



This is to certify that the

dissertation entitled

Flooding and Field Grown Maize: Above- and Below-Ground Responses and a Simulation Model

presented by

Jon I. Lizaso

has been accepted towards fulfillment of the requirements for

Ph.D. degree in Crop and Soil Sci.

wajor professor

Date July 8, 1993

LIBRARY Michigan State University

PLACE IN RETURN BOX to remove this checkout from your record. TO AVOID FINES return on or before date due.

	DATE DUE	DATE DUE	DATE DUE
-	10-14-95		
الهمين	MAY 1 1 1998		
4	<u>e</u> APR 0 8 2005		
			·

MSU Is An Affirmative Action/Equal Opportunity Institution c:circidatedus.pm3-p.1

FLOODING AND FIELD GROWN MAIZE: ABOVE- AND BELOW-GROUND RESPONSES AND A SIMULATION MODEL

Ву

Jon I. Lizaso

A DISSERTATION

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

DOCTOR OF PHILOSOPHY

Department of Crop and Soil Sciences

ABSTRACT

FLOODING AND FIELD GROWN MAIZE: ABOVE- AND BELOW-GROUND RESPONSES AND A SIMULATION MODEL

By:

Jon I. Lizaso

Problems associated with excess of water affect 12% of the world's soils. In many areas of seasonal rainfed agriculture in the tropics, heavy rainfalls in soils with limited drainage produce transient flooding that affect maize and other crops' production. However, our knowledge of seasonal responses of field grown maize to soil submergence is limited. A field facility was built to control the water table in five 2.1 m by 1.5 m plots. Pairs of transparent minirhizotrons were horizontally located to study root growth at 15, 40, 60 and 90 cm depth. Maize (Zea mays L., cv. GL 420) was flooded early (five or six leaf tip stage) or late (10 or 12 leaf tip stage) during the vegetative growth stage for four or eight days in 1990 and 1991. Leaf area was reduced by flooding and the timing of waterlogging determined the physiological process altered; early flooding was more associated with reductions in expansion growth; late flooding increased premature leaf senescence. Aboveground biomass remained unaffected during soil submergence but was reduced after drainage. Yields were halved independently of timing or duration of waterlogging. The early flood delayed the appearance of silks by two or three days. On the other hand, root growth proved to be sensitive to timing of soil submergence. Plants flooded early in the season exhibited fast reduction in root number after flooding and rapid proliferation after drainage. Plants flooded later in the season recovered the number of roots only after a short flood. The generic version of CERES is a simulation model that predicts growth and development of wheat, maize, sorghum, pearl millet and barley, considering the limitations imposed by deficient soil levels of water and nitrogen. The maize model in this generic CERES was modified to include the effect of excess of water on crop growth and development. The modified model provides an alternative for predicting the effects of transient flooding on maize, although additional adjustment and model validation are required.

To Claret, Maite and Daniel...

... for their patience and support in dealing with a full-time student and a part-time husband and father

Il n'y a pas de problème qui resiste à l'attaque soutenue de la pensée VOLTAIRE

ACKNOWLEDGEMENTS

I want to extend my gratitude to the Universidad Central de Venezuela, the institution that paid my bills and made it possible to accomplish this wonderful adventure.

I express my recognition to my advisor Dr. Joe T. Ritchie for his unique way of supervising my Ph.D. program at Michigan State University. He always let me make the decisions and face the consequences, trusting in my work and my abilities. I also would like to thank Dr. Ken Poff for his challenging lessons in the classroom, Dr. Alvin Smucker for his advise and support and to Dr. George Merva for his help in designing the field facility. All of them, as members of my guidance committee, are responsible for any error left in these pages.

I want to extend a special word of appreciation to Dr. Bud Belcher for his generous help and support during the most difficult moments of building the field facility and for always offering me a friendly hand. The constant help of Brian Graff, Tom Galecka and all the other wonderful people at the Crops Barn is greatly appreciated. My thanks are extended to Dr. Jim Bingen for providing me with the most comprehensive learning experience at MSU.

I owe a word of appreciation to the many people associated with the Nowlin Chair group. Special thanks to Sharlene Rhines for her friendly and patient review of the manuscript, to Val Snow for her comments on the first two chapters and to Brian Baer for helping with computer problems. Sharing the office with colleagues of such professional and human dimensions as Frédéric Dadoun, Reimar Carlesso and Tim Lynam was a privilege.

To be fair, I also want to give my thanks to the professors and fellow students who thought that since I came from a third world country and I spoke broken English, I had a third-class brain. They challenged me to extreme limits and helped me to grow.

TABLE OF CONTENTS

LIST OF TABLES	Page
LIST OF FIGURES	
Chapter 1. FLOODING AND CROP RESPONSES: A MAIZE-BIASSED	•
REVIEW	
Introduction	
Biochemistry of anaerobic respiration	
Effect of anoxia on water relations	
Effect of anoxia on nutrients relations	
Effect of anoxia on plant growth regulators	
Effect of anoxia on phloem transport	
Morphological adaptations to anoxia	
Metabolic adaptations to anoxia	
Simulating the effects of anoxia	18
Summary	19
Bibliography	
Chapter 2. A FIELD FACILITY FOR MONITORING WHOLE PLANT	
RESPONSES TO FLOODING	
Abstract	
Introduction	
Materials and Methods	
Results	
Conclusions	
Bibliography	43
Chapter 3. FLOODING EFFECTS ON FIELD GROWN MAIZE. I.	
ABOVEGROUND RESPONSES	
Abstract	
Introduction	
Results	
Discussion	
Conclusions	
Bibliography	
Chapter 4. FLOODING EFFECTS ON FIELD GROWN MAIZE. II. BELOW	
GROUND RESPONSES	
Abstract	9€

Introduction	. 97
Materials and Methods	
Results	
Root responses to early flooding	102
Root responses to late flooding	
Discussion	120
Conclusions	
Bibliography	
Chapter 5. FLOODING EFFECTS ON FIELD GROWN MAIZE. III.	
MODIFYING THE MAIZE MODEL IN GENERIC CERES	133
Abstract	
Introduction	
Materials and Methods	
Soil aeration index	
Predicting plant growth	
Predicting leaf growth	1/1
Predicting root growth	
Predicting plant development	140
Additional inputs	
Additional outputs	
Results	
Discussion	
Conclusions	
Bibliography	171
	4-0
CONCLUSIONS AND RECOMMENDATIONS	1/3
Appendix 1: Modified subroutines	176
Program MAIN	
Subroutine WATBAL	
Subroutine DRAINAGE	
Subroutine UPFLOW	
Subroutine NFLUXD	
Subroutine WATABLE	
Subroutine ROOTGROW	
Subroutine GROSUB	
Subroutine PHENOL	
Subroutine PHASEI	209
Appendix 2: Example of new input file	
File WT0201.MZ0	215

Appendix 3: Example	of 1	mo	di	fie	d	ar	nd	n	81	V	ou	tp	ul	: fi	le	3					 216
File OUT1.MZ																					 216
File OUT6.MZ																	 				 216
File OUT7.MZ																	 				 217

LIST OF TABLES

		Page
Table	1.1: World cereals production during 1984-1988 (million tons)	. 1
Table	3.1: Stomatal conductance, measured at 1400 h, after the onset of a flooding period of zero, four or eight days in plants at the 12 leaf tip stage. Values between parenthesis are standard errors	
Table	3.2: Yield and yield components of plants that were flooded for 0, 4 or 8 days at 6 (early) or 12 (late) leaf tip stages. Values between parenthesis are standard errors. 1991	. 78
Table	3.3: Delay in the time of occurrence of tasseling and silking of plants that were flooded for four or eight days at six (early) or 12 (late) leaf tip stage as compared with non-flooded plants. 1991	. 79
Table	3.4: Time between tasseling and silking in plants that were flooded for zero, four or eight days at six (early) or 12 (late) leaf tip stage. 1991	. 79
Table	3.5: Photosynthetic rate measured at 1400 h after the onset of a flooding period of zero, four or eight days in plants that were at the 12 leaf tip stage. Values between parenthesis are standard errors. 1991	. 80
Table	4.1: Number of roots at selected days and depths. Maize was flooded for zero, four or eight days at the six (early) leaf tip stage. Values between parenthesis are standard errors	
Table	4.2: Number of roots at selected days and depths. Maize was flooded for zero, four or eight days at the 12 (late) leaf tip stage. Values between parenthesis are standard errors	115
Table	5.1: Yields predicted by CERES-Maize and by a modified version, and field measured. Maize was flooded for zero, four or eight days at the six or 12 leaf tip stage. Values between parenthesis are standard errors.	158
Table	5.2: Silking date predicted by CERES-Maize and by a modified version, and field measured. Maize was flooded zero, four or eight days at the six or at the 12 leaf tip stage	166

LIST OF FIGURES

	Page
Figure 2.1: Plan view of the five plot facility with dimensions in meters	_
Figure 2.2: Detail in perspective of main components of a single plot with dimensions in meters	. 37
Figure 2.3: Detail of paired minirhizotrons located at 15, 40, 60 and 90 cm depth	. 39
Figure 2.4: Effect of zero, four or eight days flooding on maize leaf area during 1990. Each point is the average of four plants. Vertical lines are standard errors (for clarity only positive or negative side is shown).	. 41
Figure 2.5: Root distribution as affected by an eight day flooding period during 1990. Legends indicate days after emergence	. 42
Figure 3.1: Daily maximum and minimum temperatures experienced at MSU Box Farm during the growing periods of 1990 and 1991	. 54
Figure 3.2: Incident solar radiation and rainfall at the MSU Box Farm during the growing periods of 1990 and 1991	. 55
Figure 3.3: Leaf area per plant as affected by soil submergence of zero, four and eight days. In 1990 flooding was applied by raising the water table above the surface at five or ten leaf tip stages; in 1991 at six or 12 leaf tip stages	. 56
Figure 3.4: Detail of maize leaf area growth as affected by a flooding period of zero, four or eight days when plants were at six leaf tip stage. 1991	. 58
Figure 3.5: Detail of whole plant leaf senescence as affected by a flooding period of zero, four or eight days when plants were at six leaf tip stage. 1991	. 59
Figure 3.6: Plant leaf senescence as affected by a single flooding period of zero, four or eight days when plants were at the six leaf tip stage. 1991	

Figure 3.7: Leaf length of individual leaves as affected by a flooding event of zero, four or eight days of duration when plants were at six leaf tip stage. 1991	. 61
Figure 3.8: Leaf extension rates averaged for the whole period of expansion of the 6th, 7th and 8th leaves, as affected by a flooding event of zero, four or eight days. Vertical lines are standard errors. 1991	. 63
Figure 3.9: Final leaf length of selected leaves as affected by a flooding period of zero, four and eight days. Vertical lines are standard errors. 1991	. 64
Figure 3.10: Plant leaf area as affected by a flooding period of zero, four or eight days when plants were at 12 leaf tip stage. Vertical lines are standard errors. 1991	. 65
Figure 3.11: Plant leaf senescence as affected by a flooding period of zero, four or eight days when plants were at 12 leaf tip stage. Vertical lines are standard errors. 1991	. 66
Figure 3.12: Plant leaf senescence as affected by a flooding period of zero, four or eight days when plants were at 12 leaf tip stage. Vertical lines are standard errors. 1991	. 67
Figure 3.13: Length of leaves 13, 14 and 15 as affected by a flooding period of zero, four and eight days when plants were 12 leaf tip stage. Vertical lines are standard errors. 1991	. 69
Figure 3.14: Rate of extension of the 13th, 14th and 15th leaves, of plants flooded at the 12 leaf tip stage for zero, four and eight days. Vertical lines are standard errors. 1991	. 70
Figure 3.15: Final leaf length of selected leaves of plants flooded for zero, four and eight days at 12 leaf tip stage. Vertical lines are standard errors. 1991	. 71
Figure 3.16: Seasonal changes in plant height as affected by a flooding period of zero, four or eight days either at six leaf tip or 12 leaf tip stages. Vertical lines indicate standard errors. 1991	. 72
Figure 3.17: Length of the internodes above the ground measured at silking in plants that were flooded for zero, four or eight days at the six leaf tip stage, 1991.	. 74

in p	3: Length of the internodes above the ground measured at silking lants that were flooded zero, four or eight days at the 12 leaf tip ge. 1991	5
(abo	9: Daily evolution of stomatal conductance measured 50 days ove) or 70 days (below) after the onset of a flooding period of po, four or eight days at the 12 (above) or at the six (below) leaf stages. 1991	7
four	0: Daily changes in photosynthetic rate in plants flooded for zero, r and eight days at the 12 (above) or at the six (below) leaf tip ge	1
and	1: Aboveground biomass measured on 183 (before), 193 (after) 1213 (silking) days of the year. Plants were flooded for zero, four eight days at the 12 (late) leaf tip stage during 1991	2
org: yea	2: Proportional aboveground biomass distribution among different ans on 183 (before), 193 (after) and 213 (silking) days of the r. Plants were flooded for zero, four or eight days at the 12 (late) tip stage during 1991	3
(bet	3: Aboveground plant biomass and leaf area measured on 183 fore), 193 (after) and 213 (silking) days of the year. Plants were oded for zero, four or eight days at 12 (late) leaf tip stage during 00 and 1991	5
wer	: Root distribution on selected days after planting (DAP). Plants re flooded for zero, four or eight days at the six (early) leaf tip ge. Horizontal lines are standard errors	3
four	: Calculated total root length per plant in maize flooded for zero, r or eight days at the six (early) leaf tip stage. Vertical lines are ndard errors. Horizontal arrows indicate the flooding period 10)5
for : line	: Number of roots observed at 15 cm depth. Plants were flooded zero, four or eight days at the six (early) leaf tip stage. Vertical s are standard errors. Horizontal arrows show the flooding iod)6
for line	: Number of roots observed at 40 cm depth. Plants were flooded zero, four or eight days at the six (early) leaf tip stage. Vertical are standard errors. Horizontal arrows show the flooding iod)7

Figure	e 4.5: General root distribution on selected days after planting (DAP) in plants that were flooded for zero, four or eight days at the 12 (late) leaf tip stage. Horizontal lines are standard errors	110
Figure	4.6: Calculated total root length per plant in maize flooded for zero, four or eight days at the 12 (late) leaf tip stage. Vertical lines are standard errors. Horizontal arrows indicate the flooding period	111
Figure	4.7: Number of roots observed at 15 cm depth. Plants were flooded for zero, four or eight days at the 12 (late) leaf tip stage. Vertical lines are standard errors. Horizontal arrows indicate the flooding period.	112
Figure	4.8: Number of roots observed at 40 cm depth. Plants were flooded for zero, four or eight days at the 12 leaf tip stage. Vertical lines are standard errors. Horizontal arrows indicate the flooding period	113
Figure	e 4.9: Ratio total plant root length divided by total plant leaf area, calculated with the averages per treatment in maize flooded for zero, four or eight days at the six (early) leaf tip stage. Arrows show the flooding period	116
Figure	e 4.10: Ratio total plant root length divided by total plant leaf area, calculated with the averages per treatment, in maize flooded for zero, four or eight days at the 12 (late) leaf tip stage. Arrows show the flooding period.	118
Figure	e 4.11: Seasonal plant ratio of total root length:total leaf area, calculated with averages per treatment, in maize flooded zero, four or eight days at the six (early) or 12 (late) leaf tip stage. Arrows show the flooding period.	119
Figure	5.1: Leaf area index predicted by CERES-Maize and by a modified version, and field measured values. Vertical lines are standard errors of the measured values.	151
Figure	e 5.2: Leaf area index predicted by CERES-Maize and by a modified version, and field measured values in plants that were flooded four or eight days at the six leaf tip stage. Vertical lines are standard errors of measured values.	152

Figure 5.3: Leaf area index predicted by CERES-Maize and by a modified version, and field measured values in plants that were flooded four or eight days at the 12 leaf tip stage. Vertical lines are standard errors of measured values	153
Figure 5.4: Aboveground biomass predicted by CERES-Maize and by a modified version, and field measured values. Vertical lines are standard errors of measured values.	155
Figure 5.5: Aboveground biomass predicted by CERES-Maize and by a modified version, and field measured values. Maize was flooded four or eight days at the six leaf tip stage. Vertical lines are standard errors of measured values	156
Figure 5.6: Aboveground biomass predicted by CERES-Maize and by a modified version, and field measured values. Maize was flooded four and eight days at 12 leaf tip stage. Vertical lines are standard errors of measured values	157
Figure 5.7: Root length density predicted by CERES-Maize and by a modified version, and field measured values. Vertical lines are standard errors of measured values	159
Figure 5.8: Root length density at 15 cm depth predicted by CERES-Maize and by a modified version, and measured values. Maize was flooded four or eight days at the six leaf tip stage. Vertical lines are standard errors of measured values.	161
Figure 5.9: Root length density at 15 cm depth predicted by CERES-Maize and by a modified version, and measured values. Maize was flooded four or eight days at the 12 leaf tip stage. Vertical lines are standard errors of measured values.	162
Figure 5.10: Leaf tip appearance predicted by CERES-Maize and by a modified version, and field measured values.	163
Figure 5.11: Leaf tip emergence predicted by CERES-Maize and by a modified version, and field measured values. Maize was flooded four or eight days at the six leaf tip stage. Vertical lines are standard errors of measured values.	164

Figure 5.12: Leaf tip appearance predicted by CERES-Maize and by a	
modified version, and field measured values. Maize was flooded four	
or eight days at the 12 leaf tip stage. Vertical lines are standard	
errors of measured values	169

Chapter 1

FLOODING AND CROP RESPONSES: A MAIZE-BIASSED REVIEW.

Introduction

Although maize (*Zea mays* L.) is cultivated worldwide, the main production comes from two geographical bands located between latitudes 30° and 50° N. and 15° to 35° S. (Guidry, 1964). In the equatorial zone, maize grows from near the sea level to several thousand meters above sea level (Shaw, 1988).

Maize accounts for one-fourth of the world's total cereal production (Table 1.1), with the USA being responsible for almost half this output (USDA, 1984). In 1986-1987, USA farmers harvested 26 million hectares of maize yielding 7,500 Kg per hectare (FAO, 1989).

Table 1.1: World cereals production during 1984-1988 (million tons).

		
Total cereals production	1,811.8	100.0
Wheat ·	517.4	28.6
Rice	472.7	26.1
Maize	457.8	25.3

Source: FAO, 1989.

Soils with excess of water are widespread. Ponnamperuma (1972) estimates that submerged soils or sediments cover 72% of the earth's surface. Dudal (1976) calculates that about 12% of the world's soils have excess water problems. In addition, heavy rainfalls in imperfectly drained soils produce transient flooding in many areas of seasonal rainfed agriculture in the tropics (Sandhu *et al.*, 1986).

The aim of this review is to focus on the responses of the maize crop to transient periods of soil hypoxia and anoxia. To gain a better understanding of these responses, the biochemistry of anaerobic respiration is examined. Successive sections will analyze hydric, nutritional and hormonal relations in the plant as affected by oxygen deprivation. Morphological and metabolic responses proposed as having some meaning in the maize ability to survive oxygen stress will follow. The last part will review the attempts to summarize our present knowledge of maize responses to flooding, in a mathematical simulation model. Information on other crops and species is included whenever they add relevant details to the discussion. However, a premeditated bias towards maize is acknowledged.

Biochemistry of anaerobic respiration

In the evolutionary process, aerobic respiration succeeded the anaerobic respiration developed when there was no atmospheric molecular oxygen and reductive conditions were the norm (Vartapetian, 1978). Much later, after oxygen

accumulated in the atmosphere because of photosynthesis, new metabolic strategies were possible. The new aerobic cell kept the older system of anaerobic energy generation and added an aerobic system to take advantage of the new atmospheric conditions. The result was an integrated and much more efficient system, with oxygen as the final electron acceptor, and an 18-fold increase in potential energy yield.

The new aerobic respiratory system has three main components that take place in three different cell compartments:

- 1. Glycolysis (the anaerobic former system), in the cytosol.
- 2. Krebs cycle, in the mitochondria matrix.
- 3. Electron transport system, in the mitochondria inner membrane.

Most of the biologically useful energy produced during aerobic respiration is coupled with the electron transport process. The process is called oxidative phosphorylation (Salisbury and Ross, 1992; Nobel, 1991). In fact, the nicotinamide adenine dinucleotide (NADH+H⁺) from glycolysis, and the NADH+H⁺ and flavin adenine dinucleotide produced during the Krebs cycle are oxidized in the electron transport system coupled with the ATPase enzyme system, regenerating 89% of the adenosine triphosphate (ATP) produced in aerobic respiration. Thus when the oxygen supply is limiting, the resultant decrease in ATP greatly reduces the energy available for metabolism. Under such conditions, the rate of glycolysis may increase in a process known as the *Pasteur effect* (Salisbury and Ross, 1992).

The process will provide more ATP than under normal glycolytic rate, but at a larger cost in carbon compounds.

Impaired functioning of the Krebs cycle and the electron transport system due to anaerobic conditions cause NADH+H⁺ and pyruvic acid (the end product of glycolysis) to accumulate in the cytoplasm. This condition activates the fermentative metabolism of pyruvate, leading to either lactic acid or ethanol, both considered toxic for plant cells. Crawford (1978) found correlation between ethanol production and anaerobic injury. He proposed that irrespective of species or tissue, ethanol accumulation during flooding periods must be small for plants to survive significant periods of anoxia (Crawford, 1977; Crawford and Baines, 1977).

The role of fermentative metabolism and ethanol and lactate production has been investigated extensively during the last decade (Saglio *et al.*, 1980; Jackson *et al.*, 1982; Roberts *et al.*, 1984b; Pradet *et al.*, 1985; Walker *et al.*, 1987; Thomson and Greenway, 1991). Davies (1980) and Jackson *et al.* (1982) questioned the association of plant injury during anoxia with fermentative ethanol production. Evidence accumulated since then, indicates that ethanol fermentation is an acclimative response to oxygen deprivation (Walker *et al.*, 1987; see also later section on metabolic adaptations). Today's view (Drew, 1992) is that the end products of fermentation are not harmful because lactate, and especially ethanol, diffuse across the plasmalemma into the external medium.

Effect of anoxia on water relations

Field grown waterlogged plants may exhibit some of the symptoms connected with drought, as lack of leaf turgor, growth reduction and yellowish appearance. Early reports associated plant responses to low soil oxygen with those of water stress under the term "physiological drought". Kramer (1940 and 1951) found a reduction in root permeability as a cause of decreased root water absorption by flooded plants. Since then several experiments have provided consistent evidence to support the view of an increased resistance to the radial flow of water under limited oxygen (Parsons and Kramer, 1974; Bradford and Hsiao, 1982; Everard and Drew, 1987; Everard and Drew, 1989a). However, Trought and Drew (1980a) were not able to detect any increase in the root resistance to water movement in wheat. The significance of this last report remains unclear.

Stomatal behavior under limiting soil oxygen seems to be a field of contradictory evidence as well. Sojka and Stolzy (1980) in their review found that stomatal closure was consistently reported in response to low soil oxygen. Kozlowski and Pallardy (1984) classified plant responses to limiting soil oxygenation in two main groups according to the presence or absence of leaf dehydration associated with stomatal closure. In an experiment with sunflower, Everard and Drew (1989b) measured a decline in leaf water potential within the first hour after imposing anaerobiosis to the roots. Recovery of the leaf water status occurred at the beginning of the second day without stomatal closure.

Bradford and Hsiao (1982) found a reduction in both stomatal and root conductance without a concomitant decrease in leaf water potential. In their experiments they found indirect evidence for a role of the root system in maintaining a partial stomatal opening.

Further indirect evidence on an inadequate leaf water status is the reduction in leaf expansion associated with soil oxygen deficiency (Trought and Drew, 1980a; Wenkert et al., 1981). Since it is well known that leaf growth is highly sensitive to low leaf water potentials (Boyer and Westgate, 1984), the immediate reduction in leaf elongation after anoxia treatments may be an indication of lack of the turgor pressure required for cell elongation.

On the other hand, an early flood response as leaf epinasty, the downward orientation of leaves, requires an active process involving turgor. Bradford and Hsiao (1982) did not find any reduction in leaf water potential in stressed tomato plants, recording an epinastic response on the second day after flooding. Everard and Drew (1989b) measured a decrease in leaf water potential within one hour after flooding in sunflower, and leaf epinasty started on the second day simultaneously with the recovery of the leaf water potential.

Studying the water movement through anaerobic roots of maize, Everard and Drew (1987) found that anoxia appreciably reduced the root water flow rate. They concluded that the reduction in water flow across the roots was due primarily to the disappearance of the diurnal rhythm (Parsons and Kramer, 1974) in hydraulic conductivity and that the osmotic component had only a small effect.

Several plant responses to flooding formerly were ascribed to altered water relations. However, today it is generally accepted that they are controlled by plant growth regulators. This is the case of epinasty regulated by ethylene (Bradford and Yang, 1981) and stomatal movements affected by several factors including abscisic acid (Bradford, 1983; Jackson and Hall, 1987; Zhang and Davies, 1987).

Effect of anoxia on nutrients relations

Soil oxygen level affects soil nutrients bioavailability and plant mineral status. In oxygen depleted soils, mineral nutrients have altered chemical and biological dynamics. Nitrate disappears from the soil solution as a consequence of leaching and/or microbial denitrification, whereas nutrients such as phosphorus, iron and manganese may become more available (Kozlowski and Pallardy, 1984; Sposito, 1989). Early investigations on this subject, using solution culture, found a quick inhibition in absorption and translocation of nutrients (Hopkins *et al.*, 1950; Hammond et al., 1955; Hopkins, 1956; Rao and Raines, 1976). Whole plant experiments conducted in anaerobic environments showed reduced accumulation of nitrogen, phosphorus and potassium in the shoots; calcium and magnesium remained unchanged and sodium increased under hypoxic environment (Letey et al., 1961a, 1961b, 1962, 1965; Shalhevet and Zwerman, 1962; Lal and Taylor, 1969; Chaudhary et al., 1975). Increased temperature escalated the differences in shoot nutrients accumulation between normoxic and hypoxic plants (Letey et al., 1961b: Trought and Drew. 1982).

Timing of reduced soil aeration has a major effect in field grown plants. Chaudhary et al. (1975) flooded maize for one to four days at two, four or eight weeks after planting. They found that early submergence was most harmful to total nutrient uptake. Shandhu et al. (1986) studied the effect of intermittent submergence for 10-day periods at 20 and 40 days after planting. Significant reductions in leaf concentrations of nitrogen, phosphorus and potassium were measured only in the earlier hypoxic treatment.

Reductions in absorption and translocation of inorganic nutrients to the shoots are usually detected within two days of hypoxia, long before nutrient concentration in the rooting media has declined (Drew and Sisworo, 1977, 1979). Trought and Drew (1980b) found translocation of nitrogen, phosphorus and potassium from the older leaves of wheat to the growing ones during waterlogging. Calcium and magnesium did not translocate. The nitrogen movement was associated with the onset of premature senescence in older leaves and additions of nitrate or ammonium to the soil surface, or foliar sprays of urea delayed the senescence symptoms.

The inability of plant roots to maintain adequate rates of nutrient uptake and transport are associated with low energy levels under fermentative respiration (Drew and Stolzy, 1991). Spek (1984a, 1984b) found that the sharp decrease in nitrogen content was a consequence of the combination of continuing shoot growth and a major reduction of the transport from the roots. His data also

suggest that nitrogen transport is more dependent on the supply of oxygen than nitrogen uptake.

Many non-wetland plants exhibit the ability to develop nodal roots with interconnected free space (aerenchyma) in response to anoxic events. Molecular oxygen can diffuse through these lacunae from the aerial organs into the roots, maintaining the oxygen supply for aerobic respiration to a certain extent. However, these roots may be less efficient in absorption and transport of ions, since they lose extensive apoplastic and symplastic pathways at the root cortex. Drew and his colleagues (Drew et al. 1980; Drew and Saker, 1986) showed that under well aerated conditions aerenchymatous roots were as efficient as ordinary roots. Rates of uptake of phosphate, potassium (⁸⁶Rb⁺) and chloride were the same in both types of roots. It seems reasonable here to advise some caution with the common practice of identifying Rb results with K, since recent evidence shows that, at least under certain experimental settings, absorption and especially transport may be quite different (Brauer et al., 1987).

Sodium seems to behave differently than the other cations under restricted soil aeration. Maize tolerance to salinity is associated with the exclusion of sodium from leaves (Yeo *et al.* 1977). Since plasma membranes are permeable to Na⁺, it has been proposed an active K⁺-dependant efflux mechanism (Jeschke, 1984). Drew *et al.* (1988) studied the combined effects of salinity and anoxia. Addition of NaCl to the anoxic solution culture, enhanced Na⁺ transport to the shoots while it depressed that of K⁺. Under their experimental conditions, the ratio Na⁺/K⁺

transported to the shoots by anoxic roots increased by a factor of 860. The authors discussed that this abnormal ionic ratio in other salt sensitive species are known to produce physiological alterations including stomatal misfunctioning and reductions in photosynthetic rate and ribulose bisphosphate carboxylase-oxygenase activity (Drew et al., 1988).

Effect of anoxia on plant growth regulators

Since root systems are capable of synthesizing all plant growth regulators known today (Itai and Birnbaum, 1991), it is reasonable to inquire about the effects that a major metabolic disruption to the root tissues, lack of oxygen, may have on these substances and their regulatory role. Reid and Bradford (1984) in their review found that limiting oxygen inhibits synthesis of auxins, gibberellins and cytokinins. It has been found also that abscisic acid (ABA) levels increase in shoots (Jackson and Hall, 1987; Zhang and Davies, 1987) and ethylene accumulates both in submerged soils (Smith and Russell, 1969; Smith and Restall, 1971; Smith and Dowdell, 1974) and in hypoxic plant tissues (Jackson, 1985).

Unlike the other plant growth regulators ethylene is a gas with restricted solubility (Jackson, 1985). For that reason it cannot be significantly translocated in solution through the plant aqueous medium (Yang and Hoffman, 1984), but it moves mainly by diffusion. The estimated diffusion coefficient of ethylene decreases 10,000 times when moved from gaseous medium to water (Jackson,

1985). This limited mobility does not seem to be a problem for plants since all plant cells seem capable of producing the gas (Roberts and Hooley, 1988).

Ethylene is associated with the regulation of several plant responses to flooding such as epinasty (Bradford and Dilley, 1978; Bradford and Yang, 1981), the promotion of adventitious roots, and aerenchyma formation (Luxmoore and Stolzy, 1969; Yu et al. 1969; Drew et al. 1979 and 1981; Jackson et al. 1981; Konings, 1982; Everard and Drew, 1989b). The signal to produce these responses appears to result from an increase in ethylene concentration within the roots. Kawase (1981) proposed that ethylene increases cellulase activity, thus leading to cell wall lysis and air space formation. However, the experimental evidence to support this theory is lacking (Jackson, 1985). Moreover, most of the root cells are likely to be in contact with the gaseous ethylene, however aerenchyma formation is tissue specific. Cell lysis occurs specifically in the root cortex suggesting some unknown controlling mechanism (Drew, 1990).

Ethylene production by maize roots is stimulated by hypoxia but ceases during anoxia, which further halts aerenchyma development (Drew et al. 1979). However, synthesis of the ethylene precursor aminocyclopropane carboxylic acid (ACC) is stimulated under anoxia (Atwell et al. 1988). This suggests that ACC formed in anoxic root tips may be transported and converted to ethylene in better oxygenated portions of the root system closer to the surface (Bradford et al. 1982; Drew, 1990). Recent reports show that aerenchyma formation may also be associated with the plant mineral nutrition, in which case the process is not

necessarily related to an enhanced biosynthesis or accumulation of ethylene (Drew et al. 1989a and 1989b).

The accumulation of ABA in leaves during flooding events has received much attention during the last decade (Bradford, 1983; Jackson and Hall, 1987; Zhang and Davies, 1987; Jackson et al., 1988; Neuman and Smit, 1991). Although it was known for its role in stomatal control (Walton, 1980), it was only after failing to explain stomatal responses to root oxygen deficits based on ethylene evolution that ABA received attention (Bradford and Yang, 1981; Bradford and Hsiao, 1982). Today there seems to exist agreement that accumulation of foliar ABA will control stomatal behavior under waterlogged conditions. However, the source of the regulator remains unclear. Jackson and Hall (1987) proposed the inhibition of the transport out of the shoots as the accumulating mechanism; Zhang and Davies (1987) concluded that ABA accumulation in leaves might originate in the roots.

Effect of anoxia on phloem transport

Previous sections followed the hypothesis that a stress localized at the root level could have a significant effect on the shoots. In this section we will find that the opposite communication pathway, shoot to root, can also be affected.

In 1930, Münch proposed that photosynthates could move in the phloematic stream because of the difference in hydrostatic pressure generated by an osmotic gradient between the source and the sink (Münch, 1930). Münch's pressure-flow model was based on a simple physical model that can be built in the laboratory

(see Salisbury and Ross, 1992 for details). After much research and some additions, the pressure-flow model seems to still be favored today (Lucas and Madore, 1988; Nobel,1991; Salisbury and Ross, 1992).

Among the additions to the original pressure-flow model, the concepts of phloem loading and unloading were required for sustained functioning of the model. Münch thought that the high solute concentration required at the source could be provided by an active current of photosynthates produced in the mesophile cells. At the sink end, sugars were kept low through metabolism and/or storage in specialized cells or organelles. Investigations of the spatial distribution of specific solute concentrations strongly suggest the presence of a selective energy-dependent loading mechanism for the main compounds in phloem sap (Lucas and Madore, 1988). The movement of sucrose and other solutes to the sites of utilization or storage are also energy dependent (Eschrich, 1986). During anoxia the root system switches to the less energy-efficient anaerobic respiratory path (Saglio *et al.*, 1980).

In maize roots, Giaquinta et al. (1983) identified the pathway of phloem unloading. Their results showed that sucrose was unloaded from the phloem, symplastically transferred to adjacent cells and hydrolyzed by a vacuolar invertase prior to metabolism. Saglio and Pradet (1983) demonstrated that strict anoxia halts sucrose transport though the phloem. Since the sink strength for sugar metabolism remained unaffected (Saglio et al., 1980), their data suggested that the unloading process was impaired (Saglio and Pradet, 1983; Saglio, 1985). One

possible explanation was the occurrence of reversible structural modifications affecting the continuity of the cytoplasmic path, perhaps at the plasmodesma level (Saglio, 1985). An alternative explanation may be a disruption in the regulation of membrane potential at the tonoplast level. A recent report (Xia and Saglio, 1990) provides some evidence in support of the latter alternative.

Morphological adaptations to anoxia

Field grown maize exhibits a series of adaptive mechanisms to adverse soil aeration. Indeed, maize plants are relatively resistant to hypoxia (Grinieva, 1981). This resistance has a profound effect on the ability of the plant to survive. Unfortunately, it may not be as significant in avoiding loss of grain production.

According to the general concept of stress (Levitt, 1980) resistance can be achieved by avoidance and/or tolerance of the stress factor. Cannell and Jackson (1981) identified four types of avoidance mechanisms to oxygen stress: accelerated elongation, production of replacement roots, construction of internal channels (aerenchyma) within the root, and shoots responses which minimize injury. Tolerance to oxygen stress includes both the avoidance of toxic metabolite accumulation and true tolerance to toxic buildup. In this section, I will refer to the morphological adaptive responses of maize, more associated with the avoidance of the stress.

Several morphological responses that may have acclimative meaning have been reported in maize. They include inhibition of root (Purvis and Williamson, 1972; Wenkert et al., 1981; Meyer et al., 1987) and shoot growth (Purvis and Williamson, 1972; Wenkert et al., 1981), foliar senescence (Purvis and Williamson, 1972; Wenkert et al., 1981), adventitious rooting (Drew et al., 1979; Wenkert et al., 1981), and aerenchyma development (Luxmoore and Stolzy, 1969; Yu et al., 1969; Drew et al., 1979 and 1981; Jackson et al., 1981; Konings, 1982).

The significance of aerenchyma developed in response to hypoxia for the whole plant metabolism remains unclear. Vartapetian et al. (1978) found that the oxygen transported through aerenchyma tissue alone, could not provide normal aerobic metabolism to the root cells of pumpkin or cotton. Their calculations showed that only 8% of the total root oxygen requirement could be provided by diffusion via the cortical air spaces. Drew et al. (1985) calculated the quantitative contribution of the aerenchyma-diffused oxygen to the maintenance of high levels of adenylate energy charge. Although cortical lysis helped to maintain a high respiration rate over distances of at least 21 cm (the longest roots in their experiment), the oxygen diffusion was insufficient to maintain the energetic levels of fully aerobic roots.

Metabolic adaptations to anoxia

Kennedy et al. (1992) summarized the attempts to explain the metabolic adaptations of plants to flooding into two main groups:

1. Flood tolerance is dependent upon reduced activity of alcohol dehydrogenase (ADH) so leading to reduced ethanol production.

Proposed by Crawford and coworkers (McManmon and Crawford, 1971; Crawford, 1978), the theory identifies flooding injury with ethanol production, hence the *Pasteur effect* is a response of non-tolerant species. The tolerant species accumulate malic acid, as an alternative to ethanol, because malic enzyme is absent.

2. Flood tolerance is dependent upon fine regulation of the synthesis of lactate and acetaldehyde-ethanol. Proposed by Davies (1980), the theory recognized the regulatory role of the cytoplasmic pH on the activities of lactate dehydrogenase and pyruvate decarboxylase. The hypothesis associates flooding injury with cytoplasmic acidosis.

Many indications support the hypothesis of enhanced glycolysis and ethanol production as an acclimative response to anoxia. Several anoxia tolerant species and organs have a well regulated glycolysis and ethanol production (Drew, 1990). Ethanol is the main end-product of fermentation in rice, and ethanol production is quantitatively associated with the growth of rice embryos (Pradet *et al.*, 1985). Ethanol is also the main product in anoxic maize roots, where the metabolic energy level, as expressed by adenylate energy charge (Atkinson, 1977) was quantitatively related to the ethanol fermentative pathway (Saglio *et al.*, 1980). In studies of hypoxic acclimation of maize to anoxia (Saglio *et al.*, 1988; Hole *et al.*, 1989; Johnson *et al.*, 1989), longer viability during anoxia and higher ATP levels of the acclimated roots have been consistently associated, with an induced *Pasteur effect*, increased ethanol production and high ADH activity.

The work of Roberts *et al.*, (1984a and 1984b) in hypoxic maize root tips presented evidence in support of Davies' hypothesis of cytoplasmic acidosis. After an initial drop in pH, associated with lactic acid production, the cytoplasmic pH stabilized, within 20 minutes, at 0.5 pH units lower than the original value. This pH stabilization was associated with an active ethanol production and reduced lactate synthesis. Mutants without an active ADH, unable to shift from lactate to ethanol, continued producing lactate and the pH never stabilized. In all tested cases, early cell death was correlated with cytoplasmic acidosis.

Our understanding of the complexity of the maize metabolic adaptations to oxygen deficiency has been greatly improved after the identification of the acclimative effect of hypoxic periods previous to the anoxic treatment (Saglio et al., 1988; Johnson et al., 1989). Field grown maize will experience hypoxia before a complete depletion of oxygen, hence the hypoxic acclimation should be the dominant scenario in nature (Drew, 1990). This acclimation implies longer viability and, when in anoxia, higher energy levels, immediate expression of the *Pasteur effect* (Hole et al., 1989) and high ADH activity. Recently Xia and Saglio (1992) added another feature to the hypoxic acclimation. They measured an increased efflux of lactic acid from hypoxic-pretreated root tips as part of the adaptive responses. They speculate it may be a parallel of the detoxification systems found in hypoxic-treated cells of mammals.

Simulating the effects of anoxia

Modeling oxygen diffusion within the soil-plant system has received some attention. Luxmoore et al. (1970) proposed a model which included longitudinal and radial diffusion into a cylindrical root surrounded by a water film. Uniform root thickness was assumed and the respiratory sink of the tissue is modeled as a function of oxygen concentration and position along the root. Armstrong and Wright (1976) proposed an electrical circuit analogue to simulate root aeration in anaerobic environments. These ideas were further developed by Armstrong (1979). More recently Armstrong and Beckett (1985 and 1987) proposed a multishelled model to account for differences in concentric root tissues. This model provides a mathematical tool to predict quantitatively oxygen diffusion through specific root tissues with large differences in porosity as cortex and stele. It is interesting to note the existence of experimental evidence showing the presence of an anaerobic stele surrounded by a normoxic or hypoxic cortex (Thomson and Greenway, 1991).

A common feature of the above mentioned models is that they focus on the diffusion of oxygen through individual roots. No attempt is made to predict the effects that impaired root aeration may have at the whole plant level (Armstrong, 1979). Recently, Jones et al. (1991) proposed a generic model to simulate root growth that considers aeration stress. The model can be linked to the CERES family (Jones and Kiniry, 1986) of simulation models and hence be used to simulate maize responses to flooding. Jones et al. (1991) used the fraction of

water filled pore space as an index of soil aeration. A layer aeration factor is calculated as a function of the water filled pore fraction. Different processes of root growth including rooting depth, branching and senescence are eventually affected by the aeration factor.

Recently Smucker and Aiken (1992) proposed some of the needs for the next generation of simulation models. The authors emphasized the need for more mechanistic description of causes and effects at the root and soil interface that includes temporal and spatial variability. The ability to collect and process below ground information and the quantity and quality of such information will be critical to meet such expectations.

Summary

A maize crop during periods of waterlogging endures substantial alterations of the physical, chemical and biclogical environment of its root system. These alterations produce several changes in the plants and in the soil-plant relationships. Some of the biochemical processes associated with the respiratory path and the shift from aerobic to anaerobic respiration were reviewed and the changing views on the role of ethanol as a major agent of plant injury during hypoxia were discussed. Ethanol production and enhanced glycolysis is viewed today as an acclimative response that allows plant cells to survive extended periods of time. However, they are not able to provide enough energy to fully

sustain metabolic rates and cells eventually die due to the inability of maintaining the required pH compartmentalization.

At the whole plant level, substantial changes in the hydric, nutritional and hormonal levels were reported as a consequence of root anoxic events. The decreased energy level in the roots is not able to maintain normal rates of nutrient uptake. However, many aspects involving plant responses in terms of water relations still need further examination. For instance, stomatal closure seems to respond to the accumulation of abscisic acid in the leaves during hypoxia, but stomatal closure generally persists well beyond the actual soil oxygen deficit (Sojka, 1992). The lower energy level in roots may also have a role in impairing the normal phloematic current through the disturbance of the unloading process.

Several mechanisms associated in the literature with maize survival to soil submergence were reviewed. Although the mechanisms may warrant the opportunity to survive transient flooding periods, they imply a higher cost in carbon compounds utilized at the root level.

Some mechanistic models have tried to mathematically describe oxygen diffusion through the soil and individual roots. However, to the best of the author's knowledge no model has been published so far to simulate whole plant responses to anoxic events.

Bibliography

- Armstrong, W. 1979. Aeration in higher plants. Adv. Bot. Res. 7: 225-331.
- Armstrong, W. and P. M. Beckett. 1987. Internal aeration and the development of stelar anoxia in submerged roots: a multishelled mathematical model combining axial diffusion of oxygen in the cortex with radial losses to the stele, the wall layers and the rhizosphere. New Phytol. 105:221-245.
- Armstrong, W. and P. M. Beckett. 1985. Root aeration in unsaturated soil: a multi-shelled mathematical model of oxygen diffusion and distribution with and without sectorial wet-soil blocking of the diffusion path. New Phytol. 100:293-311.
- Armstrong, W. and E. J. Wright. 1976. An electrical analogue to simulate the oxygen relations of roots in anaerobic media. Physiol. Plant. 36:383-387.
- Atkinson, D. E. 1977. Cellular energy metabolism and its regulation. Academic Press, New York.
- Atwell, B. J., M. C. Drew and M. B. Jackson. 1988. The influence of oxygen deficiency on ethylene synthesis, 1-aminocyclopropane- 1-carboxilic acid levels and aerenchyma formation in roots of *Zea mays* L. Physiol. Plant. 72:15-22.
- Boyer, J. S. and M. E. Westgate. 1984. Water transport for cell enlargement. p. 96-102. *In* W. J. Cram, K. Janacek, R. Rybova and K. Sigler (Ed.) Membrane transport in plants. John Wiley, Chichester. West Sussex.
- Bradford, K. J. 1983. Involvement of plant growth substances in the alteration of leaf gas exchange of flooded tomato plants. Plant Physiol. 73:480-483.
- Bradford, K. J. and D. R. Dilley. 1978. Effects of root anaerobiosis on ethylene production, epinasty and growth of tomato plants. Plant Physiol. 61:506-509.
- Bradford, K. J., T. C. Hsiao and S. F. Yang. 1982. Inhibition of ethylene synthesis in tomato plants subjected to anaerobic root stress. Plant Physiol 70:1503-1507.

- Bradford, K. J. and T. C. Hsiao. 1982. Stomatal behavior and water relations of waterlogged tomato plants. Plant Physiol. 70: 1508-1513.
- Bradford, K. J. and S. F. Yang. 1981. Physiological responses of plants to waterlogging. Hortscience 16(1):25-30.
- Brauer, D., J. E. Leggett and D. B. Egli. 1987. Changes in K, Rb, and Na transport to shoots after anoxia. Plant Physiol. 83:219-224.
- Cannell, R. Q. and M. B. Jackson. 1981. Alleviating aeration stresses. *In G. F. Arkin and M. Taylor (Ed.) Modifying the root environment to reduce crop stress.*ASAE. Monograph No. 4, St. Joseph, Michigan.
- Chaudhary, T. N., V. K. Bhatnagar and S. S. Prihar. 1975. Corn yield and nutrient uptake as affected by water table depth and soil submergence. Agron. J. 67:745-749.
- Crawford, R. M. 1978. Metabolic adaptations to anoxia. p. 119- 136. *In D. Hook and R. Crawford (Ed.) Plant life in anaerobic environments. Ann Arbor, Michigan.*
- Crawford, R. M. 1977. Tolerance of anoxia and ethanol metabolism in germinating seeds. New Phytol. 79:511-517.
- Crawford, R. M. and M. A. Baines. 1977. Tolerance of anoxia and the metabolism of ethanol in tree roots. New Phytol. 79:519-526.
- Davies, D. D. 1980. Anaerobic metabolism and the production of organic acids. p. 581-611. *In* D. D. Davies (Ed.) The biochemistry of plants. Vol. 2. Academic Press, New York.
- Drew, M. C. 1992. Aeration and plant metabolism. Soil Science 154(4):259-268.
- Drew, M. C. 1990. Sensing soil oxygen. Plant Cell Environ. 13: 681-693.
- Drew, M. C., A. Chamel, J. P. Garrec and A. Fourcy. 1980. Cortical air spaces (aerenchyma) in roots of corn subjected to oxygen stress; structure and influence on uptake and translocation of 86rubidium ions. Plant Physiol. 65:506-511.
- Drew, M. C., J. Guenther and A. Lauchli. 1988. The combined effects of salinity and root anoxia on growth and net Na+ and K+ accumulation in *Zea mays* grown in solution culture. Ann. Bot. (London) 61(1):41-53.

- Drew, M. C., C. J. He and P. W. Morgan. 1989a. Decreased ethylene biosynthesis, and induction of aerenchyma, by nitrogen- or phosphate-starvation in adventitious roots of *Zea mays* L. Plant Physiol. 91(1):266-271.
- Drew, M. C., C. J. He and P. W. Morgan. 1989b. Ethylene synthesis and sensitivity in the formation of aerenchyma in response to deficiencies of N and P in roots of *Zea mays*. p. 323-330. *In* H. Clijsters, M. De Proft, R. Mancelle and M. Van Poucke (Ed.) Biochemical and physiological aspects of ethylene production in lower and higher plants. Kluwer Academic Publishers, Dordrecht.
- Drew, M. C., M. B. Jackson and S. Giffard. 1979. Ethylene- promoted adventitious rooting and development of cortical air spaces (aerenchyma) in roots may be adaptive responses to flooding in *Zea mays* L. Planta 147:83-88.
- Drew, M. C., M. B. Jackson, S. C. Giffard and R. Campbell. 1981. Inhibition by silver ions of gas space (Aerenchyma) formation in adventitious roots of *Zea mays* L. subjected to exogenous ethylene or to oxygen deficiency. Planta 153:217-224.
- Drew, M. C., P. H. Saglio and A. Pradet. 1985. Larger adenylate energy charge and ATP/ADP ratios in aerenchymatous roots of *Zea mays* in anaerobic media as a consequence of improved internal oxygen transport. Planta 165:51-58.
- Drew, M. C. and L. R. Saker. 1986. Ion transport to the xylem in aerenchymatous roots of *Zea mays* L. J. of Exp. Bot. 37(174):22-33.
- Drew, M. C. and E. J. Sisworo. 1979. The development of waterlogging damage in young barley plants in relation to plant nutrient status and changes in soil properties. New Phytol. 82: 301-314.
- Drew, M. C. and E. J. Sisworo. 1977. Early effects of flooding on nitrogen deficiency and leaf chlorosis in barley. New Phytol. 79: 567-571.
- Drew, M. C. and L. H. Stolzy. 1991. Growth under oxygen stress. p. 331-350. *In* Y. Waisel, A. Eshel and U. Kafkafi (Ed.) Plant roots; the hidden half. Marcel Dekker, New York.
- Dudal, R. 1976. Inventory of the major soils of the world with special reference to mineral stress hazards. p. 3-13. *In M. J. Wright (Ed.) Plant adaptation to mineral stress in problem soils. Cornell University Press, Ithaca, New York.*

- Eschrich, W. 1986. Mechanisms of phloem unloading. p. 225-230. *In J. Cronshaw*, W. J. Lucas and R. T. Giaquinta (Ed.) Phloem transport. Alan R. Liss, New York.
- Everard, J. D. and M. C. Drew. 1989a. Mechanisms controlling changes in water movement through the roots of *Helianthus annuus* L. during continuous exposure to oxygen deficiency. J. Exp. Bot 40(210):95-104.
- Everard, J. D. and M. C. Drew. 1989b. Water relations of sunflower (*Helianthus annuus*) shoots during exposure of the root system to oxygen deficiency. J. Exp. Bot. 40(220):1255-1264.
- Everard, J. D. and M. C. Drew. 1987. Mechanisms of inhibition of water movement in anaerobically treated roots of *Zea mays* L. J. Exp. Bot 38(192):1154-1165.
- FAO. 1989. Production yearbook, 1988. FAO, Rome.
- Giaquinta, R. T., W. Lin, N. L. Sadler and V. R. Franceschi. 1983. Pathway of phloem unloading of sucrose in corn roots. Plant Physiol. 72:362-367.
- Grinieva, G. M. 1981. The effect of flooding on metabolism and structure of maize roots. p. 323-326. *In* R. Brouwer, O. Gasparikova, J. Kolek and B. C. Loughman (Ed.) Structure and function of plant roots. Martinus Nijhoff-Dr. W. Junk Publishers, The Hague.
- Guidry, N. P. 1964. A graphic summary of world agriculture. USDA Misc. Pub. 705. U.S. Gov. Print. Office, Washington, DC.
- Hammond, L. C., W. H. Allaway and W. E. Loomis. 1955. Effects of oxygen and carbon dioxide upon absorption of potassium by plants. Plant Physiol. 30:155-161.
- Hole, D., P. Hole, J. R. Johnson, B. G. Cobb and M. C. Drew. 1989. Rates of glycolysis in aerobic and anaerobic maize root tips. Plant Physiol. 4, Supp:127.
- Hopkins, H. T. 1956. Absoption of ionic species of orthophosphate by barley roots: Effects of 2,4-dinitrophenol and oxygen tension. Plant Physiol. 31:155-61.
- Hopkins, H. T., A. W. Specht and S. B. Hendricks. 1950. Growth and nutrient accumulation as controlled by oxygen supply to the plant roots. Plant Physiol. 25:193-209.

- Itai, C. and H. Birnbaum. 1991. Synthesis of plant growth regulators by roots. p. 163-177. *In* Y. Waisel, A. Eshel and U. Kafkafi (Ed.) Plant roots; the hidden half. Marcel Dekker, New York.
- Jackson, M. B. 1985. Ethylene and responses of plants to soil waterlogging and submergence. Ann. Rev. Plant Physiol. 36:145- 174.
- Jackson, M. B., M. C. Drew and S. C. Giffard. 1981. Effects of applying ethylene to the root system of *Zea mays* on growth and nutrient concentration in relation to flooding tolerance. Physiol. Plant. 52:23-28.
- Jackson, M. B. and K. C. Hall. 1987. Early stomatal closure in waterlogged pea plants is mediated by abscisic acid in the absence of foliar water deficits. Plant Cell Envir. 10:121-130.
- Jackson, M. B., B. Herman and A. Goodenough. 1982. An examination of the importance of ethanol in causing injury to flooded plants. Plant Cell Environ. 5:163-172.
- Jackson, M. B., S. F. Young and K. C. Hall. 1988. Are roots a source of abscisic acid for the shoots of flooded pea plants? J. Exp. Bot. 39:1631-1637.
- Jeschke, W. D. 1984. K+-Na+ exchange at cellular membranes, intracellular compartmentation of cations and salt tolerance. p. 37-66. *In* R. C. Staples and G. H. Toennissen (Ed.) Salinity tolerance in plants. John Wiley, New York.
- Johnson, J., B. G. Cobb and M. C. Drew. 1989. Hypoxic induction of anoxia tolerance in root tips of *Zea mays*. Plant Physiol. 91: 837-841.
- Jones, C. A., W. L. Bland, J. T. Ritchie and J. R. Williams. 1991. Simulation of root growth. p. 91-123. *In J. Hanks and J. T. Ritchie (Ed.) Modeling plant and soil systems*. ASA, CSSA, SSSA, Madison, Wisconsin.
- Jones, C. A. and J. R. Kiniry. 1986. CERES-Maize: a simulation model of maize growth and development. Texas A&M Univ. Press, College Station, Texas.
- Kawase, M. 1981. Anatomical and morphological adaptation of plants to waterlogging. Hortscience 16(1):30-34.
- Kennedy, R. A., M. E. Rumpho and T. C. Fox. 1992. Anaerobic metabolism in plants. Plant Physiol. 100:1-6.

- Konings, H. 1982. Ethylene promoted formation of aerenchyma in seedling of *Zea mays* L. under aerated and non-aerated conditions. Physiol. Plant. 54:119-124.
- Kozlowski, T. T. and S. G. Pallardy. 1984. Effect of flooding on water, carbohydrate and mineral relations. p. 165-193. *In* T. T. Kozlowski (Ed.) Flooding and plant growth. Academic Press, Orlando.
- Kramer, P. J. 1940. Causes of decreased absorption of water by plants in poorty aerated media. Am. J. Bot. 27:216-220.
- Kramer, P. J. 1951. Causes of injury to plants resulting from flooding of the soil. Plant Physiol. 26:722-736.
- Lal, R. and G. S. Taylor. 1969. Drainage and nutrient effects in a field lysimeter study: I. Corn yield and soil conditions. Soil Sci. Soc. Am. Proc. 33:937-941.
- Letey, J., O. R. Lunt, L. H. Stolzy and T. E. Szuszkiewicz. 1961a. Plant growth, water use and nutritional response to rhizosphere differentials of oxygen concentration. Soil Sc. Soc. Proc. 25:183-186.
- Letey, J., L. H. Stolzy, G. B. Blank and O. R. Lunt. 1961b. Effect of temperature on oxygen-diffusion rates and subsequent shoot growth, root growth and mineral content of two plant species. Soil Sci. 92:314-321.
- Letey, J., L. H. Stolzy, N. Valoras and T. E. Szuszkiewicz. 1962. Influence of soil oxygen on growth and mineral concentration of barley. Agron. J. 54:538-540.
- Letey, J., L. H. Stolzy and N. Valoras. 1965. Relationships between oxygen diffusion rate and corn growth. Agron. J. 57:91- 92.
- Levitt, J. J. 1980. Responses of plants to environmental stresses. 2nd Ed. Academic Press, New York.
- Lucas, W. J. and M. A. Madore. 1988. Recent advances in sugar transport. p. 35-84. *In* J. Preiss (Ed.) The biochemistry of plants. Vol. 14. Academic Press, New York.
- Luxmoore, R. L., L. H. Stolzy and J. Letey. 1970. Oxygen diffusion in the soil-plant system I. A model. Agron. J. 62:317- 322.
- Luxmoore, R. J. and L. H. Stolzy. 1969. Root porosity and growth responses of rice and maize to oxygen supply. Agron. J. 61:202- 204.

- McManmon, M. and R. M. Crawford. 1971. A metabolic theory of flooding tolerance: the significance of enzyme distribution and behavior. New Phytol. 70:299-306.
- Meyer, W. S., H. D. Barrs, A. R. Mosier and N. L. Schaefer. 1987. Response of maize to three short-term periods of waterlogging at high and low nitrogen levels on undisturbed and repacked soil. Irrig. Sci. 8(4):257-272.
- Münch, E. 1930. Die stoffbewegungen in der pflanze. Fischer, Jena.
- Neuman, D. S. and B. A. Smit. 1991. The influence of leaf water status and ABA of leaf growth and stomata of *Phaseolus* seedlings with hypoxic roots. J. Exp. Bot. 42:1499-1506.
- Nobel, P. S. 1991. Physicochemical and environmental plant physiology. Academic Press, London.
- Parsons, L. R. and P. J. Kramer. 1974. Diurnal cycling in root resistance to water movement. Physiol. Plant. 30:19-23.
- Ponnamperuma, F. N. 1972. The chemistry of submerged soils. Adv. Agron. 24:29-95.
- Pradet, A., B. Mocquot, P. Raymond, C. Morisset, L. Aspart and M. Delseny. 1985. Energy metabolism and synthesis of nucleic acids and proteins under anoxic stress. p. 227-245. *In* J. Key and T. Kosuge (Ed.) Cellular and Molecular Biology of Plant Stress. Alan R. Liss, Inc., London.
- Purvis, A. C. and R. E. Williamson. 1972. Effects of flooding and gaseous composition of the root environment on growth of corn. Agron. J. 64:674-678.
- Rao, K. P. and D. W. Rains. 1976. Nitrate absorption by barley. I. Kinetics and energetics. Plant Physiol. 57:55-88.
- Reid, D. M. and K. J. Bradford. 1984. Effects of flooding on hormone relations. p. 195-219. *In* T. T. Kozlowski (Ed.) Flooding and plant growth. Academic Press, Orlando.
- Roberts, J. K., J. Callis, O. Jardetzky, V. Walbot and M. Freeling. 1984a. Cytoplasmic acidosis as a determinant of flooding intolerance in plants. Proc. Nat. Acad. Sci. 81:6029- 6033.

- Roberts, J. K., J. Callis, D. Wemmer, V. Walbot and O. Jardetzky. 1984b. Mechanism of cytoplasmic pH regulation in hypoxic maize root tips and its role in survival under hypoxia. Proc. Nat. Acad. Sci. 81:3379-3383.
- Roberts, J. A. and R. Hooley. 1988. Plant growth regulators. Chapman and Hall, New York.
- Saglio, P. H. 1985. Effect of path or sink anoxia on sugar translocation in roots of maize seedlings. Plant Physiol. 77(2): 285-290.
- Saglio, P. H., M. C. Drew and A. Pradet. 1988. Metabolic acclimation to anoxia induced by low (2-4 kPa partial pressure) oxygen pretreatment (hypoxia) in root tips of *Zea mays*. Plant Physiol. 86(1):61-66.
- Saglio, P. and A. Pradet. 1983. Effet du manque d'oxygène sur l'alimentation en sucres de la jeune racine de maïs. p. 331-338. *In* A. Gallais (Coordinateur.) Physiologie du maïs. INRA, Paris.
- Saglio, P. H., P. Raymond and A. Pradet. 1980. Metabolic activity and energy charge of excised maize root tips under anoxia. Plant Physiol. 66:1053-1057.
- Salisbury, F. B. and C. W. Ross. 1992. Plant Physiology. 4th ed. Wadsworth Publishing Co, Belmont, California.
- Sandhu, B. S., Balwinderjit Singh, Baldev Singh and K. L. Khera. 1986. Maize response to intermittent submergence, straw mulching and supplemental N-fertilization in subtropical region. Plant Soil 96(1):45-56.
- Shalhevet, J. and P. J. Zwerman. 1962. Nitrogen response of corn under variable conditions of drainage. A lysimeter study. Soil Sci. 93:172-182.
- Shaw, R. H. 1988. Climate requirements. p. 609-638. *In G. F. Sprague and J. W. Dudley (Ed.) Corn and corn improvement.* 3rd Edition. ASA-CSSA-SSSA, Madison, Wisconsin.
- Smith, K. A. and R. J. Dowdell. 1974. Field studies of the soil atmosphere I. Relationship between ethylene, oxygen, soil moisture content and temperature. J. Soil Sci. 25(2):217-230.
- Smith, K. A. and S. W. Restall. 1971. The ocurrence of ethylene in anaerobic soil. J. Soil Sci. 22(4):430-443.

- Smith, K. A. and R. S. Russell. 1969. Occurrence of ethylene and its significance in anaerobic soil. Nature (London) 222:769-771.
- Smucker, A. J. and R. M. Aiken. 1992. Dynamic root responses to water deficits. Soil Science 154(4):281-289.
- Sojka, R. E. 1992. Stomatal closure in oxygen-stressed plants. Soil Sci. 154(4):269-280.
- Sojka, R. E. and L. H. Stolzy. 1980. Soil-oxygen effects on stomatal response. Soil Sci. 130(6):350-358.
- Spek, L. Y. 1984a. Response of plants to nitrogen nutrition. I. Effects of interruption of the nitrate supply and aeration of the nutrient solution on absorption and distribution of nitrogen in maize plants. Proc. Koninklijke Nederlandse Akademic Wetenschappen 87(3):319-326.
- Spek, L. Y. 1984b. Response of plants to nitrogen nutrition. II. Response of maize plants to interruptions of the nitrogen nutrition and root aeration. Proc. Koninklijke Nederlandse Akademie Wetenschappen 87(3):327-336.
- Sposito, G. 1989. The chemistry of soils. Oxford University Press, New York.
- Thomson, C. J. and H. Greenway. 1991. Metabolic evidence for stelar anoxia in maize roots exposed to low O2 concentrations. Plant Physiol. 96(4):1294-1301.
- Trought, M. C. and M. C. Drew. 1982. Effects of waterlogging on young wheat plants (*Triticum aestivum* L.) and on soil solutes at different soil temperatures. Plant Soil 69:311-326.
- Trought, M. C. and M. C. Drew. 1980a. The development of waterlogging damage in wheat seedlings (*Triticum aestivum* L.) I. Shoot and root growth in relation to changes in the concentrations of dissolved gases and solutes in the soil solution. Plant Soil 54:77-94.
- Trought, M. C. and M. C. Drew. 1980b. The development of waterlogging damage in wheat seedlings (*Triticum aestivum* L.) II. Accumulation and redistribution of nutrients by the shoot. Plant Soil 56:187-199.
- USDA. 1984. Agricultural statistics. USDA U.S. Gov. Print. Office, Washington, DC.

- Vartapetian, B. B. 1978. Introduction. Life without oxygen. p. 1- 12. *In D. Hook and R. Crawford (Ed.) Plant life in anaerobic environments. Ann Arbor, Michigan.*
- Walker, J. C., D. J. Llewellyn, L.E. Mitchell and E. S. Dennis. 1987. Anaerobically regulated gene expression; molecular adaptations of plants for survival under flooded conditions. Oxford Surveys Plant Molecular & Cell Biology (4):71-93.
- Walton, D. C. 1980. Biochemistry and physiology of abscisic acid. Annu. Rev. Plant Physiol. 31:453-489.
- Wenkert, W., N. R. Fausey and H. D. Watters. 1981. Flooding responses in *Zea mays* L. Plant Soil 62:351-366.
- Xia, J. H. and P. H. Saglio. 1992. Lactic acid efflux as a mechanism of hypoxic acclimation of maize root tips to anoxia. Plant Physiol. 100:40-46.
- Xia, J. H. and P. H. Saglio. 1990. H+ efflux and hexose transport under imposed energy status in maize root tips. Plant Physiol. 93(2):453-459.
- Yang, S. F. and N. E. Hoffman. 1984. Ethylene biosynthesis and its regulation in higher plants. Annu. Rev. Plant Physiol. 35: 155-189.
- Yeo, A. R., D. Kramer, A. Läuchli and J. Gullasch. 1977. Ion distribution in salt-stressed mature *Zea mays* roots in relation to ultrastructure and retention of sodium. J. of Exp. Bot. 28:17- 29.
- Yu, P. T., L. H. Stolzy and J. Letey. 1969. Survival of plants under prolonged flooded conditions. Agron. J. 61:844-847.
- Zhang, J. and W. J. Davies. 1987. ABA in roots and leaves of flooded pea plants. J. Exp. Bot 38:649-659.

Chapter 2

A FIELD FACILITY FOR MONITORING WHOLE PLANT RESPONSES TO FLOODING

Abstract

Interpretation of root aeration studies performed on plant organs, tissues or organelles may require extreme caution to apply the findings to flooded crops. To gain a better understanding of whole plant responses to hypoxic and anoxic events, close and simultaneous monitoring of shoots' and roots' behavior may be helpful. A field facility designed and built with these purposes is described. A water table can be managed independently on each of five 2.1 m by 1.5 m plots, through a mini-scale subirrigation system. Pairs of horizontal minirhizotrons located at 15, 40, 60 and 90 cm provided an opportunity for non-destructive root growth monitoring. Maximum plant leaf area was reduced 30% or 40% when plants were flooded for four or eight days at 10 leaf tip stage. Roots showed a post-stress regrowth at 15 and 40 cm depth 24 days after flooding, whereas deeper zones did not have major changes in root growth.

Introduction

Most of the knowledge we have about plant responses to limiting soil oxygen conditions comes from research in which organs (many times only sections), tissues or organelles were the experimental material (Saglio *et al.*, 1980; Giaquinta *et al.*, 1983; Roberts *et al.*, 1984a and 1984b; Bacic and Ratkovic, 1987; Saglio *et al.*, 1988; Hole *et al.*, 1989; Johnson *et al.*, 1989; Thomson and Greenway, 1991; Xia and Saglio, 1990 and 1992). In cases where whole plants were used, artificial environments were provided with growth chamber and greenhouse facilities (Bradford, 1983a and 1983b; Drew *et al.*, 1985 and 1988; Veen, 1988; Thomson *et al.*, 1990). Although these artificial settings are designed to reduce the "noise" produced by uncontrolled factors, they may obscure the effect of unknown, but important, relationships and interactions.

An example may illuminate the point. In the late 1980s several reports demonstrated the hypoxic acclimation of maize roots to anoxia (Saglio et al., 1988; Hole et al., 1989; Johnson et al., 1989). When a flooding event occurs in nature, the complete depletion of soil oxygen may take a period from hours to days (Drew and Stolzy, 1991), depending on soil characteristics and temperature. So, field grown plants experience hypoxia before anoxia. In many experiments however, root anoxia is imposed suddenly by bubbling nitrogen gas into the nutrient solution, thus preventing the plants from undergoing hypoxic acclimation. In that view, some investigations may yield irrelevant or misleading information to improve our understanding of crop responses to flooding events.

Closely monitoring the behavior of shoot and root systems of field grown plants, under controlled submergence and water table scenarios, will help in understanding crop responses to anoxic periods. However, managing the water table in experimental plots, kept close enough to avoid uncertainty associated with soil variability (Benz et al., 1978) is difficult. Literature provides an interesting diversity of experimental techniques designed for this purpose. The most common method is using lysimeters of different sizes and designs (Hiler et al., 1971; Chaudhary et al., 1975; Cannell et al., 1980; Meyer et al., 1985). Barrett-Lennard et al., (1986) and Mukhtar et al., (1990) built hydrologically isolated plots, surrounded by plastic materials. A system of drainage-subirrigation with tiles buried in the plot perimeter and connected to a vertical pipe, allowed the control of the water table. Shallow back-filled plastic pans, were the solution employed by Fausey and McDonald (1985). Whereas Mason et al., (1987) simply retained water into closed furrows for extended periods. Ghodrati et al. (1990) utilized corrosion-resistant metal strips extending 20 cm into the soil to pond small plots.

This chapter describes a subirrigation research facility in which the water table can be independently controlled on each individual plot, function as a subirrigation system in microscale and have the capability to measure root systems non-destructively. Leaf area and root growth data obtained when corn was flooded for different durations are presented.

Materials and Methods.

A 4.86 ha subirrigation system was installed in 1985 at the Michigan State University Box Farm. The soil is mapped as Capac Loam (fine-loamy, mixed, mesic Aeric Ochraqualf) with 10 to 15% inclusions of Colwood, Marlette and Owosso soils (USDA-SCS, 1979). Plastic corrugated drainage tiles, 10 cm in diameter, were placed at 1.12 m depth and 11 m apart.

In 1990, the location of one of the tiles was chosen as a site to construct the root observation facility. A layout of the plots is shown in Figure 2.1. The soil at the facility matches the description of the Capac series: a very dark grayish brown loam surface of about 23 cm. The subsoil is described as having increasing contents of clay and clay films on the faces of peds.

A trenching machine was used to dig trenches 15 cm wide to a depth of about 1.35 m. Three 12 m long trenches parallel to the tile direction were first excavated. Then plywood forms, 1.22 m by 1.22 m by 15 cm wide, were slid into the open trench. Cross trenches were then dug with just enough room for the chain of the trencher to dig between them. The forms prevented the soil from caving in when the perpendicular trenches were excavated. With this plot arrangement, the original tile was sectioned into five pieces and became the subirrigation system of five, 2.13 m by 1.52 m plots. Upstream of each plot a plastic tile cap was inserted onto the tile. Downstream an outlet system (Figure 2.2) which would allow management of the water table in the plot was fitted. In the north-east corner of each plot a vertical 15.24 cm PVC pipe provided an input for

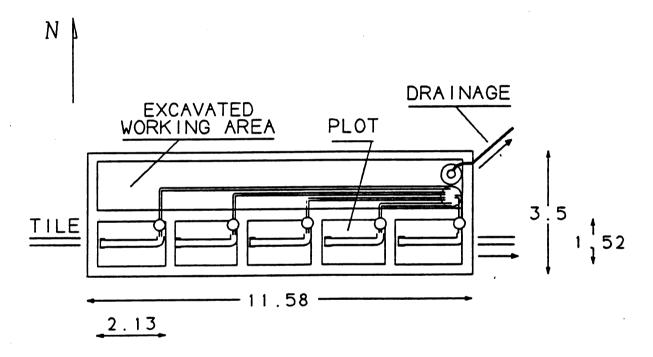


Figure 2.1: Plan view of the five plot facility with dimensions in meters.

PVC reductions. To irrigate the plots, black polyethylene tubing was used to conduct water by gravity from an elevated tank into the vertical pipe (see Figure 2.2). A valve controlled the water supply to each plot. Depth of water table was managed by adjusting the length of the float rod in the outlet float valve.

Inside the trenches, facing the working area (Figure 2.1), a network of reinforcing steel rods was used to reinforce the concrete walls. The other trenches had steel mesh for reinforcement.

One form was made for the working wall location of each plot to provide access holes for placing eight plastic minirhyzotron tubes, at 15, 40, 60 and 90 cm depths, through the concrete wall. Concrete was poured into the trenches using a concrete vibrator (see Figure 2.3 for a detail). Two days later, the soil inside the walls of the working area (Figure 2.1) was removed. The bottom of the working area was hand worked to provide a uniform slope west-east of about 1:100. A 200 liter plastic drum was cut in half and the two halves were placed with their open sides upwards in the lowest part of the working area to serve as sumps. Steel mesh was laid down in the working area and a 3.81 cm PVC pipe with two inlets were longitudinally located to provide drainage. Concrete was poured, starting by the zone surrounding the plastic sumps, to build the floor of the working area. PVC valves of 3.8 cm diameter were connected to each of the pipes coming out of the plots through the concrete wall and PVC 90 degrees elbows and pipe 3.81 cm in diameter were used as required to conduct the drainage flow to the sumps.

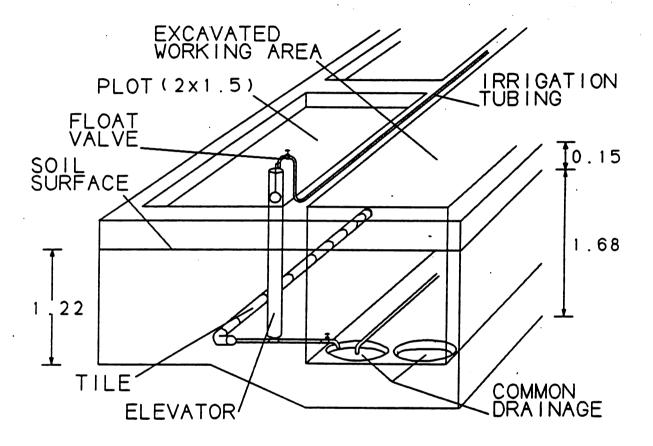


Figure 2.2: Detail in perspective of main components of a single plot with dimensions in meters.

An orifice 1.5 cm in diameter was drilled at 5 cm from the bottom, to connect both sumps. A 248.7 watt automatic electric sump pump was located at the bottom of one of the sumps and connected through a 2.5 cm polyethylene tubing, buried at 1 m depth, to the main drainage of the field.

A soil auger was used to open horizontal holes for the minirhizotrons, from the working area through the plots. A cylindrical wire brush, smaller in diameter than the opened hole, was used to scratch the soil surface in the hole and then polybuterate transparent tubes, 5 cm i.d., 5.7 cm o.d. and 152 cm long were driven into the holes. Black rubber stoppers (number 11) were inserted into the end of the tube before it was driven into the soil. The ends of the rhizotrons extending from the wall were painted black first to exclude light from the tubes and white later to avoid heating. Black rubber stoppers were placed in the painted ends.

Two vertical PVC pipes were located in the middle of each plot down to 1.2 m. The 5 cm pipe with rubber stoppers in both ends, was used as access tube for neutron probe measurements. The 1.75 cm pipe perforated and wrapped with filter cloth, was utilized as an observation well to monitor water table depth.

Results

As an example of the performance of the facility, preliminary information on maize growth in the summer of 1990 is given. During periods of inundation, the water table of the flooded plots was between 3 and 5 cm above the soil surface,

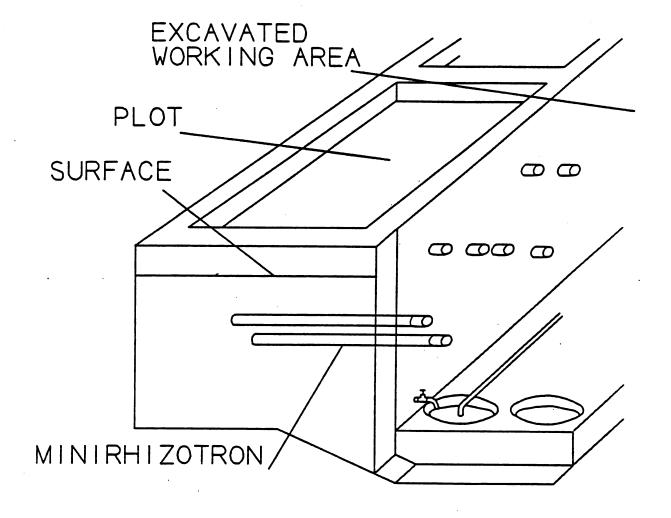


Figure 2.3: Detail of paired minirhizotrons located at 15, 40, 60 and 90 cm depth.

while the remaining plots kept low water tables without interference. Typically the water table rose above the surface within 12 hours after initiating the inundation. Drainage took longer, but usually the top 60 cm of the soil were drained within 24 hours.

The leaf area per plant appears in Figure 2.4. In one case, plants were flooded from 35 to 39 days after emergence; in the other, from 37 to 45 days. Results demonstrated a clear reduction in leaf growth between the stressed plants and the well aerated ones following the onset of the inundation period. At tasseling, the four day flooding resulted in a 30% reduction in leaf area, whereas the eight days flooding had an extra 10% decrease.

Figure 2.5 shows the distribution of roots at four dates for the control and the eight day inundation treatments. The control displayed apparently normal increase in the number of roots as the season progressed. The flooded plot did not reveal any decrease in roots by three days after the onset of the inundation. The two uppermost layers showed a proliferation of after-stress root growth 26 days after drainage. Deeper layers did not have major changes in roots. Conclusions.

The facility described herein provided a good opportunity to study the effects of flooding and limited soil aeration on whole-plant growth.

Crop growth data provided the evidence to support the adequate behavior of the structure. The results require further analysis. However they illustrate general patterns and tendencies.

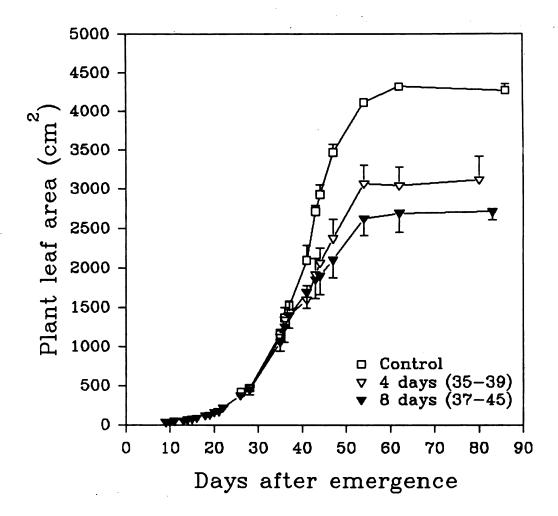


Figure 2.4: Effect of zero, four or eight days flooding on maize leaf area during 1990. Each point is the average of four plants. Vertical lines are standard errors (for clarity only positive or negative side is shown).

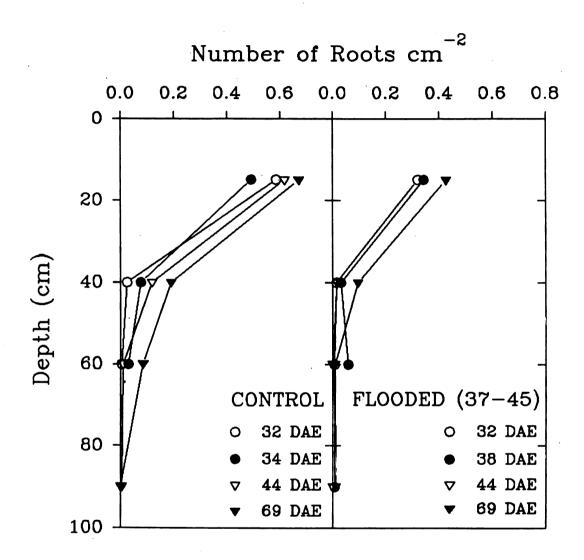


Figure 2.5: Roots distribution as affected by an eight day flooding period during 1990. Legends indicate days after emergence.

Bibliography

- Bacic, G. and S. Ratkovic. 1987. NMR studies of radial exchange and distribution of water in maize roots: the relevance of modelling of exchange kinetics. J. Exp. Bot. 38(193):1284-1297.
- Benz, L. C., G. A. Reichman, E. J. Doering and R. F. Follett. 1978. Water table depth and irrigation effects on applied water use efficiencies of three crops. Trans. of the ASAE 21(4):723-728.
- Barrett-Lennard, E. G., P. D. Leighton, I. R. McPharlin, T. Setter and H. Greenway. 1986. Methods of experimentally control waterlogging and measure soil oxygen in field trials. Aust. J. Soil Res. 24:477-483.
- Bradford, K. J. 1983a. Effects of soil flooding on leaf gas exchange of tomato plants. Plant Physiol. 73:475-479.
- Bradford, K. J. 1983b. Involvement of plant growth substances in the alteration of leaf gas exchange of flooded tomato plants. Plant Physiol. 73:480-483.
- Cannell, R. Q., R. K. Belford, K. Gales and C. W. Dennis. 1980. A lysimeter system used to study the effect of trasient waterlogging on crop growth and yield. J. Sci. Food Agric. 31: 105-116.
- Chaudhary, T. N., V. K. Bhatnagar and S. S. Prihar. 1975. Corn yield and nutrient uptake as affected by water table depth and soil submergence. Agron. J. 67:745-749.
- Drew, M. C., J. Guenther and A. Lauchli. 1988. The combined effects of salinity and root anoxia on growth and net Na+ and K+ accumulation in *Zea mays* grown in solution culture. Ann. Bot. (London) 61(1):41-53.
- Drew, M. C., P. H. Saglio and A. Pradet. 1985. Larger adenylate energy charge and ATP/ADP ratios in aerenchymatous roots of *Zea mays* in anaerobic media as a consequence of improved internal oxygen transport. Planta 165:51-58.
- Drew, M. C. and L. H. Stolzy. 1991. Growth under oxygen stress. p. 331-350. *In* Y. Waisel, A. Eshel and U. Kafkafi (Ed.) Plant roots; the hidden half. Marcel Dekker, New York.

- Fausey, N. R. and M. B. Jr McDonald. 1985. Emergence of inbred and hybrid corn following flooding. Agron J. 77(1):51-56.
- Ghodrati, M., F. F. Ernst and W. A. Jury. 1990. Effective design for small flood-irrigated field plots. Soil Sci. Soc. Am. J. 54: 927-930.
- Giaquinta, R. T., W. Lin, N. L. Sadler and V. R. Franceschi. 1983. Pathway of phloem unloading of sucrose in corn roots. Plant Physiol. 72:362-367.
- Hiler, E. A., R. N. Clark and L. J. Glass. 1971. Effects of water table height on soil aeration and crop response. Trans. of the ASAE 14(5):879-882.
- Hole, D., P. Hole, J. R. Johnson, B. G. Cobb and M. C. Drew. 1989. Rates of glycolysis in aerobic and anaerobic maize root tips. Plant Physiol. 4, Supp:127.
- Johnson, J., B. G. Cobb and M. C. Drew. 1989. Hypoxic induction of anoxia tolerance in root tips of *Zea mays*. Plant Physiol. 91: 837-841.
- Mason, W. K., K. E. Pritchard and D. R. Small. 1987. Effects of early season waterlogging on maize growth and yield. Aust. J. Agric. Res. 38(1):27-35.
- Meyer, W. S., H. D. Barrs, R. C. Smith, N. S. White, A. D. Heritage and D. L. Short. 1985. Effect of irrigation on soil oxygen status and root and shoot growth of wheat in a clay soil. Aust. J. Agric. Res. 36:171-185.
- Mukhtar, S., J. L. Baker and R. S. Kanwar. 1990. Corn growth as affected by excess soil water. Trans. of the ASAE 33(2):437-442.
- Roberts, K. M., J. Callis, O. Jardetzky, V. Walbot and M. Freeling. 1984a. Cytoplasmic acidosis as a determinant of flooding intolerance in plants. Proc. Natl. Acad. Sci. USA 81: 6029-6033.
- Roberts, K. M., J. Callis, D. Wemmer, V. Walbot and O. Jardetzky. 1984b. Mechanism of cytoplasmic pH regulation in hypoxic maize root tips and its role in survival under hypoxia. Proc. Natl. Acad. Sci. USA 81:3379-3383.
- Saglio, P. H., M. C. Drew and A. Pradet. 1988. Metabolic acclimation to anoxia induced by low (2-4 kPa partial pressure) oxygen pretreatment (hypoxia) in root tips of *Zea mays*. Plant Physiol. 86(1):61-66.
- Saglio, P. H., P. Raymond and A. Pradet. 1980. Metabolic activity and energy charge of excised maize root tips under anoxia. Plant Physiol. 66:1053-1057.

- Thomson, C. J., W. Armstrong, I. Waters and H. Greenway. 1990. Aerenchyma formation and associated oxygen movement in seminal and nodal roots of wheat. Plant Cell Environ. 13(4):395-403.
- Thomson, C. J. and H. Greenway. 1991. Metabolic evidence for stelar anoxia in maize roots exposed to low O2 concentrations. Plant Physiol. 96(4):1294-1301.
- USDA-SCS. 1979. Soil survey of Ingham county, Michigan, United States. Department of Agriculture. Soil Conservation Service.
- Veen, B. W. 1988. Influence of oxygen deficiency on growth and function of plant roots. Plant Soil 111:259-266.
- Xia, J. H. and P. Saglio. 1990. H+ efflux and hexose transport under imposed energy status in maize root tips. Plant Physiol. 93(2):453-459.
- Xia, J. H. and P. H. Saglio. 1992. Lactic acid efflux as a mechanism of hypoxic acclimation of maize root tips to anoxia. Plant Physiol. 100:40-46.

Chapter 3

FLOODING EFFECTS ON FIELD GROWN MAIZE.

I. ABOVEGROUND RESPONSES.

Abstract

This study was conducted to examine the effect of single flooding periods of four or eight days when maize was at the five-six or the 10-12 leaf tip stage. The research was done in a field facility built for this purpose. The water table was managed on each of the five 2.1 by 1.5 m² plots and roots were monitored through pairs of minirhizotrons located at 15, 40, 60 and 90 cm depth. Flooding reduced plant growth and yield, and delayed plant development. Reduction in plant leaf area depended more on reduced expansion rate of leaves in the earlier flooding and on premature senescence of the older leaves in the later flooding. Aboveground biomass remained unaffected during the flooding but was significantly decreased after drainage. Flooding reduced yields to half, independently of timing or duration of the submergence period. The early flooding delayed the appearance of silks by two or three days. However, the impact of this delay on yield remains unclear. Long lasting effects on plant carbon assimilation and stomatal regulation suggests slow post-stress recovery.

Introduction

Most crops reduce growth and yield under conditions of restricted soil aeration due to shallow water table or poor drainage. Limitations imposed by limited rooting depth due to the presence of a water table are extensively documented (e.g. Lal and Taylor, 1969; Williamson and Kriz, 1970; Benz et al., 1978; Shih and Rosen, 1985; Alvino and Zerbi, 1986).

After the development of the platinum microelectrode technique (Lemon and Erickson, 1952), efforts were focused on the study of crop responses to soil hypoxic environments as expressed by the oxygen diffusion rate. Evaluated crops included snapdragon [Antirrhinum sp.] (Letey et al., 1961a), sunflower (Letey et al., 1961b; Letey et al., 1962), cotton (Letey et al., 1961b), barley (Letey et al., 1962), soybeans, cabbage, grain sorghum, and sweet and dwarf field com (Williamson, 1964) and maize (Letey et al., 1965).

Another line of research has focused on the effects that transient flooding events have on plant growth and yield (Purvis and Williamson, 1972; Wenkert et al., 1981; Bradford and Hsiao, 1982; Zhang and Davies, 1986 and 1987; Mason et al., 1987; Smit et al., 1989; Schildwacht, 1989). In this case, considerable effort has been devoted to address the still largely unknown issue of the water relations in flooded plants. Since the earlier reports of Kramer (1940 and 1951) showing reduced root permeability as a cause of decreased water absorption in flooded plants, researchers have been confronting new findings, many times with contradictory evidence. In a recent review, Sojka (1992) documented altered

stomatal resistance with poor soil aeration for at least 58 species. However, stomatal closure and reduced growth have occurred without any detectable change in leaf water status (Bradford and Hsiao, 1982). The opposite, initial decline in leaf water potential and subsequent recovery without stomatal closure has been reported as well (Everard and Drew, 1989). At least one possible explanation for these discrepancies was evident from the work of Schildwacht (1989). This author found that the anaerobic reduction of leaf growth had two distinct phases. The first one, detectable within a few hours after imposing the stress, was fully explained by a lowered leaf water status. The second one was independent of the leaf water status since it occurred despite full recovery of the leaf water potential. This second phase may be associated with a reduction in cell wall extensibility as reported for peas (Zhang and Davies, 1986) and for a *Populus* hybrid (Smit et al., 1989). However, there is a lack of documentation on the relative contributions of senescence and reduced expansion to the decrease in leaf area growth experienced by whole plants through the season.

Crop yields have been reported to be reduced most when flooding occurs early in the season (Chaudhary et al., 1975; Sandhu et al., 1986; Meyer et al., 1987; Mukhtar et al., 1990). Yet very little attention has been directed to the effect that soil submergence may have on the timing of phenological events, especially those associated with the reproductive stages (Hiler et al., 1971; Meyer et al., 1987).

Photosynthetic assimilation has received limited attention. Data from Bradford (1983) suggests a decrease in carbon assimilation in flooded tomato. Oosterhuis et al. (1990) working with soybeans and Vu and Yelenosky (1991) working with Citrus found comparable results. On the other hand, Meyer et al. (1987) found an increased photosynthetic rate in maize on the third day of a flooding period imposed 40 days after sowing. However, the assimilation rate decreased over larger periods when compared with the control crop.

Reports on biomass accumulation show a reduction in the final biomass of flooded crops (Chaudhary et al., 1975; Sandhu et al., 1986; Meyer et al., 1987) with a higher reduction when the flooding occurs earlier in the season (Mukhtar et al., 1990). However, the final biomass provides little insight about the timing of dry matter accumulation affected by flooding.

This chapter will study the responses of field grown maize to individual flooding events during the vegetative growth stage either early (five-six leaf tip stage) or late (10-12 leaf tip stage) for four or eight days. The attention will focus on the growth process of the aboveground organs trying to fill some of the gaps identified in previous paragraphs. A general literature review provided a comprehensive theoretical framework in the first chapter, while the second chapter described the field facility built to control the water table in experimental plots. This chapter will discuss the aboveground maize responses to flooding in the vegetative growth stage during the summers of 1990 and 1991.

Materials and Methods

During the summers of 1990 and 1991, maize (*Zea mays* L., cv. GL 420) was grown in the field facility described in chapter 2. The facility allows independent control of the water table in five (2.1 by 1.5 m²) plots through a drain located at 1.10 m depth. Special care was taken to avoid disturbing the soil during the building process. The soil at the site is a Capac loam (Aeric Ochraqualf), with increasing clay content with depth, and with an estimated average of 169 mm of plant available water in the upper 1.25 m. Plant available water is defined as the difference between the highest volumetric water content in the field after drainage and the lowest measured water content when plants are very dry and leaves are dead or dormant (Ritchie, 1981).

In July 1991, a minimum data set automatic weather station (LICOR 1200) was installed in the experimental site. The automatic station provided daily information for maximum and minimum air temperatures, rainfall, and solar radiation.

Seeds were planted in excess and thinned out after emergence to the desired density of five plants m⁻² in 1990 and eight plants m⁻² in 1991. Sowing in 1990 was on July 20, soon after the facility was completed, providing the opportunity to study only the vegetative growing period. In 1991, sowing was on May 25. In 1990, fertilizer was applied at a rate of 210 Kg N ha⁻¹, 53.2 Kg P ha⁻¹ and 53.2 Kg K ha⁻¹. Nitrogen was split into two applications: at planting and 28 days after emergence. In 1991, all the fertilizer was applied at planting at the

following rates: 53.1 Kg N ha⁻¹, 53.8 Kg P ha⁻¹ and 53.8 Kg K ha⁻¹.

The water table was maintained close to, but not interfering with, the observed growing roots. Plots were watered at the surface using a garden-hose as required. Treatments were imposed by raising the water table between 20 and 50 mm above the soil surface once during the vegetative growth stage and for the following durations:

- 1. Early vegetative, for four days (E4)
- 2. Early vegetative, for eight days (E8)
- 3. Late vegetative, for four days (L4)
- 4. Late vegetative, for eight days (L8)
- 5. Control (C).

In 1990, the early and late submergence periods were imposed when plants were at five and 10 leaf tip stages (about V3 and V6 according to Ritchie and Hanway, 1984). In 1991 early and late were six and 12 leaf tip stages (V3 and V6).

On each plot, four plants were randomly selected and identified for measurements of leaf area and plant height through the season. Leaf area was determined by measuring maximum width and length of leaves or visible portion of leaves expanding and multiplying by a factor obtained by regression analysis. Two plants from each plot were randomly sampled at three different times during the vegetative stage in 1991 to provide information for the leaf area regression analysis. Actual leaf area, obtained with a leaf area meter (LICOR, model 1500, Lincoln NB), was correlated with measurements of length and width on each leaf

to derive the following expression:

Leaf Area
$$(cm^2) = 0.765 * length (cm) * width (cm) (r^2 = 0.9746)$$

Plant height was recorded as the distance from the soil surface up to the point at which the edges of the uppermost expanding leaf first separate from each other, or, when available, up to the collar of the flag leaf.

In 1990 and 1991, two plants were sampled from the two late flooding and control treatments before and after the flooding period for above ground biomass determinations. At silking two plants were sampled from each of the five plots. In 1990, the last sample was taken one week after silking and four plants were collected per plot for biomass determinations. In 1991 eight plants were sampled at harvest. Stems, leaves, ears and grains were separated. Grain dry weight was used to estimate treatments yield. Six additional ears were used to evaluate yield components.

In 1990, the occurrence of tasseling and silking was evaluated in the four plants where leaf area was measured. In 1991, all the plants on each plot were used to register these phenological events.

Photosynthesis and stomatal conductance were evaluated in 1991 simultaneously under conditions of complete sunshine in four randomly selected plants of each plot. A portable open gas exchange system (Analytical Development Corporation, Hodesdan, UK) equiped with an infrared gas analyzer

(IRGA) was used on four randomly selected plants. On each plant, a young fully expanded leaf, fully exposed to solar radiation was clamped into the instrument chamber and exposed to the incoming radiation in a perpendicular orientation. Between 30 and 60 seconds elapsed before obtaining a stable reading. The program described by Moon and Flore (1986) was used to calculate assimilation rate and stomatal conductance.

Results

The temperature during 1990 was approximately normal for plant growth only until tasseling that occurred between 70 and 74 days after planting. After tasseling, low temperatures abnormaly delayed plant growth. Figure 3.1 shows the daily maximum and minimum temperatures during the growing seasons of 1990 and 1991. The amount of radiant energy provides an estimate of the potential for carbon assimilation. The incident solar radiation for both years, together with the daily rainfall is shown in Figure 3.2. Rainfall was abundant and well distributed during 1991.

The growth of the leaf surface during 1990 and 1991 is depicted in Figure 3.3. Arrows indicate the onset of the flooding periods. For both years, the submergence periods of four and eight days significantly reduced the growth of the foliar surface, especially the early flooding event. The main difference between the response in 1990 and that of 1991 was in the four days early flooding treatment, which showed little impact in 1990. In 1990 it was difficult to maintain

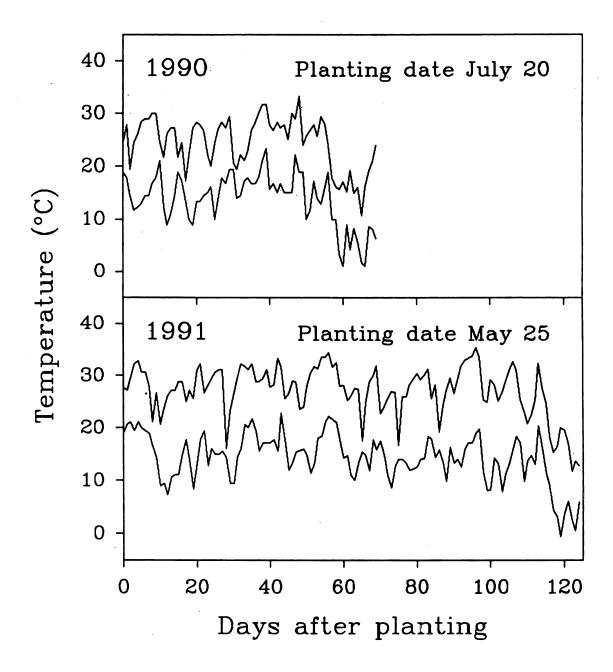


Figure 3.1: Daily maximum and minimum temperatures experienced at MSU Box Farm during the growing periods of 1990 and 1991.

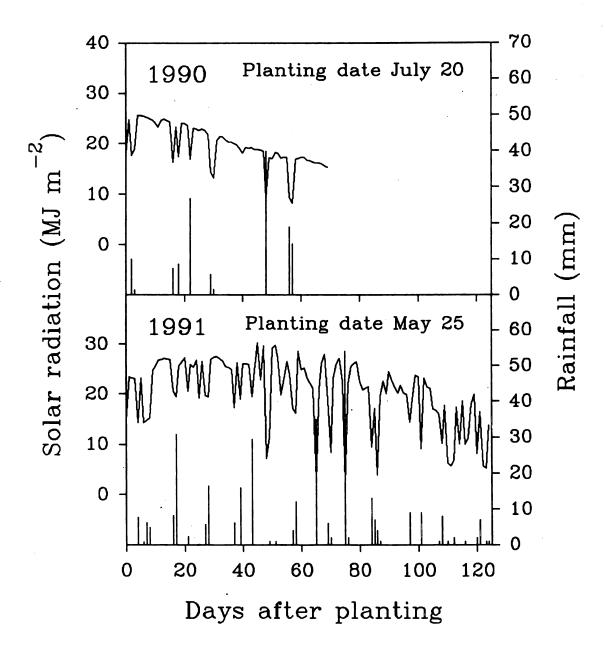


Figure 3.2: Incident solar radiation and rainfall at the MSU Box Farm during the growing periods of 1990 and 1991.

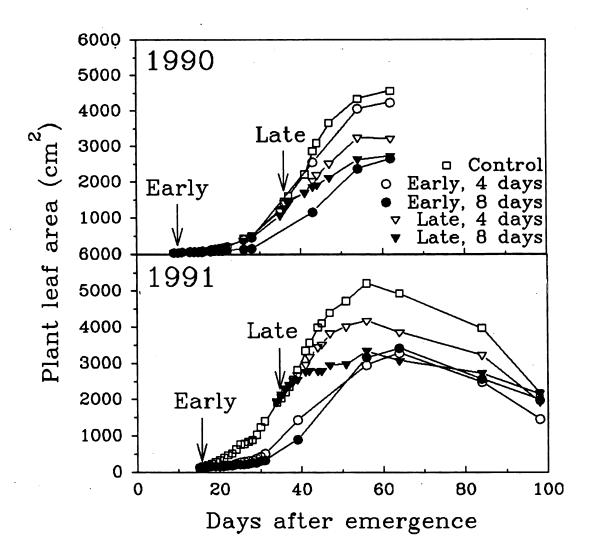


Figure 3.3: Leaf area per plant as affected by soil submergence of zero, four and eight days. In 1990 flooding was applied by raising the water table above the surface at five or 10 leaf tip stages; in 1991 at six or 12 leaf tip stages.

a constant head of water because of several leaks in the top edges of the wall in that particular plot. The reductions observed in the total plant leaf area in Figure 3.3 may have been caused by a reduction in leaf expansion of younger leaves, by an earlier senescence of older leaves, or by a combination of both.

Figure 3.4 is a daily record of the average plant foliar surface for the period of two weeks after the water table was raised. Careful measurements showed that, for plants of this size, there was a discernible difference in whole plant leaf area even from the first day after imposing the stress. Leaf senescence was responsible for a limited share of this difference (Figure 3.5). However, Figure 3.5 showed only a reduced period after the submergence event. Figure 3.6 corroborates that the differences in whole plant leaf area, shown in Figure 3.4, cannot be attributed to a main effect of premature leaf senescence, but rather to changes in leaf expansion rate.

Leaf elongation was studied by comparing the changes in leaf length of individual leaves that were actively expanding during the stress period. Figure 3.7 shows the growth and final length of three such leaves. A careful examination of the extension pattern of the sixth leaf shows three differences between flooded and non-flooded plants: the final length was shorter for stressed plants; the extension rate was lower; and, the duration of the period of expansion was longer. Observing the seventh and eighth leaf lengths the different patterns of recovery between the leaves of the shorter and longer submergence events becomes evident. Leaf eight exhibited a two-day delay in the time of appearance.

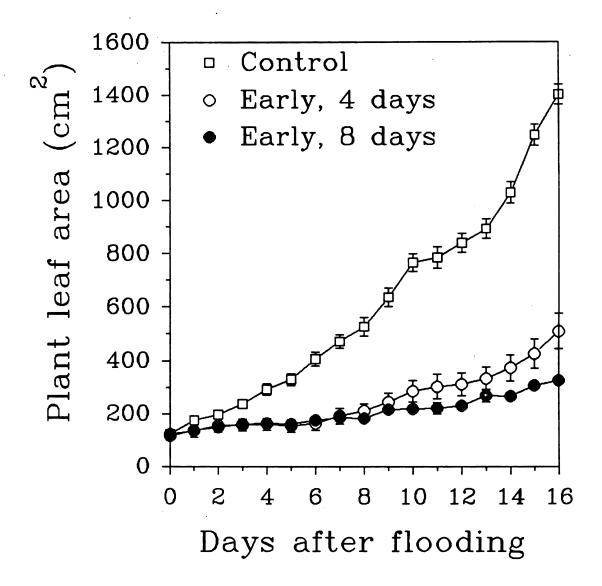


Figure 3.4: Detail of maize leaf area growth as affected by a flooding period of zero, four or eight days when plants were at six leaf tip stage. 1991.

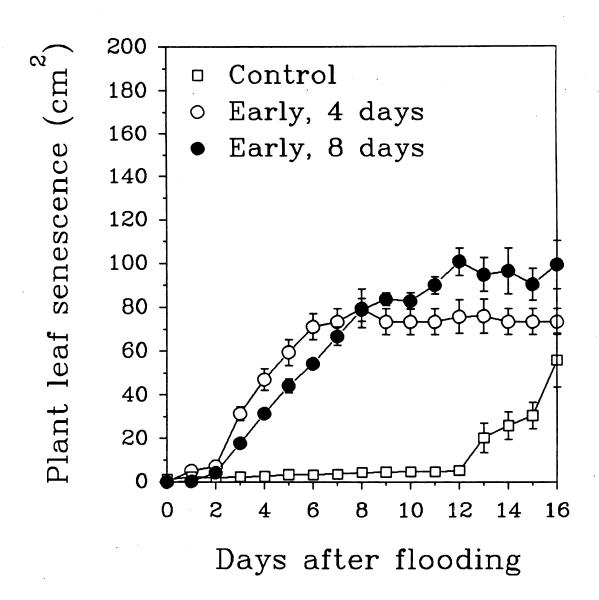


Figure 3.5: Detail of whole plant leaf senescence as affected by a flooding period of zero, four or eight days when plants were at six leaf tip stage. 1991.

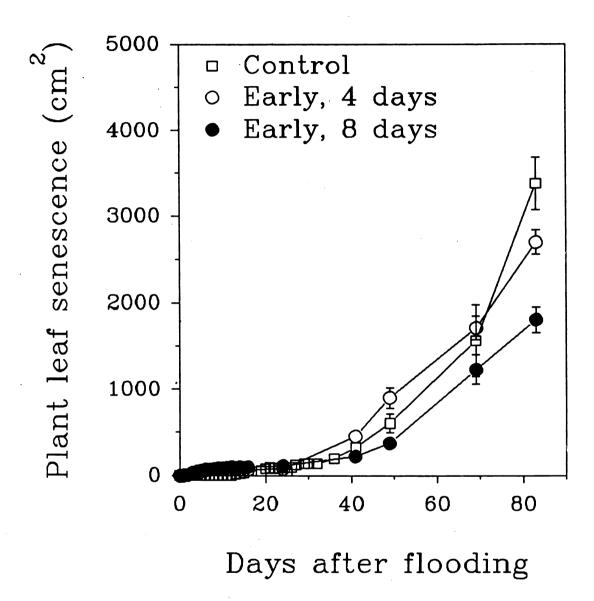


Figure 3.6: Plant leaf senescence as affected by a single flooding period of zero, four or eight days when plants were at the six leaf tip stage. 1991.

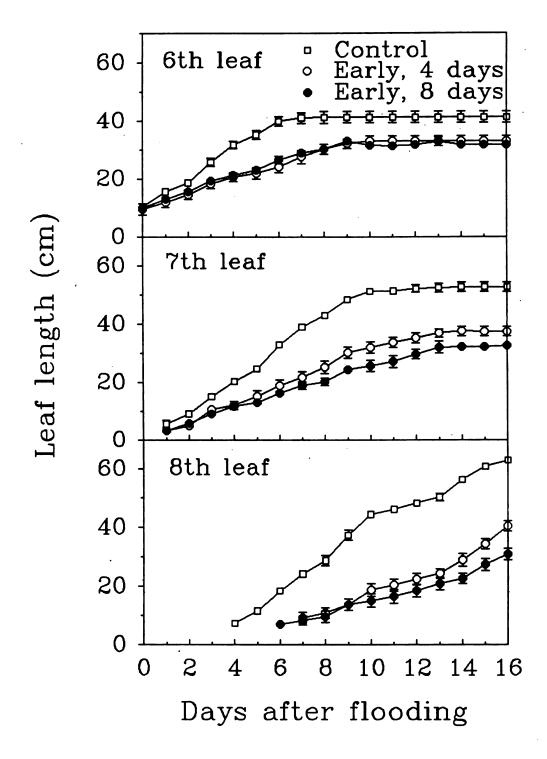


Figure 3.7: Leaf length of individual leaves as affected by a flooding event of zero, four or eight days of duration when plants were at six leaf tip stage. 1991.

Figure 3.8 shows the extension rates of leaves six, seven and eight calculated as the average of the rates through the whole period of expansion of each leaf. Two factors are responsible for the differences observed: the slower rate of growth goes together with the longer period of extension as shown in Figure 3.7. Early flooding had a long lasting effect on the process of leaf expansion (Figure 3.9). Four days of flooding reduced the length up to the 10th leaf, whereas eight days affected up to the 12th leaf.

The later flooding event was imposed when plants were in the 12th leaf tip stage. By this time (see Figure 3.10) plants had already accumulated 2,000 cm² of foliar surface, as compared with 100 cm² in the earlier stress. In this case, significant differences in whole plant leaf area between flooded and non-flooded plants were measured after the third day of flooding. Also note that there is an increase in leaf area variability, as expressed by the standard errors, associated with the duration of the submergence period.

Figure 3.11 shows the senescence responses in the two weeks following the initiation of the later flooding period. After six days there were differences between treatments. However, 10 days later plant senescence was more than three and seven times larger in the four and eight days flooding as compared with the control. The seasonal behavior of whole plant leaf senescence is depicted in Figure 3.12 for the treatments that were flooded later in the vegetative stage. From this figure, senescence clearly was a major contributing factor in reducing the leaf area of the late flooding treatments after the initial five days. This response is

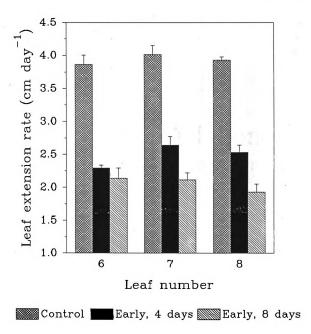


Figure 3.8: Leaf extension rates averaged for the whole period of expansion of the 6th, 7th and 8th leaves, as affected by a flooding event of zero, four or eight days. Vertical lines are standard errors. 1991.

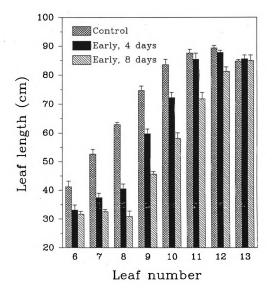


Figure 3.9: Final leaf length of selected leaves as affected by a flooding period of zero, four and eight days. Vertical lines are standard errors. 1991.

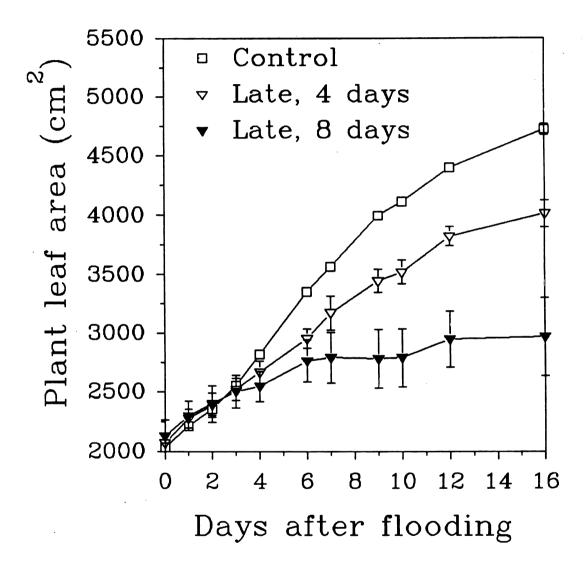


Figure 3.10: Plant leaf area as affected by a flooding period of zero, four or eight days when plants were at 12 leaf tip stage. Vertical lines are standard errors. 1991.

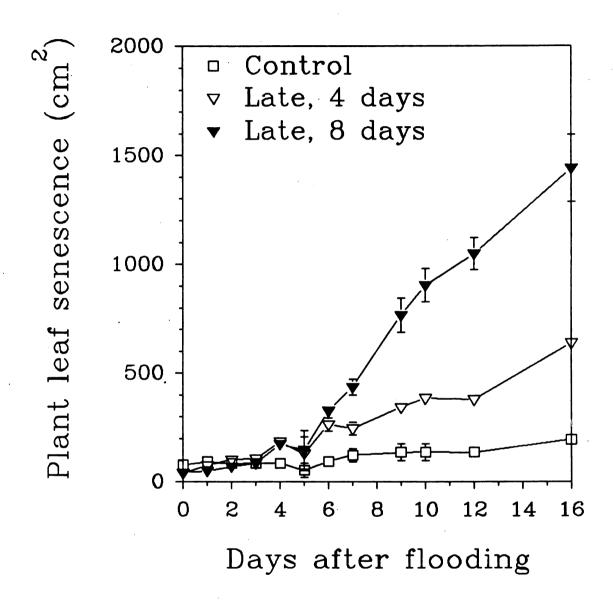


Figure 3.11: Plant leaf senescence as affected by a flooding period of zero, four or eight days when plants were at 12 leaf tip stage. Vertical lines are standard errors. 1991.

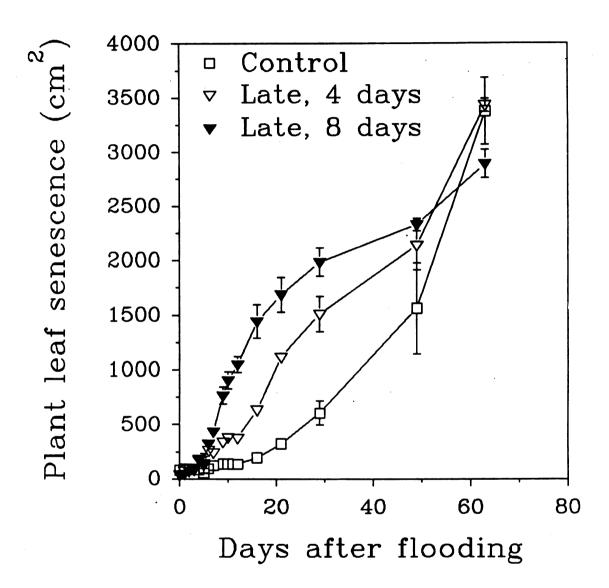


Figure 3.12: Plant leaf senescence as affected by a flooding period of zero, four or eight days when plants were at 12 leaf tip stage. Vertical lines are standard errors. 1991.

different from the one previously discussed for the early flooding, where premature senescence was a minor component in the reduction of plant leaf area.

The seasonal evolution of leaf expansion for individual leaves is shown in Figure 3.13. The general growth pattern of leaves 13, 14 and 15 showed small differences between flooded and non-flooded treatments. Although expansion rates appear to be smaller for the eight day flood than for the control, final leaf sizes are only slightly different in the 15th leaf. Average extension rates for the same leaves are in Figure 3.14. In this case, the extension of the flooding period from four to eight days did not affect the rate at which leaves expanded. However, leaves from the eight day flooding treatment did expand slower as compared with leaves from the treatment without stress. The same thing can be said about final leaf size (Figure 3.15). Leaves 14 through 17 were shorter in plants flooded eight days as compared with leaves from non-flooded plants. The length of the flag leaf was not affected.

In summary, all the flooding treatments imposed in this experiment significantly reduced the plant photosynthetic surface. The timing of the flooding altered the magnitude of the leaf area reductions. Earlier flooding mostly decreased leaf expansion and later flooding mostly promoted premature senescence.

Another plant attribute that may be affected when cell expansion becomes limiting for growth is plant height which has a fairly direct relationship with internode elongation. Figure 3.16 provides a perspective of the seasonal changes

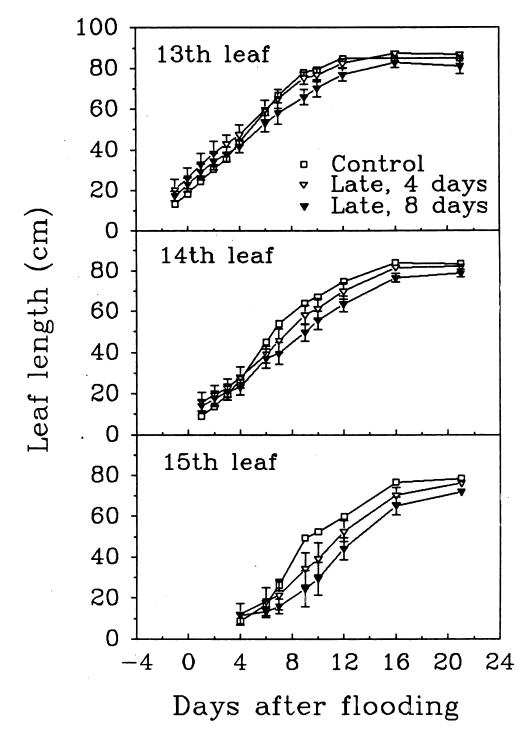
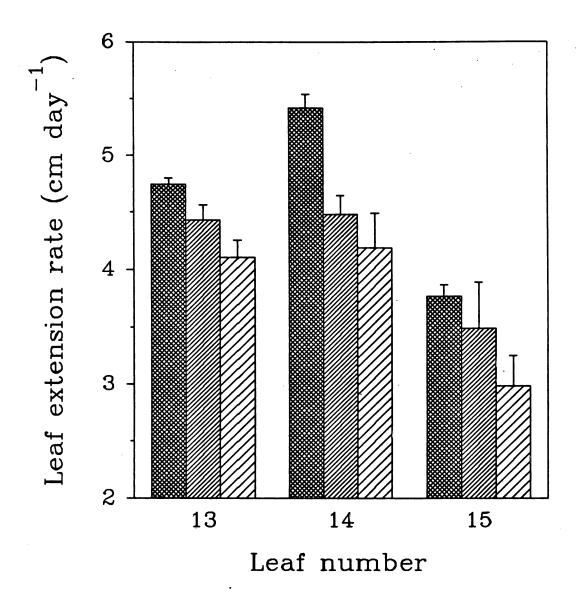


Figure 3.13: Length of leaves 13, 14 and 15 as affected by a flooding period of zero, four and eight days when plants were 12 leaf tip stage. Vertical lines are standard errors. 1991.



Control Late, 4 days Late, 8 days

Figure 3.14: Rate of extension of leaves 13th, 14th and 15th of plants flooded at the 12 leaf tip stage for zero, four and eight days. Vertical lines are standard errors. 1991.

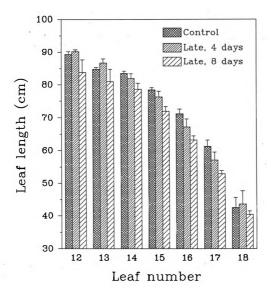
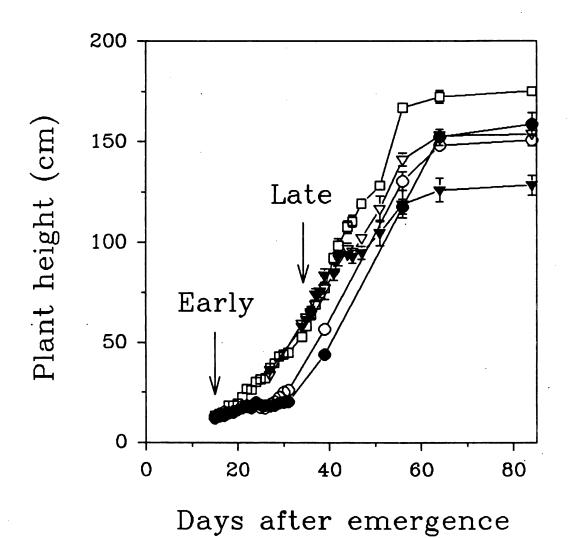


Figure 3.15: Final leaf length of selected leaves of plants flooded for zero, four and eight days at 12 leaf tip stage. Vertical lines are standard errors. 1991.



- Control
- Early, 4 days ▽ Late, 4 days
- Early, 8 days ▼ Late, 8 days

Figure 3.16: Seasonal changes in plant height as affected by a flooding period of zero, four or eight days either at six leaf tip or 12 leaf tip stages. Vertical lines indicate standard errors. 1991.

in plant height as affected by different times and durations of flooding. A rapid reduction in plant height was evident after the early flooding. Strong winds affected the experimental site 40 days after emergence. At that time, the longer late flooding treatment was under soil submergence and the shorter flooding treatment was just drained. Plant lodging produced a bend at the stem base that eventually affected the measured plant height in these treatments.

If plant height was decreased during the early flooding, then a reduction in the length of the internodes that were extending at that time could be expected. Plants in this experiment produced 17 internodes and 18 leaves. Usually the first five internodes are very short and below ground after full expansion (Ritchie and Hanway, 1984), so out of 12 internodes measured in destructive sampling at silking, the lowermost internode should be the sixth. The length of the internodes of early-flooded plants measured at silking are shown in Figure 3.17. When comparing the corresponding internodes of the flooded and non-flooded treatments, the progressive recovery of length was clearly faster in the treatment with the shorter submergence period.

The corresponding lengths of the internodes of late-flooded plants are shown in Figure 3.18. Smaller differences in internode length between flooded and non-flooded treatments as compared with the earlier flooding period are evident.

Reductions in organ extension, such as those reported above for leaves and stems, are often associated with decline in the organ water status. Under such conditions, the plant's fastest response is to close their stomata to avoid

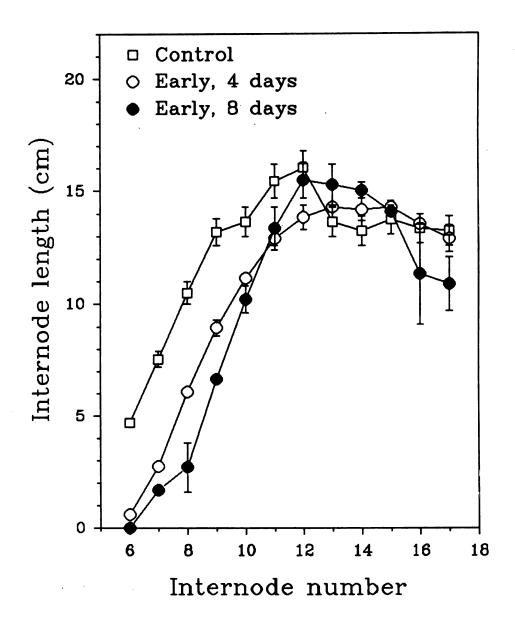


Figure 3.17: Length of the internodes above the ground measured at silking in plants that were flooded for zero, four or eight days at the six leaf tip stage. 1991.

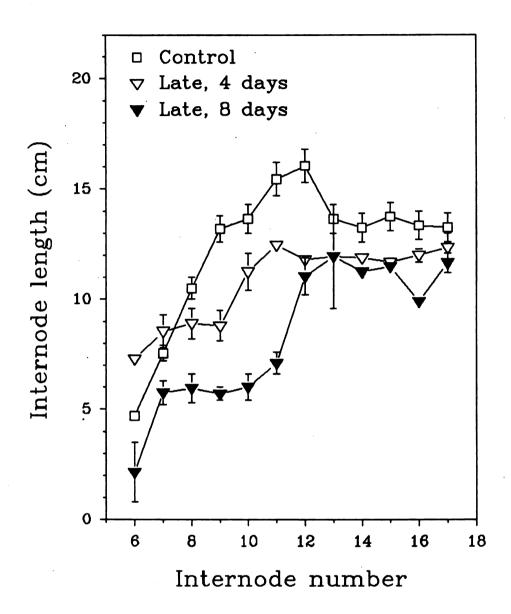


Figure 3.18: Length of the internodes above the ground measured at silking in plants that were flooded zero, four or eight days at the 12 leaf tip stage. 1991.

Table 3.1: Stomatal conductance, measured at 1400 h, after the onset of a flooding period of zero, four or eight days in plants at the 12 leaf tip stage. Values in parentheses are standard errors.

DAF	Control	Late, 4 days	Late, 8 days
	***************************************	μmol m ⁻² s ⁻¹	
4	127.33	117.22	114.71
	(5.68)	(5.09)	(9.58)
8	101.59	83.47	73.27
	(2.55)	(2.76)	(7.26)
50	170.42	173.00	162.26
	(2.55)	(17.77)	(12.63)

dehydration. Table 3.1 shows the evolution of stomatal conductance measured around 2:00 pm in the plots that were flooded later in the season. Four days after the onset of the submergence treatment, differences between flooded and non-flooded plants were still part of the variability associated with the measurement. The distinction in stomatal conductance was larger eight days after the initiation of the soil submergence. Table 3.1 shows that 50 days after flooding the soil the recovery of the treated plants seems to be complete. However, looking at this last measurement in a daily context (Figure 3.19), while morning and mid-day evaluations of the plants failed to detect differences in stomatal opening between flooded and non-flooded plants, the flooded seemed to close their stomata earlier in the afternoon. Even the plants that were flooded earlier in the season showed the same early afternoon stomata closing (Figure 3.19).

One of the main reasons why farmers grow crops is to obtain a profitable

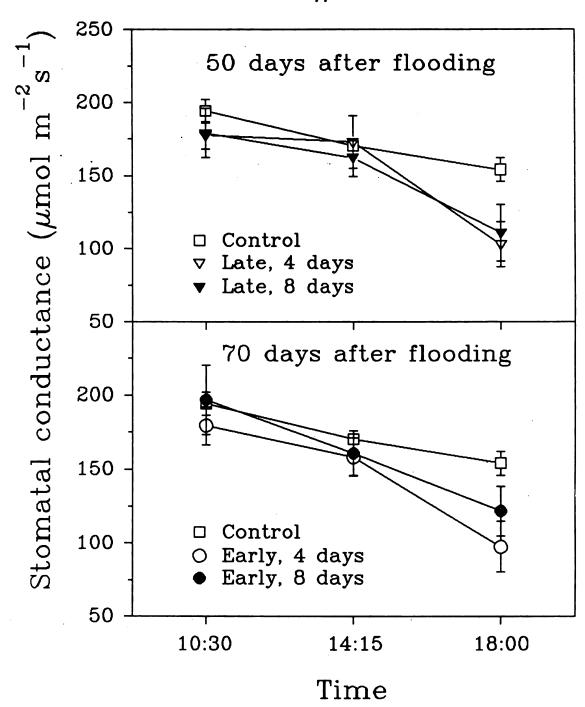


Figure 3.19: Daily evolution of stomatal conductance measured 50 days (above) or 70 days (below) after the onset of a flooding period of zero, four or eight days at the 12 (above) or at the six (below) leaf tip stages. 1991.

Table 3.2: Yield and yield components of plants that were flooded for 0, 4 or 8 days at six (early) or 12 (late) leaf tip stages. Values in parentheses are standard errors. 1991.

Flooding treatment	Number of rows	Row length	Number of grains	Avg kernel wt	Yield
		mm ⁻		9	g/plant
Early, 4	15.33	108.0	373.83	0.220	83.78
	(0.67)	(6.9)	(34.46)	(0.02)	(12.67)
Early, 8	15.33	100.5	357.83	0.217	78.20
	(0.42)	(3.9)	(19.12)	(0.01)	(6.06)
Late, 4	14.00	96.8	336.50	0.234	78.74
	(1.03)	(4.4)	(30.86)	(0.01)	(8.50)
Late, 8	15.33	98.0	336.50	0.233	78.80
	(1.33)	(4.7)	(30.36)	(0.01)	(9.09)
Control	17.33	152.7	664.83	0.230	153.38
	(0.67)	(6.2)	(28.58)	(0.01)	(12.26)

yield, usually in terms of grain weight per unit of cultivated land. Table 3.2 shows the grain yield and the components of yield for all the treatments. In all cases, the flooded plants yielded about one-half that of the control plants. Both the number and the length of the rows in the ear were reduced as a consequence of flooding but the individual kernel weight was not affected. The data also suggest a trend to yield fewer and heavier grains when plants were flooded later. However, the large variability in the number of grains obscured the possible significance of this trend.

The flooding stress induced a delay in the phenological events associated with the reproductive phase. Both tasseling and silking were delayed (Table 3.3)

Table 3.3: Delay in the time of occurrence of tasseling and silking of plants that were flooded for four or eight days at six (early) or 12 (late) leaf tip stage as compared with non-flooded plants. 1991.

		Flooding	treatment	
Event	Early 4 days	Early 8 days	Late 4 days	Late 8 days
	days			
Tasseling	3.9	6.5	0.8	1.8
Silking	5.2	8.0	1.1	2.5

Table 3.4: Time between tasseling and silking in plants that were flooded for zero, four or eight days at six (early) or 12 (late) leaf tip stage. 1991.

Flooding treatment				
Control	Early 4 days	Early 8 days	Late 4 days	Late 8 days
*****	****************	days		
2.8	4.7	5.75	2.4	3.8
		Difference v	with Control	
	+1.9	+3.0	- 0.4	+1.0

with a stronger effect in the earlier and longer flooding. Also the synchronization between male and female floral structures was affected. Table 3.4 shows the time interval between tasseling and silking. This interval was extended up to three extra days as a consequence of the longer and earlier flooding event.

Many times the plant photosynthetic capability is disrupted as a

Table 3.5: Photosynthetic rate measured at 1400 h after the onset of a flooding period of zero, four or eight days in plants that were at the 12 leaf tip stage. Values in parentheses are standard errors. 1991.

DAF	Control	Late, 4 days	Late, 8 days
		μmol m ⁻² s ⁻¹	
4	32.66	27.39	26.82
	(1.00)	(1.48)	(2.03)
8	26.07	19.06	18.55
	(0.87)	(0.87)	(0.60)
50	29.07	25.32	25.94
	(1.80)	(2.45)	(0.85)

consequence of stresses. In this experiment, the assimilation rate was promptly reduced by flooding which had a long lasting effect. Table 3.5 shows the photosynthetic rate measured at mid-day. By 50 days after the onset of the submergence, there was no discernible differences in the variability of the measurements in the flooded and non-flooded plants. However, by late afternoon (Figure 3.20) the decline in the assimilation rate as compared with the control was evident not only in the later flooded plants but also in the earlier flooded plants.

Plant biomass accumulation was expected to decrease since the photosynthetic rate was reduced as a consequence of the submergence. However, as depicted in Figure 3.21 the aboveground dry biomass grew at about the same rate in flooded and non-flooded plants during the flooding interval. The effect of impaired photosynthesis was evident only after drainage. Figure 3.22 shows how the total biomass in Figure 3.21 is distributed among different plant organs. Flooded plants diverted some carbon to build an early adventitious root

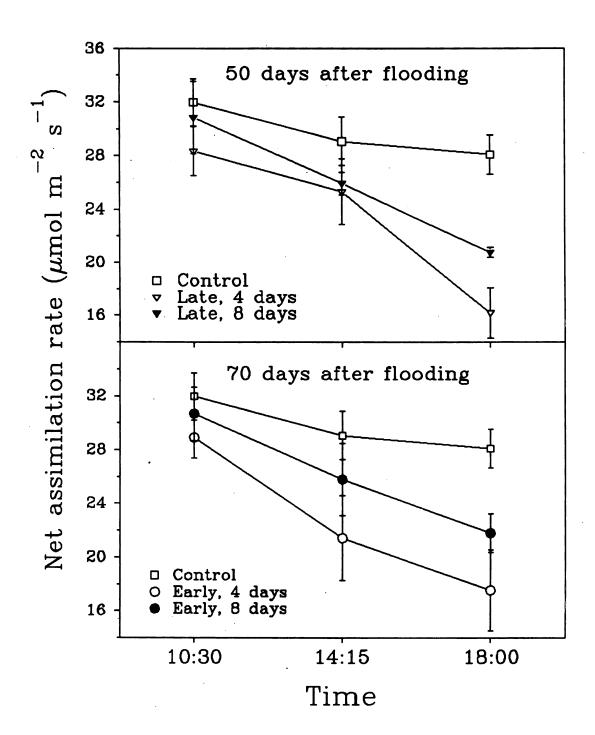


Figure 3.20: Daily changes in photosynthetic rate in plants flooded for zero, four and eight days at the 12 (above) or at the six (below) leaf tip stage.

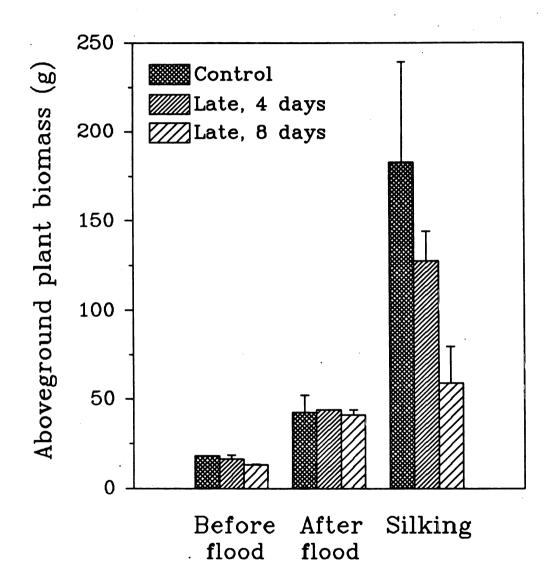
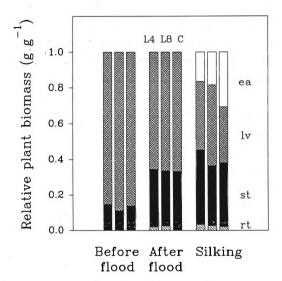


Figure 3.21: Aboveground biomass measured on 183 (before), 193 (after) and 213 (silking) days of the year. Plants were flooded for zero, four or eight days at the 12 (late) leaf tip stage during 1991.



ea: ear lv: leaves st: stem rt: aboveground adventitious roots

Figure 3.22: Proportional aboveground biomass distribution among different organs on 183 (before), 193 (after) and 213 (silking) days of the year. Plants were flooded for zero, four or eight days at the 12 (late) leaf tip stage during 1991.

system during the flooding period. Also non-flooded plants were allocating twice as much of the aboveground carbon into the ears than the flooded plants by silking. Part of this difference in carbon allocation is attributed to the different phenological stage in non-flooded plants.

Figure 3.23 is a summary of the aboveground growth process experienced by plants in 1990 and 1991 as affected by a late vegetative flooding occurrence. In both years, despite large differences in planting dates and environmental conditions, trends showed good agreement. An immediate reduction in foliar surface was evaluated after the submergence period in flooded plants, whereas aboveground biomass grew the same in flooded and non-flooded plants. Only after drainage was the biomass accumulation diminished in flooded plants.

Discussion

Results of soil submergence causing leaf area reduction agrees with Hiler et al. (1971) who found decreased leaf area in sorghum during the vegetative growth for the shallower water tables they tested (30 and 60 cm). Similar results reported by Smit et al. (1989) in *Populus* and Purvis and Williamson (1972) and Meyer et al. (1987) in maize. None of these reports had a reference to premature leaf senescence. Major differences were found in the behavior of the foliar surface when comparing early vs. late vegetative flooding. The results showed that, in the first 16 days, an early flooding reduced the foliar surface two and four times more than a late vegetative flooding when the submergence lasted eight or four days.

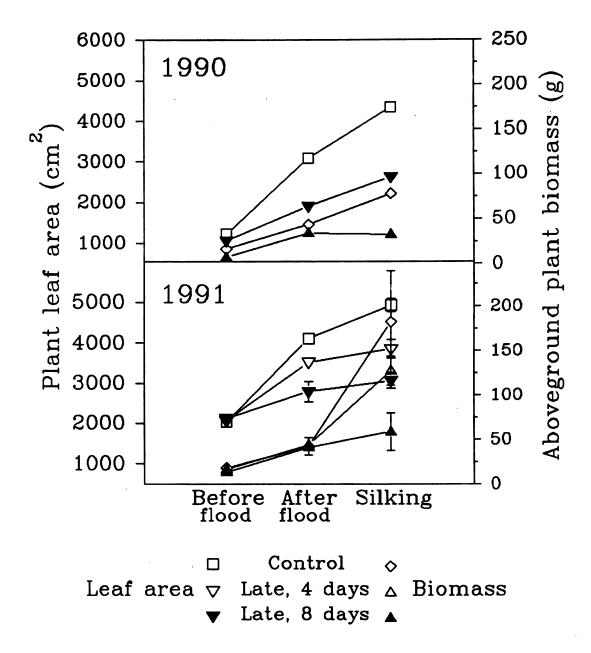


Figure 3.23: Aboveground plant biomass and leaf area measured on 183 (before), 193 (after) and 213 (silking) days of the year. Plants were flooded for zero, four or eight days at 12 (late) leaf tip stage during 1990 and 1991.

In the same period, senescence, though insignificant in the early flooding, accounted for about two thirds of the reductions that a late flooding had on green leaf area. Several reasons may be responsible for these differences between early and late vegetative flooding. A six leaf tip plant is a very small one. It has only two fully expanded leaves, its apical meristem is still below ground and the root system is quite superficial and little branched. Schildwacht (1989) reported that imposing anoxia to the roots of seven leaf tip plants reduced the shoot water status in the first hours, with an immediate decrease in extension growth. A later effect due to reduced cell wall extensibility (Zhang and Davies, 1986; Smit et al. 1989) is possible, and may be triggered by accumulation of ABA (Zhang and Davies, 1987), impaired uptake and transport of potassium (Zhang and Davies, 1986), or some unknown mechanism. Root apices of these small plants are close to the surface and are more likely to survive or to remain viable longer than deeper roots of older plants. Younger plants also require less nutrients and leaves are smaller and younger. Under waterlogging, plants can dismantle part of the less efficient productive machinery. Small plants are less likely to do this.

On the other hand, a 12 leaf tip plant is considerably larger. It has eight totally expanded leaves plus four or five expanding ones. By this time nutrient requirements are high and a period of rapid nutrient uptake and plant growth is about to begin. If the initial unbalance in shoot water relations is caused by a decreased root hydraulic conductivity as reported by Everard and Drew (1987), the phenomenon should occur equally in smaller plants as in larger plants.

However, some regulatory mechanism seems to play a major role in larger plants. As reviewed by Dale (1988) substantial evidence shows osmotic adjustment as a major regulatory mechanism in maintaining leaf extension under restricted hydraulic conditions (Morgan, 1984). Acevedo et al. (1979) showed data of an expanding maize leaf 41 days after planting that was comparable to the age of the late flooding plants in this experiment. Values of leaf water potential oscillated in a day period between almost 0 and less than -1.2 MPa, with no evident reduction on the concurrent leaf elongation. Osmotic adjustment was responsible for maintaining the high turgor pressure required for continued leaf expansion. The same mechanism may be expected to act in flooded plants.

If the osmotic adjustment cannot assure the maintenance of leaf expansion in younger plants during water deficits, or if there is some additional mechanism involved is still open to speculations. Michelena and Boyer (1982) imposed water deficits to maize plants at the six leaf tip stage, the same as the early flooding here. They found that inhibition of elongation occurred when solute accumulation in the expanding region of leaves was sufficient to maintain turgor. They concluded that some factor other than photosynthate supply and turgor also was responsible for decreased leaf expansion.

Larger plants also have larger resource demands, nitrogen among them, that an impaired root system may not be able to supply. In 1991, only 53.1 Kg of N ha⁻¹ was applied at planting. So nitrogen may have been a limiting factor when a larger demand was met by an impaired uptake and transport system. Under

these conditions, a major remobilization may be expected within the plant from older to younger organs, increasing premature senescence in older leaves. Trought and Drew (1980) flooded 11 day old wheat plants and were able to associate premature senescence of the first leaf with a net movement of nitrogen out of that leaf. Sandhu et al. (1986) studied nutrient accumulation in maize subjected to two periods of 10-11 days each of intermittent flooding at 20 and at 40 days after planting. Nitrogen was evaluated on the two uppermost fully-developed leaves. They measured major reductions in the foliar nitrogen content only in the early flooding, but failed to detect significant differences in the late flooding. One possible explanation is that nitrogen translocation from older leaves obscured the effect of reduced nitrogen uptake and nitrogen transport. Unfortunately they did not evaluate senescence (Sandhu et al., 1986).

An interesting finding of this research was the consistent association of flooding with the delay in crop phenology. Hiler et al. (1971) reported a delay of two weeks in flowering when the maize grew with the water table at 60 cm. However, when the water table was at 30 cm no delay was detected although the yield was 30% less than with a 60 cm deep water table. Meyer et al. (1987) found a delay of one or two days in the appearance of silks associated with the flooded treatments. No effect was found in the occurrence of tasseling or pollen shedding.

An assumption can be made that the thermal regime experienced by the growing meristem of earlier flooded plants was different than the non-flooded plants. Beauchamp and Lathwell (1967) found that the soil temperature was

responsible for the early development of maize, since it affected the meristematic region of shoots and thereby regulated plant development during the period of leaf initiation. Trought and Drew (1982) reported slower development in flooded wheat plants growing at 6° C than at 14° and 18° C. According to Ritchie and Hanway (1984), the growing apex is below the surface up to the total expansion of the sixth leaf. By the end of the early flooding period, plants had totally expanded five leaves. Thus the apex was continuously influenced by the lower thermal regime imposed by submergence. Plants flooded later should have had the meristem above the level of the ponded water during the entire submergence period. However, plant lodging experienced during the last three days of the eight day flooding might have moved the meristematic region down closer or into the flooded zone. The effect that a limited supply of oxygen due to soil submergence had on the shoot meristem is unknown.

Yield reductions due to waterlogging have been reported (Hiler et al., 1971; Chaudhary et al., 1975; Sandhu et al., 1986; Meyer et al., 1987; Mukhtar et al., 1990). In this experiment, any single flooding treatment reduced final grain production by about half irrespective of time or duration of the stress. Previous reports showed consistently that an earlier flooding is more harmful to yields (Chaudhary et al., 1975; Sandhu et al., 1986; Mukhtar et al., 1990). Although largely different in the timing and the way of imposing submergence, some additional factor seemed to reduce the grain harvested in the later stress tested here. One such factor may have been nitrogen. In the three above mentioned

reports (Chaudhary et al., 1975; Sandhu et al., 1986; Mukhtar et al., 1990), nitrogen application exceeded by more than two and three times the amounts applied in this research. However, while lack of nitrogen probably was a main factor in lowering the yields of the later flooded plants, it is still unclear if the delay of two or three extra days in the emergence of silks had a significant impact on the yields of earlier flooded plants.

The aboveground dry matter measured at the end of the later flooding period showed that biomass accumulation in the shoots was not reduced during the stress, despite a depressed photosynthetic rate and probable nitrogen shortages. Decreased dry weight was evident after drainage. Impaired transport of assimilates to the root system may explain these results. Saglio and Pradet (1983) demonstrated the cessation of the phloem transport of sucrose under anoxia, probably due to impaired unloading at the sink level (Saglio and Pradet, 1983; Saglio, 1985). These repressed carbon compounds might constitute an important source to build the adventitious root system developed in response to flooding (see Figure 3.24).

Conclusions

Complete submergence of the soil for a period of four or eight days during the vegetative growth phase of maize significantly reduced the plant growth and yield, and delayed plant development. Long lasting effects in stomatal behavior and photosynthetic assimilation suggested a slow physiological recovery of the plants after drainage. The results always showed a decline in the source of photosynthates as a consequence of soil waterlogging that extended for at least four days. Timing of flooding dictated the physiological process disturbed. The expansion growth was more sensitive to soil submergence early in the season. Plants developed more efficient mechanisms of adjustment to waterlogging later in the season including senescence of older leaves.

Yields were halved by every period of submergence independently of timing or duration. The data implied, however, that the reductions in yield were caused by two different factors during early and late flooding. Plants flooded early in the season had smaller leaf area and delayed silk emergence affecting the yields. Plants flooded later had the root system impaired (see chapter four) during the period of rapid nutrient accumulation which, associated with low soil nitrogen, may have led to nitrogen deficient plants for the remainder of the season.

Aboveground biomass accumulation during the submergence remained unaffected, suggesting a repressed flow of assimilates toward the root system. These repressed assimilates may have had an acclimative role in the development of adventitious roots in response to flooding.

Bibliography

- Acevedo, E., E. Fereres, T. C. Hsiao and D. W. Henderson. 1979. Diurnal growth trends, water potential, and osmotic adjustment of maize and sorghum leaves in the field. Plant Physiol. 64:476-480.
- Alvino, A. and G. Zerbi. 1986. Water Table Level Effect on the Yield of Irrigated and Unirrigated Grain Maize. Trans. of the ASAE 29:1086-1089.
- Beauchamp, E. G. and D. J. Lathwell. 1967. Root-zone temperature effects on the yearly development of maize. Plant Soil 26(2):224- 234.
- Benz, L. C., G. A. Reichman, E. J. Doering and R. F. Follett. 1978. Water table depth and irrigation effects on applied water use efficiencies of three crops. Trans. of the ASAE 21(4):723-728.
- Bradford, K. J. 1983. Involvement of plant growth substances in the alteration of leaf gas exchange of flooded tomato plants. Plant Physiol. 73:480-483.
- Bradford, K. J. and T. C. Hsiao. 1982. Stomatal behavior and water relations of waterlogged tomato plants. Plant Physiol. 70: 1508-1513.
- Chaudhary, T. N., V. K. Bhatnagar and S. S. Prihar. 1975. Corn yield and nutrient uptake as affected by water table depth and soil submergence. Agron. J. 67:745-749.
- Dale, J. E. 1988. The control of leaf expansion. Ann. Rev. Plant Physiol. Plant Mol. Biol. 39:267-295.
- Everard, J. D. and M. C. Drew. 1987. Mechanisms of inhibition of water movement in anaerobically treated roots of *Zea mays* L. J. Exp. Bot 38(192):1154-1165.
- Everard, J. D. and M. C. Drew. 1989. Water relations of sunflower (*Helianthus annuus*) shoots during exposure of the root system to oxygen deficiency. J. Exp. Bot. 40(220):1255-1264.
- Hiler, E. A., R. N. Clark and L. J. Glass. 1971. Effects of water table height on soil aeration and crop response. Trans. of the ASAE 14(5):879-882.
- Kramer, P. J. 1940. Causes of decreased absorption of water by plants in poorly aerated media. Am. J. Bot. 27:216-220.

- Kramer, P. J. 1951. Causes of injury to plants resulting from flooding of the soil. Plant Physiol. 26:722-736.
- Lal, R. and G. S. Taylor. 1969. Drainage and nutrient effects in a field lysimeter study: I. Corn yield and soil conditions. Soil Sci. Soc. Am. Proc. 33:937-941.
- Lemon, E. R. and A. E. Erickson. 1952. The measurement of oxygen diffusion in the soil with a platinum microelectrode. Soil Sci. Soc. Proc. 16(2):160-163.
- Letey, J., O. R. Lunt, L. H. Stolzy and T. E. Szuszkiewicz. 1961a. Plant growth, water use and nutritional response to rhizosphere differentials of oxygen concentration. Soil Sc. Soc. Proc. 25:183-186.
- Letey, J., L. H. Stolzy, G. B. Blank and O. R. Lunt. 1961b. Effect of temperature on oxygen-diffusion rates and subsequent shoot growth, root growth and mineral content of two plant species. Soil Sci. 92:314-321.
- Letey, J., L. H. Stolzy, N. Valoras and T. E. Szuszkiewicz. 1962. Influence of oxygen diffusion rate on sunflower growth at various soil and air temperatures. Agron. J. 54:316-319.
- Letey, J., L. H. Stolzy and N. Valoras. 1965. Relationships between oxygen diffusion rate and corn growth. Agron. J. 57:91- 92.
- Mason, W. K., K. E. Pritchard and D. R. Small. 1987. Effects of early season waterlogging on maize growth and yield. Aust. J. Agric. Res. 38(1):27-35.
- Meyer, W. S., H. D. Barrs, A. R. Mosier and N. L. Schaefer. 1987. Response of maize to three short-term periods of waterlogging at high and low nitrogen levels on undisturbed and repacked soil. Irrig. Sci. 8(4):257-272.
- Michelena, V. A. and J. S. Boyer. 1982. Complete turgor maintenance at low water potentials in the elongating region of maize leaves. Plant Physiol. 69:1145-1149.
- Moon, J. W. and J. A. Flore. 1986. A Basic computer program for calculation of photosynthesis, stomatal conductance and related parameters in an open gas exchange system. Photosynt. Res. 7:269-279.
- Morgan, J. M. 1984. Osmoregulation and water stress in higher plants. Ann. Rev. Plant Physiol. 35:299-319.

- Mukhtar, S., J. L. Baker and R. S. Kanwar. 1990. Corn growth as affected by excess soil water. Trans. of the ASAE 33(2):437-442.
- Oosterhuis, D. M., H. D. Scott, S. D. Wullscleger and R. E. Hampton. 1990. Photosynthetic and yield responses of two soybeans cultivars to flooding. Ark. Farm Res. 39:11.
- Purvis, A. C. and R. E. Williamson. 1972. Effects of flooding and gaseous composition of the root environment on growth of corn. Agron. J. 64:674-678.
- Ritchie, J. T. 1981. Water dynamics in the soil-plant-atmosphere system. Plant Soil 58:81-96.
- Ritchie, S. W. and J. J. Hanway. 1984. How a corn plant develops. Iowa State University, Coop. Ext. Serv. Spec. Rep. 48.
- Saglio, P. H. 1985. Effect of path or sink anoxia on sugar translocation in roots of maize seedlings. Plant Physiol. 77(2): 285-290.
- Saglio, P. and A. Pradet. 1983. Effet du manque d'oxygène sur l'alimentation en sucres de la jeune racine de maïs. p. 331-338. *In* A. Gallais (Coordinateur.) Physiologie du maïs. INRA, Paris.
- Sandhu, B. S., Balwinderjit Singh, Baldev Singh and K. L. Khera. 1986. Maize response to intermittent submergence, straw mulching and supplemental N-fertilization in subtropical region. Plant Soil 96(1):45-56.
- Schildwacht, P. M. 1989. Is a decreased water potential after withholding oxygen to roots the cause of the decline of leaf- elongation rates in *Zea mays* L. and *Phaseolus vulgaris* L.? Planta 177:178-184.
- Shih, S. F. and M. Rosen. 1985. Water Table Effects on Root Development and Nutrient Contents of Celery, Lettuce and Sweet Corn. ASAE Paper 85-2570.
- Smit, B., M. Stachowiak and E. Van Volkenburg. 1989. Cellular processes limiting leaf growth in plants under hypoxic root stress. J. Exp. Bot. 40(210):89-94.
- Sojka, R. E. 1992. Stomatal closure in oxygen-stressed plants. Soil Science 154(4):269-280.
- Trought, M. C. and M. C. Drew. 1982. Effects of waterlogging on young wheat plants (*Triticum aestivum* L.) and on soil solutes at different soil temperatures. Plant Soil 69:311-326.

- Trought, M. C. and M. C. Drew. 1980. The development of waterlogging damage in wheat seedlings (*Triticum aestivum* L.) II. Accumulation and redistribution of nutrients by the shoot. Plant Soil 56:187-199.
- Vu, J. C. and G. Yelenosky. 1991. Photosynthetic response of citrus trees to soil flooding. Physiol. Plant. 81:7-14.
- Wenkert, W., N. R. Fausey and H. D. Watters. 1981. Flooding responses in *Zea mays* L. Plant Soil 62:351-366.
- Williamson, R. E. 1964. The effect of root aeration on plant growth. Soil Sci. Soc. Am. Proc. 28:86-90.
- Williamson, R. E. and G. J. Kriz. 1970. Response of Agricultural Crops to Flooding, Depth of Water Table and Soil Gaseous Composition. Trans. of the ASAE 13(2):216-220:
- Zhang, J. and W. J. Davies. 1987. ABA in roots and leaves of flooded pea plants. J. Exp. Bot 38:649-659.
- Zhang, J. and W. J. Davies. 1986. Chemical and hydraulic influences on the stomata of flooded plants. J. Exp. Bot 37(183): 1479-1491.

Chapter 4

FLOODING EFFECTS ON FIELD GROWN MAIZE.

II. BELOW GROUND RESPONSES.

Abstract

The purpose of this research was to analyze the dynamics of the maize root system associated with single flooding periods during the vegetative growth stage. The water table was raised above the soil surface in small 2.1 m by 1.5 m plots, at six (early) or at 12 (late) leaf tip stages for four or eight days during the summer of 1991. Root systems were closely monitored by recording and counting the number of root segments viewed through the upper side of plastic transparent pairs of minirhizotron tubes, horizontally located at 15, 40, 60 and 90 cm depth. Timing of flooding proved to have a major effect on root responses to flooding. Plants flooded early in the season, when they had small roots, showed a fast decrease in root number after soil submergence and rapid proliferation after drainage. Plants flooded for eight days experienced root regrowth only in the upper soil layers. When flooding occurred later in the vegetative stage, plants recovered only after a short flooding (four days). Root number did not increase after eight days of flooding. The relation of root dynamics with leaf area dynamics

showed that an early flooding increased the sink strength of the roots. A short, late flooding maintained the sink strength of the roots. A late flooding of eight days reduced the sink strength of the roots.

Introduction

A comprehensive body of information has been produced during the last 15 years about root responses to anoxic and hypoxic environments. Among them however, just a few reports have addressed the complexities involved with field grown plants during periods of soil submergence (Wenkert et al., 1981; Meyer et al., 1985; Meyer et al., 1987). The experimental procedures used artificial environments in other reports, and were useful to understand the role of individual factors related to soil subirrigation. Uncertainty always arises however, as to how individual factors interact in the field with other environmental constraints. Most of the experimental material used in this type of research was excised roots or seedlings. Waters et al. (1991) found different responses in excised root tips and in intact plants. They found that during anoxia, the ability to elongate was retained longer in intact seedlings than in excised root tips supplied with glucose. Thus, the effects that plant ontogenesis have in modulating responses to the environment have remained mostly unexplored.

During periods of limiting aeration, maize and other cereal plants have been shown to increase the development of nodal roots with increased porosity compared to the usual root system (Drew et al., 1979; Drew et al., 1985; Ramírez

and Rodríguez, 1987; Thomson et al., 1990). Formation of air spaces leading to enhanced root porosity occurs in maize by cell death and disintegration, also called lysigeny, (Jackson and Drew, 1984; Drew and Stolzy, 1991) in a process mediated by ethylene (Drew et al., 1979). Pre-existing seminal roots do not seem to be able to develop aerenchyma in maize (Ramírez and Rodríguez, 1987). In wheat, however, Thomson et al. (1990) found aerenchyma in nodal and in seminal roots when they were shorter than 10 to 20 cm. Roots lacking these air channels had reduced phloem transport (Saglio, 1985; Waters et al., 1991) apparently because of impaired phloem unloading (Saglio and Pradet, 1983; Saglio, 1985).

Research has shown that aerenchymatous roots maintained larger levels of metabolically active energy as compared to non-aerenchymatous roots associated with enhanced aerobic respiration (Drew *et al.*, 1985). Aerenchymatous roots, however, had lower energy than fully aerated roots (Drew *et al.*, 1985).

Reports have shown reduced nutrient uptake of oxygen deficient plants (Spek, 1981, 1984a, 1984b; Ramírez and Rodríguez, 1987; Veen, 1988). Since aerenchymatous roots have lost extensive portions of the cortex, researchers question whether these roots are less efficient in providing adequate mineral nutrition to the plant. Evidence obtained by Drew and coworkers (Drew et al., 1980; Drew and Saker, 1986), seems to support the view that, after drainage, aerenchymatous roots are as efficient (per unit volume) as roots with an intact cortex. However, maize roots developed aerenchyma under deficient mineral nutrition without an enhanced biosynthesis or accumulation of ethylene (Drew et

al., 1989a, 1989b) adding complexity to the problem. The possible significance of this loss of root cortex for mineral deficient plants remains unknown.

The emission of adventitious roots with lysigenous air space is not the only acclimative response to soil submergence found in maize plants. Grinieva and coworkers (Grinieva, 1981, 1991; Grinieva et al. 1987) have unveiled a coordinated pattern of plant adaptations to flooding involving adventitious roots, stem base and even leaf sheaths. These authors, working with ten day old maize plants, described a reorganization in the structure of adventitious roots that, beyond the aerenchyma production, included increased diameter of xylem vessels and their new formation. Sclerenchyma developed surrounding vascular bundles in the base of the stem. Conducting bundles of leaf sheaths had larger metaxylem vessels, and large air-filled lacunae as compared with control plants. These profound structural modifications, probably built at a large cost in energy and carbon, may not be as meaningful for the plant after drainage. No report could be found however, on the longevity of adventitious roots after soil submergence.

An important adaptive response for field grown plants is the hypoxic acclimation to anoxia (Johnson *et al.* 1989). Roots that were pre-treated at low oxygen concentration before a complete oxygen deprivation extended their viability at least four times that of non-pretreated roots (Saglio *et al.* 1988; Johnson *et al.* 1989). Increased viability was associated with an enhanced glycolysis (Hole *et al.* 1989), higher metabolic energy level and high activity of alcohol dehydrogenase. Since field grown plants always experience hypoxia before anoxia (Drew, 1990),

this mechanism should operate in enhancing crop performance after a transient waterlogging.

Additional information is required to improve our ability to integrate these pieces of knowledge into a comprehensive predictive tool to forecast crop responses to flooding. A more careful consideration of the effect of periods of soil submergence on plant ontogenesis is especially needed. The short term dynamics of field grown maize roots is reported in this chapter as related to single flooding events imposed during the vegetative growth stage. The information complements the analysis of the aboveground crop responses presented in Chapter 3.

Materials and Methods

Maize (*Zea mays* L., cv. GL 420) was planted on May 25, 1991 in the field facility described in Chapter 2. The undisturbed Capac loam soil (Aeric Ochraqualf) had plants growing in 76.2 cm row spacing, with a population of 8.61 plants m⁻². Additional information about crop management is provided in Chapter 3.

Each treatment consisted of a single-event flooding that lasted four or eight days. The flooding was imposed at six (early) or at 12 (late) leaf tip stages. The control plot had the water table below the rooting depth through the season. Soil submergence was achieved by raising the water table between 20 and 50 mm above the soil surface. All plots had the water table at 60 cm depth at the

beginning of the season. After plants were 35 days old, the water table was allowed to drop between 80 and 100 cm depth.

Polybuterate transparent tubes 5 cm in diameter were located horizontally, in pairs, at 15, 40, 60 and 90 cm depth according to the layout depicted in Figure 2.3. The tubes were perpendicular to the maize rows and extended into the plot, crossing a concrete wall, for distances from the wall between 96 and 126 cm.

Roots of plants flooded early in the season, and control plants, were recorded every two days, between day of the year 162 and 178. Roots of plants flooded late in the season, and control plants, were recorded every two days between day of the year 182 and 198. All treatments were additionally recorded later in the season on day of the year 205, 212 and 232. Roots were recorded and counted up to the maximum observable depth of 60 cm during the early flooding and 90 cm during the late flooding. A flexible video-imagescope (Olympus IV12D2-30 Scope and IV-2 Camera Control Unit) 12.6 mm in diameter and 3 m long was used with a 150 W halogen lamp light source (Olympus ILK-5) to observe the roots. The system was connected to a portable TV-VCR (Symphonic 13 TVCR MKII) to record the images in standard VHS 120 minute tapes. A portable minicomputer (Tandy, Model 100), connected to the camera control unit generated the labels appearing on the recorded images. The videoimagescope was pushed into the end of the tube and a label identifying date, plot and tube was generated and recorded for several seconds. After deleting the label to have complete vision of the frame being viewed, the scope was pulled back at 2.5 cm space intervals until reaching the concrete wall.

The number of root segments intercepting the upper surface of the tube was counted on each frame recorded. Each frame was considered independent of the others and root number was the only attribute registered. Root count was expressed as the number per unit area. Due to different lengths of tubes and the possibility of a border effect of the concrete wall, the number of roots reported is the average count of a 40 cm length of the minirhizotron tube, centered below the row closest to the wall. Root counts were converted to root length densities following the assumption proposed by Upchurch and Ritchie (1983). These authors proposed that roots intersecting minirhizotron tubes at different angles have, on the average, a length equal to the tube diameter. The soil volume is assumed a rectangular prism of surface equal to the area of the frame and altitude equal to the tube diameter. Root length densities per layer were later converted into total root length per plant by accumulating the total length of roots down to the rooting depth and assuming each plant occupies an average area of 76.2 cm by 15.24 cm. The average total plant root length and leaf area for each treatment were used to calculate the ratio of root length to leaf area.

Results

Root responses to early flooding

Figure 4.1 shows the distribution of roots during the 16 day period associated with the early submergence treatment and the control. During this

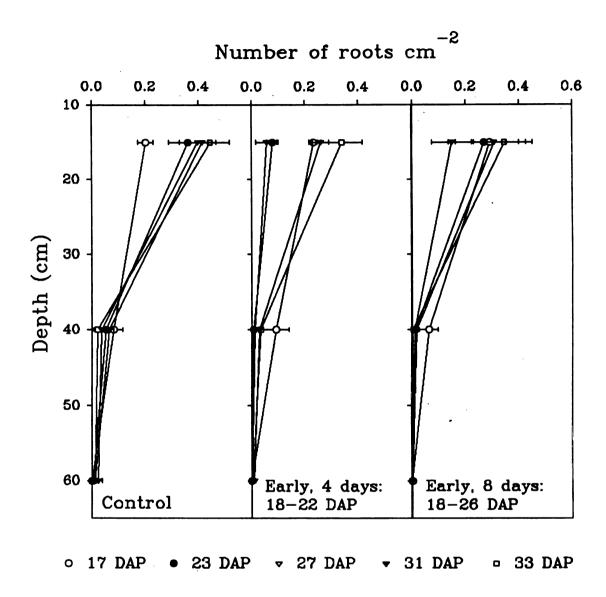


Figure 4.1: Root distribution on selected days after planting (DAP). Plants were flooded for zero, four or eight days at the six (early) leaf tip stage. Horizontal lines are standard errors.

time, roots exhibited limited growth below 40 cm. Flooding caused an immediate reduction in the number of observed roots. Non-flooded plants showed a decreased number of roots at 40 cm depth during this period, but later this trend was reversed. The estimated total root length per plant during the early flooding is depicted in Figure 4.2. The control exhibited a general trend to extend the total length of roots an average of 4 m day⁻¹. Most of this growth occurred in the first week of the period studied in Figure 4.2, whereas the second week did not exhibit a net increase in root length. Flooded plants, on the contrary, reduced the length of their root systems between 50 and 80% in the three days after the onset of the submergence. However, five days after the initiation of the flooding there was a consistent trend to increase the number of observed roots in flooded plants. The increase was slight in the plot being drained and more intense in the plot being kept below water for eight days. In both flooded plots, the lowest number of roots was observed three days after the beginning of the drainage. Flooded plants experienced a period of fast root growth after drainage and eventually had approximately the same length as control plants.

Most of the changes in total plant root length were observed in the uppermost minirhizotrons located at 15 cm depth, as shown in Figure 4.3. Growth dynamics in deeper roots (Figure 4.4) were reduced as compared with roots in the upper soil layers. Root growth in non-flooded plants seemed to be restricted to the more superficial layers during this period. Plants that were flooded for four days promptly recovered in root growth at depths of 15 and 40 cm after drainage.

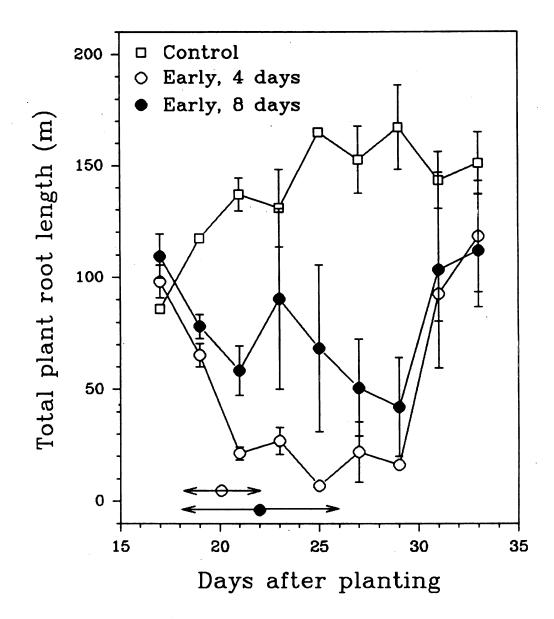


Figure 4.2: Calculated total root length per plant in maize flooded for zero, four or eight days at the six (early) leaf tip stage. Vertical lines are standard errors. Horizontal arrows indicate the flooding period.

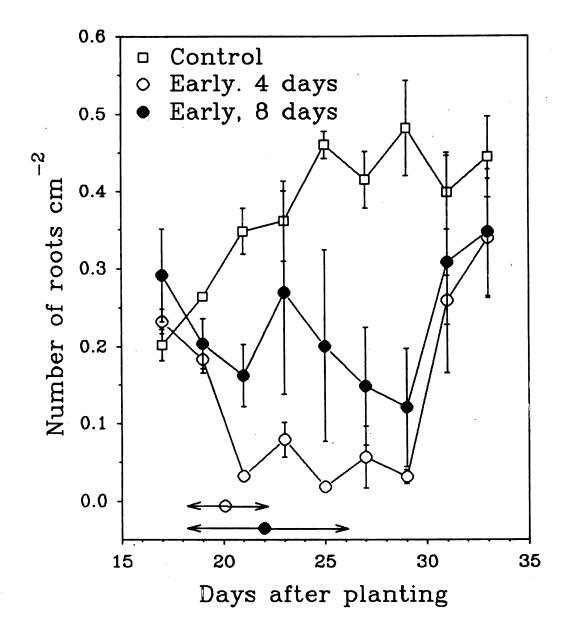


Figure 4.3: Number of roots observed at 15 cm depth. Plants were flooded for zero, four or eight days at the six (early) leaf tip stage. Vertical lines are standard errors. Horizontal arrows show the flooding period.

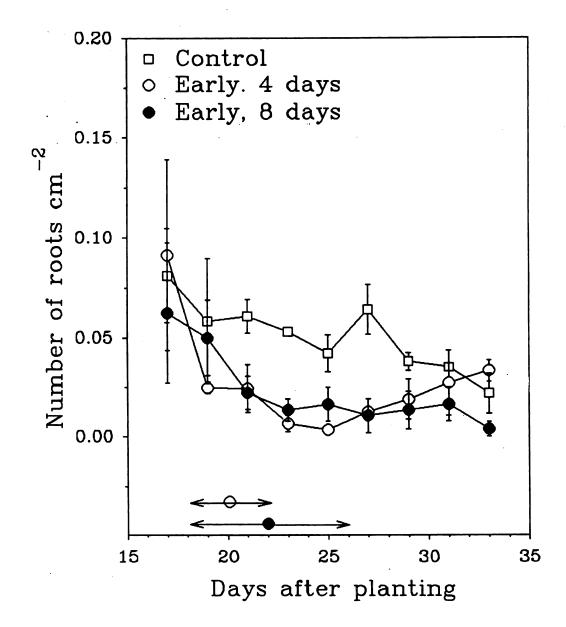


Figure 4.4: Number of roots observed at 40 cm depth. Plants were flooded for zero, four or eight days at the six (early) leaf tip stage. Vertical lines are standard errors. Horizontal arrows show the flooding period.

Table 4.1: Number of roots at selected days and depths. Maize was flooded for zero, four or eight days at the six (early) leaf tip stage. Values in parentheses are standard errors.

Day of the year _	Depth (cm)				
	15	40	60	90	
	Number of roots cm ⁻²				
205	2.075	0.265	0.225	0.015	
	(0.385)	(0.025)	(0.015)	(0.015)	
212	2.475	0.445	0.225	0.065	
	(0.845)	(0.055)	(0.015)	(0.065)	
232	1.260	0.120	0.155	0.050	
	(0.430)	(0.040)	(0.015)	(0.050)	
		Early,	4 days		
205	1.245	0.815	0.335	0.005	
	(0.445)	(0.205)	(0.045)	(0.005)	
212	1.120	0.590	0.355	0	
	(0.180)	(0.100)	(0.025)	(0)	
232	0.545 (0.185)	0.320 (0.060)	0.210 (0)	0 (0)	
	Early, 8 days				
205	1.855	1.455	0.065	0	
	(0.075)	(0.205)	(0.005)	(0)	
212	1.350	1.310	0.115	0.005	
	(0.030)	(0.060)	(0.005)	(0)	
232	0.590	0.425	0.060	0	
	(0.030)	(0.075)	(0.050)	(0)	

Plants that were flooded for eight days had root growth recovery only at the 15 cm depth. No net increase in root number was observed at 40 cm the week following drainage. The number of roots observed later in the season is depicted in Table

4.1. Despite the large variability, the data suggested that the recovery after drainage in number of roots may have not been complete.

Root responses to late flooding

Roots reached 90 cm depth, the maximum observable depth, by the time the late flooding was imposed. However, results shown in Figure 4.5 indicate that little root growth occurred at or below a 60 cm depth. A limited increment in root growth occurred at 60 cm late in the season, when the net number of roots observed in upper layers was decreasing. High soil water content close to the drain tube likely prevented root growth at 90 cm depth through the season.

The calculated total root length per plant appears in Figure 4.6. Plants had accumulated almost 300 m of roots by the time the late flooding was imposed. Roots of non-flooded plants rapidly increased at a rate of 50 m day⁻¹ during this period. Plants that endured late flooding did not show an immediate reduction in the number of roots as compared to plants subjected to the early flooding. A decrease in the trend of root growth was evident only after three days of the initiation of soil submergence in late flooded plants. The total root length was reduced by 20 to 50% as a consequence of late flooding. Plants that were flooded four days exhibited rapid root regrowth after drainage, doubling the length of their roots in just four days. On the contrary, plants that were flooded eight days had limited root regrowth after drainage.

Figure 4.7 shows the root growth as observed at 15 cm depth during the

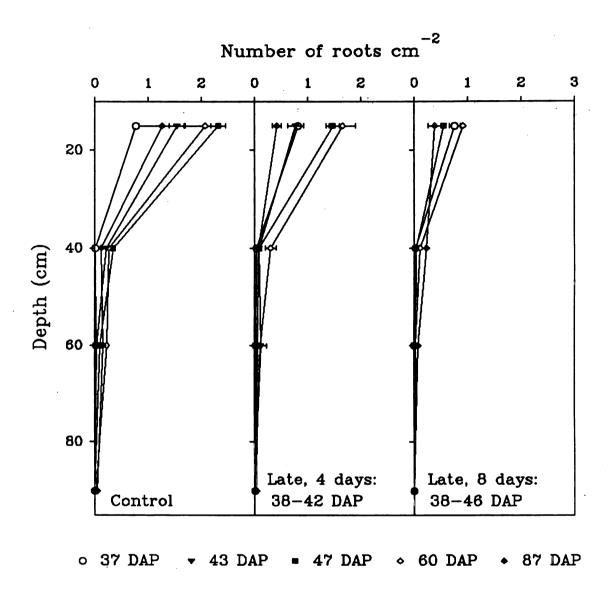


Figure 4.5: General root distribution on selected days after planting (DAP) in plants that were flooded for zero, four or eight days at the 12 (late) leaf tip stage. Horizontal lines are standard errors.

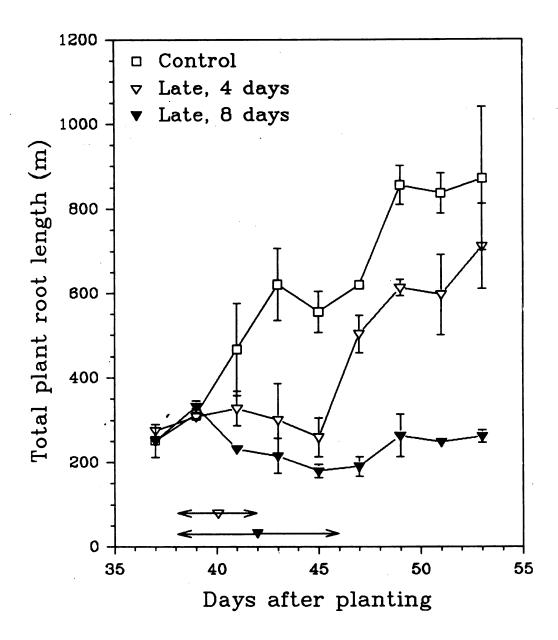


Figure 4.6: Calculated total root length per plant in maize flooded for zero, four or eight days at the 12 (late) leaf tip stage. Vertical lines are standard errors. Horizontal arrows indicate the flooding period.

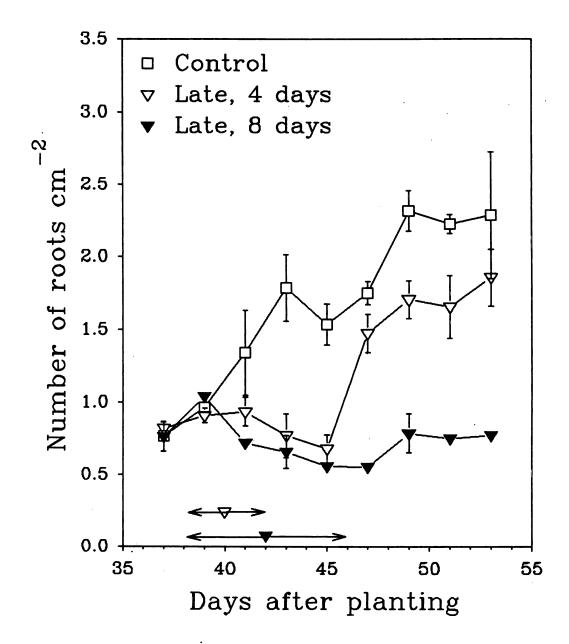


Figure 4.7: Number of roots observed at 15 cm depth. Plants were flooded for zero, four or eight days at the 12 (late) leaf tip stage. Vertical lines are standard errors. Horizontal arrows indicate the flooding period.

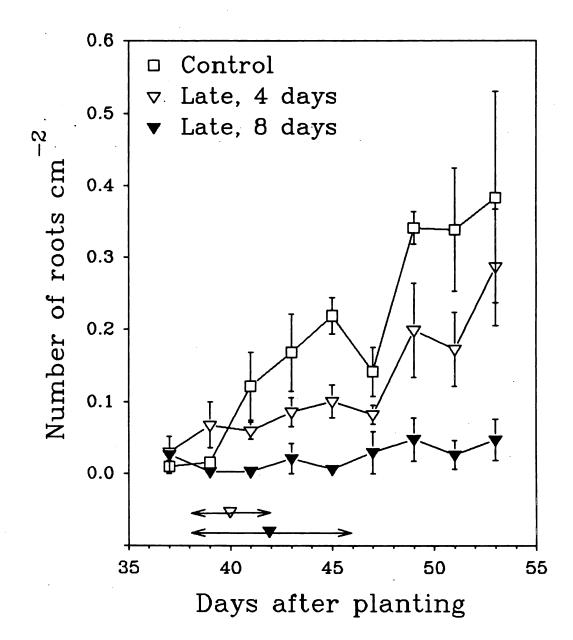


Figure 4.8: Number of roots observed at 40 cm depth. Plants were flooded for zero, four or eight days at the 12 leaf tip stage. Vertical lines are standard errors. Horizontal arrows indicate the flooding period.

late flooding period. The correspondence with the trends discussed above for the whole plant root system is evident. However, deeper roots showed different behavior. Roots growing at 40 cm depth (Figure 4.8) did not clearly exhibit increased root death in response to soil submergence. The number of roots remained the same during the inundation. After drainage, plants flooded for four days showed a fast increase in root number at 40 cm. Plants flooded for eight days had a limited initial root growth at 40 cm depth. Table 4.2 shows that non-flooded plants reached the maximum root number during the flowering and pollination stages. Decreasing number of roots were observed during the grain filling stage. Plants flooded for eight days maintained a reduced number of roots at 15 cm through the season. Late in the season, however, root growth was observed at 40 cm, reaching the same root number as plants flooded for four days.

To explore the relative responses of shoots and roots to the submergence a ratio was calculated by dividing the treatment averages of total root length by total leaf area. Figure 4.9 shows the seasonal changes in the ratio during the early flooding. All plants produced larger numbers of roots per unit of foliar surface earlier in the season. Non-flooded plants had a general trend to decrease the relative proliferation of the roots as compared with the expansion of foliar surface during this period, going from 70 m of roots per cm² of leaves down to 10 or 20 m cm⁻² and remaining at this level for the remainder of the season. Flooded plants had a larger reduction in the ratio during the first three days. Figure 4.9

Table 4.2: Number of roots at selected days and depths. Maize was flooded for zero, four or eight days at the 12 (late) leaf tip stage. Values in parentheses are standard errors.

Day of the year	Depth (cm)					
	15	40	60	90		
_	Number of roots cm ⁻² Control					
205	2.075	0.265	0.225	0.015		
	(0.385)	(0.025)	(0.015)	(0.015)		
212	2.475	0.445	0.225	0.065		
	(0.845)	(0.055)	(0.015)	(0.065)		
232	1.260	0.120	0.155	0.050		
	(0.430)	(0.040)	(0.015)	(0.050)		
		Late,	4 days			
205	1.654	0.301	0.099	0.012		
	(0.242)	(0.101)	(0.017)	(0.000)		
212	1.038	0.202	0.096	0.021		
	(0.319)	(0.098)	(0.049)	(0.003)		
232	0.416 (0.083)	0.070 (0.045)	0.056 (0.031)	0.035 (0.029)		
	Late, 8 days					
205	0.916 (0.028)	0.109 (0.091)	0.020 (0.009)	0 (0)		
212	0.721	0.268	0.012	0		
	(0.046)	(0.004)	(0.012)	(0)		
232	0.389	0.231	0.074	0		
	(0.123)	(0.034)	(0.043)	(0)		

shows a consistent increase in the trend of the relation of root to leaf area five days after the onset of the flooding, with the larger increase in the eight day flooded plants. After drainage, flooded plants increased the number of roots per

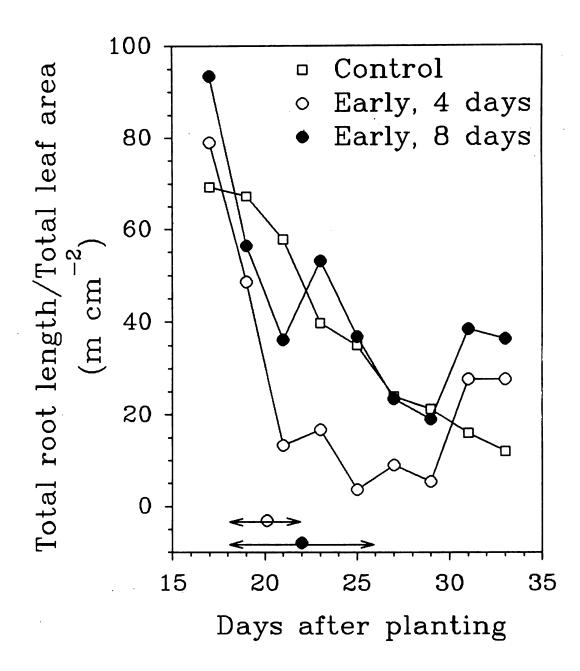


Figure 4.9: Ratio total plant root length divided by total plant leaf area, calculated with the averages per treatment in maize flooded for zero, four or eight days at the six (early) leaf tip stage. Arrows show the flooding period.

unit of leaf area to double the number of the non-flooded plants. These changes were mostly associated with variations in root length.

During the period when the late flooding occurred (Figure 4.10), non-flooded plants had between 10 and 20 m of roots per cm² of leaf area. Plants that were flooded, on the contrary, exhibited a constant decrease in the relation of root to leaf area due to a larger reduction in root length than in leaf area. After the soil was drained, plants that were flooded four days extended their root system faster than their foliar surface, with a net increase in the root-leaf ratio to levels similar to those in the non-flooded plants. Plants that were flooded for eight days had a small increase in the root-leaf ratio.

The contrasting behavior in the root-leaf ratio between plants that were flooded earlier as opposed to plants that were flooded later is evident from Figure 4.11. Plants that were flooded earlier seemed to produce more roots per unit leaf surface after drainage than non-flooded plants for the remaining of the vegetative growth stage and beginning of grain filling. In this case, root length returned to levels close to non-flooded plants after drainage, while leaf area remained lower for the remainder of the season. On the other hand, plants flooded later did not experience the rapid proliferation of roots relative to the size of the leaf area. After drainage, plants flooded for four days exhibited the same proportion of roots and leaf area as non-flooded plants, due to the same relative reductions in root length and leaf area. Plants flooded for eight days showed limited recovery in the ratio through the remainder of the season. Root length in this case was reduced in a

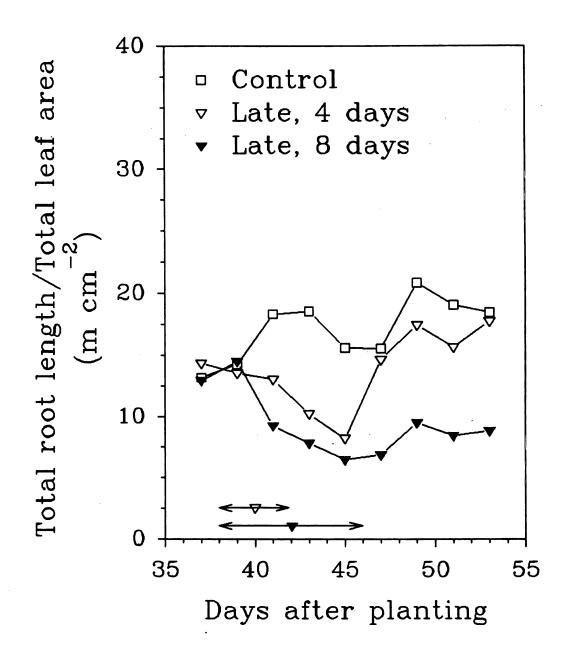


Figure 4.10: Ratio of total plant root length divided by total plant leaf area, calculated with the averages per treatment, in maize flooded for zero, four or eight days at the 12 (late) leaf tip stage. Arrows show the flooding period.

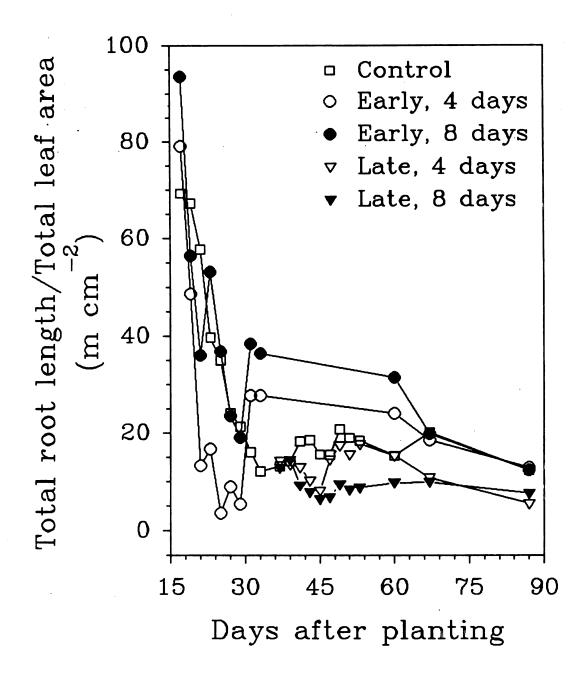


Figure 4.11: Seasonal plant ratio of total root length:total leaf area, calculated with averages per treatment, in maize flooded zero, four or eight days at the six (early) or 12 (late) leaf tip stage. Arrows show the flooding period.

larger proportion than leaf area.

Discussion

The growth of roots is a dynamic process that is sensitive to soil microenvironments. There is always a gap between soil and minirhizotron surface which is going to provide an abnormal microenvironment for root growth with the potential to affect the results and to mislead the interpretations. Recent examples showed how soil conditions caused differential root growth (Nuñez-Barrios, 1991) and root clustering (Amato, 1991). Meyer and his colleagues (Meyer et al., 1985; Meyer et al., 1987) reported consistent differences in wheat and maize root growth between lysimeters filled with undisturbed or repacked soil. Much effort was made to assure the presence of undisturbed soil in our experimental setting. Steps were also taken during the installation of minirhizotrons to minimize the gap between the soil and the surface of the tube. Results reported here were obtained one year after positioning the tubes. None of these efforts however, are expected to have completely eliminated the effect of the soil-tube interface in root growth that, although irrelevant for the whole root system, might have biassed the actual number of roots being counted.

Roots were closely monitored in this experiment during the two weeks following the onset of the submergence periods. This provided a unique opportunity to detect and follow short-term and transient changes in the dynamics of the rhizosphere in response to inundation. Horizontal minirhizotrons granted more intense exploration of roots at each depth, but limited the number of possible

depths studied. In this experiment only four depths (15, 40, 60 and 90 cm) were evaluated.

Recording roots through transparent tubes gave the ability to non-destructively monitor and repeatedly evaluate specific scenarios as required. However, the source of information was a visual image that had to be interpreted before being computed. Our instrumentation yielded images of good quality in terms of color and resolution. However, the orientation of the light source sometimes produced misleading reflections. On the other hand, the physical dimensions of the working area (see Figure 2.2) with concrete walls impeded the use of a camera handler as the one reported by Ferguson and Smucker (1989). Thus, frames of a successive date might not be focussed on exactly the same area as frames of a previous day.

Interpreting minirhizotron images was not a straight forward task. Observed roots grew in a continuum of superimposed planes parallel to the tube surface. This yielded a continuum of root images going from the clearly visible root growing directly against the tube surface to the diffuse image of roots extending several mm away from the tube surface. This was complicated even more by the highly variable background field with multiple colors, voids, worm holes, etc.

Deciding if the root was alive or dead was an important difficulty in interpreting root images. The decision was mainly based on color and appearance. Darker colors were usually associated with root death. Extensive work with field grown maize by McCully (1987) and McCully and Canny (1989)

provided excellent descriptions of morphological changes during root ontogenesis. When mature maize plants were gently excavated they identified two main groups of roots. The first group had older, long, bare, highly-branched roots with lost or undistinguishable tips. The second group had younger, unbranched or poorly-branched roots with white elongating tips and a persistent soil sheath tightly adhered to the rest of the root (McCully, 1987). This dimorphism seemed to be determined by root age and by the maturation of the late metaxylem (McCully and Canny, 1989). Therefore the development of a soil sheath as the late metaxylem matures may be interpreted in a video image as root death.

In this experiment, roots flooded for several days did not always exhibit a uniform decay. Localized necrotic darker areas usually were surrounded by healthy-looking clear tissue. In these cases, the root was considered dead only when more than 50% of the root segment had necrotic tissue.

The early flooding showed a consistent trend of increased roots on the fifth day after the onset of the submergence. This increase was observed only in the upper soil layer at 15 cm depth. At 40 cm, no rise was detected during the inundation. This elevated number of roots may reflect the arrival of adventitious and probably aerenchymatous roots extending from the stem nodes and reaching this depth. Visually identifying aerenchymatous roots that had lost large portions of the cortex with the epidermis and the stele intact was not possible in these images. Aboveground, the emission of adventitious roots from nodes above the soil surface, either above or below the water level, was not observed during the

early flooding. However, adventitious roots may have extended from nodes at or below the soil surface and remained unnoticed. Klepper (1985) discussed the regular sequential emergence of nodal roots from successive whorls in cereals. Drew et al. (1979) removed oxygen from the culture solution of 10-day-old maize plants, without pre-acclimation, and followed the successive emergence of adventitious roots from sequential nodes. Each whorl developed four or five nodal roots. The first whorl roots, which were 5 cm long at the onset of the anoxic treatment, extended into the oxygen free solution only one-third the distance that aerated roots did. The second and third whorl roots extended earlier but at the same extension rate as the aerated control roots did. The fourth whorl roots emerged and extended only in the anoxic plants by the end of the investigation (Drew et al., 1979). Nodal roots may have developed below ground in this experiment following a similar pattern in response to flooding. During this period, root activity was observed above the soil surface. Few fine white root tips extending over the soil surface were evident by the fourth day of submergence. These roots died immediately following drainage. This diageotropic root growth in response to flooding was reviewed by Jackson and Drew (1984).

Plants flooded early in the season showed an explosive proliferation of roots after drainage. Plants flooded for four days increased the number of roots at 15 and 40 cm depth. Plants flooded for eight days increased the number of roots only in the upper layer. A permanent damage to main axis roots may be the reason for this difference when the submergence lasted eight days. Renewed root

growth after drainage may be originated from axis or branches existing prior to the flooding, from adventitious roots formed during the flooding, or from both. Since adventitious roots produced during submergence reaching 40 cm depth is unlikely (Thomson et al., 1990), the growth of roots at 40 cm experienced by the four-days flooded plants should have occurred through extension and branching of preexisting roots. The origin of the root growth experienced in upper layers remains unclear.

Plants flooded late in the season did not show a major reduction in number of roots during the submergence nor had any increase that might be related to newly formed adventitious roots. During late flooding however, an active growth of adventitious roots was observed from above ground. Spongy roots grew in an ordered sequence (Klepper, 1985) from nodes either below or at the water line. Non-flooded plants showed thicker and firmer adventitious roots only in the node located at the soil surface during this period. Wenkert et al. (1981) showed a picture of the excavated upper root system of a 53-day-old maize plant flooded 13 days and a non-flooded plant. Adventitious roots grew from the first and second nodes above the surface in flooded plants, whereas non-flooded plants had adventitious roots growing from the first node only. These authors showed the flooded plants having a shallow and slightly branched adventitious root system with massive loss of the preflooding roots. In the experiment discussed herein, a similar adventitious root system might have developed. The poor branching of the adventitious root system may have passed unnoticed among the decaying but highly branched root system present at the time.

Limited branching of adventitious roots may be advantageous during the inundation. The initiation of laterals originates in angiosperms at the pericycle, inside the endodermis (Russell, 1977; Mauseth, 1988; Charlton, 1991). In wellaerated maize roots, the first noticed changes during the initiation of lateral primordia were the thinning of the cell wall and the loss of lignin (Bell and McCully, 1970; Karas and McCully, 1973). In comparative anatomy studies, the lignification of hypodermis, cortical sclerenchyma and endodermis has been associated with tolerance to drought and to flooding in nodal roots of cereals (Galamay et al., 1992). Grinieva et al. (1987) found that adventitious roots formed in response to flooding had increased sclerenchyma. In rice the thickening of the hypodermis and adjacent cortical cells was assumed to reduce radial loss of the oxygen being transported internally in the root (Armstrong, 1971; Jackson and Drew, 1984). In hypoxic maize roots, metabolic evidence suggested a strong compartmentalization in oxygen transport through aerenchymatous roots (Thomson and Greenway. 1991). Thus limited branching of the newly developed adventitious roots, under soil submergence, would reduce oxygen demand from root apices and limit radial leakage of oxygen associate with mechanical disruption of protective tissues in the root due to lateral emergence (Charlton, 1991).

After drainage the plants flooded for four days had different responses in root growth than the plants flooded for eight days. Plants flooded for four days increased their roots to levels close to non-flooded plants, suggesting an active

process of root elongation and branching post-drainage. Plants flooded for eight days did not experience any major recovery after drainage, but rather maintained a constant number of roots through the remainder of the season. The spongy adventitious roots formed aboveground during the submergence, shrank and became hard immediately after drainage. A possible reason, in accordance with Wenkert et al. (1981) results, is that the pre-flooding roots were extensively damaged after eight days of flooding and the new adventitious root system continued extending with moderate branching. The small increase in root number that plants flooded for eight days had late in the season at 40 cm seems consistent with this suggestion.

The consequences of flooding on shoot growth was discussed in the previous chapter. The decrease found in leaf area suggests important reductions in the source of photosynthates after flooding. The calculation of the total number of roots produced per unit of leaf area was an attempt to explore the effect that these reductions had on the relative sink strength of flooded roots as compared with non-flooded roots. Sink strength is the integration of sink size and sink activity. Root numbers indirectly indicate the size component of the sink. The ratio total root length to total leaf area provides an approximation to evaluate sink activity, which is defined as the capacity to use photosynthates (Brown, 1984). Roots were an active sink early in the season but the activity decreased later in the season. These data suggest important differences associated with the timing of the flooding in the post-drainage recovery. Small plants flooded early in the

season seemed to increase the sink activity of the root system after drainage for most of the season. Larger plants flooded later had different response. Plants flooded four days recovered the sink activity to a level similar to non-flooded plants. Plants flooded eight days never recovered the sink activity exhibited prior to soil submergence.

Conclusions

Evaluating the dynamics of roots using video images obtained in minimizotrons proved to be a successful method for monitoring non-destructively, short-term changes in the rhizosphere. A careful consideration of the limitations of the method however, will assist in an adequate interpretation of the results.

Soil submergence during the vegetative growth stage affected the growth of maize roots, their distribution in the soil profile and the relation with above ground organs. Different responses in early and in late flooding showed the importance of the timing of waterlogging. Early flooding produced an immediate and fast decrease in the number of roots and an explosive regrowth after drainage. A more detailed examination revealed that when plants were flooded for eight days regrowth occurred only in the upper layers. Plants flooded later did not exhibit such dramatic changes. Plants that were under soil submergence four days recovered the number of roots after drainage whereas plants flooded eight days did not. These results, together with field observations suggest the presence of a new, weakly branched, adventitious root system in flooded plants. The

pattern of adventitious root elongation from successive root whorls in this new root system follows the same sequence observed in non-flooded plants, but occurred earlier. Timing and duration of the submergence period, determines if the former pre-flooded roots will regain the ability to elongate and branch or if the later flood-developed system will be the only one responsible for root growth. A submergence duration between four and eight days seemed critical to produce a permanent damage to the pre-flooded main axes.

This data also suggests that the role of maize roots as a sink for photosynthates may be strengthened as a consequence of an early flooding. A late soil submergence is expected to have a minor impact in root sink strength after drainage, unless the waterlogging is prolonged sufficiently as to impair the ability of the roots to recover the sink strength under aerated conditions.

Bibliography

- Amato, Mariana. 1991. Spatial distribution and water uptake of roots in structured growth media. Ph.D. diss. Michigan State University, East Lansing.
- Armstrong, W. 1971. Radial oxygen losses from intact rice roots as affected by distance from the apex, respiration and waterlogging. Physiol. Plant. 25:192-197.
- Bell, J. K. and M. E. McCully. 1970. A histological study of lateral root initiation in *Zea mays* L. Protoplasma 70:179-205.
- Brown, R. H. 1984. Growth of the green plant. p. 153-174. *In M. B. Tesar (Ed.)* Physiological basis of crop growth and development. ASA, CSSA, Madison, Wisconsin.
- Charlton, W. A. 1991. Lateral root initiation. p. 103-128. *In* Y. Waisel, A. Eshel and U. Kafkafi (Ed.) Plant roots; the hidden half. Marcel Dekker, New York.
- Drew, M. C. 1990. Sensing soil oxygen. Plant Cell Environ. 13:681-693.
- Drew, M. C., A. Chamel, J. P. Garrec and A. Fourcy. 1980. Cortical air spaces (aerenchyma) in roots of corn subjected to oxygen stress; structure and influence on uptake and translocation of ⁸⁶rubidium ions. Plant Physiol. 65:506-511.
- Drew, M. C., C. J. He and P. W. Morgan. 1989a. Decreased ethylene biosynthesis, and induction of aerenchyma, by nitrogen- or phosphate-starvation in adventitious roots of *Zea mays* L. Plant Physiol. 91(1):266-271.
- Drew, M. C., C. J. He and P. W. Morgan. 1989b. Ethylene synthesis and sensitivity in the formation of aerenchyma in response to deficiencies of N and P in roots of Zea mays. p. 323-330. In H. Clijsters, M. De Proft, R. Mancelle and M. Van Poucke (Ed.) Biochemical and physiological aspects of ethylene production in lower and higher plants. Kluwer Academic Publishers, Dordrecht.
- Drew, M. C., M. B. Jackson and S. Giffard. 1979. Ethylene- promoted adventitious rooting and development of cortical air spaces (aerenchyma) in roots may be adaptive responses to flooding in *Zea mays* L. Planta 147:83-88.

- Drew, M. C., P. H. Saglio and A. Pradet. 1985. Larger adenylate energy charge and ATP/ADP ratios in aerenchymatous roots of *Zea mays* in anaerobic media as a consequence of improved internal oxygen transport. Planta 165:51-58.
- Drew, M. C. and L. R. Saker. 1986. Ion transport to the xylem in aerenchymatous roots of *Zea mays* L. J. of Exp. Bot. 37(174):22- 33.
- Drew, M. C. and L. H. Stolzy. 1991. Growth under oxygen stress. p. 331-350. *In* Y. Waisel, A. Eshel and U. Kafkafi (Ed.) Plant roots; the hidden half. Marcel Dekker. New York.
- Ferguson, J. C. and A. J. Smucker. 1989. Modifications of the minirhizotron video camera system for measuring spatial and temporal root dynamics. Soil Sci. Soc. Am. J. 53(5):1601-1605.
- Galamay, T. O., A. Yamauchi, T. Nonoyama and Y. Kono. 1992. Acropetal lignification in protective tissues of cereal nodal root axes as affected by different soil moisture conditions. Jpn. J. Crop Sci. 61(3):511-517.
- Grinieva, G. M. 1981. The effect of flooding on metabolism and structure of maize roots. p. 323-326. *In* R. Brouwer, O. Gasparikova, J. Kolek and B. C. Loughman (Ed.) Structure and function of plant roots. Martinus Nijhoff-Dr. W. Junk Publishers, The Hague.
- Grinieva, G. M. 1991. Physiological and morphological changes in maize plants under various flooding conditions. p. 81-87. *In* B. L. McMichael and H. Persson (Ed.) Plant roots and their environment. Elsevier, Amsterdam.
- Grinieva, G. M., T. A. Borisova, A. F. Garkavenkova, G. M. Akhrif and T. V. Bragina. 1987. Effect of flooding time on exudation, respiration, and anatomical structure of corn roots. Sov. Plant. Physiol. 33(5,pt.2):760-767.
- Hole, D., P. Hole, J. R. Johnson, B. G. Cobb and M. C. Drew. 1989. Rates of glycolysis in aerobic and anaerobic maize root tips. Plant Physiol. 4, Supp:127.
- Jackson, M. B. and M. C. Drew. 1984. Effects of flooding on herbaceous plants. p. 47-128. *In* T. T. Kozlowski (Ed.) Flooding and plant growth. Academic Press, Orlando, Florida.
- Johnson, J., B. G. Cobb and M. C. Drew. 1989. Hypoxic induction of anoxia tolerance in root tips of *Zea mays*. Plant Physiol. 91: 837-841.

- Karas, I. and M. E. McCully. 1973. Further studies of the histology of lateral root development in *Zea mays* L. Protoplasma 77:243-269.
- Klepper, B. 1987. Origin, branching and distribution of root systems. p. 103-124. In P. J. Gregory, J. V. Lake and D. A. Rose (Ed.) Root development and function. Cambridge University Press, Cambridge.
- Mauseth, J. D. 1988. Plant anatomy. Benjamin/Cummings Publishing Co., Menlo Park, California.
- McCully, M. E. 1987. Selected aspects of the structure and development of field-grown roots with special reference to maize. p. 53-70. *In P. J. Gregory*, J. V. Lake and D. A. Rose (Ed.) Root development and function. Cambridge University Press, Cambridge.
- McCully, M. E. and M. J. Canny. 1989. Pathways and processes of water and nutrient movement in roots. p. 3-14. *In* B. C. Loughman, O. Gasparikova and J. Kolek (Ed.) Structural and functional aspects of transport in roots. Kluwer Academic Publishers, Dordrecht.
- Meyer, W. S., H. D. Barrs, R. C. Smith, N. S. White, A. D. Heritage and D. L. Short. 1985. Effect of irrigation on soil oxygen status and root and shoot growth of wheat in a clay soil. Aust. J. Agric. Res. 36:171-185.
- Meyer, W. S., H. D. Barrs, A. R. Mosier and N. L. Schaefer. 1987. Response of maize to three short-term periods of waterlogging at high and low nitrogen levels on undisturbed and repacked soil. Irrig. Sci. 8(4):257-272.
- Nuñez-Barrios, Abelardo. 1991. Effect of soil water deficits on the growth and development of dry beans (*Phaseolus vulgaris* L.) at different stages of growth. Ph.D. diss. Michigan State University, East Lansing.
- Ramírez, R. and B. Rodríguez. 1987. Corn responses to oxygen deficiency applied to nodal and/or seminal roots. J. Plant Nutr. 10(9-16):1281-1288.
- Russell, R. S. 1977. Plant root systems. McGraw Hill, Maidenhead, U.K.
- Saglio, P. H. 1985. Effect of path or sink anoxia on sugar translocation in roots of maize seedlings. Plant Physiol. 77(2): 285-290.
- Saglio, P. H., M. C. Drew and A. Pradet. 1988. Metabolic acclimation to anoxia induced by low (2-4 kPa partial pressure) oxygen pretreatment (hypoxia) in root tips of *Zea mays*. Plant Physiol. 86(1):61-66.

- Saglio, P. and A. Pradet. 1983. Effet du manque d'oxygène sur l'alimentation en sucres de la jeune racine de maïs. p. 331-338. *In* A. Gallais (Coordinateur.) Physiologie du maïs. INRA, Paris.
- Spek, L. Y. 1981. Influence of nitrate and aeration on growth and chemical composition of *Zea mays* L. p. 395-398. *In* R. Brouwer, O. Gasparikova, J. Kolek and B. C. Loughman (Ed.) Structure and function of plant roots. Martinus Nijhoff-Dr. W. Junk Publishers, The Hague.
- Spek, L. Y. 1984. Response of plants to nitrogen nutrition. I. Effects of interruption of the nitrate supply and aeration of the nutrient solution on absorption and distribution of nitrogen in maize plants. Proc. Koninklijke Nederlandse Akademic Wetenschappen 87(3):319-326.
- Spek, L. Y. 1984. Response of plants to nitrogen nutrition. II. Response of maize plants to interruptions of the nitrogen nutrition and root aeration. Proc. Koninklijke Nederlandse Akademie Wetenschappen 87(3):327-336.
- Thomson, C. J., W. Armstrong, I. Waters and H. Greenway. 1990. Aerenchyma formation and associated oxygen movement in seminal and nodal roots of wheat. Plant Cell Environ. 13(4):395-403.
- Thomson, C. J. and H. Greenway. 1991. Metabolic evidence for stelar anoxia in maize roots exposed to low O2 concentrations. Plant Physiol. 96(4):1294-1301.
- Upchurch, D. R. and J. T. Ritchie. 1983. Root observations using a video recording system in mini-rhizotrons. Agron. J. 75:1009- 1015.
- Veen, B. W. 1988. Influence of oxygen deficiency on growth and function of plant roots. Plant Soil 111:259-266.
- Waters, I., P. J. Kuiper, E. Watkin and H. Greenway. 1991. Effects of anoxia on wheat seedlings. I. Interaction between anoxia and other environmental factors. J. Exp. Bot. 42(244): 1427-1435.
- Wenkert, W., N. R. Fausey and H. D. Watters. 1981. Flooding responses in *Zea mays* L. Plant Soil 62:351-366.

Chapter 5

FLOODING EFFECTS ON FIELD GROWN MAIZE.

III. MODIFYING THE MAIZE MODEL IN GENERIC CERES.

Abstract

CERES is a dynamic daily-step simulation model that predicts growth and development of five user-selected cereals: wheat, maize, sorghum, pearl millet and barley. The model predicts the effects of limited soil water and nitrogen on crop growth. The maize model in CERES was modified to include the effects of limited soil aeration on crop growth and development. The modified model includes the newest routines available to simulate soil temperature and the water and nitrogen balances. A new input file is required only if a controlled water table option is selected. The new input file provides input on the depth of the controlled water table for each day of simulation. The modified model produced logical and reasonable results when flooding was simulated. Under well aerated conditions, growth and yield was somewhat underestimated. Predictions of crop phenology required adjustment. The new model provides an alternative for predicting maize crop performance when the crop is affected by waterlogging.

Introduction

Mechanistic models have been proposed to describe oxygen diffusion through individual roots (Luxmoore et al., 1970; Armstrong and Wright, 1976; Armstrong, 1979; Armstrong and Beckett 1985 and 1987). These models however, do not attempt to predict whole root system behavior under conditions of limited soil aeration.

Several models have been developed to simulate whole root systems (e.g. Gerwitz and Page, 1974; Hoogenboom and Huck, 1986). Luxmoore and Stolzy (1987) recently reviewed several whole root systems models. None of these models consider the limitations imposed by deficient soil aeration on root growth. Jones et al. (1991) proposed a model to predict root growth that includes soil constraints affecting root growth. This model differentiates between static and dynamic factors according to the change experienced during the growing season. Static factors such as the presence of rocks, toxic or cemented horizons show little seasonal change. Soil temperature, aeration and strength rapidly change on a daily scale. The model uses the fraction of water filled pore space as an aeration index to affect root attributes such as rooting depth, branching, and senescence.

Maize crop responses to soil submergence during the vegetative growth stage were analyzed in Chapters three and four. In this chapter, a predictive tool capable of forecasting maize growth and development under adequate and limited soil water was modified to extend the predictions into environments with excessive soil water. The CERES model simulates growth and development of wheat, maize,

sorghum, pearl millet and barley, yet the modifications introduced were implemented only for the maize model.

Materials and Methods

The generic version of CERES, a combination of the simulation models of maize, wheat, sorghum, pearl millet and barley, was used to simulate the effects of flooding on maize growth, development, and yields. The CERES family of models was developed in a multidisciplinary international effort coordinated through the International Benchmark Sites Network for Agrotechnology Transfer (IBSNAT) Project. The generic version was developed at the International Fertilizer Development Center in Muscle Shoals, Alabama, USA (U. Singh, D. Godwin and C. Humpries, 1992, personal communication). The maize model in generic CERES is CERES-Maize described by Jones and Kiniry (1986). Version 2.1 of CERES-Maize is used here to compare the predictions of the modified generic CERES.

Simulation of infiltration and runoff in CERES-Maize has recently been modified using a time-to-ponding approach (Chou, 1990). A new water balance routine, already linked to generic CERES (A. Gerakis, 1992, personal communication), provided the capability to simulate water table fluctuations within the soil profile. The new water balance routine was modified to include a different logic when simulating the presence of a controlled water table. New routines to simulate up-flow and down-flow of water and nitrogen were obtained from Godwin and Ritchie (1992, personal communication) and linked into CERES. These

routines consider the effects of the water table and a restricting soil layer in the drainage. Simulation of nitrogen movement in the soil considers two fractions with different mobilities. A new soil temperature model (Dadoun, 1993) was also linked into generic CERES to provide better estimation of the effect of soil water content on soil temperature.

Soil aeration index

The routine that calculates root growth (ROOTGROW) was modified to include the calculation of an aeration factor on each soil layer. The aeration factor is passed to a new routine (OXSTRESS) that computed a soil aeration index. Aeration indexes are calculated in terms of soil porosity since oxygen diffusion depends on the air-filled pore space. Total porosity (TPORE) and water-filled porosity (WFPS) are calculated for each layer as:

$$TPORE_i = 1 - \frac{BD_i}{2.65}$$
 [5.1]

$$WFPS_i = \frac{SW_i}{TPORE_i}$$
 [5.2]

where BD_i is the bulk density of layer i, assuming a soil particle density of 2.65 g cm⁻³ and SW_i is the volumetric water content of the layer in cm³ cm⁻³. The water filled pore space at saturation is assumed to have a maximum value (XWFPS) of 0.93 to account for trapped air in the soil profile. Whenever the water filled pore space in a soil layer is larger than a critical value (CWFPS) a layer aeration factor

(LAF) was calculated as:

$$LAF_{i} = \frac{1 - WFPS_{i}}{1 - CWFPS}$$
 [5.3]

where CWFPS is equal to 0.45 (W. Meyer, 1990, personal communication). A soil layer with low air-filled porosity may limit oxygen diffusion into deeper layers. Thus, a layer with WFPS of 0.9 or larger limits the aeration of lower layers. In the OXSTRESS routine, root length density (RLV) of each soil layer is used to weight the layer aeration factor in the calculation of a whole rhizosphere aeration factor (WRAF):

$$WRAF = \frac{\sum (LAF_i \times RLV_i)}{\sum (RLV_i)}$$
 [5.4]

Two aeration stress indexes, ASD and ASD2, were calculated using WRAF to simulate the cumulative aeration status experienced by the plant. Both indexes increased following the same calculation as the soil aeration decreased but they differed during the recovery period. The model compares yesterday's and today's values of WRAF to decide if the soil aeration improved. When the aeration in any day is more limiting for root growth than the previous day, the aeration indexes are (ASD and ASD2) increased according to:

$$ASD_{DAY} = ASD_{DAY-1} + (1-WRAF)$$

$$ASD_{DAY} = ASD_{DAY-1} + (1-WRAF)$$
[5.5]

During the recovering period ASD will decrease as:

 $ASD_{DAY} = ASD_{DAY-1} - WRAF \times (WRAF - WRAFY) \times 0.855 \times ISTAGE^2$ [5.6]

This formulation implies that the decrease in the stress index ASD will be modulated by the current status of soil aeration (WRAF), by the daily increase in soil aeration (WRAF-WRAFY), and by the phenological stage (ISTAGE), assuming faster recovering later in the season. ASD2 recovers early in the vegetative growth stage (XSTAGE less than 2.5) in two steps. When ASD2 is large (larger than 4.0):

$$ASD2_{DAY} = ASD2_{DAY-1} - WRAF \times ASD2_{DAY-1} \times 0.8$$
 [5.7]

When ASD2 is small (less than 4.0):

$$ASD2_{DAY} = ASD2_{DAY-1} - WRAF \times ASD2_{DAY-1} \times 0.1$$
 [5.8]

During the remainder of the season (XSTAGE larger than 2.5) ASD2 will recover as:

$$ASD2_{DAY} = ASD2_{DAY-1} - WRAF \times ASD2_{DAY-1} \times 0.5$$
 [5.9]

Both aeration indexes are maintained in the range between zero and 10. A cumulative aeration stress index (CASD), similar to the soil water and nitrogen stress indexes in CERES-Maize, is calculated:

$$CASD = \sum (1-WRAF)$$
 [5.10]

CASD will provide an average aeration stress index per phenological stage to be printed.

Predicting plant growth

CERES-Maize calculates daily dry matter production by multiplying the potential dry matter production (PCARB) by the most limiting of three zero-to-unity stress factors due to temperature, limited soil water, and nitrogen. A new soil aeration deficit factor (SADEF) was computed to affect the actual dry matter production under conditions of excessive soil water. The calculation of SADEF assumes that a maize crop may endure up to two days of complete soil submergence without a noticeable disruption in the ability of the crop to accumulate biomass. A period between two and four days is critical in affecting dry matter production. Beyond four days of complete soil submergence no additional damage is predicted. A slow recovery after drainage is assumed to occur only during the vegetative growth stage. When the maximum number of days under complete soil submergence or its equivalent (XASD2) is between two and four, SADEF is calculated as follows:

$$SADEF = 1.36-0.18 \times AAFF$$
 [5.11]

where AAFF is made equal to XASD2 and is updated every time XASD2 increases. In successive days AAFF is reduced by 0.095 units each day during the vegetative growth stage. When XASD2 is larger than four SADEF is calculated as:

$$SADEF = e^{-AAF \times 0.15}$$
 [5.12]

where AAF has an initial value of four and every day is decreased by 0.095 units during the vegetative growth stage. Actual dry matter production (CARBO) is then

calculated as:

CARBO = PCARB×AMIN1(PRFT,SWDF1,NDEF1,SADEF) [5.13]

where PCARB is potential dry matter production and AMIN1 is a FORTRAN function that selects the most limiting stress factor due to temperature (PRFT), soil water deficit (SWDF1), nitrogen (NDEF1) and soil aeration (SADEF).

CARBO is partitioned among the different organs growing in any phenological stage. The CERES-Maize model allocates the biomass in aboveground growing organs according to several algorithms and the remaining biomass is assigned to root growth. The model checks, however, if a minimum proportion of CARBO is going to roots. The transport of photosynthates to the roots during the vegetative growth stage is impaired under waterlogging. The program was modified to calculate a labile fraction of the biomass (LABIO) being allocated into the roots which will be maintained temporarily aboveground until soil aeration improves. This labile biomass was prevented from increasing the calculated plant leaf area (PLA). LABIO was calculated during the vegetative growth stage as a function of the aeration stress index ASD2:

$$SADF1 = e^{-ASD2 \times 0.6}$$
[5.14]
$$LABIO = GRORT \times (1 - SADF1)$$

where GRORT is the biomass being allocated into the roots. LABIO was subtracted from GRORT and added to leaf biomass (GROLF) early in the season (ISTAGE = 1 or ISTAGE = 2). Late in the vegetative growth stage (ISTAGE = 3)

LABIO will be added to stem biomass (GROSTM) instead of leaf biomass. LABIO allocated in leaves and stems is accumulated in separated variables which are used to return the labile biomass to the roots after drainage. When soil aeration improves, the labile biomass temporarily stored in leaves returns to roots at a fraction of the biomass allocated that day into leaves according to the following equations:

$$LFWT_{DAY} = LFWT_{DAY-1}$$
-GROLF×PROP

$$GRORT_{DAY} = GRORT_{DAY-1}$$
+GROLF×PROP

[5.15]

$$TLABIOL_{DAY} = TLABIOL_{DAY-1}$$
-GROLF×PROP

The proportion (PROP) was made equal to 0.85 early in the season (XSTAGE less than 1.75). For the remainder of the season the proportion is equal to one. Similar equations are used to return labile biomass from stems to the roots:

$$STMWT_{DAY} = STMWT_{DAY-1}$$
-GROSTM×PROP

$$GRORT_{DAY} = GRORT_{DAY-1}$$
+GROSTM×PROP

[5.16]

$$TLABIOS_{DAY} = TLABIOS_{DAY-1}$$
-GROSTM×PROP

Predicting leaf growth

The simulation of leaf growth and rate of leaf appearance was changed.

The modifications introduced in the calculation of leaf appearance will be discussed later in the section on plant development. The CERES-Maize model

simulates separately the effect that environmental stresses have on expansion of leaves and on leaf senescence. Potential leaf area growth (PLAG) during the vegetative growth stage is calculated using several equations according to the phenological stage of the crop. In all the equations, PLAG is calculated as a function of the number of emerged leaves (XN), the accumulated fraction of thermal time required for a new leaf to appear (TI), and the most limiting of two stress factors due to limited soil water and nitrogen (SWDF2 and NDEF2). The formulation was modified to include the effect of reduced soil aeration (ASD). During the juvenile stage (ISTAGE = 1):

$$SADF2 = e^{-ASD \times 0.2}$$
[5.17]
$$PLAG = 2 \times XN^2 \times TI \times AMIN1(SWDF2, SADF2)$$

From the end of the juvenile stage to tassel initiation (ISTAGE = 2):

$$PLAG = 2 \times XN^2 \times TI \times AMIN1(SWDF2,NDEF2,SADF2)$$
 [5.18]

After tassel initiation three equations are used according to the number of emerged leaves (XN). When XN is less than 12, between 12 and the last three leaves, or during the expansion of the last three leaves, PLAG is calculated as:

$$SADF3 = e^{-ASD \times 0.1}$$

$$PLAG = 3.5 \times XN^2 \times TI \times AMIN1(SWDF2,NDEF2,SADF3)$$
[5.19]

$$SADF3 = e^{-ASD \times 0.1}$$
 $PLAG = 3.5 \times 170 \times TI \times AMIN1 (SWDF2, NDEF2, SADF3)$
[5.20]

$$SADF3 = e^{-ASD \times 0.05}$$

$$PLAG = \frac{3.5 \times 170 \times TI}{\sqrt{XN + 3 - TLNO}} \times AMIN1(SWDF2,NDEF2,SADF3)$$
[5.21]

Two new stress coefficients due to limited nitrogen or soil aeration, were included in the calculation of leaf senescence. The nitrogen stress coefficient (SLFN) is used only during the reproductive stages and allows a daily leaf senescence of up to 2% if the crop has not endured a severe soil submergence (XASD2 less than six):

$$SLFN = 0.98 + 0.02 \times NDEF2$$
 [5.22]

Otherwise, leaf senescence may increase up to 5%. The aeration stress coefficient (SLFA) increases daily leaf senescence up to 2% according to:

$$SLFA = 0.98 + 0.002 \times (10 - ASD)$$
 [5.23]

The rate of leaf senescence (PLAS) during the vegetative growth stage is calculated as:

 $PLAS = (PLA-SENLA) \times (1-AMIN1(SLFW,SLFC,SLFT,SLFA))$ [5.24] where PLA is the total plant leaf area in cm² and SENLA is daily senescence per plant in cm². The formulation uses the most limiting stress factor associated with

limited soil water (SLFW), plant competition (SLFC), air temperature (SLFT) and soil aeration (SLFA). During the reproductive stages, the nitrogen stress factor (SLFN) is included in the calculations.

Predicting root growth

The routine that calculates root growth was modified to predict the effects of excessive soil water. Two root attributes received attention: root depth and number of roots per layer. In CERES-Maize, root depth increases through the whole season and the maximum daily increase in root depth is calculated as 0.22 cm per unit of thermal time accumulated in that day. This growth may be slowed down by limited soil water or stopped when the maximum depth in the soil profile is reached. In the modified routine, the growth in root depth occurs only up to the silking stage unless the rooting depth by that time is less than 50 cm. If the rooting depth by the beginning of the linear phase of grain filling is still less than 30 cm, additional growth in root depth is allowed. In any case, root depth growth was stopped when the rooting front arrived at a saturated soil layer or at the water table. If the rooting front stayed in a saturated layer for more than five days, root death was assumed and the new root depth was set equal to the middle of the nearest non-saturated upper layer. The modified formulation, however, maintained a minimum rooting depth to simulate the presence of aerenchymatous roots (Drew et al. 1985; Thomson et al. 1990). A minimum distance of 20 cm from the rooting front to the soil surface or to the ponding water surface was maintained. In the new formulation, increases in root depth were slowed down by limited soil aeration according to:

$$SADF4 = LAF_{j} \times 3$$

$$RTDEP_{DAY} = RTDEP_{DAY-1} + DTT \times 0.22$$

$$\times AMIN1((SWDF1 \times 2), SWDF, SADF4)$$

$$SADF4 = e^{-ASD2 \times 0.3}$$

$$RTDEP_{DAY} = RTDEP_{DAY-1} + DTT \times 0.22$$

$$\times AMIN1((SWDF1 \times 2), SWDF, SADF4)$$
[5.25]

where DTT is the thermal time accumulated in the day, SWDF1 and SWDF are water deficit coefficients for the whole rhizosphere or for the layer where root depth is calculated, and SADF4 is an aeration deficit factor. LAF_i represents the aeration status in the soil layer where the rooting front is growing, and ASD2 estimates the current status of the plant in terms of root aeration. The first equation to calculate SADF4 is used if the plants have not experienced any significant period of soil submergence (maximum registered value of ASD2 less than two). Otherwise, the second equation is selected.

To calculate the effect of inadequate soil aeration on the number of roots in each soil layer, a new variable (RLVLOSS) was introduced. RLVLOSS will reduce a fraction of the root length density of each soil layer (RLV_i) according to the aeration status of that layer (LAF_i). During the vegetative growth stage two equations were used to calculate RLVLOSS: the first was used before tassel initiation (ISTAGE = 2) and the second after (ISTAGE = 3),

$$RLVLOSS = (1-LAF_i) \times 0.075 \times ASD \times RLV_i$$

$$[5.26]$$
 $RLVLOSS = (1-LAF_i) \times 0.025 \times ASD \times RLV_i$

These equations imply that during the vegetative growth stage the fraction of roots lost in each soil layer due to insufficient soil aeration depends upon the aeration in the soil layer (LAF_i) and the current rhizosphere aeration (ASD). During the reproductive stages the calculation of RLVLOSS differs according to the existence or non-existence of a previous submergence period (maximum ASD2 recorded less than two):

$$RLVLOSS_i = (1-LAF_i) \times 0.01 \times TRLVY \times RLV_i$$

$$[5.27]$$
 $RLVLOSS_i = (1-LAF_i) \times 0.02 \times TRLVY \times RLV_i$

Root loss in this case is a function of the aeration of the soil layer (LAF_i) and of the accumulated root length density of the previous day (TRLVY).

Root length density (RLV_i) is updated every day considering the new component RLVLOSS and increasing root senescence from 0.5% during the vegetative growth stage to 5% during the reproductive stage.

Predicting plant development

Plant development is estimated in CERES-Maize in two routines: PHENOL and PHASEI. PHENOL determines the beginning of a new growth stage and PHASEI initializes and calculates variables used in the following growth stage. Several changes were introduced to simulate the delay of phenological events as

a consequence of soil submergence. Thermal time, calculated as the accumulation of degrees centigrade above a base temperature, was calculated using the mean soil temperature, instead of the mean air temperature, from sowing to tassel initiation. During this period, the base temperature was set 0.5 °C above the values used in CERES-Maize. After tassel initiation, the shoot meristem is assumed to be above the soil surface (Ritchie and Hanway, 1984). Thus, air temperature was used to calculate the thermal time. The base temperature was set to 8.0 °C as in CERES-Maize.

The actual thermal time that the modified model accumulates may be reduced early in the vegetative growth stage (XSTAGE less than two) as a consequence of inadequate soil aeration (ASD larger than one):

$$SADF5 = e^{-ASD \times 0.4}$$

$$TT = DTT \times SADF5$$
[5.28]

where DTT is the thermal time accumulated in the day, ASD is the aeration stress index calculated earlier and TT is the actual thermal time used to estimate plant development.

CERES-Maize estimates that a new leaf emerges every time a certain amount of thermal time, a phyllochron, is accumulated. A new variable (LFDELAY) was introduced to account for the delay in leaf emergence associated with limited soil aeration. LFDELAY is calculated as a function of the soil aeration early (XSTAGE less than two) or late in the season as:

$$SADF6 = e^{-ASD \times 0.01}$$

 $SADF6 = e^{-ASD \times 0.15}$ [5.29]
 $LFDELAY = SADF6$

LFDELAY is used later in the calculation of the phyllochron:

$$CUMPH = \sum TI \times LFDELAY$$
[5.30]
$$CUMDELAY = \sum TT \times (1 - LFDELAY)$$

where CUMPH is the accumulated number of phyllochrons, which corresponds with the number of emerged leaves, TI is the fraction of the phyllochron accumulated in the day, and TT is the accumulated thermal time as calculated in equation 5.26. CUMDELAY is used during the reproductive growth stage to modify the calculation of the normal plant senescence (SLAN). In CERES-Maize, SLAN during the reproductive stage is calculated as a function of the accumulated thermal time during the phenological stage. The modified version calculates SLAN as a function of the accumulated thermal time plus CUMDELAY.

Additional inputs

The new additions allowing the simulation of a water table by considering three possible scenarios: without a water table, with a fluctuating water table updated daily and with a controlled water table which depth is read from an input file. In the third option the model calculates the depth of the water table according to the inputs and outputs of the system, as in the second option, and then

computes subirrigation or drainage as required to move up or down the simulated depth of water table to match the read depth.

Each experiment and treatment simulated using the controlled water table scenario must have an additional input file with two variables per line: day of the year (RDOY) and soil layer number where the water table is (RWTLAYR). Both variables are integers with four and three fields (I4 and I3 format code in FORTRAN). The file name has six characters and the extension MZ0. The six characters are: WT for water table, two digits for the experiment number and two digits for treatment number. Thus a file named "WT0201.MZ0" corresponds to the water table input file for experiment two, treatment one.

Additional outputs

The modified model prints the aeration stress index together with the water and nitrogen stress indices in the summary output file (OUT1.MZ) and on the computer screen. Two new output files are written and numbered six and seven according to the terminology used by CERES-Maize (OUT6.MZ and OUT7.MZ). The sixth file is optional and contains a daily water balance of the entire soil profile. It identifies the day of the year and depth of the water table, as well as main inputs and outputs to the system associated with the water table fluctuation as subirrigation, drainage, ponding and runoff. For every soil layer the model prints the input of ascending water (FLOWU_i) and the output of descending water (FLOWD_i), the resulting layer water content (SW_i) and the layer saturated water

content (SAT_i). The eighth file prints a line each day of simulation where all the components of the water balance are written. The file was used for checking purposes.

Results

Field data obtained in 1991 and analyzed in Chapters three and four was used to compare the predictions of CERES-Maize (Version 2.1) and the modified version. Figure 5.1 shows the leaf area index predicted for both models and the measured values in the control plot. CERES-Maize underestimated leaf growth because it predicted a major nitrogen deficiency after tassel initiation (ISTAGE = 3). The nitrogen stress factor that affected the simulation of leaf growth (CNSD2) during this period was 0.47 as compared with 0.30 in the modified version of generic CERES. A value of 0.47 means that the plant had on the average 47% of the required nitrogen for normal growth during this period. The modified version underestimated leaf expansion during the last week of leaf growth.

When an early flooding was simulated (Figure 5.2) CERES-Maize predicted larger leaf area when the crop was flooded for eight days rather than when it was flooded for four days. No effect was predicted on the time of occurrence of maximum leaf surface. The modified version predicted a delay of one week in the occurrence of maximum leaf area between the four and eight days flooding that was similar to the field measured plants, but the peaks of both curves fell below the measured leaf area.

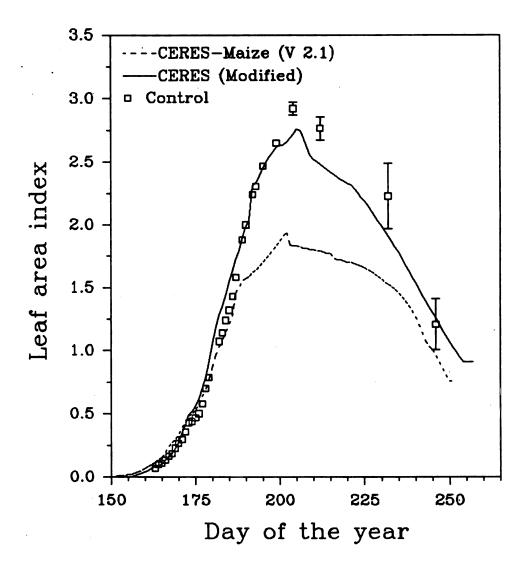


Figure 5.1: Leaf area index predicted by CERES-Maize and by a modified version, and field measured values. Vertical lines are standard errors of the measured values.

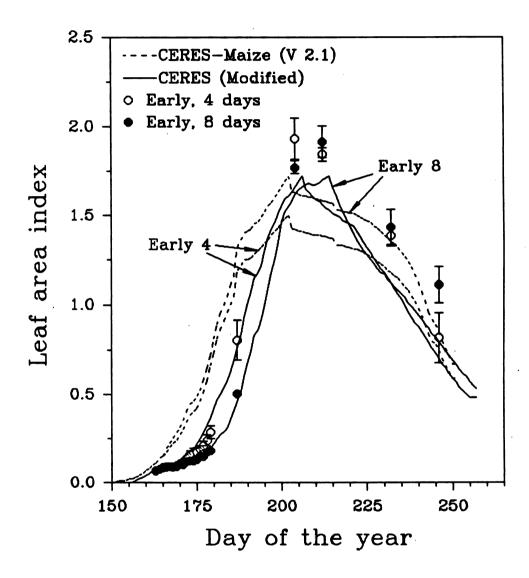


Figure 5.2: Leaf area index predicted by CERES-Maize and by a modified version, and field measured values in plants that were flooded four or eight days at the six leaf tip stage. Vertical lines are standard errors of measured values.

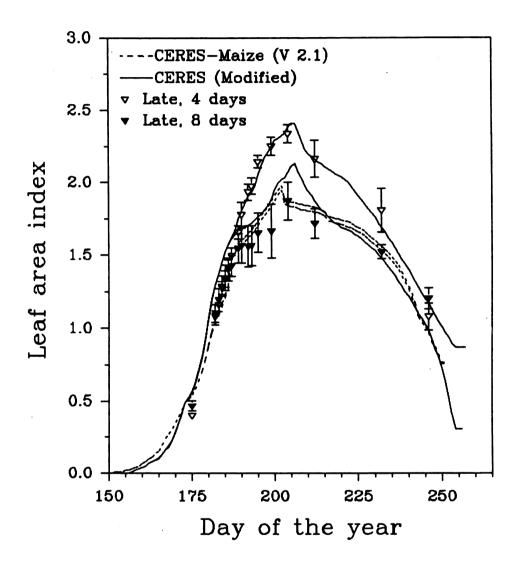


Figure 5.3: Leaf area index predicted by CERES-Maize and by a modified version, and field measured values in plants that were flooded four or eight days at the 12 leaf tip stage. Vertical lines are standard errors of measured values.

Figure 5.3 shows the leaf area predicted when a flooding was simulated late in the vegetative growth stage. CERES-Maize predicted the same leaf area when four or eight days of waterlogging were simulated. The modified version on the other hand, yielded excellent predictions with a slight overprediction of the maximum leaf area when eight days of flooding was simulated.

Limited field information on plant biomass and the large variability associated with the measurements increased the uncertainty about desired changes to be introduced in the modified model. Figure 5.4 shows that, despite a better performance, the modified model still seems to underestimate biomass accumulation in the conditions tested in this experiment. Similar to the trend observed in leaf area index, CERES-Maize predicted more biomass in plants flooded for eight days than in plants flooded for four days (Figure 5.5). The modified model predicted differences in biomass through the season after an early flooding of four or eight days. However, the total biomass at the end of the season seemed in excess of that measured in the field. Similar results were obtained when a late flooding was simulated using the modified model (Figure 5.6). CERES-Maize did not show any effect on the predicted plant biomass of an increased duration of flooding.

One of the most important reasons to develop simulation models is to forecast crop yields accurately under a wide range of field conditions. Table 5.1 shows the predicted yields by CERES-Maize and the modified version of generic CERES together with the measured values. CERES-Maize predicted yields

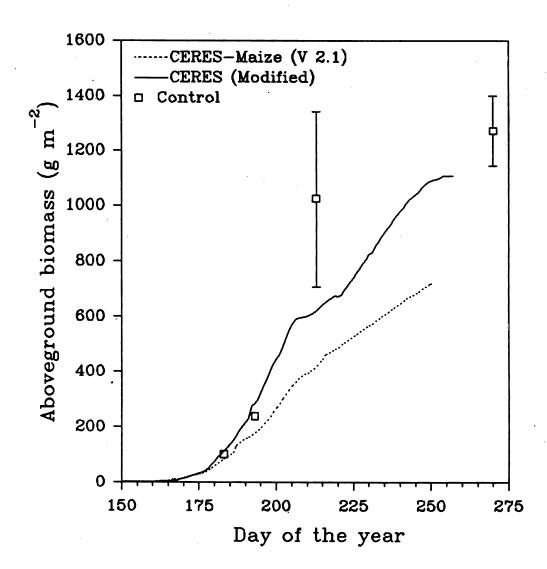


Figure 5.4: Aboveground biomass predicted by CERES-Maize and by a modified version, and field measured values. Vertical lines are standard errors of measured values.

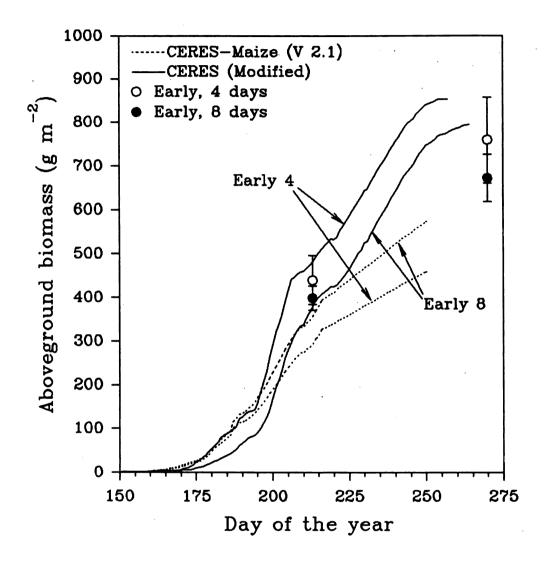


Figure 5.5: Aboveground biomass predicted by CERES-Maize and by a modified version, and field measured values. Maize was flooded four or eight days at the six leaf tip stage. Vertical lines are standard errors of measured values.

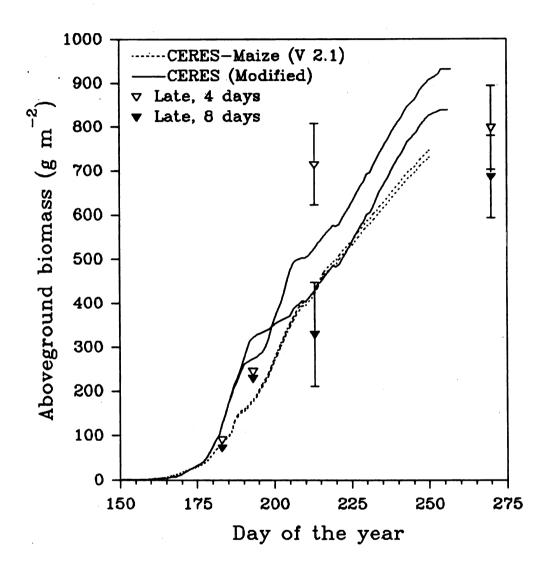


Figure 5.6: Aboveground biomass predicted by CERES-Maize and by a modified version, and field measured values. Maize was flooded four and eight days at 12 leaf tip stage. Vertical lines are standard errors of measured values.

Table 5.1: Yields predicted by CERES-Maize and by a modified version, and field measured. Maize was flooded for zero, four or eight days at the six or 12 leaf tip stage. Values in parentheses are standard errors.

Treatment	Measured	Predicted	
		CERES-Maize (V 2.1)	Gen. CERES (Modified)
	Kg ha ⁻¹		
Control	8605 (687.8)	3310	5594
Early, 4 days	4700 (710.6)	1760	4272
Early, 8 days	4387 (340.1)	2347	4227
Late, 4 days	4417 (477.0)	3415	4399
Latė, 8 days	4421 (509.9)	3500	4585

between 38% and 80% of the field measured yields. The modified generic CERES accurately predicted grain yields of the flooded plants. Yields of non-flooded plants were underestimated by 35%.

The prediction of root growth in CERES-Maize is insensitive to excessive soil water and also seems to overpredict root growth under well aerated conditions. Figure 5.7 shows the pattern of root growth as predicted at 15 cm depth by CERES-Maize and by the modified generic CERES as compared with the field measured root number. At this depth, CERES-Maize predicted that the maximum root length density of 5 cm cm⁻³ was reached in 25 days and the same value was maintained through the season. The measured values, on the contrary, showed

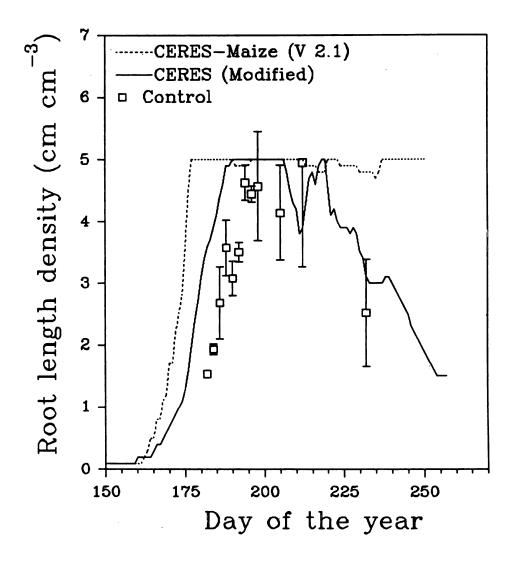


Figure 5.7: Root length density at 15 cm depth predicted by CERES-Maize and by a modified version, and field measured values. Vertical lines are standard errors of measured values.

a slower rate of root growth with a mid-season plateau around 4 and 5 cm cm⁻³ and decreasing root numbers during the grain filling. The modified generic CERES followed the described trend although it seemed to overpredict root growth early in the season.

When an early season flooding was simulated (Figure 5.8) CERES-Maize predicted the same root growth as without soil submergence. The modified model predicted a delay in root growth, associated with an early soil submergence, before a fast proliferation of roots. This predicted delay, especially in the longer inundation, was not observed in the roots measured in the field. When the flooding period was simulated late during the vegetative growth stage (Figure 5.9), field data showed a fast but incomplete recovery in root number after drainage in the short flooding (four days) and no recovery in the long flooding (eight days). The modified model accurately predicted root growth in the short flooding, but predicted a recovery after the long flooding that did not occur.

One of the main features of the CERES family of simulation models is the emphasis put on simulating crop phenology. Figure 5.10 shows that when simulating well aerated soil conditions, little difference was observed between the predictions of CERES-Maize and the modified generic CERES in the predictions of leaf appearance. Both models predicted a faster emergence of the last two leaves and one or two leaves more than the observed values in the field.

The simulation of an early flooding in the season is shown in Figure 5.11. Field measurements showed a delay between the flooding occurrence and the

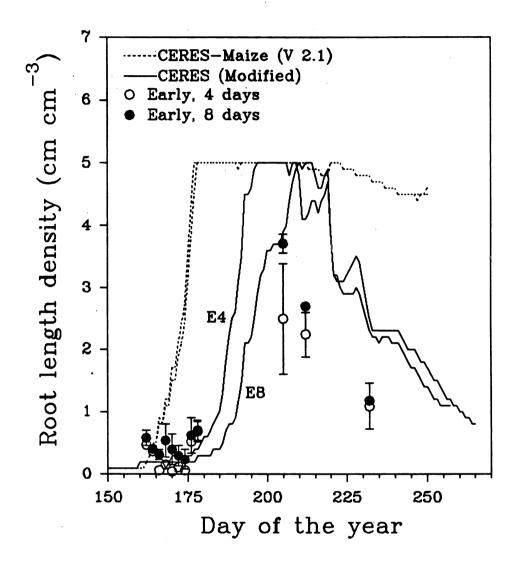


Figure 5.8: Root length density at 15 cm depth predicted by CERES-Maize and by a modified version, and measured values. Maize was flooded four or eight days at the six leaf tip stage. Vertical lines are standard errors of measured values.

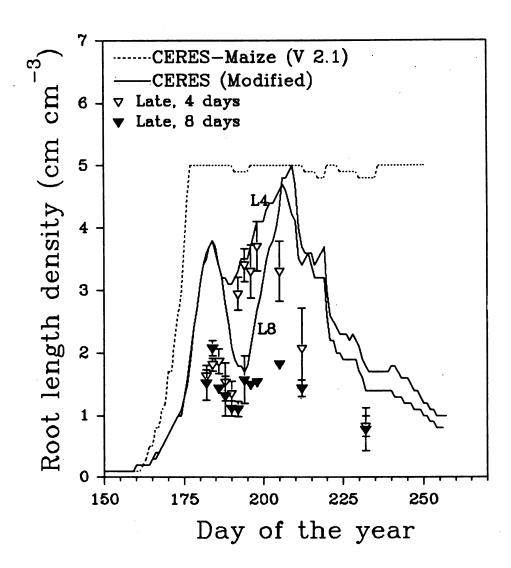


Figure 5.9: Root length density at 15 cm depth predicted by CERES-Maize and by a modified version, and measured values. Maize was flooded four or eight days at the 12 leaf tip stage. Vertical lines are standard errors of measured values.

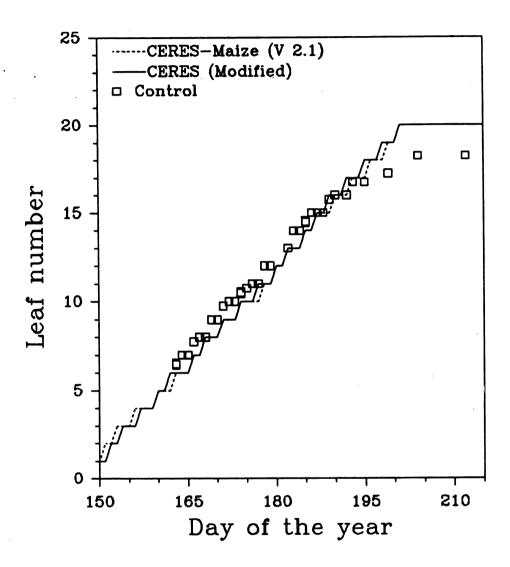


Figure 5.10: Leaf tip appearance predicted by CERES-Maize and by a modified version, and field measured values.

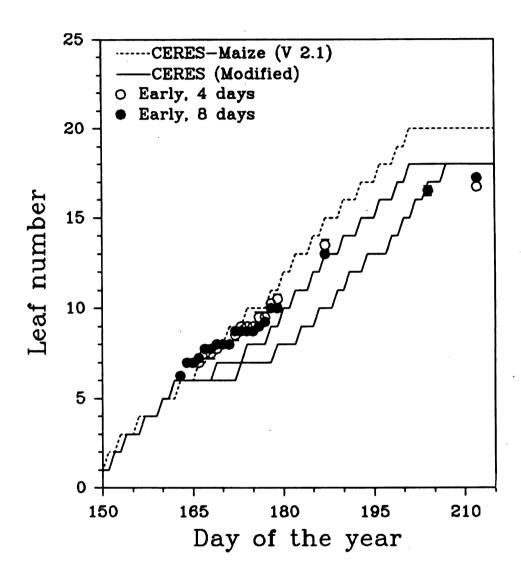


Figure 5.11: Leaf tip emergence predicted by CERES-Maize and by a modified version, and field measured values. Maize was flooded four or eight days at the six leaf tip stage. Vertical lines are standard errors of measured values.

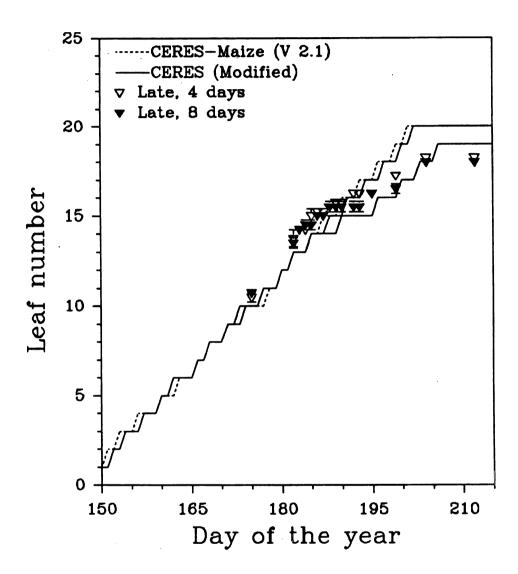


Figure 5.12: Leaf tip appearance predicted by CERES-Maize and by a modified version, and field measured values. Maize was flooded four or eight days at the 12 leaf tip stage. Vertical lines are standard errors of measured values.

between the shorter and the longer flooding. The modified version of generic CERES predicted an extra leaf and overpredicted the impact of soil submergence on the rate of leaf appearance, especially in the eight days flooding. When simulating waterlogging late in the vegetative growth stage (Figure 5.12), generic CERES predicted a slower rate of leaf appearance and one leaf less between the four and the eight days flooding. Field data showed that after a delay of ten days, the shorter flooding had an extra emerged leaf as compared with the longer flooding. Flooded and non-flooded plants had the same final number of leaves.

Table 5.2: Silking date predicted by CERES-Maize and by a modified version, and field measured. Maize was flooded zero, four or eight days at the six or at the 12 leaf tip stage.

Treatment	Measured	Predicted		
		CERES-Maize (V 2.1)	Gen. CERES (Modified)	
	**********	Day of the year		
Control	205	202	206	
Early, 4 days	210	202	206	
Early, 8 days	213	202	214	
Late, 4 days	206	202	206	
Late, 8 days	208	202	206	

The day when floral stigmata first appear (silking date) has received attention to evaluate crop phenology in simulation models. Table 5.2 shows the predicted and observed silking dates in the experiment here evaluated. CERES-

Maize predicted the same silking date for all the treatments. The predicted appearance of silks was three days earlier than the observed date in the field for non-flooded plants. The modified version of generic CERES was only sensitive to the larger delay observed in the early flooding when plants were in saturated soil for eight days.

Discussion

Three areas in the simulation of maize growth and development were modified in CERES to simulate soil submergence: aboveground growth, root growth and plant phenology. Before attempting to introduce any change, the latest modifications available were linked into the simulation model and modified or adjusted as required. Nitrogen cycle simulation required special attention. The field experiment received only 53.1 kg ha⁻¹ of nitrogen. When attempting to simulate this condition with CERES-Maize or with the original generic version of CERES the models predicted an early season nitrogen depletion and consequently, plant growth was underestimated (see Figure 5.1). Attempts to adjust the calculation of the nitrogen stress factors (NFACTO routine) were unsuccessful and the original equations as derived from Jones (1983) were maintained. Changes in nitrogen denitrification (NTRANS) and nitrification rate (NTRANS) were evaluated without success.

Three new routines developed by Ritchie and Godwin (1992, personal communication) were important in developing a reasonable simulation system that

was later modified to include predictions of the effects of poor aerated soils: DRAINAGE simulates saturated flow through the soil profile, UPFLOW simulates water redistribution in the soil profile associated with soil evaporation, NFLUXD simulates the movement of nitrogen with the flow of water.

The modified version of generic CERES produced reasonable estimations of aboveground plant growth in flooded conditions. Under well aerated conditions however, predictions seemed to be consistently less than field measured values. Combined underestimates of leaf area and biomass accumulation resulted in inaccurate crop yield forecasts.

The measured root numbers in minirhizotrons were converted to root length densities using the relation described by Melhuish and Lang (1968). The model proposed by Upchurch and Ritchie (1983) provided values of root length density that were too low. Bland and Dugas (1988) reported better correlations between root length densities calculated using the relation of Melhuish and Lang (1968) and roots washed from soil cores working with cotton. In sorghum however, they could not find a simple relation (Bland and Dugas, 1988). The modified version of generic CERES seemed to provided reasonable estimates of root growth, although the model still forecasts faster root growth than the observed in well aerated conditions.

More accurate predictions of crop development will require further model adjustments. The simulation of the rate of leaf appearance when soil waterlogging occurs early in the season showed limited agreement between observed and

predicted values. Leaf emergence rate was estimated using the new variable LFDELAY calculated as a function of the aeration index (Equation 5.28). Calculation of LFDELAY may require additional adjustment and the inclusion of a delay before the reduction of the leaf emergence rate.

Conclusions

Significant periods of soil submergence, during the vegetative growth stage of a maize crop, introduce changes in the soil-plant atmosphere relationships that extend well beyond the period of limited root aeration, and affect plant growth and development. Timing of occurrence of soil submergence had a significant effect on plant responses. To the best of the author's knowledge, this is the first attempt to address comprehensively the complex array of factors and interactions involved in forecasting the whole season performance of a maize crop affected by waterlogging. Therefore, this effort is a first attempt that requires additional refinements.

The availability of field data with seasonal information of crop growth and development associated with periods of limited soil aeration is a major limitation for future model improvements. Two areas of information are critically required: phenological changes and root growth. A more accurate register of phenological adjust the model equations. Information about short term root evolution during periods of waterlogging is also required. Converting root counts obtained with

minirhizotrons into root length densities requires additional review before a standard method can be proposed.

Bibliography

- Armstrong, W. 1979. Aeration in higher plants. Adv. Bot. Res. 7:225-331.
- Armstrong, W. and P. M. Beckett. 1987. Internal aeration and the development of stelar anoxia in submerged roots: a multishelled mathematical model combining axial diffusion of oxygen in the cortex with radial losses to the stele, the wall layers and the rhizosphere. New Phytol. 105:221-245.
- Armstrong, W. and P. M. Beckett. 1985. Root aeration in unsaturated soil: a multi-shelled mathematical model of oxygen diffusion and distribution with and without sectorial wet-soil blocking of the diffusion path. New Phytol. 100:293-311.
- Armstrong, W. and E. J. Wright. 1976. An electrical analogue to simulate the oxygen relations of roots in anaerobic media. Physiol. Plant. 36:383-387.
- Bland, W. L. and W. A. Dugas. 1988. Root length density from minirhizotron observations. Agron. J. 80:271-275.
- Chou, T. 1990. Modeling infiltration using time-to-ponding and a storm generator approach. PhD. diss. Michigan State University, East Lansing, Michigan.
- Dadoun, F. A. 1993. Modeling tillage effects on soil physical properties and maize (*Zea mays* L.) development and growth. PhD. diss. Michigan State University, East Lansing, Michigan.
- Drew, M. C., P. H. Saglio and A. Pradet. 1985. Larger adenylate energy charge and ATP/ADP ratios in aerenchymatous roots of *Zea mays* in anaerobic media as a consequence of improved internal oxygen transport. Planta 165:51-58.
- Gerwitz, A. and E. R. Page. 1974. An empirical model to describe plant root systems. J. Appl. Ecol. 11:773-787
- Hoogenboom, G. and M. G. Huck. 1986. ROOTSIMU v 4.0: A dynamic simulation of root growth, water uptake and biomass partitioning in a soil-plant-atmosphere continuum: uptake and documentation. Agron. and Soils Dept. Series 109. Auburn University, Auburn, AL.

- Jones, C. A. 1983. Effect of soil texture on critical bulk densities for root growth. Soil Sci. Soc. Am. J. 47:1208-1211.
- Jones, C. A., W. L. Bland, J. T. Ritchie and J. R. Williams. 1991. Simulation of root growth. p. 91-123. *In J. Hanks and J. T. Ritchie (Ed.) Modeling plant and soil systems. ASA, CSSA, SSSA, Madison, Wisconsin.*
- Jones, C. A. and J. R. Kiniry. 1986. CERES-Maize: a simulation model of maize growth and development. Texas A&M Univ. Press, College Station, Texas.
- Luxmoore, R.L. and L. H. Stolzy. 1987. Modeling belowground processes of roots, the rhizosphere and soil communities. p. 129-153. *In* K. Wisiol and J. D. Hesketh (Ed.) Plant growth modeling for resource management: Vol II. Quantifying Plant Processes. CRC Press, Boca Raton, Florida.
- Luxmoore, R. L., L. H. Stolzy and J. Letey. 1970. Oxygen diffusion in the soil-plant system I. A model. Agron. J. 62:317- 322.
- Melhuish, F. M. and A. R. Lang. 1968. Quantitative studies of roots in soil. I. Length and diameters of cotton roots in a clay loam soil by analysis of surface-ground blocks of resin- impregnated soil. Soil Sci. 106(1):16-22.
- Ritchie, S. W. and J. J. Hanway. 1984. How a corn plant develops. Iowa State University, Coop. Ext. Serv. Spec. Rep. 48.
- Thomson, C. J., W. Armstrong, I. Waters and H. Greenway. 1990. Aerenchyma formation and associated oxygen movement in seminal and nodal roots of wheat. Plant Cell Environ. 13(4):395-403.
- Upchurch, D. R. and J. T. Ritchie. 1983. Root observations using a video recording system in mini-rhizotrons. Agron. J. 75:1009- 1015.

CONCLUSIONS AND RECOMMENDATIONS

The objective of the present research was to study the main responses of field grown maize to soil submergence during the vegetative growth stage and to develop a forecasting tool to simulate such responses. The effect of timing and duration of flooding on above and below ground plant growth and the changes in phenology were investigated. CERES-Maize, linked into a generic cereal simulation model, was modified to simulate the results of waterlogging on crop growth and development.

Flooding the maize crop for at least four days during the vegetative growth stage produced major reductions in plant growth and yields and delayed plant development especially when the flooding occurred early in the season. Evaluations of photosynthetic assimilation and stomatal conductance suggested long lasting effects on plant physiology.

The foliar surface was consistently reduced by the flooding treatments but the timing of flooding determined the main physiological process disturbed. The expansion growth was more sensitive early in the season, whereas later in the season plants increased leaf senescence in response to soil submergence. On

the other hand, aboveground biomass was not affected during the flooding, suggesting a repressed transport of assimilates that may be due to impaired phloem unloading.

Yields were reduced by half regardless of timing or duration of flooding. Yield reductions early in the season may have been caused by smaller leaf area and delayed silk emergence. Plants flooded later in the season endured soil submergence when the period of rapid nutrient accumulation was about to start which may have impaired plant nitrogen nutrition associated with limited soil fertilization.

Root growth, root distribution and the relation with aboveground organs were altered by flooding during the vegetative growth stage. Timing of flooding determined plant responses. Plants flooded earlier immediately reduced root numbers and exhibited a fast regrowth after drainage. Root growth responses on plants flooded later depended on the duration of the submergence. Plants flooded four days later in the season recovered the root numbers after drainage. Plants flooded eight days maintained low number of roots for the remainder of the season, suggesting the presence of a new adventitious, little branched, root system in these plants. The relations of root growth with leaf area growth suggested that the sink strength of maize root systems may be enhanced after an early flooding. A late vegetative flooding would have a minor effect on the sink strength of roots for photosynthates unless soil submergence lasts long enough to impair the recovery of sink strength after drainage.

The modified model described herein provides an alternative for simulating maize growth and development as affected by soil submergence, although additional adjustments are needed, especially related with the phenology model. Testing the model under different environmental conditions, including well aerated and poor aerated soils will provide additional information about required changes and adjustments. Critically needed are field data on crop phenology and root growth associated with waterlogging. The conversion of root counts obtained with minirhizotron tubes into root length densities seems to require additional attention.

In this study, timing of flooding consistently had a main effect in modulating crop responses. However, only soil submergence during the vegetative growth stage was explored. It remains unclear from literature the impact that flooding during the reproductive phase may have on crop growth and yields.

The appropriate assessment of the level of accuracy associated with the technique used to evaluate morphological and physiological crop parameters is important to assist in the interpretation of field results. In this experiment for instance, leaf area was accurately evaluated whereas root counts provided an uncertain estimation on total root length. Consequently, the total length of roots reported have a relative meaning for comparison among treatments. On the other hand, rates of leaf expansion or leaf senescence measured provided a clear picture of the physiological process being disturbed by flooding.

Appendix 1: Modified subroutines

```
C
      CERES GENERIC NITROGEN MODEL
      This is an effort to combine all the models into one generic
C
C
      model. All routines are generally the same except for some crop
C
      specific ones (nfact, menu2, grosub).
C
C
      CERES MAIZE MODEL -
C
      CERES WHEAT MODEL -
C
      CERES SORGHUM MODEL
C
      CERES PEARL MILLET MODEL
C
      CERES BARLEY MODEL
      CERES CEREAL GENERIC MODEL DEVELOPED BY SINGH, GODWIN AND HUMPRIES -IFDC
C
      NITROGEN ROUTINES DEVELOPED BY GODWIN, JONES, ET AL
SDEBUG
      Include 'gen1.blk'
      Include 'gen2.blk'
      Include 'gen3.blk'
      Include 'gen4.blk'
      Include 'Ntrc1.Blk'
      Include 'Ntrc2.Blk'
      Include 'comibs.blk'
      Include 'predob.blk'
      Include 'Nmove.Blk'
      Include 'Enviro.Blk'
      Include 'soilox.blk'
      Include 'nwatbal.blk'
      logical iechon, FEXIST, Lrun, Lbegin, OUTSOPEN, FCROP
      Dimension Store(12,50)
      character*1 iehvc
      character*2 Cropa(6)
      character*12 FFile1, FileC, FileD
      character*12 DRAINFILE, WTFILE, CALCEVFILE
      CHARACTER*1 RESP2
                                                                         ! AG
      INTEGER ISWAT, DECTRT, UNTRT, DECEXP, UNEXP
      Data Cropa/'MZ','WH','SG','ML','BA','FA'/
      OPEN (UNIT=77, FILE='NBAL.OUT', STATUS='UNKNOWN')
10
      ioutpt=.true.
      Lbegin=.false.
      OUTSOPEN=. FALSE.
      NSENS = 0
      NREP = 0
      NOUTO = 40
      NOUT1 = 41
      NOUT2 = 42
      NOUT3 = 43
      NOUT4 = 44
      Nout5 = 45
      KOUTWA = 1
      KOUTGR = 1
      Koutnu = 1
      POND = 0.0
                                                                         IAG
      PONDMAX = 10.0
                                                                         ! AG
C
      DRAINFILE = 'OUT7.MZ'
      CALCEVFILE = 'OUT6.MZ'
C
      INQUIRE(FILE='CROP.DAT', EXIST=FCROP)
      IF(FCROP)OPEN(UNIT=2, FILE='CROP.DAT', STATUS='OLD')
      INQUIRE(FILE='BATCH.$$$',EXIST=FEXIST)
      IF(FEXIST) OPEN(5,FILE='BATCH.$$$',STATUS='OLD')
C
      OPEN (UNIT = NOUTO, FILE = 'SIM.DIR', STATUS='UNKNOWN')
      Call Clear
Write(*,100)
format(///,20x,'Welcome to the C E R E S Model Version 1.99'
     1,//,20x,'Incorporates new menu structure, includes
     2',/,20x,'soil stresses (water, nitrogen and oxygen),
     31,/,20x,'supports multi-year and multi-treatment
```

```
41,/,20x,'simulation and also provides output support
     5',/,20x,'
                     for IBSNAT graphics and DSSAT'
     6.//////, Press Enter to Continue')
                     Read(5,'(a1)')a
      IF(FCROP) THEN
         READ(2,*) NCROP
         If(ncrop.eq.2.) then
           Ichoice=5
         Elseif(ncrop.eq.5) then
           Ichoice=1
         Elseif(ncrop.eq.6) then
           Ichoice=4
         Elseif(ncrop.eq.10) then
           Ichoice=3
         Elseif(ncrop.eq.12) then
           Ichoice=2
         Else
           Ichoice=7
         Endif
      ENDIF
      IF(.NOT.FCROP.OR.ICHOICE.EQ.7) THEN
110
      call clear
        Write(*,115)
115
        Format(///, 1
                      Which of the following models do you want to run:
     11,//
     2,20x, 1.
                        Maize ',/
                        Wheat ','
Sorghum ','
Millet ','
     3,20x, 2.
4,20x, 3.
     5,20x, 4.
     6,20x, 5.
                        Barley ',/
                        Fallow ',/////,
     7,20x, 6.
     8' Please enter your choice:')
        Read(5,'(12)') Ichoice
        Call Selpro(1,6,1choice, Index, Ierr)
        IF(Index.eq.2) goto 110
      ENDIF
      Crop=Crope(Ichoice)
C
C
      simulation loop
C
      Runall=.false.
200
      Imulti=.false.
      Runend=.false.
      Imoutf=1
      Iphout=.true.
      Numy=0
      Nrep=Nrep+1
300
      Iret=0
      Call Clear
      CALL IPEXP
      FileC=FileB
      Write(FileC(12:12),301)
301 Format('C')
      FileD=FileB
      Write(FileD(12:12),302)
302
      Format('D')
      FFile1=File1
      If(Runend) then
        Nrep=Nrep-1
        go to 3500
      Endif
      Change=.false.
      If(nyr.gt.1)Then
           Imulti=.true.
           Write(*,400)nyr
400
           Format(' Multiple Year Run ', i5,' Years')
      Endif
      If(.not.Imulti)Call Clear
      if(runall)then
```

```
nsens=0
             go to 1100
       endif
          file1t=ffile1
500
       WRITE (*,600) POND, PONDMAX
      FORMAT(/,2X, 'RUN-TIME OPTIONS: ',

1 //2X,'0) RUN SIMULATION ',

2 /2X,'1) SELECT SIMULATION CUTPUT FREQUENCY'

3 /2x,'2) MODIFY SELECTED MODEL VARIABLES INTERACTIVELY.'
600
              //7X, 49(1H*) ,
               /7X, 'POND IS INITIALIZED AT ',F3.1,' AND PONDMAX AT ',F4.1,
                   ' cm',/7X, 49(1H*) )
                                                                                              ! AG
       if(Imulti)write(*,700)
700
       Format( 2X, '3) RUN MULTI-YEAR SIMULATION')
       Write(*,800)
       Format(//2X,'<=== CHOICE? [ DEFAULT = 0 ]')
read (5,900,iostat=ierr) NSENS
800
900
       FORMAT(12)
       Call Selpro(0,3,Nsens,Index,Ierr)
       IF(Index.eq.2) goto 500
       If(Nsens.eq.O.and.Imulti)Then
             Imulti=.false.
             Write(*,1000)
Format(' Single season simulation only')
1000
       Endif
       If(Nsens.eq.3)call ipmulti
       IF (NSENS .EQ. 1) then
             CALL IPFREQ
             GO TO 500
       Endif
1100
       If(.not.Change)CALL IPTRT
       If(.not.Change)CALL IPSWIN
       If(Isuco2.eq.1) goto 1111
       If(.not.Change) then
         TCHANGE=0.
         Tchmin=0.
         Rchange=1.
         Schange=1.
       Endif
1111 If(Nsens.EQ.2) Then
             Call MENU(iret)
             Change=.true.
             Ffile1=File1
             If(Imulti)go to 500
       Endif
           if(change)ffile1=file1t
       If(iret.EQ.1) then
             Close(11)
             Go to 300
       Endif
       CALL IPWTH
       If(Runall)then
             Titler=' '
             WRITE (*,1200)
1200
             FORMAT(/,T21, '<=== ENTER UP TO HERE RUN IDENTIFIER. '.
      1'<cr> FOR NONE.')
             read (5,1300) TITLER FORMAT(A20)
1300
       Endif
       IF (TITLER.EQ.' ')
      1 TITLER=TITLET
       ifirst=1
C
        IF(Nrep.gt.1) Goto 1500
C
       Open files to direct drain outputs from watbal
       and read water table depth:
```

```
DECTRT = INT(NTRT/10) + 48
      UNTRT = NTRT - INT(NTRT/10)+10 + 48
      DECEXP = INT(NFEXP/10) + 48
      UNEXP = NFEXP - INT(NFEXP/10)^{+}10 + 48
      WTFILE = 'WT'//CHAR(DECEXP)//CHAR(UMEXP)//CHAR(DECTRT)//
                 CHAR(UNTRT)//'.MZO'
C
      OPEN (380, FILE=DRAINFILE, STATUS='UNKNOWN')
                                                                           IAG
      OPEN (410, FILE=WTFILE, STATUS='UNKNOWN')
                                                                           IAG
      IF(Nrep.gt.1) Goto 1500
C
      Select water table switch:
                                                                           IAG .
      ISWIT = 0
                                                                           IAG
      WRITE(*,'(A,/,2(28x,A,/))')' ENTER WATER TABLE SWITCH: 0 = OFF',
     1 '1 = WT W/O CONTROL', '2 = CONTROLLED WT'
     IAG
      READ (*,'(11)' ) ISWAT
                                                                           ! AG
C
    Initialize DEPWT to depth of soil profile
      CUMDEP = 0.
DO L=1, NLAYR
         CUMDEP=CUMDEP+DLAYR(L)
      ENDDO
      DEPWT=CUMDEP
C
      WRITE (380,1400) NREP, TITLER
C
      Ask to write Water Table results to a file.
      IF (ISWAT.GE.1) THEN
          RESP2 = 'N'
                                                                              IAG
         PRINT*
                                                                               ! AG
         WRITE(*,'(A \)')' WANT TO WRITE DAILY WATER TABLE RESULTS TO A
     1 FILE? (Y/N) '
          READ (*,'(A1)') RESP2
                                                                              ! AG
          IF (RESP2.EQ.'Y'.OR.RESP2.EQ.'Y') THEN
                                                                              ! AG
            OPEN (370, FILE=CALCEVFILE, STATUS='UNKNOWN')
                                                                              LAG
            WRITE (370,1400) NREP, TITLER
          ENDIF
                                                                              ! AG
      END I F
 1400 FORMAT (1X, 'RUN ',12,8X,A20)
      OPEN (UNIT=HOUT1, FILE=OUT1, STATUS='UNKNOWN')
      OPEN (UNIT=NOUT2, FILE=OUT2, STATUS='UNKNOWN')
      OPEN (UNIT=NOUT3, FILE=OUT3, STATUS='UNKNOWN')
      OPEN (UNIT=NOUT4, FILE=OUT4, STATUS='UNKNOWN')
      IF(OUTS.NE.
                         ') then
       OPEN (UNIT=NOUTS, FILE=OUTS, STATUS='UNKNOWN', RECL=270)
       OUTSOPEN=.TRUE.
      ENDIF
      WRITE (NOUTO, 1600) OUT1, OUT2, OUT3, OUT4, OUT5
1500 IF(.NOT.OUT5OPEN.AND.OUT5.NE.' ') OPEN(UNIT=NOUT5,
     1 FILE=OUT5, STATUS='UNKNOWN', RECL=270)
      Inquire(File=FileC,Exist=Fexist)
      If(.not.Fexist) FileC='
      Inquire(File=FileD,Exist=Fexist)
      If(.not.Fexist) FileD='
      WRITE (NOUTO, 1700) TITLER, FILEB, FILEC, FILED
1600 FORMAT(1X,4(A7,1,1),A7)
1700
      FORMAT(1X,A20,21X,A12,1X,A12,1X,A12)
       iechon=.true.
       lrun=runall
      ihvon=.false.
      If(Lrun) invon=.true.
      If(Imulti)then
           If(numy.ne.0)iechon=.false.
            ihvon=.false.
            lrun=.true.
      endif
      if(.not.lrun)then
       ihvon=.true.
C
       else
           write(*,1800).
```

```
format(' Do you want post harvest comparison with observed da
     1ta' ,/,' displayed on the screen (Y/N) ? ')
           read(5,1900) iehvc
1900
           format(a)
           if(iehvc.eq.'Y'.or.iehvc.eq.'y')ihvon=.true.
      endif
2000 READ (11,4200,END=2500) IYR,DOY,SOLRAD,TEMPHX,TEMPHN,RAIN
      If (solrad.le.0.0.or.rain.lt.0.0.or.tempmx.eq.-99.0.or.tempmn.
     1eq.-99.) write (*,2100)FFILE1,IYR,DOY,SOLRAD,TEMPMX,TEMPMN,RAIN
2100 Format(2x, Please correct your weather file - ',A12,'.',
     2/,2x,'Missing solar radiation, temperature or rainfall data.'
     3//,2X, 'Year Day Solar Rad. Max. Temp. Min. Temp. Rain',
     4/,3x,12,4x,13,6x,f5.2,2(8x,f5.1),4x,f5.1,
     5//,2x,' <Ctrl> <Break> to change missing values. ')
      If(DOY.NE.Isim) Goto 2000
      Lbegin=.true.
      TEMPMX=TEMPMX+TCHANGE
      TEMPMN=TEMPMN+TCHmin
      SOLRAD=SOLRAD*Schange
      RAIN=RAIN*Rchange
c**** zero out accumulators for multi-year run
      If(imulti)then
           igsl=0
           yield=0.0
           biomas=0.0
           abioms=0.0
           garain=0.0
           train=0.0
           tlch=0.0
           tnox=0.0
           If(numy.ne.0)then
              cell reinit
              nrep=nrep+1
           Endif
      Endif
      CALL PROGRI
      ifirst=2
      CALL SOILTHI
      IF (ISWSWB.NE.0) CALL SOILRI
      IF (ISWNIT.NE.0) CALL SOILNI
C
       IF (ISWNIT.NE.O) CALL OMINIT(CEC)
      IF (ISWNIT.NE.O) CALL NBAL(1)
      If(Doy.EQ.Isim) Backspace 11
      if(numy.eq.0) then
       call echo(iechon)
       nline=0
       if(iphout) write(*,2001)
      Endif
2001
      FORMAT (/,15x,'SIMULATION HAS BEGUN....PLEASE WAIT.'/
     1 10X, 'DON''T TOUCH THE TERMINAL UNTIL IT PROMPTS YOU.')
      if(numy.eq.0.and..not.iphout)then
           Call Clear
           IF(nline.eq.0) Write(*,2950)
           Write(nout1,2950)
      Endif
2400 YTEMPHX = TEMPHX
      READ (11,4200,END=2500) IYR,DOY,SOLRAD,TEMPHOK,TEMPHN,RAIN
      If (solrad.le.0.0.or.rain.lt.0.0.or.tempmx.eq.-99.0.or.tempmn.
     1eq.-99.) write (*,2100)FFILE1,IYR,DOY,SOLRAD,TEMPMX,TEMPMN,RAIN
      TEMPMX=TEMPMX+TCHANGE
      TEMPMN=TEMPMN+TCHmin
      SOLRAD=SOLRAD*Schange
      RAIN=RAIN*Rchange
      Tempm=(Tempmx+Tempmn)*0.5
       if(iswnit.ne.0)
      Call Solt(YTEMPMX)
      IF (DOYX.EQ.367) CALL CALDAT
      IF (ISWSWB.NE.O) CALL WATBAL (ISWWT, RESP2)
       IF (ISMNIT.NE.0) CALL OMCYCLE(TCO2)
```

```
IF (ISWNIT.NE.O) CALL NTRANS
      IF (ISTAGE.LT.6.AND.CROP.EQ.'MZ') CALL GROSUB(CUMDELAY)
      IF (ISTAGE.LT.6.AND.CROP.EQ.'WH') CALL WGROSUB
      IF (ISTAGE.LT.6.AND.CROP.EQ.'SG') CALL SGROSUB
      IF (ISTAGE.LT.6.AND.CROP.EQ.'ML') CALL MGROSUB
      IF (ISTAGE.LT.6.AND.CROP.EQ.'BA') CALL WGROSUB
      IF(DOY.EQ.ISOW.OR.ISTAGE.NE.7)CALL PHENOL(iret,CUMDELAY)
      IF(Imulti) then
        Train=Train+Rain
         If(Istage.lt.6)then
            Igsl=Igsl+1
            Garain=Garain+Rain
        Endif
      Endif
      If(iret.eq.1)go to 2800
      IF (ISWNIT.NE.O) CALL NURITE
      CALL WRITE
      GO TO 2400
2500 Read(FFile1(11:12),2600) Kyr
      Kyr=Kyr+1
       If(Kyr.gt.99) Kyr=10
2600 Format(12.2)
      Write(FFile1(11:12),2600) Kyr
      Inquire(File=FFile1,Exist=Fexist)
       If(Fexist) then
            Open(11,File=FFile1)
            READ(11,2700) LAT,XLONG,PARFAC,PARDAT FORMAT(4X,2(1X,F6.2),2(1X,F5.2))
2700
            IF(LBEGIN)Goto 2400
            GOTO 2000
      Endif.
C
      WRITE (nout1,4300)
      write(*,4300)
2800 Lbegin=.false.
       IF (ISWNIT.NE.O) CALL NBAL(3)
      If(imulti)then
            numy=numy+1
            nline=nline+1
            Call Phasei(CUMDELAY)
            Iret=0
            Store(1, numy)=yield
            Store(2, numy)=biomas*10.
            Store(3, numy)=abioms*10.
            Store(4, numy)=totnup
            Store(5, numy)=Tlch+Tnox
            Store(6, numy)=Igsl
            Store(7, numy)=gsrain
            STore(8, numy)=Si1(1)
            Store(9, numy)=Si1(5)
            Store(10, numy)=Si3(1)
            Store(11, numy)=Si3(5)
            Store(12, numy)=numy
            If(nline.ge.22) nline=0
            If(.not.iphout) then
             If(nline.eq.0) write(*,2950)
             Write(*,3000)numy,(Store(j,numy),j=1,12)
            Endif
            If(Float(Ny/15).eq.15.and..not.iphout)Then
                 Call Clear
                 Write(*,3300)
Read(5,'(a1)')a
            Endif
            if(numy.eq.nyr)go to 3100
            go to 2000
3100
            Call Psort(Store, 12, Numy)
            Call Clear
            Write(*,3200)
3200
            Format(' Simulation Outputs sorted according to yield')
```

```
Write(nout1,3200)
           Write(*,2950)
           Write(Nout1,2950)
           Do 3400 ny=1, numy
                 Write(*,3000)ny,(store(j,ny),j=1,12)
                 If(Float(Ny/15).eq.15)Then
                      Call Clear
                      Write(*,2950)
                      Write(*,3300)
Format(' Press Enter to Continue')
3300
                      Read(5,'(a1)')a
                 Endif
                 Write(Nout1,3000)ny,(store(j,ny),j=1,12)
3400
            Continue
           Write(*,3300)
Read(5,'(a1)')a
      Endif
3500 If(.Not.Runall)Then
         If(.NOT.FCROP) THEN
           Write(*,3600)
            format(' Simulation complete for this treatment.',/,
3600
     1 ' Do you want to :',/,
     2 ' 1 Return to Experiment and Treatment Menu',/,
     3 1 2 Display Detailed Outputs on Screen',/,
     4 ' 3 Choose another crop',/,
     Š ' 4 Quit',//,
     6 1
            Input a number (default is 1)')
         Else
           Write(*,3650)
3650
           format(' Simulation complete for this treatment.',/,
     1 ' Do you want to :',/,
2 ' 1 Return to Experiment and Treatment Menu',/,
     3 ' 2 Display Detailed Outputs on Screen',/,
     5 ' 3 Quit',//,
     6 1
             Input a number (default is 1)')
         Endif
            read(5,'(i2)',iostat=ierr) igo
           Call selpro(0,4, igo, index, ierr)
            Goto (3700,3800), index
           If(igo.eq.0) igo=1
3700
            IF(FCROP.AND.IGO.EQ.3) IGO=4
            Goto (3800,3900,4050,4100),igo
      Endif
3800
      CLOSE(11)
      go to 200
3900
      If(Imulti)Then
           Write(*,4000)
Format(' Option not available under Multiple Year Setting')
4000
           Go to 3500
      Else
           If(Runend) then
               Write (*,4400)
               Go to 3500
            Endif
           Call disout
           Goto 3500
      Endif
4050 Close(11)
      Goto 10
4100 ENDFILE(NOUTO)
      ENDFILE(NOUT1)
      write (nout2,*)
      ENDFILE(NOUT2)
      ENDFILE(NOUT3)
      ENDFILE(NOUT4)
      If(OUT5.NE.' ') ENDFILE(NOUT5)
      CLOSE(NOUTO)
      CLOSE(NOUT1)
      CLOSE(NOUT2)
```

```
CLOSE(NOUT3)
       CLOSE(NOUT4)
       IF (OUT5.NE.' ') CLOSE(NOUT5)
       stop
2950 Format(2x,'#',3x,'GRAIN',2x,'MATURE',2x,'ANTHES',5x,'N'
1 ,5x,'N',2x,'E-M',3x,'E-M',2(3x,'WAT'),2(3x,'NIT'),1x,'YR'
2 ,/,6X,'YIELD',2(1X,'BIOMASS'),1X,'UPTAKE',2X,'LOSS',1X,
3 'DAYS',2X,'RAIN',2(1X,'STRS1',1x,'STRS5'))
3000 Format(1x,12,3f8.0,2f6.0,f5.0,f6.0,4f6.1,1x,f3.0)
4200 FORMAT (5x,12,1x,13,f6.2,2(1x,f5.1),1x,f5.1,1x,f6.2)
4300 FORMAT (6X, 'END OF WEATHER DATA')
4400
       Format(' Option not available under Multi-Treatment Setting')
       END
       SUBROUTINE WATBAL (ISWAT, RESP2)
C
         Modified by:
C
                            J. Lizaso
C
                            September, 1992
C
$DEBUG
                                                                                   IAG
       Include 'GEN1.BLK'
       Include 'GEN2.BLK'
       Include 'GEN3.BLK'
       Include 'GEN4.BLK'
       Include 'NMOVE.BLK'
       Include 'NTRC1.BLK'
       Include 'NTRC2.BLK'
       Include 'COMIBS.BLK'
       Include 'ENVIRO.BLK'
       INCLUDE 'NWATBAL.BLK'
       INCLUDE 'SOILOX.BLK'
C
       REAL FLOWN(21), LEFTWAT, OVERFLOW, PINF, PONDY, SNOWLT,
             TRATIO, TSWY, WINF
       INTEGER ISMAT, EVFLAG, RDOY, RWTLAYR CHARACTER*(*) RESP2
       LOGICAL AIRTEST, WITEST
C
       Initialize variables
       SUBIRR=0.
       DRANGE=0.
       DEPIR=0.
       DRAIN = 0.0
       EO = 0.0
       EP = 0.0
       ES = 0.0
       ET = 0.0
       EOS= 0.0 .
       EOP= 0.0
       EVFLAG = 0
       ICSDUR=ICSDUR+1
       IOFF=0.
       PINF = 0.0
       PONDY = POND
                                    ! for error checking only
                                                                                    IAG
       PRECIP=0.
        RAIN = RAIN / 10.0
                                    I convert to cm
       RUNOFF = 0.0
       WINF = 0.0
       WTLAYR = NLAYR + 1 !default value
       WTTEST = .FALSE.
C
       Yesterday's water will be used for error checking(in cm )
                                                                                    IAG
        tswy = 0.0
        do 101, L = 1, nlayr
            TSWY = TSWY + sw(l)*dlayr(l)
101
        continue
```

```
LEFTWAT = TSWY + POND
                                     ! Total leftover water from yesterday !AG
      DO 602 L=1,NLAYR
          FLOWU(L)=0.
          WFPS(L)=0.
602
      CONTINUE
       IF (IIRR.EQ.2.OR.IIRR.EQ.3) CALL IRRIGE
      DEPIR = DEPIR / 10.0 ! convert to cm because irrigation is in mm
C
       Precipitation is rain plus irrigation:
       PRECIP=RAIN+DEPIR
       SWDEF=0.
C
       IF (TEMPHOX.LE.1..OR .SNOW.NE.O.) THEN
         CALL SNOWFALL (TEMPMX, PRECIP, RAIN, SNOWLT, SNOW)
       ENDIF
       TPRECP=PRECIP
C
       CALL CALEO
c
C
  If there has been any precip or if water remains in the pond
c call the ponding routine
       If(Pond.Gt.O.O.or.Precip.Gt.O.O)Then
           CALL PONDING (KSMACRO, KSMTRX, PINF, POND, PONDMAX, PRECIP.
                           RUNOFF, SAT, SW)
           Idrsw-.True.
      Endif
C
      Error checking in ponding:
C
                                                                                  IAG
       ERROR = PONDY + PRECIP - RUNOFF - PINF - POND
                                                                                  IAG
       IF (ERROR*ERROR . GT. 0.00001) then
                                                                                  IAG
          WRITE(*,1245) ERROR, DOY
      FORMAT (/, 15X, 1H<sub>F</sub>, 50(1H=), 1H<sub>1</sub> , /, 15X,

1 '| ERROR IN WATER BALANCE (PONDING)=',(F8.4),' DOY=',I3,'|

2 /,15X, 1H<sup>L</sup>, 50(1H=), 1H<sup>L</sup>)

ENDIF
                                                                                  IAG
1245
                                                                                  IAG
                                                                                 IAG
                                                                                  ! AG
                                                                                 LAG
C
       WINF = PINF
       CALL DRAINAGE(Dlayr, Dul, Sat, Sw, Flowd, Kamecro, Overflow,
                      Wtlayr, Wlayr, Winf, Idraw, RWTLAYR, WTTEST)
c If there has been overflow generated by backup add this to the pond
       Pond=Pond+Overflow
       If(Pond.gt.Pondmax)Then
          Runoff=Runoff+Pond-Pondmax
          Pond=Pondmax
       Endif
       Drain=Flowd(Nlayr)
       If(Iswwt.ge.1)Drain=Flowd(Wtlayr-1)
       IF (ISWNIT.NE.O) THEN
         CALL NFLUXD(Sat, Dul, Sw, Nlayr, Dlayr, Flowd, Swcon, SNo3, NNout)
       IF (ISWNIT.NE.O.AND.IUON) THEN
         CALL NFLUXD(Sat, Dul, Sw, Nlayr, Dlayr, Flowd, Swcon, Urea, NNout)
       ENDIF
                                                                                 IAG
C
        Error checking in drainage:
                                                                                 IAG
                                                                                 ! AG
       tsw = 0.0
                                                                                 IAG
      do 204, L = 1, nlayr
TSW = TSW + sw(L)*dlayr(L)
                                                                                 IAG
                                                                                 IAG
204
      continue
                                                                                 IAG
       ERROR = LEFTWAT + PRECIP - RUNOFF - ES - EP - POND - TSW - DRAIN
                                                                                IAG
C
       DRAIN is set to 0.0 if WT is on.
                                                                                 IAG
```

```
IAG
                                                                    IAG
1246
                                                                    IAG
                                                                    IAG
C
     CALL UPFLOW(Dlayr, Flowu, Sw, LL, SAT, Ad, EOS, Es, Nlayr, DOY, DUL)
C
     IF (ISWNIT.NE.O) THEN
       CALL NFLUXU (Nlayr, Sw. Dlayr, Sno3, Flowu, NNout)
     FMOIF
     IF (ISWNIT.NE.O.AND.IUON) THEN
       CALL NFLUXU (Niayr, Sw, Dlayr, Urea, Flowu, NNout)
     ENDIF
     CES=CES+ES
C
                                                                    IAG
      Error checking in UPFLOW:
                                                                    IAG
                                                                    ! AG
     tsw = 0.0
                                                                    IAG
     do 205, L = 1, nlayr
                                                                    IAG
         TSW = TSW + sw(L)*dlayr(L)
                                                                    IAG
205
     continue
                                                                    IAG
     IF (WTLAYR.GT.1) THEN I we dont want WTLAYR-1 to be 0
                                                                    IAG
        ERROR = LEFTWAT + PRECIP - RUNOFF - ES - EP - POND - TSW-DRAIN
                                                                    IAG
     IAG
                                                                    IAG
                                                                    IAG
1247
                                                                    ! AG
                                                                    IAG
                                                                    IAG
C
     IF (ISWNT.EQ.2) THEN
C
C
          If WT switch is 2, read depth of WT from input file
Č
        READ (410, '(14,13)') RDOY, RWTLAYR
        DO WHILE (.NOT. EOF(410) .AND. (RDOY .LT. DOY))
           READ (410, '(14,13)') RDOY, RWTLAYR
        END DO
        IF (EOF (410)) THEN
           WRITE(*,*) 'WARNING: Not found proper WTLYR in WATABLE file'
        EMDIF
     ENDIF
     IF (ISWAT.GE.1) THEN
C
C
C
                If WT switch is 1 or 2, call WT routine
Č
C
        CALL WATABLE (DEPWT, DL1, NLAYR, SAT, SW, WTLAYR, DLAYR,
                      SUBIRR, ISUNT)
     ENDIF
C
     IF (ISWWT.EQ.2) THEN
C
     If WT switch is 2 then:
C
                 * subirrigate when simulated WT is below read WT
                 * drain
C
                              when simulated WT is above read WT
        IF (RWTLAYR.LT.WTLAYR) THEN
   Simulated WT below read WT ----> subirrigate
           DO 1000 L = RWTLAYR, WTLAYR
```

SUBIRR = SUBIRR+(SAT(L)-SW(L))*DLAYR(L)

```
IF ((SAT(L)-SW(L)) .LT. 0.0) THEN
                  WRITE (*,*) 'Problem with WT in WATBAL(266)'
             ENDIF
             SW(L)=SAT(L)
1000
             CONTINUE
          ELSEIF (RWTLAYR.GT.WTLAYR) THEN
    Simulated WT above read WT ----> drain
             CALL DRAINAGE(Dlayr, Dul, Sat, Sw, Flowd, Kamecro, Overflow,
                             Wtlayr, Nlayr, Winf, Idrau, RWTLAYR, WTTEST)
             DRAIN = FLOWD(RWTLAYR-1)
          ENDIF
          WTLAYR = RWTLAYR
          IF (SUBIRR .GE. DRAIN) THEN
             SUBIRR = SUBIRR - DRAIN
             DRAIN = 0.0
             DRAIN = DRAIN - SUBIRR
             SUBIRR = 0.0
          ENDIF
      ENDIF
C
        DEPWT = DL1(WTLAYR)
   ** Write in 'OUT6' output file **
C
       IF ((RESP2.EQ.'Y'.OR.RESP2.EQ.'Y').AND.(ISWAT.GE.1) ) THEN
        WRITE(370, 1178) DOY, DEPHT, SUBIRR, DRAIN, POND, RUNOFF
FORMAT (/,'DOY ',13,7x,' DEPHT = ',F6.2,','SUBIRR = ',F5.2,
' DRAIN = ',F5.2,' POND = ',F5.2,' RUNOFF = ',F5.2)
      ENDIF
      Print out results for each layer:
                                                                                IAG
      IF (RESP2.EQ.'Y'.OR.RESP2.EQ.'Y') THEN
                                                                                IAG
          IF (ISWAT.EQ.0) THEN
                                                                                IAG
             WRITE (370, '(/,A, 13,A, F9.4,A, F9.4)' ) ' DOY = ', DOY,
     1' DEPWT = ',DEPWT
                                                                                IAG
          WRITE (370, 1210) DEPTH', FLOWD', FLOWU', SH(L)', SAT(L)'
          DO 1150 L = 2, NLAYR
WRITE(370, 1200) DL1(L), FLOWD(L), FLOWU(L), SW(L), SAT(L)
                                                                                IAG
1150
          CONTINUE
                                                                                IAG
1210
          FORMAT (A5,A9,1X,A9,4X,A6,3X,A8)
1200
          FORMAT (F4.0, 4(1X, F9.4))
      ENDIF
                                                                                IAG
C
              Calculate water deficit for automatic irrigation
      If(Iirr.eq.3)Then
          CALL WATDEF (ATHETA, CUMDEP, DLAYR, DSOIL, DUL, LL.
                        NLAYR, SW, SWDEF)
      Endif
      Add up PESW throughout the soil profile:
       PESW = 0.0
      DO 300, L = 1,NLAYR
          PESW = PESW + ((SW(L) - LL(L)) * DLAYR(L))
300
      CONTINUE
      IF (ISTAGE.GE.6) THEN ! if no plants, that is, no need for roots, uptake
        ET=ES
        CET=CET+ET
         CRAIN=CRAIN+PRECIP
      ELSE
```

```
If(ISWC02.EQ.1) then
             CALL ETRATIO (LAI, RLF, RLFC, Tempm, UAVG, TRATIO, CO2)
         Else
             Tratio=1.0
         Endif
2800
         Continue
         IF (GRORT.GT.O.O .OR. (CROP .EQ. 'MZ' .AND. ASD .GT. O.O) .OR.
             (CROP .EQ. 'MZ' .AMD. ASD2 .GT. 0.0)) THEN
             CALL ROOTGROW (CROP, CUMDEP, DEPMAX, DLAYR, DTT, DUL, ESW,
                             GRORT, ISLMIT, L1, LL, NLAYR, NO3, NH4, PHINT, PLANTS, RLV, RLDF, RNFAC, RTDEP, SW, SMDF, SMDF1, SMDF3, MR, BD, DEPWT, ISTAGE, LRTDEP,
     1
     2
     3
                              POND, SAT, utlayr, iswut)
             K = 1
             CUMDEP = DLAYR(K)
             DO WHILE (CUMDEP.LT.RTDEP)
                 K = K + 1
                 CUMDEP = CLIMDEP+ DLAYR(K)
             ENDDO
             LRTDEP = K
         ENDIF
         IF (CROP.EQ.'MZ') THEN
             AIRTEST = .FALSE.
             DO 2000, L = 1, LRTDEP
                  IF (WFPS(L).GT.CWFPS) THEN
                      AIRTEST = .TRUE.
                  ENDIF
2000
             CONTINUE
         ENDIF
C
С
                                Oxygen Stress Routine
C
         IF ((AIRTEST.OR.ASD.GT.O..OR.ASD2.GT.O.).AND.CROP.EQ.'MZ') THEN
            CALL OXSTRESS (LRTDEP, DEPWT)
         ENDIF
3300
         Continue
         CALL MUPTAKE (RMUCON, SW, LI, RIV, Dlayr, Eop, EP, Niayr, LAI, EO, ES,
                        TRATIO, POTRIUT)
C
         CALL WSTRSS (CSD1, CSD2, EP, EOP, POTRMUT, SMDF1, SMDF2)
С
         ET = ES + EP
3800
         CEP=CEP+EP
         CET=CET+ET
         CRAIN=CRAIN+PRECIP
      ENDIF ! end if plants exist in the field
c Calculate net water flow
      Do L=1,Nlayr
         Flown(L)=Flowd(L)-Flowu(L)
       Enddo
c Writing headings for output file
       IF (MOD(DOY, 21).EQ.2) THEN
                                                                                  IAG
        WRITE(380,3000) 'DOY', 'TSW ', 'TSW', 'ES', 'EP', 'PREC', 
'IRRI', 'SUBIR', 'DRAIN', 'POND', 'RUNOF', 
('SW(',J,')', J = 1, NLAYR)
      ENDIF
      Write daily output:
С
      IF (ISWNT.EQ.0) THEN
         WRITE (380, 3001) DOY, TSW, TSWY, ES, EP, PRECIP, DEPIR, ' N/A '
                             DRAIN, POND, RUNOFF, (SW(J), J = 1, NLAYR)
      ELSEIF (ISWIT.EQ.1) THEN
         WRITE (380, 3002) DOY, TSW,TSWY,ES,EP,PRECIP, DEPIR, ' N/A ',
                      \cdot N/A ', POND, RUNOFF, (SW(J), J = 1, NLAYR)
```

```
ELSE
         WRITE (380, 3003) DOY, TSW,TSWY,ES,EP,PRECIP, DEPIR, SUBIRR,
                              DRAIN, POND, RUNOFF, (SU(J), J = 1, NLAYR)
       ENDIF
3000 FORMAT (/,A4,10(1X, A7), 20(1X, A4, I2, A2), / )
3001 FORMAT (I4, 6(1X, F7.2),1X,A7,3(1X,F7.2),20(1X, F8.4))
3002 FORMAT (I4, 6(1X, F7.2),2(1X,A7),2(1X,F7.2),20(1X, F8.4))
3003 FORMAT (I4, 10(1X, F7.2),20(1X, F8.4))
       RETURN
       END
       SUBROUTINE DRAINAGE(Dlayr, Dul, Sat, Sw, Flowd, Ksmacro, Overflow
      1 , Wtlayr, Nlayr, Winf, Idraw, RWTLAYR, WTTEST)
C
c
           This subroutine drains water downward. The routine also
c
           accompdates the effects of a water table and a layer restricting
c
           drainage.
c
       Real Dlayr(*), Dul(*), Flcon, Sweq1, Sweq2, Flowd(0:*), Sat(*),
      & Sw(*), Swy, Winf, Excess, Overflow, Ksmacro(*), Hold, Wexcess(21)
       Integer
                    Nlayr, Wtlayr, RWTLAYR, WT
       Logical Idraw, WTTEST
       Idrsw=.False.
       FLCON = -0.2
       EXCESS = 0.0
       OVERFLOW = 0.0
C
     Zero out Excess array before calculating drainage
       IF(.NOT.WTTEST) THEN
            Flowd(0) = Winf
            Do L=1,nlayr
                Floud(L)=0.0
            Enddo
       ENDIF
       DO L=1,NLAYR
            WEXCESS(L)=0.0
       ENDDO
C
     Drainage Loop - down to water table layer WTLAYR (or RWTLAYR), if any:
       ISTART=1
       WT=WTLAYR
       IF (WTTEST) THEN
            ISTART=WTLAYR-1
                                    ! maybe =WTLAYR-1 ??????
           WT=RWTLAYR
       ENDIF
C
       Do L = ISTART, Amin1(WT-1, Wlayr)
            Swy = Sw(L)
c
     Only drain water above DUL
C
            If(Sw(L)+Flowd(L-1)/Dlayr(L).Gt.Dul(L)+0.001)Then
C
     Calculate equilibrium water content for both held water(SWEQ1)
c
     and drained water(SWEQ2) and potential flow from that layer
                Sweq1 = Dul(L) + (Sat(L)-Dul(L))*
      2
                 (1-Exp(Flowd(L-1)*flcon))
                Sweq2 = Swy - ((Swy - Dul(L))*0.5)
                Sw(L) = Amax1(Sweq1, Sweq2)
                IF (SW(L).GT.SAT(L)) THEN
                     WEXCESS(L)=SW(L)-SAT(L)
```

```
SU(L)=SAT(L)
               ENDIF
               Flowd(L) = (Swy+WEXCESS(L)+Flowd(L-1)/Dlayr(L)-Sw(L))
     £
                           *Dlayr(L)
               IF (FLOND(L).LT.O.) THEN
                  SW(L)=SW(L)+FLOWD(L)/DLAYR(L)
                  FLOWD(L)=0.
               ENDIF
               Idraw=.True.
    Check that KeMacro does not constrict potential flow - if so compute
C
C
    an excess which will be used to back water up
               IF (.NOT.WTTEST) THEN
                  IF (Flowd(L).gt.Ksmacro(L+1).or.L.eq.wtlayr-1) Then
                    Excess=Floud(L)-Ksmacro(L+1)
                     Flowd(L)=Ksmacro(L+1)
    If necessary back water up from Excess - loop starts where we are at
C
    and runs back to surface - if there is still excess this is put into
    the pond. Excess must be an array since there may be more than one
C
    flow constriction point in the profile
                    DO WHILE ((K.GT.0).AND.(EXCESS.GT.0.0))
                        Idraws.True.
                        Hold=(Sat(K)-Sw(K))*Dlayr(K)
                        If(Excess.lt.Hold)Then
                           Sw(K)=Sw(K)+Excess/Dlayr(K)
                           Excess=0.0
                        Else
                           Sw(K)=Sat(K)
                           Excess=Excess-Hold
                        Endif
                        K = K - 1
                     ENDDO
                  Endif
               ENDIF
    When a low KsMacro occurs it will redirect flow upward from
    the layer where the restriction occurs - it is correct that
    FLOWD(L) should be negative then - but it is doubtful these
    circumstances would generate mass flow of nitrate - hence
C
C
    Flowd(L) is set to zero
               If (Flowd(L).lt.0.0) THEN
                  WRITE (*,*) 'FLOND<0. L, FLOND', L, FLOND(L)
                  Flowd(L)=0.0
               ENDIF
C
C
    If water content is less than DUL, no flows:
               SW(L)=SW(L)+FLOND(L-1)/DLAYR(L)
               Flowd(L)=0.0
          Endif
    Excess water from surface layer is redirected to the pond
c
      Overflow=overflow + Excess
      ENDDO ! End drainage loop for this layer--move one deeper
      WTTEST = .TRUE.
      Return
      End
```

```
SUBROUTINE UPFLOW(Dlayr, Flowu, Sw., LL, SAT, Ad, EOS, Es, Nlayr, DOY, DUL)
C
    Subroutine to simulate water redistribution in the profile
c
C
    following evaporation
c
    Compute Maximum water loss from top three layers as a function
C
    of their moisture contents
C
$DEBUG
      INTEGER DOY
      Real Ad(3), Dlayr(*), Dsh(3), Flowu(0:20), Sh(*), Ll(*), SAT(*),
           EOS, Es, Diff, DUL(*)
C
C
    FLOMU(L) is initialized at the begining of WATBAL
      Do L=1.3
         Ad(1)=(0.109+0.469*(LL(L)-0.35)**2) *LL(L)
      Enddo
      Dsw(1)=0.5*(0.5+EOS)*(Sw(1)-Ad(1))**1.4*Dlayr(1)
      IF(SW(1).GT.DUL(1)-0.02) DSW(1)=(SW(1)-0.02-AD(1))+0.80+DLAYR(1)
      Dsw(2)=0.075*(Sw(2)-Ad(2))**1.4*Dlayr(2)
      IF(SW(2).GT.DUL(2).0.02) DSW(2)=(SW(2).0.02-AD(2))*0.12*DLAYR(2)
      Dsw(3)=0.04*(Sw(3)-Ad(3))**1.4*Dlayr(3)
      IF(SW(3).GT.DUL(3)-0.02) DSW(3)=(SW(3)-0.02-AD(3))+0.032+DLAYR(3)
C
    Soil evaporation is the sum of these
C
      Es=Dsu(1)+Dsu(2)+Dsu(3)
c
    Ensure ES does not exceed EOS - if so scale back DSW
      If(Es.Gt.EOS)Then
        Do L=1.3
           Dsw(L)=Dsw(L)*EOS/Es
        Enddo
        FREFOS
      Endif
C
    Compute a temporary change in water content of layer 3
         Su(3)=Su(3)-Dsu(3)/Dlayr(3)
         Flowu(2)=0.0
C
    Calculate diffusivities and fluxes for layers 4 to Nlayr
c
C
      IF (SW(3).LT.DUL(3)) THEN
         Do L=3,Nlayr-1
             K=L-1
             M=L+1
             Diff=0.5*Exp(40.0*((Sw(M)-LL(M))+
                   (Sw(L)-Flowu(K)/Dlayr(L)-LL(L)))/2.0)
             If(Diff.Gt.50.0)Diff=50.0
             Flowu(L)=(Sw(M)-DUL(M)+Flowu(K)/Dlayr(L)-Sw(L)+DUL(L))*
                      Diff/((Dlayr(L)+Dlayr(M))/2.0)
             IF(FLOHU(L).LT.0.) FLOHU(L) = 0.
    Flowu(k) Moves water from L to L-1 , Flowu(L) from L+1 to L
             Sw(L)=Sw(L)-Flowu(K)/Dlayr(L)+Flowu(L)/Dlayr(L)
         Enddo
         Flowu(Nlayr)=0.0
         Sw(Nlayr)=Sw(Nlayr).Flowu(Nlayr-1)/Dlayr(Nlayr)
      ELSE
         DO L=3, NLAYR
            FLOWU(L)=0.
         ENDDO
      ENDIF
C
C
    Compute moisture content and Flows in top two layers
c
```

```
Flowu(2)=Dsw(3)
      Flowu(1)=Flowu(2)+Dsw(2)
      FLOWU(0)=FLOWU(1)+DSW(1)
      Sw(2)=Sw(2)-Dsw(2)/Dlayr(2)
      Sw(1)=Sw(1)-Dsw(1)/Dlayr(1)
   Some checking ....
     DO L=1,NLAYR-1
          IF(FLOWU(L).LT.O.) THEN
             WRITE (*,*) 'FLOWU <0.', DOY,FLOWU(L) FLOWU(L) = 0.
          ENDIF
          IF(SW(L).GT.SAT(L)) THEN
             WRITE (*,*) 'SW > SAT; SW, SAT: ',DOY,SW(L),SAT(L)
SW(L)=SAT(L)
          ENDIF
      ENDDO
      Return
      End
      SUBROUTINE NFLUXD(Sat, Dul, Sw. Nlayr, Dlayr, Flow, Sucon, Spec, NNout)
C
    Downward flow Leaching routine
C
c
                         D. Godwin
C
              by:
                         September, 1992
C
C
C
     modified by:
                         J. Lizaso
                         November, 1992
C
c
    Leaching subroutine - depends on Flow from water Balance subroutine
C
SDEBUG
C
        Real Sat(*),Dul(*),Sw(*),FLow(*),Spec(*),NNout(*),Swcon(*),
     & Dlayr(*), Outn, Egcoeff, Wool, Dmax, Fast, SLow, Voleq, Outn1, Outn2
c
    Spec(*) is soil nitrogen species - can be either Nitrate or urea
C
        Integer Nlayr,L
        Outn=0.0
        Eqcoeff=0.05
        Do L=1,Nlayr
            Spec(l)=Spec(l)+Outn
C
    If No flow bypass for this layer
C
C
            If(Flow(L).Gt.0.0)Then
c
c
    Calculate volume of water in layer and maximum drainage from this layer
c
              Wvol=Sw(l)*Dlayr(L)
              Dmax=(Sat(l)-Dul(l))*Swcon(l)
    If Flow is greater than drainage - partition it into slow and fast
C
              If(Flow(l).gt.Dmax)Then
                   Fast=Flow(L)-Dmax
                   Slow=Flow(L)-Fast
              Else
                   Fast=0.0
                   Slow=Flow(L)
              Endif
    Leach out nitrate with piston flow for slow drainage
c
              Outn1=Slow/Wvol*Spec(L)
c
```

```
C
    For fast drainage calculate the number of volume equivalents
    passing through the layer
C
C
             Voleq = 1.0
             if (fast.gt.0.) Voleq=Fast/Wvol
    Eqcoeff could be a soil property determining degree of equilibration
c
C
    of nitrate with fast moving water
C
             Outn2=Fast/(Fast+Wvol)*Voleq*Spec(L)*eqcoeff
c
C
    Move leachate from L - will be added to L+1 at top loop
C
             Outn=Outn1+Outn2
             Spec(l)=Spec(l)-Outn
           Else
              Outn=0.0
           Endif
           NNout(l)=Outn
       Enddo
       Return
       End
      SUBROUTINE WATABLE (DEPWT, DL1, NLAYR, SAT, SW, WTLAYR, DLAYR,
                          SUBIRR, ISWAT)
C
C
        Modified by:
                        J. Lizaso
C
                        September, 1992
C
$DEBUG
C
      REAL DEPUT, DL1(*), SAT(*), SW(*), DLAYR(*)
      INTEGER ISMAT, NLAYR, WILAYR
C
      IF ((SW(NLAYR) .LT. SAT(NLAYR)) .AND. (ISMIT .EQ. 2)) THEN
         SUBIRR = SUBIRR + (SAT(NLAYR)-SU(NLAYR)) * DLAYR(NLAYR)
      ENDIF
      DEPWT = DL1(NLAYR)
      SW(NLAYR) = SAT(NLAYR)
      K = NLAYR - 1
                        I a temporary layer counter
      DO WHILE ((ABS(SW(K)-SAT(K)).LT.0.00001).OR.
                (ABS(SW(K-1)-SAT(K-1)).LT.0.00001).AND.(K.GE.1))
         DEPWT = DL1(K)
         K = K - 1
      ENDDO
      WTLAYR = K + 1
      DO 755 L = WTLAYR, NLAYR
         SW(L) = SAT(L) ! saturate all layers below wt layer
755
      CONTINUE
      RETURN
      END
      SUBROUTINE ROOTGROW(CROP, CUMDEP, DEPMAX, DLAYR, DTT, DUL, ESW
                          GRORT, ISLNIT, L1, LL, NLAYR, NO3, NH4, PHINT,
     2
3
                          PLANTS, RLV, RLDF, RNFAC, RTDEP, SW, SWDF,
                          SWDF1, SWDF3, WR, BD, DEPWT, ISTAGE, LRTDEP,
                          POND, SAT, wtlayr, iswwt)
C
C
        Modified by:
                        J. Lizaso
C
                        August, 1992
C
SDEBUG
      INCLUDE 'SOILOX.BLK'
C
      REAL CUMDEP, DLAYR(*), DEPMAX, DTT, DUL(*), ESW(*), GRORT, LL(*),
```

```
1 PHINT, PLANTS, MO3(*), NH4(*), BD(*), TRLDF, RLDF(*), RNLF,
     2 RLNEW, RLV(*), RLVF, RNFAC, RTDEP, SW(*), SAT(*), SWDF, SWDF3,
     3 WR(*)
      INTEGER L1, ISWNIT, ISWAT, NLAYR
      CHARACTER CROP*(*)
C
    Critical CWFPS and Maximum XWFPS Water Filled Pore Space
C
C
      CWFPS = 0.45
      XWFPS = 0.93
C
      TRLDF = 0.
      CUMDEP = 0.
      SWDF3 = 0.0
      RNFAC = 1.0
      TRLVY = 0.
      TRLVLOSS = 0.
      DO L = 1, NLAYR
         RLVLOSS(L) = 0.
         TRLVY = TRLVY + RLV(L)
      END DO
C
      IF (Crop.Eq.'WH' .OR. Crop.Eq.'BA') RLNEW = GRORT*1.05*PLANTS
      IF (Crop.EQ.'SG') RLNEW = GRORT+1.00+PLANTS
      IF (Crop.EQ.'ML') RLNEW = GRORT+0.80+PLANTS
      IF (Crop.EQ.'MZ') THEN
         IF ((ISTAGE.LE.3) .AND. (XASD2.GT.2.0)) THEN
            IF (DAX .GT. 15) THEN
               RLNEW = GRORT*1.0*PLANTS
               RLNEW = GRORT*0.5*PLANTS
            ENDIF
         ELSE
            RLNEW = GRORT+0.70+PLANTS
         ENDIF
      ENDIF
C
      DO L = 1, NLAYR
         L1 = L
C
C
      Total porosity TPORE and water filled pore space WFPS
C
         TPORE(L) = 1.0 - (80(L)/2.65)
         WFPS(L) = SW(L)/TPORE(L)
         IF (WFPS(L) .GT. XWFPS) WFPS(L) = XWFPS
C
C
      Layer aeration factor LAF
C
         LAF(L) = (1. - WFPS(L))/(1. - CWFPS)
         IF (WFPS(L) .LE. CWFPS) LAF(L) = 1.
         IF (L .GT. 1) THEN
            IF (LAF(L - 1) . LE. (0.1/(1. - CWFPS))) LAF(L) = LAF(L - 1)
         END IF
C
         CUMDEP = CUMDEP + DLAYR(L)
         SWDF = 1.
         IF (SW(L) - LL(L) .LT. 0.25*ESW(L)) SWDF = 4.*(SW(L) - LL(L))
         /ESW(L)
         IF (SWDF .LT. 0.) SWDF = 0.
         IF (ISWNIT .NE. 0) THEN
            RNFAC = 1.0 - (1.17*EXP( - 0.15*(NO3(L) + NH4(L))))
            IF (CROP .EQ. 'WH' .OR. CROP .EQ. 'BA') THEN
               IF (RNFAC .LT. 0.01) RNFAC = 0.01
            ELSE
              IF (RNFAC .LT. 0.1) RNFAC = 0.1
            END IF
         END IF
C
```

```
RLDF(L) = AMIN1(SUDF, RNFAC, LAF(L))*WR(L)
         IF (CUMDEP .GE. RTDEP) GOTO 10
         SMDF3 = SMDF3 + (SW(L) - LL(L))/(DUL(L) - LL(L))*DLAYR(L)
         TRLDF = TRLDF + RLDF(L)
      END DO
      GOTO 20
10
      IF (CROP .EQ. 'WH' .OR. Crop .EQ. 'BA') THEN
         RTDEP = RTDEP + DTT+0.22*AMIN1((SMDF1*2.0), SMDF)*95./PHINT
         IF (ISTAGE .LE. 3 .OR. (ISTAGE .EQ. 4 .AMD. RTDEP .LT. 50.)
          .OR. (ISTAGE .EQ. 5 .AND. RTDEP .LT. 30.)) THEN
            IF (NOF .EQ. 0) THEN
               IF (XASD2 .GT. 2.0) THEN
                  RTDEP = RTDEP + DTT*0.22*AMIN1((SMDF1*2.0), SMDF, EXP
                   ( - ASD2*0.3))
     1
               ELSE
                  RTDEP = RTDEP + DTT*0.22*AMIN1((SNDF1*2.0), SNDF, LAF
     1
                   (L)*3.0)
               END IF
            END IF
            IF (RTDEP .GT. DEPHT .OR. SAT(L) - SH(L) .LT. 0.0001) THEN
               NDF = NDF + 1
            ELSE
               NDF = 0
            END IF
            IF (NOF .GT. 5) THEN
               IF (ISWAT .LT. 1) THEN
                  RTDEP = 0.
                  II = 1
                  DO WHILE (SAT(II) - SW(II) .LT. 0.0001 .AND. II .GT.
     1
                   1)
                     II = II - 1
                  END DO
                  DO I = 1, II
                     RTDEP = RTDEP + DLAYR(I)
                  END DO
                  RTDEP = RTDEP - DLAYR(II)/2.
               ELSE IF (WTLAYR .GE. 2) THEN
                  RTDEP = DEPWT - DLAYR(wtlayr - 1)/2.
               ELSE
                  RTDEP = DEPWT
               END IF
               ndf = 0
    See Thomson et al. (1990) and Drew et al. (1985)
    for references on depth of aerenchymatous roots
               IF (RTDEP .LT. 20. - POND) THEN
                  RTDEP = 20. - POND
                  NDF = 1
               END IF
               N = 1
               DEPCUM = DLAYR(N)
               DO WHILE (RTDEP .GT. DEPCUM)
                  N = N + 1
                  DEPCUM = DEPCUM + DLAYR(N)
               END DO
               LRTDEP = N
               L1 = N
            END IF
         END IF
         IF (ISTAGE .EQ. 4 .AND. RTDEP .GT. 50. .AND. NDF .GT. 0) THEN
            NDF = 0
            RTDEP = DEPWT
         END IF
      END IF
      IF (RTDEP .GT. DEPMAX) RTDEP = DEPMAX
      RLDF(L) = RLDF(L)*(1. - (CUMDEP - RTDEP)/DLAYR(L))
      TRLDF = TRLDF + RLDF(L)
      SWDF3 = SWDF3/CUMDEP
      IF (TRLDF .GE. RLNEW*0.00001) THEN
```

```
RNLF = RLNEW/TRLDF
         IF (CROP .EQ. 'WH' .OR. Crop .EQ. 'BA') CUMDEP = 0.
         DO L = 1, L1
            IF (CROP .EQ. 'WH' .OR. Crop .EQ. 'BA') THEN
               CUMDEP = CUMDEP + DLAYR(L)
               RLV(L) = RLV(L) + RLDF(L)*RNLF/DLAYR(L) - 0.01*RLV(L)
               IF (CUMDEP .GE. 115.) THEN
RLVF = 0.377 - 0.0015*CUMDEP
                   IF (Crop .EQ. 'BA') RLVF = 4.*10E-5*(CUMDEP - 220.)*
     1
                  IF (RLV(L) .GT. RLVF) RLV(L) = RLVF
               END IF
            ELSE
               IF (ISTAGE .LE. 2) THEN
                  RLVLOSS(L) = (1. - LAF(L))*0.075*ASD*RLV(L)
               ELSE IF (ISTAGE .EQ. 3) THEN
                  RLVLOSS(L) = (1. - LAF(L))*0.025*ASD*RLV(L)
               ELSE IF (XASD2 .LT. 2.0) THEN
                  RLVLOSS(L) = (1. - LAF(L))*0.01*TRLVY*RLV(L)
                  RLVLOSS(L) = (1. - LAF(L))*0.02*TRLVY*RLV(L)
               END IF
               IF (RLVLOSS(L) .GT. RLV(L)) RLVLOSS(L) = RLV(L)
               TRLVLOSS = TRLVLOSS + RLVLOSS(L)
               IF (ISTAGE.LE.3) THEN
                    RLV(L)=RLV(L)+RLDF(L)*RNLF/DLAYR(L)-0.005*RLV(L)-
     1
                             RLVLOSS(L)
                    RLV(L)=RLV(L)+RLDF(L)*RNLF/DLAYR(L)-0.05*RLV(L)-
     1
                             RLVLOSS(L)
               ENDIF
               IF (RLV(L) .GT. 5.0) RLV(L) = 5.0
            END IF
            IF (RLV(L) .LT. 0) RLV(L) = 0.001
         END DO
         DO l = l1 + 1, nlayr
            IF (RLV(L) .GT. 0.) THEN
RLVLOSS(L) = RLV(L)
               TRLVLOSS = TRLVLOSS + RLVLOSS(L)
               rlv(l) = 0.
            END IF
         END DO
      END IF
      RETURN
      END
      SUBROUTINE GROSUB (CUMDELAY)
        Modified by:
                         J.Lizaso
                         September, 1992
$DEBUG
      INCLUDE 'gen1.blk'
      INCLUDE 'gen2.blk'
      INCLUDE 'gen3.Blk'
      INCLUDE 'gen4.blk'
      INCLUDE 'Ntrc1.Blk'
      INCLUDE 'Ntrc2.BLK'
      INCLUDE 'Comibs.Blk'
      INCLUDE 'Enviro.Blk'
      INCLUDE 'Soilox.Blk'
      REAL LABIO, LFDELAY, NSINK, NPOOL1, NPOOL2, NPOOL, NSDR
      IF (ISWNIT .NE. 0 .AND. Istage .LT. 7) CALL NFACTO
      PAR = 0.5*SOLRAD
      tt = 0.92*exp( - 0.82356*ROWSPC)
      y1 = \exp(-0.65*lai)
```

C C

C Č

C

C

```
y2 = 0.7*exp( - tt*lai)
      PCARB = 4.5*per/plants*(1. - amax1(y1, y2))
  Adjusts photosynthesis rate for variable CO2
      IF (ISMCO2 .EQ. 1) PCARB = PCARB*PCO2
      PRFT = 1. - 0.0025*((0.25*TEMPHN + 0.75*TEMPHX) - 26.)**2
      IF (PRFT .LT. 0.) PRFT = 0.
      IF (XASD2 .GT. 4.0) THEN
         IF (XASD2.GT.XXASD2) THEN
            XXASD2=XASD2
         ELSEIF (ISTAGE .LE.3) THEN
            AAF = AAF - 0.095
            IF(AAF.LT.O.) AAF=O.
         ENDIF
         SADEF = EXP(-AAF * 0.15)
      ELSE IF(XASD2.LT.2.) THEN
         XXASD2=XASD2
         AAF = 4.0
         SADEF=1.0
      ELSE
         IF (XASD2.GT.XXASD2) THEN
            XXASD2=XASD2
            AAFF=XASD2
         ELSEIF (ISTAGE .LE. 3) THEN
            AAFF = AAFF-0.095
            IF (AAFF.LT.O.) AAFF=O.
         ENDIF
         SADEF = 1.36 - 0.18 * AAFF
      ENDIF
      CARBO = PCARB*AMIN1(PRFT, SWDF1, NDEF1, SADEF)
C
      IF (Dtt .LT. 0.) Dtt = 0.
C
      IF (ISTAGE .LE. 3 .AND. xn .LT. tlno) THEN
         LFDELAY = 1.
         IF (ASD .GT. 1.) THEN
            IF (XSTAGE .LE. 2.0) THEN
LFDELAY = EXP( - ASD*0.01)
            ELSE IF (ASD .GT. 2.0) THEN
               LFDELAY = EXP( - ASD*0.15)
            END IF
         END IF
C
         PC = 1.
         IF (CUMPH .LT. 5) PC = .66 + 0.068 + \text{CUMPH}
         TI = DTT/(38.9*PC)
         CUMPH = CUMPH + TI*LFDELAY
         CUMDELAY=CUMDELAY+DTT*(1.-LFDELAY)
         XN = CUMPH + 1.
         LN = XN
      END IF
      IF (ISTAGE .EQ. 2) THEN
         PLAG = 2.0*XN*XN*TI*amin1(ndef2, swdf2, EXP( - ASD
          *0.2))
         PLA = PLA + PLAG
         XLFWT = (PLA/267.)**1.25
         GROLF = XLFWT - LFWT + TLABIOL
         IF (GROLF .GE. CARBO*0.75) THEN
            GROLF = CARBO*0.75
            PLA = (LFWT - TLABIOL + GROLF) +0.8+267.
         END IF
         GRORT = CARBO - GROLF
         IF(ASD2.GT.1.0) THEN
            LABIO=GRORT*(1.-EXP(-ASD2*0.6))
            GRORT=GRORT-LABIO
            GROLF=GROLF+LABIO
            TLABIOL=TLABIOL+LABIO
C
             PLA = (LFWT + GROLF - TLABIOL)**0.8*267.
         LFWT = LFWT + GROLF
```

```
SLAN = SUMDTT*PLA/10000.
LFWT = LFWT - SLAN/600.
ELSE IF (ISTAGE .EQ. 3) THEN
    IF (XN .LT. 12.) THEN
       PLAG = 3.5*XN*XN*TI* AMIN1(SWDF2,NDEF2,EXP( - ASD
        *0.1))
       GROLF = 0.00116*PLAG*PLA**0.25
       GROSTM = GROLF*0.0182*(XN - XNTI)**2
   ELSE IF (XN .GE. TLNO - 3.) THEN
PLAG = 170.*3.5/((XN + 3. - TLNO)**0.5)*TI*
         AMIN1(SUDF2, NDEF2, EXP( - ASD+0.05))
       GROLF = 0.00116*PLAG*PLA**0.25
       GROSTM = 3.5*3.1*TI*AMIN1(SHDF2,NDEF1,EXP(-ASD*0.05))
   ELSE
       PLAG = 3.5*170.*TI*AMIN1(SHDF2,NDEF2,EXP(-ASD
        *0.1))
1
       GROLF = 0.00116*PLAG*PLA**0.25
       GROSTM = GROLF*0.0182*(XN - XNTI)**2
    END IF
    GRORT = CARBO - GROLF - GROSTM
    IF (GRORT.LT.0.10*CARBO) THEN
       IF (GROLF .GE. 0.0 .OR. GROSTM .GE. 0.) THEN
          GRF = CARBO*0.90/(GROSTM + GROLF)
          GRORT = CARBO+0.10
       ELSE
          GRF = 1.0
       END IF
       GROLF = GROLF*GRF
       GROSTM = GROSTM*GRF
    END IF
    PLA = (LFWT + GROLF)**0.8*267.
    IF( ASD2.GT.1.0) THEN
       LABIO=GRORT*(1.-EXP(-ASD2*0.6))
       GRORT=GRORT-LABIO
       GROSTM=GROSTM+LABIO
       TLABIOS=TLABIOS+LABIO
    ENDIF
    LFWT = LFWT + GROLF
    SLAN = PLA/1000.
    LFWT = LFWT - SLAN/600.
    STMUT = STMUT + GROSTM
 ELSE IF (ISTAGE .EQ. 4) THEN
    GROEAR = 0.22*DTT*amin1(ndef2, swdf2)
    GROSTM = GROEAR*0.40
    GRORT = CARBO - GROEAR - GROSTM
    IF (GRORT .LT. 0.08*CARBO) THEN
       IF (GROEAR .GT. 0.0 .OR. GROSTM .GE. 0.) THEN
          GRF = EARBO*0.92/(GROEAR + GROSTM)
          GRORT = CARBO*0.08
       ELSE
          GRF = 1.0
       END IF
       GROEAR = GROEAR*GRF
       GROSTM = GROSTM*GRF
    END IF
    SLAN=PLA*(0.05+(SUNDTT+CUMDELAY)/200.*0.05)
    LFWT = LFWT - SLAN/600.
    EARWT = EARWT + GROEAR
    STMUT = STMUT + GROSTM
    SUMP = SUMP + CARBO
    IDURP = IDURP + 1
 ELSE IF (ISTAGE .EQ. 5) THEN
    IF (PLANTS .EQ. 0.01) GOTO 40
    IF (CARBO .EQ. O.) GOTO 10
   SLAN = PLA*(0.1 + 0.50*((SUNDTT+CUMDELAY)/P5)**3)
   LFWT = LFWT*0.9990
   RGFILL = 0.0
   DO I = 1, 8
       TTMP = TEMPNN + TMFAC(I)*(TEMPNX - TEMPNN)
```

```
IF (TTMP .GT. 6.0) RGFILL = RGFILL + (1.0 - 0.0025*(TTMP -
     1
             26.)**2)/8.
         END DO
         GROGRN = RGFILL*GPP*G3*0.001*(0.45 + 0.55*sudf1)
         IF (RGFILL .GT. 0.1) GOTO 20
         EMAT = EMAT + 1
         IF (EMAT .EQ. 1) GOTO 30
10
         SUMDIT = P5
         IF (IPHOUT) WRITE (*, 5000) DOY
         IF (IPHOUT) WRITE (nout1, 5000) DOY
         EMAT = 0
20
30
         GRORT = 0.
         GROSTM = CARBO - GROGRN
         IF (GROSTM .LT. O.) THEN
            STMUT = STMUT + CARBO - GROGRN
            IF (STMUT .LE. SUMIN+1.07) THEN
                STHAT = STHAT + LFWT+0.0050
                IF (STMUT .LT. SUMIN) THEN
                   STMUT = SLMIN
                   GROGRN = CARBO
               END IF
            END IF
         ELSE
            STMUT = STMUT + GROSTM*0.50
            GRORT = GROSTM*0.50
         END IF
IF (ISWNIT .NE. 0) THEN C******** GRAIN N ALLOWED TO VARY BETWEEN .01 AND .018.
C************* HIGH TEMP., LOW SOIL WATER, AND HIGH N INCREASE GRAIN N SFAC = 1.125 - .125*sudf2
            TFAC = 0.69 + 0.0125*TEMPM
            GNP = (0.004 + 0.013*NFAC)*AMAX1(SFAC, TFAC)
            NSINK = GROGRN*GNP
            IF (MSINK .NE. O.O) THEN
               RMNC = 0.75*RCNP
                IF (RANC .LT. RMNC) RANC = RMNC
                VANC = STOVN/STOVUT
                IF (VANC .LT. VMNC) VANC = VMNC
                MPOOL1 = STOVWT+(VANC - VMNC)
                NPOOL2 = RTWT*(RANC - RMNC)
               xnf = 0.15 + 0.25*nfac
                tnlab = xnf*npool1
               rnlab = xnf*npool2
               npool = tnlab + rnlab
                IF (ICSDUR .EQ. 1) GPP = AMIN1(GPP*NDEF3, (NPOOL/(.062
                 *.0095)))
     1
               NSDR = NPOOL/NSINK
                IF (medr .LT. 1.0) meink = meink*medr
                IF (neink .GT. tnlab) THEN
                   STOWN = STOWN - tnlab
                   rnout = nsink - tnlab
                   rootn = rootn - rnout
                   RANC = ROOTN/RTWT
               ELSE
                   STOVN = STOVN - NSINK
                   VANC = STOVN/STOVUT
               END IF
            END IF
            GRAINN = GRAINN + NSINK
         END IF
         GRNWT = GRNWT + GROGRN
         EARWT = EARWT + GROGRN
         IF (STMUT .GT. SWMAX) STMUT = SWMAX
      ELSE IF (ISTAGE .EQ. 6) THEN
         GOTO 40
      ELSE
C
    Istage=1
```

```
PLAG = 2.0°XN°XN°TI°AMIN1(swdf2, EXP( - ASD°0.2))
IF (XN .LT. 4.) PLAG = 1.0°XN°TI°AMIN1(swdf2,
                                 EXP(-ASD*0.2))
         PLA = PLA + PLAG
         XLFWT = (PLA/250.)**1.25
         IF (XLFWT .LT. LFWT-TLABIOL) XLFWT = LFWT-TLABIOL
         GROLF = XLFWT - LFWT + TLABIOL
         GRORT = CARBO - GROLF
         IF (GRORT .LE. 0.25*CARBO) THEN
            GRORT = CARBO*0.25
            SEEDRY = SEEDRY + CARBO - GROLF - GRORT
             IF (SEEDRY .LE. O.) THEN
               SEEDRY = 0.
               GROLF = CARBO*0.75
               PLA = (LFWT - TLABIOL + GROLF)++0.8+267.
            END IF
         END IF
         IF (ASD2.GT.1.0) THEN
            LABIO=GRORT*(1.-EXP(-ASD2*0.6))
             GRORT=GRORT-LABIO
             GROLF=GROLF+LABIO
            TLABIOL=TLABIOL+LABIO
C
             PLA = (LFWT + GROLF - TLABIOL)**0.8*267.
         ENDIF
         LFWT = LFWT + GROLF
         IF (GROLF .GT. 0.) SLAN = SUMDTT*PLA/10000.
         LFWT = LFWT - SLAN/600.
      END IF
C End of IF according to ISTAGE
      IF (CARBO .EQ. 0.0) CARBO = 0.001
      PDWI = PCARB*(1.0 - GRORT/CARBO)
      PGRORT = PCARB*GRORT/CARBO
      SLFW = 0.95 + 0.05*SWDF1
      SLFN = 0.95 + 0.05*NDEF2
      IF (ISTAGE.EQ.4 .AND. XASD2.LT.6.0) SLFN = 0.98 + 0.02*NDEF2
      SLFA = 0.98 + 0.002*(10. - ASD)
      SLFC = 1.0
      IF (LAI .GT. 4.) SLFC = 1. - 0.008*(LAI - 4.)
      IF (TEMPM .LE. 6.0) SLFT = 1. - (6.0 - TEMPM)/6.0
      IF (TEMPMN .GT. 0.0) THEN
         ICOLD = 0
      ELSE
         SLFT = 0.0
         ICOLD = ICOLD + 1
      END IF
      IF (SLFT .LT. 0.) SLFT = 0.
      PLAS = (PLA - SENLA)*(1.0 - AMIN1(SLFW, SLFC, SLFT, SLFA))
      IF (ISTAGE.GT.3) THEN
         PLAS = (PLA - SENLA)*(1.0-AMIN1(SLFW, SLFN, SLFC, SLFT, SLFA))
      ENDIF
      SENLA = SENLA + PLAS
      IF (SENLA .LT. SLAN) SENLA = SLAN
      IF (SENLA .GE. PLA) SENLA = PLA
C
       WRITE (57, '(13,7F10.3)') DOY, PLA, PLAS, SLAN, SENLA, SLFA, ASD, ASD2
      LAI = (PLA - SENLA)*PLANTS*0.0001
      IF (LN .GT. 4 .AND. LAI .LE. O. .AND. ISTAGE .LE. 4 .AND. icold
     1 .GT. 4) THEN
         WRITE (*, 5010)
         WRITE (NOUT1, 5010)
         ISTAGE = 6
      ELSE IF (ICOLD .GE. 10) THEN
         WRITE (*, 5010)
         WRITE (NOUT1, 5010)
         ISTAGE = 6
      IF (XSTAGE .LT. 1.75) THEN
```

```
PROP = 0.85
      ELSE
         PROP = 1.0
      ENDIF
      IF (TLABIOL.GT.O. .OR. TLABIOS.GT.O. .AND. ASD2.LT.1.0) THEN
         IF (TLABIOL.GE.GROLF*PROP) THEN
            LFWT=LFWT-GROLF*PROP
            GRORT=GRORT+GROLF*PROP
            TLABIOL=TLABIOL-GROLF*PROP
         ELSE
            LFWT=LFWT-TLABIOL
            GRORT=GRORT+TLABIOL
            TLABIOL=0.
         ENDIF
         IF (TLABIOS.GE.GROSTM*PROP) THEN
            STMUT=STMUT-GROSTM*PROP
             GRORT=GRORT+GROSTM*PROP
             TLABIOS=TLABIOS-GROSTM*PROP
         ELSE
            STMUT=STMUT-TLABIOS
            GRORT=GRORT+TLABIOS
            TLABIOS=0.
         ENDIF
      ENDIF
      IF (TRLVY .EQ. 0.) TRLVY = 0.00001
      RTWT = RTWT + 0.5*GRORT - 0.005*RTWT - TRLVLOSS/TRLVY*RTWT
      BIOMAS = (LFWT + STMWT + EARWT)*PLANTS
      DM = BIOMAS*10.0
      STOWT = LFUT + STMUT
      PTF = (LFWT+STHWT+EARWT)/(RTWT+LFWT+STHWT+EARWT)
      IF (ISWNIT .NE. 0) CALL NUPTAK
40
      RETURN
5000 FORMAT (2X, 'CROP MATURE ON JD', 14,
1 ' BECAUSE OF SLOWED GRAIN FILLING')
5010 FORMAT (2X, 'CROP FAILURE GROWTH PROGRAM TERMINATED ')
      END
      SUBROUTINE PHENOL(iret, CUMDELAY)
      Include 'GEN1.BLK'
      Include 'GEN2.BLK'
      Include 'GEN3.BLK'
      Include 'GEN4.BLK'
      Include 'NTRC1.BLK'
      Include 'NTRC2.BLK'
      Include 'COMIBS.BLK'
      Include 'PREDOB.BLK'
      Include 'ENVIRO.BLK'
      Include 'SOILOX.BLK'
C
      Character*28 String(5), Whstag(5), Bastag(5)
      Character*3 jmon
      Data String/
     1 'EMERGENCE
                         END JUVENILE',
     2 'END JUVENIL - FLORAL INIT',
     3 'FLORAL INIT - END LF GROWTH',
     4 'END LF GRTH - BEG GRAIN FILL',
     5 'GRAIN FILLING PHASE'/
      Data Whstag/
                          TERM SPIKLT',
     1 'EMERGENCE -
     2 'END VEG - BEG EAR GROWTH',
     3 'BEGIN EAR - END EAR GROWTH',
     4 'END EAR GRTH - BEG GRN FILL',
     5 'LINEAR GRAIN FILL PHASE'/
      Data Bastag/
     1 'EMERGENCE - MAX PRIMORDIA',
2 'MAX PRIM - BEG EAR GROWTH',
     3 'BEGIN EAR - END EAR GROWTH'.
```

```
4 'END EAR GRTH . BEG GRN FILL',
     5 'LINEAR GRAIN FILL PHASE'/
      XANC=TANC+100.0
      APTNUP=STOVN+10+PLANTS
      iret=0
      IF(CROP.EQ.'WH'.OR.CROP.EQ.'BA') THEN
        TEMPCN=TEMPHN
        TEMPCX=TEMPMX
        TOTHUP=APTHUP
        XS=SNOL
        IF (XS.GT.15.) XS=15.
        IF (TEMPMN.LT.O.) TEMPCN=2.+TEMPMN*(0.4+0.0018*(XS-15.)**2)
        IF (TEMPHX.LT.O.) TEMPCX=2.+TEMPHX*(0.4+0.0018*(X8-15.)**2)
        TEMPCR=(TEMPCX+TEMPCN)/2.
        ***** CALCULATES THERMAL TIME FOR WHEAT OR BARLEY *******
C
        DTT=TEMPCR-TBASE
        tdif=Tempcx-tempcn
        if(tdif.eq.0)tdif=1.0
        IF (TEMPCX.GE.TBASE) GOTO 1001
        DTT=0.
        GOTO 20
1001
        IF (TEMPCN.GT.TBASE) GOTO 2001
        TCOR=(TEMPCX-TBASE)/tdif
        DTT=(TEMPCX-TBASE)/2.*TCOR
2001
        IF (TEMPCX.LE.26.) GOTO 20
        TCOR=(TEMPCX-26.)/tdif
        DTT=13.*(1.+TCOR)+TEMPCN/2.*(1.-TCOR)
        IF(TEMPCN.LE.26.) GOTO 3001
        DTT=26.
3001
        IF ( TEMPCX.LT.34.) GOTO 20
        TCOR=(TEMPCX-34.)/tdif
        DTT=(60.-TEMPCX)*TCOR+26.*(1.-TCOR)
        IF (TEMPCN.GE.26.) GOTO 20
        TCOR=(26.-TEMPCN)/tdif
        DTT=DTT*(1.-TCOR)+(TEMPCN+26.)/2.*TCOR
        - GO TO 20
      ENDIF
c
c ****** Using soil temperature to calculate GDD when appropriate
      IF (ISTAGE.GE.8) THEN
           STMP=ST(RDLAYR)
        EL SE
           STMP=ST(1)
      ENDIF
      ATT=TEMPM-TBASE
      STT=STMP-TBASE
      if (istage.le.2 .or. istage.ge.8) then
           dtt=stt
           if (stmp .lt. tbase) dtt = 0.0
           if (stmp .gt. 34.) dtt = 34. - tbase
         else
           dtt=att
           IF (TEMPMN .LE. TBASE .OR. TEMPMX .GE. 34.0) THEN
              IF (TEMPMX .LT. TBASE) THEN
                 DTT = 0.0
              ELSE
                 DTT = 0.0
                 DO 90 I = 1,8
                    TTMP = TEMPMN + TMFAC(I) * (TEMPMX - TEMPMN)
IF (TTMP .GT. TBASE .AND. TTMP .LE. 34.) THEN
                       DTT = DTT+(TTMP-TBASE)/8.
                     ELSE IF (TTMP .GT. 34 .AND. TTMP .LT. 44.) THEN
                       DTT=DTT+(34.-TBASE)*(1.-(TTMP-34.)/10.)/8.
                     ENDIF
   90
                 CONTINUE
              ENDIF
           ENDIF
      end if
```

```
IF (ASD.GT.1. .AND. XSTAGE.LE.2) THEN
        DTTRED=EXP(-ASD*0.4)
        DTT=DTT*DTTRED
     EMOLE
   20 SUNDTT=SUNDTT+DTT
     TEMPOTT=TEMPOTT+DTT
C****** CALCULATE DAYLENGTH ***********************
     IF(ISTAGE.EQ.9.OR.ISTAGE.LE.2) THEN
       IF(CROP.EQ.'BA') YDL=HRLT
       DEC=0.4093*SIN(0.0172*(DOY-82.2))
       DLV=((-S1*SIN(DEC)-0.1047)/(C1*COS(DEC)))
       IF(DLV_LT_-0.87)DLV=-0.87
       HRLT=7.639*ACOS(DLV)
       IF(CROP.EQ.'BA') CHGDL=HRLT-YDL
     ENDIF
GO TO (1,2,3,4,5,6,7,8,9), ISTAGE
C****** DETERMINE SOUING DATE *************************
   7 CALL CALDAT
    FORMAT(1X,12,1x,a3,F6.0,' SOWING',18X,'g/m^2',7x,'kg/ha', 1 8x,4('-'),'mm',5('-'),3x,'cm')
500
    FORMAT(/,
                DATE COTT PHENOLOGICAL STAGE
                                                    BION LAI'
    1 , NUPTK NX CET RAIN PESH')
     IF(Iphout)WRITE (*,600)
     IF(Iphout)Write (Nout1,600)
IF(Iphout)WRITE (*,500) ND,MONTH,cumdtt
     IF(Iphout)Write(Nout1,500)ND,MONTH,cumdtt
     NDAS=0.
     CALL PHASEI (CUMDELAY)
     IF (ISWSWB.EQ.0) RETURN
     CLIMDEP=0.
     DO 100 L=1,NLAYR
       CUMDEP=CUMDEP+DLAYR(L)
       IF (SDEPTH.LT.CUMDEP) GO TO 110
  100 CONTINUE
 110 LO=L
     RETURN
C****** DETERMINE GERMINATION DATE
   8 IF (ISWSWB.EQ.0) GO TO 210
     IF (SW(L0).GT.LL(L0)) GO TO 210
     SWSD=(SW(L0)-LL(L0))*0.65+(SW(L0+1)-LL(L0+1))*0.35
     NDAS=NDAS+1
     IF (NDAS.LT.40) GO TO 200
     IF (NDAS.LT.90.AND.CROP.EQ.'WH') GO TO 200
     IF (NDAS.LT.90.AND.CROP.EQ.'BA') GO TO 200
     ISTAGE=6
     PLANTS=0.00
     gpp=1.
     GRNWT=0.
     IF(Iphout)WRITE(*,3600)
     IF(Iphout)Write(Nout1,3600)
3600 FORMAT(1X, 'CROP FAILURE BECAUSE OF LACK OF GERMINATION',
     1' WITHIN 40 DAYS OF SOWING')
     RETURN
 200 IF (SWSD.LT.0.02) RETURN
 210 CALL CALDAT
     IF(Iphout)WRITE (*,1200) nd,month,Cumdtt,Cet,Crain,Pesw
IF(Iphout)WRITE (Nout1,1200) nd,month,Cumdtt,Cet,Crain,Pesw
     Format(1x, 12, 1x, a3, f6.0, GERMINATION', 39x, f4.0, 1x, f5.0, 2x, f4.0)
     iprint=0
     CALL PHASEI (CUMDELAY)
     RETURN
9 NDAS=NDAS+1
     IF (CROP.EQ.'WH'.OR.CROP.EQ.'BA') THEN
        RTDEP=RTDEP+0.1*DTT
        XSTAGE=SUMDTT/P9
```

```
CALL COLD
      ELSE
         RTDEP=RTDEP+0.15*DTT
         IDUR1=IDUR1+1
      ENDIF
      IF (SUMDTT.LT.P9) RETURN
      IF (P9.GT.150.) THEN
        ISTAGE=6
        PLANTS=0.00
        gpp=1.
        GRNWT=0.
        IF(Iphout)WRITE (*,1399)
        IF(Iphout)WRITE (nout1,1399)
        RETURN
      ENDIF
      CALL CALDAT
      IF(CROP.EQ.'BA') THEN
        PHINT=77.5-232.6*CHGDL
        IF(Iphout)WRITE (*,1401) nd,month,Cumdtt,PHINT,CHGDL,Cet;
        Crain, Pesw
        IF(Iphout)WRITE (nout1,1401) nd,month,Cumdtt,PHINT,CHGDL,
        Cet, Crain, Pesw
      ELSE
        IF(Iphout)WRITE (*,1400) nd,month,Cumdtt,Cet,Crain,Pesw
        IF(Iphout)WRITE (nout1,1400) nd,month,Cumdtt,Cet,Crain,Pesw
      ENDIF
1399 FORMAT(' SEED PROBABLY RAN OUT OF METABOLITE DUE TO DEEP PLANTING
     1.')
1400 Format(1x,12,1x,a3,f6.0,' EMERGENCE',41x,f4.0,1x,f5.0,2x,f4.0)
1401 Format(1x,12,1x,a3,f6.0,' EMERGENCE, PHINT=',F8.1,' CHGDL=',F6.3,
     1 12x, f4.0, 1x, f5.0, 2x, f4.0)
      CALL PHASEI (CUMDELAY)
      RETURN
1 NDAS=NDAS+1
      IF (CROP.EQ.'WH'.OR.CROP.EQ.'BA') GO TO 1650
      XSTAGE=2*SUMDTT/P1
      IF(CROP.EQ.'MZ') XSTAGE=SUMDTT/P1
      IDUR1=IDUR1+1
      IF (SUMDTT.LT.P1) RETURN
      CALL CALDAT
      IF(Iphout)WRITE (*,1600) nd,month,Cumdtt,Biomes,Lai,Aptnup,
     1 XANC, CET, CRAIN, PESW
      IF(Iphout)WRITE (Nout1,1600) nd, month, Cumdtt, Biomas, Lai, Aptnup,
     1 XANC, CET, CRAIN, PESW
1600 Format(1x,12,1x,a3,f6.0,' END JUVENILE',12x,f6.0,1x,f5.2,1x,f5.1,
     1 2x, f4.2, 2x, f4.0, 1x, f5.0, 2x, f4.0
      GO TO 300
      *****DETERMINE DURATION OF VEGETATIVE PHASE FOR WHEAT & BARLEY***
1650 CALL COLD
      IF (VF.LT.0.3) GO TO 1660
      DF=1.-P1D*(20.-HRLT)**2
1660 IF(CROP.EQ.'WH') THEN
        TDU=TDU+DTT*AMIN1(VF,DF)
        XSTAGE=TDU/400.0+1.0
        IF (TDU.LE.400.*(PHINT/95.)) RETURN
        CALL CALDAT
        If(Iphout)WRITE (nout1,1750) nd,month,CUMDTT,CUMVD,BIOMAS,
        LAI, aptnup, xanc, cet, CRAIN, PESW
        If(Iphout)WRITE (*,1750) nd, month, CUMDTT, CUMVD, BIOMAS, LAI,
         aptnup, xanc, cet, CRAIN, PESW
      ELSEIF(CROP.EQ.'BA') THEN
        TDU=TDU+DTT*AMIN1(VF,DF)*LIF2
        XSTAGE=TDU/300.0+1.0
        IF (TDU.LE.300.*(PHINT/75.)) RETURN
        CALL CALDAT
        If(Iphout)WRITE (nout1,1751) nd,month,CUMDTT,CUMVD,BIOMAS,
        LAI, aptnup, xanc, cet, CRAIN, PESW
        If(Iphout)WRITE (*,1751) nd, month, CUMDTT, CUMVD, BIOMAS, LAI,
```

```
1
       aptnup, xanc, cet, CRAIN, PESW
     ENDIF
1750 FORMAT(1X,12,1x,a3,F6.0,' T SPKLT VE DAYS=',F3.0,5x,F6.0,1X,
1 F5.2,1X,F5.1,2X,F4.2,2X,F4.0,1X,F5.0,2X,F4.0)
1751 FORMAT(1X,12,1x,a3,F6.0,' MAX PRIM VE DAYS=',F3.0,5x,F6.0,1X,
    1 F5.2, 1x, F5.1, 2x, F4.2, 2x, F4.0, 1x, F5.0, 2x, F4.0)
     GO TO 300
2 NDAS=NDAS+1
     IF (CROP.EQ.'WH'.OR.CROP.EQ.'BA') GO TO 1810
     XSTAGE=2.0+SIND
     IF(CROP.EQ.'MZ') XSTAGE=1.0+0.5*SIND
     IDUR1=IDUR1+1
     PDTT=DTT
     IF(ISWSWB.NE.1) ICSDUR=ICSDUR+1
      IF(ICSDUR.EQ.1) PDTT=SUMDTT-P1
     IF(CROP.EQ.'MZ') P20=12.5
      IF(DLITE.GT.O.) HRLT=DLITE
      IF (HRLT.LT.P20) HRLT=P20
     IF(CROP.EQ.'SG') THEN
      RATEIN=1./92.
      IF (HRLT.GT.P20) RATEIN=1./(102.+P2R*(HRLT-P20))
      ELSEIF (CROP.EQ.'ML') THEN
      RATEIN=1./68.
      IF (HRLT.GT.P20) RATEIN=1./(68.+P2R*(HRLT-P20))
      ELSEIF (CROP.EQ.'MZ') THEN
      RATEIN=1./(4.+P2*(HRLT-P20))
      POTT=1.
     Endif
     SIND=SIND+RATEIN*POTT
     IF (SIND.LT.1.0 .OR. XSTAGE.LT.1.5) RETURN
     CALL CALDAT
      IF(Iphout)WRITE (*,1800) nd,month,Cumdtt,Biomes,Lai,Aptnup,
     1 XANC, CET, CRAIN, PESW
     IF(Iphout)WRITE (nout1,1800) nd,month,Cumdtt,Biomes,Lai,Aptnup,
    1 XANC, CET, CRAIN, PESW
1800 Format(1x, 12, 1x, a3, f6.0, ' FLORAL INITIATION', 7x, f6.0, 1x, f5.2, 1x,
    1 f5.1,2x,f4.2,2x,f4.0,1x,f5.0,2x,f4.0)
     GO TO 300
      1810 XSTAGE=SUMDTT/P2+2
     IF (SUMDTT.LT.P2) RETURN
     CALL CALDAT
     CLAI=LAI
     If(Iphout)WRITE (nout1,1910) nd, month, CUMDTT, BIOMAS, LAI, APTMUP,
     1XANC, CET, CRAIN, PESW
     If (Iphout) WRITE (*, 1910) nd, month, CUMDTT, BIOMAS, LAI, APTNUP,
     1 XANC, CET, CRAIN, PESW
1910 FORMAT(1X,12,1x,a3,F6.0,' END VEG BEGIN EAR GROWTH',F6.0,1X,F5.2
    1 ,1X,F5.1,2X,F4.2,2X,F4.0,1X,F5.0,2X,F4.0)
     GO TO 300
3 NDAS=NDAS+1
     XSTAGE=3.0+2.0*SUMDTT/P3
     IF(CROP.EQ.'MZ') XSTAGE=1.5+3.0*SUMDTT/P3
     IF(CROP.EQ.'WH'.OR.CROP.EQ.'BA') XSTAGE=SUMDTT/P3+3.0
     IDUR1=IDUR1+1
     IF (SUMDTT.LT.P3) RETURN
     CALL CALDAT
     If(Crop.eq.'MZ'.or.Crop.eq.'SG') MAXLAI=LAI
     IF(CROP.EQ.'MZ') THEN
       ISDATE=DOY
       ABIOMS=BIOMAS
       IF(Iphout)WRITE (*,2000) nd,month,Cumdtt,Biomes,
    1 Lai, Aptnup, XANC, CET, CRAIN, PESW
       IF(Iphout)WRITE (nout1,2000) nd,month,Cumdtt,
      Biomas, Lai, Aptnup, XANC, CET, CRAIN, PESW
     ELSEIF(CROP.EQ.'WH'.OR.CROP.EQ.'BA') THEN
C
       ******DETERMINE END OF PRE-ANTHESIS EAR GROWTH**********
```

```
If (Iphout) WRITE (nout1, 2010) nd, month, CUMDIT, TPSM, BIOMAS, LAI,
     1 APTNUP, XANC, CET, crain, PESW
        If(Iphout)WRITE (*,2010)nd,month,CUMDTT,TPSM,BIONAS,LAI,
     1 APTNUP, XANC, CET, crain, PESW
     ELSE
        IF(Iphout)WRITE (*,2020) nd,month,Cumdtt,Biomes,
     1 Lai, Aptnup, XANC, CET, CRAIN, PESW
        IF(Iphout)WRITE (nout1,2020) nd,month,Cumdtt,
     1 Biomes, Lai, Aptrup, XANC, CET, CRAIN, PESW
      ENDIF
2000 Format(1x,12,1x,a3,f6.0,' 75% SILKING',13X,F6.0,1X,F5.2,1X,F5.1,2X,
     1 F4.2,3(1X,f5.0))
2010 FORMAT(1X,12,1x,a3,F6.0,' END EAR GR. EARS=',F5.0,2x,F6.0,1X,F5.2,
     1 1x,F5.1,2x,F4.2,2x,F4.0,1x,F5.0,2x,F4.0)
2020 Format(1x,12,1x,a3,f6.0, END LF GRTH',13X,F6.0,1X,F5.2,1X,F5.1,2X,
     1 F4.2,2x,f4.0,1x,f5.0,2x,f4.0)
     GO TO 300
C****** DETERMINE END OF PANICLE GROWTH ********
    4 NDAS=NDAS+1
        IF(CROP.EQ.'MZ') GOTO 299
        IF(CROP.EQ.'WH'.OR.CROP.EQ.'BA') GOTO 350
        If(Crop.eq.'ML') then
         pflowr=50.0
        Else
          pflowr=2.5*phint+30.0
        Endif
        XSTAGE=5.0+SUMDTT/pflowr
        IF (SUMDTT.LE.pflowr) IDUR1=IDUR1+1
        IF (SUMDTT.GE.pflowr.AND.IPRINT.EQ.0)THEN
           CALL CALDAT
           JANTH=DOY
           BIOMS2=BIOMAS/PLANTS
           ISDATE=DOY
           Abiome=Biomes
C***** ANTHESIS IS 150. DEGREE DAYS INTO THIS PHASE FOR SORGHUM *****
C****
        ANTHESIS IS 50. DEGREE DAYS INTO THIS PHASE FOR MILLET *****
           IF(Iphout)WRITE (*,2200) nd,month,Cumdtt,Biomas,Lai,Aptnup,
     1
             XANC, CET, CRAIN, PESW
           IF(Iphout)WRITE (nout1,2200) nd,month,Cumdtt,Biomas,Lai,
             Aptnup, XANC, CET, CRAIN, PESW
2200
           FORMAT(1x, 12, 1x, a3, f6.0, 'ANTHESIS', 16x, F6.0, 1x, F5.2, 1x,
             F5.1,2x,F4.2,2x,f4.0,1x,f5.0,2x,f4.0
           IPRINT=1
        END IF
      IF (SUMDTT.LT.P4) RETURN
      CALL CALDAT
     IF(Iphout)WRITE (*,2201) nd,month,Cumdtt,Biomes,Lai,Aptnup,
     1 XANC, CET, CRAIN, PESW
      IF(Iphout)WRITE (nout1,2201) nd,month,Cumdtt,Biomes,Lai,Aptnup,
     1 XANC, CET, CRAIN, PESW
     FORMAT(1x, 12, 1x, a3, f6.0, ' END PAN GRTH', 12x, F6.0, 1x, F5.2, 1x,
     1 F5.1,2X,F4.2,2x,f4.0,1x,f5.0,2x,f4.0)
      IF (GPP.LE.O.O) GPP=1.0
      If (Crop.eq.'ML') MAXLAI=LAI
      GO TO 300
C*****DETERMINE BEGINNING OF EFFECTIVE GRAIN FILLING PERIOD FOR MAIZE*
299 XSTAGE=4.5+5.5*SUMDTT/(P5*.95)
      IF (SUMDIT.LT.170.) RETURN
      PSKER=SUMP*1000/IDURP*3.4/5.0
      GPP=G2*PSKER/7200+50
      IF (GPP.GT.G2) GPP=G2
      IF (GPP.LT.0.0) GPP=0.0
      EARS=PLANTS
C****** DETERMINE BARRENNESS FOR MAIZE**********************
      IF (GPP.LE.51.) GPP=51.
      IF (GPP.LT.G2*0.15) EARS=PLANTS*((GPP-50.)/(G2-50.))**0.33
      IF (EARS.LT.O.O) EARS=0.0
      GPSM=GPP*EARS
350
     IF(CROP.EQ.'WH'.OR.CROP.EQ.'BA') THEN
```

```
C
        if(CROP.EQ.'BA'.AND.sumdtt.gt.60)go to 2370
        if(sumdtt.gt.80)go to 2370
        ISDATE=DOY
        Abioms=Biomas
        CALL CALDAT
        JMD=MD
        JMON=MONTH
2370
        XSTAGE=SUMDTT/p4+4.0
        IF (SUMDIT.LT.p4) RETURN
C****
           anthesis is 80 (WH) and 60 (BA) deg days into this phase
        IF(IPHOUT.AND.CROP.EQ.'BA')WRITE(*,2371)JND, JMON, ISDATE
        IF(IPHOUT.AND.CROP.EQ.'BA')WRITE(NOUT1,2371)JND, JMON, ISDATE
        GPP=STMUT*G1
        GPSM=GPP*PLANTS
        if(gpsm.lt.100)then
           If(Iphout)write(nout1,2380)
           If(Iphout)WRITE(*,2380)
           plants=0.
           EARS=0.
           gpp=1.
           If(imulti)Iret=1
           istage=6
2380
           format(' Crop failure growth program terminated')
           RETURN
        end if
      ENDIF
      CALL CALDAT
      IF(IPHOUT)WRITE (*,2202) nd,month,Cumdtt,Biomes,Lai,Aptnup,Xanc,
     1 Cet, CRAIN, PESW
      IF(IPHOUT)WRITE (nout1,2202) nd,month,Cumdtt,Biomes,Lai,Aptnup,
     1 Xanc, Cet, CRAIN, PESW
 2202 FORMAT(1x,12,1x,a3,f6.0,' BEGIN GRAIN FILL',8X,F6.0,1X,F5.2,1X,
     1 F5.1,2X,F4.2,3(1X,F5.0))
2371 FORMAT(' Ear Emergence occured on ',i2,1x,a3,' Day of Year =',i4)
      GO TO 300
C****** DETERMINE END OF EFFECTIVE FILLING PERIOD FOR MAIZE***
    5 MDAS=NDAS+1
      IF (CROP.EQ.'MZ') THEN
        XSTAGE=4.5+5.5*SUMDTT/P5
        IF (SUMDIT.LT.P5*0.95) RETURN
      ELSEIF (CROP.EQ.'WH'.OR.CROP.EQ.'BA') THEN
        *****DETERMINE END OF GRAIN FILLING FOR WHEAT & BARLEY ********
C
        XSTAGE=SUMDTT/P5+5.0
        IF (PLANTS.GT.O.) GO TO 2710
        yield=0.
        GRNUT=0.
        gnup=0.
        stover=0.
        totnup=0.
        ISTAGE=6
        GO TO 2720
2710
        IF (SUMDTT.LT.P5) RETURN
      ELSE
C******DETERMINE END OF GRAIN FILLING FOR MILLET AND SORGHUM*******
        XSTAGE=6.5+2.5*SUMDTT/P5
        IF (SUMDTT.LT.P5) RETURN
      ENDIF
2720 CALL CALDAT
      IF(Crop.eq.'ML') then
       IF(ISM.GT.O)THEN
        IF(TGROPAN.GT.O.5)RETURN
        EMAT=EMAT+1
        IF(EMAT.LT.2)RETURN
        IF(IPHOUT) WRITE (NOUT1, 1095) ND, MONTH, CUMDTT, BIOMAS, LAI, APTNUP,
     1 XANC, CET, CRAIN, PESW
        IF(IPHOUT) WRITE (*,1095) ND, MONTH, CUMDTT, BIOMAS, LAI, APTNUP,
     1 XANC, CET, CRAIN, PESW
        GO TO 300
```

```
ELSE
       I SH=1
        IF(IPHOUT) WRITE (NOUT1, 1090) ND, MONTH, CUMDTT, BIOMAS, LAI, APTHUP,
     1 XANC, CET, CRAIN, PESW
     IF(IPHOUT) WRITE (*,1090) ND, MONTH, CUMDTT, BIONAS, LAI, APTNUP, XANC, CET, CRAIN, PESW
       RETURN
      END IF
      ENDIF
     IF(IPHOUT)WRITE (*,2400) nd,month,Cumdtt,Biomes,Lai,
     1 Aptnup, Xanc, Cet, CRAIN, PESW
      IF(IPHOUT)WRITE (nout1,2400) nd,month,Cumdtt,Biomes,Lai,
     1 Aptnup, Xanc, Cet, CRAIN, PESW
 2400 FORMAT(1X,12,1x,a3,F6.0,' END GRAIN FILL',10X,f6.0,1x,f5.2,1x,
     1 f5.1,2x,f4.2,3(1x,f5.0))
 1090 FORMAT(1X,12,1x,a3,F6.0,' END MAIN GRN FILL',7X,F6.0,
     1 1X,F5.2,1X,F5.1,2X,F4.2,2X,F4.0,1X,F5.0,2X,F4.0)
 1095 FORMAT(1X,12,1x,a3,F6.0, 'END TILR GRN FILL',7X,F6.0,
     1 1x,F5.2,1x,F5.1,2x,F4.2,2x,F4.0,1x,F5.0,2x,F4.0)
     GO TO 300
6 IF (CROP.EQ.'MZ') THEN
         IF (DTT.LT.2.0) SUMDTT=P5
         IF (SUMDTT.LT.P5) RETURN
         GO TO 301
      ENDIF
      IF (CROP.EQ.'WH') GO TO 301
      IF (DTT.LT.2.0) RETURN
      IF (SUMDTT.LT.2.0) RETURN
  301 CALL CALDAT
      iprint=0
      MDATE=DOY
      IF(Iphout)WRITE (*,2600) nd,month,Cumdtt,Biomas,Lai,Aptnup,
     1 XANC, CET, CRAIN, PESW
      IF(Iphout)WRITE (nout1,2600) nd,month,Cumdtt,Biomes,Lai,Aptnup,
     1 XANC, CET, CRAIN, PESW
2600 Format(1x,12,1x,a3,f6.0,' PHYSIOLOGICAL MATURITY',2x,F6.0,1x, 1 F5.2,1x,F5.1,2x,F4.2,3(1x,F5.0))
      IF(CROP.EQ.'SG') THEN
         GRNWT=PANWT*0.8
         GRAINN=GRAINN-0.2*PANWT*TANC
         STOVN=STOVN+0.2*PANWT*TANC
         APTNUP=STOVN+10+PLANTS
      ENDIF
      IF(CROP.EQ.'ML') GRNWT=PANWT+0.75
      YIELD=GRNWT*10.*PLANTS
      IF(CROP.EQ.'MZ') YIELD=GRNWT*10.*EARS
      If(Plants.eq.0.)go to 300
      IF(GPP.LE.O.)GPP=1.
      SKERWT=GRNWT/GPP
      IF(CROP.EQ.'ML'.OR.CROP.EQ.'SG') GPSM=GPP*PLANTS
      IF(CROP.EQ.'MZ') GPSM=GPP*EARS
      STOVER=BIOMAS*10.-YIELD
      IF(CROP.EQ.'MZ') YIELD=YIELD/0.845
      YIELDB=YIELD/62.8
      IF(CROP.EQ.'WH'.OR.CROP.EQ.'BA') THEN
        IF(SKERWT.LT.0.02) THEN
          GPSM=YIELD*5.
          SKERWT=0.02
        ENDIF
        YIELDB=YIELD/67.
       CGPE=GPSM/TPSM
      ENDIF
      pgrnwt=SKERWT*1000.0
      IF(Crop.eq.'SG') then
        pgrnwt=grnwt/gpp*1000.0
         if(pgrnwt.gt.28.)pgrnwt=28.
         if(pgrnwt.lt.15.)pgrnwt=15.
         if(pgrnwt.EQ.15.or.pgrnwt.EQ.28.) then
```

```
skerwt=pgrnwt/1000.
            gpp=grnwt/skerwt
            gpem=gpp*plants
         endi f
      ENDIF
      IF(iswnit.eq.0)then
        Xgnp=0.0
        Xptn=0.0
        Gnup=0.0
      Else
        IF(GRWWT.GT.O.) THEN
          XGNP=(GRAINN/GRNUT)*100.0
          XPTN=XGNP*6.25
          GNUP=GRAINN*PLANTS*10.
          IF(CROP.EQ.'MZ') GNUP=GRAINN*EARS*10.
        FMDIF
      Endif
      Totnup=Gnup+Aptnup
       SI1(Istage)=0.0
       $12(Istage)=0.0
       SI3(Istage)=0.0
       SI4(Istage)=0.0
       SI5(ISTAGE)=0.0
300
      If(iswswb.eq.0) GOTO 305
       SI1(ISTAGE)=CSD1/ICSDUR
       SI2(ISTAGE)=CSD2/ICSDUR
       SI3(ISTAGE)=CNSD1/ICSDUR
       $14(ISTAGE)=CNSD2/ICSDUR
       SI5(ISTAGE)=CASD/ICSDUR
305
      IF (ISTAGE.EQ.6) GO TO 2800
      CALL PHASEI (CUMDELAY)
      RETURN
2800 IF(Iphout)Write(*,3800)yield,yieldb,gpsm,pgrnwt
      IF(Iphout)Write(nout1,3800)yield,yieldb,gpem,pgrnwt
      If(.not.Runall.and.Iphout)then
         Write(6,3301)
3301 Formet(' Please press ENTER to continue')
         Read(5, '(a1)')a
      Endif
      IF(Iphout)WRITE (*,3900)
      IF(Iphout)Write(nout1,3900)
      DO 2900 I=1,5
        IF (CROP.EQ.'WH') THEN
           IF(Iphout)WRITE (*,4000) I,SI1(I),SI2(I),SI3(I),
     1
           SI4(I), Whstag(i)
           IF(Iphout)WRITE (nout1,4000) I,SI1(I),SI2(I),
           $13(1),$14(1),Whstag(i)
        ELSEIF (CROP.EQ. 'BA') THEN
           IF(Iphout)WRITE (*,4000) I,SI1(I),SI2(I),SI3(I),
           SI4(I),Bastag(i)
           IF(Iphout)WRITE (nout1,4000) 1,SI1(I),SI2(I),
           $13(1),$14(1),Bastag(i)
        ELSE
           IF(Iphout)WRITE (*,4000) I,SI1(I),SI2(I),SI3(I),
           $14(1),$15(1),$tring(i)
           IF(Iphout)WRITE (nout1,4000) I,SI1(I),SI2(I),
           $13(1),$14(1),$15(1),$tring(i)
        ENDIF
2900 CONTINUE
      IF(Iphout)Write(*,5000)
      IF(Iphout)Write(nout1,5000)
      IF(.not.RUNALL.and.Iphout) then
       Write(6,*)' Press "ENTER" to continue.'
Read(5,'(A1)') a
      Endif
      if(iirr.eq.2.or.iirr.eq.3)then
        write(*,3000)nirr,effirr
3000
           format(/, i6, ' IRRIGATION APPLICATIONS AT ', F5.2, ' EFFICIENCY'
     1,/)
```

```
LINES=NIRR/14
         IF(LINES*14.LT.NIRR)LINES=LINES+1
         DO 3100 I=1,LINES
            11=14*(1-1)+1
            12=11+13
            IF(I2.GT.NIRR)I2=Nirr
            WRITE(NOUT1,3200)(Iday(MPX),MPX=I1,I2)
            WRITE(NOUT1,3300)(AIRR(MPX),MPX=11,12)
           WRITE(*,3200)(Iday(MPX),MPX=11,12)
WRITE(*,3300)(AIRR(MPX),MPX=11,12)
3100
         CONTINUE
         FORMAT(1X, 'JUL. DAY ',14(13,2X))
FORMAT(1X, 'AMOUNT mm ',14(F4.0,1X))
3200
3300
         totir=0.0
         do 3400 i=1,nirr
3400
         totir=totir+airr(i)
         WRITE(NOUT1,3500)TOTIR
         WRITE(*,3500)TOTIR
3500
         FORMAT(/1X, 'IRRIGATION THIS SEASON : ',F5.0,' mm')
       endif
       if(.not.Imulti)call opharv
       If(OUTS.NE.' ') CALL FOUTS
       CALL PHASEI (CUMDELAY)
       if(runall.and.iphout) then
          SUDF1=1.
           SWDF2=1.
           NDEF1=1.
          MFAC=1.
           NDEF2=1.
       endif
       iret=1
3800 Format(/,1x,'YIELD (KG/HA)=',F6.0,1X,'(BU/ACRE)=',F5.1,1X,
1 'FINAL GPSM=',F7.0,1X,'KERNEL WT.(mg)=',f5.1)
3900 FORMAT (/,1X,'ISTAGE',4X,'CSD1',4X,'CSD2',3X,'CNSD1',3X,
1 'CNSD2',4X,'CASD',2X,'S T A G E O F G R O W T H'
4000 FORMAT (1X,16,5F8.2,3X,A28)
5000 FORMAT(** NOTE: In the above table, 0.0 represents minimum stress*
      1,/,'
                     and 1.0 represents maximum stress for water (CSD)'
                     nitrogen (CNSD) and aeration (CASD) respectively.')
       RETURN
       END
       SUBROUTINE PHASEI (CUMDELAY)
       Include 'GEN1.BLK'
       Include 'GEN2.BLK'
       Include 'GEN3.BLK'
       Include 'GEN4.BLK'
       Include 'NTRC1.BLK'
       Include 'SOILOX.BLK'
C
       CNSD1=0.0
       CNSD2=0.0
       CSD1=0.
       CSD2=0.
       CASD=0.
       ICSDUR=0
    10 GO TO(1,2,3,4,5,6,7,8,9), ISTAGE
     1 ISTAGE=2
       SIND=0.
       BIOMS1=0.1
       BIOMS2=0.1
       IF(CROP.EQ.'WH'.OR.CROP.EQ.'BA')THEN
         SUMDTT=0.
         If(Crop.eq.'BA') Sumdtt=dtt
         P2=PHINT*3.
         IF(CROP.EQ.'BA') P2=225
         IF(TILN*PLANTS.GT.1000.)TILN=1000./PLANTS
       ENDIF
```

```
RETURN
    2 ISTAGE=3
      IF(Crop.eq.'WH'.OR.CROP.EQ.'BA') then
       P3=PHINT*2.
        IF(CROP.EQ.'BA') P3=150
        SUMDTT=SUMDTT-P2
        GROLF=0.
        GPLA=PLA-SENLA
        RETURN
      ENDIF
      TLNO=(CUMDTT/35.+6.0)
     BIOMS1=BIOMAS/PLANTS
      Xnti=Sumdtt/43.
      If(Crop.eq.'SG') then
         pp3=275.+0.19*sumdtt
         p3=6.50*phint+0.25*sumdtt
C
         p3=7.0*phint+0.25*sumdtt
         p4=4.0*phint+38.
         IDUR1=0
      Elseif(Crop.eq.'ML') then
        p3=370.+0.135*Sumdtt
        p4=150.
      Elseif(Crop.eq.'MZ') then
        TBASE=8
        TLNO=IFIX(CUMDTT/(21.-2.)+6.)
        P3=(TLNO-2.)*38.9+96.-SUMDIT
        XNTI=XN
        GOTO 24
      Endif
      PLANX=PLA
      IDUR=0.0
      TDUR=0.0
      TCON=0.0
      SUMRTR=0.
   24 SUMDTT=0.
   25 RETURN
   3 ISTAGE=4
      If(Crop.eq.'WH'.OR.CROP.EQ.'BA') then
        P4=200.
        SUMIN-STMUT
        GPLA=PLA-SENLA
        GO TO 35
      Elseif(Crop.eq.'MZ') then
        EARWT=0.167*STMWT
        STMUT=STMUT-EARWT
        SWMIN=STMWT*0.85
        SUMP=0.
        IDURP=0
        PLAMX=PLA
      ELSE
        PGC=0.
        PAF=0.1
        MGROLF=0.0
        MPLA=0.0
        TSIZE=EXP(-0.15*(PLANTS-2.0))
      ENDIF
      PTF=1.0
   35 SUMDTT=SUMDTT-P3
      RETURN
    4 ISTAGE=5
      VANC=TANC
      VMNC=TMNC
      IF(CROP.EQ.'WH'.OR.CROP.EQ.'BA') THEN
        TBASE=1.
        GPLA=PLA-SENLA
        GRNWT=0.0035*GPP
        GO TO 45
      ELSEIF (CROP.EQ.'MZ') THEN
        SKERWT=0.
```

```
SUNAX=STMUT
      GO TO 46
    ENDIF
    PANUT=0.3*STHUT
    IF(CROP.EQ.'SG') THEN
       AG2=G2*0.05
       PANWT=STMWT*AG2
       GRAINN=PANWT*TCMP
       STOVN=STOVN-GRAINN
       STOWT-STOWT-PANUT
    ENDIF
    STMUT=STMUT-PANUT
    MPANWT=0.25*MSTMWT
    TPANWT=0.3*TSTMWT
    MSTMUT=MSTMUT-MPANUT
    TSTMUT=TSTMUT-TPANUT
    IF(CROP.EQ.'SG') THEN
      SUMIN=STMUT*.8
      LWMIN=LFWT*0.95
      SUMAX=STMUT
      PGC=PANWT*AG2
      GPP=1340.*((BIOMS2-BIOMS1)/IDUR1)
    ELSEIF(CROP.EQ.'ML') THEN
      SUMIN=MSTMUT*.8
      LWMIN=MLFWT*0.85
      SUMAX=MSTMUT
      PGC=MPANWT*0.11
      ISM=0
      GPP=3130.*(BIOMS2/IDUR1)
    ENDIF
45 SUNDTT=SUNDTT-P4
 46 EMAT=0.0
    RETURN
  5 ISTAGE=6
    IF(CROP.EQ.'WH'.OR.CROP.EQ.'BA') LAI=0.
    RETURN
  6 ISTAGE=7
    CUMDTT=0.
    CRAIN=O.
    CES=O.
    CEP=0.
    CET=0.
    DTT=0.
    RATIO=0.
    CUMRAT=0.
    RTWT=0.
    RETURN
  7 ISTAGE=8
    RTDEP=SDEPTH
    IF(CROP.EQ.'WH'.OR.CROP.EQ.'BA') RETURN
    IF(CROP.EQ.'MZ') TBASE=TBASE+0.5
    SUMDTT = 0.
    Y1=0.0
    Y2=0.0
    ASD=0.
    ASD2=0.
    RETURN
  8 ISTAGE=9
    CET=0.
    CES=0.
    CEP=0.
    CUMDTT=0.
    NDEF1=1.0
    NDEF2=1.0
    CRAIN=O.
    SUMDTT=0.
    TBASE=10.
    IF(CROP.EQ.'SG') P9=20.+6.*SDEPTH
    IF(CROP.EQ.'ML'.OR.CROP.EQ.'MZ') THEN
```

```
TBASE=TBASE+0.5
      P9=15.+6.*SDEPTH
  ENDIF
  IF(CROP.EQ.'WH'.OR.CROP.EQ.'BA') THEN
    P9=40.+10.2*SDEPTH
    TBASE=2.
    VF=0.
    CLIMVD=0.
    IF(CROP.EQ.'BA') P9=50.+10.4*SDEPTH
  ENDIF
  RETURN
9 ISTAGE=1
  SUMDTT=SUMDTT-P9
  GROSTM=0.
  GRNWT=0.
  SENLA=0.
  GRORT=0.
  WRAFY=0.
  TILN=1.0
  gropen=0.
grolf=0.
  IF(CROP.EQ.'WH'.OR.CROP.EQ.'BA') THEN
    DTT=SUMDTT
    TDU=0.0
    DF=0.01
    ILO=1
    LN=0
    LAI=PLANTS*4.E-6
    IF(CROP.EQ.'BA') LAI=PLANTS*4.E-4
    PLA=0.04
    LFWT=0.00034
    SEEDRY=0.012
    STMVT=0.
    STOWT=SEEDRY*0.5
    RTWT=SEEDRY*0.5
    BIOMAS=0.
    CUMPH=0.
    TILSW=0.01
    TBASE=0.
    TPSM=PLANTS
    PLSC(1)=0.
    GO TO 29
  ENDIF
  slan=0.
  TBASE=8.0
  REGM=1.
  IDUR=0.
  TLNO=30.
  LN=1
  PLAY=1.0
  IF(CROP.EQ.'MZ') THEN
    TBASE=TBASE+0.5
    CUMPH=0.514
    PLA=1.0
    SEEDRV=0.2
    LFWT=0.2
    STMWT=0.2
    RTWT=0.2
    EARWT=0.
    STOWIT=0.4
    NDF=0
    CUMDELAY=0.
    TLABIOL=0.
    TLABIOS=0.
    XASD2=0.
    RTNLAB=0.
  ELSE
    CUMDTT=CUMDTT-P9
    TPSM=1.
```

```
PLAN=0.
      PLATO=0.
      PLA0=0.5
      PLA=0.5
      MPLA=0.5
      TPLA=0.5
      MPLAG=0.0
      TPLAG=0.0
      LFWT=0.01
      MLFWT=0.01
      TLFWT=0.005
      SLW=0.
      RTWT=0.006
      STMUT=0.006
      MSTMWT=0.006
      TSTMWT=0.001
      PANDW=0.
      PANUT=0.
      MPANWT=0.
      TPANWT=0.
      MGROSTM=0.
      TGROSTM=0.
      TGROLF=0.
      MGROLF=0.
      MGROPAN=0.
      TGROPAN=0.
      TCARBO=0.
      TDUR=0.
      SUMRTR=0.
      TILSW=0.5
    ENDIF
    IF(CROP.EQ.'SG') THEN
      CUMPH=SUMDTT/PHINT
      STOWNT=0.016
      PLAY=0.13+0.003*G1
      SEEDRV=0.02
    ELSEIF(CROP.EQ.'ML') THEN
      CUMPH=SUMDTT/43.
      IDUR1=0
      STOVWT=LFWT
      SEEDRV=0.006
    ENDIF
    LAI=PLANTS*PLA*0.0001
    BIOMAS=STOWNT
    RWID=0.023
29 CUMDEP=0.
   IF (ISWSWB.EQ.0) RETURN
DO 30 L=1,NLAYR
      CUMDEP=CUMDEP+DLAYR(L)
      RLV(L)=0.20*PLANTS/DLAYR(L)
      IF(CROP.EQ.'WH'.OR.CROP.EQ.'BA')
        RLV(L)=0.0024*PLANTS/DLAYR(L)
      IF (CUMDEP.GT.RTDEP) GO TO 40
 30 CONTINUE
 40 RLV(L)=RLV(L)*(1.-(CUMDEP-RTDEP)/DLAYR(L))
   L1=L+1
    IF(L1.GE.NLAYR) GO TO 65
   DO 60 L=L1,Nlayr
      RLV(L)=0.
 60 CONTINUE
 65 DO 70 L=1,Nlayr
      RWU(L)=0.
 70 CONTINUE
   IF (ISWNIT.EQ.0) GO TO 80
   RANC=0.025
   TANC=0.050
   GRAINN=0.0
   IF(CROP.EQ.'WH'.OR.CROP.EQ.'BA') THEN
      RANC=0.045
```

TANC=0.045
ELSEIF(CROP.EQ.'MZ') THEN
RANC=0.022
TANC=0.044
c tanc=0.0457
ENDIF
ROOTH=RANC*RTWT
STOVM=STOVWT*TANC
80 RETURN
END

Appendix 2: Example of new input file

File: WT0201.NZ0

Appendix 3: Example of modified and new output files

File: OUT1.MZ

THE PROGRAM STARTED ON JULIAN DATE 100

DATE	COTT PHE	NOLOGICAL	STAGE	BI	DM	LAI	NUPTK	MX	CET	RAIN	PESW
25 May	0. SC	WING		g/m	^2	1	kg/ha		m	m	CIR
26 May	13. GE	RMINATION		•			_		9.	10.	17.
		IERGENCE								1.	
•		D JUVENIL			3.	.05	1.1	3.84		3.	
		ORAL INIT									
25 111	940 75	X SILKING		7	,, ,, ,	47	43.7	4 40	24	45	14.
		GIN GRAIN									
11 Sep	1465. EN	ID GRAIN F	ILL	8:	38.	.31	9.3	.31	43.	30.	12.
14 Sep	1493. PI	ID GRAIN F IYSIOLOGIO	AL MATU	RITY &	38.	.31	9.3	.31	43.	31.	11.
YIELD	(KG/HA)=	4585. (BL	J/ACRE)=	73.0 FIN	AL GPS	M=	1816.	KERNEL	. WT.(mg)=21	3.4
ISTAGE	CSD1	CSD2	CNSD1	CNSD2	CASE) S	TAG	E 0	F G	ROW	TH
1	.00	.00	.00	.00	.02	2 (EMERGE	NCE -	EN	D JUVE	NILE
2		.00									
2 3	.00	.00	10	40	22		FINDAL	INIT	- END	I F GP	ALTH
4		.05	.10	72			FUR I F	COTH	250	COATH	54 I I
											FILL
5	.12	.19	. 19	.52	.02	2 (GRAIN	FILLING	i PHAS	Ε	
* NOTE:		above tabl represent									
	nitroger	(CNSD)	and aera	tion (CAS	D) rea	spec.	tively				

File: OUT6.NZ

D1 104	•	Cambra / dama
RUN		Early, 4 days,

DOY 100		DEPWT =	77.00			
SUBIRR =	.96	DRAIN =	.00 POND =	.00 RUNOFF	=	.00
DEPTH	FLOUD	FLOWU	SW(L)	SAT(L)		
2.	.0000			.5280		
7.	.0000		.2227	.4510		
15.	.0000		.2231	.4510		
26.	.0630		.2880	.3440		
40.	.0573	.0430	.2972	.3260		
57.	.0525	.0066	.2949	.3160		
77.	.0474	.0007	.3160	.3160		
100.	.0000	.0036	.3160	.3160		
DOY 101		DEPWT =	77 00			
		DRAIN =		.00 RUNOFF		nn
DEPTH	FLOWD	FLOW		SAT(L)	_	
2.	.0000			.5280		
7.	.0000			.4510		
15.	.0000			.4510		
26.	.0000			.3440		
40.	.0000			.3260		
57.	.0000			.3160		
77.	.2415			.3160		
100.	.0000	.0046		.3160		
		.00-0	.5100	.5100		
DOY 102		DEPWT =	77.00			
SUBIRR =	.05	DRAIN =	.00 POND =	.00 RUNOFF	=	.00
DEPTH	FLOUD	FLOHU	SW(L)	SAT(L)		
2.	.0000	.0722	.1792	.5280		
7.	.0000	.0394	.2397	.4510		
15.	.0000	.0804	.2263	.4510		
26.	.0000	.0963		.3440		
40.	.0000	.0465	.2937	.3260		
57.	.0184	.0230	.2981	.3160		

77. .2599 .0472 .3160 .3160 100. .0000 .0043 .3160 .3160

File: QUT7.NZ

RUN 1 Late, 8 days.

DOY	TSW	TSWY	ES	EP	PREC	IRRI	SUBIR	DRAIN	POND	RUNOF	SW(1)	SW(2
	3) Sk			SW(6)	SW(7)							
107	35.82	35.99	.16	.00	.00	.00	.03	.00	.00	.00	.1237	.2242
.271	7 .25	80	.2801	.2906	.2934	.3011	.3160					
108	35.71	35.86	.15	.00	.00	.00	.03	.00	.00	.00	.1030	.2155
.268			.2818	.2904	.2933	.3017	.3160					
109	37.67	35.74	.25	.00	2.18	.00	.00	.00	.00	.00	.2715	.3246
.310			.3016	.2917	.2933	.3017	.3160					
110	_37.63	37.67	.24	.00	.20	.00	.00	.00	.00	.00	.1945	.2798
.291			.3039	.3018	.2965	.3149	.3160				2404	05.77
111	37.49	37.63	.24	.00	.10	.00	.00	.46	.00	.00	.2194	.2573
.281			.3002	.2997	.3014	.3055	.3160				4/00	2704
112	ຼ36.83	37.13	.30	.00	.00	.00	.01	.00	.00	.00	.1688	.2301
.278		74 OF	.2989	.2997	.2992	.3095	.3160	4 07	00	00	.3254	.3171
113 .313	37.95 ~	36.85	.30 .3057	.00	1.40	.00 .3055	.00 .3160	1.03	.00	.00	.3234	.3171
	37.89	738 38.32		.3027 .00	.2993 .00	.00	.00	.67	.00	.00	.1542	.2641
114 .285			.42 .3013	.3004	.3055	.3055	.3160	.07	.00	.00	. 1342	.2041
115	36.96	37.23	.3013	.00	.00	.00	.01	.00	.00	.00	.1236	.2342
.281			.2997	.3004	.3014	.3134	.3160	.00	.00	.00	. 1230	.6376
116	36.81	~2 36.97	.16	.00	.00	.00	.00	.00	.00	.00	.1003	.2250
.277		582	.2988	.3001	.3006	.3144	.3160	.00	.00	.00	. 1003	
117	37.32	36.82		.00	.86	.00	.00	.53	-00	.00	.3023	.2913
.296			.3013	.3003	.2979	.3055	.3160	100				
118	37.38	37.65		.00	.05	.00	.00	.39	.00	.00	.2027	.2605
.281		544	.3003	.2998	.2975	.3055	.3160		•••	• • •		
119	36.88	37.05		.00	.13	.00	.02	.00	.00	.00	.1704	.2467
.280		500	.2994	.2995	.2976	.3082	.3160		• • •			
120	36.68	36.90	.27	.00	.05	.00	.02	.00	.00	.00	.1592	.2208
.277	4 .2!	578	.2985	.2994	.2977	.3087	.3160					
121	36.63	36.70	.25	.00	.18	.00	.02	.00	.00	.00	. 1535	.2162
.276		570	.2979	.2992	.2978	.3092	.3160					
122	36.48	36.65	.16	.00 .	.00	.00	.01	.00	.00	.00	.1233	.2080
.274		550	.2969	.2989	.2978	.3096	.3160					
123	36.35	36.50		.00	.00	.00	.01	.00	.00	.00	.1018	.2002
.272		534	.2958	. 2985	.2978	.3099	.3160					
124	36.23	36.37	.13	.00	.00	.00	.01	.00	.00	.00	.0847	.1929
.270		519	.2947	.2980	.2978	.3102	.3160					
125	36.13	36.25	.12	.00	.00	.00	.01	.00	.00	.00	.0722	.1860
.268			.2937	.2975	.2977	.3104	.3160					
126	_36.03	36.14		.00	.00	.00	.01	.00	.00	.00	.0630	.1794
.267		691	.2926	.2969	.2976	.3105	.3160				AFF /	4336
127	35.93	36.04			.00	.00	.01	.00	.00	.00	.0554	.1732
.265	. 24	179	.2916	.2964	.2975	.3106	.3160					

HICHIGAN STATE UNIV. LIBRARIES
31293008850905