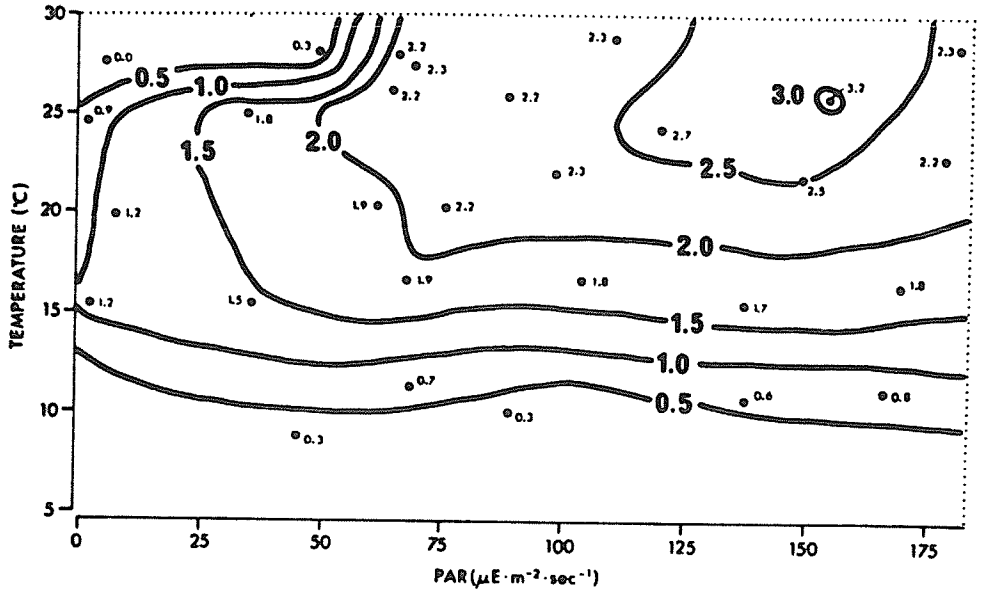
The response surface modelled by the submerged leaf elongation rate function is illustrated in Figure 5.5.

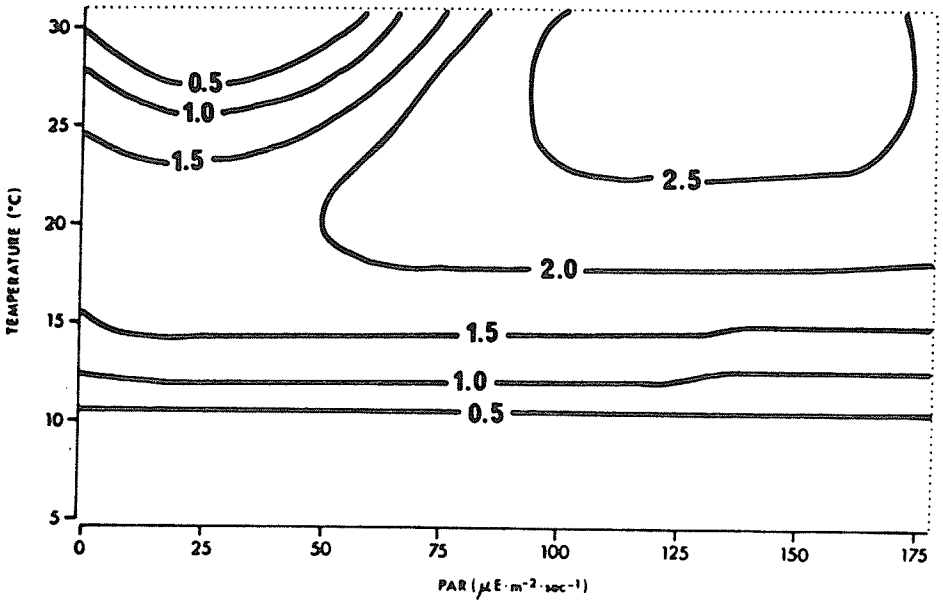
The submerged leaf shoot elongation rate model was examined for goodness of fit with the data reported in chapter 4 and found to account for 42% of the total variation in the data set. An examination of the residualts (Fig. 5.5) shows that the model tends to over-estimate elongation rate at PAR levels of less than 80 $uE \cdot m^{-2} \cdot s^{-1}$ and to under-estimate elongation rate above this PAR level. The most serious bias in the model is the over-estimation at very low PAR levels and high temperatures. This results from the model failing to properly account for the photo-compensation point.

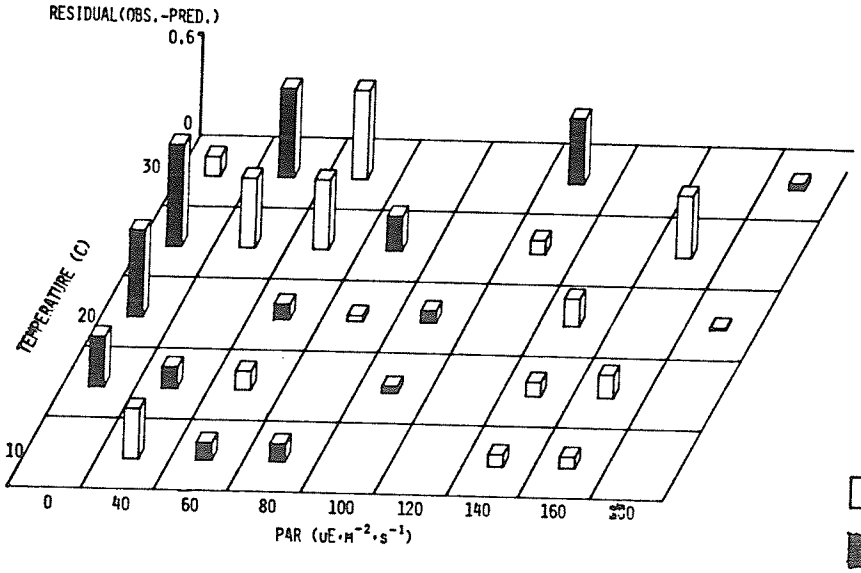
Discussion

The submerged leaf growth model makes several rather sweeping assumptions about the behaviour of both the plants and the environment. Three important assumptions were made with regard to plant response: firstly, that the pattern of shoot elongation in response to time-invariant PAR and water

Figure 5.5: Characteristics of shoot elongation model.
(a) Top - data used in model development. Shoot elongation rate ($\%\cdot hr^{-1}$) data from chapter 4.
(b) Middle - response surface generated by shoot elongation model. (elongation rate).
(c) Bottom - error of model in predicting real system (residuals).







positive residual

negative residual

temperature observed in chapter 4 approximates the relationship which occurs under field conditions; secondly, that elongation responses observed with plants grown in 30cm would be the same as those observed at other depths given the same conditions of PAR and temperature; and finally, that the relationship of elongation rate to PAR level was saturated at PAR levels above 175 $uE \cdot m^{-2} \cdot s^{-1}$.

The assumptions made and the lack of evidence to either support or reject them highlights the need for further work. The periodicity of the field data collected by me, and those found in the literature (eg. Lee (1979)), precludes the calculation of shoot elongation rate under field conditions. Further investigation is required, both under laboratory and field conditions. For example, primary productivity estimates using ^{14}C would help to elucidate the light saturation and photo-inhibition of net primary production at PAR levels above 150 $uE \cdot m^{-2} \cdot s^{-1}$ (chapter 4).

Other assumptions made in the shoot elongation model relate to the calculation of hourly levels of the environmental factors from mean daily values and total daily values. The modelling of hourly PAR levels as a sine curve may consistently underestimate the highest PAR levels and overestimate the early morning and evening levels since the assumption of a 16 hour light and 16 hour dark photoperiod was necessary in order to calculate hourly light levels in a 16 hour daylight period.

The scope of geographic and temporal validity of the data reported in chapter 4 are also unknown. The submerged leaf phenophase experiments of chapter 4 tested only one seed lot from Lac du Bois. How wild rice plants grown from seed of other years, or different lakes, would respond to PAR and temperature under laboratory conditions is unknown.

Despite the limitations of the shoot elongation module imposed by the variety of assumptions made, the estimates of plant elongation over time under various conditions seem plausible. The module should be quite adequate for generating hypotheses but should be used very cautiously in making predictions as further investigations are required to validate the module in terms of actual field conditions, and other seed sources and years.

5.1.2.5 Plant dry weight module

Purpose

The plant dry weight module models the total dry weight of a wild rice plant at the end of the submerged leaf phenophase as a function of its length and the average PAR and temperature conditions in which it grew (Fig. 5.1).

Method

The data reported in chapter 4 provide estimates of the weight of wild rice plants, grown in 30cm of water in known conditions of PAR and temperature, at the end of the submerged leaf phenophase. These plant weight data were mod-

elled as a function of the PAR and temperature conditions in which the plants had been grown similar to the method used to model the shoot elongation data (described previously). Plant weight was interpolated from the response surfaces found in chapter 4 along a series of "temperature transects" (10, 15, 20, 25, and 28°C) and across the range of PAR levels tested (0 to 175 $uE \cdot m^{-2} \cdot s^{-1}$). These "transects" are found in Figure 5.3. The data for each of the five "temperature transects" were then fit to:

$$\text{PLANT WEIGHT(mg)} = B_0 + B_1 * \text{PAR} + B_2 * \text{PAR}^2 \quad (3)$$

using SAS PROC REG to perform a least-squares linear regression.

The parameters: B_0, B_1, and B_2 describing each of the five "temperature transects" were then in turn modelled as a function of temperature. The same model (3) gave a reasonably good fit to the parameters B_0 and B_1 but the parameter B_2 was fit to the following model using SAS PROC SYSNLIN:

$$B_2 = a + b * \text{temperature} + \text{temperature}^c$$

where; temperature is the temperature of the "transect", and a, b, and c are regression constants.

The estimated parameters were then substituted back into the original model (3) to describe plant weight as a function of PAR and temperature.

The resulting model was examined for goodness of fit by plotting residuals and calculating the proportion of variance explained as described for the germination model.

Results

The modelled response surface is illustrated in Figure 5.6 along with the data from which it was generated for comparison.

The plant dry weight model was examined for goodness of fit with the data reported in chapter 4 and found to account for 48% of the total variation in the data set. Residuals were uncorrelated with either PAR or temperature; therefore, estimates of plant dry weight should be unbiased.

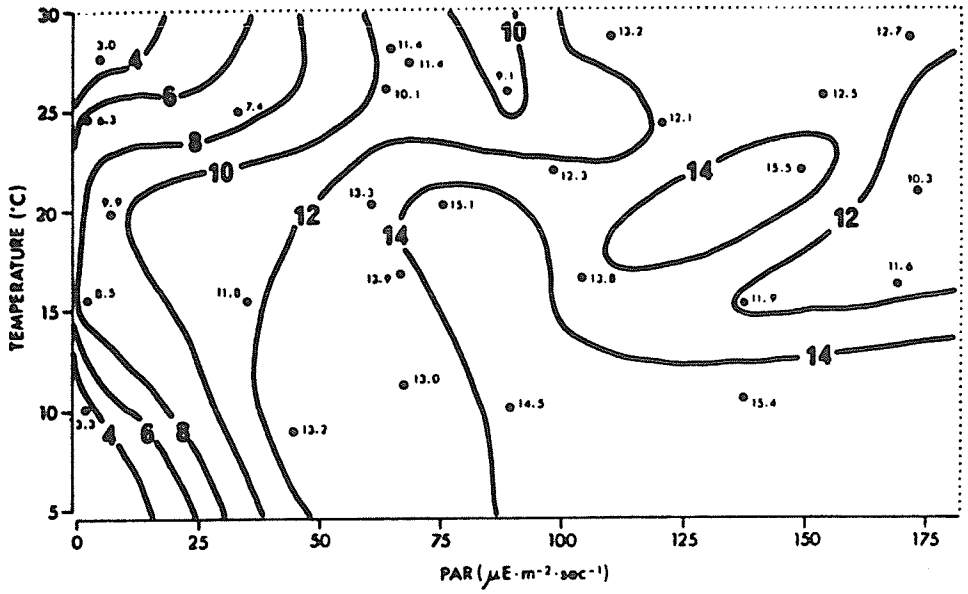
The program listing for the shoot elongation module is found in Appendix I in program segment Remote Block SUBWT.

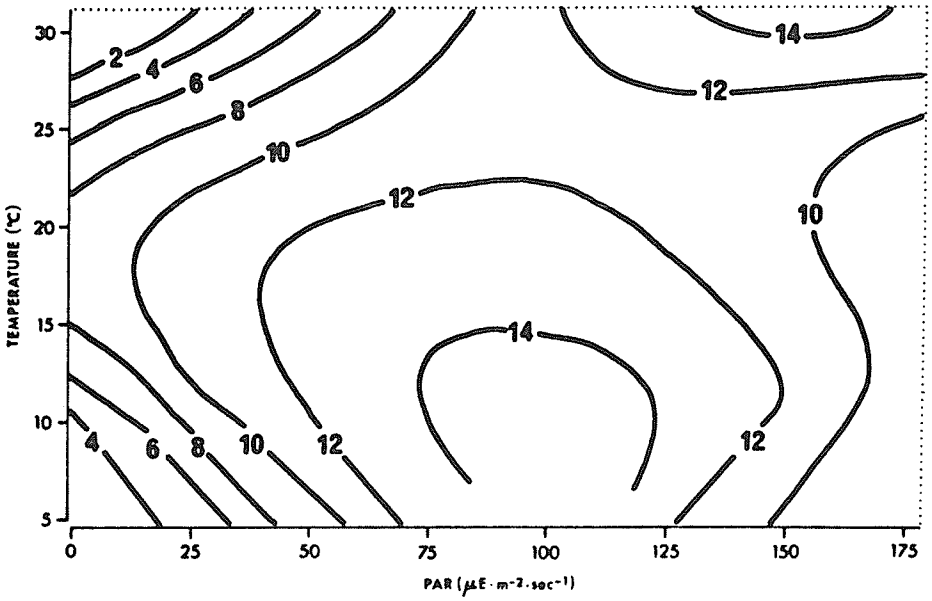
Discussion

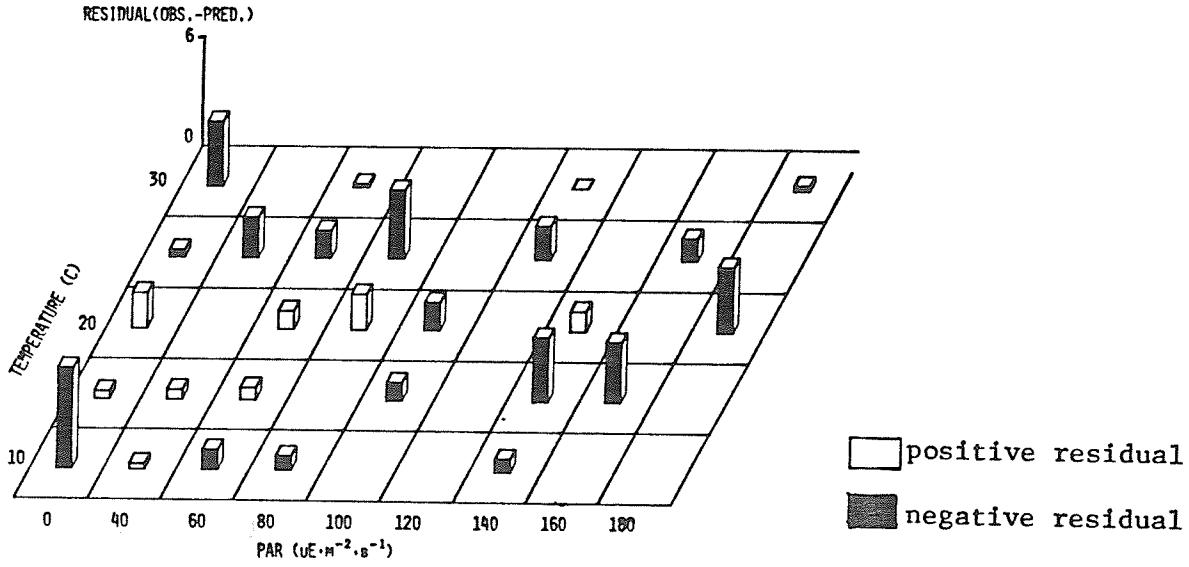
The plant weight model provides a good description of the data reported in chapter 4. The model used to describe plant weight as a function of PAR and temperature, however, is empirical and so should not be used to extrapolate beyond the range of conditions for which it was developed (Hall and Day, 1977).

For the purposes of the growth model, plants were assumed to be growing under saturated PAR conditions at levels above 175 $uE \cdot m^{-2} \cdot s^{-1}$. In the controlled environment experiments (chapter 4) it was found that net primary production reached a plateau or decreased at PAR levels above 150-175 $uE \cdot m^{-2} \cdot s^{-1}$. Investigation of the inhibition of growth of wild rice at PAR levels above 150 $uE \cdot m^{-2} \cdot s^{-1}$ is required. If inhibition is occurring at higher PAR levels, many of the

Figure 5.6: Characteristics of plant dry weight model.
(a) Top - data used in model development. Plant dry weight (mg) data from chapter 4.
(b) Middle - response surface generated by plant dry weight model.
(c) Bottom - error of model in predicting real system (residuals).


TEMPERATURE (°C)
PAR (μE·m⁻²·sec⁻¹)


TEMPERATURE (°C)
PAR (μE·m⁻²·sec⁻¹)


RESIDUAL(OBS.-PRED.)
TEMPERATURE (C)
PAR (uE·M⁻²·S⁻¹)
positive residual
negative residual

current water level management practices and recommendations should be modified.

It was assumed that the weight of plants grown in the field in varying water depths and under time-varying conditions of PAR and temperature could be approximated by the data of chapter 4 which were from plants grown in 30cm of water and in time-invariant conditions of PAR and temperature. This assumption requires testing. Neither are the effects of seed source and seed lot on submerged leaf plant weight known. The assumption implicit in using the plant weight model is that the data reported in chapter 4 describe the relationship of plant weight to PAR and temperature of wild rice plants in general. Again, further investigation is required to either support or negate these assumptions.

5.2 DISCUSSION

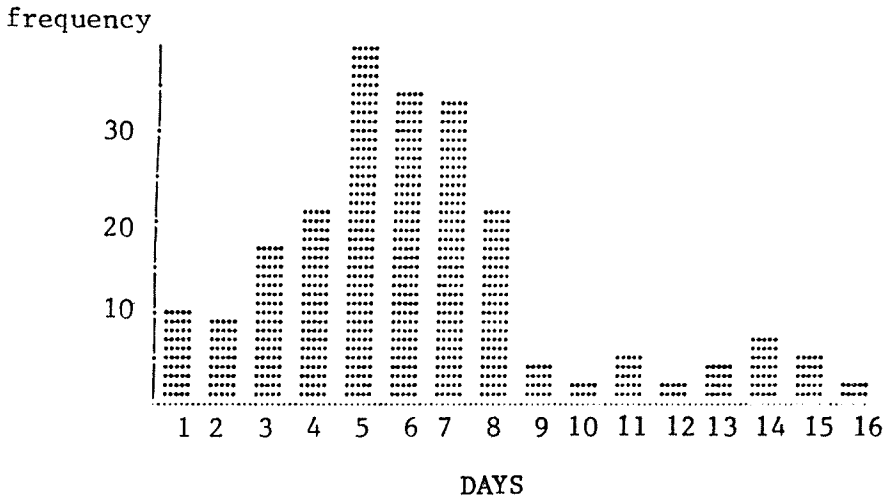
This is the first attempt to model wild rice growth as an integrative process - that is, one that builds upon itself. Figure 5.7 illustrates the graphical output from one run of the model in which 324 seeds were modelled to demonstrate model usage. The importance of the decision to use a batch-mode program interfaced with an interactive "frontend" program is well illustrated by this modelling exercise which required the execution of over 2.3 million statements! It should be noted that in this example the two forcing functions PAR and temperature alone have resulted in a very wide range of plant developmental stages over time (Fig. 5.7).

Figure 5.7: Summary of graphical output from pre-floating leaf stages growth model.

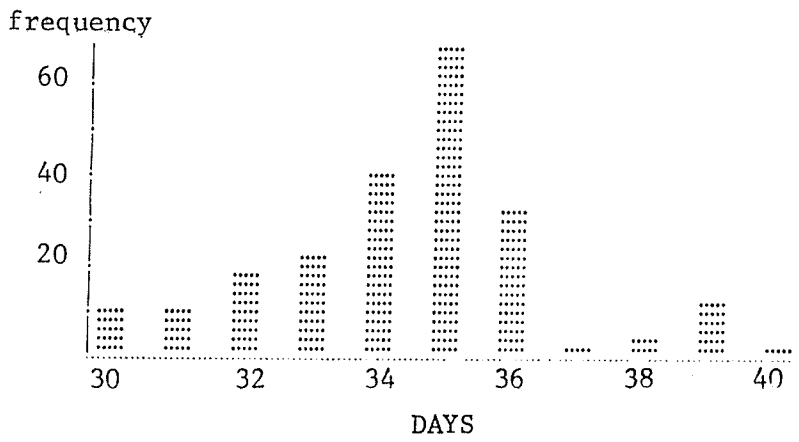
INITIAL CONDITIONS

SEEDS PER SQ METER	324
FRACTION WINTER KILLED	0.10
WATER DEPTH(CM)	100.
COEF LIGHT EXT	0.04
PAR BIAS	0.0
SEDIMENT BIAS	0.0
WATER BIAS	0.0

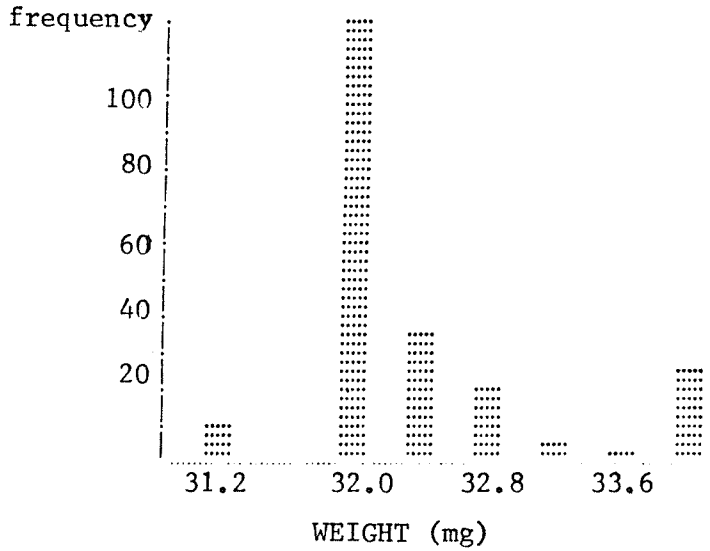
DAYS TO GERMINATION FREQUENCY DISTRIBUTION



DAYS TO END OF SUBMERGED LEAF STAGE FREQUENCY DISTRIBUTION



WEIGHT AT END OF SUBMERGED LEAF STAGE FREQUENCY DISTRIBUTION



This reflects the life-history strategy discussed in chapter 3 of spreading population development over time as a means of risk aversion.

The predicted plant weights of approximately 31-34mg·plant^{-1} (Fig. 5.7) are within the range of values found at Lac du Bois (Atkins and Stewart, 1985). This is encouraging, but does not lessen the need to collect field data to validate the model.

An obvious shortcoming of the model is the absence of a feedback loop to integrate intra-specific competition and individual plant growth. Undoubtedly competition must affect the later developing plants most strongly, but this is not reflected in the model. Further work with the model and the collection of individual plant field data may yield insight into the importance of intra-specific competition in the early growth of wild rice.

Another aspect of the model which requires further investigation is the assumption that the growth "events" are Markov processes. The model assumes that the change in growth parameters at any point in time is dependent only upon the current environmental state variables and not upon the past history of the plant. The manner in which the individual parameters were modelled also assumes an independence of growth parameters which is known to be untrue. The degree of co-action among growth parameters in the model results the interrelatedness of the growth parameters in the dataset from which the model was developed.

Figure 5.8 summarizes the plant parameter predictions from a further 9 runs of the model in a 3X3 factorial experiment examining model sensitivity. PAR was controlled at three levels (coefficient of light extinction=.02, .04, and .06); and sediment and water temperatures run at three bias levels (-4°C, 0°C, and 4°C). (Bias is added to the mean daily temperature data to change mean daily temperature upward or downward as specified).

The results of the 3X3 factorial experiment indicate a wide range of plant performance over the range of PAR and temperature biases tested. The model predicts a 2-fold increase in plant weight from the most stressful to the least stressful conditions tested (Fig. 5.8). Light was indicated to have a greater influence on plant weight in the conditions tested than did temperature.

These results are based on the assumption that high light levels do not decrease net assimilation as was the case in chapter 4 where photoinhibition appeared to occur. Comparison of the model results with field data from a wide range of sites is needed to further understand the role of PAR in determining submerged leaf phenophase plant growth.

The modelled role of PAR and temperature in the time taken to germinate and to reach the floating leaf phenophase is also shown in Figure 5.8. The degree to which the temperature and PAR treatments are independent of one another is striking in light of the modelling techniques used which should recover an interaction. This is consistent with the

Figure 5.8: Summary of 3 X 3 factorial model-sensitivity test.

Days to Germination

Coefficient of Light Extinction	-4	0	+4
.06	9.5	6.2	4.2
.04	9.5	6.2	4.2
.02	9.5	6.2	4.2

Temperature Bias

Days to End of Submerged Leaf Stage

Coefficient of Light Extinction	-4	0	+4
.06	54.1	40.4	33.2
.04	47.1	34.4	28.2
.02	46.0	32.8	26.1

Temperature Bias

Plant Weight

Coefficient of Light Extinction	-4	0	+4
.06	23.5	28.5	30.8
.04	27.3	32.3	34.3
.02	47.0	46.5	44.4

Temperature Bias

canonical correlation results (chapter 4) which also showed independent effects.

The examples given above demonstrate the model's potential as a research tool and as a means of elucidating alternate management strategies. The modular approach to model formation should easily accomodate the upgrading of individual growth stage modules and allow the inclusion of other factors not considered here such as interspecific competition.

The model successfully integrates the data regarding the germination of fully afterripened seed (chapter 2) and submerged leaf phenophase growth as influenced by PAR and temperature (chapter 4). It was not possible to integrate the induction of secondary dormancy specifically as a process due to insufficient data. Therefore, the role of the seed bank in the stand dynamics of wild rice was omitted. As well, data from the literature such as those of Svare (1960) remain to be incorporated.

The generalization of the database demonstrated earlier shows that the model can lead to insights regarding the ecological relationships of wild rice. Despite the very limited database on which to develop the model the predictions are in line with the limited field data available on the early developmental stages of wild rice. If anything, the database is being over extended. The fact that the predictions are plausible suggests that the microcosm studies such as the growth chamber study reported in chapter 4 can lead to insights into ecological relationships of wild rice.

Development of the model has identified a number of areas in which further research is warranted. These include: further investigation of the factors which induce secondary dormancy in wild rice seed; factors influencing winter mortality of seed; factors influencing the emergence of wild rice seedlings from the sediments and the role of emergence in stand dynamics; the role of intra-specific competition during the submerged leaf phenophase; and the impact of reduced submerged leaf growth on later developmental stages. A major weakness identified in present studies is the periodicity of the sampling cycle. The two week sampling period commonly used is too long to study the submerged leaf phenophase. A sampling cycle of 2-3 days would yield much more useful information.

Perhaps one of the most important aspects of the development of the pre-floating leaf stages growth model is that it provides a framework within which to test hypotheses and within which to integrate and to evaluate new information.

Modeling is a cyclic process with constant feedback (Hall and Day, 1977). The model presented in this chapter is the first cycle. The next step is to gather more information in the areas indicated during development and model usage. The pre-floating leaf stages growth model can be used as a powerful tool in furthering our knowledge of the ecological relationships of wild rice.

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```
*//ATKINS JOB ',,T=1M,F=BAI1'
*// EXEC WATFIV,SIZE=2000K
*//GO.SYSIN DD *
$JOB  WATFIV   ,NOLIST,NOEXT,NOWARN
C ******************************************************************
C *               WILD RICE SUBMERGED STAGES GROWTH MODEL          *
C *                                                                *
C *                     WRITTEN BY:  TREVOR ATKINS                 *
C *                                                                *
C *                              JULY, 1986.                       *
C ******************************************************************
C
C ******************************************************************
C *               PARTIAL VARIABLE LISTING                         *
C *                                                                *
C * DAY     (I) DAYS FROM GERMINATION - SIMULATION TIME SCALE      *
C * DAYS    (R) FLOATING POINT VALUE OF DAY                        *
C * DSEED   (D) SEED FOR RANDOM NUMBER GENERATOR                   *
C * FLUC_   (R) DAILY TEMPERATURE FLUCTUATION (SEDIMENTS)          *
C * GGUD    (R) IMSL FUNCTION TO GENERATE RANDOM NUMBERS           *
C * GRMPC   (R) FUNCTION TO CALC % GERMINATION FROM TEMP DATA      *
C * MDT_    (R) MEAN DAILY TEMPERATURE (SEDIMENTS)                 *
C * NWKILL  (I) INTEGER NUMBER OF SEEDS WINTER KILLED              *
C * NOSEED  (I) TOTSD-NWKILL = # OF SEEDS SURVIVING THE WINTER     *
C * RAND    (I) VECTOR IDENTIFYING  RANDOMLY SELECTED SEEDS        *
C * STATUS  (I) PLANT STAGE "STATUS BOARD" - RECORDS 5 STAGES      *
C *             -1 WINTER KILLED SEED                              *
C *             -2 GERMINATION DAY                                 *
C *             -3 DAY OF EMERGENCE FROM SEDIMENTS                 *
C *             -4 DAY OF ARRIVAL AT WATER SURFACE                 *
C *             -5 SUMMER KILLED SEED                              *
C * TOTSD   (I) TOTAL # OF SEEDS PER SQ M AT BEGINNING OF SIMULATION*
C * WKILL   (R) PERCENTAGE OF SEEDS WHICH DIE DURING WINTER        *
C *                                                                *
C *                                                                *
C ******************************************************************
C
C
C DECLARATIONS
C
      INTEGER STATUS(3025,5),DAY,RAND(302500),NWKILL,TOTSD
      INTEGER GMSLCT(3025)
      INTEGER NOSEED
      DOUBLE PRECISION DSEED
      REAL WKILL,DAYS,GRMPC,MDT,MDT2,MDT3,FLUC,FLUC2,FLUC3,A1,B1,C1
      REAL SUBLEN(3025),PLNTWT(3025),WATTMP(123),SEDTMP(123)
      REAL AVGTMP(3025),AVGPAR(3025)
      INTEGER PARTYM(3025),TMPTYM(3025),PARTOT(123)
C
C SET RANDOM NUMBER GENERATOR SEED
C
      DSEED=14566.0D0
C
C READ IN NUMBER OF SEEDS AND REDUCE TO A SQUARE.
```

```
C NO MORE THAN 3025 SEEDS PER SQUARE METER ARE ALLOWED
C
      READ(20,*)TOTSD
      TOTSD=(IFIX(SQRT(FLOAT(TOTSD))))**2
      IF(TOTSD .GT. 3025)TOTSD=3025
C
C READ IN FRACTION OF SEEDS THAT WILL NOT SURVIVE THE WINTER
C
      READ(20,*)WKILL
C
C READ IN WATER DEPTH, COEFFICIENT OF LIGHT EXTINCTION AND
C ENVIRONMENTAL "ADJUSTERS" TO BIAS ENVIRONMENTAL DATA
C
      READ(20,*)WATDEP
      READ(20,*)COEFEX
      READ(20,*)PARADJ
      READ(20,*)SEDADJ
      READ(20,*)WATADJ
C
C INITIALIZE THE STATUS BOARD
C
C COLUMNS 1 AND 5 ARE WINTER AND SUMMER DEAD SEEDS
C THEY ARE INITIALIZED TO 1 = ALIVE
C
C COLUMNS 2,3,4 ARE EMERGENCE,SUBMERGED LEAF, AND POST-FLOATING LEAF
C THEY ARE INITIALIZED TO 0 = NOT IN STAGE YET
C
      DO 1 I=1,TOTSD
      STATUS(I,1)=1
      STATUS(I,2)=0
      STATUS(I,3)=0
      STATUS(I,4)=0
      STATUS(I,5)=1
C
C INITIALIZE THE SUBMERGED LEAF LENGTH TO 1CM, WITH WEIGHT 0.0,
C THE PAR AND WATER TEMPERATURE ACCUMULATORS TO 0, AND PARTYM
C AND TMPTYM (NUMBER OF OBS IN AVGPAR AND AVGTMP) TO 0.
C
      SUBLEN(I)=1.0
      PLNTWT(I)=0.0
      AVGPAR(I)=0.0
      PARTYM(I)=0
      TMPTYM(I)=0
1     AVGTMP(I)=0.0
C
C READ IN WATER TEMPERATURE, PAR DATA, AND SEDIMENT
C TEMPERATURE DATA FOR 123 DAYS AND APPLY BIAS VALUE
C
      DO 27 DAY=1,123
      READ(17,*)PARTOT(DAY)
      PARTOT(DAY)=PARTOT(DAY)+PARADJ
      READ(18,*)WATTMP(DAY)
      WATTMP(DAY)=WATTMP(DAY)+WATADJ
      READ(19,*)SEDTMP(DAY)
```

```
27    SEDTMP(DAY)=SEDTMP(DAY)+SEDADJ
C
C SET THE WATER TEMPERATURE DAILY FLUCTUATION LEVEL
C
      TMPFLC=8.0
C
C BEGIN SIMULATION BY REDUCING SEED POPULATION TO REFLECT
C WINTER KILL
C
      EXECUTE WMORT
C
C CYCLE THROUGH PLANTS FOR 60 DAYS
C UNGERMINATED SEEDS GO TO SELECTION VECTOR FOR DAY
C GERMINATED SEEDS ARE GROWN ACCORDING TO THEIR GROWTH STAGE
C
      DO 7 DAY=1,60
      NUMB=0
      DO 2 I=1,TOTSD
C
C BYPASS DEAD SEEDS
C
      IF(STATUS(I,1) .NE. 1)GO TO 2
      IF(STATUS(I,5) .NE. 1)GO TO 2
C
C UNGERMINATED SEED - ADD TO TALLY OF UNGERMINATED SEED NUMBER - "NUMB"
C AND LIST IN SELECTION VECTOR
C
      IF(STATUS(I,2) .EQ. 0)GO TO 3
C
C GROW AS GERMINATED BUT NOT EMERGED PLANT
C
      IF(STATUS(I,3) .LE. 0)GO TO 4
C
C GROW AS SUBMERGED LEAF PLANT
C
      IF(STATUS(I,4) .EQ. 0)GO TO 5
C
C FLOATING LEAF PLANT - SKIP OVER
C
      IF(STATUS(I,4) .NE. 0)GO TO 2
3     EXECUTE SELECT
      GO TO 2
4     EXECUTE EMERGE
      GO TO 2
5     EXECUTE SUBMRG
2     CONTINUE
C
C SEED GERMINATION CAN NOW PROCEED FOR DAY
C
      EXECUTE GERMIN
C
C END OF DAY - START NEXT DAYS SIMULATION
C
7     CONTINUE
```

```
C
C END OF SIMULATION PERIOD... THOSE WHICH WERE GOING TO
C SURVIVE HAVE DONE SO!
C NOW CALCULATE TOTAL PLANT WEIGHT FOR EACH PLANT AT END
C OF THE SUBMERGED LEAF GROWTH STAGE.
C
      EXECUTE SUBWT
C
C OUTPUT SOME DATA FOR THE MASSES AND TO EXTERNAL DEVICE
C
      WRITE(6,814)TOTSD,WKILL,WATDEP,COEFEX,PARADJ,SEDADJ,WATADJ
      WRITE(6,812)
      DO 200 II=1,TOTSD
      WRITE(6,800)(STATUS(II,JJ),JJ=1,4),PLNTWT(II)
200   WRITE(21,813)(STATUS(II,JJ),JJ=1,4),PLNTWT(II)
      WRITE(6,815)
800   FORMAT(' ',T8,I5,T23,I5,T41,I5,T61,I5,T76,F6.1)
810   FORMAT(' ','WEIGHT  ',F6.1,'  TEMP   ',F4.1,'  PAR  ',F6.1)
812   FORMAT('1',T5,'WINTER KILL',T20,'DAYS TO GERM.',T35,
     1'DAYS TO EMERGE',T55,'DAYS TO FL. LEAF',T73,'PLANT WT(MG)')
813   FORMAT(4(I5,2X),F6.1)
814   FORMAT('1',T20,'INITIAL CONDITIONS'/
     1'0','SEEDS PER SQ METER',T30,I5/
     1'0','FRACTION WINTER KILLED',T30,F4.2/
     1'0','WATER DEPTH(CM)',T30,F6.0/
     1'0','COEF LIGHT EXT',T30,F6.2/
     1'0','PAR BIAS',T30,F5.1/
     1'0','SEDIMENT BIAS',T30,F5.1/
     1'0','WATER BIAS',T30,F5.1/)
815   FORMAT('1')
999   CONTINUE
      STOP
C ***************************************
C ***************************************
C **                                   **
C **           REMOTE BLOCKS           **
C **                                   **
C ***************************************
C ***************************************
C
C
C ***************************************
C *         REMOTE BLOCK WMORT          *
C ***************************************
C
C REMOTE BLOCK WMORT CALCULATES NUMBER OF SEEDS DYING BETWEEN
C SEED DISPERSAL AND ICE BREAKUP (FROM INPUT MORTALITY FRACTION)
C AND RANDOMLY DISTRIBUTES MORTALITY AMONGST ALL SEEDS
C
      REMOTE BLOCK WMORT
C
C RANDOMLY GENERATE NUMBER SEQUENCE FROM WHICH "NWKILL" NON-RECURRING
C NUMBERS WILL BE PICKED TO BE WINTER KILLED SEED.
C IF NO WINTER KILL OCCURS GO AROUND THIS SECTION
```

```
C
      NWKILL=IFIX(WKILL*FLOAT(TOTSD))
      IF(NWKILL .EQ. 0) GO TO 11
      CALL GGUD(DSEED,TOTSD,NWKILL*100,RAND)
C
C UPDATE STATUS BOARD TO REFLECT WINTER DEATH
C
      ITEST=0
      ITOP=NWKILL*100
      DO 10 I=1,ITOP
      IF(STATUS(RAND(I),1) .NE. 1)GO TO 10
      STATUS(RAND(I),1)=0
      ITEST=ITEST+1
      IF(ITEST-NWKILL .EQ. 0)GO TO 11
10    CONTINUE
      WRITE(6,801)
801   FORMAT(' FAILURE TO GENERATE SUFFICIENT RNDM NOS FOR WINT. KILL')
      STOP
C
C CALCULATE NUMBER OF SEEDS WHICH SURVIVE INTO SUMMER
C
11    NOSEED=TOTSD-NWKILL
      END BLOCK
C
C
C ***************************************
C *        REMOTE BLOCK SELECT          *
C ***************************************
C
      REMOTE BLOCK SELECT
      NUMB=NUMB+1
      GMSLCT(NUMB)=I
      END BLOCK
C
C ***************************************
C *         REMOTE BLOCK GERMIN         *
C ***************************************
C
C GERMINATE SEEDS FROM GERMINATION SELECTION VECTOR
C
      REMOTE BLOCK GERMIN
C
C CALCULATE SEDIMENT TEMPERATURE (MEAN AND FLUCTUATION)
C
      MDT=SEDTMP(DAY)
      IF(DAY .EQ. 1)FLUC=ABS(1.5*(SEDTMP(2)-SEDTMP(1)))
      IF(DAY .NE. 1)FLUC=ABS(1.5*(SEDTMP(DAY)-SEDTMP(DAY-1)))
C
C DETERMINE THE PERCENTAGE OF SEEDS GERMINATING AS F(MDT,FLUC)
C
      IF(DAY .EQ. 1)GRMS=GRMPC(MDT,FLUC,DAY)
      IF(DAY .NE. 1)GRMS=GRMPC(MDT,FLUC,DAY)-GRMPC(MDT,FLUC,DAY-1)
C
C DETERMINE NUMBER OF SEEDS TO GERMINATE (PROPORTION OF POPULATION
```

```
C TO GERMINATE * TOTAL NUMBER OF SEEDS WHICH SURVIVED WINTER).
C ROUND TO INTEGER VALUE.
C
      XGERM=(GRMS/100.0)*(FLOAT(NOSEED))
      TEST=XGERM-(FLOAT((IFIX(XGERM*10))/10))
      IF(TEST .LT. 0.5)NOGERM=IFIX(XGERM)
      IF(TEST .GE. 0.5)NOGERM=IFIX(XGERM)+1
C
C IF NO SEEDS ARE TO BE GERMINATED
C OR IF NO SEEDS REMAIN TO BE GERMINATED
C THEN SKIP GERMINATION SECTION
C
      IF(NUMB .EQ. 0)GO TO 13
      IF(NOGERM .EQ. 0)GO TO 13
      PRINT,NOGERM,' SEEDS TO BE GERMINATED ON DAY   ',DAY
C
C NOW IF NUMBER OF SEEDS TO BE GERMINATED EQUALS OR IS GREATER
C THAN NUMBER OF SEEDS REMAINING UNGERMINATED THEN ALLOW
C ALL NON-GERMINATED BUT ALIVE SEEDS TO GERMINATED
C
      IF(NOGERM .LT. NUMB)GO TO 15
      DO 16 II=1,NUMB
16    STATUS(GMSLCT(II),2)=DAY
      GO TO 13
C
C RANDOMLY GENERATE NUMBER SEQUENCE FROM WHICH "NOGERM" UNGERMINATED
C SEEDS WILL BE PICKED FOR GERMINATION
C
15    CALL GGUD(DSEED,NUMB,NOGERM*100,RAND)
C
C SELECT SEEDS FOR GERMINATION AND
C UPDATE STATUS BOARD TO REFLECT GERMINATION
C
      ITEST=0
      ITOP=NOGERM*100
      DO 12 JJ=1,ITOP
      IF(STATUS(GMSLCT(RAND(JJ)),2) .NE. 0)GO TO 12
      IF(STATUS(GMSLCT(RAND(JJ)),1) .NE. 1)PRINT,'GERM. SLCT ERROR A'
      IF(STATUS(GMSLCT(RAND(JJ)),5) .NE. 1)PRINT,'GERM. SLCT ERROR B'
      STATUS(GMSLCT(RAND(JJ)),2)=DAY
      ITEST=ITEST+1
      IF(ITEST-NOGERM .EQ. 0)GO TO 13
12    CONTINUE
      WRITE(6,802)
802   FORMAT(' FAILURE TO GENERATE SUFFICIENT RNDM NOS FOR GERMINATION')
13    CONTINUE
      END BLOCK
C
C ***************************************
C *         REMOTE BLOCK EMERGE         *
C ***************************************
C
C GROW COLEOPTILE TO SURFACE (PLUS ONE CENTIMETER!)
C
```

```
      REMOTE BLOCK EMERGE
C
C ALLOW 4 DAYS TO EMERGE - BEGIN SUBMERGED LEAF GROWTH
C 5 DAYS AFTER GERMINATION
C
      IF(STATUS(I,2) .EQ. 0)GO TO 18
      IF(STATUS(I,3) .GT. 0)GO TO 18
      IF(STATUS(I,1) .NE. 1)GO TO 18
      IF(STATUS(I,5) .NE. 1)GO TO 18
      IF(STATUS(I,4) .NE. 0)GO TO 18
      STATUS(I,3)=STATUS(I,3)-1
      IF(STATUS(I,3) .LE. -4)STATUS(I,3)=DAY
18    CONTINUE
      END BLOCK
C
C ****************************************
C *         REMOTE BLOCK SUBMRG          *
C ****************************************
C
C GROW THE SUBMERGED LEAF PLANT
C
      REMOTE BLOCK SUBMRG
C
C GROWTH IS A FUNCTION OF PAR AND TEMPERATURE
C PLANTS ARE GROWN EVERY HOUR
C
C
C SUBLEN IS CURRENT LENGTH OF SUB LEAF PLANT
C WATDEP IS WATER DEPTH
C
      REFLCT=.40
C
C PARTOT IS THE PAR INTEGRATED FOR DAY... EINSTEINS OF PAR.
C THIS NEEDS TO BE BROKEN DOWN TO GIVE HOURLY PAR LEVELS.
C "A" IS THE AMPLITUDE OF SINE CURVE FOR GIVEN TOTAL PAR FOR
C THE DAY AND IS IN E PER HOUR.  THIS IS THEN CONVERTED TO
C UE PER SECOND TO MATCH PAR NEEDED FOR RATE CALCULATION.
C
      A=(FLOAT(PARTOT(DAY))*3.14159)/32.0
      A=(A*1000000)/3600
C
C CYCLE THROUGH THE DAY AND GROW PLANT EVERY HOUR
C
      DO 20 IHOUR=1,24
      IF(SUBLEN(I) .GT. WATDEP)GO TO 20
C
C CALCULATE HOURLY TEMPERATURE FROM SINE WAVE WITH AMPLITUDE
C OF HALF OF DAILY TEMP FLUCTUATION. 14 IS ADDED TO THE
C TIME OF DAY TO SHIFT MAXIMUM TEMPERATURE TO 4 IN THE AFTERNOON.
C THIS TEMP IS ADDED TO TEMPERATURE ACCUMULATOR FOR USE IN PLANT
C WEIGHT CALCULATION.
C
       TEMP=((.5*TMPFLC)*SIN(FLOAT(IHOUR+14)*3.14159/12.0))+WATTMP(DAY)
       AVGTMP(I)=AVGTMP(I)+TEMP
```

```
      TMPTYM(I)=TMPTYM(I)+1
C
C CALCULATE HOURLY PAR FROM SINE CURVE WITH AMPLITUDE "A" AND
C MAXIMUM AT 1 IN THE AFTERNOON (16 HOUR PHOTOPERIOD)
C
      PAR=A*SIN(3.14159*(FLOAT(IHOUR)+27)/16.0)
      IF(PAR .LE. 0)GO TO 20
      PARINS=(PAR*(1.0-REFLCT))
      EFFPAR=EXP(ALOG(PARINS)-(COEFEX*(WATDEP-(.5*SUBLEN(I)))))
      IF(EFFPAR .LT. 1.0)GO TO 20
C
C ACCUMULATE EFFPAR FOR PLANT WEIGHT CALCULATION
C
      AVGPAR(I)=AVGPAR(I)+EFFPAR
      PARTYM(I)=PARTYM(I)+1
C
C THE GROWTH RATE (% ELONGATION PER HOUR = F(WATTMP AND PAR)
C IF PAR IS OVER 175 UE THEN GROW AT SATURATED RATE.
C
      IF(EFFPAR .GT. 175)EFFPAR=175
      X=WATTMP(DAY)-8.0
      Y=.5981+.00233*EFFPAR-.0000418*EFFPAR**2+.000000156*EFFPAR**3
      Z=.081+.00087*EFFPAR-.0000189*EFFPAR**2+.0000000747*EFFPAR**3
      IF(Z*X .LT. 0 .OR. X*Y .LT. 0)RATE=0.0
      IF(Z*X .GE. 0 .AND. X*Y .GE. 0)RATE=(X**Y)-EXP(Z*X)
C
C CONVERT TO FRACTION
C
      RATE=RATE/100.0
      IF(RATE .LT. 0)RATE=0.0
      SUBLEN(I)=SUBLEN(I)+(RATE*SUBLEN(I))
      IF(SUBLEN(I) .GT. WATDEP)STATUS(I,4)=DAY
20    CONTINUE
      END BLOCK
C
C ***************************************
C *         REMOTE BLOCK SUBWT          *
C ***************************************
C
      REMOTE BLOCK SUBWT
C
C SUBMERGED LEAF PLANT WEIGHT IS CALCULATED AS A FUNCTION OF
C THE AVERAGE TEMPERATURE AND LIGHT CONDITIONS DURING
C GROWTH.  VECTORS AVGPAR AND AVGTMP HAVE ACCUMULATED
C THE TOTAL PAR AND WATER TEMPERATURES. VECTOR PARTYM
C HAS THE ACCUMULATED NUMBER OF OBSERVATIONS WHICH GO INTO
C MAKING UP AVGPAR AND AVGTMP
C
      DO 25 I=1,TOTSD
      IF(SUBLEN(I) .EQ. 1)GO TO 25
      AVGPAR(I)=AVGPAR(I)/FLOAT(PARTYM(I))
      AVGTMP(I)=AVGTMP(I)/FLOAT(TMPTYM(I))
C
C WEIGHT IS MODELLED FOR 30CM PLANT FROM EXPERIMENTAL DATA
```

```
C AND PROPORTIONATELY CHANGED TO REFLECT DIFFERENCE IN LENGTH.
C GROWN AS LIGHT SATURATED IF PAR IS ABOVE 175 UE.
        B0=-16.860+2.797*AVGTMP(I)-.076*AVGTMP(I)**2;
        B1=.583-.047*AVGTMP(I)+.00112*AVGTMP(I)**2;
        B2=-1.005-.00008*AVGTMP(I)+AVGTMP(I)**.00202;
        PAR=AVGPAR(I)
        IF(AVGPAR(I) .GT. 175)PAR=175
        PLNTWT(I)=(B0+B1*PAR+B2*PAR**2)*(SUBLEN(I)/30.0);
25     CONTINUE
       END BLOCK
      END
C
C GRMS IS A FUNCTION RETURNING GERM% FROM MDT,FLUC, AND DAY
C
      REAL FUNCTION GRMPC(MDT,FLUC,DAY)
      REAL MDT,FLUC,DAYS,MDT2,MDT3,FLUC2,FLUC3,A1,B1,C1
      INTEGER DAY
      DAYS=FLOAT(DAY)
      MDT2=MDT**2
      MDT3=MDT**3
      FLUC2=FLUC**2
      FLUC3=FLUC**3
C
C GERMINATION TIME COURSE FOR INDIVIDUAL TEMP TRT DESCRIBED BY
C LOGISTIC EQUATION
C
      A1=58.33497+1.18756*FLUC+.19486*MDT2-.02637*FLUC2-.006092*MDT3
      B1=3.67490297-.00001852*MDT3
      C1=-.082711-.00637935*MDT2+.00016792*MDT3+.00001234*FLUC3
      GRMPC=A1/(1.0+EXP(B1+C1*DAYS))
      IF(GRMPC .LT. 0.0)GRMPC=0.0
      RETURN
      END
$ENTRY
*//FT17F001 DD DSN=ATKINS.MODEL(PAR),DISP=SHR
*//FT18F001 DD DSN=ATKINS.MODEL(H2OTEMP),DISP=SHR
*//FT19F001 DD DSN=ATKINS.MODEL(SEDTEMP),DISP=SHR
*//FT20F001 DD DSN=ATKINS.MODEL(ICODE),DISP=SHR
*//FT21F001 DD DSN=ATKINS.MODEL.OUTPUT,DISP=(OLD,PASS)
*// EXEC SAS
*//DATA DD DSN=ATKINS.MODEL.OUTPUT,DISP=(OLD,PASS)
*//SYSIN DD *
DATA YUP;
INFILE DATA;
INPUT WKILL GERM EMERGE ENDSL WT;
IF GERM=0 THEN GERM=.;
IF EMERGE=0 THEN EMERGE=.;
IF ENDSL=0 THEN ENDSL=.;
IF WT=0 THEN WT=.;
PROC CHART;
VBAR WKILL /DISCRETE;
TITLE WINTER KILL FREQUENCY DISTRIBUTION;
PROC CHART;
VBAR GERM/DISCRETE;
```

```
TITLE DAYS TO GERMINATION FREQUENCY DISTRIBUTION;
PROC CHART;
VBAR EMERGE/DISCRETE;
TITLE DAYS TO EMERGENCE FREQUENCY DISTRIBUTION;
PROC CHART;
VBAR  ENDSL/DISCRETE;
TITLE DAYS TO END OF SUBMERGED LEAF STAGE FREQUENCY DISTRIBUTION;
PROC CHART;
VBAR WT;
TITLE WEIGHT AT END OF SUBMERGED LEAF STAGE FREQUENCY DISTRIBUTION;
PROC MEANS  N MEAN VAR;
VAR GERM EMERGE ENDSL WT;
TITLE MEAN AND VARIANCE OF PLANT PARAMETERS;
```

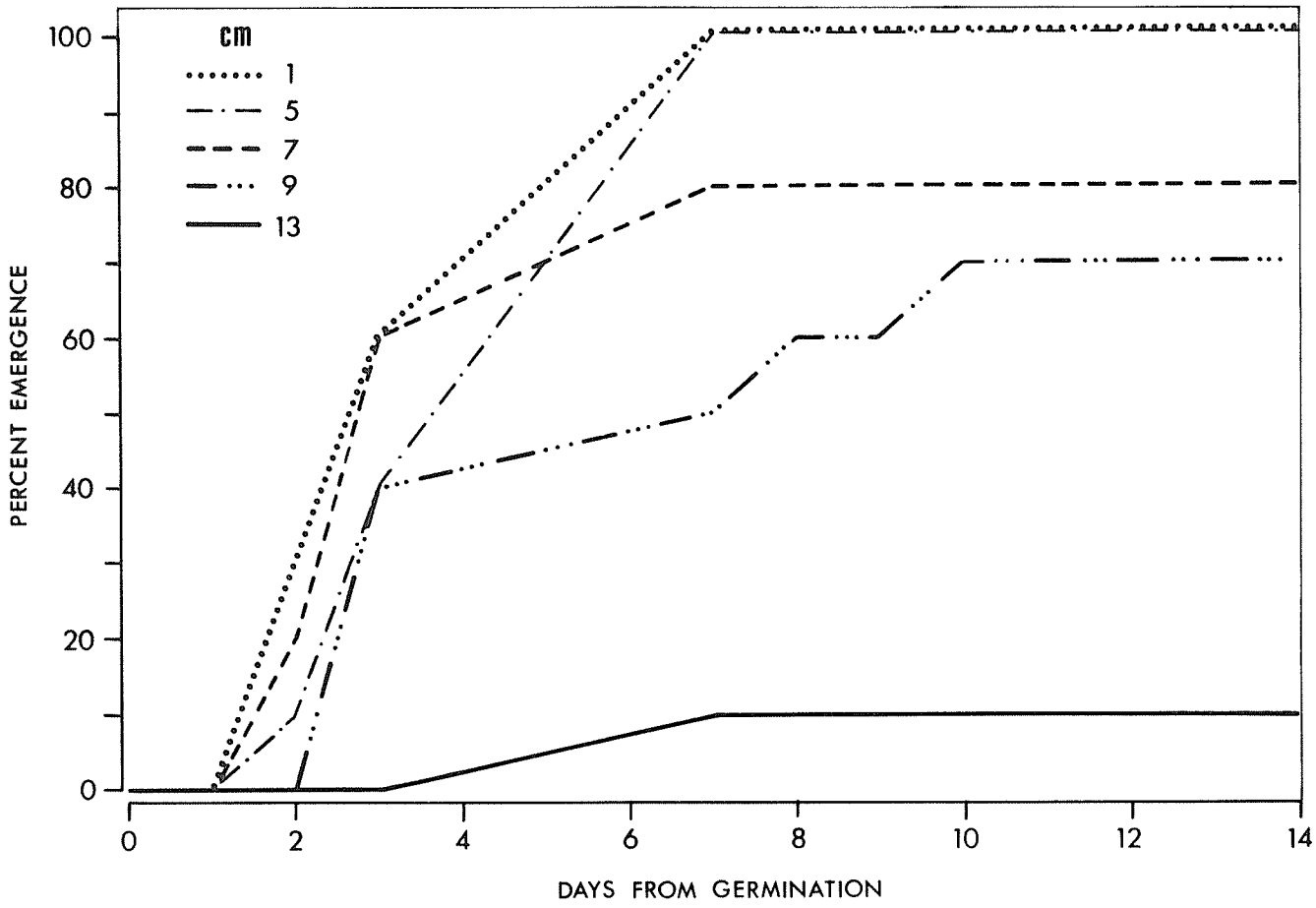
Appendix B

RESULTS OF SEEDLING EMERGENCE PRELIMINARY EXPERIMENT

The rate and success of seedling emergence were examined as follows. Five pails were filled with 15cm of sediments dredged from the West Bay of Lac du Bois. Ten germinated seeds were planted in each pail as pseudo-replicates. Planting depth ranged from 1cm to 13cm. The pails were placed in a growth chamber set to 20°C, without light, and emergence monitored daily.

The data are plotted in Figure B.1.

Figure B.1: Results of seedling emergence preliminary experiment.


cm
1
5
7
9
13
100
80
60
40
20
0
PERCENT EMERGENCE
0
2
4
6
8
10
12
14
DAYS FROM GERMINATION