

71-20,076

WANJURA, Donald Frank, 1938-
A MODEL OF COTTON GERMINATION AND EMERGENCE

The University of Arizona, Ph.D., 1971
Agronomy

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A MODEL OF COTTON GERMINATION AND EMERGENCE

by

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A Dissertation Submitted to the Faculty of the

DEPARTMENT OF AGRONOMY

In Partial Fulfillment of the Requirements
For the Degree of

DOCTOR OF PHILOSOPHY

In the Graduate College

THE UNIVERSITY OF ARIZONA

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ACKNOWLEDGMENTS

I express sincere thanks to my major advisor, Dr. D. R. Buxton, for his advice and guidance throughout this study. The encouragement and assistance of Professor H. N. Stapleton during the course of the work is also noted.

My appreciation is extended to Drs. K. K. Barnes, R. E. Briggs, and M. A. Massengale for their help in serving on my graduate committee and assistance in reviewing the manuscript.

The support of the Departments of Agronomy and Agricultural Engineering is acknowledged for providing greenhouse facilities and constant temperature water bath tanks for conducting experiments.

The author is grateful to the Agricultural Engineering Research Division of Agricultural Research Service for the opportunity to attend graduate school.

The Cotton Producers Institute is recognized for their interest and financial support of the cotton plant simulation work at The University of Arizona.

The patience, understanding, and sacrifice of my wife, Sue, is greatly appreciated.

TABLE OF CONTENTS

	Page
LIST OF TABLES	vi
LIST OF ILLUSTRATIONS	x
ABSTRACT	xiii
 CHAPTER	
1. INTRODUCTION	1
2. LITERATURE REVIEW	5
Metabolism of Germinating Seeds	5
Water Absorption	7
Seed Moisture Content	8
Temperature	11
Physical Impedance	12
Aeration	13
Chilling Effect	14
Seedling Vigor	16
The Systems Concept	18
Plant Response Modeling	21
3. EMPIRICAL TESTS	25
Field Emergence	25
Controlled Environment	28
Radicle Emergence	28
Hypocotyl and Radicle Elongation	32
4. RESULTS AND DISCUSSION	35
Field Emergence	35
Controlled Environment Studies	37
Radicle Emergence	37
Seed Water Uptake	42
Seed-Moisture Percentage at	
Radicle Emergence	51
Hypocotyl and Radicle Elongation	54
Maximum Hypocotyl and Radicle	
Lengths	62

TABLE OF CONTENTS--Continued

CHAPTER	Page
5. EMERGENCE MODEL	69
Radicle-Emergence Model	70
System Description	70
Mathematical Definition	72
Evaluation of Model Constant	73
Model Verification	75
Model Application	82
Hypocotyl-Elongation Model	85
System Description	88
Mathematical Definition	89
Evaluation of Model Constant	91
Model Verification	93
6. SUMMARY AND CONCLUSIONS	98
APPENDIX A. MEASUREMENTS OF COTTON SEEDLING GROWTH, STATISTICAL ANALYSES, AND FLOW CHARTS FOR COMPUTER PROGRAMS	103
APPENDIX B. COMPUTER PROGRAM FOR SIMULATING THE 3-mm RADICLE EMERGENCE EVENT	129
APPENDIX C. COMPUTER PROGRAM FOR SIMULATING HYPOCOTYL ELONGATION	132
ABBREVIATIONS AND SYMBOLS	137
LITERATURE CITED	139

LIST OF TABLES

Table	Page
1. Average percentage emergence of cotton-seed planted at four depths in the field on April 15, 1969	36
2. Average measurements made on germinating seedlings prior to emergence for test planted April 15, 1969	39
3. Radicle-emergence time in hours for five soil temperatures and four moistures (average of six observations)	44
4. Accumulated R^2 values of regression model terms for seed moisture uptake over four soil moisture levels	45
5. Average seed-moisture percentage at the time radicles had emerged an average of 3 mm for five soil temperatures and four soil moisture levels (average of six observations)	51
6. Maximum hypocotyl lengths in cm for five temperatures, three moisture levels, and four physical-impedance levels	64
7. Maximum radicle lengths in cm for five temperatures, three moisture levels, and four physical impedance levels	65
8. Ratios of maximum hypocotyl/radicle lengths for five temperatures, three moisture levels, and four physical impedance levels	67
9. Radicle-emergence times in hours computed from Equation (4-5) (R) and predicted (P) by the seed-water-uptake model for four moisture levels and five temperatures	79

LIST OF TABLES--Continued

Table	Page
10. Comparison of observed and predicted 3-mm radicle-emergence times under variable environmental conditions	81
11. Statistics for estimating goodness of fit between observed and simulated hypocotyl elongation for fluctuating temperature with constant soil moisture and physical impedance	95
12. Daily maximum and minimum seed-depth temperatures (C) for four planting depths in test planted April 15, 1969 . . .	104
13. Average soil-moisture values for four depths of planting in test planted April 15, 1969	105
14. Average soil-impedance values for four depths of planting expressed in kg/cm ² in test planted April 15, 1969	105
15. Analysis of variance for maximum hypocotyl lengths	106
16. Analysis of variance for maximum radicle lengths	107
17. Analysis of variance for ratios of maximum mean hypocotyl lengths to radicle lengths	108
18. Chi-Square test of fit between actual and predicted imbibitional seed-water uptake	109
19. Average time-wise hypocotyl and radicle lengths at 15.6 C and .3-bar soil moisture for four levels of physical impedance	111
20. Average time-wise hypocotyl and radicle lengths at 15.6 C and 3.0-bars soil moisture for four levels of physical impedance	112

LIST OF TABLES--Continued

Table	Page
21. Average time-wise hypocotyl and radicle lengths at 15.6 C and 10.0-bars soil moisture for four levels of physical impedance	113
22. Average time-wise hypocotyl and radicle lengths at 21.1 C and .3-bar soil moisture for four levels of physical impedance	114
23. Average time-wise hypocotyl and radicle lengths at 21.1 C and 3.0-bars soil moisture for four levels of physical impedance	115
24. Average time-wise hypocotyl and radicle lengths at 21.1 C and 10.0-bars soil moisture for four levels of physical impedance	116
25. Average time-wise hypocotyl and radicle lengths at 26.7 C and .3-bar soil moisture for four levels of physical impedance	118
26. Average time-wise hypocotyl and radicle lengths at 26.7 C and 3.0-bars soil moisture for four levels of physical impedance	119
27. Average time-wise hypocotyl and radicle lengths at 26.7 C and 10.0-bars soil moisture for four levels of physical impedance	120
28. Average time-wise hypocotyl and radicle lengths at 32.2 C and .3-bar soil moisture for four levels of physical impedance	121
29. Average time-wise hypocotyl and radicle lengths at 32.2 C and 3.0-bars soil moisture for four levels of physical impedance	122

LIST OF TABLES--Continued

Table	Page
30. Average time-wise hypocotyl and radicle lengths at 32.2 C and 10.0-bars soil moisture for four levels of physical impedance	123
31. Average time-wise hypocotyl and radicle lengths at 37.8 C and .3-bar soil moisture for four levels of physical impedance	124
32. Average time-wise hypocotyl and radicle lengths at 37.8 C and 3.0-bars soil moisture for two levels of physical impedance	125
33. Average time-wise hypocotyl and radicle lengths at 37.8 C and 10.0-bars soil moisture for two levels of physical impedance	125
34. Values of K and R ² for the model of hypocotyl elongation for several combinations of constant temperature, moisture, and physical impedance	126

LIST OF ILLUSTRATIONS

Figure	Page
1. Methodology of applying systems theory in biology proposed by Mesarovic (1968)	19
2. The "black box" problem presented by biological systems	21
3. Ten seed in a soil cup arranged in a 5.7-cm-diameter circle for water uptake tests	31
4. Cups containing soil and 10 seed covered with Saran Wrap setting on a metal rack in a controlled-temperature, water-bath tank during seed water uptake tests	31
5. Relationship between maximum emergence percentage and planting depth from April 15, 1969 field test	38
6. Radicle-emergence time versus temperature for four soil moisture levels as computed from Equation (4-5)	43
7. Accumulated seed moisture for six temperatures at .3-bar soil moisture	47
8. Accumulated seed moisture for six temperatures at 1.0-bar soil moisture	48
9. Accumulated seed moisture for six temperatures at 3.0-bars soil moisture	49
10. Accumulated seed moisture for six temperatures at 10.0-bars soil moisture	50
11. Hypocotyl and radicle lengths versus time at 32.2 C and .3-bar soil moisture for four levels of physical impedance	56

LIST OF ILLUSTRATIONS--Continued

Figure	Page
12. Hypocotyl and radicle lengths versus time at .3-bar soil moisture and .23 kg/cm ² physical impedance for five temperatures	57
13. Hypocotyl and radicle lengths versus time at 32.2 C and .23 kg/cm ² physical impedance for three soil moisture levels	59
14. Cotton seedlings after 5 days at 32.2 C, 3.0-bars soil moisture, and .23 kg/cm ² physical impedance showing elongated hypocotyls and radicles with lateral roots	61
15. Cotton seedlings after 5 days at 32.2 C, 10.0-bars soil moisture, and .23 kg/cm ² physical impedance showing elongated radicles without hypocotyl growth	61
16. Time-constant values for different levels of soil temperature and moisture computed from Equation (5-5)	76
17. Change in imbibitional, seed-moisture percentage (ΔM) for different environments prior to the 3-mm radicle-emergence event as predicted by the seed-water-uptake model	78
18. Total and predicted, imbibed-seed-water content at .3-bar soil moisture for different temperatures at 3-mm radicle emergence	83
19. Total and predicted imbibed-seed-water content at 1.0-bar soil moisture for different temperatures at 3-mm radicle emergence	84
20. Total and predicted imbibed-seed-water content at 3.0-bars soil moisture for different temperatures at 3-mm radicle emergence	86

LIST OF ILLUSTRATIONS--Continued

Figure	Page
21. Total and predicted imbibed-seed-water content at 10.0-bars soil moisture for different temperatures at 3-mm radicle emergence	87
22. Flow chart of computer program for simulating the 3-mm radicle-emergence event	110
23. Flow chart of computer program for simulating hypocotyl elongation	128

ABSTRACT

This investigation measured the influence of soil temperature, moisture, and physical impedance at steady-state levels on cottonseed (Gossypium hirsutum L.) water uptake and seedling elongation. Each parameter was varied over the range of values normally encountered under field conditions. The information obtained provided the basis for formulating a model of imbibitional seed water uptake and hypocotyl elongation.

As temperature increased from 15.6 to 32.2 C, time required for 3-mm radicle extension decreased while total length and elongation rate of hypocotyls and radicles increased. When temperature was increased to 37.8 C, these relationships were reversed. This high temperature was found to be more severe on hypocotyl than radicle growth, especially when soil moisture was limiting. Seed-moisture percentage at 3-mm radicle emergence was highest for the extreme temperatures.

Increasing soil moisture from .3 to 10.0 bars decreased rate of imbibitional-water uptake and seed-moisture percentage at radicle emergence, and increased time required for 3-mm radicle extension. Both high soil-moisture tension and high physical impedance exerted a

greater limiting effect on final hypocotyl than radicle length.

Values of parameters in the mathematical models were estimated from the data and functionally related to soil environment. Accumulation of imbibitional water was used to model the 3-mm radicle emergence event. The basis of the model is a linear differential equation with a single lumped constant, $T \frac{dW}{dt} + W = W_S$. Environmental influence on rate of seed-water uptake ($\frac{dW}{dt}$) is reflected by the parameter, T . W is seed-water content and W_S is the steady-state level of imbibitional seed water. W_S was found to be a constant (80% dry basis moisture) for the range of soil temperatures and moistures studied. Discrete simulations were performed using time intervals of 1 hour. Predicted radicle-emergence times under fluctuating temperature regimes were within 10% of observed values. Simulations of constant environmental conditions suggested that the major portion of the seed's moisture at radicle emergence results from imbibition.

Average hypocotyl elongation of a population of emerging seedlings was modeled using a nonlinear differential equation that describes the dynamics of an autocatalytic reaction, $\frac{dE}{dt} = KE(E_S - E)$. Elongation rate is represented by $\frac{dE}{dt}$, K is a constant, E is hypocotyl length, and E_S is maximum attainable length for a given steady-state environment. Environment affects elongation rate by

changing the magnitudes of K and E_S . The model satisfactorily simulated hypocotyl elongation at the .05 level of significance under fluctuating temperatures in 8 of 10 comparisons. There was a tendency to underestimate growth when temperatures exceed 32.2 C. This suggests a temperature by time-duration interaction above the optimum temperature for growth where elongation is increasingly depressed by longer duration of high temperatures.

FORTTRAN programs for the radicle emergence and hypocotyl elongation phases of the model are documented in the report. The model predicts mean response. Distribution of the population could be described if its variance were known for different conditions.

CHAPTER 1

INTRODUCTION

Problems encountered in obtaining a healthy stand of cotton (Gossypium hirsutum L.) plants are frequently related to eagerness of the grower to begin the crop season and unpredictability of weather during the early planting period. Provided the grower plants vigorous, viable seed, failure to obtain satisfactory emergence is caused directly or indirectly by the environment. The work of Bowen (1966) has demonstrated that the soil parameters most commonly limiting are temperature, moisture, physical impedance, and aeration.

The planting to emergence period of cotton production may not be the most critical phase in the productive life of the plant; however, it is the first critical phase. Stress during this period results in either an inadequate number of plants for profitable production or a highly diverse plant population which makes crop management difficult. Replanting because of an inadequate stand requires additional expense and loss of part of the growing season. Nonuniform stands magnify the difficulty in determining the optimum time of performing subsequent production operations. Poorly timed operations usually reduce profits.

The cotton fiber industry has lost much of its market to synthetic fibers since World War II. This situation has caused a reduction in cotton acreage and fiber price. Consequently, today much of cotton production research is oriented toward cost reduction. For the grower, cost reduction means the crop must be managed more effectively. Efficient management requires an understanding by the manager of the system which he is attempting to control. The ultimate understanding of a system can be represented by a model whereby the system can be simulated. The ability to realistically model a system depends on how well the system is understood.

Modeling can be very beneficial, even if the initially developed models are not sufficiently realistic for accurate simulation. An immediate result from initial attempts at modeling is the clarification of what is known about the system. Then as model development progresses, critically lacking areas of information are highlighted, which is often the first benefit derived from a model. It is the availability of critical information which determines whether a realistic model can be developed. Once the knowns and unknowns are clearly established, future research can be effectively pursued. The model thus helps to define areas of fruitful research.

Every researcher should have a general model concept for the system to which his research relates. Once the

overall system model is visualized, the areas requiring research are evident. The important decision remaining is that of assigning priorities. The most important problems, then, can be studied first and the study of lesser problems delayed. An orderly sequence in approaching research offers the likelihood of reducing redundancy to a minimum.

A properly conceived model has the potential of a decision making aid for growers or managers. If the inputs to the model are parameters that can be monitored by the producer, he can provide the necessary information for simulating the growth of his crop. The process of providing a record of inputs to the crop will increase the producer's personal knowledge of its progress. A more-aware producer having the aid of a model to simulate the progress of his crop is likely to make better management decisions, especially in marginal situations.

The research documented in this report was undertaken to provide a better understanding of the dynamics of cotton emergence. The general approach is that of input-output analysis. Inputs to the germinating and emerging seedling were controlled at specific levels and the output from the seed was measured. No attempt was made to model the internal metabolic activities in the plant.

The specific objectives of this investigation were as follows:

1. Experimentally measure the growth response of the germinating and emerging cotton seedling to soil temperature, moisture, and physical impedance.
2. Develop models for predicting the time for radicle emergence and hypocotyl elongation from the empirical data.
3. Verify the models by using them in simulation.

CHAPTER 2

LITERATURE REVIEW

Germination of cottonseed is an area of research which has received much attention. Work concerning metabolic changes during germination and the most common factors limiting germination and emergence are included in the following literature review. This section ends with a brief discussion of systems theory and current models of plant responses.

Metabolism of Germinating Seeds

As seed begin to imbibe water, the first easily observable change is an increase in respiration rate followed by a breakdown of reserve materials (Mayer and Poljakoff-Mayber, 1963). The energy required for germination is supplied by the breakdown of stored carbohydrates and lipids through respiration. Conversion of fats to glucose occurs via the glyoxylate cycle which bypasses part of the Krebs cycle. The established mechanism of respiration is that of glycolysis in which glucose is broken down to pyruvate. Pyruvate is then oxidized in the Krebs cycle. Following the degradative process of respiration the breakdown products are transported from the endosperm

or cotyledons to the growing axis and new materials are synthesized.

Marre (1967) reported total mitochondrial enzyme activity generally increased almost in parallel with water uptake and respiration in castorbean seed (Ricinus communis L.). However, the time sequence for individual enzymes showed significant differences. During early germination there was a de novo synthesis of almost all the ribosomal apparatus. Total ribonucleic acid (RNA) content increased slowly at first followed by a very rapid increase. Cherry (1963) found that the RNA content in germinating peanuts (Arachis hypogaea L.) increased threefold by the 8th day after water imbibition, followed by a rapid decline.

Phosphates play an extremely important role in many reactions. Phosphorous is required for nucleic acid (RNA and DNA) formation, which in turn is essential to protein synthesis. Phytin is a phosphorous compound frequently present in seeds and may contain up to 80% of the total phosphorous fraction. Ergle and Guinn (1959) showed that all phytin in 6-day old cotton seedlings was present in the cotyledons. The initial phytin level in the seed was high but quickly dropped during germination. Concurrently, inorganic phosphate accumulated.

One form of evidence for transport of materials in the seed during germination is the decrease in dry weight of certain seed parts. Cherry (1963) found that peanut

cotyledons decreased in weight due to a depletion of reserves. Similar results were reported for germinating cottonseed at several temperatures by Christiansen (1962).

The importance of water to seed metabolism was demonstrated by Marre (1967) using castorbean seed. Blocking seed water uptake after 40 hours of imbibition resulted in decreased enzyme activity to almost zero after 48 hours. Twenty-four hours after stopping water uptake RNA synthesis had stopped and polysomes had largely reverted to monosomes. Forty-eight hours after the seed was permitted to continue imbibition, polysome content increased and monosomes decreased. Protein synthesis was inhibited during the water stress period and this was interpreted as resulting from an inhibition of polysome formation.

Water Absorption

Dewez (1964) pointed out that when seed absorbs water, initially there is a rapid uptake phase followed by slower uptake. The rapid phase is usually attributed to physical wetting of the seed tissue while the slower phase is influenced by metabolic processes. The slower phase, which occurs at a constant rate, is a quasi-stationary state of water uptake. This state is continuously modified by changes induced by the growth process.

Based on a theoretical analysis of moisture diffusion in a silty loam soil, Hadas (1969) concluded that

total seed-soil contact areas ranging from 1 to 100% nor total water stress between field capacity and wilting point had an important effect on imbibition. However, he found that contact area, the part of the seed in contact with water, total water stress, and water uptake rate may be decisive during the "triggering" stage that follows imbibition. Collis-George, Melville, and Phillips (1969), in a later communication, disagreed with the imbibition equation used by Hadas and the use of the average diffusion coefficient for seed in his analysis.

Moisture absorption through the seed coat has been studied by several researchers. Moisture was found to diffuse through the entire seed coat of cotton exposed to moisture saturated air by Burch and Delouche (1959). Phillips (1968) concluded water was not preferentially absorbed through the micropyle. Comparing cotton, soybeans (Glycine max L.), castorbean, and oat (Avena sativa L.) seed, Burch and Delouche (1959) found that cotyledons absorbed more moisture in relation to their dry weight than did endospermous tissue.

Seed Moisture Content

Dewez (1964) reported that cottonseed placed in moisture saturated air at temperatures of 20, 30, and 47.5 C absorbed moisture to a common asymptotic value of 80% dry basis. The asymptotic value was approximately the

maximum amount of moisture absorbed by imbibition. Germination of cottonseed was obtained at .33-, 1.0-, and 4.0-bars moisture, but not at 15.0 bars in work reported by Phillips (1968). Average moisture content per germinated seed, with radicle lengths from 2 to 4 mm, was .088 g for all soil moisture levels. Burch and Delouche (1959) found a moisture content of 50 to 55% wet basis was necessary to produce 50% germination of cotton and soybeans.

Hadas (1970) studied the germination (2-mm radicle length) of clover (Trifolium alexandinum L.) and chickpea (Cicer arietinum L.) seed in soils of different moisture contents. One hundred per cent germination resulted when the relative water uptake of clover and chickpea seed reached 100 and 80% of initial seed weight, respectively. Final water content for cloverseed was the same for soil moisture percentages of 17, 14, and 11, but rates of uptake varied. It was concluded that even at relatively low soil moisture levels the limiting factor to moisture absorption was the internal moisture potential of the seed.

The influence of water on the germination of range grasses has been extensively studied by Collis-George and Sands (1959, 1962). In the moisture tension range .65 to 1.0 bar, neither percentage of seed area in contact with soil nor the orientation of the seed was important in germination. Water uptake by seed is likely controlled by soil matric potential and hydraulic conductivity when other

physical factors are constant. Collis-George and Hector (1966) concluded matric potential was important in germination because of three possible causal factors: (1) the direct effect of energy on water uptake by seed, (2) the indirect effect of controlling the wetted area of contact between seed and soil, and (3) the indirect effect of controlling strength of the soil and compression of seed. Matric potential had a greater influence on germination than did osmotic potential produced by glycerol or sodium chloride solutions. Ten bars of osmotic potential was approximately equivalent to .1 bar of matric potential. Collis-George and Sands (1962) concluded that their results supported the hypothesis that osmotic potential does not permanently manifest itself in biological systems, because there is no truly semipermeable membrane which permanently excludes the solute external to the cell. Monohar and Heydecker (1964) also showed that matric potential had a greater influence on germination of peas (Pisum sativum L.) than an equal magnitude of osmotic potential. They attributed their results to a reduction in contact area between the seed and the surrounding water film as the matric potential increased.

Hunter and Erickson (1952) reported characteristic soil moisture stresses above which seeds of a given species would not germinate. The reported values were 12.5, 7.9, 6.6, and 3.5 bars, respectively, for corn (Zea mays L.),

rice (Oryza sativa L.), soybeans, and sugar beets (Beta vulgaris L.). Hadas (1970) reached a similar but more generalized conclusion. He indicated that a given species germinates in a characteristic moisture range, depending on the seed's capabilities, the soil moisture potential, and conductivity of the soil.

Temperature

Ludwig (1932) and Mariani and Dag (1962) reported cottonseed germination on filter paper in petri dishes with a temperature as low as 12 C; however, Camp and Walker (1927) obtained no germination at 14 C in soil. The optimum germination temperature was reported to be between 33 and 36 C by Arndt (1945). The results of Camp and Walker and of Arndt indicate that the maximum temperature for cotton germination is approximately 40 C.

The cardinal temperatures for growth of the hypocotyl and radicle are similar to those for germination. Arndt (1945) reported that optimum temperature range for root elongation of 33 to 36 C for the first 3 days shifted to 27 C after a length of 50 to 80 mm was reached. The optimum temperature for radicle growth of 25 C reported by Galligar (1938) is slightly lower than that reported by Arndt. Arndt (1945) found the optimum temperature for hypocotyl elongation to be 33 C for the first 4 days, with a shift to 36 C after the 5th day when the seedling attained

a total length of 160 mm. Root optimum temperatures changed at the stage where the slower emerging but more rapidly growing hypocotyls were about equal in length to the faster emerging but slower growing primary root.

Physical Impedance

Physical impedance was one of four potentially limiting edaphic factors for seedling emergence, along with moisture, temperature, and aeration, identified by Bowen (1966). Morton and Buchele (1960) designed a "mechanical seedling" probe to simulate the seedling energy expended during emergence. Emergence energy increased directly with compaction pressure, initial moisture content, amount of soil surface drying, and indirectly with moisture content at time of measurement. Under drying conditions, emergence energy was greatly reduced by applying the initial compacting pressure at seed level rather than at the soil surface.

The results of the study by Bowen (1966) showed that at high soil moisture, increasing magnitude of surface compaction greatly increased physical impedance. A surface compaction of $.07 \text{ kg/cm}^2$ (1 psi) applied to soil near field moisture capacity limited emergence within 2 days; however, $.37 \text{ kg/cm}^2$ (5 psi) became limiting after only a few hours. A figure of merit for physical impedance was developed from the study based on the required hydraulic pressure in a buried rubber balloon needed to rupture the covering soil.

Physical impedance was considered nonlimiting if the rupture pressure during the first 8 days following planting was less than $.84 \text{ kg/cm}^2$ (11.5 psi).

In a laboratory study under nondrying conditions and 32.2 C by Garner and Bowen (1966), zero surface compaction produced the most rapid cotton hypocotyl elongation. No difference was found for compactions of $.07$, $.22$, and $.37 \text{ kg/cm}^2$ (1, 3, and 5 psi). The same study showed that maximum diameter of hypocotyls increased linearly with increasing soil compaction. The conclusion of a field study by Wanjura, Hudspeth, and Kirk (1966) using Amarillo loam and fine sandy loam soils indicated surface compaction as small as $.04 \text{ kg/cm}^2$ (.6 psi) decreased cotton emergence. Soil strength was directly related to magnitude of surface pressure applied during the planting operation. Subject to modification by other environment parameters, the maximum allowable soil strength that did not greatly affect cotton emergence was in the range of 1.4 to 2.1 kg/cm^2 (20 to 30 psi).

Aeration

Germination and emergence require aerobic respiration in which the moles of carbon dioxide evolved are approximately equal to the moles of oxygen absorbed. Excessive soil moisture usually results in a low oxygen content in the soil. Work of Coble (1965) pointed out some

interesting factors related to oxygen requirements for germinating cottonseed. Submerging cottonseed in water for 15 minutes reduced the partial pressure of oxygen in the seed almost to zero. A theoretical analysis suggested that oxygen diffusion rate through a water logged seed coat was insufficient to satisfy the aerobic respiration requirement of a germinating cottonseed. The author concluded that oxygen supply in sandy soils is sufficient when the soil moisture tension is greater than .05 bar. Bowen (1966) developed a figure of merit for aeration using measurements obtained with a specially constructed permeameter. Seven-day average of air permeability readings (beginning 2nd day after planting), taken 23 hours after application of water, must be greater than $K = .05 \times 10^{-8} \text{ cm}^2$.

Chilling Effect

Elucidating evidence has been accumulated during the past 10 years on effect of chilling during early phases of germination. Christiansen (1963) subjected germinated cotton seedlings to combinations of cold (5 and 10 C) and warm (31 C) treatments. A cold-warm regime caused root tip abortion and an initial growth lag followed by normal development. A warm-cold regime caused drastic reduction in growth rate and death or inactivation of cortex tissue.

In a later study, Christiansen (1968) allowed cottonseed to imbibe water for 4 hours at 31 C and then

air dried prior to germinating at 5 C. Chilling immunity resulted and it was hypothesized that an irreversible event, which is prevented by chilling, occurs during early seed hydration. Subsequently, Christiansen (1969a) suggested that the irreversible event occurs before 13% seed moisture is reached. Seed respiration was found to triple between 12 and 16% moisture at 30 C. Christiansen (1969b) reported germinating cotton seedlings at 5 C exuded sugars and amino acids from the radicle tip. A respiration inhibitor, sodium azide, caused exudation rates comparable to the 5 C treatment. Removing either stimulus stopped exudation. Based on the concept that respiration is essential for membrane integrity, it was suggested radicle exudation was due to deficient energy levels caused by impaired respiration.

Hayman (1969) found cotton seedlings exuded more sugars at low than high temperatures, but exudation was not correlated with rate of germination or respiration. The glucose equivalents lost by germinating cottonseed at the same physiological age (1-mm radicle extension) was 7 and 3 times greater at 18 and 24 C, respectively, than at 30 C. The seeds lost more materials in water than in moist sand and Hayman postulated higher exudation in water was due to initial uncontrolled leakage. If uncontrolled leakage occurred, it could indicate membrane damage caused by higher absorption rates in water.

Pollock and Toole (1966) found survival and size of seedling lima beans (Phaseolus lunatus L.) were greatly reduced by imbibition at 15 C followed by germination at 25 C. However, a short initial period of imbibition at 25 C almost completely avoided adverse effects of low temperature which is in agreement with the work of Christiansen. The chill sensitive stage was found to be over before the excised embryo axis reached 50% moisture based on original weight. Chilling injury caused excised embryonic axes to lose organic materials. These authors proposed that membrane damage was involved.

The laboratory results discussed above were supported by Christiansen and Thomas (1969). Cotton seedlings were chilled at 10 C for 2, 4, or 6 days during germination and transplanted to the field. Final plant height and date of first flower were linearly retarded by increasing duration of chilling. Fiber quality as measured by Micronaire reading was also adversely affected.

Seedling Vigor

The precise definition and determinant of seedling vigor are still unknown. Most studies of seedling vigor have used all or part of the criteria of rapidly emerging, healthy stands of plants which produce high yields of the desired product, as indices of vigor. Kneebone and Cremer (1955) studied the influence of seed size on vigor in five

range grass species. Their results showed larger seed emerged faster and grew more rapidly. Vigor (as measured by speed of emergence, stand, height, and early forage production) within a seed lot increased with seed size. Three cotton cultivars were separated into size classes from .40- to .67-cm diameter by Porterfield and Smith (1956). Field emergence and yield of intermediate-size seed classes were greater than the largest or smallest-diameter seed.

Wilkes, Kunze, and Niles (1968) studied seedling vigor of two cotton cultivars in field tests. Rate of emergence and total emergence were directly correlated with seed weight and density. Both cultivars showed a significant increase in free fatty acid content as the seed weight decreased.

A study by Wanjura, Hudspeth, and Bilbro (1969a) analyzed the relationship between laboratory germination percentage and field performance of one cotton cultivar. For three different emergence times from a single planting date, the percentage of surviving emerged plants decreased with increasing time for emergence and with decreasing germination percentage. The amount of time required for emergence was concluded to be a good indication of a plant's vigor.

Tupper (1969) conducted a study to correlate length, diameter, weight, volume, and density of seed from

two cotton cultivars with vigor. Seed weight had the greatest affect on seedling growth in germination tests. Seed density exerted the most influence on germination and early seedling growth in tests conducted under standard conditions (20 and 30 C) and under cold test conditions (18.3 C). In field tests, the best indicator of emergence was the percentage of normal seedlings obtained after 7 days in the cold test. Plants produced from light seed showed less uniformity in yield than those from heavy seed.

The Systems Concept

The systems approach to problem solving is relatively young as a formalized concept. Some of the fundamental ideas inherent to systems analysis have long been embodied in the researcher's scientific method. Most definitions of a system convey the same basic ideas, with the exact wording reflecting the particular viewpoint of the definer. Milsum (1966) defined a system as, "Any collection of communicating materials and processes which together perform some function in which the investigator is interested." The behavior of a system is determined by: (1) characteristics of the components, (2) structure of communication between components, and (3) input signals or variables to the system.

Mesarovic (1968) discussed the general aspects of formalized systems theory as it relates to biology.

Systems theory is based on the idea that any real life phenomena (biological or otherwise) can be represented as an image termed a model. The formal aspects of the model can be represented as a mathematical relationship. After a system has been modeled mathematically, the problem of systems theory is to study the properties of the system. The methodology of the systems approach for biological applications is schematically represented in Fig. 1 by Mesarovic. In applying the procedures in Fig. 1, steps A, B, and C are performed in a recursive rather than sequential manner.

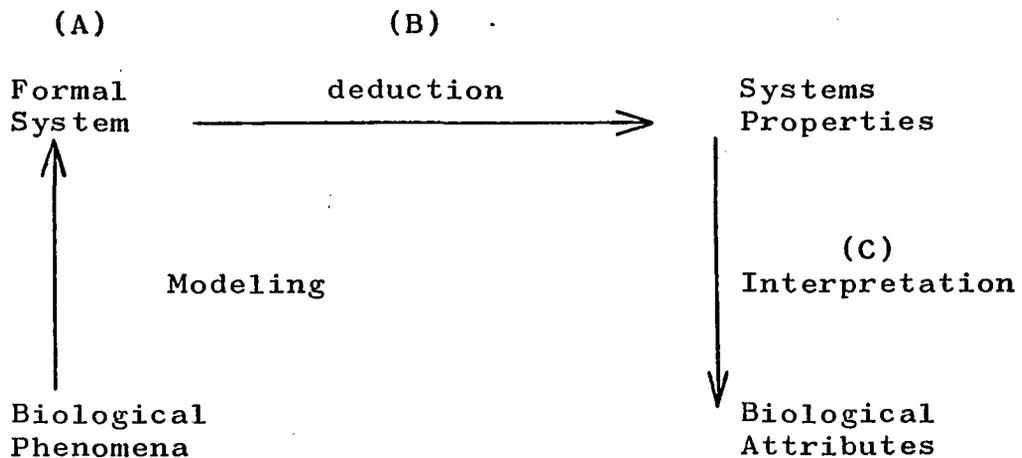


Fig. 1. Methodology of applying systems theory in biology proposed by Mesarovic (1968).

Several other ideas are presented by Mesarovic which are important in applying systems analysis to biology. Non-numerical systems specification will become

increasingly important because of biological complexity and individual variations. A given system can have many alternate constructive specifications. The specification utilized depends on the interest of the modeler. There are really two distinct areas of systems theory. The first is general systems theory which is primarily concerned with formal systems specification (step A in Fig. 1). The second area includes the various specialized branches of systems theory; such as linear control theory, automata theory, estimation theory, etc. This area is applied in step B of Fig. 1.

A final point to be drawn from Mesarovic is the idea of considering biological systems as goal seeking (i.e., teleological) in order to develop effective constructive models. However, in a complex goal-seeking system there exists a hierarchial interdependence of goals. Biological systems are in general multilevel and multigoal. Attempts to represent them as a single level (even if multivariable) system, or as an input-output system can result in a model which is valid for a narrow set of conditions.

The most common systems analysis situation encountered by the biological researcher is discussed by Grodins (1963) and depicted in Fig. 2. The input and output to the system are known, but the internal mechanism which converts the input to the observed output is unknown.

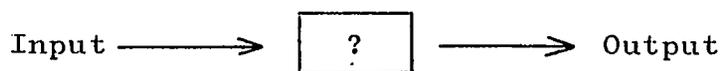


Fig. 2. The "black box" problem presented by biological systems.

This situation is often referred to as the "black box" problem. In biological systems it is often difficult to isolate the system of interest. Furthermore, all inputs may not be controllable or the system's components may vary over time. Consequently, mathematical descriptions of laws for biological systems are often statistically derived.

Plant Response Modeling

Recently, interest in modeling natural systems has greatly increased. For crop plants, earlier models were regressions relating environmental parameters to yield. Chen et al. (1969) developed functional relationships between photosynthesis, respiration, and carbohydrate accumulation. Temperature and light intensity were the inputs which produced carbohydrates. A dynamic model of vegetative growth was proposed by Curry (1969) which utilized the coupling of photosynthesis, respiration, and evapotranspiration. This model produced reasonable results using environmental inputs and basic data for corn. The

model was conceived as a first approximation of a possible dynamic modeling approach for plant growth systems.

Several models are being developed for simulating the complete plant growth cycle. Stapleton and Meyers (1969) have reported a model for cotton. This model is considered by these authors as the major subsystem in a cotton production system. Distributive analysis of plant component subsystems has resulted in usable models for evapotranspiration, photosynthesis, vegetative growth, and fruit development and maturation. ELCROS (Elementary Crop Growth Simulator) is a model proposed by Wit and Brouwer (1968) for simulating the total crop plant response. Plant condition and environmental inputs are used in models of respiration, photosynthesis, and transpiration. Growth is simulated by accounting for temperature, reserves, age of tissue, and water stress. Williams and Loomis (1969) are developing a model patterned after ELCROS for sugar beet growth called SUBGRO.

Previous models for predicting cotton emergence have only considered the temperature influence. For a 2.5-cm planting depth and constant temperature levels, Bowen (1966) related the number of degree-hours above a base of 12.8 C to produce cotton emergence. The required degree-hours varied from 2600 at 19 C to 3360 at 40 C, with a minimum of 2450 at 25 C. Wilkes, Cochran, and Niles (1968) concluded 1200 degree-hours in the range of 18.3 to

26.7 C were needed for initial emergence under field conditions from a 5-cm depth.

A growth chamber study by McQuigg and Calvert (1966) related soil temperature and elapsed time to average cotton emergence. Temperature-duration regimes were also identified which produced no emergence, some emergence, and acceptable emergence.

The work of Riley et al. (1964) showed that minimum, maximum, and average, seed-depth temperature can be used to predict the number of days required from planting to initial cotton emergence. Results of Wanjura, Hudspeth, and Bilbro (1967, 1969b) agreed with those of Riley et al. From field studies, relationships were established between time of initial emergence, time to reach 45% of final emergence, and accumulated daily minimum, seed-depth temperature. As a rule of thumb, 103 hours of temperature above 18 C were needed to achieve initial emergence from a 5-cm depth.

An average hypocotyl elongation model was developed by Wanjura, Buxton, and Stapleton (1970). This model utilized average, temperature-dependent growth rates computed from data published by Arndt (1945). Since average growth rates were utilized, the model only simulated true hypocotyl length at emergence. The model did predict emergence time for a 5-cm planting depth, even though the time-wise predictions of hypocotyl length were

not accurate. In addition to the limitation of a single planting depth, all other potentially influencing factors of hypocotyl growth were required to be nonlimiting.

CHAPTER 3

EMPIRICAL TESTS

The average, hypocotyl-elongation model reported by Wanjura et al. (1970) assumed that temperature was the only input to seedling emergence. This condition is approached during planting under many field conditions. For many adverse circumstances, however, the model is not applicable. A cotton-emergence model having wide applicability must include the main environmental factors that are often limiting under field situations. Consequently, the work reported here was undertaken to develop a cotton emergence model having wide applicability.

Past research, particularly the work of Bowen (1966), showed that soil environmental parameters of temperature, moisture, and physical impedance were important inputs to cotton emergence. These are the only parameters considered in the following tests. It is recognized that other environmental factors can influence emergence, but in most situations the parameters listed above determine emergence.

Field Emergence

The first attempt to obtain data for an emergence model was in a field test where soil temperature, moisture,

physical impedance, and plant development were monitored. A variable depth planting test was begun in clay loam soil at The University of Arizona Campbell Avenue Farm, Tucson on April 15, 1969. A preemergence herbicide, Prefar (0,0-dissopropyl phosphorodithioate S-ester with N-[2-mercaptoethyl] benzenesulfonamide), was applied and incorporated on March 25th at the rate of 2.24 kg/ha of active material. The site was broadcast with 100 kg/ha nitrogen (N) using ammonium nitrate on April 1 followed by sprinkler irrigation. The experimental design was a randomized complete block with four replications using planting depths of 2.5, 5, 7.5, and 10 cm. Commercially produced, acid-delinted cottonseed of the cultivar 'Deltapine 16' treated with Ceresan (methyl mercury acetate, methyl mercury 2,3-dihydroxy propyl mercaptide) was hand planted at 2.5-cm intervals with a total of 100 seed per replication. The seed lot had a germination of 91% in the standard test (alternate 20 and 30 C) and 61% under a constant 18 C temperature.

The seed furrow was formed with a cultivating sweep on a sled runner. After the seed were placed in the furrow, they were pressed into the soil with a standard seed firming wheel, and the furrow was closed with a hoe and rake. The following data were taken after planting: Soil temperature at each planting depth at hourly intervals, soil moisture at planting depth at 2-day intervals,

soil physical impedance measurements at 2-day intervals, seedling germination, growth measurements prior to emergence from the soil, and plant emergence.

Soil temperatures were measured with a Honeywell Elektronik 15 strip chart multipoint recorder. Three copper-constantan thermocouples connected in parallel were inserted into the soil at each planting depth. Soil moisture samples were taken with a 2.5-cm diameter, split-tube, soil sampler. The sample was taken in the interval plus and minus 1.25 cm from the actual planting depth. Moisture was determined gravimetrically and expressed in bars. Physical impedance measurements were taken with a Chatillon push-pull gauge with a .4-cm diameter blunt probe. Measurements were made by observing the maximum force required to push the probe 2.5 cm into the soil.

Measurements were made of developing seedlings prior to the time of emergence by digging up seedlings at various intervals. Total seedling length, percentage germination, and number of plants observed at each sampling were recorded. Measurements were made up to 167 hours after planting; from that time on the radicle was too long to permit removal of the entire plant without losing part of the radicle.

Preliminary evaluation of the field study results indicated that information obtained would not be suitable for use in a model development. Seedling development could

not be accurately measured until emergence. Environmental parameters could be monitored, but they could not be controlled over a sufficiently wide range. Data gathered, however, could be useful in evaluating a model developed from other data. Due to shortcomings of the field study, it was decided that the desired information could best be obtained in studies under controlled conditions.

Controlled Environment

The study of germination and emergence of cotton seedlings was divided into two phases: (1) planting until the radicle extended 3 mm outside the seed coat (germination), and (2) 3-mm radicle extension until the hypocotyl emerged from the soil (emergence). These two phases of young seedling growth are sufficiently different to require individual consideration in a realistic model of these stages of development. These studies were conducted in temperature-controlled water baths in the Department of Agronomy Greenhouse on The University of Arizona Campus, Tucson.

Radicle Emergence

Tests were conducted to measure rate of water uptake by cotton seed under several soil moisture and temperature regimes. Commercial Deltapine 16, acid-delinted seed, treated with Ceresan was used. Initial seed moisture content was 8.0% on a dry weight basis. The seed

were visually examined and seed with a cracked seed coat, extremely small in size, or irregular in shape were discarded. After screening, the seed were separated into groups of 10; weighed to the nearest .01 g, and placed in small packets. An added limitation was imposed requiring a group of 10 seed to weigh between .9 to 1.1 g.

Soil utilized in all tests was a mixture of 75% soil obtained from the Avra Valley area and 25% sand from the Rillito River bed. Both materials were obtained from Tucson Sand and Soil Company, Tucson. A curve of soil moisture tension versus soil moisture percentage on a dry weight basis was obtained from the Soil and Water Testing Laboratory of the Agricultural Chemistry and Soils Department. A soil texture analysis using the hydrometer method indicated that the mixture was: 78.4% sand, 14.1% silt, and 7.5% clay, resulting in a textural classification of sandy loam. The soil mixture had a pH of 7.9.

In preparing for radicle emergence tests, soil was poured in thin layers on a concrete slab and dried in the sun. After drying, the soil was put through a 3.5-mm mesh screen and the moisture content determined gravimetrically. Next, 300 g of air-dried soil were poured into plastic cups with a diameter of 10 cm and a depth of 4.5 cm. This amount of soil filled the cups to a 3.8-cm depth.

Before placing seed in each cup, 125 g of soil were removed. Then 10 seed were uniformly placed around a

5.7-cm-diameter circle in a horizontal plane with the aid of a templet (Fig. 3). After the seed were pressed into the soil, the 125 g of soil were replaced. At the beginning of a test, the proper amount of water was added to each cup to bring the soil to the desired moisture level. The water was first conditioned to the proper, treatment temperature.

The cups were covered with Saran Wrap and placed on metal racks in the water-bath tanks (Fig. 4). Three water-bath tanks were equipped with refrigeration units and heating cables to provide constant temperatures ± 0.5 C. The water level in each tank was maintained at 0.6 cm from the top of the cups.

Each treatment contained three replications for each sampling interval. The treatments consisted of 24 combinations of six, temperature levels (37.8, 32.2, 26.7, 21.1, 15.6, and 12.8 C) and four, soil-moisture levels (.3, 1, 3, and 10 bars). The experiment was repeated thus, the statistical design was a split plot over time with the experimental treatments conducted in a factorial arrangement. Six sampling times were utilized between the time of planting and the approximate time when radicles reached an average length of 3 mm. Each sampling was from a different seed lot and the entire test consisted of a grand total of 864 seed lots. Seed weight and radicle length were measured at each sampling interval.



Fig. 3. Ten seed in a soil cup arranged in a 5.7-cm-diameter circle for water uptake tests.

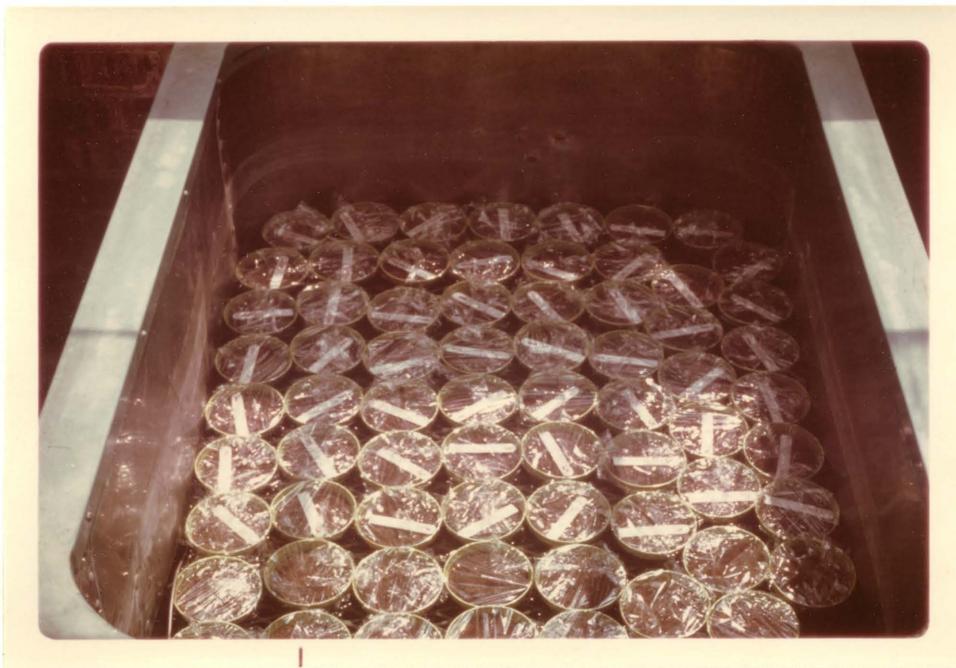


Fig. 4. Cups containing soil and 10 seed covered with Saran Wrap setting on a metal rack in a controlled-temperature, water-bath tank during seed water uptake tests.

The seed were observed by brushing soil from the seed surface and weighing the 10-seed lot to the nearest 0.01 g. In cases where radicle growth occurred, length was measured to the nearest mm.

Hypocotyl and Radicle Elongation

The hypocotyl- and root-elongation studies utilized the same soil as the radicle-emergence tests. The moisture conditioning process began by pouring 600 g of air-dry soil of known moisture content into individual plastic cups. Water was added and six cups were placed in a double plastic bag for 24 hours or more to allow the moisture to equilibrate. Prior to planting, the six cups were emptied into a plastic bag and the soil was thoroughly mixed to obtain a uniform soil mass. The soil was screened through a 3.5-mm screen into plexiglass growth boxes where seedling growth could be monitored. Soil was added to the boxes in 5-cm layers and compacted to a specific physical impedance level by hand tamping with a wooden slat before adding the next layer. A Chatillon push-pull gauge with a .4-cm diameter, blunt probe was pushed 2.5 cm into the soil layer to obtain an index of physical impedance. Force readings from the gauge were converted to pressure by dividing by area of the probe.

The plexiglass growth boxes were 70-cm long by 43-cm high by 5-cm deep. Ten cm from the top of the box,

the sides were angled 20 degrees from vertical. For the growth studies the boxes were tilted forward 15 degrees from vertical to make roots grow along the sides of the box for observation. In this position the upper-10-cm of the sides were at an angle of 5 degrees from vertical which caused hypocotyls to also grow along the sides for observation.

Pregerminated seed with radicle lengths averaging 3 mm were used in emergence tests. Seed were pregerminated by placing them in a beaker of tap water at 82 C for 1 minute, spreading in a shallow metal tray on a moist paper towel, and covering with a single layer of Saran Wrap. Germination was allowed to occur for approximately 18 hours at 32.2 C.

After adding soil to within 10 cm of the top of growth boxes, 15 pregerminated seed were placed along the side of each box. A spacing of 3.8 cm between seed was provided to minimize interference between adjacent plants. After transplanting soil was placed over the seed to a depth of 7.5 cm. The covering soil was conditioned to the same physical impedance and moisture level as the soil below the planting position. Next, the top of the box was covered with Saran Wrap to prevent soil drying. Vertical position of each seed was recorded and boxes were placed in constant-temperature, water-bath tanks at the proper angle.

Hypocotyl and radicle lengths were recorded daily. Measurements were made by recording location of the apex of the hypocotyl hook and the tip of the radicle. Seedling growth was observed until 50% of the seedlings emerged or until hypocotyls ceased to elongate. Appearance of lateral roots was also recorded. These measurements were approximate because observations were made only daily.

The experimental design for the emergence tests was a factorial arrangement. The 60 treatments included five temperatures (37.8, 32.2, 26.7, 21.1, and 15.6 C), three soil moisture levels (.3, 3.0, and 10.0 bars), and four physical impedance levels (.23, 1.12, 2.24, and 3.36 kg/cm²). Each elongation test contained 15 pregerminated seed.

CHAPTER 4

RESULTS AND DISCUSSION

This section summarizes the significant results from field emergence test and greenhouse studies. In a later section raw data from these tests are utilized in development of models for radicle-emergence time and hypocotyl elongation.

Field Emergence

Measurements of soil-environmental parameters are presented in Tables 12, 13, and 14 in Appendix A. Table 12 shows daily maximum and minimum temperature for each planting depth. Average values of soil moisture by planting depth and time after planting are presented in Table 13. In a similar manner, Table 14 summarizes the physical-impedance measurements which were taken for the various planting depths. Average percentage emergence from each planting depth is shown in Table 1.

Differences in emergence among planting depths do not seem to be related to soil temperature or moisture for ranges that were encountered in the test. Maximum percentage and rate of emergence could be best related to soil-impedance values and depth of planting. Generally, there was an increase in soil impedance with depth.

Table 1. Average percentage emergence of cottonseed planted at four depths in the field on April 15, 1969.

Time since planting, hours	Planting depth, cm			
	2.5	5.0	7.5	10.0
145	5.4	0.0	0.0	0.0
162	15.5	0.7	0.0	0.0
170	22.2	1.5	0.0	0.0
179	31.2	6.7	0.0	0.0
196	37.2	9.5	0.0	0.0
210	40.0	14.2	2.0	0.0
219	42.2	19.8	3.2	0.0
243	49.5	26.0	6.3	0.0
269	56.0	31.3	8.7	0.0
315	56.5	31.7	9.8	0.0

However, all soil-impedance values were at levels requiring considerable exertion by seedlings to emerge. Total work that a given seedling can perform to emerge from soil is related to the amount of stored seed energy, if other environmental factors are nonlimiting. With increasing depth, the seedling expends greater amounts of energy for increased length which it must attain before reaching the soil surface. A seedling emerging from a deeper depth

would have less reserve energy with which to overcome soil resistance.

Figure 5 indicates that maximum percentage emergence decreased linearly with depth up to 7.5 cm. The linear relationship may extend to zero emergence since this point may have been reached above 10 cm. Energy required to emerge from the 10.0-cm depth exceeded the capacity of the seedlings.

Measurements of seedling development prior to emergence from the soil are presented in Table 2. Seedling length (hypocotyl plus radicle) and percentage germination were similar for each of the planting depths. The fact that initial seedling development was not different among planting depths implies that difference in maximum percentage emergence was related to total energy consumption which increased with depth. When the seedling's energy status fell below some critical level while the hypocotyl was below the soil surface, emergence did not occur.

Controlled Environment Studies

Radicle Emergence

Radicle emergence for this study is defined as the event when average radicle length in a population of germinating seeds reaches 3 mm. Time required for radicle emergence in the controlled environment study is defined as

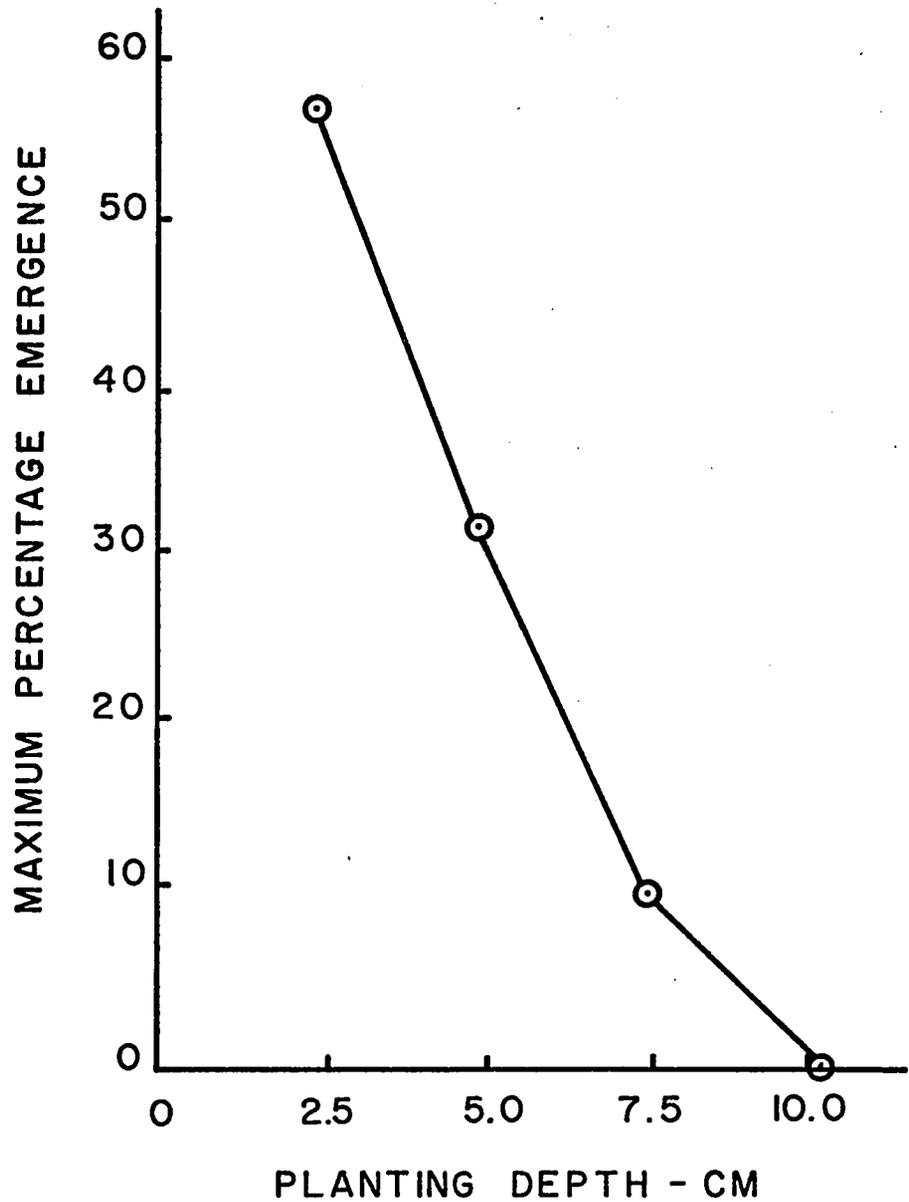


Fig. 5. Relationship between maximum emergence percentage and planting depth from April 15, 1969 field test.

Table 2. Average measurements made on germinating seedlings prior to emergence for test planted April 15, 1969.

Planting depth, cm	Plant characteristic	Time since planting, hours					
		48	72	93	117	143	167
2.5	Total length, mm*	2.0	8.1	20.5	34.2	54.5	--
	Per cent germination ⁺	12	50	80	82	95	--
	Number of plants	16	40	40	40	40	--
5.0	Total length, mm	2.0	4.6	19.6	35.6	51.4	57.5
	Per cent germination	7	32	75	80	92	87
	Number of plants	14	40	40	40	40	40
7.5	Total length, mm	3.0	4.6	17.2	35.0	44.6	55.5
	Per cent germination	6	27	60	85	80	83
	Number of plants	16	40	40	40	40	30
10.0	Total length, mm	0	4.5	18.6	32.2	47.7	58.6
	Per cent germination	0	30	60	77	97	87
	Number of plants	14	40	40	40	40	40

*This is the average length of the plants observed.

⁺Per cent germination is computed by dividing number of plants showing visible radicle extension by total number of plants examined.

the period between planting and the time when radicle-emergence occurs. Radicle emergence did not occur in the treatment combination of 15.6 C and 10.0 bars, nor in any of the moisture levels at 12.8 C.

Multiple linear regression was utilized to obtain statistical equations for expressing radicle-emergence time as a function of soil temperature and moisture. The equations below express time for radicle emergence as a function of temperature in C for four soil moisture levels. The temperature range for Equations (4-1), (4-2), and (4-3) was 15.6 to 37.8 C and 21.1 to 37.8 C for Equation (4-4).

<u>Soil moisture, bars</u>	<u>Equation</u>	<u>R²</u>	<u>Standard error of estimate</u>	<u>Equation number</u>
.3	RET = 239.3 - 13.46 S + .2027 S ²	.96	5.06	(4-1)
1.0	RET = 237.5 - 13.23 S + .1982 S ²	.97	4.65	(4-2)
3.0	RET = 274.5 - 15.47 S + .2321 S ²	.96	5.58	(4-3)
10.0	RET = 228.8 - 11.63 S + .1644 S ²	.77	7.76	(4-4)

RET = Time required for 3-mm radicle emergence, hours.

S = Soil temperature, C.

Multiple coefficients of determination (R²) for Equations (4-1), (4-2), and (4-3) are high, indicating a close fit of the empirical data. The 10.0-bar moisture level is near the

limit of cotton seed's ability to absorb moisture from soil and increased variability is reflected in the lower value of R^2 and the greater standard error of estimate. The difference between individual regressions and the common regression (shown below) was significant at the .005 level indicating there were differences in regression among moisture levels. However, in comparing the 95% confidence intervals for the coefficients of linear and second order terms in the four equations, no differences were found. Thus to compute radicle-emergence time for constant soil moisture, it is more appropriate to use the equation for the specific moisture level than a common regression equation.

A regression equation relating time for radicle emergence to soil temperature and moisture level appears below.

$$\begin{aligned} \text{RET} = & 244.2 - 13.85 S + .2091 S^2 + 3.332 M \\ & - .0808 M^2 - .0551 SM \end{aligned} \quad (4-5)$$

Where: RET = Time required for 3-mm radicle emergence, hours

S = Soil temperature, C $R^2 = .94$

M = Soil moisture, bars SE = 5.79

SE = Standard error of the estimate

The marked effect of temperature on radicle-emergence time is demonstrated by the fact that an equation containing

only linear and second order terms of temperature yielded a relationship which gave an R^2 value of .92.

Equation (4-5) is plotted in Fig. 6 for the four moisture levels. Within the limits of 15.6 and 32.2 C, the germination process follows the Van't Hoff-Arrhenius equation as shown in Brody (1945) for the reaction rate of inorganic chemical reactions as influenced by temperature. This law states that for each 10 C increase in temperature, the rate of reaction at least doubles. Leveling-off of radicle-emergence time for .3-, 1.0-, and 3.0-bar moisture levels between 32.2 and 37.8 C suggests that denaturing of certain enzymes active in metabolic pathways during seed germination may be occurring. The average time for radicle emergence measured for each soil temperature and moisture combination is shown in Table 3.

Seed Water Uptake

Moisture uptake of seed in different treatments was determined by weighing six groups of 10-seed lots at each of six sampling intervals. A different group of seed was monitored at each sampling time which introduced additional variability. The alternative of replacing seed after each observation was not used because it was felt the soil environment would be destroyed by the sampling procedure. The equations below relate percentage seed moisture to temperature and elapsed time for each moisture level. The

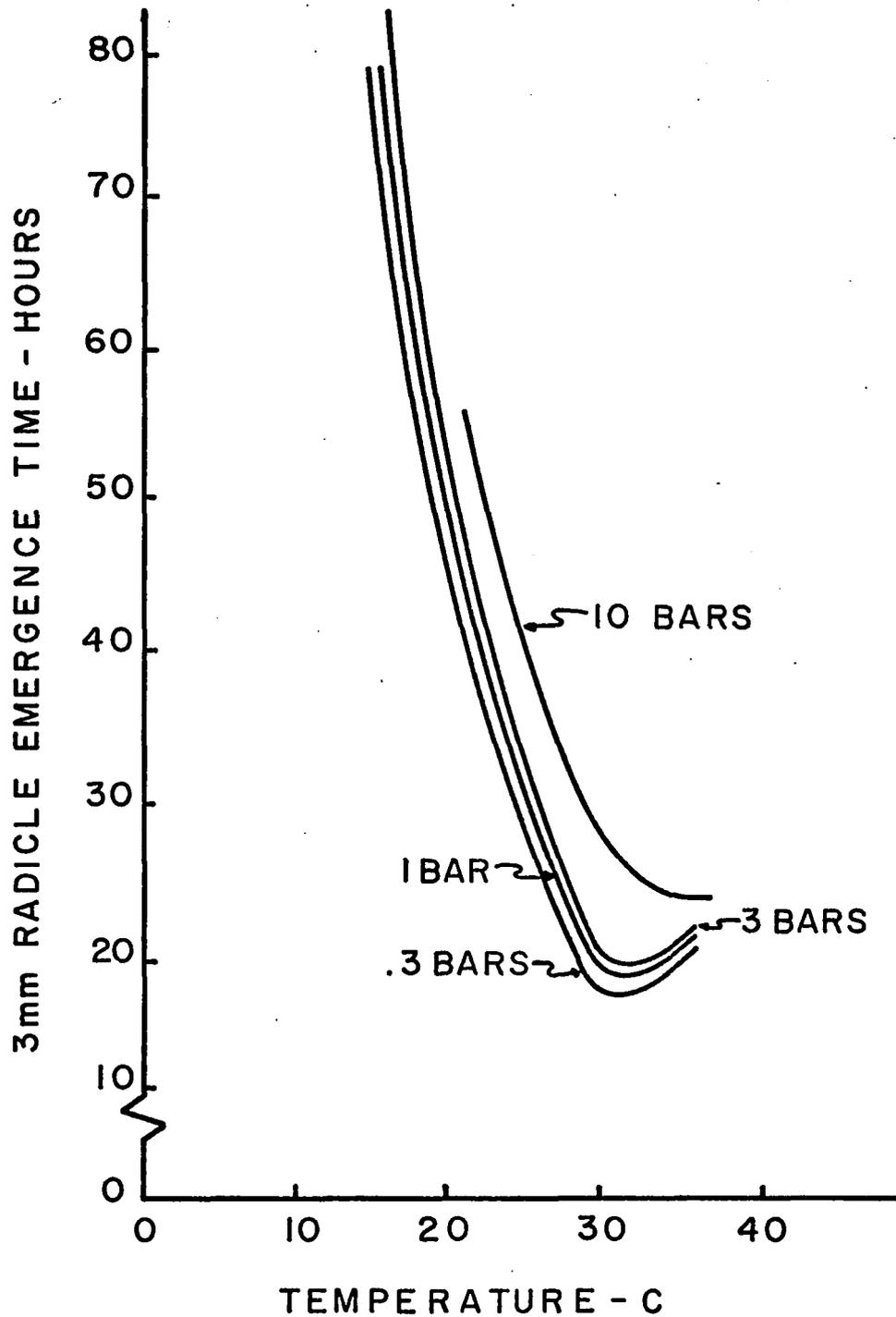


Fig. 6. Radicle-emergence time versus temperature for four soil moisture levels as computed from Equation (4-5).

Table 3. Radicle-emergence time in hours for five soil temperatures and four moistures (average of six observations).

Temperature, C	Moisture, bars				Average
	.3	1.0	3.0	10.0	
15.6	81.3	82.1	92.6	--*	
21.1	40.5	41.2	46.0	52.3	45.0
26.7	25.6	27.0	27.2	34.0	28.5
32.2	19.8	20.5	21.8	25.1	21.8
37.8	18.2	18.6	18.7	22.8	19.6
Average	37.1	37.9	41.3		

*Radicle emergence did not occur in this treatment.

applicable temperature range for the equations is from 12.8 to 37.8 C.

Soil moisture, bars	Equation	R ²	Standard error of estimate	Equation number
.3	PM = 52.91 - 2.539 S + .0504 S ² + .0245 t - .0098 t ² + .0830 St	.87	6.16	(4-6)
1.0	PM = 24.32 - .4932 S + .0173 S ² + .3580 t - .0082 t ² + .0716 St	.86	6.35	(4-7)
3.0	PM = 22.09 - .5506 S + .0239 S ² + .8391 t - .0107 t ² + .0493 St	.84	6.38	(4-8)

<u>Soil moisture, bars</u>	<u>Equation</u>	<u>R²</u>	<u>Standard error of estimate</u>	<u>Equation number</u>
10.0	PM = 35.85 + 2.963 S - .0325 S ² + 1.492 t - .0141 t ² + .0245 St	.87	5.59	(4-9)

PM = Total seed moisture, percentage dry weight.

S = Soil temperature, C.

t = elapsed time, hours.

The contribution of each term of the equation is shown by the accumulated R² values in Table 4. The vertical listing of regression terms shows their order of inclusion in Equations (4-6), (4-7), and (4-8) by using step-wise regression procedure.

Table 4. Accumulated R² values of regression model terms for seed moisture uptake over four soil moisture levels.

Regression terms	Soil moisture level, bars			
	.3	1.0	3.0	10.0
St	.71	.71	.58	*
St + t ²	.85	.84	.80	*
St + t ² + S ²	.85	.86	.82	*
St + t ² + S ² + t	.87	.86	.84	*
St + t ² + S ² + t + S	.87	.86	.84	*

*The order of entry for terms in Equation (4-9) for 10.0 bars is St, t², S, t, S² with accumulated R² values of .76, .84, .85, .86, and .87.

The interaction term of temperature and time is the most important factor for each equation. This is shown for each moisture level in Fig. 7 through 10. The R^2 values for each equation are not high, but do indicate an acceptable fit of the empirical data. The regression terms are included in the same order for all equations except the equation for 10.0 bars. The reason for this difference is not apparent.

The multiple regression equation relating soil temperature, soil moisture, and time to seed-moisture percentage appears below.

$$\begin{aligned} \text{PM} = & 13.92 + .0123 S^2 + .8207 t - .0111 t^2 \\ & + .0609 St - .0020 Smt \end{aligned} \quad (4-10)$$

$$R^2 = .85$$

$$\text{SE} = 6.22$$

Step-wise regression showed that the interaction term of temperature and time was again the most significant term. The regression model considered linear and second-order terms of all parameters plus first-order interaction terms. Criterion for including a term into the equation was the t-test of the coefficient of each entering term. A term was deleted if its coefficient was not different from zero at 0.10 probability level.

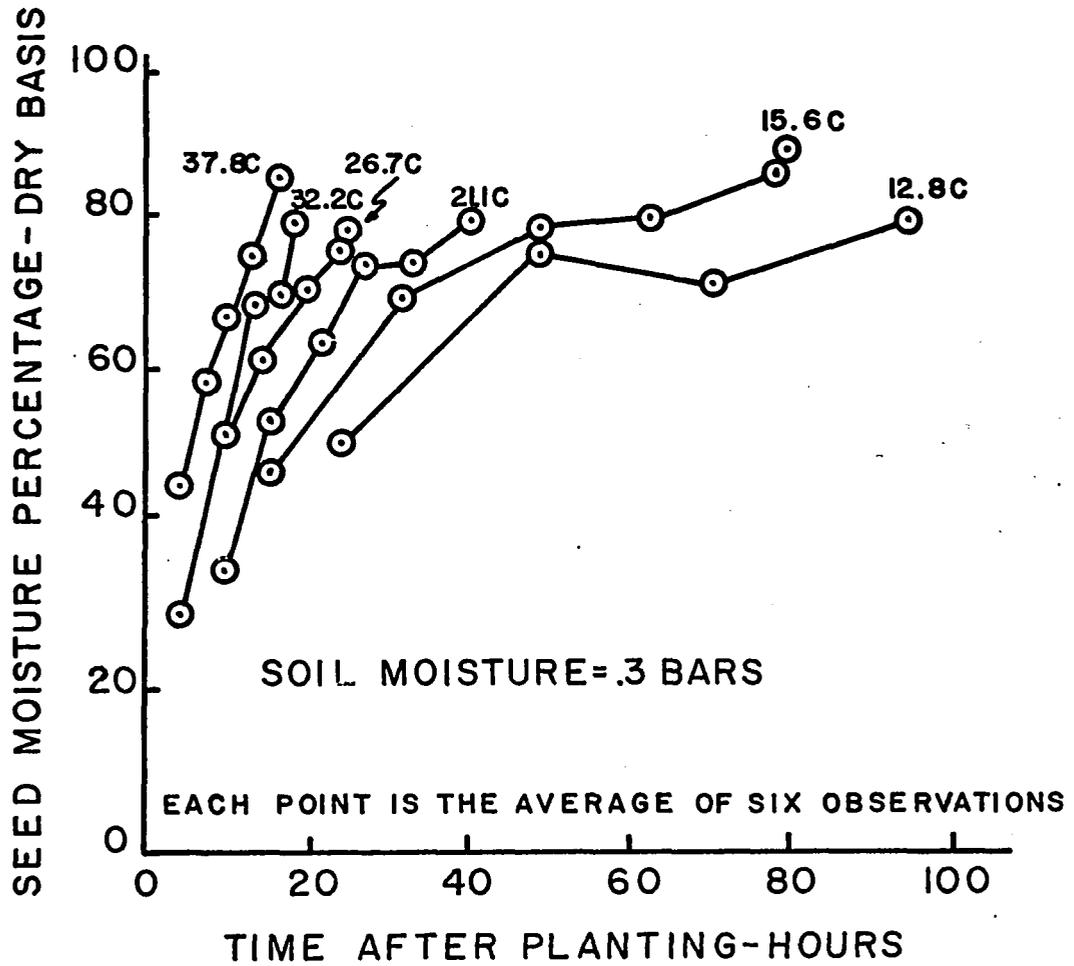


Fig. 7. Accumulated seed moisture for six temperatures at .3-bar soil moisture.

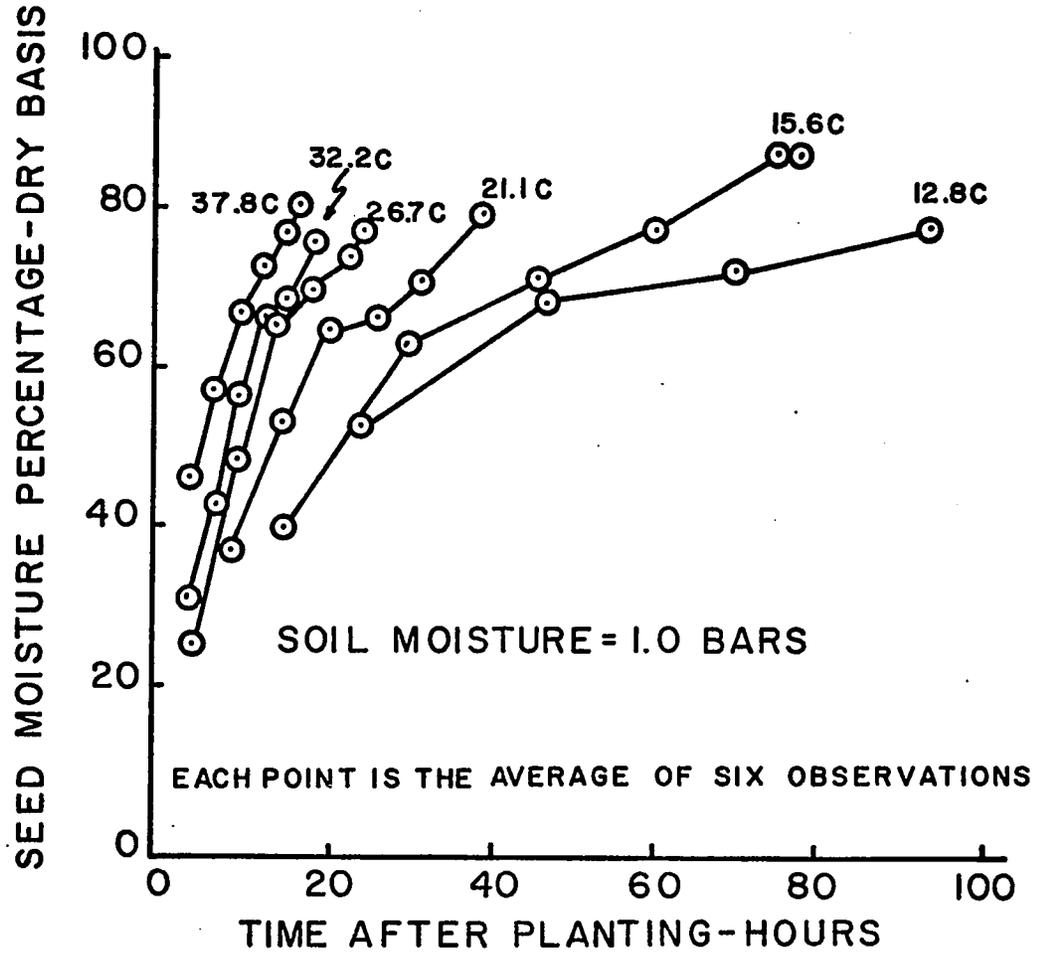


Fig. 8. Accumulated seed moisture for six temperatures at 1.0-bar soil moisture.

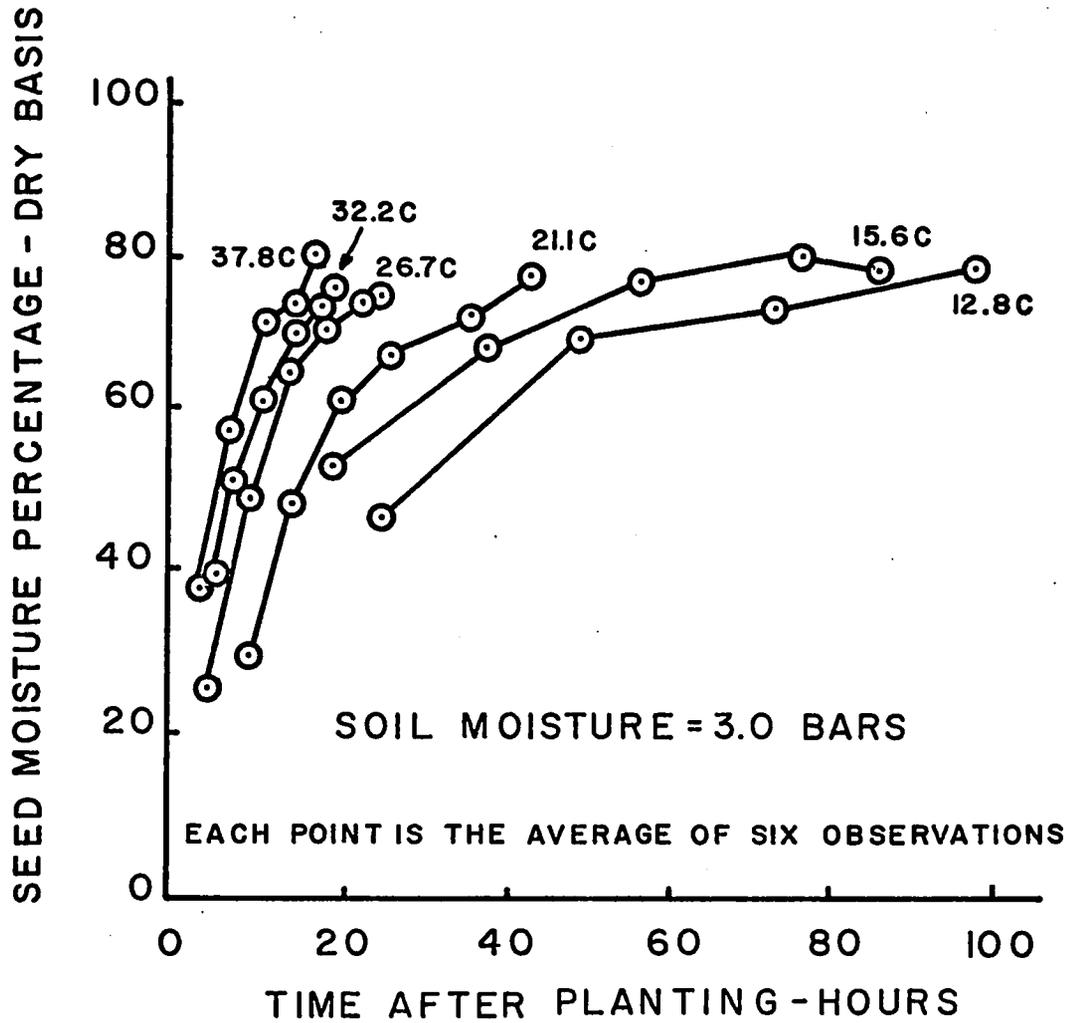


Fig. 9. Accumulated seed moisture for six temperatures at 3.0-bars soil moisture.

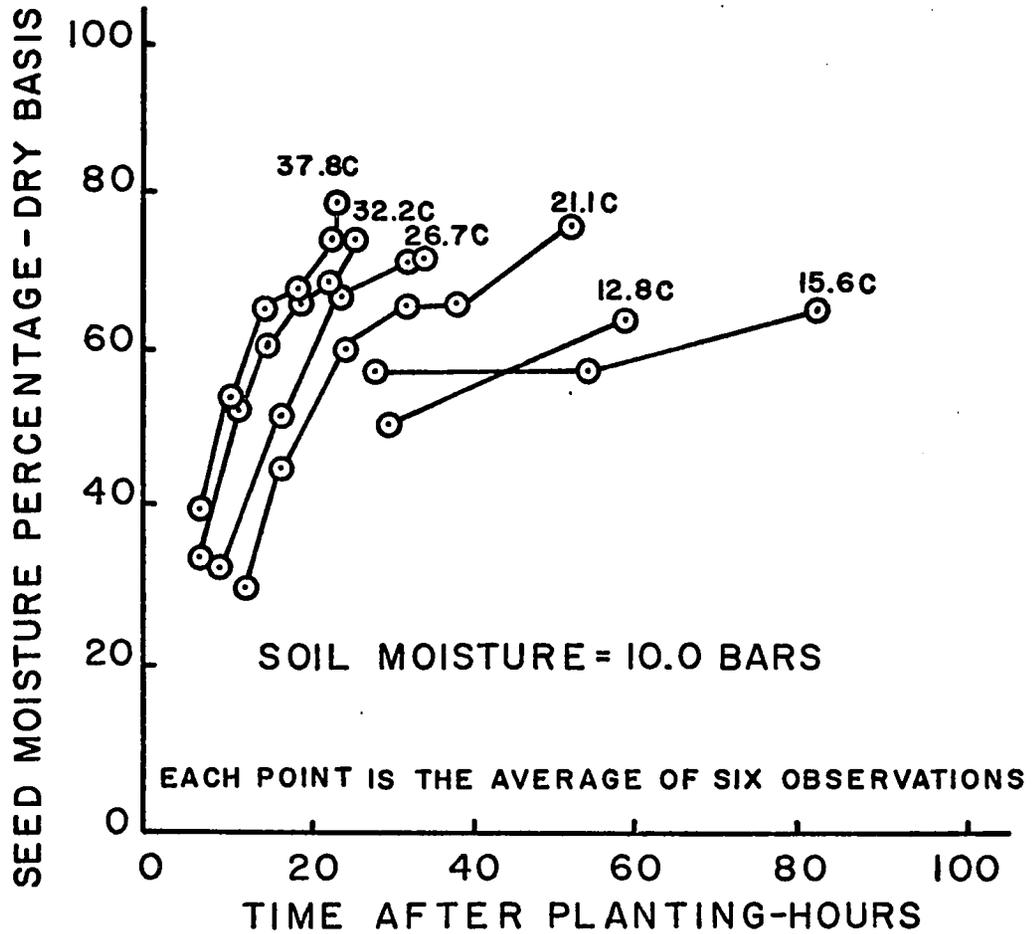


Fig. 10. Accumulated seed moisture for six temperatures at 10.0-bars soil moisture.

Seed-Moisture Percentage at Radicle Emergence

Seed-moisture percentage at radicle emergence for different treatment levels was less variable than the time for radicle emergence. Observed time for radicle emergence varied from 18.2 to 92.6 hours (Table 3) compared to a range of 73.4 to 88.0% seed moisture, shown in Table 5.

Table 5. Average seed-moisture percentage at the time radicles had emerged an average of 3 mm for five soil temperatures and four soil moisture levels (average of six observations).*

Temperature, C	Soil moisture, bars				Average
	.3	1.0	3.0	10.0 [†]	
37.8	<u>84.2</u> a	80.6 b	<u>80.2</u> a	78.0	80.8
32.2	<u>79.3</u> b	76.1 b	<u>77.0</u> a	73.4	76.5
26.7	<u>77.8</u> b	77.9 b	<u>74.6</u> a	70.2	75.1
21.1	<u>78.9</u> b	78.9 b	<u>76.9</u> a	75.9	77.7
15.6	<u>88.0</u> a	<u>87.5</u> a	<u>77.9</u> a	--	
Average	81.6	80.2	77.3		

*Numbers in the same column followed by a common letter or in the same row underscored by a common line are statistically the same at the .05 level according to Duncan's New Multiple Range Test.

[†]The 10.0-bar moisture level was not included in the analysis since radicle extension did not occur at 15.6 C.

For a given temperature, seed moisture at radicle emergence tended to decrease with soil moisture, but the differences were not statistically significant except at 15.6 C. Results of Phillips (1968) for temperatures between 21.1 and 32.2 C agreed with data reported here. He reported no differences in seed moisture content at germination with corn and cotton for soil moisture levels between .3 and 3.0 bars at a constant 28 C temperature. Within a soil-moisture level, seed moisture was highest for extreme temperatures. Differences in seed moisture among temperatures is less distinct at low soil-moisture levels. At .3-bar soil moisture, the 37.8 and 15.6 C temperature effects are significantly different from all other temperatures. At 1.0-bar soil moisture, seed moisture at 15.6 C was significantly higher than at other temperatures. All seed moistures were statistically similar at the 3.0-bar soil moisture level. No significant difference was found among seed moistures within a temperature level in an analysis that included all soil moistures between temperatures of 21.1 and 37.8 C.

Water content of seed at radicle emergence is the result of two interdependent processes: (1) rate of seed water absorption and (2) metabolic rate of the seed. Both processes are influenced by temperature and soil moisture level. Seed-water content at radicle emergence was less sensitive to water absorption than to metabolic rate. For

example, refer to .3- and 1.0-bar soil-moisture levels in Table 5. Moisture content at 15.6 C was higher than for other temperatures, indicating that increased temperature had a greater effect on radicle-emergence rate than on water uptake. Seed-moisture contents at the 3.0-bar level were not significantly different among temperatures indicating that rate of water diffusion from the soil was limiting seed water uptake. The trend of decreasing seed moisture at radicle emergence with decreasing level of soil moisture also suggests that water diffusion into the seed is governing seed-moisture content at radicle emergence.

A final point will be drawn from Table 5. The 26.7 C temperature generally has the lowest seed-moisture level among the soil-moisture levels. At this temperature, maximum radicle elongation occurred per unit of absorbed water. The higher seed-moisture levels at other temperatures suggests two possibilities: (1) under certain environments seed absorb water in excess of the minimum requirement for radicle emergence or, (2) different environments require varying amounts of water in the seed for radicle emergence. The former possibility is the most likely.

An analysis of variance for seed moisture content at 3-mm radicle extension revealed a significant time factor. Since the variances between time of replication were unequal it was necessary to use orthogonal polynomials.

to obtain a regression equation. This procedure requires equal numbers of replications. The 10.0-bar moisture level was omitted from the regression since no radicle emergence occurred for the treatment combination of 15.6 C and 10.0 bars. The regression equation for predicting seed moisture content where soil moisture levels ranged from .3 to 3.0 bars and temperatures from 15.6 to 37.8 C appears below:

$$MC = 124.1 - 3.128 S + .0534 S^2 - 4.575 M + .1125 M S$$

$$R^2 = .86$$

$$SE = 1.38 \quad (4-11)$$

Where: MC = Seed-moisture content at 3-mm radicle length, percentage dry weight

S = Soil temperature, C

M = Soil moisture, bars

Hypocotyl and Radicle Elongation

The emergence tests began with pregerminated seed with radicle lengths averaging 3 mm. Treatment levels were designed primarily to study their effect on hypocotyl elongation. Measurements were made at approximately 24-hour intervals; except for treatments at 15.6 C where readings were made at approximately 48-hour intervals. Measurements in all treatments were terminated when either 50% of planted seed emerged or all hypocotyls ceased to elongate. Duration of the tests ranged from 79 hours at 32.2 C to 523 hours at 15.6 C.

A typical time distribution of hypocotyl and radicle lengths is shown in Fig. 11. The plotted data are a family of curves for constant 32.2 C and .3-bar moisture, and results at other temperatures and moistures show a similar family of curves. Duration over which the hypocotyl will continue to elongate does not appear to be influenced by physical impedance. The duration of growth, instead, appears to be related to soil temperature and moisture level.

Radicle elongation began before hypocotyl elongation and occurred at a faster rate. Prior to the appearance of lateral roots, the radicle elongated at a constant rate. Hypocotyl elongation was exponential when it was undampened. Dampening can result from unfavorable levels of temperature, moisture, or physical impedance.

The next three sections will discuss general effects of soil temperature, moisture, and physical impedance on seedling elongation. A following section will discuss the effect of the three parameters on maximum hypocotyl length.

Temperature Effect. Rate of elongation of both hypocotyls and radicles increased between 15.6 to 32.2 C and then decreased at 37.8 C (Fig. 12). The effect of temperature on relative elongation rates of hypocotyls agreed with earlier results obtained by Arndt (1945). A

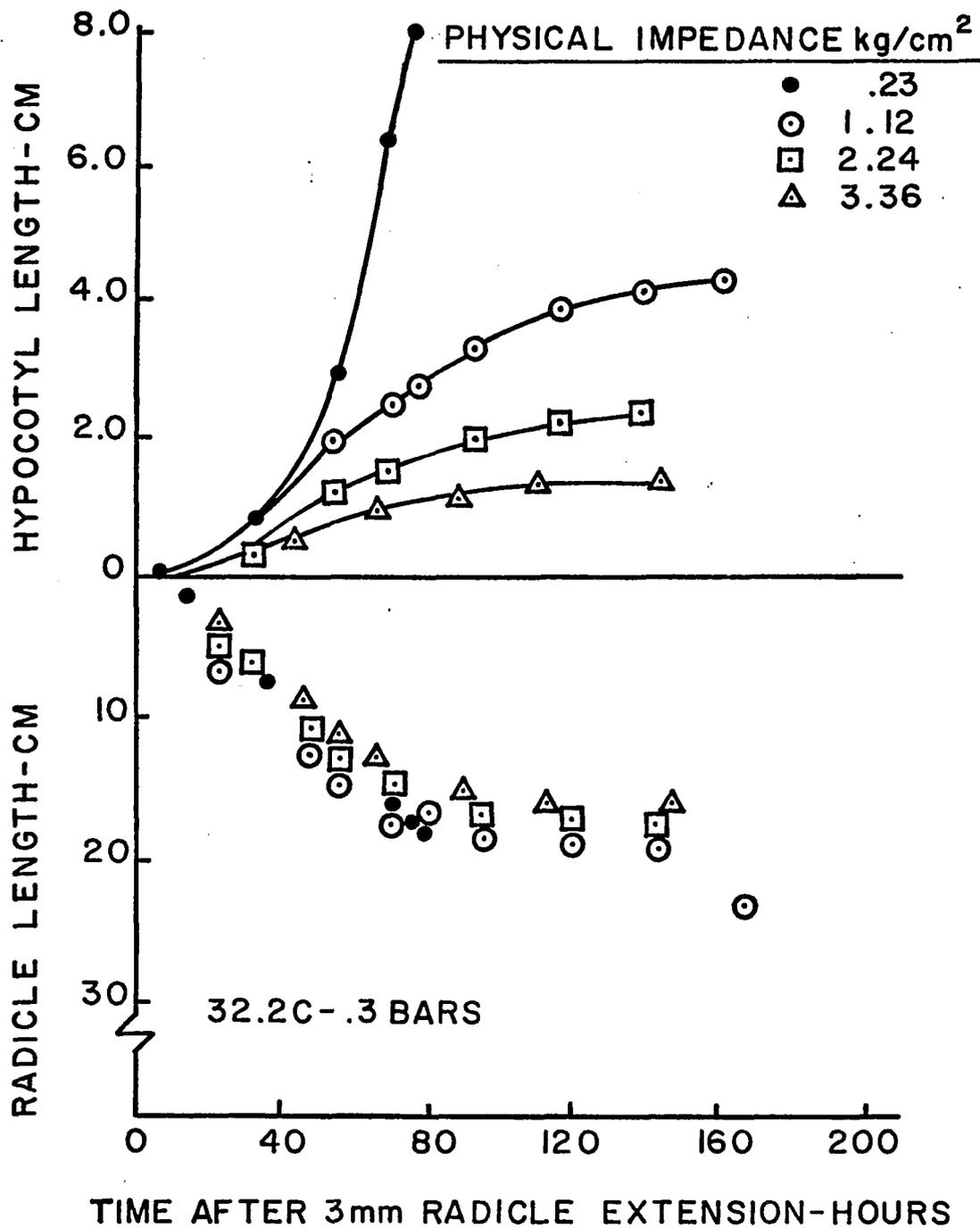


Fig. 11. Hypocotyl and radicle lengths versus time at 32.2 C and .3-bar soil moisture for four levels of physical impedance.

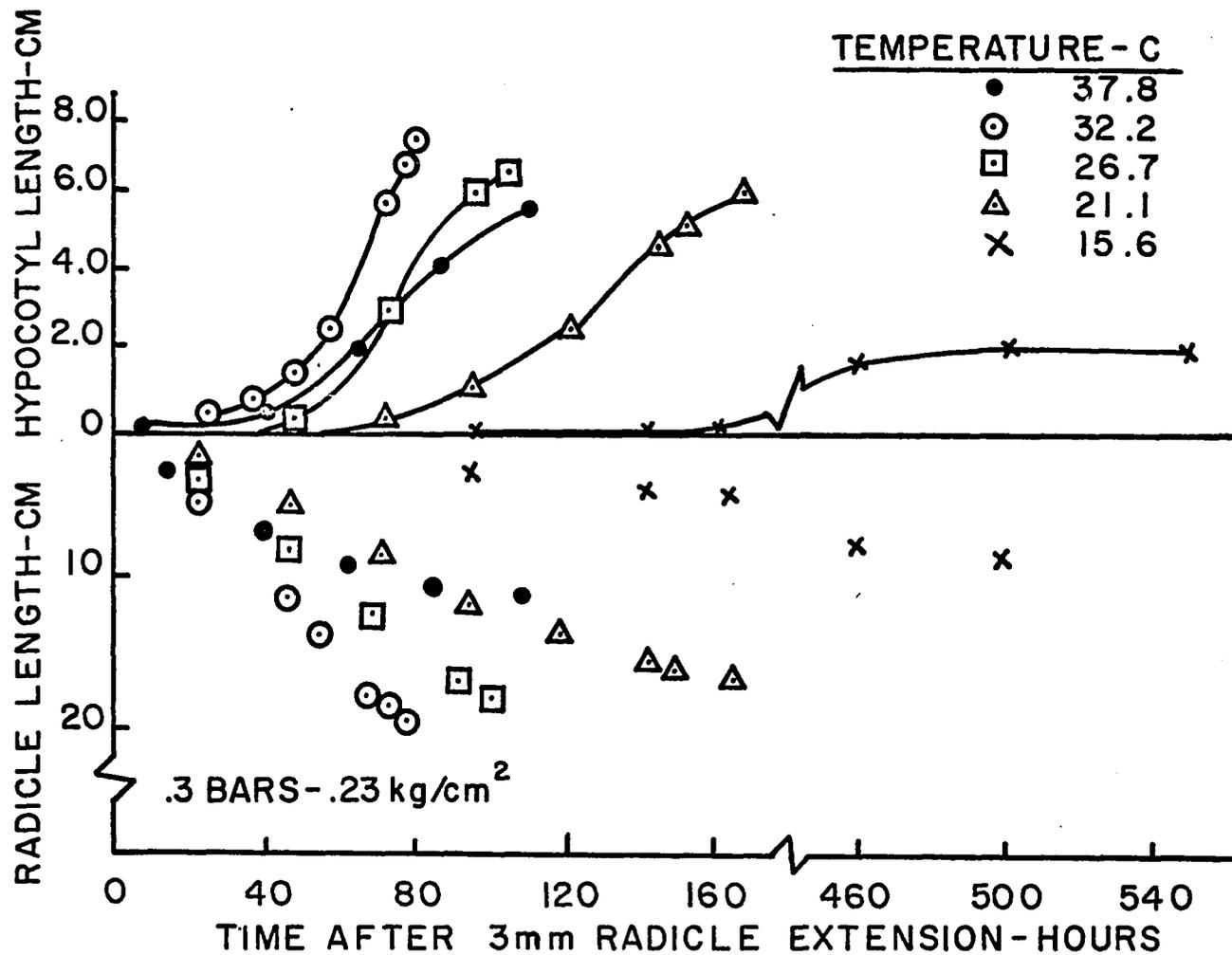


Fig. 12. Hypocotyl and radicle lengths versus time at .3-bar soil moisture and .23 kg/cm² physical impedance for five temperatures.

temperature stress was indicated by prolonged exposure to 37.8 C. Hypocotyl elongation occurred earlier at 37.8 C than at 26.7 C; however, rate of elongation and total length was greater at 26.7 C. Hypocotyl elongation was faster and greater in total length at 32.2 C than at other temperatures.

Temperature stress was more severe at high than at low temperatures and affected elongation of hypocotyls more than radicles. Diminished radicle elongation occurred at 37.8 C as soil-moisture tension was raised from 3.0 to 10.0 bars; but no hypocotyl elongation was observed at 10.0 bars. Elongation of both hypocotyls and radicles at 15.6 C was reduced as moisture level decreased, but measurable elongation occurred at all soil-moisture levels.

Moisture Effect. Moisture stress influenced hypocotyl growth by increasing the length of the lag phase, and decreasing elongation rate and maximum length (Fig. 13). The greatest effect on hypocotyl elongation occurred at 37.8 C. The pattern of elongation was similar to other temperatures at .3-bar soil moisture, but total length at 3.0 bars was .4 cm for the .23 kg/cm² physical-impedance level and no hypocotyl elongation occurred at 10.0-bar soil moisture and 37.8 C.

Elongation of radicles was less sensitive to low soil moisture than that of hypocotyls. By 120 hours after

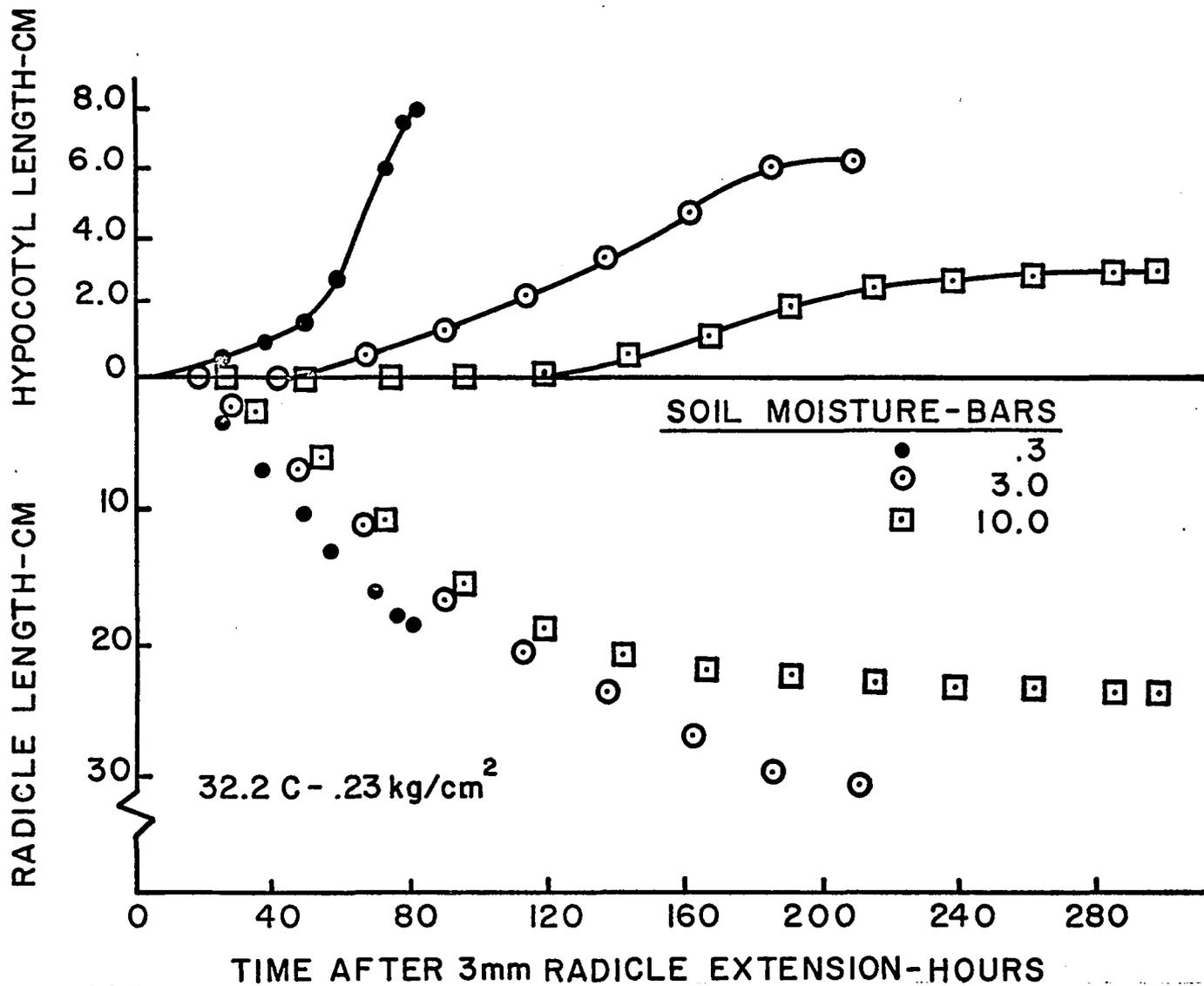


Fig. 13. Hypocotyl and radicle lengths versus time at 32.2 C and .23 kg/cm² physical impedance for three soil moisture levels.

planting hypocotyl length was 2.5 cm at 3.0-bars moisture compared to no elongation at 10.0 bars (Fig. 13). Radicle lengths for the same time and moisture levels were 21 and 19 cm, respectively. Figures 14 and 15 are photographs taken of the same treatments levels 5 days after planting. Essentially the same stage of development and degree of difference between treatments is shown in the photographs and Fig. 13. As will be seen later in Table 8, the ratio of maximum hypocotyl to maximum radicle length decreased with soil-moisture level for all temperature and physical-impedance levels.

Physical-Impedance Effect. The dampening influence on both hypocotyl and radicle elongation in Fig. 11 was due to physical impedance. Hypocotyls were more sensitive to soil physical impedance than were radicles. This was apparently due to differences in size, shape, and method of growth of the two plant organs. Growth of the radicle is limited to the tip where cell division and elongation are concentrated. This pattern of root elongation has been reported in a variety of crop plants by Baldovinos (1953), Goodwin and Avers (1956), and Garner and Bowen (1966). Radicle growth encounters minimal resistance because elongation is limited to a few mm at the tip. In the hypocotyl, however, elongation is not restricted to a single growing point. This observation has previously been

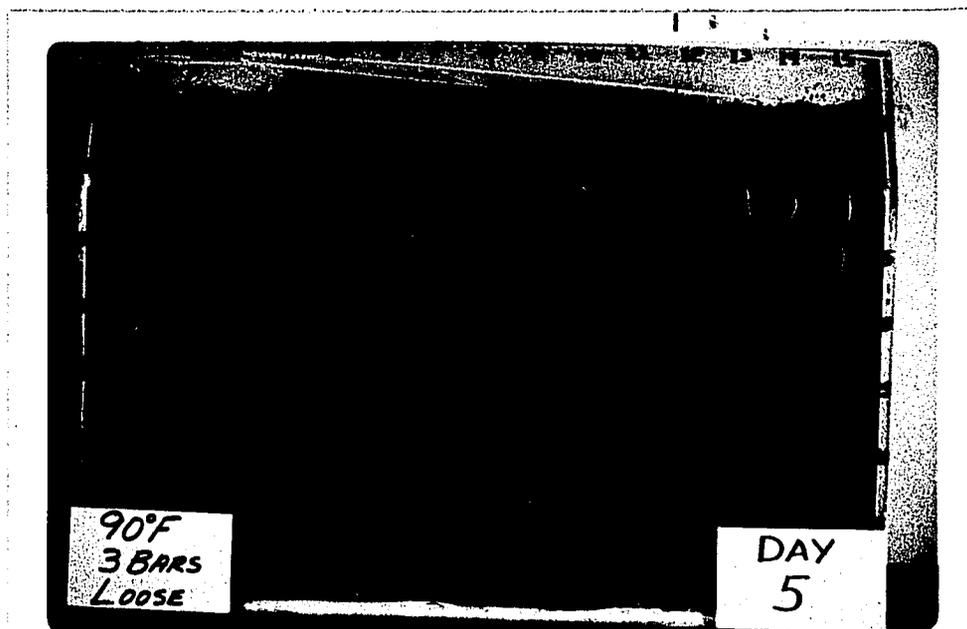


Fig. 14. Cotton seedlings after 5 days at 32.2 C, 3.0-bars soil moisture, and $.23 \text{ kg/cm}^2$ physical impedance showing elongated hypocotyls and radicles with lateral roots.

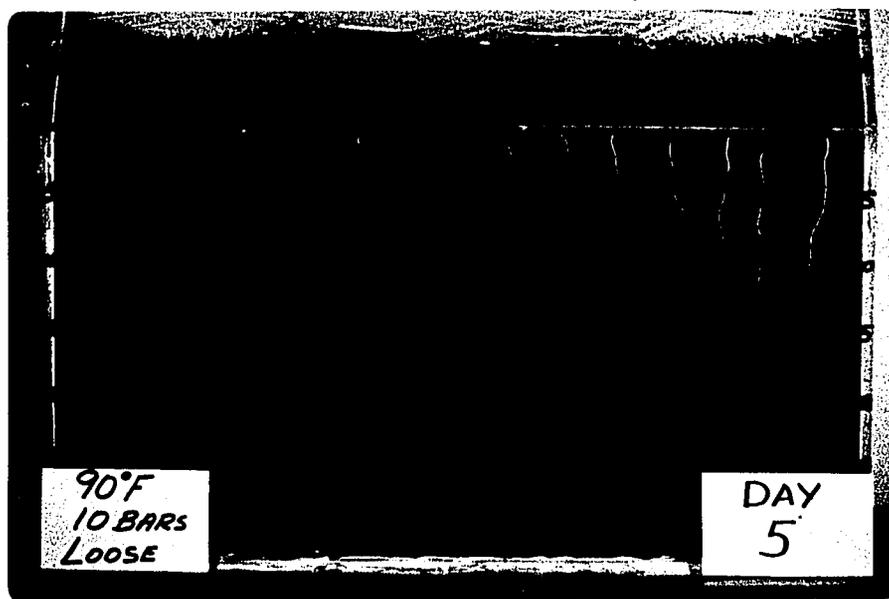


Fig. 15. Cotton seedlings after 5 days at 32.2 C, 10.0-bars soil moisture, and $.23 \text{ kg/cm}^2$ physical impedance showing elongated radicles without hypocotyl growth.

noted by Beck and Andrus (1943), Brian and Stover (1937), Ropp (1951), and Arnold and Alston (1961). The region immediately below the cotyledons elongates fastest but elongation occurs throughout the hypocotyl. Thus, a large portion of the hypocotyl must be moved as the hypocotyl grows. Also, the hypocotyl with attached cotyledons generates more resistance to movement through the soil mass than does the cylindrical radicle with its pointed root tip.

Measurements were not made but it was observed that hypocotyl diameter enlarged with increasing magnitude of physical impedance. This effect was not observable for radicles. Garner and Bowen (1966) reported a positive linear relationship between soil compaction level and maximum hypocotyl diameter.

Increasing physical impedance also caused the hypocotyl to arch and have a pronounced hook. In several instances hypocotyls were observed to break in the hook section. Increasing physical impedance caused more horizontal deviations in growth of radicles. This growth pattern was apparently the result of roots attempting to grow along the path of least soil resistance.

Maximum Hypocotyl and Radicle Lengths

Maximum hypocotyl lengths for all combinations of temperature, moisture, and physical impedance appear in

Table 6. The effect of increasing physical impedance or decreasing soil moisture was to decrease hypocotyl length. Length of hypocotyls increased with temperatures between 15.6 and 32.2 C and then declined at 37.8 C.

The analysis in Table 15 in Appendix A indicates that both main effects and interactions are significant. Interaction means, however, show the same general trend found for individual main effects. Thus, while interactions are significant their influence is dwarfed by main effects of temperature, moisture, and physical impedance. The dominance of main effects is indicated by the F-values in Table 15 which are much greater than those of interactions.

The influence of temperature, moisture, and physical-impedance level on radicle length at the time of maximum hypocotyl length is shown in Table 7. Increasing physical impedance generally caused a slight reduction in radicle length, but the reduction was much less than for hypocotyls. The 3.0-bar soil-moisture level produced the longest radicle. This also contrasts with the effect on hypocotyls where length consistently decreased with reduced soil moisture. Temperature's effect on radicle length was greater than other main effects and similar to the response for hypocotyls. Increasing lengths occurred for temperatures from 15.6 to 32.2 C with a decrease at 37.8 C. Decrease in hypocotyl and radicle length between

Table 6. Maximum hypocotyl lengths in cm for five temperatures, three moisture levels, and four physical-impedance levels.

Temperature, C	Soil moisture, bars	Physical impedance, kg/cm ²			
		.23	1.12	2.24	3.36
15.6	.3	2.7	1.2	.8	.5
	3.0	1.6	.7	.5	.3
	10.0	.7	.2	.1	.2
21.1	.3	6.8(7.8)*	3.0	1.6	1.3
	3.0	4.7(4.9)*	2.8	1.4	.9
	10.0	1.1	.7	.3	.1
26.7	.3	7.2(8.2)*	3.5	2.3	1.5
	3.0	5.8(6.2)*	2.8	1.5	1.0
	10.0	2.9	.6	.3	.2
32.2	.3	7.9(9.8)*	4.1	2.2	1.2
	3.0	6.5(7.5)*	2.9	1.5	.6
	10.0	3.5	1.0	.3	0.0
37.8	.3	6.2(7.0)*	2.7	1.5	.7
	3.0	.4	.2	0.0	0.0
	10.0	0.0	0.0	0.0	0.0

*Numbers on the left are hypocotyl lengths at 50% emergence. Those in parentheses are estimates of maximum hypocotyl length obtained by an analog solution of Equation (5-9) in Chapter 5.

Table 7. Maximum radicle lengths in cm for five temperatures, three moisture levels, and four physical impedance levels.

Temperature, C	Soil moisture, bars	Physical impedance, kg/cm ²			
		.23	1.12	2.24	3.36
15.6	.3	7.9	8.7	5.5	6.9
	3.0	10.7	9.0	8.2	7.3
	10.0	9.5	6.4	6.9	5.6
21.1	.3	15.6*	19.9	15.1	11.8
	3.0	23.6*	19.9	19.5	15.0
	10.0	17.8	20.4	16.9	17.8
26.7	.3	17.2*	19.7	13.9	15.2
	3.0	29.9*	20.5	21.3	18.0
	10.0	22.3	24.2	24.0	22.6
32.2	.3	18.3*	23.8	18.2	16.6
	3.0	29.7*	28.2	27.0	21.8
	10.0	22.5	18.5	18.8	18.2
37.8	.3	10.2*	10.5	9.7	9.2
	3.0	12.9	12.4	0.0	0.0
	10.0	0.0	0.0	0.0	0.0

*Indicates treatments where 50 per cent of the seedlings emerged from 7.5 cm.

32.2 and 37.8 C is probably caused by impaired respiration. Arndt (1945) reported a reduction in elongation rate between 33 and 39 C, and reduced total length between 33 and 36 C for cotton hypocotyls and radicles germinated in agar gel.

The analysis of variance of treatment factors in Table 16 (Appendix A) shows all main effects and interactions to be significant. The F-values of main effects are higher than for interactions, especially for temperature. Trends for interaction means were similar to those of main effects.

Ratios of maximum hypocotyl length divided by maximum radicle length are presented in Table 8. The ratios show a dramatic change in the proportioning between hypocotyl and radicle due to moisture and physical impedance, but are statistically insensitive to temperature (Table 17, Appendix A). The ratios decrease sharply between physical impedance levels of .23 and 1.12 kg/cm². The same drastic change often occurred between .3- and 3.0-bars soil moisture. A relatively greater effect of both factors on hypocotyls is indicated by the changing ratios. The analysis of variance shows that the primary influence on the ratios is due to physical impedance and moisture. Results of Harris (1914) agree with the moisture effect noted in this study. He reported a decrease in the

Table 8. Ratios of maximum hypocotyl/radicle lengths for five temperatures, three moisture levels, and four physical impedance levels.

Temperature, C	Soil moisture, bars	Physical impedance, kg/cm ²			
		.23	1.12	2.24	3.36
15.6	.3	.34	.13	.14	.07
	3.0	.14	.07	.06	.04
	10.0	.07	.03	.01	.03
21.1	.3	.43*	.15	.10	.11
	3.0	.19*	.14	.07	.06
	10.0	.06	.03	.01	.01
26.7	.3	.41*	.17	.16	.09
	3.0	.19*	.13	.07	.05
	10.0	.13	.02	.01	.01
32.2	.3	.43*	.17	.12	.07
	3.0	.21*	.10	.05	.02
	10.0	.15	.05	.01	.00
37.8	.3	.60*	.25	.15	.07
	3.0	.03	.01	--	--
	10.0	--	--	--	--

*Indicates treatments where 50 per cent of the seedlings emerged from 7.5 cm.

shoot/root ratio during germination with decreasing soil moisture for corn and wheat seedlings.

The effect of physical impedance is attributable to the greater sensitivity of hypocotyls because of their shape and manner of growth as discussed earlier. The effect of moisture may be due to an internal mechanism of the germinating seedling. Development of an adequate root system to supply water takes priority over elongation of the hypocotyl when the water status of the seedling is low.

CHAPTER 5

EMERGENCE MODEL

The previous studies provided information about hypocotyl and radicle elongation in different soil environments. While some physiological aspects of emergence were studied, the primary objective was to obtain data for developing an emergence model.

The hypocotyl- and radicle-elongation tests were conducted under constant levels of soil temperature, moisture, and physical impedance. In context of systems analysis this represents step inputs of each parameter to the developing seedling.

The model of cotton seedling emergence was divided into two subsystems: (1) a model of radicle emergence time, and (2) a model of hypocotyl elongation.

The general approach used in developing models for each of the subsystems was that of "black box" analysis. External inputs (temperature, moisture, and physical impedance) to the germinating seedling and outputs (seed moisture and seedling elongation) were known. The form of the dynamic relationship that would produce the same response was then estimated. Experimental data were utilized to obtain estimates of coefficients in

hypothesized mathematical equations. The final step in the procedure was verification of mathematical models.

Radicle-Emergence Model

Little physical change is observable in the seed prior to radicle emergence, except for seed swelling. Increase in seed volume is due to water absorption. Imbibition is the dominant influence on water diffusion into the seed before the radicle emerges. Therefore, a model of imbibition was developed to predict the occurrence of radicle extension averaging 3 mm.

Imbibition by seed is generally considered to be a passive process. Since little metabolic energy is required for water absorption during imbibition, the process is primarily dependent on the difference in water potential between seed and surrounding environment, and resistance to moisture flow into the seed. Meyer and Anderson (1965) stated that seed may imbibe water either as a vapor or in liquid state; however, the greatest amount of water absorbed by seed from soil at high soil-moisture levels is probably in liquid form.

System Description

The system under consideration is the water uptake and radicle emergence of acid-delinted cottonseed germinating in soil. Driving force for movement of water into the seed is the difference in water potential between the

soil and the seed. Rate at which moisture moves into seed is dependent on the levels of moisture in the seed, soil moisture, and soil temperature. The soil parameters and ranges considered are soil moisture (.3 to 10.0 bars) and temperature (12.8 to 37.8 C).

Within the limits of soil conditions specified, it is assumed that the moisture content of the fully imbibed seed, before the radicle breaks through the seed coat, reaches a constant value. This implies that soil environment, within the limits of temperature and moisture specified, will influence the rate at which seed is absorbing water, but the final steady-state moisture level is an inherent property of the seed. The condition stated above can only be true if imbibitional forces within the seed are great compared to matric forces in the soil. Shull (1916) found that cocklebur seeds absorbed some moisture in osmotic solutions approaching 1000 bars.

The assumption of a constant, steady-state, seed-moisture level is substantiated by Dewez (1964) who found that the common asymptotic moisture level for cottonseed at three different temperatures in moisture saturated air was 80% on a dry weight basis. Hadas (1970) reported a constant, steady-state, moisture level for clover seed at three different soil moistures. In the radicle-emergence tests discussed in Chapter 4, no germination was obtained at 12.8 C regardless of soil moisture level. However, the

moisture level in the seed of these treatments was approximately 80% on a dry weight basis after steady-state moisture conditions were reached. Assuming that little metabolic activity occurred in the seed since the radicles did not emerge, absorbed seed water must have resulted almost entirely from imbibition. Based on the evidence above a steady-state imbibitional seed moisture level of 80% dry basis was used in the following model development.

Mathematical Definition

The rate at which seed takes up water during the imbibitional phase is dependent on the difference between actual and steady-state seed water. This is mathematically expressed by:

$$\frac{dW}{dt} = \frac{1}{T} (W_S - W) \quad (5-1)$$

Where: $\frac{dW}{dt}$ = Rate of seed-water uptake

W_S = Steady-state level of imbibitional water in the seed

W = Accumulated imbibitional water content of the seed

T = Time constant which reflects total resistance to water absorption by the seed.

The constant, T , is a lumped constant since it represents all of the seed-soil system resistances to water absorption. This constant accounts for moisture-flow resistances as influenced by temperature, soil moisture, seed coat, and

internal seed constituents. T is indicative of the water-uptake rate. It has dimensions of time and is referred to as the time constant by Milsum (1966).

By rearranging terms Equation (5-1) can be represented in standard form.

$$T \frac{dW}{dt} + W = W_S \quad (5-2)$$

Equation (5-2) is a linear, first-order, differential equation for describing a simple diffusion process. Specification of seed-water absorption due to imbibition is represented by the left side of the equation. The term on the right side is the input to the system. For the limits of temperature and soil-moisture tension specified, input to the seed is a constant represented by W_S . Output of this system is obtained by integration.

Solution of Equation (5-2) for a step input and an initial moisture condition of W_0 is given by:

$$W = W_S + (W_0 - W_S) \exp(-t/T) \quad (5-3)$$

The general shape of Equation (5-3) is a logarithmic curve which has a rapid rise in its early phase and then becomes asymptotic to a steady-state value.

Evaluation of Model Constant

Equation (5-3) indicates that seed water content can be predicted if values of W_S , W_0 , and T were known.

The value of W_S was estimated from the previous experiments as 80% dry-basis moisture and W_o , the initial seed moisture, was measured. Therefore, T remained the only unknown parameter. Water uptake measurements from the radicle-emergence tests were employed to obtain estimates of T . Data used were restricted to the early phase of germination where it was certain that metabolic activities within the seed had little influence on water absorption. This resulted in utilizing data only from the steep-sloped portion of the seed-water, uptake curve (the first four values for each treatment in Fig. 7 through 10).

The value of T was calculated for each treatment level by minimizing the least-squares error in Equation (5-3) with respect to T . Using this criterion the equation below was derived by taking the partial derivative with respect to T and equating to zero. Discrete time values are indicated by t_i .

$$T = \frac{\sum t_i^2}{\ln(W_o - W_S) \sum t_i - \sum \ln(W - W_S) t_i} \quad (5-4)$$

Values of T from each treatment were used to obtain the regression equation below which expresses $1/T$ as a function of soil temperature and moisture tension.

$$\frac{1}{T} = .033776 + .000086 S^2 - .003479 M \quad R^2 = .96$$

$$SE = .009 \quad (5-5)$$

S = Soil temperature, C

M = Soil moisture, bars

Values of the time constant generated by Equation (5-5) are plotted in Fig. 16. The magnitude of T is greatest at combinations of low temperature and high soil-moisture tension. Temperature has more influence on T than does moisture over the range of values studied; however, the effect of temperature increases most rapidly at low moisture levels. Part of the effect of temperature is due to the changing physical properties of liquid water. Fluidity increases by a factor of 1.8 between 12.8 and 37.8 C.

The T values were evaluated by comparing predicted values of seed moisture percentage from the model with the first-four, observed, moisture values of each curve in Fig. 7 through 10. The Chi-Square test at the 0.10 level of probability was utilized in making comparisons. There were no differences between observed and predicted water-uptake values in 21 of 24 treatment comparisons as shown in Table 18 of Appendix A.

Model Verification

The water-uptake model represented by Equation (5-2) was used to simulate average radicle extension of 3 mm. The flow chart in Fig. 22 (Appendix A) shows the logic of the model and the computer program is presented in Appendix B. The model was utilized for estimating

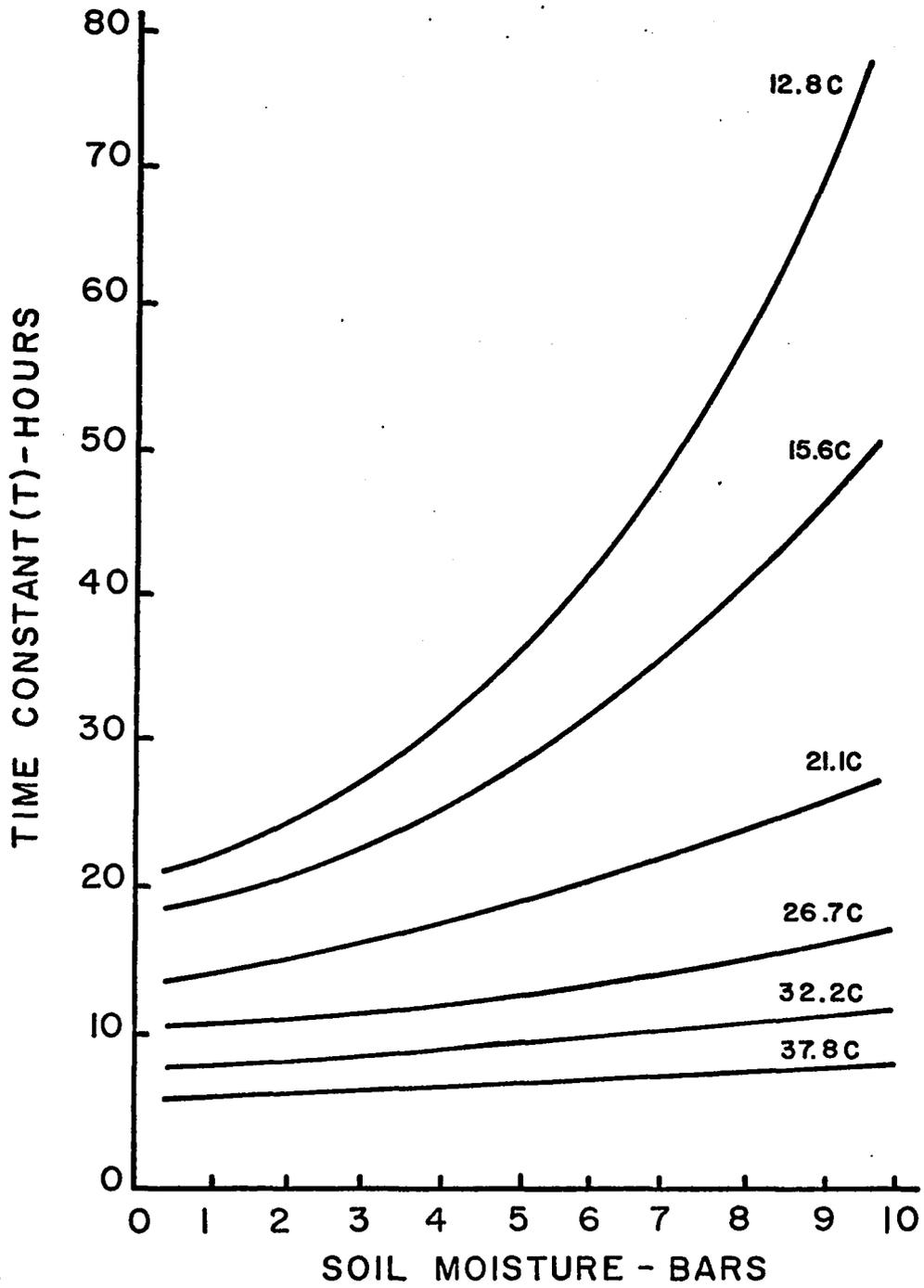


Fig. 16. Time-constant values for different levels of soil temperature and moisture computed from Equation (5-5).

radicle emergence even though it simulates imbibitional and not total water content of germinating seed. This was possible because time of occurrence and seed-moisture content at 3-mm radicle extension were known from the germination tests for various combinations of soil temperature and moisture. Change in percentage moisture (ΔM) due to imbibition during the hour immediately preceding radicle extension predicted by the water-uptake model was calculated for all combinations of constant temperature and soil moisture in the radicle-emergence tests. These values are shown in Fig. 17. Input to the model consists of hourly values of soil temperature and moisture. After each iteration the increase in seed-moisture percentage is compared to values in Fig. 17 for the same temperature and moisture, and the model predicts occurrence of the 3-mm radicle-extension event when the incremental change of percentage moisture is less than the corresponding value in the figure.

The flow chart of the radicle-emergence model in Fig. 22 shows that temperature must exceed 15.5 C for seed to absorb moisture in the model. Seed actually continue to take up some water at temperatures below 15.5 C, but practically no metabolic activity occurs. Since seed-water status is utilized to indicate stage of germination, zero water uptake in the model interrupts the simulated germination progress. No germination was observed in

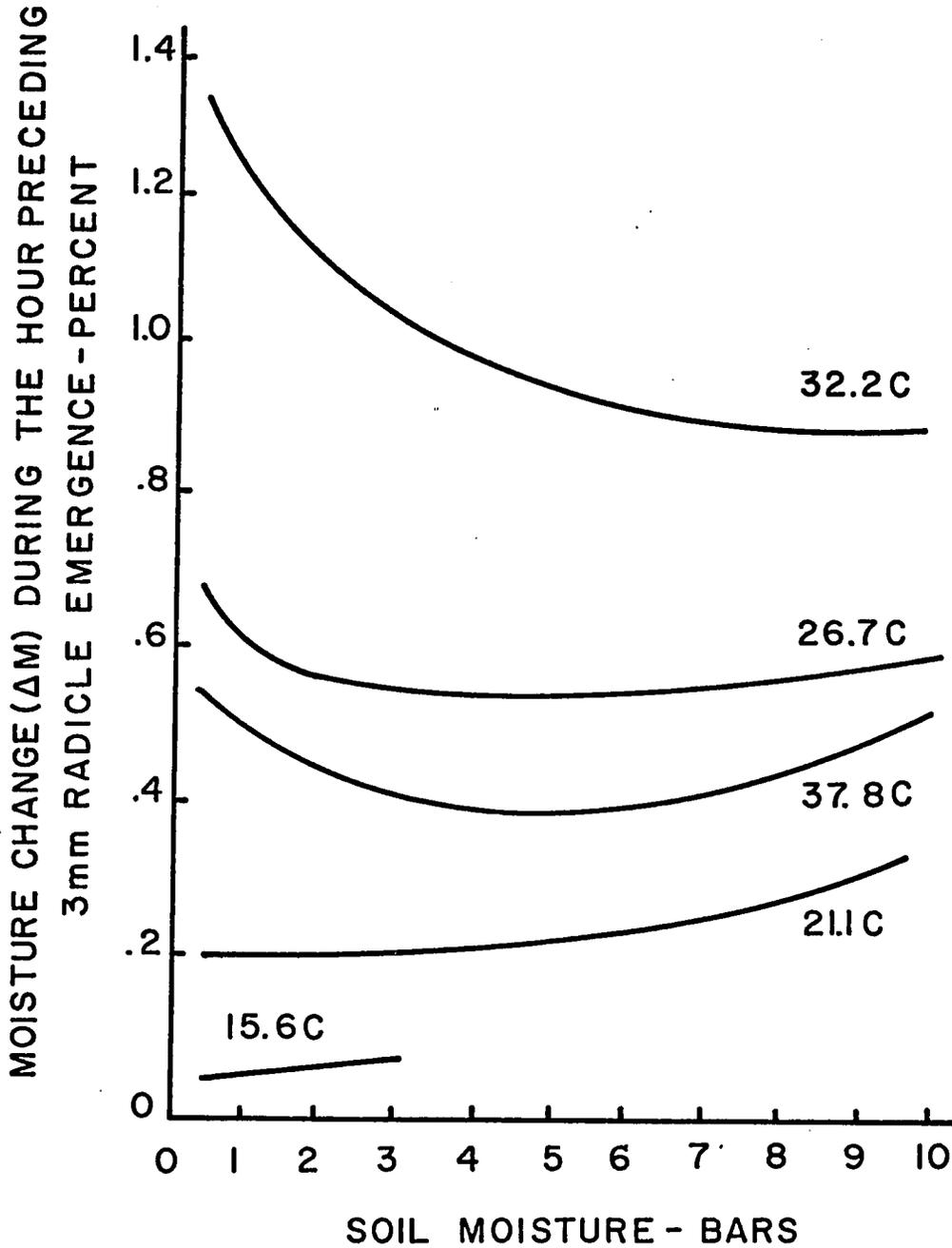


Fig. 17. Change in imbibitional, seed-moisture percentage (ΔM) for different environments prior to the 3-mm radicle-emergence event as predicted by the seed-water-uptake model.

radicle-emergence tests reported in Chapter 4 for 15.6 C and 10.0-bar moisture. Camp and Walker (1927) also failed to obtain germination of cottonseed in soil at 14 C.

Table 9 shows a comparison between radicle emergence computed from Equation (4-5) (regression equation based on test data) and those predicted by the water-uptake model. It can be seen that the model accurately simulated the 3-mm radicle-emergence event for constant environments; however, this comparison is a restricted verification of the model.

Table 9. Radicle-emergence times in hours computed from Equation (4-5) (R) and predicted (P) by the seed-water-uptake model for four moisture levels and five temperatures.

Temperature, C	Moisture level, bars							
	.3		1.0		3.0		10.0	
	R	P	R	P	R	P	R	P
37.8	20	20	20	21	22	23	24	24
32.2	15	17	16	18	19	20	22	24
26.7	24	26	25	27	28	31	34	36
21.1	46	47	47	48	51	51	59	62
15.6	80	80	82	83	86	91	--	--

A more general evaluation of the model is shown in Table 10 for germination occurring under fluctuating conditions. The first-four comparisons were taken from the field planting; the last two are from tests conducted at ambient temperatures in the greenhouse using the same cup containers as for the germination tests. Detailed environmental information for the field planting is shown in Tables 12, 13, and 14 (Appendix A). The deviation of predicted from observed values in Table 10 is greater than those in Table 9; however, all deviations are less than 10%.

A partial explanation for less accuracy in simulating under a variable environment lies in differences between the real system and the model. Seed-water absorption in a fluctuating environment is a time-varying process. The model used to simulate seed-water absorption is piecewise linear. In other words, the time-varying process is estimated by repeated use of a linear time invariant model of short duration. If duration of each interval is sufficiently small, the real system can be closely approximated. Environment is treated as a constant during each interval and the coefficient for each period is changed based on the input. State of the environment during each interval is reflected in the magnitude of T from Equation (5-2).

Table 10. Comparison of observed and predicted 3-mm radicle-emergence times under variable environmental conditions.

Description of soil environment	Time, hours	
	Observed	Predicted
2.5-cm planting depth, fluctuating temperature, 7 to 25 C, Moisture, .3 to .8 bars	65	71
5-cm planting depth, fluctuating temperature, 9 to 24 C, Moisture, .3 to .8 bars	76	73
7.5-cm planting depth, fluctuating temperature, 10 to 25 C, Moisture, .3 to .9 bars	79	73
10-cm planting depth, fluctuating temperature, 12 to 26 C, Moisture, .3 to .8 bars	78	72
.3-bars moisture, fluctuating temperature, 25 to 33 C	24	23
3.0-bars moisture, fluctuating temperature, 26 to 32 C	25	25

Model Application

The water-uptake model makes possible a more intensive examination of early phases of cottonseed germination than was possible from empirical measurements of seed-water content. Since the model primarily simulates water-uptake by imbibition, inputting values of temperature and moisture used in the germination tests, allows an estimate of the portion of the seed's moisture resulting from imbibition and that resulting from metabolic activity. Results from this operation indicate that water content of the seed when radicle extension averages 3 mm is primarily the result of imbibition. This conclusion is reached by comparing total-moisture content of seed at 3-mm extension as shown in Table 5 to that predicted by the model for imbibitional-water absorption.

Figures 18 and 19 show total- and predicted-imbibed, seed-moisture values at .3- and 1.0-bar soil moisture. At both soil-moisture levels, greatest difference between observed and predicted values occurs at 32.2 C, which is the temperature nearest to the optimum temperature range for germination (33 to 36 C) reported by Arndt (1945). The difference between total and predicted imbibed-moisture values is postulated to result from increased, seed-moisture absorption because of metabolic activity in seed. This seems to be a realistic interpretation since largest differences are noted in the optimum

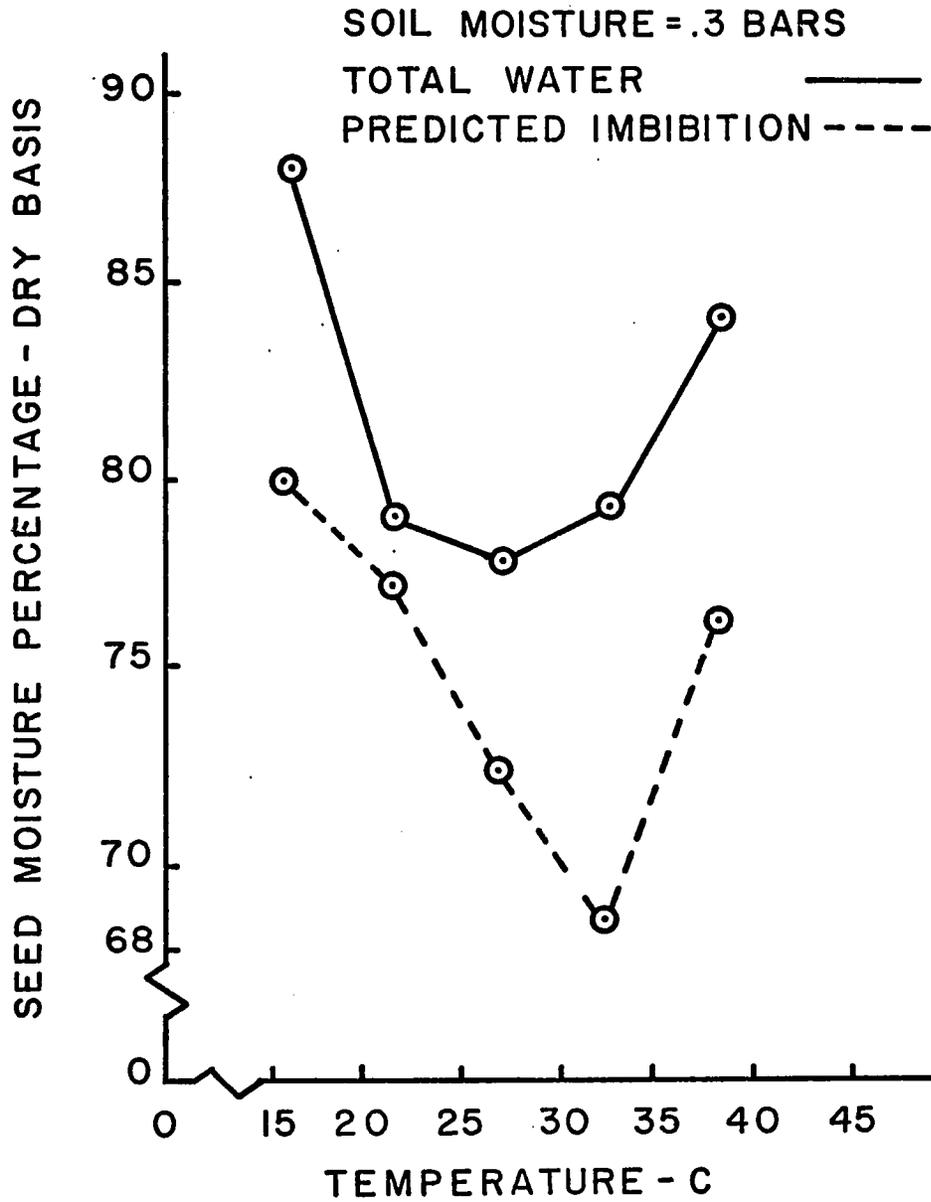


Fig. 18. Total and predicted, imbibed-seed-water content at .3-bar soil moisture for different temperatures at 3-mm radicle emergence.

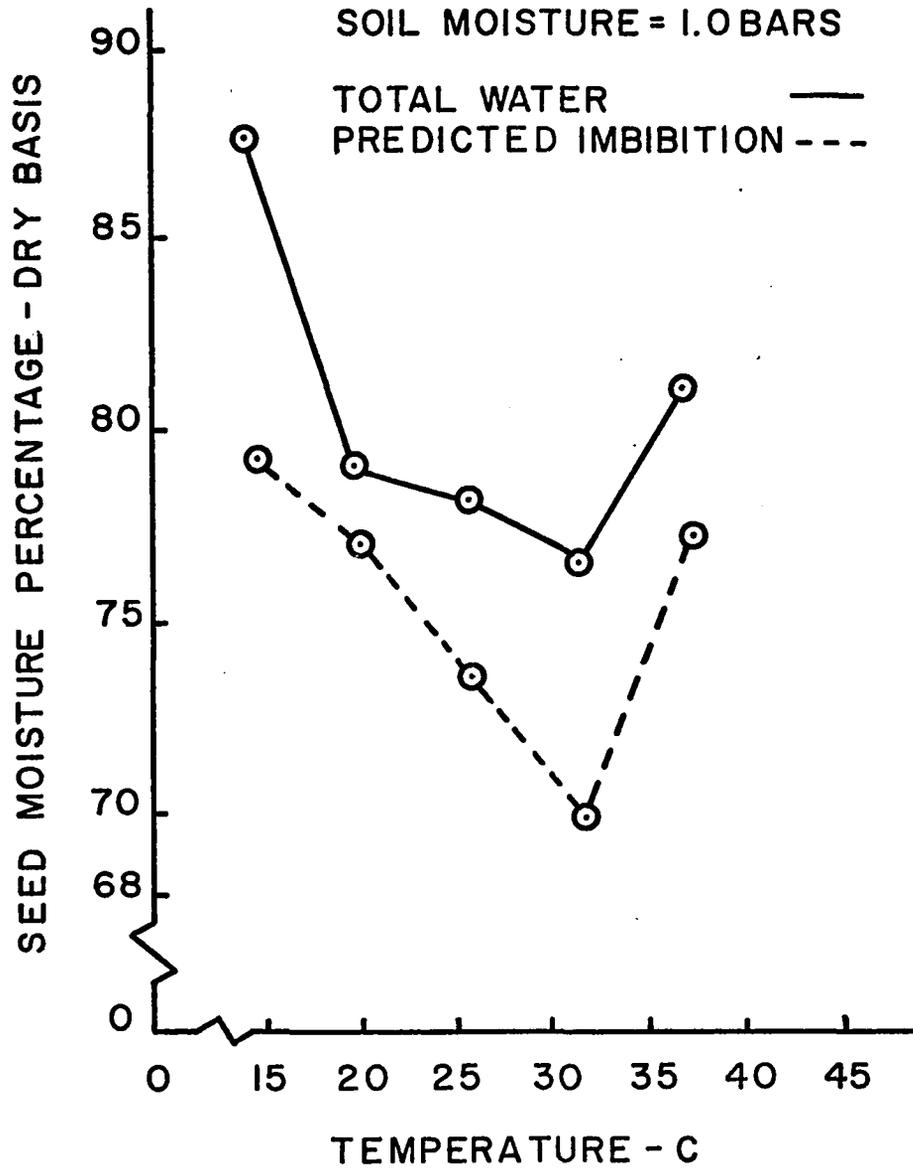


Fig. 19. Total and predicted imbibed-seed-water content at 1.0-bar soil moisture for different temperatures at 3-mm radicle emergence.

range for germination which would have the highest metabolic rate.

Differences between total water and predicted imbibed seed water are less distinct at lower temperatures for soil moistures of 3.0 and 10.0 bars (Fig. 20 and 21). In these instances, seed metabolism must have had a smaller effect on water absorption. Some temperatures show little difference between total and predicted imbibed water. This could be an indication that metabolic activity is not essential for radicle emergence. However, in favorable environments the 3-mm radicle-extension event occurs more rapidly because of metabolic activity.

Hypocotyl-Elongation Model

The hypocotyl of a germinating cotton seedling begins to elongate after the radicle has begun to lengthen. The hypocotyl and attached cotyledons increase in size and normally shed the seed coat before emerging. Pressure from the enlarging seedling and resistance from soil work simultaneously in removing the seed coat.

During emergence the hypocotyl forms a hook in its upper portion where the cotyledons are attached. The hook is formed early in emergence and is maintained until the apex of the hook breaks through the soil surface and is exposed to light. Red light stimulates opening of the hook. Powell and Morgan (1970) found that cotyledons are

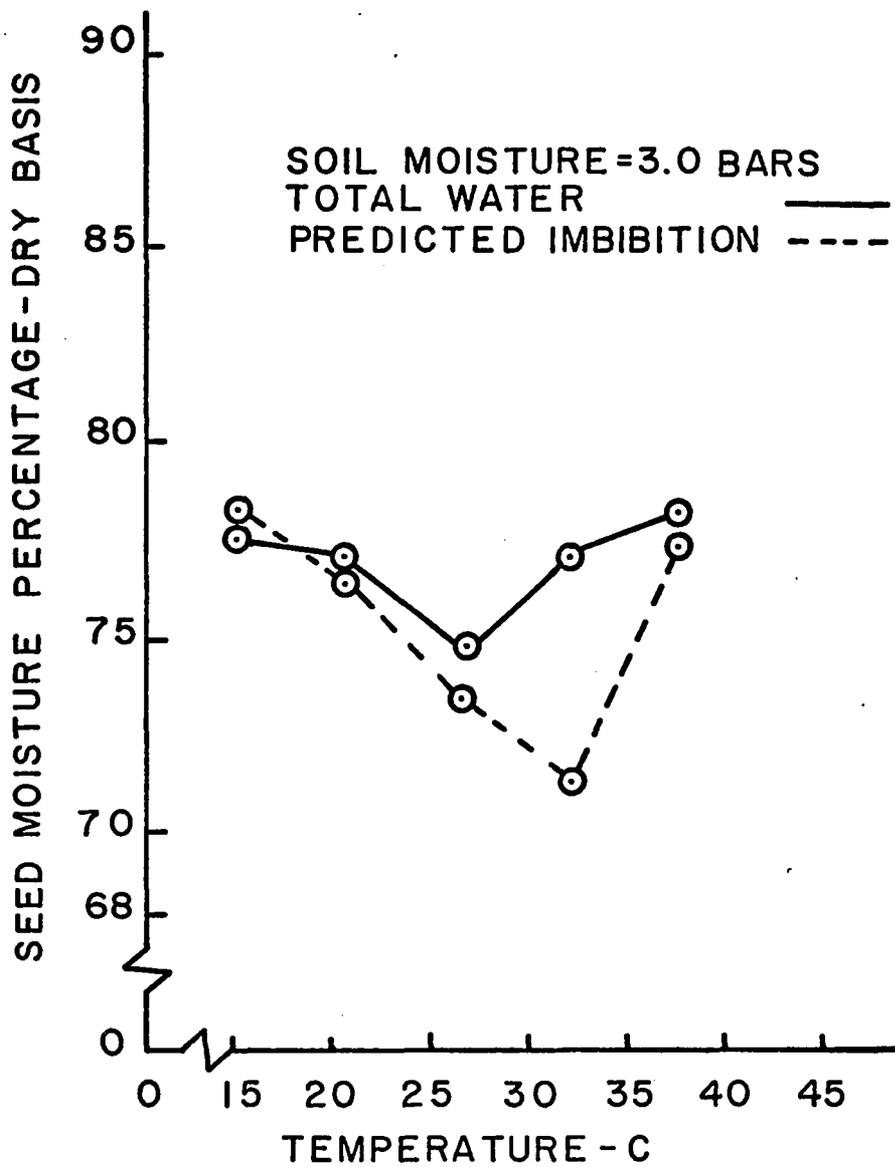


Fig. 20. Total and predicted imbibed-seed-water content at 3.0-bars soil moisture for different temperatures at 3-mm radicle emergence.

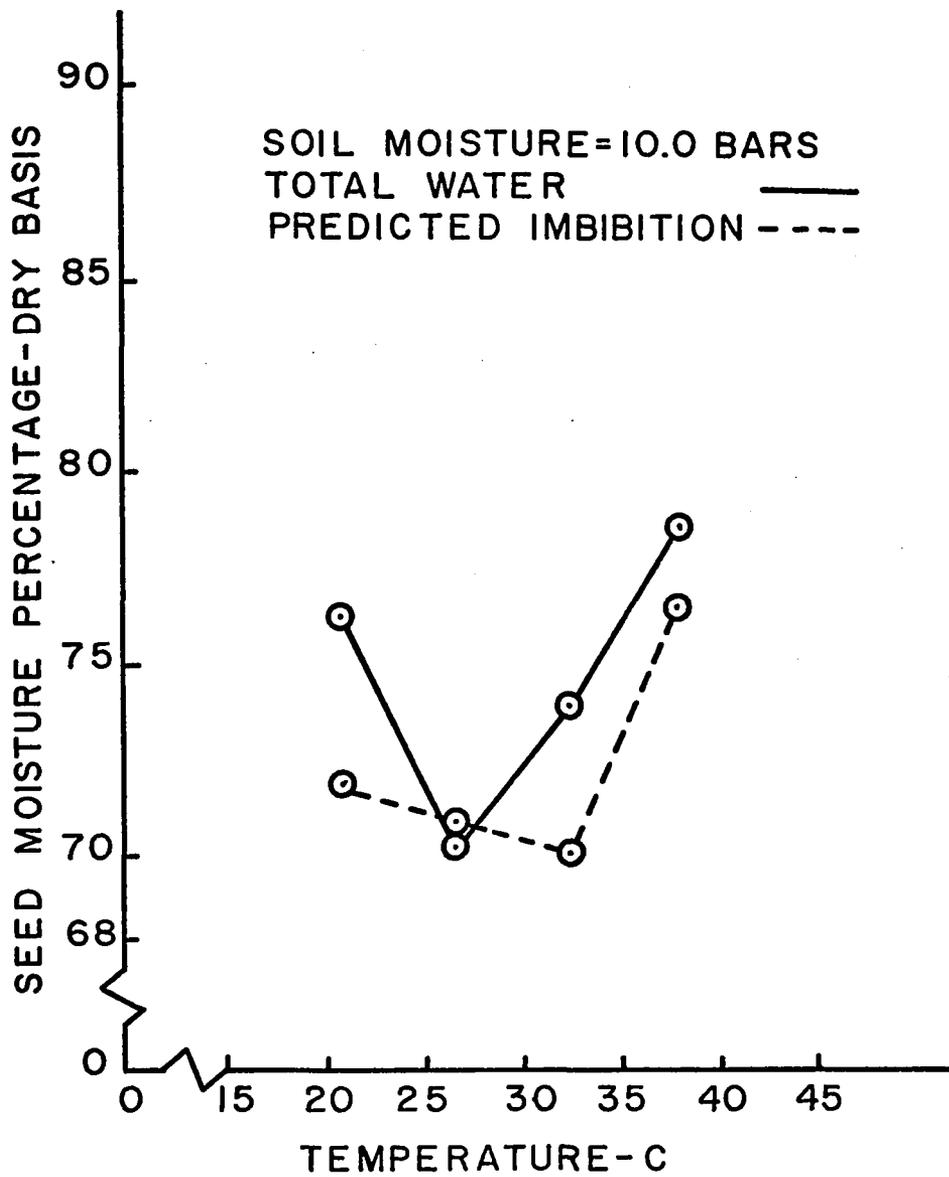


Fig. 21. Total and predicted imbibed-seed-water content at 10.0-bars soil moisture for different temperatures at 3-mm radicle emergence.

required for hook opening in cotton. In addition, the lower hypocotyl and root tissue can stimulate hook opening. These authors reported that hooks opened equally well when hypocotyls or cotyledons, or both were exposed to light. Ethylene inhibited the light induced opening of bean (Phaseolous vulgaris L.) hypocotyl hook in a study conducted by Kang, Burg, and Ray (1967). They also concluded that auxin inhibited hook opening by inducing production of ethylene.

System Description

Elongation rate and total length of hypocotyls are determined by the state of the system. Important parameters are soil moisture, soil temperature, seedling vigor, and soil resistance. Seedling vigor, which is related to energy supply, was not considered in this analysis. Other potential parameters such as toxic chemical compounds, disease, and deficient aeration were also omitted.

During emergence the only energy available is that available from storage materials in seed. Consequently, each seedling has a fixed, potential source of energy for growth during emergence. If the supply is low or the soil environment unfavorable, the seedling either fails to emerge or does so in a weakened condition.

Mathematical Definition

For the purpose of formulating a mathematical description, it is assumed that hypocotyl elongation results from cell elongation and division which are not confined to a single region. Furthermore, the quantity of energy is fixed. Rate of elongation is defined by:

$$\frac{dE}{dt} = K E Z \quad (5-6)$$

Where: $\frac{dE}{dt}$ = Rate of hypocotyl elongation

K = Constant of hypocotyl elongation

E = Hypocotyl length

Z = Unused energy

The parameter Z is critical because for any seed it represents a fixed quantity of available energy. Z can be defined as

$$Z = Z_0 - Z' \quad (5-7)$$

Where: Z_0 = Available energy at time zero

Z' = Amount of consumed energy

Elongation which results from Z is more convenient to measure than energy. Therefore, to replace Z in Equation (5-6) elongation which resulted from Z is expressed as:

$$E' = E_S - E \quad (5-8)$$

Where: E' = Unrealized hypocotyl length

E_S = Maximum hypocotyl length

E = Hypocotyl length

Substituting the elongation equivalent of Z from Equation (5-8) into Equation (5-6) results in

$$\frac{dE}{dt} = KE(E_S - E) \quad (5-9)$$

Output of Equation (5-9) generates a sigmoid curve for a constant value of K . This same form of differential equation dynamically describes an autocatalytic reaction in chemistry. During growth, the rate of increase in size is initially proportional to size, but the rate of increase decreases as maximum size is approached. Elongation rate is small at first because E is small. Decrease in elongation rate as E approaches E_S is due to the decreasing difference between E_S and E . dE/dt is greatest for intermediate values of E . In Equation (5-9), the quantity of unused energy is represented by $E_S - E$.

Maximum elongation values, E_S , which are a function of energy and environment, are shown in Table 6. Treatments that produced 50% emergence were terminated before maximum elongation occurred. E_S was estimated for these treatments by fitting an analog solution of Equation (5-9) to the observed response. These values are enclosed by parentheses in Table 6.

The solution of Equation (5-9) for constant conditions is

$$E = \frac{E_o E_S}{E_o + (E_S - E_o) \exp(-KE_S t)} \quad (5-10)$$

E_o is hypocotyl length at time zero and t represents time. All other terms are as previously defined. The product, KE_S , has dimensions of reciprocal time.

Evaluation of Model Constant

The influence of fluctuating environment on elongation is accounted for in a manner similar to that utilized for the seed-water-uptake model. Hypocotyl elongation was measured for a number of constant environmental conditions. The soil-environmental parameters held at constant levels were temperature, moisture, and physical impedance. From tests, all terms in Equation (5-10) except E_o and K were measured. A value of .05 mm was picked as a good estimate of E_o based on trial and error solutions. Using a logarithmic transformation, Equation (5-10) which is non-linear, is represented in linear form:

$$\frac{\ln \left(\frac{\frac{E_o E_S}{E} - E_o}{E_S - E_o} \right)}{E_S} = -K t \quad (5-11)$$

Linear regression analyses of experimental data in Tables 19 through 33 (Appendix A) were used to estimate the value

of K for each environment. Observed values were compared with those predicted by Equation (5-10) using appropriate K values computed from Equation (5-11). The R^2 criterion was used to measure goodness of fit between observed and predicted values. The Chi-Square test was not applicable since a considerable number of observed values had magnitudes less than one. Values of K and R^2 are included in Table 34 of Appendix A. The combination of the parameters E_S and K characterize the favorableness of the soil environment for hypocotyl growth. The product of E_S and K is indicative of rate of growth, with larger magnitudes representing more rapid elongation.

Hypocotyl elongation was simulated by using Equation (5-9) for 51 combinations of constant, soil-environmental conditions of temperature, moisture, and physical impedance. In 36 of 51 comparisons, Equation (5-9) fitted observed growth curves with an R^2 value greater than .90 (Table 34 in Appendix A). Considering only environments which produced maximum hypocotyl lengths of 1 cm or more (Table 6) only one comparison had an R^2 value less than .90. In general the model was least accurate in simulating hypocotyl elongation in environments which caused severe seedling stress. From these results Equation (5-9) is concluded to be an acceptable model for describing the average time distribution of hypocotyl

length for a population of cotton seedlings emerging in a constant environment.

Model Verification

The applicability of Equation (5-9) as a model of average hypocotyl elongation in a population of cotton seedlings received additional evaluation under fluctuating conditions. Observations of hypocotyl elongation were made under varying temperature conditions in plexiglass growth boxes with constant soil moisture and physical impedance levels. Temperature was picked as the variable parameter because it changes most under natural conditions and was the easiest parameter to vary and measure.

Equation (5-9) was utilized for simulating hypocotyl elongation under variable temperatures. Figure 23 (Appendix A) shows the flow chart and Appendix C contains the computer program of the hypocotyl-elongation model. The flow chart outlines the general logic of the model. Incremental growth was computed on an hourly basis using values of K and E_S as defined by temperature, moisture, and physical impedance. Two conditions are necessary for growth to occur during any hour. First, temperature has to be higher than 15.5 C. Secondly, E_S for the hourly environment has to be greater than the accumulated elongation, E . This constraint is utilized to prevent Equation (5-9) from indicating a negative increment of growth.

One additional logic element in the computer program is included to estimate when maximum hypocotyl elongation is reached. This is necessary to stop the computer model from "growing" the hypocotyl in a fluctuating environment after the seedling's "energy is exhausted." To prevent this, the portion of the total possible growing time that elapsed during an hour is estimated from the state of the environment. This is accomplished by using a regression equation which relates total growing time in hours for a constant environment to temperature and moisture. The portion of total growing time consumed during a given hour is taken as the reciprocal of total growing time predicted by the regression equation for that soil environment. The hourly reciprocal values are accumulated. Maximum elongation is considered to occur when the accumulated reciprocal values reached .85. This value was chosen after comparing the results of simulating hypocotyl elongation under varying temperatures. After reaching .85 the observed hypocotyl lengths tended to markedly deviate from those simulated by the model. This is interpreted to mean that the energy level of the seedling was too low to sustain normal elongation. Furthermore, energy utilization may be different for constant and variable temperature regimes.

Results from simulating hypocotyl elongation under fluctuating temperatures are shown in Table 11. The

Table 11. Statistics for estimating goodness of fit between observed and simulated hypocotyl elongation for fluctuating temperature with constant soil moisture and physical impedance.⁺

Description of soil environment [‡]	Observed maximum hypocotyl length, cm	Linear regression coefficient	t-value	R ²	Standard error of estimate
16 to 42, 3.0, .23	4.1	.78	4.13* (6)	.98	.31
23 to 38, 3.0, 1.12	1.9	.86	2.28 (6)	.98	.19
25 to 38, 3.0, .23	4.0	.93	2.48* (6)	.99	.16
26 to 36, .3, 1.12	3.0	.93	.99 (4)	.98	.32
25 to 36, 1.3, .23	6.2	1.06	1.83 (5)	.99	.31
25 to 37, .3, 1.6	2.0	1.16	2.61 (3)	.99	.15
32.2, .3, .23	4.4	1.10	1.26 (4)	.98	.43
20 to 31, .5, .23	7.5	.99	.71 (7)	.99	.22

Table 11.--Continued

32.2, .3, .23	6.9	.91	1.39 (5)	.98	.68
24 to 32, 3.0, .47	3.4	.99	.01 (6)	.93	.64

*Indicates a significant difference between the coefficient and 1.0 at the .05 level. Numbers in parentheses are degrees of freedom.

+Goodness of fit was evaluated by checking the linear regression between observed and predicted hypocotyl lengths.

#From left to right the numbers represent soil temperature range in C, moisture in bars, and physical impedance in kg/cm².

procedure for estimating goodness of fit was to calculate a linear regression between observed and predicted values. The linear regression coefficients in Table 11 have a value of 1.0 when the model is unbiased. The t-values indicate that the model was biased in two of the ten comparisons. In these two cases, the predicted tended to be less than the observed values. Standard error of the estimate was less than 10% of maximum length, except for the last comparison which approached 20%. The overall results in Table 11 indicated the hypocotyl model satisfactorily simulated elongation under fluctuating temperatures.

It may be significant that the comparisons in Table 11 which had regression coefficients statistically different from 1.0 were subjected to more temperatures above 32.2 C than the other comparisons. The model was developed from data collected under constant conditions. The growth rate observed at the constant temperature of 37.8 C, which is near the maximum temperature for cotton growth, may be less than would occur at the same temperature existing for only a short duration. This could explain the model under estimating hypocotyl elongation in these comparisons. The existence of a temperature-time factor near the upper temperature limit for an organism was postulated by Blackman (1905). He presented analytical proof for this phenomena, but added it would be difficult to verify experimentally.

CHAPTER 6

SUMMARY AND CONCLUSIONS

The study was undertaken to measure growth of cotton seedlings during emergence with constant levels of soil temperature, moisture, and physical impedance and to use those data to develop models of radicle-emergence time and hypocotyl elongation. These models were subsequently used to simulate growth under fluctuating temperatures.

Emergence was divided into two parts for empirical tests and model development. The first phase covered the period from planting until the radicle length averaged 3 mm. The second phase began with 3-mm radicle extension and ended when the hypocotyl emerged from the soil or reached maximum length.

Radicle-emergence tests (first phase) were conducted in soil with 10-seed lots. Water absorption was measured until 3-mm radicle emergence occurred for 6 temperatures (12.8, 15.6, 21.1, 26.7, 32.2, and 37.8 C) and 4 soil moisture levels (.3, 1.0, 3.0, and 10.0 bars). The second phase measured hypocotyl and radicle elongation for groups of 15 pregerminated seed. Observations were made at 5 temperatures (15.6, 21.1, 26.7, 32.2, and 37.8 C), 3 soil moistures (.3, 3.0, and 10.0 bars), and 4 physical

impedance levels (.23, 1.12, 2.24, and 3.36 kg/cm²). These tests were continued until 50% emergence or all hypocotyls stopped elongating.

The time of 3-mm radicle extension decreased between 15.6 and 32.2 C, and leveled off at 37.8 C. Decreasing soil moisture increased radicle emergence time less than temperature.

Rate of imbibitional water uptake decreased as seed-moisture content increased. High, soil-moisture levels and temperatures resulted in faster water uptake. Seed-moisture percentage at the 3-mm radicle-emergence event was highest for the extreme temperatures (15.6 and 37.8 C) with lower percentages at intermediate temperatures. Low soil moisture tended to result in reduced seed moisture at radicle emergence.

Total length, rate of elongation of both hypocotyls and radicles, and radicle-emergence time increased from 15.6 to 32.2 C and then decreased at 37.8 C. The most severe reduction in hypocotyl elongation with decreasing soil moisture occurred at 37.8 C.

Low soil moisture and high physical impedance decreased hypocotyl elongation more than radicles. A more pronounced arch in the hypocotyl was observed at higher physical-impedance levels. Differences in sensitivity between the hypocotyl and radicle to soil moisture and physical impedance are related to differences in shape, and

manner of growth. The hypocotyl with attached cotyledons elongates throughout its length and encounters greater soil resistance. A relatively longer radicle was observed at lower soil moisture levels. The effect of soil moisture likely results from an internal mechanism which strives to develop an adequate root system at the expense of the hypocotyl when plant-water status is low.

The radicle-emergence time model accumulates imbibitional seed water as a measure of seed-germination status. The basis of the model is a linear differential equation with a single lumped constant, $T \frac{dw}{dt} + W = W_S$. The magnitude of the lumped constant reflects environmental influences on seed imbibition. The model predicts the 3-mm radicle-emergence event when seed-water level exceeds the moisture level observed in tests at corresponding environmental conditions. The model simulated radicle-emergence within 10% of actual observations under variable temperature conditions.

Simulation with the radicle-emergence model showed that most of the seed's water content at 3-mm radicle extension is the result of imbibition. The largest difference between total-water content of the seed and imbibitional water occurred at 32.2 C.

Hypocotyl elongation was modeled by using a non-linear differential equation that describes the dynamics of an autocatalytic reaction, $\frac{dE}{dt} = KE(E_S - E)$. In this

equation, environment influences the elongation rate by changing the magnitude of K and E_S . Simulations with the model under fluctuating temperatures indicated that the model satisfactorily estimated observed hypocotyl growth, but tended to underestimate hypocotyl growth when temperatures exceeded 32.2 C. The model was developed from data obtained under constant conditions. It is possible that growth response under steady-state conditions at 37.8 C is lower than that which occurs at similar but fluctuating temperatures.

The following conclusions were drawn from the results of the study:

1. Radicle-emergence time between .3- and 3.0-bars soil moisture is primarily influenced by temperature.
2. Seed water absorption up to 3-mm radicle extension is predominantly by imbibition.
3. A linear-differential equation of diffusion containing a single-lumped constant can be used to simulate seed water absorption by imbibition.
4. Decreasing levels of soil moisture cause a delay in initiation of hypocotyl elongation and reduce final length.
5. The nonlinear differential equation of an autocatalytic reaction also describes average hypocotyl

elongation for a population of emerging cotton seedlings.

6. One-hour time intervals are sufficiently small for discrete simulation of growth during cotton emergence.
7. The model of hypocotyl elongation can be utilized in a model for simulating time distribution of seedling emergence if the randomness of the population is known.

APPENDIX A

MEASUREMENTS OF COTTON SEEDLING GROWTH, STATISTICAL
ANALYSES, AND FLOW CHARTS FOR COMPUTER PROGRAMS

Table 12. Daily maximum and minimum seed-depth temperatures (C) for four planting depths in test planted April 15, 1969.

Date, and day since planting	Planting depth, cm							
	2.5		5.0		7.5		10.0	
	Max	Min	Max	Min	Max	Min	Max	Min
April 15- 0	25.0	11.7	23.3	13.3	22.8	14.4	22.2	15.6
16- 1	23.9	7.8	21.7	9.4	21.7	10.6	22.8	11.7
17- 2	29.4	7.2	25.6	8.9	25.0	10.0	25.6	11.7
18- 3	31.7	7.8	27.8	9.4	27.2	10.6	26.7	12.8
19- 4	32.2	11.1	28.3	12.2	28.3	13.3	27.8	15.6
20- 5	35.6	11.1	31.1	12.8	30.0	14.4	28.9	15.6
21- 6	36.7	12.8	32.2	13.9	31.1	15.6	29.4	16.7
22- 7	36.1	12.8	31.7	14.4	31.1	16.1	29.4	17.8
23- 8	36.7	12.8	32.8	14.4	31.7	16.1	30.0	17.8
24- 9	37.2	13.9	33.3	15.0	31.7	16.7	30.0	18.3
25-10	35.6	13.3	31.7	15.0	30.6	16.7	29.4	18.3
26-11	33.9	11.7	30.6	13.3	28.9	15.0	27.8	16.7
27-12	35.0	10.0	31.7	12.2	29.4	14.4	27.8	15.6
28-13	36.7	11.1	32.8	13.3	30.6	15.0	28.9	16.7

Table 13. Average soil-moisture values for four depths of planting in test planted April 15, 1969.*

Time since planting, hours	Planting depth, cm			
	2.5	5.0	7.5	10.0
24	.3	.3	<.3	<.3
69	.8	1.0	.9	.8
118	2.4	2.4	1.2	.9
168	9.3	3.2	1.9	1.2
219	10.3	6.7	1.7	1.7

*Soil moisture was sampled in the seed drill +1.25 cm of planting depth and is expressed in bars.

Table 14. Average soil-impedance values for four depths of planting expressed in kg/cm² in test planted April 15, 1969.*

Time since planting, hours	Planting depth, cm			
	2.5	5.0	7.5	10.0 [‡]
26	3.45	3.66	4.15	4.50
71 [†]	6.19	6.19	6.26	--
119	2.04	3.30	4.01	--
169	5.77	5.91	7.52	--

*Penetrometer measurements were made with a Chatillon push-pull gauge having a .4-cm-diameter, blunt probe.

[†]The soil crust was broken after impedance measurements were made.

[‡]The length of the penetrometer probe did not permit taking readings below 7.5 cm when physical impedance exceeded 4.50 kg/cm².

Table 15. Analysis of variance for maximum hypocotyl lengths.

Source	Degrees of freedom	Mean squares	F
Physical Impedance (P)	3	488.25	279.00**
Moisture (M)	2	408.99	233.71**
Temperature (T)	4	131.22	74.98**
PXM	6	46.94	26.82**
PXT	12	24.97	14.27**
MXT	8	19.46	11.12**
PXMXT	24	3.62	2.06**
Error	840	1.85	
Total	899		

**Indicates significance at the .01 level.

Table 16. Analysis of variance for maximum radicle lengths.

Source	Degrees of freedom	Mean squares	F
Physical Impedance (P)	3	890.60	69.47**
Moisture (M)	2	894.25	74.04**
Temperature (T)	4	10,390.70	810.51**
PXM	6	283.23	22.09**
PXT	12	31.20	2.43**
MXT	8	689.23	53.77**
PXMXT	24	76.62	5.98**
Error	840	11.10	
Total	899		

**Indicates significance at the .01 level.

Table 17. Analysis of variance for ratios of maximum mean hypocotyl lengths to radicle lengths.

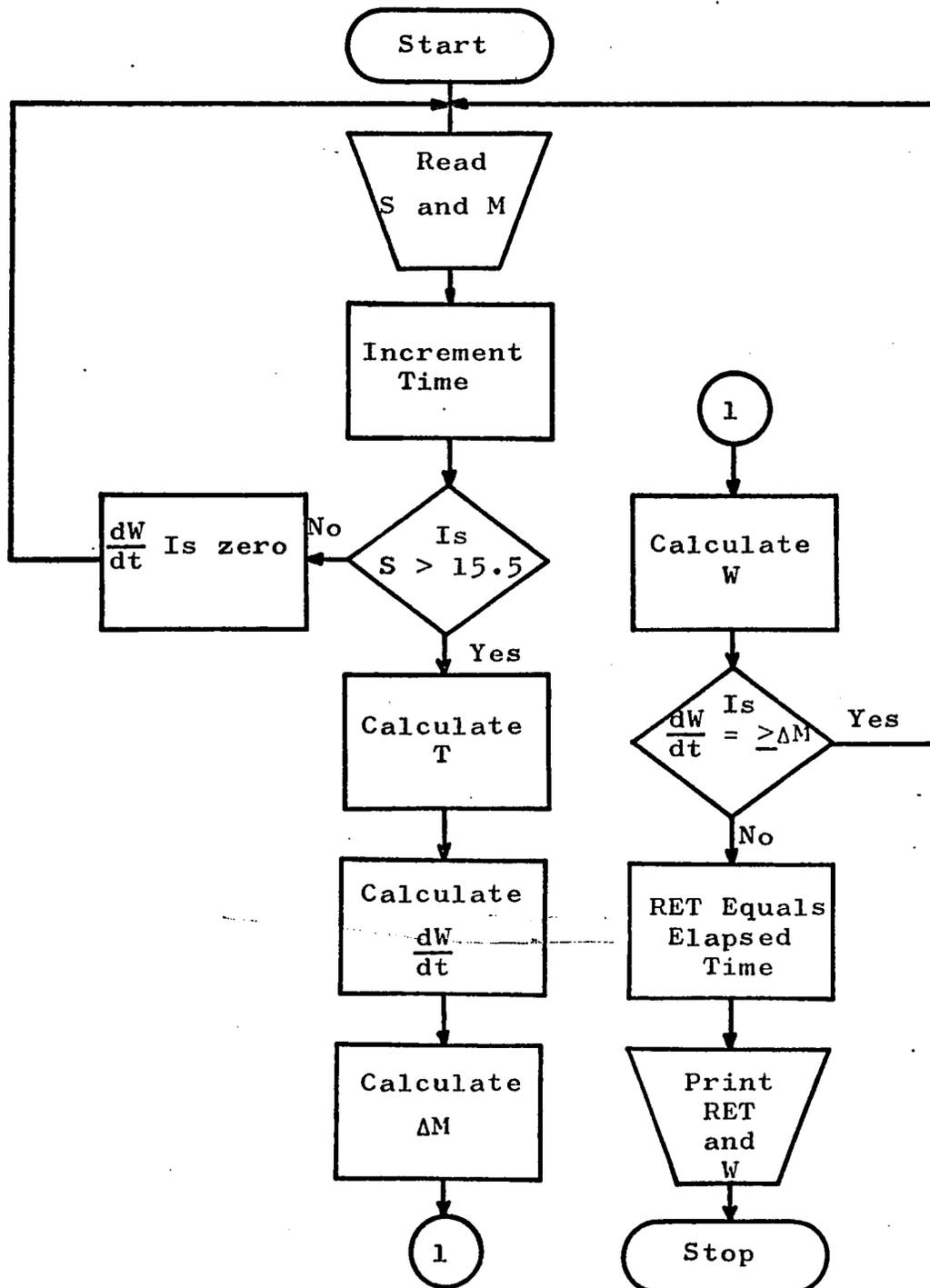
Source	Degrees of freedom	Mean squares	F
Physical Impedance (P)	3	.1009	66.26**
Moisture (M)	2	.1655	108.68**
Temperature (T)	4	.0019	1.28
PXM	6	.0238	15.65**
PXT	12	.0009	.56
MXT	8	.0060	3.97**
PXMXT	24	.0015	
Total	59		

**Indicates significance at the .01 level.

Table 18. Chi-Square test of fit between actual and predicted imbibitional seed-water uptake.*

Soil moisture, bars	Chi-Square	Probability level
	<u>12.8</u>	
.3	1.45	.50 < P < .75
1.0	.35	.90 < P < .95
3.0	1.02	.75 < P < .90
10.0	11.93	.005 < P < .01
	<u>15.6</u>	
.3	1.98	.50 < P < .75
1.0	1.92	.50 < P < .75
3.0	.12	.975 < P < .99
10.0	6.33	.05 < P < .10
	<u>21.1</u>	
.3	3.35	.25 < P < .50
1.0	1.18	.75 < P < .90
3.0	5.10	.10 < P < .25
10.0	3.18	.25 < P < .50
	<u>26.7</u>	
.3	1.65	.50 < P < .75
1.0	3.26	.25 < P < .50
3.0	.69	.75 < P < .90
10.0	.52	.90 < P < .95
	<u>32.2</u>	
.3	8.31	.025 < P < .05
1.0	5.20	.10 < P < .25
3.0	.02	.995 < P
10.0	.55	.90 < P < .95
	<u>37.8</u>	
.3	.14	.975 < P < .99
1.0	.03	.995 < P
3.0	.19	.975 < P < .99
10.0	1.61	.50 < P < .75

*The underlined numbers are soil temperature in C. Degrees of freedom for each comparison were three. Calculated Chi-Square must be larger than 6.25 to be significant at the 0.10 level.



See page 137 for description
of abbreviations

Fig. 22. Flow chart of computer program for simulating the 3-mm radicle-emergence event.

Table 19. Average time-wise hypocotyl and radicle lengths at 15.6 C and .3-bar soil moisture for four levels of physical impedance.*

Time	Hypocotyl	Radicle	Time	Hypocotyl	Radicle
<u>PI = .23</u>			<u>PI = 1.12</u>		
24	0	.7	27	0	.5
46	0	1.2	55	0	1.1
96	0	2.3	67	0	1.2
144	.2	3.4	91	0	1.9
166	.3	3.8	115	.1	2.2
192	.3	4.2	139	.2	2.7
214	.5	4.5	163	.2	3.2
264	1.0	5.1	188	.3	3.6
286	1.3	5.3	235	.5	4.6
312	1.6	5.5	259	.6	5.1
334	1.8	5.8	307	.7	5.8
360	2.0	6.0	356	.7	6.3
432	2.2	6.7	403	1.0	7.0
454	2.2	6.9	451	1.0	7.5
507	2.7	7.5	499	1.1	8.1
550	2.7	7.9	523	1.2	8.3
			571	1.2	8.7
<u>PI = 2.24</u>			<u>PI = 3.36</u>		
27	0	.2	44	0	0
55	0	.6	68	0	.5
67	0	.7	116	.1	1.9
91	0	1.2	164	.1	2.1
115	.2	1.5	216	.2	3.0
139	.2	1.8	288	.3	4.1
163	.2	2.2	336	.4	4.7
188	.2	2.5	384	.4	5.3
235	.4	3.1	408	.5	5.6
259	.4	3.4	456	.5	6.0
307	.5	3.9	504	.5	6.3
356	.7	4.3	578	.5	6.9
403	.8	4.7			
451	.8	5.0			
499	.8	5.3			
523	.8	5.4			
571	.8	5.5			

*Lengths are in cm, time is in hours, and physical impedance is in kg/cm².

Table 20. Average time-wise hypocotyl and radicle lengths at 15.6 C and 3.0-bars soil moisture for four levels of physical impedance.*

Time	Hypocotyl	Radicle	Time	Hypocotyl	Radicle
<u>PI = .23</u>			<u>PI = 1.12</u>		
17	0	.2	17	0	.3
43	0	.9	43	0	1.0
65	0	1.9	65	0	1.6
115	0	3.5	115	0	3.0
163	0	4.6	163	0	4.0
185	.2	5.2	185	0	4.4
211	.2	5.7	211	0	4.9
283	.6	6.8	283	.2	6.0
305	1.0	7.2	305	.3	6.5
358	1.3	7.9	358	.5	6.7
401	1.4	8.5	401	.6	7.2
449	1.5	9.1	449	.6	7.6
497	1.6	9.7	497	.7	8.5
545	1.6	10.4	545	.7	8.7
569	1.6	10.7	569	.7	9.0
<u>PI = 2.24</u>			<u>PI = 3.36</u>		
21	0	.2	43	0	.5
68	0	1.1	91	0	1.5
92	0	1.9	139	0	2.3
140	0	3.0	187	.1	3.4
189	.1	4.1	235	.1	4.2
236	.2	5.0	307	.2	5.1
284	.3	5.4	355	.2	5.7
332	.4	5.9	403	.3	6.2
356	.4	6.2	427	.3	6.5
404	.4	6.7	475	.3	6.8
452	.4	7.2	523	.3	7.2
500	.5	7.7	542	.3	7.3
572	.5	8.2			

*Lengths are in cm, time is in hours, and physical impedance in kg/cm².

Table 21. Average time-wise hypocotyl and radicle lengths at 15.6 C and 10.0-bars soil moisture for four levels of physical impedance.*

Time	Hypocotyl	Radicle	Time	Hypocotyl	Radicle
	<u>PI = .23</u>			<u>PI = 1.12</u>	
21	0	0	46	0	0
68	0	1.4	118	0	0
92	0	2.1	166	0	.6
140	0	3.6	214	0	1.9
189	0	4.6	238	0	2.7
236	.1	5.6	286	0	3.8
284	.3	6.2	334	.1	4.7
332	.4	6.8	382	.1	5.3
356	.5	7.1	454	.1	5.7
404	.6	7.6	502	.2	6.0
452	.7	8.2	550	.2	6.4
500	.7	8.8			
572	.7	9.5			
	<u>PI = 2.24</u>			<u>PI = 3.36</u>	
46	0	0	45	0	0
118	0	2.0	93	0	1.2
166	0	2.8	141	0	1.8
214	0	3.2	189	0	2.3
238	0	3.7	237	0	3.0
286	0	4.7	309	.1	3.4
334	0	5.4	357	.1	3.8
382	0	5.9	405	.1	4.1
454	.1	6.5	429	.2	4.2
502	.1	6.9	477	.2	4.5
			525	.2	4.9
			549	.2	5.6

*Lengths are in cm, time is in hours, and physical impedance is in kg/cm².

Table 22. Average time-wise hypocotyl and radicle lengths at 21.1 C and .3-bar soil moisture for four levels of physical impedance.*

Time	Hypocotyl	Radicle	Time	Hypocotyl	Radicle
<u>PI = .23</u>			<u>PI = 1.12</u>		
24	0	1.7	21	0	.9
48	.3	4.5	45	.3	3.7
72	.5	7.5	69	.5	6.7
95	1.3	11.0	93	1.1	10.6
121	2.9	13.0	121	2.0	13.8
144	5.2	14.4	145	2.3	16.0
152	5.7	15.0	165	2.8	16.3
168	6.8	15.6	189	3.0	18.4
			213	3.0	19.7
			237	3.0	19.9
<u>PI = 2.24</u>			<u>PI = 3.36</u>		
23	0	1.2	22	0	.5
47	.1	3.4	46	0	2.1
75	.2	6.0	70	.1	4.5
99	.5	9.0	94	.2	6.7
119	.9	10.7	118	.5	8.3
143	1.1	12.4	142	.9	9.7
167	1.4	13.3	166	1.1	10.5
191	1.5	14.2	194	1.2	11.3
215	1.6	14.7	218	1.3	11.8
239	1.6	15.1	242	1.3	11.8
			266	1.3	11.8

*Lengths are in cm, time is in hours, and physical impedance is in kg/cm².

Table 23. Average time-wise hypocotyl and radicle lengths at 21.1 C and 3.0-bars soil moisture for four levels of physical impedance.*

Time	Hypocotyl	Radicle	Time	Hypocotyl	Radicle
<u>PI = .23</u>			<u>PI = 1.12</u>		
21	0	1.2	23	0	.9
45	0	4.5	47	.1	3.1
69	0	7.7	71	.2	5.4
93	.2	10.8	95	.3	8.0
117	.9	13.8	119	.8	10.4
141	1.6	16.3	143	1.3	12.7
165	2.0	18.5	167	1.7	15.8
189	2.3	20.0	191	1.9	17.3
213	3.0	21.2	215	2.3	19.4
237	3.4	22.1	239	2.6	19.4
261	3.9	22.7	263	2.8	19.4
285	4.3	23.1	287	2.8	19.9
309	4.6	23.4			
333	4.7	23.6			
<u>PI = 2.24</u>			<u>PI = 3.36</u>		
18	0	.8	22	0	0
42	0	2.5	46	0	1.9
66	.1	4.9	70	.1	3.5
91	.2	7.5	94	.2	4.9
115	.4	9.5	118	.2	6.6
139	.7	12.2	142	.4	8.9
163	1.0	14.1	166	.5	10.7
187	1.1	15.8	190	.6	12.2
211	1.3	17.3	214	.7	13.6
235	1.3	18.4	238	.9	14.5
259	1.4	19.0	262	.9	14.5
283	1.4	19.5	286	.9	15.0

*Lengths are in cm, time is in hours, and physical impedance is in kg/cm².

Table 24. Average time-wise hypocotyl and radicle lengths at 21.1 C and 10.0-bars soil moisture for four levels of physical impedance.*

Time	Hypocotyl	Radicle	Time	Hypocotyl	Radicle
<u>PI = .23</u>			<u>PI = 1.12</u>		
19	0	.3	23	0	1.0
43	0	1.6	47	0	3.1
67	0	3.4	71	0	4.1
91	0	5.0	95	.1	5.6
115	.1	6.6	119	.1	7.7
139	.2	8.0	143	.2	9.3
163	.2	9.6	167	.2	10.7
187	.2	10.6	191	.2	12.0
211	.2	12.0	215	.2	13.2
235	.4	13.2	239	.3	14.3
259	.6	14.1	263	.3	15.2
283	.7	14.9	287	.3	16.4
307	.8	15.6	311	.3	17.2
331	.9	16.2	335	.4	17.8
355	.9	16.6	359	.4	18.6
379	1.0	16.9	383	.4	18.8
403	1.0	17.3	407	.6	18.8
427	1.1	17.7	431	.6	20.3
451	1.1	17.8	455	.7	20.4
<u>PI = 2.24</u>			<u>PI = 3.36</u>		
18	0	.4	46	0	.7
42	0	.8	70	0	1.8
66	0	2.1	94	0	2.8
90	0	3.6	118	0	4.0
114	0	5.1	142	0	5.2
138	0	6.2	166	0	6.1
162	0	7.0	190	0	7.5
186	0	8.3	214	0	8.6
210	.1	9.1	238	0	9.7
234	.1	10.3	262	0	10.4
258	.1	11.5	286	0	11.9
282	.2	12.3	310	0	12.8
306	.2	13.0	334	0	13.9
330	.2	13.9	358	0	14.2
354	.2	14.5	381	.1	15.7
378	.2	15.2	406	.1	16.7
402	.2	15.7	430	.1	17.4

Table 24.--Continued

426	.3	16.2	454	.1	17.5
450	.3	16.6	478	.1	17.8
474	.3	16.9			

*Lengths are in cm, time is in hours, and physical impedance is in kg/cm^2 .

Table 25. Average time-wise hypocotyl and radicle lengths at 26.7 C and .3-bar soil moisture for four levels of physical impedance.*

Time	Hypocotyl	Radicle	Time	Hypocotyl	Radicle
<u>PI = .23</u>			<u>PI = 1.12</u>		
23	0	2.7	21	0	2.4
47	.4	7.5	45	.3	7.2
71	2.8	11.9	69	1.6	11.8
94	6.6	16.2	93	2.1	15.4
103	7.2	17.2	117	2.4	18.0
<u>PI = 2.24</u>			141	3.0	19.5
23	.1	2.0	165	3.5	19.7
47	.3	5.9	189	3.5	19.7
72	.6	9.7	<u>PI = 3.36</u>		
99	1.1	11.6	21	.1	1.3
123	1.4	13.2	45	.2	5.1
143	1.9	13.6	69	.4	9.0
167	2.1	13.8	93	.7	12.2
187	2.1	13.9	117	1.0	14.0
212	2.2	13.9	141	1.4	14.7
235	2.3	13.9	165	1.5	15.0
			189	1.5	15.2
			213	1.5	15.2
			237	1.5	15.2

*Lengths are in cm, time is in hours, and physical impedance is in kg/cm².

Table 26. Average time-wise hypocotyl and radicle lengths at 26.7 C and 3.0-bars soil moisture for four levels of physical impedance.

Time	Hypocotyl	Radicle	Time	Hypocotyl	Radicle
<u>PI = .23</u>			<u>PI = 1.12</u>		
24	0	2.6	22	0	1.5
46	0	6.3	46	0	4.6
70	0	10.7	70	.1	7.9
94	.1	15.4	94	.2	10.8
118	.5	19.2	118	.5	13.7
142	1.3	24.6	142	1.2	16.2
166	2.2	27.9	166	2.0	18.2
189	3.7	29.4	190	2.8	19.3
214	5.1	29.4	214	2.8	20.1
238	5.8	29.9	238	2.8	20.5
<u>PI = 2.24</u>			<u>PI = 3.36</u>		
23	0	1.3	23	0	1.3
47	0	4.8	47	0	4.3
71	.1	8.3	71	0	5.8
95	.3	12.1	95	.1	11.0
119	.7	15.4	119	.4	13.6
143	1.2	18.1	143	.8	15.5
167	1.3	19.8	167	.9	16.8
191	1.4	20.6	191	1.0	17.6
215	1.5	21.0	215	1.0	17.9
239	1.5	21.3	239	1.0	18.0

*Lengths are in cm, time is in hours, and physical impedance is in kg/cm².

Table 27. Average time-wise hypocotyl and radicle lengths at 26.7 C and 10.0-bars soil moisture for four levels of physical impedance.*

Time	Hypocotyl	Radicle	Time	Hypocotyl	Radicle
<u>PI = .23</u>			<u>PI = 1.12</u>		
22	0	1.2	22	0	1.1
47	.1	4.0	46	0	2.8
71	.2	6.7	72	0	5.0
95	.3	9.6	95	0	7.1
119	.3	12.2	118	0	8.9
143	.4	14.4	142	0	11.0
167	.6	16.7	164	0	12.6
191	.8	18.4	188	0	14.4
215	1.1	19.8	212	.1	16.1
239	1.3	20.5	236	.2	17.8
263	1.6	21.0	260	.3	19.3
287	1.8	21.4	284	.4	20.5
311	2.1	21.7	308	.4	21.8
335	2.1	21.9	332	.5	23.0
359	2.3	22.0	356	.6	23.7
383	2.6	22.1	380	.6	24.0
407	2.7	22.2	405	.6	24.2
432	2.8	22.3			
455	2.9	22.3			
<u>PI = 2.24</u>			<u>PI = 3.36</u>		
20	0	.9	20	0	1.1
44	0	2.9	44	0	3.1
68	0	5.8	68	0	5.1
92	0	8.5	92	.1	7.3
116	0	11.2	116	.1	9.4
140	.1	13.5	140	.1	10.7
164	.1	15.0	164	.1	13.0
188	.1	16.9	188	.1	13.6
215	.1	17.4	215	.1	16.3
237	.1	20.0	237	.1	17.5
260	.2	21.1	260	.2	18.9
285	.3	22.0	285	.2	19.8
308	.3	22.7	308	.2	20.7
332	.3	23.5	332	.2	22.0
357	.3	24.0	357	.2	22.6

*Lengths are in cm, time is in hours, and physical impedance is in kg/cm².

Table 28. Average time-wise hypocotyl and radicle lengths at 32.2 C and .3-bar soil moisture for four levels of physical impedance.*

Time	Hypocotyl	Radicle	Time	Hypocotyl	Radicle
<u>PI = .23</u>			<u>PI = 1.12</u>		
7	0	.4	24	.3	5.3
24	.5	3.9	47	1.5	12.1
36	.8	7.3	56	1.9	14.2
48	1.5	10.6	72	2.4	17.0
57	2.9	13.1	80	2.6	17.7
71	6.2	16.8	96	3.2	18.7
76	7.4	17.7	120	3.8	19.4
79	7.9	18.3	144	4.0	19.6
			168	4.1	23.8
<u>PI = 2.24</u>			<u>PI = 3.36</u>		
22	.2	4.0	22	.3	3.3
31	.2	6.3	45	.5	8.8
48	.9	11.3	66	.9	12.8
56	1.2	13.1	90	1.0	15.3
71	1.4	14.9	113	1.2	16.3
95	1.9	17.1	138	1.2	16.5
120	2.1	17.3	161	1.2	16.6
143	2.2	18.2	185	1.2	16.6

*Lengths are in cm, time is in hours, and physical impedance is in kg/cm².

Table 29. Average time-wise hypocotyl and radicle lengths at 32.2 C and 3.0-bars soil moisture for four levels of physical impedance.*

Time	Hypocotyl	Radicle	Time	Hypocotyl	Radicle
<u>PI = .23</u>			<u>PI = 1.12</u>		
18	0	2.0	21	0	2.7
42	0	6.3	45	0	7.3
66	.4	11.3	69	0	12.6
90	1.2	16.6	92	.5	18.5
114	2.3	20.3	115	1.2	22.9
138	3.5	23.4	137	1.5	25.6
162	4.9	26.3	163	2.0	27.1
186	6.3	28.7	185	2.4	27.7
210	6.5	29.7	211	2.6	28.1
			233	2.9	28.2
			261	2.9	28.2
<u>PI = 2.24</u>			<u>PI = 3.36</u>		
18	0	1.9	18	0	1.7
42	0	7.6	42	0	5.4
66	.1	14.1	66	0	9.1
91	.5	19.7	91	.1	12.9
114	.9	22.4	114	.2	16.5
138	1.1	24.8	138	.4	18.4
162	1.3	26.0	162	.4	20.0
186	1.5	26.4	186	.6	20.9
210	1.5	26.6	210	.6	21.5
234	1.5	27.0	234	.6	21.8

*Lengths are in cm, time is in hours, and physical impedance is in kg/cm².

Table 30. Average time-wise hypocotyl and radicle lengths at 32.2 C and 10.0-bars soil moisture for four levels of physical impedance.*

Time	Hypocotyl	Radicle	Time	Hypocotyl	Radicle
<u>PI = .23</u>			<u>PI = 1.12</u>		
21	0	2.5	20	0	1.2
46	0	6.6	44	.1	3.9
70	0	11.1	68	.2	6.7
94	0	15.3	92	.3	9.6
118	.1	18.6	116	.3	13.2
142	.6	20.5	140	.3	14.2
166	1.2	21.5	165	.3	14.4
190	1.8	21.9	188	.4	16.2
214	2.7	22.2	212	.5	17.2
238	2.9	22.3	236	.7	17.8
262	3.2	22.4	260	.8	18.5
286	3.4	22.4	284	.9	18.5
310	3.5	22.5	308	1.0	18.5
			332	1.0	18.5
<u>PI = 2.24</u>			<u>PI = 3.36</u>		
23	0	1.9	23	0	.9
47	0	4.2	47	0	3.3
71	.1	6.7	71	0	5.0
95	.1	8.5	95	0	6.2
119	.2	10.5	119	0	7.8
143	.2	11.9	143	0	8.8
167	.2	13.0	167	0	10.7
191	.2	14.2	191	0	10.7
215	.2	15.1	215	0	13.5
239	.2	15.8	239	0	14.9
263	.2	16.5	264	0	17.7
288	.3	17.1	287	0	18.2
312	.3	18.8			
336	.3	18.8			
359	.3	18.8			

*Lengths are in cm, time is in hours, and physical impedance is in kg/cm².

Table 31. Average time-wise hypocotyl and radicle lengths at 37.8 C and .3-bar soil moisture for four levels of physical impedance.*

Time	Hypocotyl	Radicle	Time	Hypocotyl	Radicle
	<u>PI = .23</u>			<u>PI = 1.12</u>	
17	0	2.4	17	0	1.8
41	.5	6.6	41	.2	6.5
65	2.3	8.5	65	.7	8.0
87	4.6	9.7	89	1.2	9.7
111	6.2	10.2	113	1.8	10.2
	<u>PI = 2.24</u>		137	2.3	10.5
15	0	2.1	161	2.5	10.7
39	.2	6.8	185	2.6	10.8
63	.7	8.6	207	2.7	10.8
87	1.0	9.0		<u>PI = 3.36</u>	
111	1.4	9.4	23	0	4.0
135	1.5	9.6	47	.3	7.6
159	1.5	9.7	71	.5	8.9
183	1.5	9.7	99	.6	9.1
			123	.7	9.2
			147	.7	9.2
			171	.7	9.2
			195	.7	9.2

*Lengths are in cm, time is in hours, and physical impedance is in kg/cm².

Table 32. Average time-wise hypocotyl and radicle lengths at 37.8 C and 3.0-bars soil moisture for two levels of physical impedance.*

Time	Hypocotyl	Radicle	Time	Hypocotyl	Radicle
	<u>PI = .23</u>			<u>PI = 1.12</u>	
19	0	2.2	19	0	1.9
43	0	6.5	43	0	6.1
67	0	8.1	67	0	8.1
91	.1	9.4	91	.1	9.4
115	.1	10.0	115	.1	10.3
139	.4	11.0	139	.1	11.9
163	.4	12.3	163	.2	11.9
187	.4	12.9	187	.2	12.4

*Lengths are in cm, time is in hours, and physical impedance is in kg/cm².

Table 33. Average time-wise hypocotyl and radicle lengths at 37.8 C and 10.0-bars soil moisture for two levels of physical impedance.*

Time	Hypocotyl	Radicle	Time	Hypocotyl	Radicle
	<u>PI = .23</u>			<u>PI = 1.12</u>	
21	0	2.0	21	0	1.4
45	0	3.7	45	0	3.8
69	0	4.5	69	0	5.9
93	0	4.5	93	0	7.1
117	0	4.7	117	0	7.4
141	0	4.7			

*Lengths are in cm, time is in hours, and physical impedance is in kg/cm².

Table 34. Values of K and R² for the model of hypocotyl elongation for several combinations of constant temperature, moisture, and physical impedance.*

Soil moisture, bars	Physical impedance, kg/cm ²			
	.23	1.12	2.24	3.36
			<u>15.6</u>	
.3	.0049	.0092	.0140	.0193
	.98	.97	.94	.98
3.0	.0075	.0101	.0163	.0120
	.93	.77	.88	.81
10.0	.0113	.0071	--	.0103
	.86	.33	--	.44
			<u>21.1</u>	
.3	.0050	.0128	.0188	.0200
	.99	.99	.99	.96
3.0	.0047	.0092	.0172	.0198
	.98	.99	.98	.98
10.0	.0114	.0138	.0133	--
	.97	.97	.53	--
			<u>26.7</u>	
.3	.0079	.0128	.0153	.0253
	.97	.98	.99	.99
3.0	.0043	.0067	.0191	.0235
	.94	.94	.95	.86
10.0	.0056	.0122	.0226	.0431
	.99	.73	.75	.55
			<u>32.2</u>	
.3	.0084	.0147	.0272	.0486
	.99	.99	.99	.97
3.0	.0046	.0098	.0199	.0264
	.98	.95	.96	.83
10.0	.0065	.0163	.0563	--
	.93	.98	.88	--
			<u>37.8</u>	
.3	.0090	.0149	.0331	.0629
	.99	.99	.99	.97

Table 34.--Continued

3.0	.0225	.0435	--	--
	.75	.55	--	--

*Upper numbers for each soil moisture are K values and lower numbers are R² values. Underlined numbers are soil temperature in C.

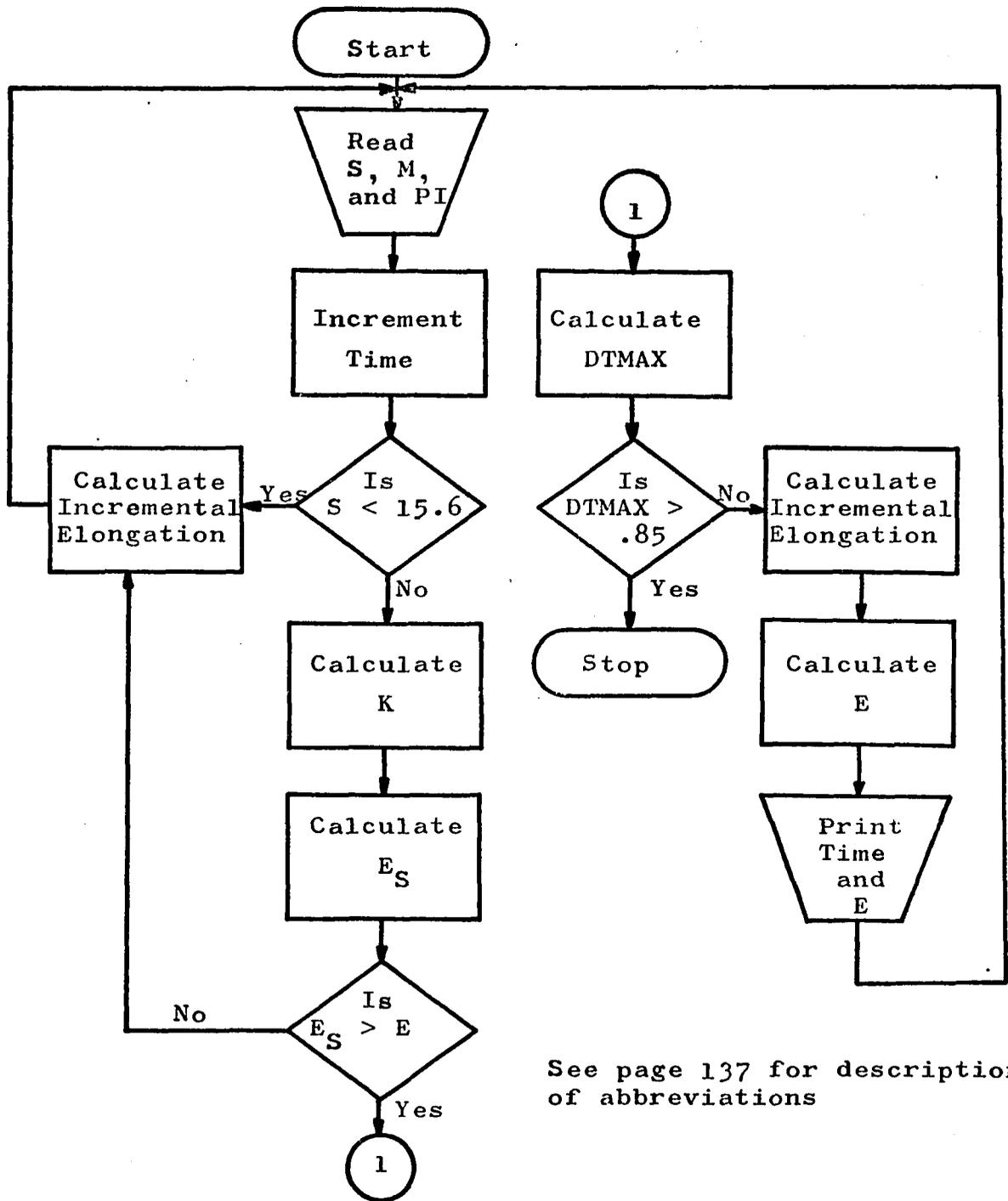


Fig. 23. Flow chart of computer program for simulating hypocotyl elongation.

APPENDIX B

COMPUTER PROGRAM FOR SIMULATING THE 3-mm
RADICLE EMERGENCE EVENT

```

PROGRAM RACET(INPUT,OUTPUT,TAPE1=INPUT)
C PROGRAM FOR COMPUTING THE 3-MM RADICLE EMERGENCE EVENT
C BY SIMULATING THE IMBIBITIONAL WATER UPTAKE OF COTTON
C SEED. THE INPUTS ARE HOURLY SOIL TEMPERATURE F, AND
C SOIL MOISTURE IN BARS.
DIMENSION T(16)
REAL KL, MOS
T WATERL=0.
D WATER=0.
TIME=0
1 PRINT 40
D RET=0.
TIME=0
T WATERL=0.
READ 95, MOS
60 J=0
READ 50, (T(I),I=1,16)
IF(EOF,1)1,61
61 J=J+1
IF(J.GT.16) GO TO 60
TEMP=(T(J)-32.)*(5./9.)
TIME=TIME + 1
IF(TEMP.LT.15.55555) GO TO 15
IF(TEMP.GE.15.55555) GO TO 90
90 KL= .0337762 + .0000855456*TEMP**2. - .00347882*MOS
91 D WATER=KL*(80.0 - T WATERL)
IF((TEMP.GE.26.56).AND.(TEMP.LT.32.2)) GO TO 63
IF(TEMP.GT.32.2) GO TO 66
IF((TEMP.GT.21.2).AND.(TEMP.LT.26.55)) GO TO 65
IF((TEMP.LE.21.2).AND.(TEMP.GE.15.55)) GO TO 62
62 DELMOS=-.1133196 + .000705254*(TEMP**2.) -.001347778*
1MOS + .001177446*(MOS**2.)
GO TO 64
63 DELMOS= -.6954544 + .001961955*(TEMP**2.) + .0833515*
1MOS + .007526679*(MOS**2.) - .006411228*MOS*TEMP
GO TO 64
65 DELMOS= -.3583704 + .001383181*(TEMP**2.) -.03509194*
1MOS + .003506748*(MOS**2.)
GO TO 64
66 DELMOS= 3.392908 - .00197022*(TEMP**2.) - .3693547*MO
1S + .008647528*(MOS**2.) + .007305203*TEMP*MOS
GO TO 64
64 RET= 245.5 - 13.90*TEMP + .2100*(TEMP**2.) + 2.555*MO
1S - .0580*TEMP*MOS

```

```
DRET= (1.0/RET) + DRET
IF(DWATER.LT.DELMOS)GO TO 10
TWATER= TWATERL + DWATER
GO TO 16
15 KL=0.0
   DWATER=0.0
   DELMOS=0.0
   TWATERL=TWATERL
16 PRINT 51,TIME, TEMP, MOS, KL, DWATER, DELMOS, TWATER,
   1DRET
   TWATERL=TWATER
   GO TO 61

10 TWATER=TWATERL + DWATER
   PRINT 51,TIME, TEMP, MOS, KL, DWATER, DELMOS, TWATER
   GERMT=TIME
   PRINT 52, GERMT
   DWATER=0.
   TWATERL=0.
   DRET=0.
20 GO 21 I=1,500
   READ 50,TCHECK
   IF(EOF,1)1,22
22 IF(TCHECK.GT.999.) STOP
21 CONTINUE
40 FORMAT(1H1,5X,*TIME*,6X,*TEMP*,5X,*MOS*,6X,*KL*,5X,*D
   1WATER*,5X,*DELMOS*,3X,*TWATER*,4X,*DRET*/)
50 FORMAT(16F5.0)
51 FORMAT(8F10.5)
52 FORMAT(10X,*GERMINATION TIME EQUALS*,F5.0)
95 FORMAT(F5.2)
   STOP
   END
```

APPENDIX C

COMPUTER PROGRAM FOR SIMULATING
HYPOCOTYL ELONGATION

```

PROGRAM HYPCCT(INPUT,OUTPUT,TAPE 1=INPUT)
C THIS PROGRAM CALCULATES HYPOCOTYL ELONGATION IN CM
C USING HOURLY INPUTS OF SOIL TEMPERATURE F, SOIL
C MOISTURE IN BARS, AND PHYSICAL IMPEDANCE IN PSI
DIMENSION KT(6,4,5), EST(6,4,5), A(16)
REAL M,PI,K,MOS,KNL
READ 10,(((KT(I,J,K),K=1,5),J=1,4),I=1,6)
10 FORMAT(5F10.0)
PRINT 16,(((KT(I,J,K),K=1,5),J=1,4),I=1,6)
READ 10,(((EST(I,J,K),K=1,5),J=1,4),I=1,6)
PRINT 16,(((EST(I,J,K),K=1,5),J=1,4),I=1,6)
16 FORMAT(9X,*3.3 PSI*,9X,*16 PSI*,9X,*
1*32 PSI*,9X,*48 PSI*,9X,*50 PSI*/5F15.10)
20 READ 30, TEMP, MOS, PI, IDATE
PRINT 31,TEMP,MOS,PI,IDATE
19 PRINT 22
DTIME=0.
TIME=0.
ELST=.05
ELONG=0.
22 FORMAT(12X,*TIME*,2X,*TEMPERATURE*,5X,*DE*,5X,*
1*ELONGATION*,17X,*KNL*,10X,*EMAXT*,10X,*DTIME*/)
30 FORMAT(F5.0,F5.0,F5.0,5X,A10)
M= MOS
31 FORMAT(1X//20X,*TEMPERATURE IS*,F7.1,5X,*MOISTURE IS*
1,F5.2,5X,*PHYSICAL IMPEDANCE IS*,F5.1,5X,*DATE IS*,A1,
10//)
60 J=0
READ 32,(A(I),I=1,16)
32 FORMAT(16F5.0)
IF(A(1).GT.399.) STOP
IF(EOF,1)20,61
51 J= J + 1
IF(J.GT.16) GO TO 60
T=A(J)
TIME= TIME + 1
IF(T.LT.60.) GO TO 46
70 IF(K(T,M,PI,EST).LT.ELST) GO TO 47
65 DE=K(T,M,PI,KT)*ELST+(K(T,M,PI,EST) - ELST)
IF(DE.LT.0.) DE=-DE
S= (T - 32)*.555555
IF(S.LT.21.1111) GO TO 90
IF((S.GE.21.1111).AND.(S.LE.32.2222)) GO TO 91
IF(S.GT.32.2222) GO TO 92
90 CON=.202744E-06
TMAX=492.599 -CON*EXP(S) - 17.6902*M - 1.50139*(M**2)
1+ 2.75729*M
GO TO 93
91 DON=.436166E-12

```

```

      TMAX=471.445 - 13.6641*S + DON*EXP(S) + 62.4350*M
1- 2.35255*(M**2) - .548660*S*M
      GO TO 33
92 TMAX=82.8945+96.9449*M-2.25039*(M**2)-1.69967*S*M
93 DTIME=1.0/TMAX + DTIME
      IF(DTIME.GT..35) GO TO 40
      ELONG= ELONG + DE
      EMAXT=K(T,M,PI,EST)
      KNL=K(T,M,PI,KT)

      PRINT 34,TIME,T, DE, ELONG,KNL,EMAXT,DTIME
34 FORMAT(12X,F4.0,5X,F4.0,7X,F5.3,8X,F7.3,10X,F15.10,5X
1,F5.2,7X,F6.5)
      ELST= DE + ELST
      GO TO 61
46 DE=0.
      KNL= 0.
      EMAXT= 0.
      PRINT 34,TIME,T, DE, ELONG,KNL,EMAXT,DTIME
      GO TO 61
47 DE= 0.
      EMAXT= K(T,M,PI,EST)
      KNL= K(T,M,PI,KT)
      PRINT 34,TIME,T, DE, ELONG,KNL,EMAXT,DTIME
      GO TO 61
40 DO 45 I=1,500
      READ 32,CHECK
      IF(ECF,1)20,41
41 IF(CHECK.GT.999.) STOP
45 CONTINUE
      STOP
      END
      REAL FUNCTION K(T,M,PI,KT)
      THIS FUNCTION CALCULATES THE VALUE OF ES AND K AS A
      C FUNCTION OF TEMPERATURE F, MOISTURE IN BARS, AND
      C PHYSICAL IMPEDANCE IN PSI BY USING LINEAR
      C INTERPCLATION
      DIMENSION TA(6),MA(4),PIA(5)
      DIMENSION KT(6,4,5)
      REAL MA,KT,M,KL,KU,KSUB
      DATA TA/60.0,70.0,80.0,90.0,100.0,110.0/,MA/0.33,3.0,
110.0,11.0/,PIA/3.3,16.0,32.0,48.0,50.0/
      ITL=ITU=0
      DO 1 I=1,6
      IF(T.GE.TA(I)) GO TO 1
      ITL=I-1
      ITU=I
      GO TO 3

```

```

1 CONTINUE
3 DT=(T-TA(ITL))/(TA(ITU)-TA(ITL))
  IF(DT.EQ.0.) ITU=ITL
  IMU=IML=J
  DO 2 I=1,4
  IF(M.GE.MA(I)) GO TO 2
  IML=I-1
  IMU=I
  GO TO 4
2 CONTINUE
4 DM=(H-MA(IML))/(MA(IMU)-MA(IML))
  IF(DM.EQ.0.) IMU=IML
  IPL=IPU=0
  DO 5 I=1,5
  IF(PI.GE.PIA(I)) GO TO 5
  IPL=I-1
  IPU=I
  GO TO 6
5 CONTINUE
6 DP=(PI-PIA(IPL))/(PIA(IPU)-PIA(IPL))
  IF(DP.EQ.0.) IPU=IPL
  D=SQRT(DP**2. + DM**2. + DT**2.)
  KL=KT(ITL,IML,IPL)
  KU=KT(ITU,IMU,IPU)

  IF((KL.GT.KU).AND.(T.LT.90.)) GO TO 11
9 K=D*(KU-KL) + KL
  GO TO 10
11 IF((DT.GT.0.).AND.(DM.GT.0.)) GO TO 12
  IF((DT.GT.0.).AND.(DP.GT.0.)) GO TO 13
  GO TO 9
C CALCULATIONS TO FIND PROPER VALUE OF K WHEN
C TEMPERATURE AND MOISTURE ARE OFF THE TABLE AXES.
12 IF(DP.GT.0.) GO TO 9
  DIFML=(MA(IML)-M)/(MA(IML)-MA(IMU))
  SUBL1=(DIFML)*(KT(ITL,IML,IPL) - KT(ITL,IMU,IPL))
  SUBL2=KT(ITL,IML,IPL) - SUBL1
  DIFMU=(MA(IML) - M)/(MA(IML) -MA(IMU))
  SUBU1=(DIFMU)*(KT(ITU,IML,IPL) - KT(ITU,IMU,IPL))
  SUBU2=KT(ITU,IML,IPL) - SUBU1
  KSUB=((SUBU2-SUBL2)*(TA(ITU)-T))/(TA(ITU)-TA(ITL))
  K=SUBU2 - KSUB
  GO TO 10

```

```
C      CALCULATIONS OF K WHEN TEMPERATURE AND PI OFF THE
C      TABLE AXES.
13  IF(DM.GT.0.) GO TO 9
      DIFML=(PIA(IPL)-PI)/(PIA(IPL) - PIA(IPU))
      SUBL1=(DIFML)*(KT(ITL,IML,IPL) - KT(ITL,IML,IPU))
      SUBL2=KT(ITL,IML,IPL) - SUBL1
      DIFMU=(PIA(IPL) - PI)/(PIA(IPL) - PIA(IPU))
      SUBU1=(DIFMU)*(KT(ITU,IML,IPL) - KT(ITU,IML,IPU))
      SUBU2=KT(ITU,IML,IPL) - SUBU1
      KSUB=((SUBU2-SUBL2)*(TA(ITU)-T))/(TA(ITU) - TA(ITL))
      K= SUBU2 - KSUB
10  RETURN
      END
```

ABBREVIATIONS AND SYMBOLS

- C - Temperature in centigrade
- cm - Centimeter(s)
- dE/dt - Rate of hypocotyl elongation, cm/hour
- DTMAX - Elapsed portion of total growing time, a decimal
- dW/dt - Rate of seed water uptake, percentage dry weight/
hour
- E - Hypocotyl length, cm
- E_0 - Hypocotyl length at time zero, cm
- E_S - Maximum hypocotyl length, cm
- E' - Unrealized hypocotyl length, cm
- exp - Base of natural system of logarithms (2.718)
- g - Gram(s)
- ha - Hectare(s)
- K - Constant of hypocotyl elongation, 1/cm-hr
- kg - Kilogram(s)
- M - Soil moisture, bars
- MC - Seed moisture content at 3-mm radicle length,
percentage dry weight
- mm - Millimeter(s)
- PI - Soil physical impedance, kg/cm²
- PM - Total seed moisture, percentage dry weight
- psi - Pounds/square inch
- R² - Multiple coefficient of determination

- RET - Time required for 3-mm radicle emergence, hours
- S - Soil temperature, C
- SE - Standard error of the estimate
- T - Time constant, hours
- t - Elapsed time, hours
- W - Accumulated imbibitional seed moisture, percentage dry weight
- W_0 - Seed moisture at time zero, percentage dry weight
- W_S - Steady-state level of imbibitional seed moisture, percentage dry weight
- Z - Unused energy
- Z_0 - Available energy at time zero
- Z' - Amount of consumed energy
- ΔM - Change in imbibitional seed moisture during the hour immediately preceding 3-mm radicle emergence, percentage dry weight
- % - Per cent

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