THE EFFECTS OF WATER DEPTH INCREASES ON THE PRODUCTION AND GROWTH OF WILD RICE, *Zizania aquatica* L.

by

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A thesis submitted in the partial fulfillment for requirements of the degree of Master of Science

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DECLARATION

The research presented in this thesis was carried out by the author and has not been previously submitted for credit towards any degree or diploma. The work of others, where included, has been appropriately cited.

"Had you been there you could not have heard what he heard, or had you you would not have interpreted it. You could have smelled nothing but the mustiness of decaying vegetation, which blended with the aroma of growing things."

E.R. Burroughs

ABSTRACT

Wild rice, grown in plastic buckets suspended from specially designed rafts, was subjected to increases in water depth during the submerged-leaf, first floating-leaf, second floating-leaf, and the first aerial-leaf stages. The depth was increased from the initial depth of 45cm by either 0cm (control), 15cm, 30cm, or 50cm. With the exception of the 15cm treatment, increases in water depth resulted in decreases in the vegetative characteristics of plant height, total and component (root, stem, leaf) dry weights, and the number of tillers on each plant. As water depth increased similar reductions occurred in the reproductive characteristics of the number of inflorescences per plant, the number of pedicels per plant, and the dry weights of the inflorescences. The 15cm treatment had higher production values than the control, possibly because the lower light levels at the greater depth were closer to optimum for the particular seed source used. The final biomass did not seem to be influenced by the phenological stages when these depth increases occurred.

The growth of wild rice subjected to increases in water depth was analysed using growth curves and modelling techniques. The growth of the plants in the control treatment was accurately described by the logistic equation. Growth for plants experiencing increases in water depth, for all phenological stages studied, was also described by the logistic equation. The derived parameters of K and r, in each phenological stage, were

plotted versus water depth. Equations describing the resultant relationship between r and increases in water depth was determined to be the same. This suggested that for wild rice the maximum instantaneous rate of growth is constant. Thus, under conditions of optimum nutrient levels, water depth increases have the same effect on wild rice production during all phenological stages.

ACKNOWLEDGEMENTS

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To my family which has always been most supportive I owe a great debt. They provided encouragement and love when one needs it most, as only a family can provide. My wife Marg gave me love and patience without hesitation, and Gaelan our son. Thank you for giving as much as you could, all of the time.

Those that I wish to thank come from the general ranks of academic society, the students with whom one struggles alongside to understand self-inflicted folly. Dr. Rebbeca Counts and Mr. Tim Keenan, my collegues in wild rice research, deserve much more than a heart felt thanks, but that is all that is mine to give. I wish to give special acknowledgement to Mr. George Morgan who gave me invaluable assistance in remedial statistics and showed remarkable patience in working alongside "plant people". And to all the other graduate students who I have become so attached, thanks for making Stevenson's B & G the memory that it is today,

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Chapter 1

GENERAL INTRODUCTION

Wild rice has long been a part of northwestern Ontario's economy. Once a commodity for barter among native peoples and the first Europeans (Chambliss, 1940), this crop has become an important cash crop for native and non-native residents of the region. However, the year-to-year production of wild rice is highly variable (Lee, 1979). In order to increase the present production, and to re-establish the province of Ontario as a major producer in the world market, a far better understanding of how wild rice plants grow will be required. Basic research on growth performance and factors affecting yields, would enable producers to stabilize wild rice production.

Much of the success or failure of a wild rice crop can be directly attributed to one component of its environment - water. As an annual aquatic plant, wild rice depends upon specific characteristics of the water in which it grows for successful propagation from year to year by natural seeding (Dore, 1969). Important qualities of water include depth and fluctuations in level, as well as rate of flow, pH, and transparency (Sain, 1981). The commercial success of existing stands and the establishment of new stands requires an understanding of how these factors affect plant growth and seed production.

The characteristic of water which is most important to wild rice plants is depth (Dore, 1969; Macins, 1969; Thomas and Stewart, 1969; Lee, 1975). When wild rice is seeded in lakes and streams in northwestern Ontario it grows best in 0.3 m to 1.0 m of water (Dore, 1969; Sain, 1981). Wild rice will grow in depths outside of this range but the plants are of little commercial value due to their reduced yields (Lee, 1975). Deep water plants are thin, elongated, and present in very low densities; shallow water plants, although robust, may lodge at the time of seed formation causing problems with harvesting (Dore, 1969).

Water levels in lakes and streams vary from year to year depending upon local precipitation patterns. In years of above-average snow accumulation or heavy spring rains high water levels can cause significant reductions in overall grain production (Macins, 1969; Lee, 1975). Plant growth and survival are affected by deeper water. Plants growing in deeper water mature more slowly, and take longer to progress through their successive stages of development (Rogosin, 1958; Thomas and Stewart, 1969). It has been reported (Moyle, 1944) that increases of as little as 15cm during the growing season can reduce yields by half, and higher water levels may result in a total crop failure. However, although these studies suggest that wild rice growth is severely affected by increases in water depth, there have been no quantitative comparisons of when these increases are most critical.

In this study the effects of sustained water depth increases during the submerged-leaf, first floating-leaf, second floating-leaf, and aerial-leaf stages of wild rice development were examined. Initially, wild rice plants were grown at a recommended (Oelke, et al 1982) water depth of 45cm from which depth increases of 0cm, 15cm, 30cm, or 50cm were implemented. The depth increases were chosen to represent the range of water depth increases thought to be detrimental to lake production of wild rice. Specifically, there were two objectives : (i) to examine the effects of depth increases on plant survival, and vegetative and reproductive production; and (ii) to establish whether any one phenological stage of wild rice development is influenced more by these increases in water depth than others.

CHAPTER 1

The effects of increases in water depth on vegetative and reproductive production.

INTRODUCTION

The abundant lakes and streams of northwestern Ontario are ideal for wild rice production (Lee, 1974), and the harvest of this native cereal crop is an important part of the local economy. Unfortunately, year-to-year fluctuations occur in the productivity of such unmanaged wild rice stands, and, in any four year period, there are likely to be one crop failure, one bumper crop, and two fair crops (Moyle, 1944).

Studies conducted by Rogosin (1958), Weber and Simpson (1967), and Thomas and Stewart (1969) have shown that the depth of water in which wild rice grows affects the rate of plant development and production; however, success or failure of the wild rice harvest has been attributed most frequently to increases in water depth during various phenological stages (Chambliss, 1940; Moyle, 1944; Rogosin, 1951; Dore, 1969; Macins, 1969; Lee, 1974; Sain, 1981).

During the spring, higher water levels will cause etiolation of the seedlings and they may eventually die (Dore, 1969). If the water level is increased during the floating-leaf stage, when the roots are still small, the wild rice plants may be uprooted from soft sediments by the buoyancy of their own leaves (Chambliss, 1940). After the cuticle and stomates are formed at the floating-leaf stage (Hawthorn and Stewart, 1970), flooding of the plants may impede gas exchange and cause mortality. However, although these studies suggest that wild rice growth is severely affected by increases in water depth, there have been no quantitative comparisons of when these increases are most critical.

In the present study wild rice was systematically subjected to sustained increases in water depth during the submerged-leaf, first floating-leaf, second floating-leaf, and the aerial-leaf stages. The objectives of the experiment were to determine i) if increases in water depth during these phenological stages affected the survival and/or the vegetative and reproductive characteristics of wild rice; and ii) if the final harvest biomass was related to these inundations.

METHODS

Cultivation Procedures

Wild rice was grown in eight specially designed rafts (Fig. 1). A wooden latticework separated two closed-cell polystyrene floats (25cm x 52cm x 244cm) from which plastic buckets (28cm x 35cm x 14cm) were suspended by 5mm braided polypropylene rope. The ropes were affixed to the raft's latticework by end loops, and hooked onto nails partially driven into the top surface of the struts. The buckets could be lowered or raised to facilitate transplantation of seedlings, initiation of treatments, periodic inspection of seedlings, culling, and sampling.

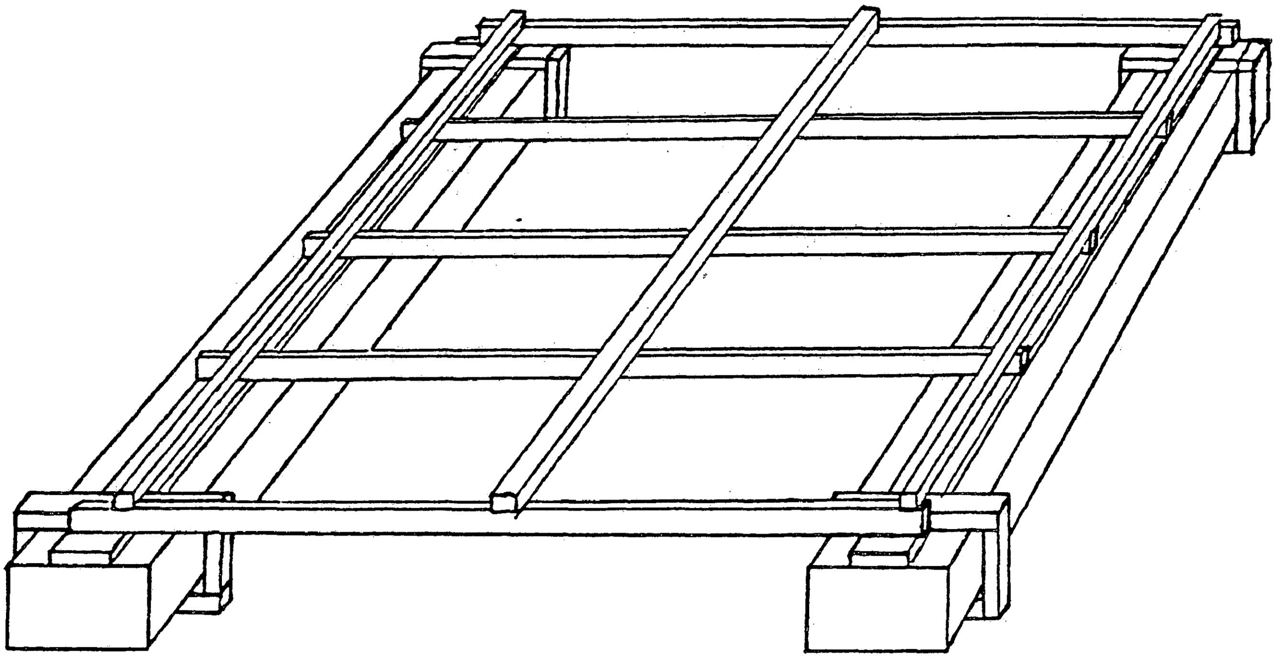
The rafts were placed on Back Lake (48^{o} 30'N, 89^{o} 30'W) located within the city limits of Thunder Bay, Ontario, Canada. Back Lake has a surface area of approximately one hectare, a maximum depth of 6.45 metres, a pH of 7.5, alkalinity of 239.4 mg/l $CaCO_3$, conductivity of 37.5 umhos/cm, and a Secchi disc reading of 3 metres (Momot, 1969). No waves large enough to upset the suspended buckets of soil are formed on this lake.

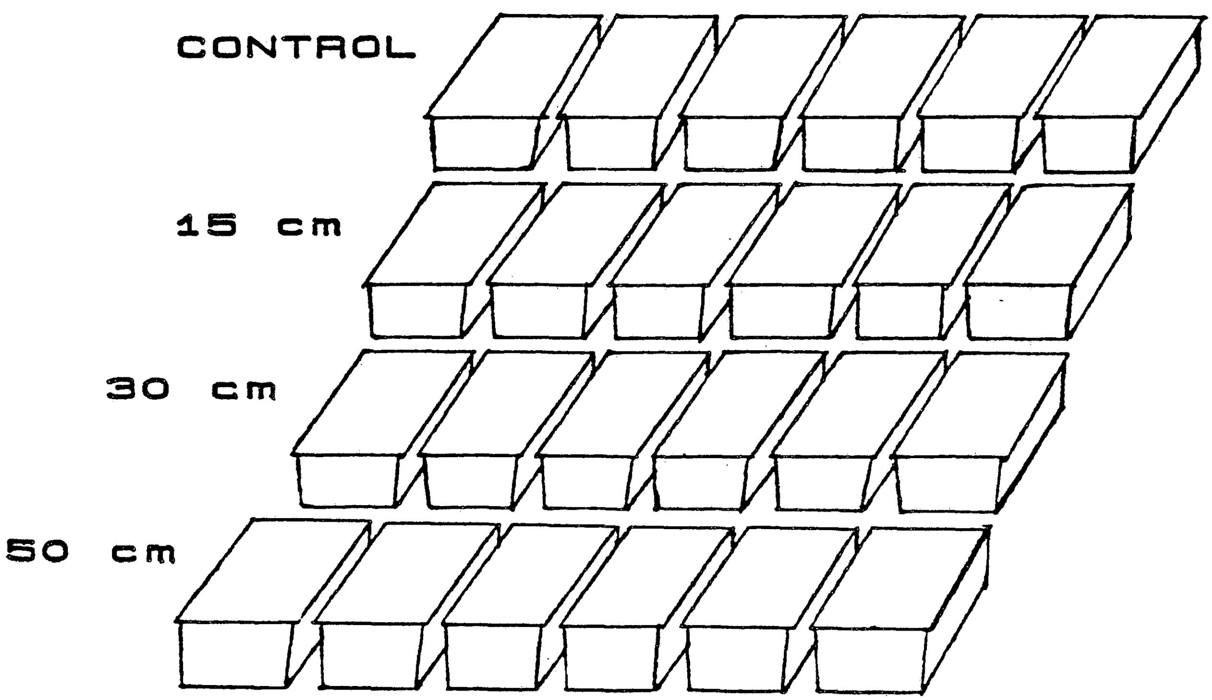
The growing medium was a highly organic soil (loss on ignition of 85%). To ensure that macronutrients would not be limiting two 20 gram, slow-release fertilizer pellets (manufactured by Sierra Chemical Co. of California in the ratio of N:P:K of 20:10:5) were added to each bucket. The soil was saturated with water for 1 week before the seedlings were transplanted. A 2-3cm layer of sand was applied to the surface of the soil to limit soil losses due to wave action.

After-ripened seed, collected from Whitedog Lake, located 50km northwest of Kenora, Ontario, was surface-sterilized for 15

Figure 1.

Rafts used to grow wild rice. Plants were grown in plastic buckets suspended from the framework of the rafts at a depth of 45cm. At the submerged, first floating-leaf, second floating-leaf, and first aerial-leaf stages, the buckets were lowered by either 0cm (control), 15cm, 30cm, or 50 cm.




CONTROL
15 cm
30 cm
50 cm

minutes in a dilute solution of 5% sodium hypochlorite (Hartmann, 1975), rinsed, and placed in distilled water to germinate. After ten days the seedlings were ready for transplanting.

Ten seedlings were transplanted into each bucket suspended from the raft's latticework at an initial depth of of 45cm on May 29. The seedlings were grown at this depth for ten days to allow them to recover from any transplant shock. Seedlings in each bucket were then culled to five plants.

A randomized block design was used for this experiment. There were four levels of water depth increase, replicated six times in each of two rafts for each of the four phenological stages. Water depth treatments that lowered the buckets from the initial water depth of 45cm by 0cm (control), 15cm, 30cm, or 50cm, were initiated at each of four phenological stages: submerged-leaf stage (raft series A-June 8), first floating-leaf stage (raft series B-June 15), second floating-leaf stage (raft series C-June 22), and the aerial-leaf stage (raft series D-July 6). There were two rafts for each of the phenological stages.

Two buckets were selected randomly from each water depth treatment in each phenological stage at weekly intervals for five weeks following inundation. All plants were removed from these buckets and transported to the laboratory in portable coolers. The final two buckets in each treatment were harvested in late August after the wild rice plants had fully matured.

Data Collection And Analyses

Data collected for each sample included: plant number (survival), plant height (the total length of the main shoot from the base of the stem to the bottom of the last leaf blade), number of tillers, number of inflorescences (the total number of stems exhibiting flowers), number of mature inflorescences (the total number of mature seed heads), potential number of grains (the number of pedicels of pistillate spikelets), and dry weights for component plant parts (roots, stems, leaves, and mature seed heads). Dry weights were determined from plant material dried at 80 ^{o} C for 48 hours in a drying oven.

Data from the plants in each sample were averaged and converted to time-independent values following the method of Lee (1979). Two-way analyses of variance of these values were then processed by the VAX/780 computer at Lakehead University using the SPSS statistical package (Nie et al, 1975). Differences between all possible pairs of group means were tested with Duncan's Multiple Range Test at the 5% level of significance.

RESULTS

Plant Survival and Vegetative Response

The vegetative and reproductive responses of wild rice varied according to the increases in water depth. However, all plants survived all treatments. Vegetative responses to the varying inundations at the four phenological stages are shown in Figures 2 - 5.

Submerged-leaf Stage

The heights of plants for each treatment group increased in proportion to the level of inundation - the greater the treatment increase in water level the greater the height of the plants in that treatment group (Fig. 2a). The greatest height was attained by the plants in the 50cm treatment. One way analyses of variance (ANOVA) revealed that differences did occur among the treatments, and Duncan's Multiple Range Test (DMRT) showed that the mean plant heights were statistically different between treatments.

With the exception of the 15cm treatment, total plant and plant component dry weights (roots, stems, and leaves) decreased in value for each successive treatment increase in water depth (Fig. 2b-2e). The 15cm treatment resulted in higher total plant dry weight and plant component dry weights than did the control treatment. ANOVA's on the time independent data showed that significant differences occurred among treatments for root, stem, and total plant dry weights. No significant differences occurred among treatments for leaf dry weight. DMRT showed that mean values were generally significantly different between all but adjacent treatment pairs. For example, mean stem weight for the

Figure 2

Vegetative characteristics of wild rice plants subjected to inundation during the submerged-leaf stage: ((a) plant heights, (b) total plant dry weights, (c) root dry weights, (d) stem dry weights, (e) leaf dry weights,(f) number of tillers per plant). Different upper-case letters on the curves indicate treatment means were signicantly different over entire curve, as judged by DMRT.

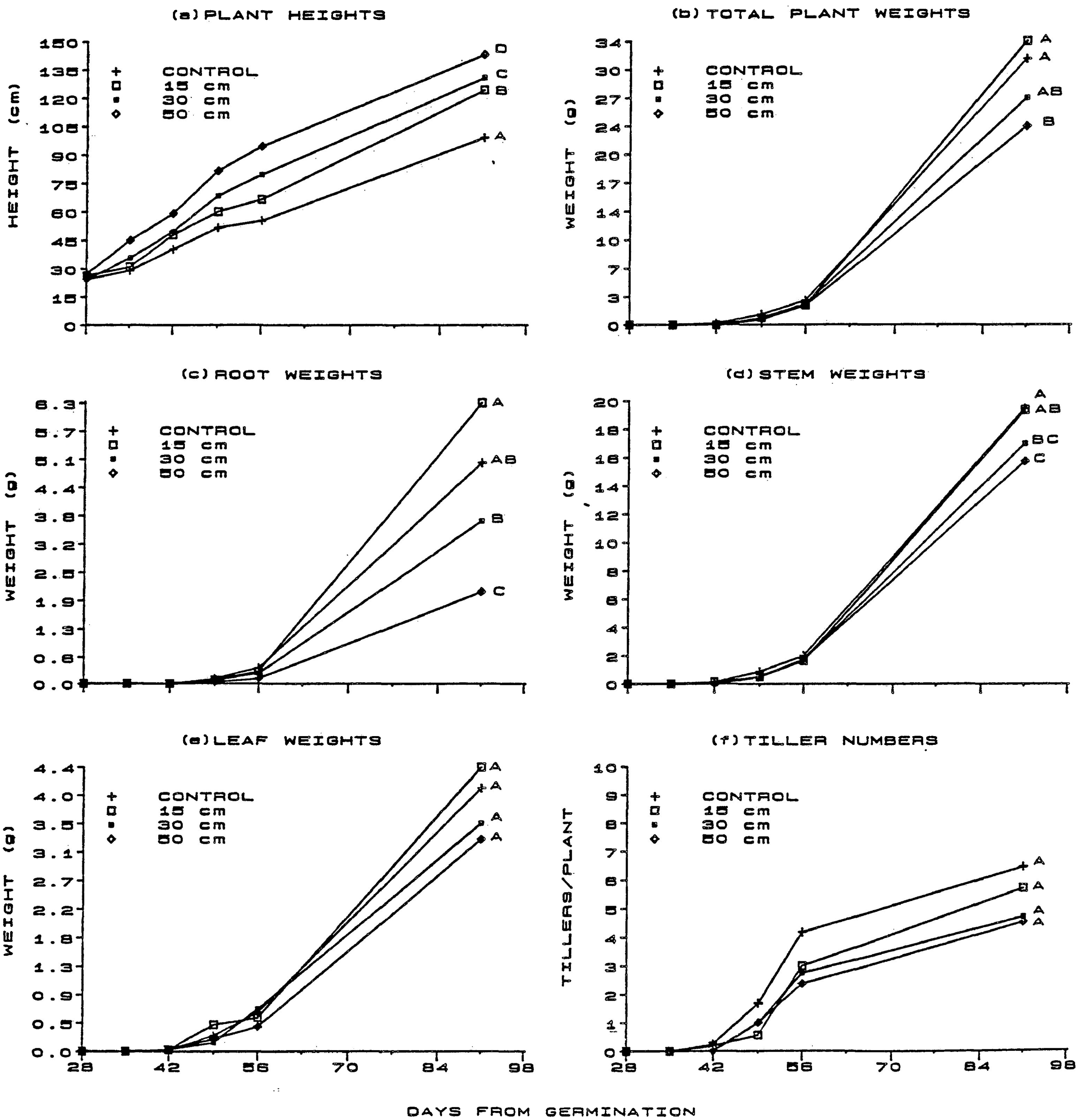

(a) PLANT HEIGHTS
HEIGHT (cm)
CONTROL
15 cm
30 cm
50 cm
D
C
B
A
(b) TOTAL PLANT WEIGHTS
WEIGHT (g)
CONTROL
15 cm
30 cm
50 cm
A
A
AB
B
(c) ROOT WEIGHTS
WEIGHT (g)
CONTROL
15 cm
30 cm
50 cm
A
AB
B
C
(d) STEM WEIGHTS
WEIGHT (g)
CONTROL
15 cm
30 cm
50 cm
A
AB
BC
C
(e) LEAF WEIGHTS
WEIGHT (g)
CONTROL
15 cm
30 cm
50 cm
A
A
A
A
(f) TILLER NUMBERS
TILLERS/PLANT
CONTROL
15 cm
30 cm
50 cm
A
A
A
A
28
42
56
70
84
98
DAYS FROM GERMINATION

Figure 3

Vegetative characteristics of wild rice plants subjected to inundation during the first floating-leaf stage: ((a) plant heights, (b) total plant dry weights, (c) root dry weights, (d) stem dry weights, (e) leaf dry weights, (f) number of tillers per plant). Different upper-case letters on the curves indicate treatment means were significantly different over the entire curve, as judged by DMRT.

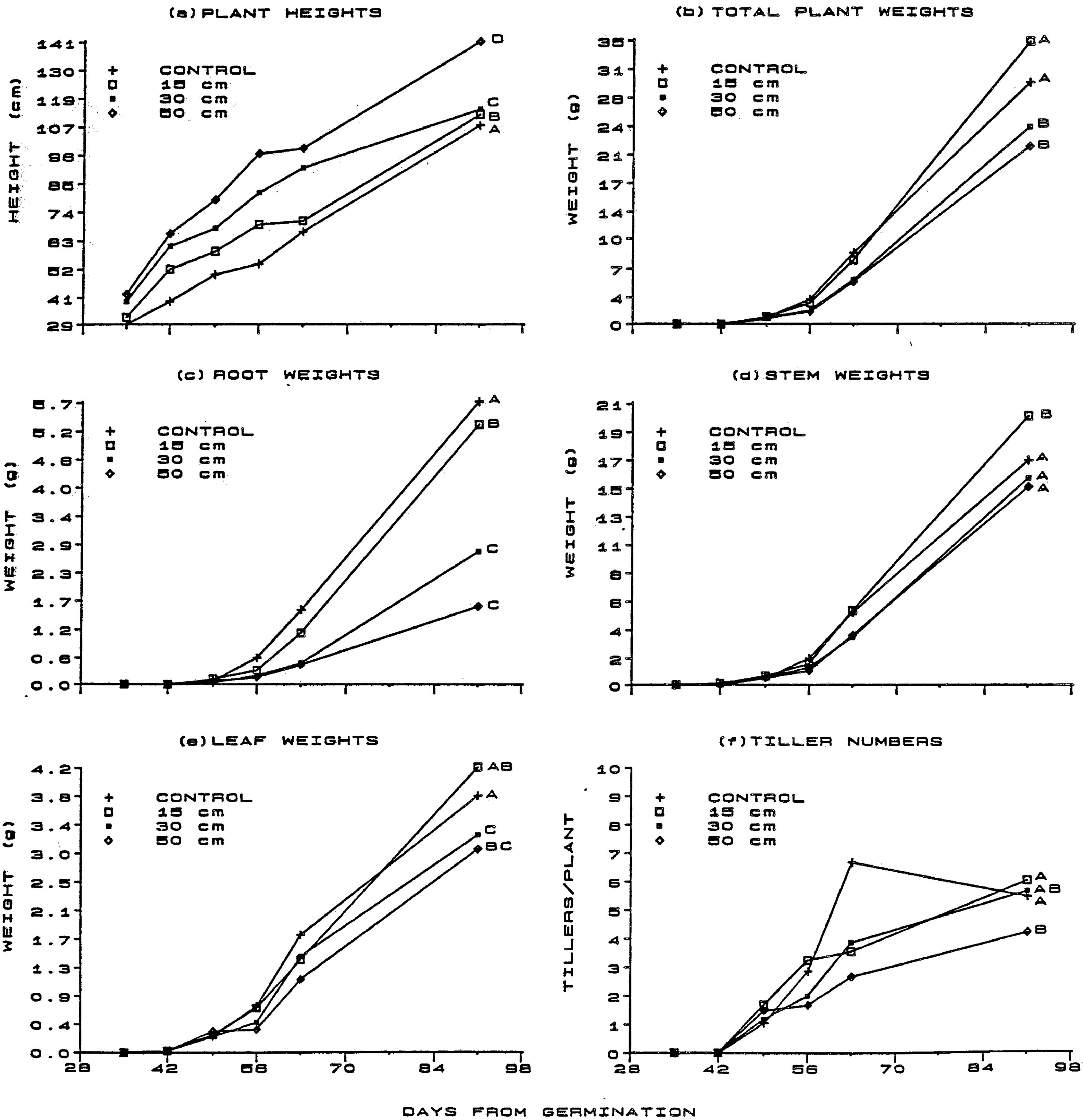
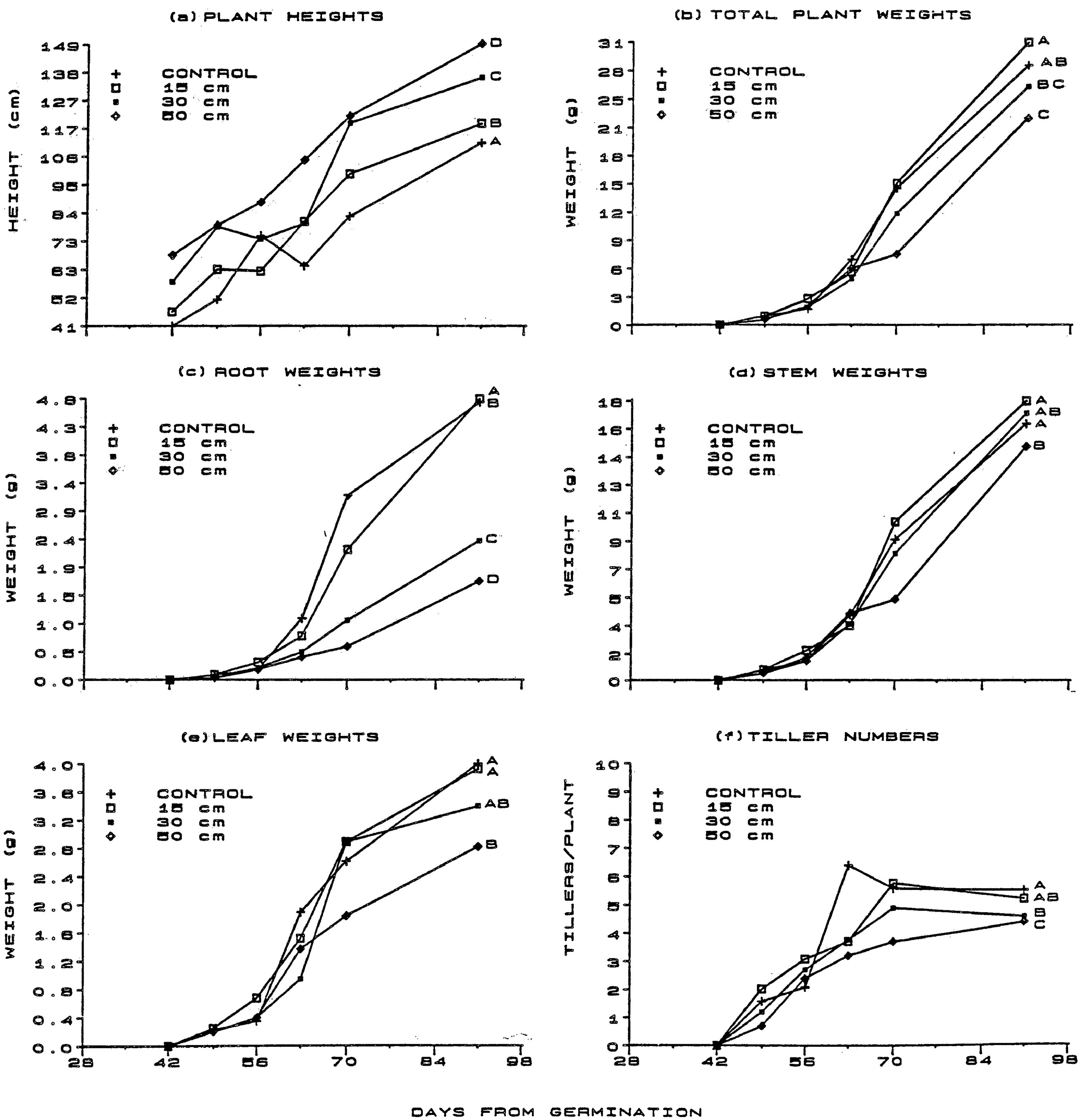

(a) PLANT HEIGHTS
(b) TOTAL PLANT WEIGHTS
(c) ROOT WEIGHTS
(d) STEM WEIGHTS
(e) LEAF WEIGHTS
(f) TILLER NUMBERS
CONTROL
15 cm
30 cm
50 cm
HEIGHT (cm)
WEIGHT (g)
TILLERS/PLANT
DAYS FROM GERMINATION

Figure 4

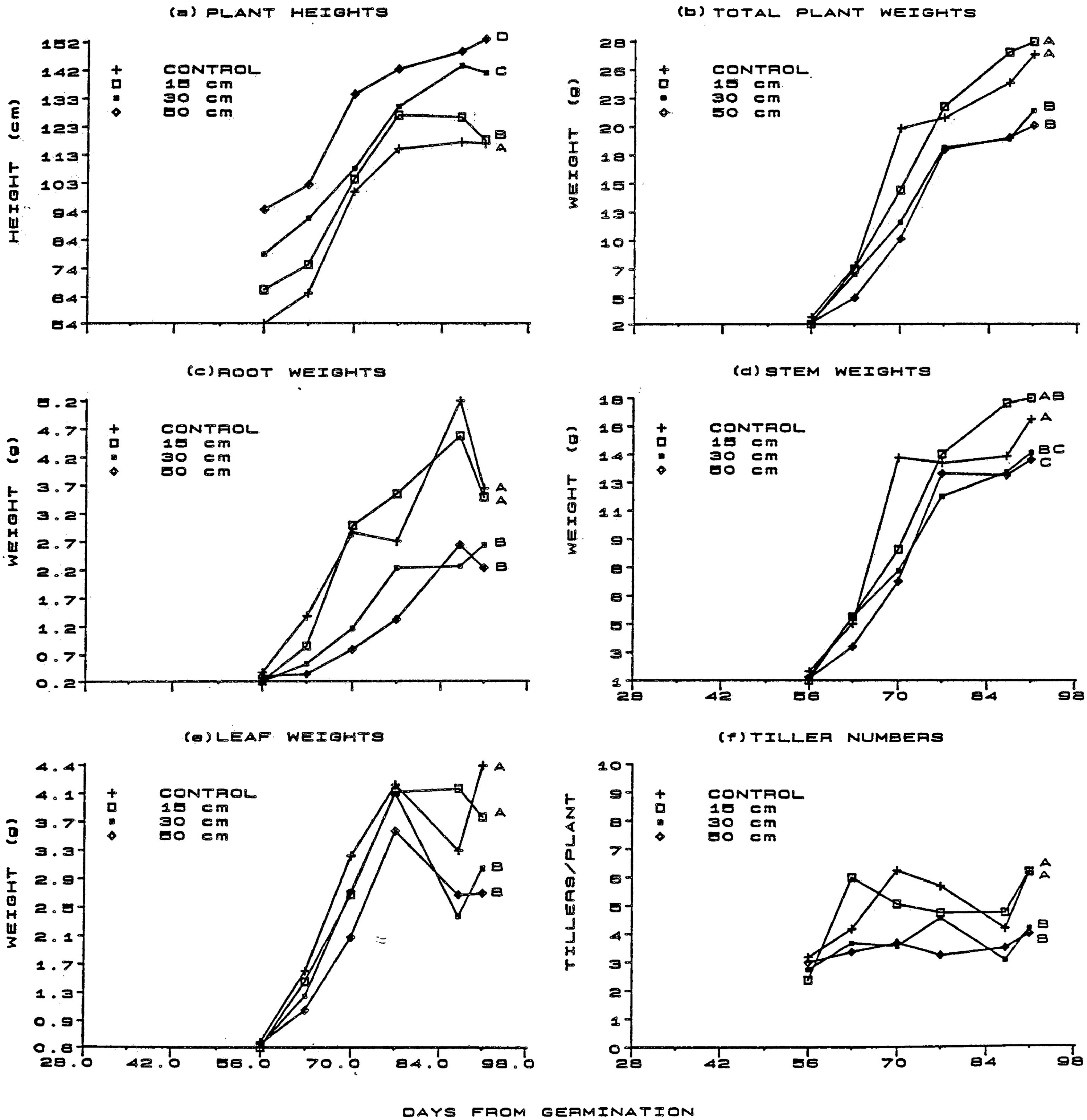
Vegetative characteristics of wild rice plants subjected to inundation during the second floating-leaf stage: ((a) plant heights, (b) total plant dry weights, (c) root dry weights, (d) stem dry weights,(e) leaf dry weights, (f) number of tillers per plant). Different upper-case letters on the curves indicate treatment means were significantly different over the entire curve, as judged by DMRT.



(a) PLANT HEIGHTS
HEIGHT (cm)
149
138
127
117
106
95
84
73
63
52
41
+ CONTROL
□ 15 cm
■ 30 cm
◇ 50 cm
D
C
B
A
(b) TOTAL PLANT WEIGHTS
WEIGHT (g)
31
28
25
21
18
15
12
9
6
3
0
A
AB
BC
C
(c) ROOT WEIGHTS
WEIGHT (g)
4.8
4.3
3.8
3.4
2.9
2.4
1.9
1.5
1.0
0.5
0.0
A
B
C
D
(d) STEM WEIGHTS
WEIGHT (g)
18
16
14
13
11
9
7
5
4
2
0
A
AB
A
B
(e) LEAF WEIGHTS
WEIGHT (g)
4.0
3.6
3.2
2.8
2.4
2.0
1.6
1.2
0.8
0.4
0.0
A
A
AB
B
(f) TILLER NUMBERS
TILLERS/PLANT
10
9
8
7
6
5
4
3
2
1
0
A
AB
B
C
28
42
56
70
84
98
DAYS FROM GERMINATION

Figure 5

Vegetative characteristics of wild rice plants subjected to inundation during the aerial-leaf stage: ((a) plant heights, (b) total plant dry weights, (c) root dry weights, (d) stem dry weights, (e) leaf dry weights,(f) number of tillers per plant). Different upper-case letters on the curves indicate treatment means were significantly different over the entire curve, as judged by DMRT.


(a) PLANT HEIGHTS
HEIGHT (cm)
CONTROL
15 cm
30 cm
50 cm
(b) TOTAL PLANT WEIGHTS
WEIGHT (g)
CONTROL
15 cm
30 cm
50 cm
(c) ROOT WEIGHTS
WEIGHT (g)
CONTROL
15 cm
30 cm
50 cm
(d) STEM WEIGHTS
WEIGHT (g)
CONTROL
15 cm
30 cm
50 cm
(e) LEAF WEIGHTS
WEIGHT (g)
CONTROL
15 cm
30 cm
50 cm
(f) TILLER NUMBERS
TILLERS/PLANT
CONTROL
15 cm
30 cm
50 cm
DAYS FROM GERMINATION

control treatment was not significantly different from the mean of the 15cm treatment; the 15cm treatment mean was not significantly different from the 30cm treatment mean; and the 30cm treament mean was not significantly different from the 50cm treatment mean. The control treatment mean was significantly different from both the 30cm and 50cm treatment means; and the 15cm treatment mean was significantly different from the 50cm treatment mean.

The number of tillers per plant seemed to decrease as the inundation depth increased (Fig. 2f), but an ANOVA revealed that these values were not significantly different.

First Floating-leaf Stage

Plants lowered during the first floating-leaf stage increased in height from the control to the 50cm treatment (Fig. 3a). An ANOVA on these plant heights revealed that there were significant differences among treatments and DMRT showed that all treatment means were significantly different from one another.

Total plant and plant component dry weights (roots, stems and leaves) generally decreased with successive increases in water depth (Fig. 3b-3e). The exception to this pattern was the 15cm treatment which had higher values for these variables than any of the other treatments. ANOVA'S showed that there were significant differences among treatments for each of the dry weight variables. DMRT revealed that for each of these variables all but adjacent treatment means were significantly different.

An ANOVA revealed that the number of tillers per plant (Fig. 3f) were significantly different among the treatments. DMRT showed that the means were significantly different between the control and the 15cm treatment, and between the control and the 50cm treatment.

Second Floating-leaf Stage

Heights for plants lowered during the second floating-leaf stage were proportional to increases in water depth (Fig. 4a). The greatest heights were achieved in the 50cm treatment. All treatment means were significantly different from one another.

Total plant dry weights and plant component dry weights decreased with increasing water depth (Fig. 4b-4e) except for the 15cm treatment which consistently achieved harvest values that were equal to or greater than those for the control treatment. Significant differences occurred among treatments for all dry weight variables. DMRT analysis of these variables showed significant differences occurred between most combinations of treatment means. The most common exception was between contiguous treatment means.

Treatment increases in water depth resulted in fewer tillers per plant (Fig. 4f). An ANOVA followed by DMRT revealed significant differences among treatments and between each pair of treatment means which were not adjacent to each other.

Aerial-leaf Stage

Plants lowered during the aerial-leaf stage increased in height with increasing water depth (Fig. 5a). All combinations of treatment means were statistically different.

At any time during the growing season, all dry weight variables (roots, stems, leaves, and total plant dry weight) generally decreased with increasing inundation (Fig. 5b-5e). The exception was the 15cm treatment which had higher harvest values for both stem and total dry weights than did any of the other treatments. ANOVA'S for these dry weight variables determined that treatment results were statistically different for each variable. DMRT determined that significant differences occurred bewtween means for all but adjacent treatments.

Following inundation, the numbers of tillers per plant decreased with increasing water depth (Fig. 5f). ANOVA on these data revealed significant differences among treatments, and DMRT showed that the means for all but adjacent treatments were statistically different.

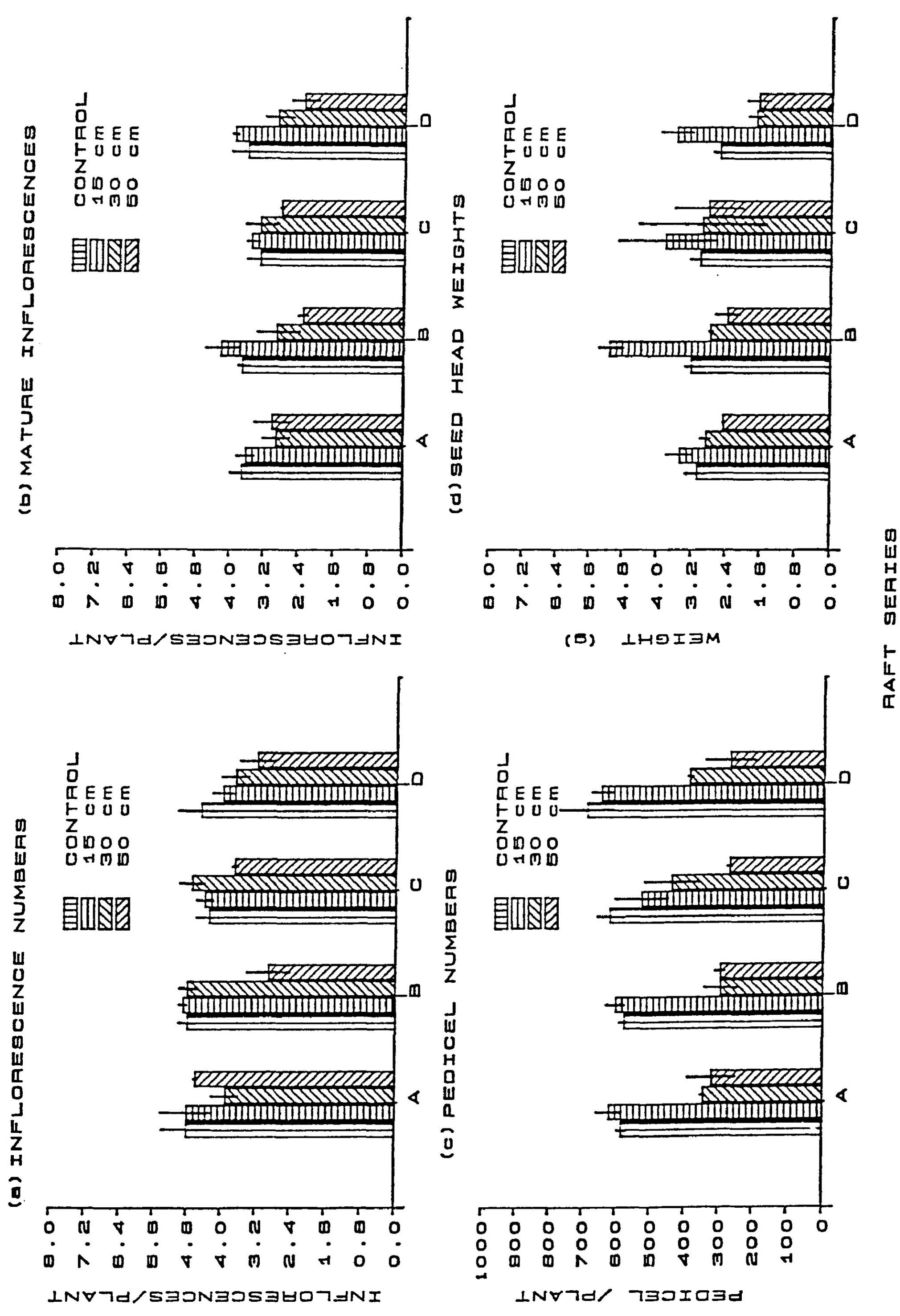
Reproductive Responses

The number of inflorescences per plant (Fig. 6a) decreased for those plants that were subjected to water depth increases during the aerial leaf stage. Increasing depth appeared to have no effect on inflorescence number of those plants lowered during the earlier phenological stages.

The other reproductive characteristics generally responded to increases in water depth in the same manner at all phenological stages. With the exception of the 15cm treatment, as water depth increased, the number of inflorescences which attained maturity (Fig. 6b), the pedicel numbers per plant (Fig. 6c), and the dry weights of mature inflorescences (Fig. 6d) all decreased in value. Plants given the 15cm treatment exceeded the control for these characteristics.

Figure 6

Reproductive characteristics ((a) inflorescence number, (b) mature inflorescences, (c) pedicel numbers, (d) seed head weights) of wild rice plants subjected to inundation during the submerged-leaf stage (A), first floating-leaf stage (B), second floating-leaf stage (C), and the first aerial-leaf stage (D). Error bars indicate one standard deviation from the mean.

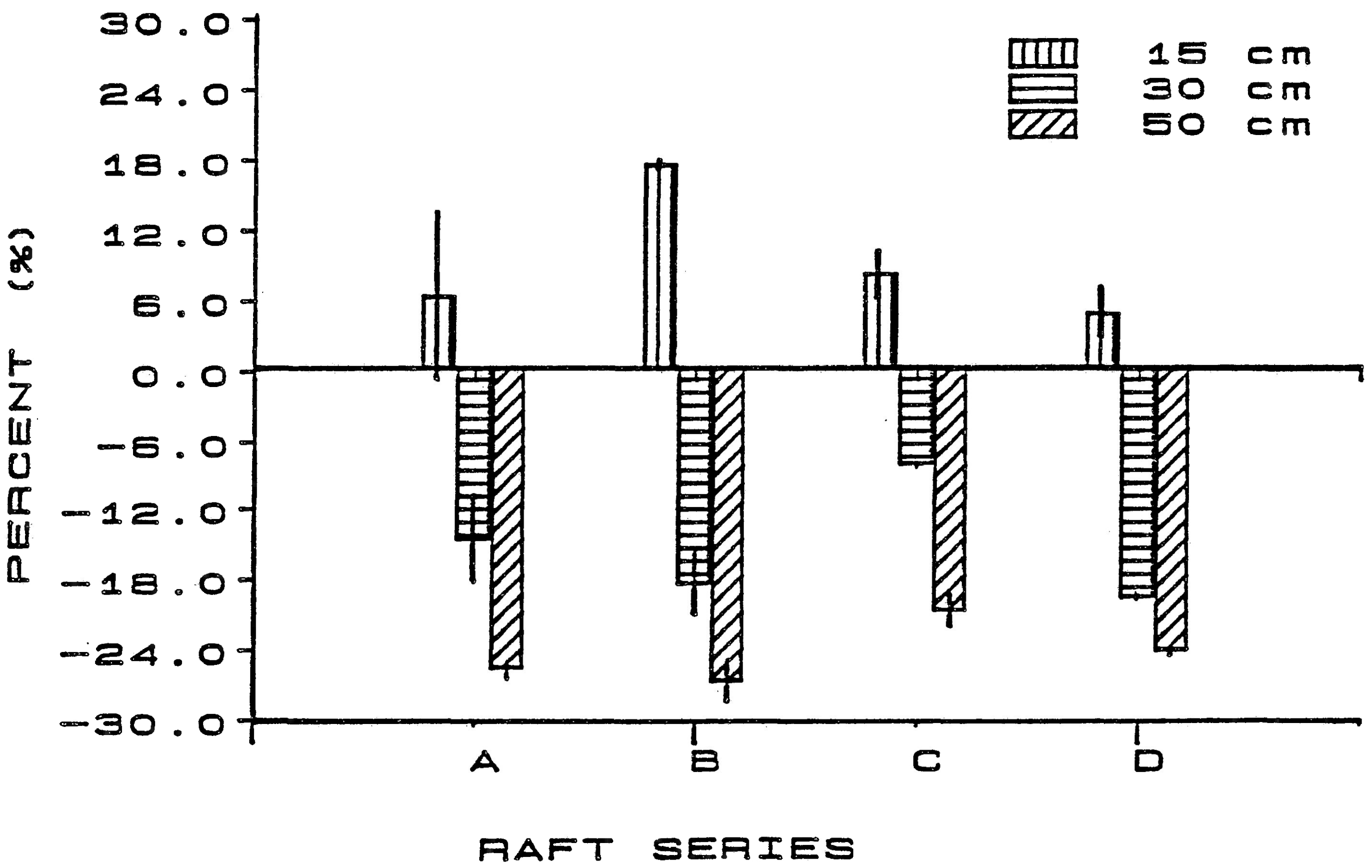

(a) INFLORESCENCE NUMBERS
(b) MATURE INFLORESCENCES
(c) PEDICEL NUMBERS
(d) SEED HEAD WEIGHTS
CONTROL
15 cm
30 cm
50 cm
INFLORESCENCES/PLANT
PEDICEL /PLANT
WEIGHT (g)
8.0
7.2
6.4
5.6
4.8
4.0
3.2
2.4
1.6
0.8
0.0
1000
900
800
700
600
500
400
300
200
100
0
A
B
C
D
RAFT SERIES

Final Harvest Biomass

The total and plant component dry weights at the end of the growing season for each of the phenological stages (Fig. 2b-2f, 3b-3f, 4b-4f, 5b-5f) varied according to the level of inundation, but not with the timing of the inundation. That is, the values obtained for the final harvest dry weights of the whole and plant component parts in each treatment during each phenological stage were within 1.96 standard deviations of the same treatment in any other phenological stage. However, the pattern among the treatments (Fig. 7) was the same for all phenological stages. In each phenological stage, plants given the 15cm treatment had higher values than the control; those given the 30cm treatment had lower values; and those subjected to the 50cm treatment experienced the greatest reductions in weight.

Figure 7

Final harvest biomass, expressed as a percent of the control, of wild rice plants subjected to inundation during the submerged-leaf stage (A), first floating-leaf stage (B), second floating-leaf stage (C), and the first aerial-leaf stage (D).



30.0
24.0
18.0
12.0
6.0
0.0
-6.0
-12.0
-18.0
-24.0
-30.0
PERCENT (%)
15 cm
30 cm
50 cm
A
B
C
D
RAFT SERIES

DISCUSSION

Absence of Plant Mortality

The most important result of this study may be the most obvious - the absence of plant mortality. Other studies have reported wild rice to be extremely sensitive to increases in water depth (Atkins, 1983; Thomas and Stewart, 1969; Weber and Simpson, 1967). In this study, mortality was prevented when the wild rice plants increased in height in response to increases in water depth. This occurred during all phenological stages (Fig. 2a, 3a, 4a, 5a).

Height of wild rice during the submerged and floating-leaf stages has been correlated with the water depth in which the plants grow (Thomas and Stewart, 1969). During these early stages the internodes elongate until the leaves reach the surface (Weir and Dale, 1960). This adaptive mechanism for increases in plant height is an important part of the plant's ability to grow in a wide range of water depths. However, in this study wild rice plants were able to increase in height during the second floating-leaf and aerial-leaf stages after they had achieved their initial height. These increases in height also may be due to internodal elongation, or posssibly, a combination of internode and leaf sheath elongation.

Spence (1974) determined that the submerged species, *Potamogeton obtusifolius* and *P. crispus*, exhibit internodal elongation at all stages of development, similar to terrestrial plants which grow in the dark or shade. Musgrave et al (1972) proposed that internal ethylene levels, mediated by gibberellic acid, are responsible for increased shoot length in *Callitriche* sp. in response to increased water depth. However, Spence and Dale (1978) suggested that a depth dependent causal agent such as ethylene was of minimal importance relative to photosynthetically active radiation (PAR). They proposed that shoot length variation was a response to the levels of red light absorbed by phytochrome. *Potamogeton crispus* grown at similar depths under low or high PAR shows promotion or inhibition of internodal elongation respectively (Spence, 1974). If this mechanism is present in wild rice, height increases in wild rice resulting from increasing water depths are a result of reductions in PAR, specifically in the far-red portion of the spectrum. Atkins (1986) demonstrated that under growth-chamber conditions wild rice did increase in length in response to lower PAR levels.

Although this may well be the mechanism by which the wild rice plants in the cultivation rafts attained their increase in height, this response is not generally seen under field conditions. More commonly widespread mortality occurs (Atkins, 1983). This would suggest that one or more additional factors that facilitate renewed stem growth may be involved.

A resumption of internodal growth in response to increases in water depth would require a readily available source of nutrients (Galston et al, 1980). Although immediate requirements could be met by plant reserves (Milthorpe and Moorby, 1974; Fitter and Hay, 1981), eventually an external source of nutrients would be required by the plant. Under field conditions this nutrient supply could be limiting. In this experiment the slow-release fertilizer provided the supply of nutrients for renewed growth.

Another factor which could explain the lack of plant mortality was seed source. It is possible that the seed source used was better able to respond to increases in water levels. Such depth-tolerant varieties have been identified in white rice (Vergara, 1977), and certain populations of wild rice have been shown to grow in deeper waters than others (Counts, 1984).

Vegetative and Reproductive Responses

Duncan's multiple range tests showed that as long as there was an increase in depth of at least 30cm, both vegetative and reproductive production were adversely affected. These effects were similar for inundations at all phenological stages. That is, although changes in production occurred at different times in the growing season, these changes were always similar in magnitude.

With the exception of the 15cm treatment, as the water depth was increased, the plants had a corresponding increase in height during each phenological stage (Fig. 2a, 3a, 4a, 5a). This was, however, at the expense of net production. The seasonal change in total dry weight per plant and dry weight for roots, stems, and leaves (Fig. 2b-2e, 3b-3e, 4b-4e, 5b-5e) decreased with increasing inundation levels. These changes in dry weights probably occurred because of reduced levels of photosynthetic light in the water column as the plants were lowered (Kirk, 1977). Jupp and Spence (1977) attributed a reduction in *Potamogeton filiformis* biomass to a decrease in light intensity caused by phytoplankton in the water column. Similarly, reductions in biomass have been reported by Barko et al (1982) for aquatic macrophytes subjected to a range of reduced light intensities.

Reproductive productivity of the wild rice plants also declined in proportion to the increases in water depth. With the exception of the 15cm treatment, as the level of inundation increased, fewer inflorescences reached maturity (Fig. 6b), and the number of potential seeds (pedicel number, Fig. 6c) and seed head dry weights (Fig. 6d) were reduced. These reductions were likely caused by the retardation effect that greater water depths have on wild rice development. The deeper the water, the longer it takes wild rice to attain successive phenological stages (Rogosin, 1958; Thomas and Stewart, 1969). The greater effort put into reaching the surface of the water reduced the amount of time in the growing season that could be dedicated to the reproductive phase.

Figure 6a revealed that there were progressively fewer inflorescences per plant for the 50cm depth treatment, for each successive phenological stage. An examination of Figure 6c, however, showed that pedicel numbers for plants experiencing an increase in water depth of 50cm were relatively constant, for all phenological stages. Inflorescences although progressively fewer in number maintained the same overall numbers of pistillate florets, thus the ratios of pistillate to staminate florets must have changed in response to this depth treatment. This suggests that a sexual strategy may exist that attempts to ensure reproductive success under stress conditions.

It is noteworthy that the plants from the 15cm depth treatments consistently had better vegetative and reproductive production than the plants from the control treatments. It is possible that the seed source used was not growing at its optimal depth at the control depth of 45cm and the increase of 15cm actually enhanced its growing environment (Counts, 1984). A second related possibility is that levels of light reaching the plants at the control depth were detrimental to their growth. Atkins (1986) determined that photoinhibition of wild rice plants occurred at shallow depths due to high light intensities and recommended that deeper water depths would provide better production.

Final Harvest Biomass

Figure 7 shows that by the end of the growing season, the plants varied in their final biomass, but the changes in production were more a factor of depth increases than the phenological stage at which they occurred. No relationship was evident between production and the time of the depth increases. This is not to say that increases in depth are not more critical at certain stages of the plant's development; only that by merely examining the final result, in terms of harvest biomass, the effect of the treatments cannot be discerned. It is possible that immediately following the inundation treatments stress is exerted on the growth of wild rice, and this stress may be greater during certain phenological stages. A future paper will concentrate on modelling the effects of these inundation treatments to determine if further analysis can identify a critical growth stage.

In conclusion, when wild rice that is growing under optimum nutrient conditions is inundated with water no mortality will occur. However, increases in depth of at least 30cm will affect both vegetative and reproductive production. The final harvest biomass is influenced by depth inundations, but it does not appear to be influenced by the phenological stage at which these inundations occur.

CHAPTER 2

An analysis of growth following increases in water depth.

INTRODUCTION

The rate at which new plant material is accumulated is an important part of a plant's response to its environment. This growth rate varies continually and cannot be quantified exactly; however, by fitting a mathematical equation to the growing plant's responses to the environment, minor irregularities in the rate of plant growth can be eliminated (Evans, 1972; Thornley, 1976). The resulting model, although a simplification of the real system, can provide useful insight into plant-environment relationships (Richards, 1969).

In a preceding study, the response of wild rice to increases in water depth (Chapter 1) revealed that under adequate nutrient conditions the plants were able to withstand large increases in water depth. It was shown that a sustained increase in water depth of 30cm or greater, was required to significantly affect the vegetative and reproductive production of these plants. The final harvest biomass was influenced by the water depth increases, but it did not appear to be affected by the phenological stage at which these inundations occurred.

The absence of plant mortality in this study and the similar final harvest biomass, suggested that no one phenological stage of wild rice development was more affected by increases in water depth. This contradicts the widespread acceptance of a critical growth phase for wild rice (Chambliss, 1940; Moyle, 1944; Rogosin, 1958; Dore, 1969; Macins, 1969; Thomas and Stewart, 1969; Lee, 1974, 1975; Sain, 1981; Atkins, 1983). However, the absence of mortality and similar harvest biomass for all phenological stages, are not in themselves conclusive. Given the growing conditions in this study, it may be that an increase in water depth imposes a stress on the plant which is evident only in an analysis of its growth performance. Richards (1969) suggests that plant growth is a good indicator of a population's ability to respond to various environmental conditions. Comparisons of growth responses to increases in water depth between each of the phenological stages studied, would provide additional evidence to prove or disprove the existence of a critical growth stage. Therefore, the purpose of this paper is to determine if any one phenological stage of wild rice development is more affected by increases in water depth. Equations, describing the growth that follows the initiation of depth treatments, will be used to develop a predictive model which will identify the existence of a critical growth stage.

Identification of this critical growth period could help explain some of the year-to-year variation in crop yields, as well as provide information for improved water level management policies and site selection.

METHODS

Cultivation Procedures

The experimental growth of wild rice plants was conducted on Back Lake, located within the City of Thunder Bay, Ontario, Canada. Plants were grown under conditions of controlled water level increases, in plastic tubs suspended from specially designed rafts. The tubs could be lowered or raised to allow transplanting of seedlings, initiation of treatments, and sampling.

Inundation Treatments And Sampling Schedule

The effects of increased water depth were examined during four phenological stages: submerged-leaf stage (raft series A), first floating-leaf stage (raft series B), second floating-leaf stage (raft series C), and the aerial-leaf stage (raft series D). At each of these phenological stages, the tubs were lowered 0cm (control), 15cm, 30cm, or 50cm. Two replicates were assigned to each of the four stages studied.

Samples were chosen at random from each depth treatment on a raft, at weekly intervals, for five weeks after the initial inundation treatment. The sixth sample, for each depth treatment on all rafts, was harvested 91 days from germination.

All plant samples were divided into their component parts of roots, stems, leaves and seed heads, and oven dried at 80^{o}C for 48 hours to obtain their dry weights.

Further details of the cultivation raft and sampling procedures are outlined in Chapter 1.

Data Analyses

Growth analysis techniques were used to quantify changes in plant growth caused by the inundation treatments. The analysis was conducted using only the total plant dry weight data since the earlier study (Chapter 1) showed that all plant component parts had similar trends. An examination of total plant weights therefore reflected all plant components.

The analyses proceeded stepwise, as follows:

a) Calculation of Weight per Plant prior to Inundation.

Initially, a baseline growth curve was established for wild rice plants which experienced no change in water depth (control treatment). The control treatment's mean dry weights per plant (Appendix I), for all phenological stages, were plotted against time. The resultant S-shaped curve, or sigmoid, is described by the logistic curve equation [1] (Poole, 1974; Lee and Stewart, 1981; Krebs, 1985):

$$W_{(t)} = K/1+e^{(c-rt)} \qquad [1]$$

where: K = maximum attainable overall mean weight per wild rice plant; c = constant ; r = maximal instantaneous rate of dry weight increase (grams per day); t = time in days from germination.

Utilizing a least sum of squares method (Poole, 1974; Zar, 1974) the parameters of this logistic weight-growth curve (K, c, and r) were calculated. These parameters were subsequently used in the resultant equation (equation [1]) to estimate the mean total dry weight per plant, for each of the four phenological stages, at the initiation of inundation treatments.

b) Calculation of Treatment Equations.

The estimates for mean dry weight per plant, at the time of treatment initiation, were then included with observed values of mean dry weight per plant, obtained from the weekly sampling which followed inundation treatments. Logistic weight-growth equations, with their respective parameters of K, c, and r, were established for all water depth treatments and phenological stages studied.

c)The Relationship of K and r to Inundation.

The values of K and r for each raft series, which were derived from the logistic weight-growth equations, were plotted against depth. The resultant non-linear plots suggested that these relationships might best be described using a polynomial expression. Multiple regression (Nie et al, 1975), was used to generate polynomial expressions for the regression of K versus water depth, and r versus water depth for each raft series. Utilizing an F test for comparing polynomial equations (Zar, 1974) the null hypothesis was tested that all raft series polynomial regression equations, for K and r respectively, estimate the same population regression model. A rejection of the null hypothesis, for either the r versus depth or the K versus depth polynomials, would indicate that at least one of the sample polynomial regression equations was significantly different from the others, and therefore, at least one phenological stage was more affected by inundation treatments.

If the null hypothesis was accepted, for either set of polynomials, then the individual values for K and/ or r, could be combined and an overall regression equation calculated. Subsequently, an F test, as described by Zar (1974), was used to test the hypothesis that the slope of the overall regression equation, for K and r respectively, was not significantly different from zero. Acceptance of the null hypothesis would indicate that the relationship was best described by a constant.

d) Time to r Following Inundation.

The parameters of K, c, and r established for the logistic weight-growth equations for all water depth treatments and phenological stages studied, were utilized to predict daily mean total plant dry weights following inundation. These values were then used to identify the daily interval experiencing the maximum rate of dry weight increase (W_2-W_1/t_2-t_1). The difference between this date and the time of inundation provides an estimate for the time to r. These times r were then compared to the control, and expressed as the difference in days from control.

RESULTS

Weight per Plant Prior to Inundation

Figure 1 shows the seasonal observed values obtained in Chapter 1 and predicted values of the mean weights per wild rice plant as calculated by the logistic weight-growth equation. In most cases, the predicted values are within one standard deviation of the observed values. The predicted mean weight per plant, at the start of inundation at the submerged-leaf, first floating-leaf, second floating-leaf, and aerial-leaf stage was 0.0103 g, 0.0316 g, 0.0971 g, and 0.8972 g, respectively.

Treatment Equations

Table 1 contains the K, r, and c values for the logistic equations describing mean dry weights per plant versus time, for all water depth treatments in each raft series.

In Figure 2, the K values, from each raft series, are plotted versus depth. All four plots exhibit two inflection points (one occuring at the 15cm depth treatment and a second at the 30cm depth treatment), and are described by cubic (third-power) polynomial regression equations (Table 2). An F test for comparing multiple regression equations (Zar, 1974) revealed that the equations were not significantly different. Therefore, the K values for each phenological stage could be combined and a relationship, described by a single polynomial regression equation, developed between K and water depth increase (Fig. 3). Results of the F test comparing the overall regression equation's slope with zero were such that the null hypothesis was rejected ($F_{(3,28)} = 15.2785$, $P < 0.05$). The overall relationship of K versus water depth increase was not a constant.

Figure 1.

Observed and predicted values of the mean weight per wild rice plant in the control treatment. (Bars indicate one standard deviation from the mean.)

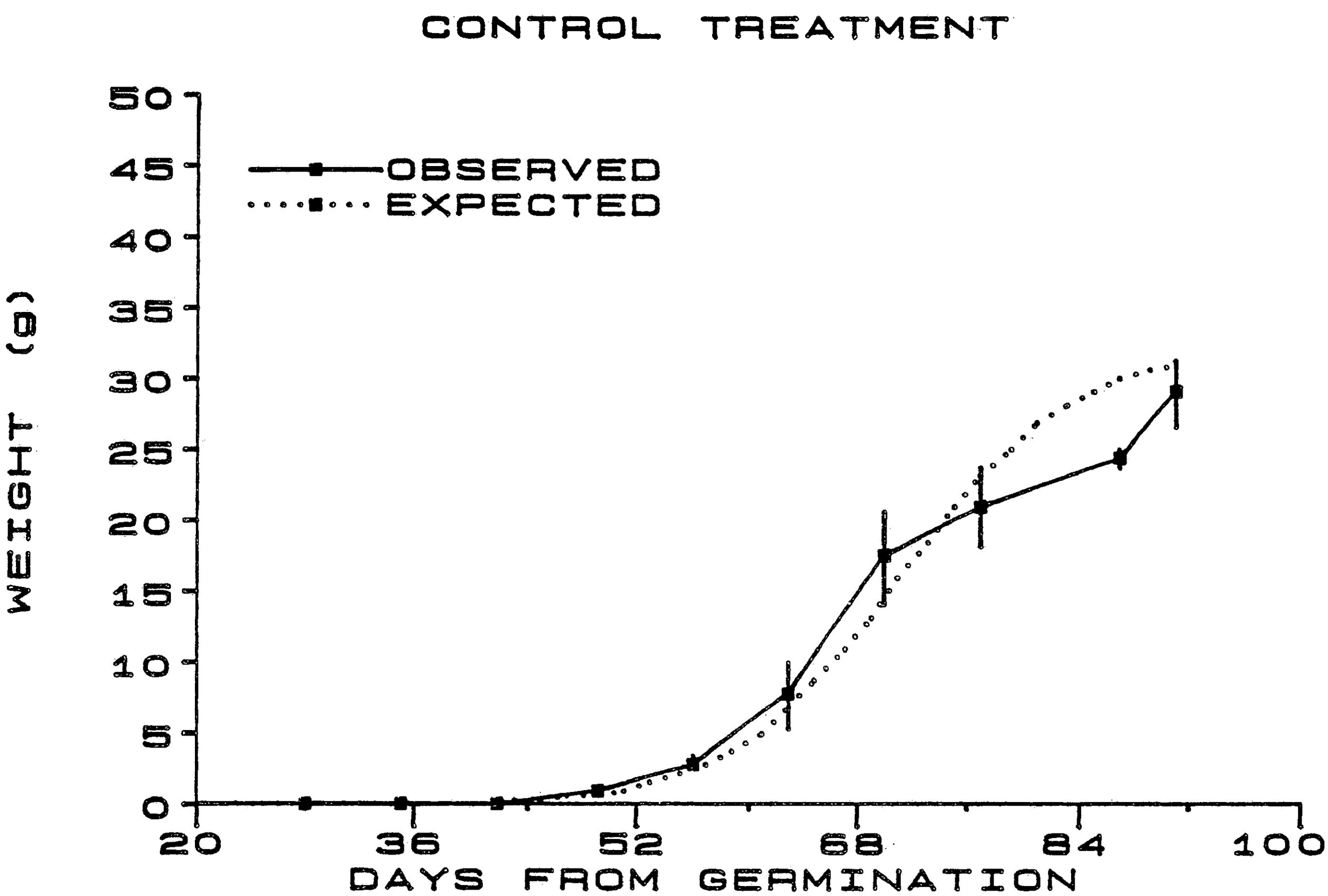

CONTROL TREATMENT
OBSERVED
EXPECTED
WEIGHT (g)
0
5
10
15
20
25
30
35
40
45
50
20
36
52
68
84
100
DAYS FROM GERMINATION

TABLE 1. Numeric values for the parameters K, r, and c, for all depth treatments in each raft series.

RAFT SERIES	DEPTH TREATMENT	K	r	c
A (submerged-leaf stage)	CONTROL	32.46	-0.1606	11.4315
	15	35.45	-0.1578	11.4043
	30	27.7	-0.168	11.6150
	50	24.25	-0.1652	11.4557
B (1st floating-leaf stage)	CONTROL	32.46	-0.1606	11.4315
	15	35.7	-0.1708	11.5958
	30	24.9	-0.1662	11.4301
	50	22.50	-0.1612	11.5203
C (2nd floating-leaf stage)	CONTROL	32.46	-0.1606	11.4315
	15	31.8	-0.1640	11.6007
	30	27.05	-0.1603	11.4300
	50	24.9	-0.1441	11.2989
D (aerial-leaf stage)	CONTROL	32.46	-0.1606	11.4315
	15	29.03	-0.1674	11.3170
	30	22.1	-0.1607	11.3923
	50	21.1	-0.1479	11.4970

Figure 2.

Mean K values for the four depth treatments (0cm, 15cm, 30cm, 50cm) in each of the phenological stages examined.

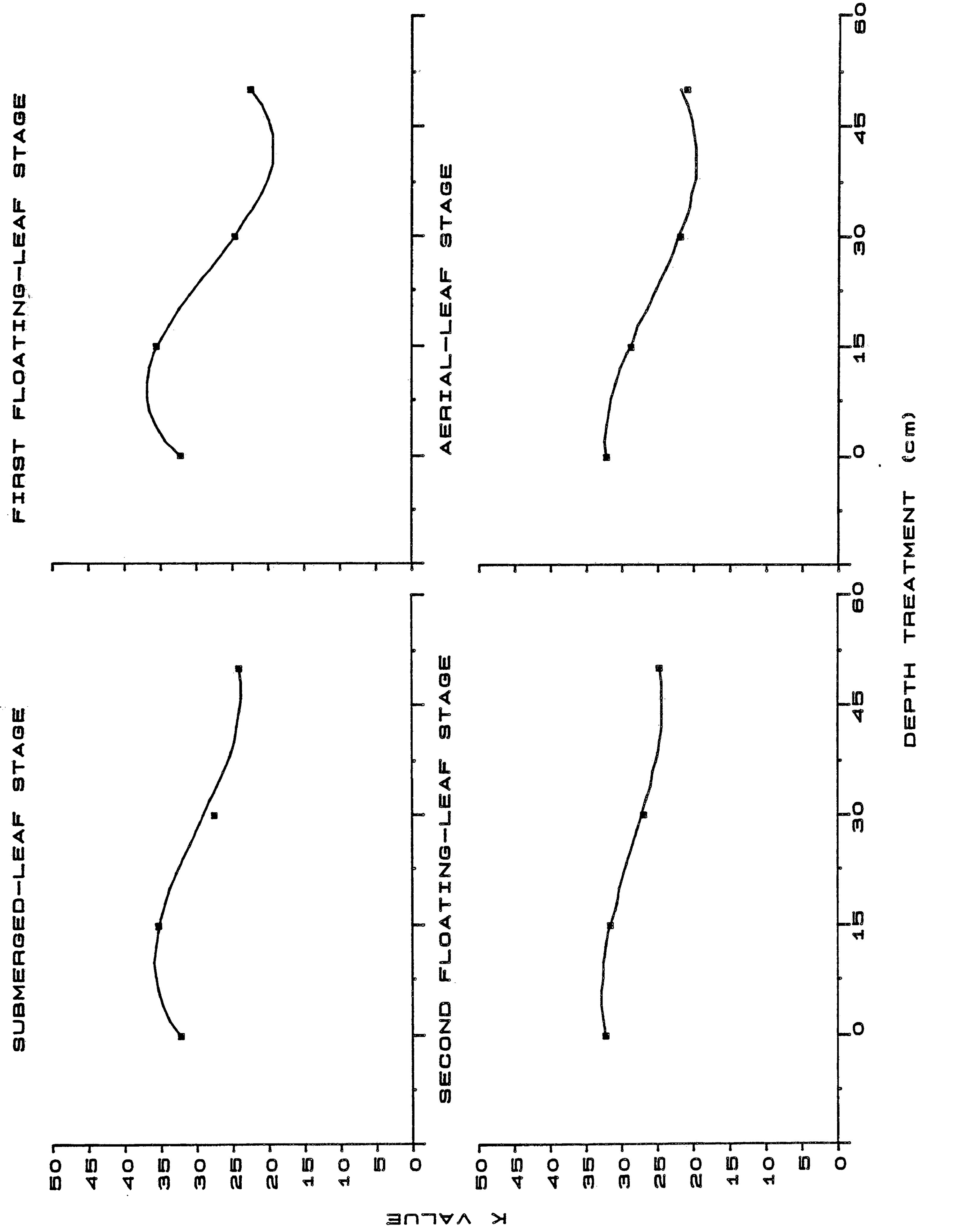
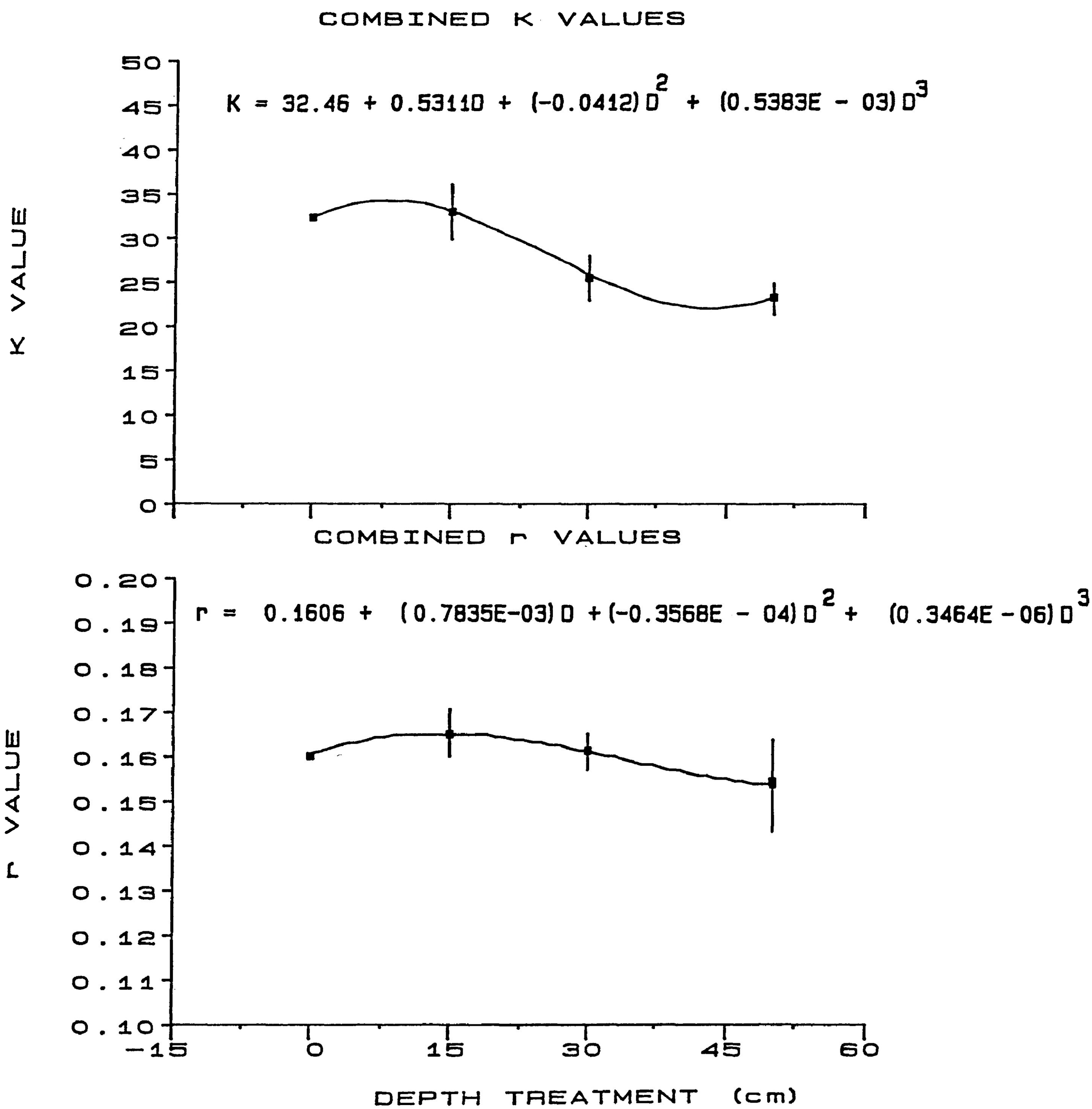

SUBMERGED-LEAF STAGE
FIRST FLOATING-LEAF STAGE
SECOND FLOATING-LEAF STAGE
AERIAL-LEAF STAGE
K VALUE
DEPTH TREATMENT (cm)
0 5 10 15 20 25 30 35 40 45 50
0 15 30 45 60

TABLE 2. Polynomial regression equations, K versus DEPTH, D, for raft series A-D.

RAFT SERIES	REGRESSION EQUATION
A (submerged-leaf stage)	$K=32.46+0.7327D-0.0434D^2+0.51E-03D^3$
B (first floating-leaf stage)	$K=32.46+1.1132D-0.0744D^2+0.9630E-03D^3$
C (second floating-leaf stage)	$K=32.46+0.1834D-0.0196D^2+0.2561E-03D^3$
D (aerial-leaf)	$K=32.46+0.0951D-0.0273D^2+0.4241E-06D^3$

Figure 3.

Relationship between combined K and r values versus water depth treatments.


COMBINED K VALUES
K = 32.46 + 0.5311D + (-0.0412)D2 + (0.5383E - 03)D3
K VALUE
50
45
40
35
30
25
20
15
10
5
0
COMBINED r VALUES
r = 0.1606 + (0.7835E-03)D + (-0.3568E - 04)D2 + (0.3464E - 06)D3
r VALUE
0.20
0.19
0.18
0.17
0.16
0.15
0.14
0.13
0.12
0.11
0.10
-15
0
15
30
45
60
DEPTH TREATMENT (cm)

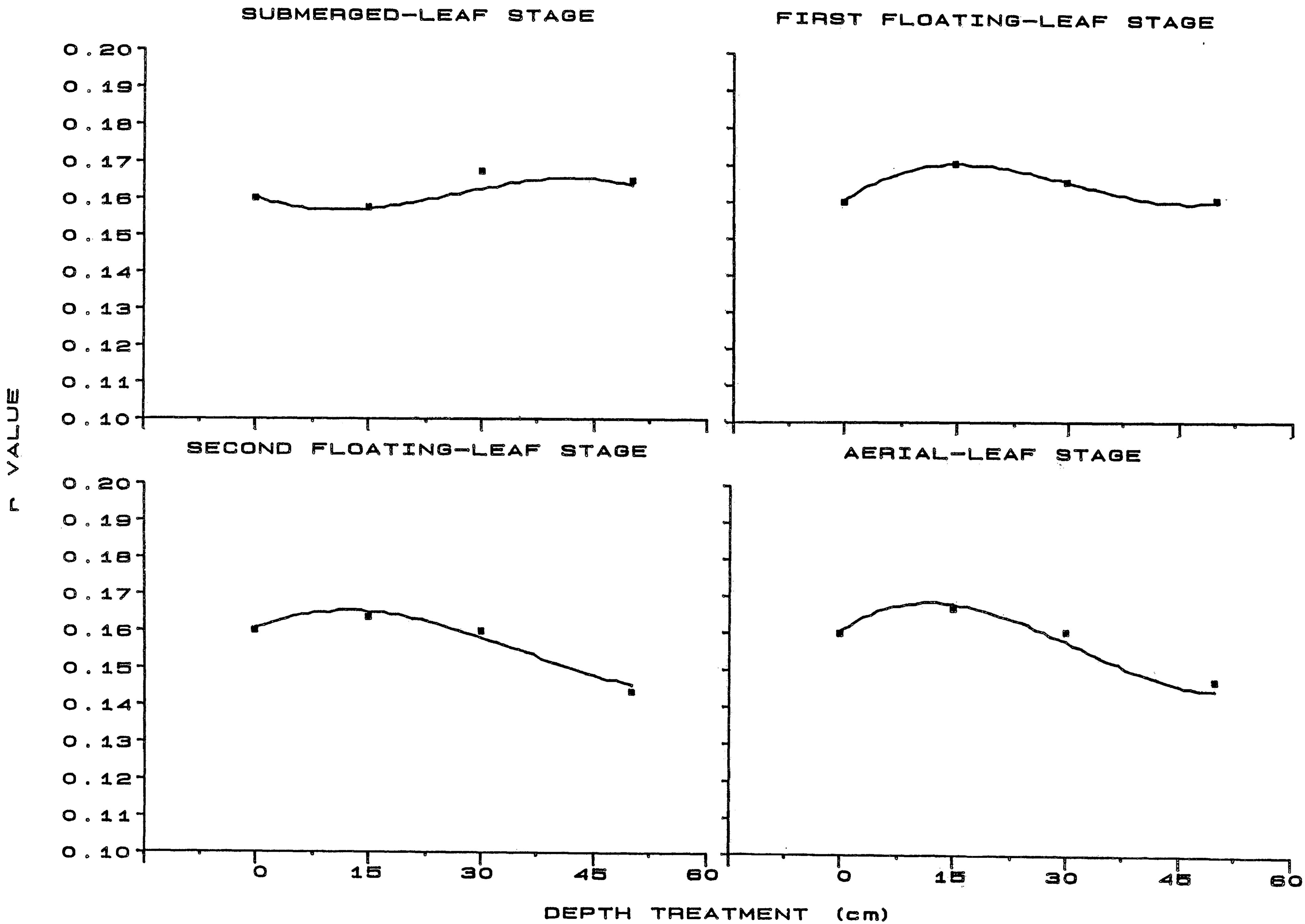
In Figure 4, the r values, from each raft series, were plotted versus depth. Regression equations that described these plots were cubic polynomials (Table 3). Results of the F test, comparing these multiple regression equations, revealed that there was no significant difference between the equations. This allowed the r values to be combined and a polynomial regression equation derived that describes the relationship of r versus depth increase (Fig.3).

An F test revealed that the slope of the overall regression equation for r was not significantly different from zero (the null hypothesis was accepted). The relationship of r versus water depth increase, was therefore best described by a constant. This constant was determined to be 0.1604 g/day, which was the mean r value from the polynomial equations for each of the four phenological stages.

The time required to attain r following inundation, for all water depth treatments and phenological stages studied, are contained in Table 4.

Figure 4.

Mean r values for the four depth treatments (0cm, 15cm, 30cm, 50cm) in each of the phenological stages examined.



SUBMERGED-LEAF STAGE
FIRST FLOATING-LEAF STAGE
SECOND FLOATING-LEAF STAGE
AERIAL-LEAF STAGE
r VALUE
0.20
0.19
0.18
0.17
0.16
0.15
0.14
0.13
0.12
0.11
0.10
0
15
30
45
60
DEPTH TREATMENT (cm)

TABLE 3. Polynomial regression equations, r versus DEPTH, D, for raft series A-D.

RAFT SERIES	REGRESSION EQUATION
A (submerged-leaf stage)	$r=0.1606+(-0.751E-03D)+0.4447E-04D^2+(-0.5613E-06D^3)$
B (1st floating-leaf stage)	$r=0.1606+0.1485E-02D+(-0.6466E-04D^2)+0.6976E-06D^3$
C (2nd floating-leaf stage)	$r=0.1606-0.9097E-03D+(+0.4543E-04D^2)+0.4275E-06D^3$
D (aerial-leaf stage)	$r=0.1606-0.1491E-02D+(-0.7708E-04D^2)+0.8217E-06D^3$

TABLE 4. Estimated time required to attain maximum instantaneous rate of dry weight increase (r) following inundation.

PHENOLOGICAL STAGE	DEPTH TREATMENT	TIME (days)	DIFFERENCE FROM CONTROL (days)
Submerged-leaf	CONTROL	43	0
	15	44	1
	30	44	1
	50	43	0
First floating-leaf	CONTROL	34	0
	15	32	-4
	30	35	1
	50	37	3
Second floating-leaf	CONTROL	29	0
	15	29	0
	30	30	1
	50	37	8
Aerial-leaf	CONTROL	15	0
	15	12	-3
	30	15	0
	50	23	8

DISCUSSION

The growth curve for wild rice, under conditions of no increase in water depth, was described accurately by the logistic growth equation [1]. Those plants experiencing an increase in water depth exhibited similar growth curves; although slopes of these growth curves differed according to the increase in water depth.

Growth At Constant Water Depth

The degree of confidence with which the logistic equation described the growth of wild rice, receiving no increase in water depth, was quite high. The predicted values very closely depicted the observed values (Fig.1). This relationship provides an accurate description of wild rice growth when not limited by nutrient and inundation stresses.

Under conditions of no increase in water depth, the K value was 29.1553 g. This K value represents the maximum dry weight per plant possible if the depth does not change. This does not imply that a greater weight could not be achieved under different environmental conditions. Although K can be given a biological reference, it does not represent a biologically significant factor upon which the growth curve depends to achieve its form (Richards, 1969). The value of K, in the mathematical equation that describes the annual growth of wild rice, was the result of the plants ability to grow under the restraint's of the natural environment; it was not a factor directing that growth.

Effects Of Water Depth Increases

When growth data from two or more experimental treatments are fitted by the same mathematical function, the treatment effects on growth appear as differences between the equations (Richards, 1969; Evans, 1972). Although the previous paper (Chapter 1) showed that total plant dry weight does vary with water depth increase, regressions of K on depth, for each raft series, were not significantly different from one another. This suggests that there is no one phenological stage of wild rice development that is more susceptible to increases in water depth. Thus, a polynomial regression equation based upon K values from all the growth curves, from all raft series (Fig. 3), is the best description of the functional relationship K has on depth following an increase in water depth.

Similarly, the regression of r on depth resulted in the establishment of a single polynomial regression equation (Fig.3) which was not dependent on the phenological stage at which inundation was initiated. In addition, r was found to be a constant (r = 0.1604), for all phenological stages studied. This suggests that the maximum instantaneous rate of plant growth, measured in terms of dry weight (grams per day), following a water level increase, is not only similar for successive phenological stages, but it is not affected by the extent of the water level increase. This implies that r, the maximal instantaneous rate of dry weight increase, may be fixed for wild rice. A decrease in photosynthetically active radiation due to an increase in water depth (Chapter 1), may result in a reduction in the rate of plant growth which is proportional to the increase in water depth. Subsequently, this reduced rate of plant growth tends to increase, usually as a result of a change in plant morphology which seeks to maximize its net assimilation rate (Fitter and Hay, 1981). The amount of time required for plants to attain this fixed r value may well be correlated with the reduction in K for increasing water depth treatments.

Estimates of the time required to attain the maximum instantaneous rate of dry weight increase (r) following inundation, for all phenological stages, revealed a similar pattern to that expressed by Duncan's Multiple Range Tests conducted on total plant dry weight data in the previous paper (Chapter 1). Plants experiencing the greatest increases in water depth (30cm and 50cm), generally took longer to attain r than did those receiving lesser levels of inundation (Table. 4). This result agreed with the conclusions of this previous work - a water depth increase of 30cm or greater was required to produce significant effects on vegetative and reproductive production. It was also evident that plants receiving the 15cm treatment maintained the advantage first described in that paper since the time to attain r for these plants was equal to, or less than, that required by control treatment plants.

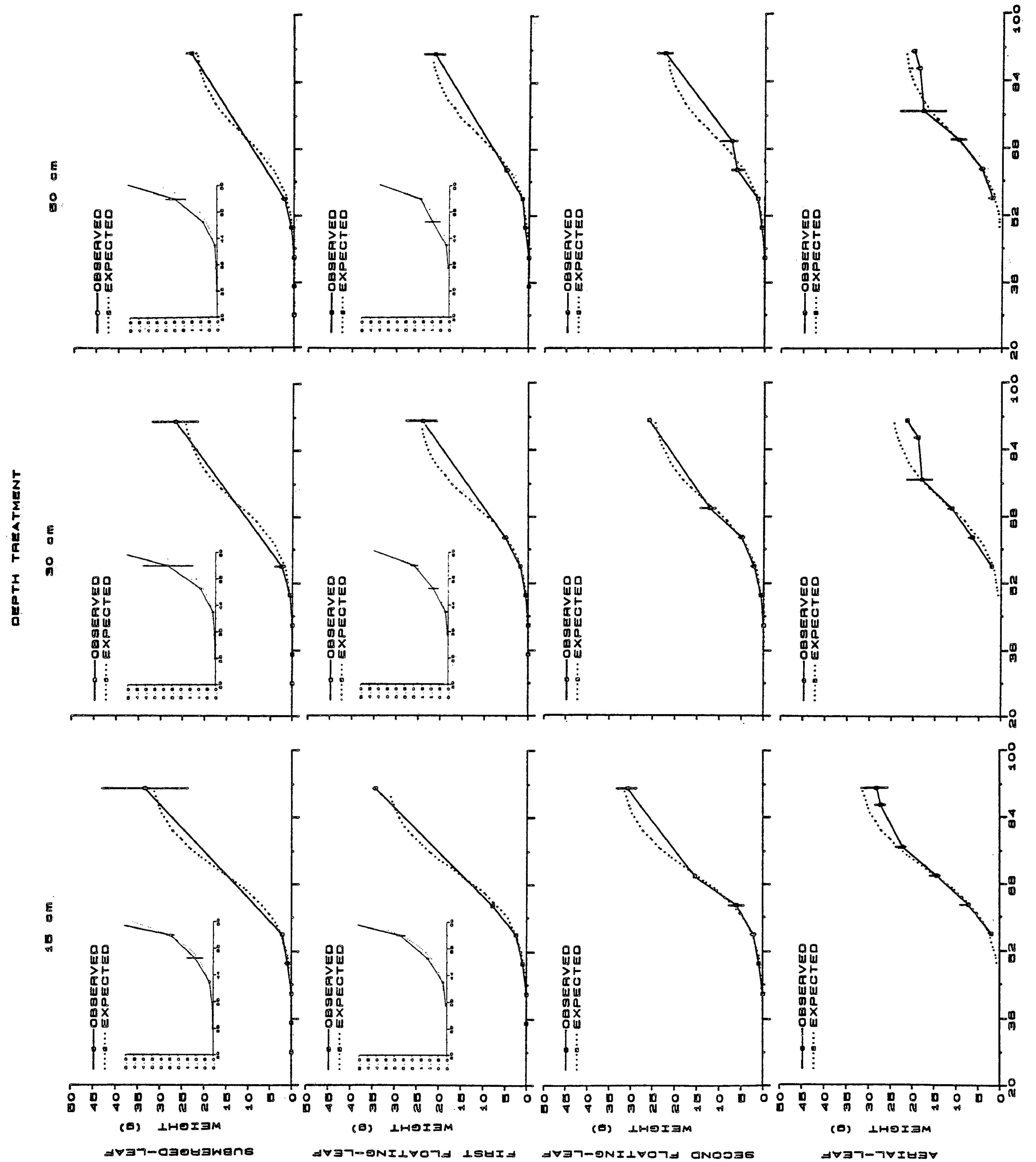
Goodness Of Fit After Inundation

Plotting predicted and observed values of mean dry weight per plant for each depth treatment and for all raft series studied (Fig. 5), reveals the goodness of fit of the model (the derivation of the model is contained in Appendix II). In almost all instances the predicted results for mean dry weight per plant are within one standard deviation of the observed value.

The excellent fit of these mathematical models of wild rice growth, gives further evidence that no one phenological stage of

Figure 5.

Observed and predicted values of mean dry weight per wild rice plant in the 15cm, 30cm, and 50cm depth treatments during the submerged-leaf, first floating-leaf, second floating-leaf, and first aerial-leaf stages. (Bars indicate one standard deviation from the mean.)


DEPTH TREATMENT
15 cm
30 cm
50 cm
OBSERVED
EXPECTED
SUBMERGED-LEAF
FIRST FLOATING-LEAF
SECOND FLOATING-LEAF
AERIAL-LEAF
WEIGHT (g)
0 5 10 15 20 25 30 35 40 45 50
DAYS FROM GERMINATION
20 36 52 68 84 100

development is affected more greatly by inundation. This conclusion is in discord with some of the views and observations reported by other authors. Moyle and Hotchkiss (1945) stated that "a rise of six inches (15cm) during June and July (floating leaf stage) frequently will greatly reduce the crop, and a rise of a foot (30cm) will nearly eliminate it." Atkins (1983) reported that a water depth increase of 18cm, during the floating-leaf stage, was the cause of widespread mortality for lake stands of wild rice. Unlike this study, these reports were based on observations of natural stands of wild rice which may have had suboptimal soil nutrient levels. A sharp rise in water levels may be associated with adverse weather conditions, and this may have a greater role in extensive plant losses than it is usually accredited. A large stand of wild rice in a sheltered inland lake experienced an increase in water depth of 20cm and recovered to produce an albeit reduced crop (Atkins pers. comm.). Thomas and Stewart (1969) identifed the submerged- and floating-leaf stages as being most susceptible to water depth fluctuations. This was based on the hypothesis that reduced photosynthetic leaf area, caused by increases in water depth during these developmental growth stages, would greatly reduce plant yield. The results of the present study, which examine directly the growth curves of wild rice plants experiencing increases in water depth, show otherwise.

In conclusion, it is possible to accurately model the effects of water depth increases on wild rice growth. Under conditions of optimum nutrient levels, water depth increases have the same effect on wild rice growth and production during all phenological stages. Caution should be exercised in applying this model, to a natural situation since it only considers the effects of water depth increases. Other factors, such as plant competition, sub-optimal soil nutrient availability, low temperatures, and reduced light quality in the water column, may well confound direct application of this model to field conditions.

In the absence of a single phenological stage that can be identified as the critical growth phase, year to year variations in crop yields cannot be strictly attributed to increases in water depth. Other factors, such as soil nutrient status and adverse weather conditions, may play an important role in the fluctuating annual crop yields of natural wild rice stands. Future research will concentrate on quantifying the effects of these factors on the depth tolerance of wild rice.

GENERAL CONCLUSIONS

Wild rice that is grown under conditions of optimum nutrient availability can survive increases in water depth at all phenological stages. Given adequate nutrition, wild rice plants will continue to grow in height, during its early vegetative stages, in response to large increases in water depth. At a later stage in plant development (aerial-leaf stage), a resumption of stem and leaf sheath growth will provide a compensating increase in plant height to increases in water depth. The continued survival of the stand is also ensured in that all plants reach reproductive maturity, regardless of the magnitude of the water depth increase. If the increase in depth is 30cm or greater, the vegetative and reproductive production of the plants are reduced. The larger the water depth increase beyond this 30cm increment, the greater the reductions in plant production. The harvest biomass is also reduced as the inundation depth increases; however this reduction is the same for all phenolgical stages.

The effects of water depth increases on wild rice production can be accurately modeled and used to produce equations for predictive growth curves. Comparisons between the equations describing these growth curves show that water depth increases have the same effect on wild rice growth and production during all developmental growth stages. Wild rice also appears to have a fixed maximum rate of growth which limits the plants ability to recover completely from the stress imposed by inundation. However, there is no evidence that a critical growth stage exists for wild rice.

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APPENDIX

APPENDIX I

MEAN TOTAL PLANT DRY WEIGHTS

DATE	A-15	SDV	A-30	SDV	A-50	SDV
28	0.0547	0.0132	0.0512	0.0006	0.0436	0.0009
35	0.0747	0.0010	0.0703	0.0075	0.0649	0.0027
42	0.2297	0.0518	0.1587	0.0389	0.1507	0.0446
49	1.0897	0.4872	0.8852	0.0696	0.8435	0.0513
56	2.4920	0.2164	2.7746	1.4419	2.4071	0.5814
91	33.7089	9.7039	27.1211	5.3469	23.6771	1.3180
	B-15	SDV	B-30	SDV	B-50	SDV
35	0.0770	0.0147	0.0507	0.0126	0.0633	0.0154
42	0.2280	0.0258	0.1751	0.0949	0.1901	0.0742
49	1.1238	0.0817	0.8885	0.3033	0.9807	0.4734
56	2.6606	0.2574	1.9960	0.2311	1.6851	0.0718
63	8.0413	0.2544	5.5723	0.6357	5.3372	1.1812
91	34.6844	0.4089	24.1284	3.6958	21.7475	2.4355
	C-15	SDV	C-30	SDV	C-50	SDV
42	0.1979	0.0395	0.1916	0.0116	0.1265	0.0685
49	1.2352	0.1487	0.8505	0.3190	0.8851	0.0334
56	2.4419	0.5785	2.4606	0.5711	1.7521	0.1566
63	5.9857	1.9597	5.2110	0.7037	6.2785	1.5037
70	15.4258	0.3784	12.2808	2.2005	7.8055	2.1879
91	30.6501	2.7627	25.9862	0.2378	22.5457	1.8855
	D-15	SDV	D-30	SDV	D-50	SDV
56	2.1644	0.0209	2.4273	0.0675	2.4318	0.9482
63	7.3454	1.7180	6.8325	0.8645	4.7525	0.7186
70	14.5361	1.4390	11.5114	0.8279	10.0252	1.9050
77	22.2102	1.6331	18.4001	3.4412	18.2202	5.3350
87	27.2745	1.3380	19.3062	0.7328	19.3681	1.8169
91	28.2939	3.4211	21.8278	0.0917	20.5639	0.4239

APPENDIX I

MEAN TOTAL PLANT DRY WEIGHTS

DATE	CONTROL	SDV
28	0.0423	0.0044
35	0.0704	0.0053
42	0.2310	0.0990
49	1.1687	0.3787
56	2.9930	0.4778
63	7.9320	2.3555
70	17.5968	3.3088
77	21.1680	2.7676
87	24.4839	0.6906
91	29.1553	2.3100

APPENDIX II

Growth Model

The control treatment's mean dry weights per plant for all phenological stages, were plotted against time. The resultant S-shaped curve, or sigmoid, is described by the logistic curve equation:

$$W_{(t)} = K/1+e^{(c-rt)} \quad [1]$$

where: K = maximum attainable overall mean weight per wild rice plant; c = constant ; r = maximal instantaneous rate of dry weight increase (grams per day); t = time in days from germination.

The weight of a wild rice plant at any time is equivalent to the accumulation of dry weight prior to inundation plus the accumulation of dry weight after inundation (Lee,1983). This can be written as:

$$[2] \qquad W_{t+\Delta t} = \int_{t_0}^{t} W(u)du + \int_{t}^{t+\Delta t} W(u)du$$

where: $W_{t+\ t}$ = weight after inundation

The first integral in equation [2] is the accumulation of dry weight prior to inundation, at time t (= W_t). The second integral is the dry weight accumulated after inundation.

Making the substitution for the first integral, the equation becomes:

$$[3] \qquad W_{t+\Delta t} = W_t + \int_{t}^{t+\Delta t} W(u)du$$

For the specific case of wild rice, the total plant weight, W(t), can be described by a logistic equation:

$$[1] \qquad W_t = K\ /\ 1+e^{(c-rt)}$$

where:

$K = 32.46$

$c = 11.4315$

$r = 0.1606$

The definite integral for equation [1] is as below.

[4] $$\int_{t}^{t+\Delta t} W(u)du = F(t+\Delta t)-F(t)$$

where $F(t) = K\{t+(1/r)\log_e(1+e^{c-rt})\}$

substituting:

$K = f(depth) = 32.46+0.5311D-0.0412D^2+0.5383E-03D^3$

$c = 11.4315$

$r = f(depth) = 0.1604$

The result from equation [4] can then be substituted into equation [3] to yield total plant dry weight at any time, t+ t, after time t, given the weight at time $t(W_t)$, and the parameters of the logistic weight-growth curve (K, c, and r).