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Introduction

I. WHY STUDY SOIL-PLANT-WATER RELATIONS?

A. Population

Of the four soil physical factors that affect plant growth (mechanical impedance, water, aeration, and temperature) (Shaw, 1952; Kirkham, 1973), water is the most important. Drought causes 40.8% of crop losses in the United States, and excess water causes 16.4%; insects and diseases amount to 7.2% of the losses (Boyer, 1982). In the United States, 25.3% of the soils are affected by drought, and 15.7% limit crop production by being too wet (Boyer, 1982).

People depend upon plants for food. Because water is the major environmental factor limiting plant growth, we need to study soil-plant-water relations to provide food for a growing population. What is our challenge?

The earth’s population is growing exponentially. The universe is now considered to be 13 billion years old (Zimmer, 2001). The earth is thought to be 4.45 billion years old (Allègre and Schneider, 1994). The earth’s oldest rock is 4.03 billion years old (Zimmer, 2001). Primitive life existed on earth 3.7 billion years ago, according to scientists studying ancient rock formations harboring living cells (Simpson, 2003). Human-like animals have existed on earth only in the last few (less than 8) million years. In Chad, Central Africa, six hominid specimens, including a nearly complete cranium and fragmentary lower jaws, have been found that are 6 to 7 million years old (Brunet et al., 2002; Wood, 2002). In 8000 B.C., at the dawn
of agriculture, the world's population was 5 million (Wilford, 1982). At the birth of Christ in 1 A.D., it was 200 million. In 1000, the population was 250 million (National Geographic, 1998a) (Fig. 1.1). By 1300, it had grown larger (Wilford, 1982). But by 1400, the population had dropped dramatically due to the Black Death, also called the bubonic plague (McEvedy, 1988), which is caused by a bacillus spread by fleas on rats. The Black Death raged in Europe between 1347 and 1351 and killed at least half of its population. It caused the depopulation or total disappearance of about 1,000 villages. Starting in coastal areas, where rats were on ships, and spreading inland, it was the greatest disaster in western European history (Renouard, 1971). People fled to the country to avoid the rampant spread of the disease in cities. The great piece of literature, The Decameron, published in Italian in 1353 and written by Giovanni Boccaccio (1313–1375), tells of 10 people who in 1348 went to a castle outside of Florence, Italy, to escape the plague. To pass time, they each told a tale a day for 10 days (Bernardo, 1982).

By 1500, the world's population was about 250,000,000 again. In 1650, it was 470,000,000; in 1750, it was 694,000,000; in 1850, it was 1,091,000,000. At the beginning of the nuclear age in 1945, it was 2.3 billion. In 1950, it was 2,501,000,000; in 1970, 3,677,837,000; in 1980,
4,469,934,000. In 1985, it was 4.9 billion, and in 1987 it was 5.0 billion (New York Times, 1987). In 1999, the world’s population reached 6 billion (National Geographic, 1999). In 2002, the population of the USA was 284,796,887 (Chronicle of Higher Education, 2002).

Note that it took more than six million years for humans to reach the first billion; 120 years to reach the second billion; 32 years to reach the third billion; and 15 years to reach the fourth billion (New York Times, 1980). It took 12 years to add the last billion (fifth to sixth billion, 1987 to 1999). The United Nations now estimates that world population will be between 3.6 and 27 billion by 2150, and the difference between the two projections is only one child per woman (National Geographic, 1998b). If fertility rates continue to drop until women have about two children each—the medium-range projection—the population will stabilize at 10.8 billion. If the average becomes 2.6 children, the population will more than quadruple to 27 billion; if it falls to 1.6, the total will drop to 3.6 billion.

The population may also fall due to plagues (Weiss, 2002) such as the one that devastated Europe in the fourteenth century. Current potential plagues may result from AIDS (acquired immune deficiency syndrome), generally thought to be caused by a virus; influenza, another viral infection—for example, there may be a recurrence of the 1918 pandemic (Gladwell, 1997); sudden acute respiratory syndrome (SARS), a deadly infectious disease caused by a coronavirus (Lemonick and Park, 2003); and mad-cow disease, which is formally called bovine spongiform encephalopathy (BSE). BSE is called Creutzfeldt-Jakob (also spelled as Creutzfeldt-Jacob) disease (CJD), when it occurs in humans (Hueston and Voss, 2000). It is thought to be caused by prions, which were discovered by Stanley Prusiner (1942–) of the University of California School of Medicine in San Francisco; the discovery won Prusiner both the Wolf Prize (1996) and the Nobel Prize (1997) in medicine. Prions are a new class of protein, which, in an altered state, can be pathogenic and cause important neurodegenerative disease by inducing changes in protein structure. Prions are designed to protect the brain from the oxidizing properties of chemicals activated by dangerous agents such as ultraviolet light.

B. The “Two-Square-Yard Rule”

The population is limited by the productivity of the land. There is a space limitation that our population is up against. Many of us already have heard of this limitation, which is a space of two square yards per person. The sun’s energy that falls on two square yards is the minimum required to
provide enough energy for a human being’s daily ration. Ultimately, our food and our life come from the sun’s energy. The falling of the sun’s energy on soil and plants is basic. We want to make as many plants grow on those two square yards per person as possible, to make sure we have enough to eat.

Let us do a simple calculation to determine how much food can be produced from two square yards, using the following steps:

1. Two square yards is 3 feet by 6 feet or 91 cm by 183 cm.

   \[91 \text{ cm} \times 183 \text{ cm} = 16,653 \text{ cm}^2\text{ or, rounding, 16,700 cm}^2.\]

2. The solar constant is 2.00 cal cm\(^{-2}\) min\(^{-1}\), or, because 1 langley = 1 cal cm\(^{-2}\), it is 2.00 langleys min\(^{-1}\). The langley is named after Samuel Pierpoint Langley (1834–1906), who was a US astronomer and physicist who studied the sun. He was a pioneer in aviation.

   The solar constant is defined as the rate at which energy is received upon a unit surface, perpendicular to the sun’s direction in free space at the earth’s mean distance from the sun (latitude is not important) (Johnson, 1954). The brightness of the sun varies during the 11-year solar cycle, but typically by less than 0.1% (Lockwood et al., 1992).

3. \[16,700 \text{ cm}^2 \times 2.00 \text{ cal cm}^{-2} \text{ min}^{-1} = 33,400 \text{ cal min}^{-1}.\]

4. \[33,400 \text{ cal min}^{-1} \times 60 \text{ min h}^{-1} \times 12 \text{ h d}^{-1} = 24,048,000 \text{ cal d}^{-1},\text{ or, rounding, 24,000,000 cal d}^{-1}.\] We multiply by 12 h d\(^{-1}\), because we assume that the sun shines 12 hours a day. Of course, the length the sun shines each day depends on the day of the year, cloudiness, and location.

5. There is 6% conversion of absorbed solar energy into chemical energy in plants (Kok, 1967). This 6% is for the best crop yields achieved; 20% (Kok, 1967) to 30% (Kok, 1976) conversion is thought possible, but it has not been achieved; 2% is the conversion for normal yields; under natural conditions, \(\leq 1\%\) is converted (Kok, 1976). The solar energy reaching the earth’s surface that plants do not capture to support life is wasted as heat (Kok, 1976). Let us assume a 6% conversion:

   \[24,000,000 \text{ cal d}^{-1} \times 0.06 = 1,440,000 \text{ cal d}^{-1}.\]

6. The food “calories” we see listed in calorie charts are in kilocalories. So, dividing 1,440,000 cal d\(^{-1}\) by 1,000, we get 1,440 kcal d\(^{-1}\), which is not very much. The following list gives examples of calories consumed per day in different countries (Peck, 2003):
| Location     | Kilocalories d⁻¹ |
|--------------|------------------|
| USA, France  | >3,500           |
| Argentina    | 3,000–3,500      |
| Morocco      | 2,500–2,999      |
| India        | 2,000–2,499      |
| Tanzania     | <2,000           |

We recognize that the above calculation of productivity from two square yards is simplified, and more complex and thorough calculations of productivity, which consider geographic location, sky conditions, leaf display, and other factors, have been carried out (e.g., de Wit, 1967). Nevertheless, the 1,440 kcal d⁻¹ is a useful number to know. It would be a starvation diet. One could live on it, but the calories probably would not provide enough for active physical work, creative intellectual activity, and reproduction. Women below a minimum weight cannot reproduce (Frisch, 1988). Civilization would advance slowly with this daily ration. People begin to die of starvation when they lose roughly a third of their normal body weight. When the loss reaches 40%, death is almost inevitable.

Triage is a system developed in World War I. It is the medical practice of dividing the wounded into survival categories to concentrate medical resources on those who could truly benefit from them and to ignore those who would die, even with treatment, or survive even without it. This practice has been advocated to allocate scarce food supplies. Wealthy countries should help only the most promising of the poorer countries since spreading precious resources too thin could jeopardize chances for survival of the strong as well as the weak. If we can grow more food, then this system does not need to be put into effect. In this book, we seek a better understanding of movement of water through the soil-plant-atmosphere continuum, or SPAC (Philip, 1966), because of the prime importance of water in plant growth.

We focus on principles rather than review the literature. Many references are given, but no attempt is made to cite the most recent papers. Articles explaining the principles are cited. They often are in the older literature, but we need to know them to learn the principles. No knowledge of calculus is required to understand the equations presented.

In this book, we divide the movement of water through the SPAC into three parts: 1) water movement in the soil and to the plant root; 2) water movement through the plant, from the root to the stem to the leaf; and 3) water movement from the plant into the atmosphere. However, before
we turn to principles of water movement in the SPAC, let us first consider plant growth curves.

II. PLANT GROWTH CURVES

A. The Importance of Measuring Plant Growth and Exponential Growth

The world-population growth curve (Fig. 1-1) is an exponential curve. What do plant growth curves look like? Because water is the most important soil physical factor affecting plant growth, it is important to quantify plant growth to determine effects of water stress. In any experiment dealing with plant-water relations, some measure of plant growth (e.g., height, biomass) should be obtained. Plant growth curves also exemplify quantitative relationships that we seek to understand basic principles of plant-water relations. If we can develop equations to show relationships, then we can predict what is going to happen. Equations describing plant-growth curves demonstrate how we can quantify, and thus predict, plant growth.

We first consider the growth of the bacterium *Escherichia coli*. In the early nineteenth century, when plants and animals were being classified, the bacteria were arbitrarily included in the plant kingdom, and botanists first studied them (Stanier et al., 1963, p. 55–56). Even though bacteria are not plants or animals, we can follow their growth to understand plant growth curves.

Under ideal conditions, a cell of *E. coli* divides into two cells approximately every 20 minutes; for the sake of simplicity we assume that it is exactly 20 minutes. Let us consider the propagation of a single cell. Our purpose is to find a relation between the number $N$ of cells at some moment in the future and the time $t$ that has elapsed. At the start of our observations, at the time 0 min, there is 1 cell. When 20 min have elapsed there are 2 cells. When 40 min have elapsed there are $2 \times 2 = 2^2$ cells. When 60 min have elapsed there are $2 \times 2^2 = 2^3$ cells; that is, when 3 time intervals of 20 min each have passed, there are $2^3$ cells. We observe a pattern developing: when $m$ time intervals each of 20 min have passed, at the time $t = 20m$ min, there are $2^m = 2^{t/20}$ cells. Thus, if $N$ denotes the number of cells present at the moment when $t$ minutes have elapsed, then the relation we seek is given by the equation

$$N = 2^{t/20}.$$  \hspace{1cm} (1.1)

Because the time $t$ appears in the exponent of the expression $2^{t/20}$, this equation is said to describe exponential growth of the number $N$ of cells (De Sapio, 1978, p. 21–23).
A famous book called *On Growth and Form* by D’Arcy Wentworth Thompson contains the following statement (Thompson, 1959, Vol. 1, p. 144): “Linnaeus shewed that an annual plant would have a million offspring in twenty years, if only two seeds grew up to maturity in a year.” Linnaeus is, of course, Carolus Linnaeus (born Karl von Linné) (1707–1778), the great Swedish botanist. We can show that what Linnaeus said is true by adapting the preceding equation, as follows:

\[ X = 2^{20}, \quad (1.2) \]

where \( X \) is the number of offspring from the plant in twenty years.

To solve this equation, we need to use logarithms. John Napier (1550–1617), a distinguished Scottish mathematician, was the inventor of logarithms. (See the Appendix, Section III, for his biography.) To solve equations using logarithms, we need to know the fundamental laws of logarithms, which are as follows (Ayres, 1958, p. 83):

1. The logarithm of the product of two or more positive number is equal to the sum of the logarithms of the several numbers. For example,

\[ \log_b (PQ) = \log_b P + \log_b Q \quad (1.3) \]

2. The logarithm of the quotient of two positive numbers is equal to the logarithm of the dividend minus the logarithm of the divisor. For example,

\[ \log_b (P/Q) = \log_b P - \log_b Q \quad (1.4) \]

3. The logarithm of a power of a positive number is equal to the logarithm of the number, multiplied by the exponent of the power. For example,

\[ \log_b (P^n) = n \log_b P \quad (1.5) \]

4. The logarithm of a root of a positive number is equal to the logarithm of the number, divided by the index of the root. For example,

\[ \log_b (P^{(1/n)}) = (1/n) \log_b P. \quad (1.6) \]

In calculus, the most useful system of logarithms is the *natural system* in which the base is a certain irrational number \( e = 2.71828 \), approximately (Ayres, 1958, p. 86). The natural logarithm of \( N \), \( \ln N \), and the common logarithm of \( N \), \( \log N \), are related by the formula

\[ \ln N = 2.3026 \log N. \quad (1.7) \]

To solve our equation, we take the logarithm of each side:

\[ \log (2^{20}) = \log X \]
Using logarithm Rule No. 3, we get
\[ 20 \log 2 = \log X \]

Solving (and reading out all the digits on our hand calculator):
\[
\log X = 20 (0.30103) = 6.0205999
\]
\[
X = 1,048,576.
\]

Linnaeus was right.

**B. Sigmoid Growth Curve**

The S-shaped, or sigmoid, curve is typical of the growth pattern of individual organs, or a whole plant, and of populations of plants (Fig. 1.2). It can be shown to consist of at least five distinct phases: 1) an initial lag period during which internal changes occur that are preparatory to growth; 2) a phase of ever-increasing rate of growth. (Because the logarithm of growth rate, when plotted against time, gives a straight line during this period, this phase is frequently referred to as the log period of growth or “the grand period of growth.”); 3) a phase in which growth rate gradually diminishes; 4) a point at which the organism reaches maturity and growth ceases. If the curve is prolonged further, a time will arrive when 5) senescence and death of the organism set in, giving rise to another component of the growth curve (Mitchell, 1970, p. 95).

**C. Blackman Growth Curve**

Since about 1900, people have used growth curves to analyze growth. Significant relationships of a mathematical nature, however, are difficult to

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**FIG. 1.2** Five phases in the sigmoid growth curve. (From Mitchell R.L., 1970, p. 95. Reprinted by permission of Roger L. Mitchell.)
apply to such a complex thing as growth (Hammond and Kirkham, 1949). One well-known theory of plant growth is the compound interest law of Blackman (1919). He related plant growth to money in a bank. When money accumulates at compound interest, the final amount reached depends on:

1. The capital originally used;
2. The rate of interest;
3. The time during which the money accumulates.

Comparing these factors to plants,

1 = the weight of the seed;
2 = the rate at which the seed material is used to produce new material;
3 = the time during which the plant increases in weight.

Blackman related the three factors into one exponential equation,

$$W_1 = W_o e^{rt}, \quad (1.8)$$

where

- $W_1$ = the final weight
- $W_o$ = the initial weight
- $r$ = the rate of interest
- $t$ = time
- $e$ = the base of natural logarithms ($2.718 \ldots$).

The Blackman equation works best for early phases of growth (the log phase of growth in the sigmoid growth curve). In later growth stages, the decreasing relative growth rate has appeared to make impossible the application of this theory to the entire growth curve. Blackman attempted to do this, nevertheless, by using the average of all the different relative growth rate values as the $r$ term in Equation 1.8. He called this term the “efficiency index” of plant growth.

Hammond and Kirkham found that the growth curves (dry weight versus time) of soybeans \([Glycine max (L.) Merr.]\) and corn \((Zea mays L.)\) were characterized by a series of exponential segments, which were related to the growth stages of the plants. The exponential equation for all segments had the form:

$$w = w_o e^{r(t-t_0)}, \quad (1.9)$$

where

- $w$ = weight of the plant at time $t$
\( w_0 \) = weight of the plant at an arbitrary time \( t_0 \)  
\( r \) = relative growth rate  
\( e \) = base of natural logarithms (2.718 . . .).

Taking the natural logarithm of each side, we get

\[
\ln w = \ln w_0 + \ln e^{r(t-t_0)}
\]
\[
\ln w_0 + [r(t-t_0)] x 1
\]
\[
\ln w_0 + r(t-t_0).
\]

Converting to common logarithms by dividing each term by 2.303, we get

\[
\log w = \log w_0 + \frac{r(t-t_0)}{2.303}.
\]

Now let

\[ y = \log w \]
\[ a = \log w_0 \]
\[ b = r/2.303 \]
\[ x = t-t_0. \]

We get \( y = a + bx \), which is the equation of a straight line.

The differential form of Equation 1.9, \( w = w_0 e^{r(t-t_0)} \), is

\[
dw/(wdt) = r \quad (1.10)
\]

where \( r \), the relative growth rate, is the increase in weight per unit weight per unit time. It is obtained by multiplying the slope, \( b \), of the line by 2.303.

Hammond and Kirkham (1949) plotted the common logarithm of dry weight versus time and found that soybeans have three growth stages, I, II, and III. The analysis showed that the plants produce dry matter at the greatest relative rate during period I; at a smaller rate during period II; and at a still smaller rate during period III. That is, the slopes declined with age (slope = \( r/2.303 \)). They saw that the dates of change in the growth curves from period I to period II were also the dates when the plants began to bloom. The dates of the second change in the growth curve, or the change from period II to period III, were the dates when the plants reached maximum height. The soybeans grew on two different soils, a Clarion loam and a Webster silt loam. The soybean plants in the Clarion soil bloomed and reached maximum height about a week earlier than the soybeans on the Webster silt loam soil. The growth curves clearly showed this difference (Fig. 1.3). Growth curves, therefore, can be used to see the effect of the soil environment on plant growth. Hammond and Kirkham (1949) did not give a reason for the difference in rate of growth on the Webster and Clarion
soils, but it must have been related to one of the four soil physical factors that affect plant growth: water, temperature, aeration, or mechanical impedance. For corn, they found four periods of growth (Fig. 1.4). The additional period in corn apparently was related to the difference in time of appearance of male and female flowers in corn. The physiological changes associated with the breaks in the curves were associated with tasseling, silk- ing, and cessation of vegetative growth. The last break occurred after the corn plants had reached maximum height. In sum, the data for soybeans and corn showed that a quantitative analysis of the complete growth curve can be accomplished if the overall growth is partitioned into segments based on the growth stages of the plants.

The equations for plant growth show that we can develop significant mathematical relationships for a quantitative analysis of plant growth. This is probably because plant growth is governed by basic chemical and physical laws. From these relationships, we can predict plant growth.

III. APPENDIX: BIOGRAPHY OF JOHN NAPIER

John Napier (1550–1617), a distinguished Scottish mathematician, was the inventor of logarithms. The son of Scottish nobility, Napier’s life was spent
amid bitter religious dissensions. He was a passionate Protestant. His great work, *A Plaine Discouery of the Whole Reuelation of Saint John* (1594), has a prominent place in Scottish ecclesiastical history as the earliest Scottish work on the interpretation of the scriptures. He then occupied himself by inventing instruments of war, including two kinds of burning mirrors, a piece of artillery, and a metal chariot from which shot could be discharged through small holes. Napier devoted most of his leisure to the study of mathematics, particularly to developing methods of facilitating computation. His name is associated with his greatest method, logarithms. His contributions to this mathematical invention are contained in two treatises: *Mirifici logarithmorum canonis descriptio* (1614; translated into English in 1857) and *Mirifici logarithmorum canonis constructio*, which was published two years after his death (1619) and translated into English in 1889. Although Napier’s invention of logarithms overshadows all his other mathematical work, he has other mathematical contributions to his credit. In 1617, he published his *Rabdologiae, seu numerationis per virgulas libri duo* (English translation, 1667). In this work, he describes ingenious methods of performing the fundamental operations of multiplication.
and division with small rods (Napier’s bones). He also made important contributions to spherical trigonometry (Scott, 1971).

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