Dr. HAFIZ Haider Ali
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5th Agronomy

Only Definitions

3. CROPS AND THEIR RELATION TO ENVIRONMENT

Abid Hussain[1]

LEARNING OBJECTIVES

After reading this chapter, a student should be able to:

- Explain the terms *environment* and *aerial environment* with reference to plants.
- Discuss the influence of environmental factors such as radiation, temperature, and water stress on plant growth processes and their effects on yield.
- Define the term *potential evapotranspiration* and explain its use in crop water studies.
- Explain boundary layer (aerodynamic) resistance of leaves and how it is influenced by wind speed.
- Calculate soil moisture deficit from a knowledge of environmental factors.

3.1 Introduction

Several factors influence the yield and quality of a crop: size, number and nature of the propagules used to raise the crop, functioning of the crop plants during growth and maturation, and the environment in which the crop is grown. After emergence, the plants start making their own constituents by combining carbon dioxide, water, and mineral elements, using radiant energy from the sun. The resultant processes of plant growth and development can be retarded by inadequate light, temperature extremes, or nutritional deficiencies.

The factors of crop environment are subject to large variations: solar radiation, temperature, and soil moisture may all change drastically from time to time. Within limits, plants can survive such changes; in fact, a certain

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[1] Dr. Abid Hussain is Associate Professor, Department of Agronomy, University of Agriculture, Faisalabad.

amount of variability in environmental factors may even be necessary for healthy plant growth (Evans 1963).

This chapter will attempt to show the influence of different environmental variables on plant growth and development and on crop yields. **Plant growth** can be defined as the increase in dry weight of a plant over time, mainly as a consequence of photosynthesis; or the increase in the size of a plant organ due to the expansion of its cells. Growth rate can be expressed as the increase of weight, volume, area, or length per unit time. **Development** is the progress of a plant from germination to maturity through a series of stages (Monteith 1981). **Phenology** is the study of the timing of these stages in relation to the calendar.

The environment. The **environment** of an organism comprises all that surrounds it. However, all the living and non–living things which surround an organism may not be significant for it. Those components of the environment which are significant for the organism they surround, comprise its *functional* or *operational* environment (Mason and Langenheim 1975). To be a component of the functional environment, an element of the environment must:

- be operationally significant to an organism.
- be directly effective at some time during its life.
- influence the sequence of its ontogeny.

The aerial environment. The atmosphere is a simple physical mixture comprising by volume about 78.8% nitrogen, 20.95% oxygen, 0.032% carbon dioxide, traces of other gases, and varying amounts of water vapour. The O_2 and CO_2 of the air affect all forms of life through the processes of photosynthesis and respiration. The main environmental factors which influence terrestrial systems are solar radiation, temperature, water, atmospheric humidity, and wind.

(r) ~~3~~.2 Radiation

3.2.1 Definition and measurement

Solar radiation is energy derived from oscillating magnetic and electrostatic fields present in the sun. It is convenient to discuss the solar radiation important for plant growth in terms of two wave bands: the visible (0.4–0.7 microns), and the infrared (0.7–3.0 microns). The visible band is effective in photosynthesis and is therefore often called **photosynthetically active radiation** (PAR).

Radiation is usually measured as a flux of energy per unit horizontal surface area per unit time. This is usually referred to as **radiant flux density.** The preferred units for measuring it are joules per square metre per
($J\ m^{-2}\ s^{-1}$) (= watts m^{-2}), or megajoules per square metre per day
$m^{-2}\ d^{-1}$). It is no longer appropriate to use former measures of 'li
intensity' such as foot–candle.

The radiant flux density incident upon plants varies throughout the day, increasing from zero at dawn to a maximum around noon and then declining to zero again at dusk. The total amount of light energy falling on plants also changes throughout the year, as well as with geographic location.

The average radiant flux density reaching the surface of the atmosphere facing the sun is about 1360 watts m^{-2}. In passing through the atmosphere, some of it is absorbed, particularly by clouds, and some is scattered by dust and other constituents of the atmosphere. The portion reaching the surface of the earth is the short-wave, global radiation. This has two components: the *direct* and the *diffuse*. The direct is that part of the radiation incident on the atmosphere which succeeds in reaching the earth without any deflection in its path. The diffuse is the part which reaches the earth after being reflected by dust, water vapour, and other constituents of the atmosphere.

On a completely clear day, about 75%, and on a completely overcast day, about 25% of the radiation impinging on the outer limit of the atmosphere succeeds in reaching the earth's surface. Of the radiation reaching the earth's surface, the diffuse component is about 10–15% on a clear day and 100% on a cloudy day. The average amount of short-wave global radiation (St) received during a certain period at any part of the globe can be calculated by the following formula:

$$St = St_e\ (0.25 + 0.51\ n/N) \qquad (3.1)$$

where:

St_e = the radiation reaching the surface of the atmosphere
n = the number of hours of bright sunshine
N = daylength in hours

About 7% of PAR and 30–40% of infrared radiation (about 25% of total incident radiation) is reflected from vegetation, against 10–20% from bare soil and about 5% from water surfaces. Table 3.1 gives the daily radiation balance on a clear summer day.

Table 3.1 Daily radiation balance on clear summer day

Income	$MJ\ m^{-2}\ d^{-1}$
Incoming radiation at the surface of the atmosphere	31.4
Incoming energy at the surface of the earth	22.0
Reflected	4.5

Income	$MJ\ m^{-2}\ d^{-1}$
Outgoing radiation	7.3
Net radiation at the surface	10.2

The net radiation received at the surface is utilized as follows:

Use	Quantity ($MJ\ m^{-2}\ d^{-1}$)	Percent of total
Evaporation	8.7	85.3
Heating air and plants	0.8	7.8
Heating soil	0.5	4.9
Plant growth	0.2	2.0
	10.2	100.0

Source: Values follow Milthorpe and Moorby (1979:29).

3.2.2 Radiation interception and plant growth

The fraction of radiation intercepted by plants depends on incident radiation, leaf area index, and the canopy architecture of the plant. The latter differs among crops, depending on whether their leaves are erect or horizontal.

Plant growth and absorbed radiation. The crop growth rate (CGR) for a crop intercepting incident PAR completely can be represented by the following formula:

$$CGR = f(\varepsilon, P_{max}, R, K, S_i) \qquad (3.2)$$

where:

ε is a measure of the average photosynthetic efficiency of leaves.

P_{max} is the average maximum rate of gross photosynthesis of individual leaves.

R is the average fraction of the gross amount of carbon fixed by crop photosynthesis that is respired.

K is an extinction coefficient describing the rate at which PAR flux density declines per unit leaf area index (L) of the canopy. A large value for K is indicative of horizontal leaves and fast extinction of light.

S_i is the solar radiation incident on the crop.

For most arable crops, none of the above variables change greatly during the grand period of growth. Most photosynthesis is carried out by directly-lit green surfaces—not by those illuminated solely by light transmitted through one or more leaves.

During the early stages of crop growth, both the number of leaves and their average size increase with time. Within a few weeks after germination, there is enough foliage to intercept more than 90% of the incident radiation under favourable environments. Most crops, regardless of climate, can intercept more than 90% of PAR with a LAI of 4–6, and achieve their maximum potential growth rates under favourable environments.

3.2.3 Light and the photosynthetic process

The photosynthetic process may be viewed as comprising three processes: the CO_2 supply process, the light (photochemical) reaction, and the dark (enzymatic) reaction.

1. The CO_2 supply process. During photosynthesis, CO_2 from the air diffuses through the plant stomata into the intercellular spaces of the leaves. From there it diffuses through the walls of the mesophyll cells, across the plasmalemma to the chloroplasts, where CO_2 reduction takes place.

2. The light (photochemical) reaction. In the photochemical reaction, which follows the CO_2 supply process, photons in the wave band 400–700 nm are absorbed by chlorophyll and associated pigment molecules. The pigments use this absorbed energy to oxidize water and produce the strong reducing compound NADPH (nicotine adenine dinucleotide phosphate) and ATP. The process can be represented as:

$$2NADP + 4H_2O \xrightarrow[\text{chlorophyll}]{\text{photons}} 2NADPH + O_2 + 2H_2O \qquad (3.3)$$

Because the light reaction is photochemical it has a small temperature coefficient, i.e. the rate of increase in reaction per unit increase in temperature is small. Biologists express this as a dimensionless ratio, Q_{10}. The Q_{10} for physical and photochemical processes generally varies from 1.0 to 1.1.

3. The dark (enzymatic) reaction. In the dark process, assuming the operation of the C_3 pathway, the NADPH and ATP (adenosine triphosphate) produced in the light are used to reduce CO_2 to carbohydrates and other compounds and to regenerate the carbon acceptor RuBP. The reaction can proceed in the dark and is temperature dependent. The reaction may be summarized as follows:

$$2NADPH + CO_2 \xrightarrow{\text{enzymes}} CH_2O + H_2O \qquad (3.4)$$

For every molecule of CO_2 released in the light reaction, a molecule of CO_2 is taken up in the dark reaction.

Because the dark reaction depends on enzymes whose activity typically stops at 0°C and below, it has a large temperature coefficient with a Q_{10} varying from 2 to 4.

Total photosynthesis is the result of these three processes.

3.2.4 Relationship between the rate of photosynthesis, the supply of light and CO_2, and temperature

Under low light intensity, light is the limiting factor for total photosynthesis, the rate of photosynthesis depending on irradiance. As light intensity increases, the rate of photosynthesis will increase up to a certain point, after which it stops increasing unless the CO_2 concentration is also increased. At the normal atmospheric concentration of CO_2 (0.03%), increasing temperature does not increase the rate of total photosynthesis. At high irradiance *and* higher CO_2 concentration, however, temperature becomes limiting, and an increase of temperature from 20 to 30°C produces a 50% increase in the rate of photosynthesis.

3.2.5 Environmental effects on photosynthesis and respiration

1. Effects on photosynthesis. Measurements of photosynthesis are usually expressed as net photosynthesis (P_n), i.e. total photosynthesis minus respiration. Net photosynthesis of a crop is mainly influenced by three environmental factors: radiation, temperature, and water stress.

Effect of radiation. In a number of crops, e.g. cotton and maize (Hesketh and Baker 1967) and sugarcane (Chu 1970), when grown with good husbandry and under climates favourable to them, intercepted radiation is the primary determinant of photosynthetic productivity during the vegetative stage of growth. Later in the growth cycle of the crop, strong sunlight causes light saturation of the photosynthetic mechanism. This is perhaps due to the reduced responsiveness of the leaf surface to intercepted radiation later in the growing season.

Effect of temperature. In general, since photochemical processes are not strongly temperature-dependent, leaf photosynthesis is relatively insensitive to temperature (Cooper and Tainton 1968), at least in C_3 plants. Measurements of net photosynthesis on young crop canopies do not show a marked response to temperature (Jeffers and Shibles 1969). Later in the growing season, however, high temperatures cause a marked decrease in crop net photosynthesis (Baker et al. 1972).

Effect of water stress. Water stress reduces the rate of net photosynthesis. The effect is perhaps caused through the closure of the stomata in water-stressed plants.

2. Effects on respiration. Crop respiration is normally measured in the dark. Measurements of respiration during the night indicate that its magnitude is apparently related to the photosynthesis of the crop during the preceding day, which is in turn determined by the insolation received during that day. The rate of respiration also increases with temperature over the range normally experienced in the field (Baker et al. 1972; Sale 1974).

3. Effects on dry matter production. Environmental factors influence the amount of dry matter produced indirectly, through their effect on photosynthesis and respiration. Early in the growing season, plant growth is mainly determined by intercepted radiation. This is because of the linear response of photosynthesis to intercepted radiation at this stage in crop growth, and also because of the small amount of respiration associated with the maintenance of established plant tissues. As the growing season advances, crop dry weight increases. So does respiration associated with the maintenance of the established tissues of the crop. This accounts for the decrease of crop growth rate with increasing temperature, and may explain why cool summers are often associated with better crop growth (Robertson 1974).

To sum up, early in the growing season crop dry matter production is mainly governed by the amount of radiation intercepted by the crop. Later in the season, when crop dry weight and the respiration associated with the maintenance of the established tissues increase, high temperature will significantly decrease crop dry matter.

(2) ~~3.3~~ Photoperiod

On the basis of photoperiod (daylength), crop species can be divided into three categories: long-day, short-day, and day-neutral.

Long-day species are those whose floral development is accelerated by daylengths of more than 16 hours. These plant species tend to have originated or be widely grown at high latitudes. Examples of such crops are wheat, barley, and pea. **Short-day species** are those whose floral development is accelerated by daylengths of less than 10 hours. These plant species tend to have originated or be widely grown at lower latitudes. Maize, soybean, and tobacco are examples of short-day plants. **Day-neutral species** are those whose floral development is not influenced by daylength outside the usual range of 10–12 hours, and is controlled mainly by temperature.

(3) ~~3.4~~ Temperature

Temperature is a relative measure of the hotness or coldness of a body. **Heat** is the *energy* which is transferred from one body to another by a thermal process such as radiation, conduction, or convection. **Temperature** is a measure of the *intensity of heat*. Temperature strongly influences growth as well as development.

potential evaporation rate (E_p) with units mm d^{-1}. The supply of water to the crop is usually taken as the sum of rainfall (R) and irrigation (I). A first step in deriving a useful index of water stress is to calculate the difference between the demand and supply of water, i.e. the potential soil moisture deficit (D) during the growing season. At any time in the growing season, D is given by:

$$D = \Sigma E_p - \Sigma(I+R) + D_s \qquad (3.7)$$

where ΣE_p and $\Sigma(I+R)$ are the accumulated potential evaporation and rainfall + irrigation respectively, and D_s is the actual soil moisture deficit when the crop was sown. For spring sowing it is usual to assume that $D_s = 0$ (i.e. the soil is at field capacity at sowing), but this is not always true. Equation (3.7) is evaluated for each day after sowing with the stipulation that D can never be negative; if calculated D turns out to be negative, it is assumed to be zero, i.e. drainage is assumed to occur. Table 3.2 gives an example of equation (3.7) being used to calculate D.

Table 3.2 Example of calculation of potential soil moisture deficit (mm)

Day	E_p	R	I	D_1*	D_2**
1	3.5	0	0	3.5	53.5
2	4.0	0	0	7.5	57.5
3	2.0	20	0	0.0	39.5
4	3.0	0	0	3.0	42.5
5	4.0	0	0	7.0	46.5
6	5.1	0	0	12.1	51.6
7	5.5	0	0	17.6	47.1
8	6.0	0	0	23.6	53.1
9	7.0	0	0	30.6	60.1
10	3.0	0	0	35.6	65.1
11	5.0	0	30	10.6	40.1
12	4.0	0	0	14.6	44.1
13	5.0	2	0	17.6	47.1

* For D_1, soil assumed to be at field capacity on sowing.
** For D_2, soil assumed to have a deficit of 50 mm.

The influence of moisture stress on the growth of an annual crop can be related to the maximum value of D reached during growth (D_m, the maximum potential soil moisture deficit) which is, in effect, an index of drought severity. To do this, it is first necessary to define a value of D beyond which growth is limited by drought; this is termed the limiting deficit (D_ℓ). To estimate the influence of drought on crop growth, it is first assumed that for a well-irrigated crop for which $D_m < D_\ell$, growth is proportional to the total potential evaporation from the crop (ΣE_p).

For most crops, the fraction of total growth harvested as economic yield (Y) is stable, and so the yield for a fully irrigated crop (Y_F) is given by:

$$Y_F = k\,\Sigma E_p \qquad (3.8)$$

where k is a constant of proportionality, typically around 11 kg dry matter (DM) ha^{-1} mm^{-1} for well-husbanded crops.

To estimate the effect of drought on yield, a further assumption is made: that if D_m exceeds D_ℓ, growth stops until more rain or irrigation is received, whereupon the crop will grow again at the full rate determined by E_p until that water is used up, when once again growth will stop. When D_m is greater than D_ℓ it follows that:

$$Y = k\,[\Sigma E_p - (D_m - D_\ell)] \qquad (3.9)$$

with the loss of yield due to drought being proportional to $(D_m - D_\ell)$. Yield decreases linearly with D_m. Non-irrigated crops affected by drought are unable to use subsequent rain as well as irrigated crops. The growth of non-irrigated crops *slows* when $D_m > D_\ell$ but does not *stop*. Monteith (1981) suggested this as the time lost for growth due to drought. If the potential evaporation rate during the main period of crop growth is stable, the lost time is given simply by $(D_m - D_\ell)/E_p$. This model for the effect of drought on yield makes some drastic assumptions but it is simple, the variables have biological and physical relevance, and it requires no measurements of actual soil moisture content.

The value of D_ℓ is crucial; it defines when irrigation is needed, for if D_m exceeds D_ℓ yield is reduced (Equation 3.9). Two factors determine D_ℓ: first, the physical characteristics of the soil; and second, the effective rooting depth of the crop. Heavy, moisture-retentive soils are associated with large values of D_ℓ, and deep-rooted crops like lucerne have large values of D_ℓ. If the available water content of a soil (A), measured in mm of available water per m depth of soil, is known, then to a first approximation:

$$D_\ell = 0.5 \times z \times A \qquad (3.10)$$

where z is the effective rooting depth in metres. Some rough values for the effective rooting depths of different crops are as follows: 0.45 m for pea and green bean; 0.6–0.7 m for pasture; around 1.0 m for cereals; and up to 1.5 m for lucerne.

Effect of moisture stress on crop growth. Water stress affects many aspects of crop growth and yield by affecting various physiological activities in the life history of a plant. Major ones are cell division and enlargement, root and shoot extension, stomatal resistance, photosynthesis, transport of nutrients for the general functioning of cell metabolism, and respiration.

3.4.1 Effect of temperature on growth

Temperature starts influencing the growth of a crop soon after the seed is sown, provided the soil is moist. Early in the season, when temperatures are low, the growth of most annual crops is limited by temperature. Low temperatures slow the rate of leaf extension and increase the time to reach full crop canopy cover. At full crop canopy cover all incoming radiation is intercepted and growth is fastest. Leaf area is important in influencing the growth rate of crops because this directly determines the amount of radiation intercepted by the foliage during the season. In agriculture, crop management generally attempts to increase plant growth and yield by influencing leaf growth rather than the rate of photosynthesis per unit leaf area.

3.4.2 Vernalization and chilling

Many biennials and temperate annuals, as well as certain fruit trees, require exposure to cold temperatures before they can flower. This is known as the **vernalization requirement** for annuals and biennials, and **chilling requirement** for fruit trees. The most effective temperature range for vernalization is 3–7°C; effectiveness is assumed to decline linearly from 3 to 0°C and from 7 to 10°C. Temperatures below 0°C and above 10°C are assumed to be ineffective for vernalization.

(4) ~~3.5~~ Water

Water, which is essential for crop growth, is becoming increasingly scarce in most parts of the world. The question of how crop growth and yield are related to water use has therefore assumed great importance. This is the topic for discussion in this section.

3.5.1 Transpiration

Transpiration is the process of loss of water from living plants. Its study is important because it is the main process through which water received as rainfall by a crop or applied in irrigation is lost to the atmosphere.

In Pakistan, evaporation from green crops which shade the ground completely and are supplied with adequate water varies from about 1 mm d^{-1} (10 t ha^{-1} [of ground] d^{-1}) in winter to about 10 mm d^{-1} (100 t ha^{-1} d^{-1}), in mid-summer. An understanding of the factors controlling water loss from plants is essential in order to modify the plant environment or the plant itself to reduce water use.

Transpiration of water vapour from plant leaves is a physical process of diffusion. Water vapour diffuses from a saturated atmosphere inside the leaf

through its stomata and a thin layer of still air at the leaf surface (the **boundary layer**) and into the drier atmosphere outside the leaf. The rate of transpiration is directly proportional to the difference in water vapour concentration between the air inside the leaf and the air above the boundary layer, and inversely proportional to the diffusive resistances of the stomata and the boundary layer.

Stomatal resistance. The resistance offered by stomata to the diffusion of water molecules is directly proportional to the number of stomata per unit leaf area, and inversely proportional to the diameters of the stomatal apertures. The size of the stomatal apertures, in turn, is influenced by a number of environmental factors: the stomata of most species open in the light and close in the dark, either as a direct response to solar radiation, or under the control of circadian rhythms. Stomata also tend to open if the CO_2 concentration in the substomatal cavity falls below a critical level. Exposure of leaves either to lower internal CO_2 concentration or to solar radiation causes the depression of the solute potential of the stomatal guard cells. Water is therefore drawn into the guard cells. This increases their turgor pressure above that of the surrounding epidermal cell: the stomata then open as a consequence of the mechanical effects of this difference in turgor pressure between the guard cells and the surrounding epidermal cells. The size of the stomatal apertures and the resistance to gaseous diffusion through the apertures depend upon the magnitude of the difference in the turgor pressure.

The fundamental response of stomata to solar radiation or to circadian rhythm can be modified by several factors. Increased respiration at high temperatures may lead to the closure of the stomata due to the accumulation of high levels of CO_2 in the leaf air spaces. This mechanism leads to water conservation. It may be the cause of mid-day closure of stomata when leaf temperatures and evaporative demand are high.

Stomata also respond to overall leaf–water relations, closing at relatively low thresholds of leaf water potential. Under certain circumstances, stomatal aperture can respond directly to changes in water vapour content of the air before changes have occurred in leaf water potential. Such a response to air humidity permits the leaf to control its water content accurately. Another mechanism of stomatal aperture control is exercised through growth substances in the leaf, in particular, abscisic acid. Abscisic acid is synthesized in the chloroplasts during water stress, and can cause the closure of stomata and their delayed opening.

These various mechanisms of transpiration control illustrate the options available to different crop species for responding to various environmental factors to achieve a favourable balance between the uptake of CO_2 for photosynthesis, and the loss of water through transpiration.

These processes must occur during the appropriate stages of development, and consequently the timing of each contribution is important. Interacting with this set of circumstances is the ability of the environment to supply light, water, and nutrients for the completion of each stage of growth.

Effect of moisture stress on vegetative growth. Vegetative growth consists of all those activities associated with the generation and expansion of leaves, the formation of apical meristems, and the concurrent expansion of the root system. Low leaf water potentials influence leaf production through their effects on leaf initiation in meristems and subsequent rates of cell division. The rate of leaf initiation may become slower or even cease as moisture stress increases, and there is evidence that cell division may be reduced. In general, cell enlargement appears to be more sensitive than cell division.

Leaf enlargement is reduced by small degrees of moisture stress long before photosynthesis is affected. Rates of enlargement are most rapid when leaf water potential is −0.15 MPa to −0.25 MPa and decline markedly when leaf water potential falls below these values. In maize, sunflower, and soybean, leaf enlargement was reduced to 25% of the well-watered controls or even less when leaf water potentials decreased to −0.4 MPa (Boyer 1970).

Short periods of moisture stress have a reversible effect on leaf growth (Acevedo et al. 1971). However, if leaf water potentials are continuously less than optimum for several days, leaves may not grow at the original rate upon rewatering (Boyer 1970). Therefore, the subsequent regrowth of the stressed plant depends also on the duration of the stress. With prolonged deficits, indirect effects arise from reduced photosynthesis, reduced mineral nutrient supply and protein synthesis, and increased sugar synthesis or other impairments of metabolism.

Under certain field situations such as saline soils, the leaves at the top grow even though leaf water potentials may be continuously more negative than −0.4 MPa. It, therefore, seems certain that leaves are capable of adjusting in some way so that enlargement is less affected than in the experiments described by Boyer (1970) and Acevedo et al. (1971).

Although low leaf water potentials have a large effect on the rate of production of new leaves (leaf area), they also cause the loss of existing leaf area. In the adaptation study in maize, leaf senescence was accelerated in the stressed plants compared to that in the controls (Boyer 1970).

Root growth is also retarded by water shortage and markedly influenced by photosynthate supply (possibly growth substances) from the leaves, with severe defoliation leading to virtual cessation of root elongation.

Respiration. Research studies generally demonstrate that dark respiration is suppressed, more or less proportionately but not very markedly, by moderate to severe water stress (Boyer 1970). Generally, rates of respiration appear to be closely coupled with rates of growth (photosynthesis).

Respiration rates of whole plants or shoots certainly include both growth and maintenance components, so changes during stress are difficult to interpret.

Effect of water stress on dry matter production. The efficiency with which intercepted radiation is used to fix CO_2 depends on leaf area, aerodynamic and stomatal resistance, internal resistance to CO_2 transfer, and the photosynthetic efficiency of individual leaves. As the CO_2 fixed by photosynthesis represents most of the dry matter (DM) accumulated by the plant, any factor that affects the photosynthetic activity of leaves is likely to affect the total dry matter (TDM).

Since cell growth is usually much more susceptible to water stress than is CO_2 assimilation, it should not be assumed that dry matter production is not affected unless plant water status falls to a level that reduces stomatal opening and photosynthesis. Stress that is mild enough not to affect photosynthesis *can* reduce the development of leaf surface area. Whether such reduction will affect dry matter yield depends on whether the leaf area is limiting the crop's assimilation of CO_2.

3.5.4 Atmospheric moisture

Humidity. The amount of water vapour that can be retained by a unit volume of air is dependent upon the temperature of that air, warm air being able to retain more water vapour per unit volume than air at a lower temperature. Thus, for a complete knowledge of the state of the air, two parameters are required: the temperature of the air and the amount of moisture in it.

Effect of humidity on transpiration. The influence of atmospheric moisture content on plant growth is exerted through its effects on plant–water relations. This results primarily from the direct effect on transpiration. The vapour pressure of the bulk air is the actual vapour pressure (e) of the air, which is a direct indicator of its moisture content. This vapour pressure is related to the saturated vapour pressure (e^*) at the same temperature by the following expression.

$$\text{Relative humidity} = (e/e^*) \times 100 \qquad (3.11)$$

Thus as air temperature changes, the relative humidity changes, even though the actual moisture content of the air remains the same. Relative humidity in itself, therefore, is not a reliable indicator of potential transpiration losses. Another measure of atmospheric moisture content is **vapour pressure deficit** (VPD), which is the difference between e^* and e ($e^* - e$) *at the same temperature*. **If leaf and air temperatures are identical, the VPD of the air is the same as ($e^* - e$), which is the leaf air information really needed for consideration of the transpiration rate.**

Boundary-layer resistance. The leaf surface is enveloped by a relatively undisturbed layer of air, called the **boundary layer. Water vapour from inside the leaf must diffuse through this boundary layer before entering the atmosphere. The thickness of the boundary layer depends upon wind velocity as well as leaf shape and size.**

The diffusive resistance of a transpiring plant is the sum of the resistances which the stomata and the boundary layer offer to diffusion of water vapour from inside the leaves to the atmosphere. Under most conditions, the stomatal resistance is the dominant component of the diffusive resistance. Stomatal apertures, therefore, determine the rate of transpiration under such circumstances. But in still air, or when wind velocity is very low, the boundary layer becomes thicker, and its resistance to diffusion can become the dominant component of the plant's diffusive resistance. In such circumstances, boundary-layer resistance can control transpiration over a range of stomatal apertures.

3.5.2 Moisture stress

Water deficit occurs in the plant whenever evapotranspiration exceeds water absorption. This may be due to excessive water loss, reduced absorption, or both. To study the effect of moisture stress on the yield of a crop, therefore, it is important to consider both the supply of water to the crop and its demand for water.

Some concepts essential for this discussion are defined here.

Potential evapotranspiration (E_p). Potential evapotranspiration (E_p) is defined as the amount of evaporation occurring from an extensive area of a short, green crop completely covering the ground and well supplied with water. For arable crops which do not cover the ground completely until some time after planting, adjustments are made according to the crop cover and the soil moisture content. This enables the determination of a value for potential evapotranspiration (E_p) for the full growing season.

Penman's equation for calculation of potential evapotranspiration. Penman's (1948) equation for calculation of potential evapotranspiration is based on the premise that the rate of potential evapotranspiration is determined by two characteristics of the prevailing weather: the drying power of the air, and the energy available for evaporation and heating. Assuming that a crop behaves like a water surface, the rate of evaporation from the crop surface will depend on wind speed and the dryness of the atmosphere in the following manner.

$$E_p = f(u)\,[e'(T_s) - e_a] \qquad (3.5)$$

where:

E_p = potential evapotranspiration'
$f(u)$ = a function depending on wind speed at 2 m above ground level

$e'(T_s)$ = **the maximum amount of water vapour that the air can hold at the temperature of the crop surface, expressed as vapour pressure in units of mb**
e_a = **the actual amount of water vapour held in the air at 2 m above ground level, expressed as vapour pressure in units of mb and** measured at 9 A.M.

This equation simply states that potential evapotranspiration (E_p) is equal to the product of a concentration difference (difference between the maximum amount of water vapour that the air can hold and the water vapour actually held), $[e'(T_s) - e_a]$, and a conductivity, $f(u)$, which depends on wind speed. According to this equation, at a constant wind speed, potential evapotranspiration increases in direct proportion to the dryness of the atmosphere. At constant dryness, E_p increases in direct proportion to wind speed.

Field capacity. Field capacity is defined operationally as the amount of water present in the soil each spring after the water from winter rains has drained out of the soil. Field capacity may differ widely from site to site in the same field, and may also vary according to the time of year. It is, therefore, not an accurate, absolute measure of soil moisture status. But it is valuable in field practice as a reference point from which potential soil water deficit can be calculated. Water deficit occurs in plants whenever evapotranspiration exceeds water absorption. This may be due to excessive water loss, reduced water absorption, or both.

Potential soil moisture deficit (D). Potential soil moisture deficit (D) is the difference between a crop's potential evapotranspiration (E_p), and the amount of rainfall (R) received by a crop plus the quantity of water delivered to it in irrigation (I):

$$D = E_p - (R+I) \qquad (3.6)$$

In equation (3.6), D is not allowed to have negative values; it is assumed that the amount of rain that falls when D=O is lost as runoff.

Maximum potential soil moisture deficit (D_m). Maximum potential soil moisture deficit (D_m) is the greatest value of potential soil moisture deficit attained during the growth of a crop. It is an index of the severity of drought during the growing season.

3.5.3 The response of crop yields to soil moisture stress

This analysis is designed to answer two questions: when is irrigation needed, and what is crop response likely to be? It is based on the simplest theory compatible with observed responses and is implicit in much, if not all, of the advice given to Pakistani farmers about irrigation.

Once full crop cover is established, the demand of a crop for water is determined largely by the weather. This demand is usually specified as a

These processes must occur during the appropriate stages of development, and consequently the timing of each contribution is important. Interacting with this set of circumstances is the ability of the environment to supply light, water, and nutrients for the completion of each stage of growth.

Effect of moisture stress on vegetative growth. Vegetative growth consists of all those activities associated with the generation and expansion of leaves, the formation of apical meristems, and the concurrent expansion of the root system. Low leaf water potentials influence leaf production through their effects on leaf initiation in meristems and subsequent rates of cell division. The rate of leaf initiation may become slower or even cease as moisture stress increases, and there is evidence that cell division may be reduced. In general, cell enlargement appears to be more sensitive than cell division.

Leaf enlargement is reduced by small degrees of moisture stress long before photosynthesis is affected. Rates of enlargement are most rapid when leaf water potential is −0.15 MPa to −0.25 MPa and decline markedly when leaf water potential falls below these values. In maize, sunflower, and soybean, leaf enlargement was reduced to 25% of the well-watered controls or even less when leaf water potentials decreased to −0.4 MPa (Boyer 1970).

Short periods of moisture stress have a reversible effect on leaf growth (Acevedo et al. 1971). However, if leaf water potentials are continuously less than optimum for several days, leaves may not grow at the original rate upon rewatering (Boyer 1970). Therefore, the subsequent regrowth of the stressed plant depends also on the duration of the stress. With prolonged deficits, indirect effects arise from reduced photosynthesis, reduced mineral nutrient supply and protein synthesis, and increased sugar synthesis or other impairments of metabolism.

Under certain field situations such as saline soils, the leaves at the top grow even though leaf water potentials may be continuously more negative than −0.4 MPa. It, therefore, seems certain that leaves are capable of adjusting in some way so that enlargement is less affected than in the experiments described by Boyer (1970) and Acevedo et al. (1971).

Although low leaf water potentials have a large effect on the rate of production of new leaves (leaf area), they also cause the loss of existing leaf area. In the adaptation study in maize, leaf senescence was accelerated in the stressed plants compared to that in the controls (Boyer 1970).

Root growth is also retarded by water shortage and markedly influenced by photosynthate supply (possibly growth substances) from the leaves, with severe defoliation leading to virtual cessation of root elongation.

Respiration. Research studies generally demonstrate that dark respiration is suppressed, more or less proportionately but not very markedly, by moderate to severe water stress (Boyer 1970). Generally, rates of respiration appear to be closely coupled with rates of growth (photosynthesis). Respiration rates of whole plants or shoots certainly include both growth and maintenance components, so changes during stress are difficult to interpret.

Effect of water stress on dry matter production. The efficiency with which intercepted radiation is used to fix CO_2 depends on leaf area, aerodynamic and stomatal resistance, internal resistance to CO_2 transfer, and the photosynthetic efficiency of individual leaves. As the CO_2 fixed by photosynthesis represents most of the dry matter (DM) accumulated by the plant, any factor that affects the photosynthetic activity of leaves is likely to affect the total dry matter (TDM).

Since cell growth is usually much more susceptible to water stress than is CO_2 assimilation, it should not be assumed that dry matter production is not affected unless plant water status falls to a level that reduces stomatal opening and photosynthesis. Stress that is mild enough not to affect photosynthesis *can* reduce the development of leaf surface area. Whether such reduction will affect dry matter yield depends on whether the leaf area is limiting the crop's assimilation of CO_2.

3.5.4 Atmospheric moisture

Humidity. The amount of water vapour that can be retained by a unit volume of air is dependent upon the temperature of that air, warm air being able to retain more water vapour per unit volume than air at a lower temperature. Thus, for a complete knowledge of the state of the air, two parameters are required: the temperature of the air and the amount of moisture in it.

Effect of humidity on transpiration. The influence of atmospheric moisture content on plant growth is exerted through its effects on plant–water relations. This results primarily from the direct effect on transpiration. The vapour pressure of the bulk air is the actual vapour pressure (e) of the air, which is a direct indicator of its moisture content. This vapour pressure is related to the saturated vapour pressure (e^*) at the same temperature by the following expression.

$$\text{Relative humidity} = (e/e^*) \times 100 \qquad (3.11)$$

Thus as air temperature changes, the relative humidity changes, even though the actual moisture content of the air remains the same. Relative humidity in itself, therefore, is not a reliable indicator of potential transpiration losses. Another measure of atmospheric moisture content is **vapour pressure deficit** (VPD), which is the difference between e^* and e ($e^* - e$) *at the same temperature*. If leaf and air temperatures are identical, the VPD of the air is the same as ($e^* - e$), which is the leaf air information really needed for consideration of the transpiration rate.

Under natural conditions, during the course of a day the temperature will change, but the vapour pressure may not change significantly. Thus, the relative humidity and VPD will change concomitantly with the temperature, even though the moisture content of the air remains the same. If leaf temperature increases, the vapour pressure inside the leaf increases, thus increasing the vapour pressure gradient from leaf to air. Thus the increase in transpiration from morning to afternoon is due not to the decrease in relative humidity or increase in VPD of the air but *to the increase in leaf temperature*. Comparison of results at similar relative humidities is dangerous unless the air temperatures are the same.

Effect of humidity on crop growth. Under many agricultural situations the moisture content of the air becomes an important growth-limiting environmental parameter. When the radiant energy load on the crop is high and air temperature is high, the moisture content of the air can impose a considerable constraint upon the growth rate of a crop. This combination of high light, warm temperatures, and low atmospheric moisture content is typical of many irrigated areas. In Pakistan, warm temperatures, a high number of cloudless days, and low rainfall dictate the use of considerable amounts of water for irrigation, which raises the cost of production.

Low atmospheric moisture content during a significant part of the growing season is probably one of the greatest limits to total productivity. For much of the time, the transpiration rate is so high that water potentials and turgor pressure are below the critical threshold for leaf growth for periods long enough to significantly limit total crop production. This effect is especially intensified when cropped areas are interspersed with non-cropped areas, as is typical in many of the irrigated areas of the world. Under such conditions, the movement of hot, dry air from over the barren soil through the cropped area leads to an advective heating of the leaves and thereby increases the amount of heat that must be dissipated by latent heat transfer or transpiration. The transpiration rate then must be high enough not only to balance the radiation load but also to compensate for the increased heat load due to advection. This is the well-known 'oasis effect'. Hanks et al. (1971) have observed this effect in wide-row sorghum crops adjacent to non-cropped areas in the Great Plains of the United States.

With the realization that the moisture content of the air in these areas is an important limiting factor to higher productivity, it becomes extremely important to find practical and cost-effective methods of modifying air humidity over and within the cropped areas.

Dew. The formation of dew occurs mainly at night because it depends on radiational cooling of leaf and soil surfaces until they reach dew-point temperatures. Dew absorption has been found to vary widely with plant species. It also depends on the intensity and duration of dewfall as well as on the soil moisture regime, being higher under dry-land conditions than under irrigation. Dew can provide only a very small proportion of the water requirements of a normally transpiring plant, but may be of some importance to plants under water stress. It may accelerate the restoration of leaf turgor at night, and in the morning can delay the onset of renewed stress. In dry regions, therefore, dew may be beneficial to plant growth and make a positive contribution to the water balance of the plant.

Fog. When a warm, saturated air mass rapidly replaces a cool, dry air mass over a cool surface, fog or mist results. During overcast nights, this may cause the deposition of relatively large amounts of water on plants and on the soil surface. Fog occurs very frequently along rather narrow coastal regions which border on oceans with cold currents that run parallel to the coast. It affects plant growth through high air humidity, wetting of the aerial parts of plants, and humidification of the soil surface. There are no accurate measurements of the amount of moisture supplied by fog to the water balance of plants, but both type and density of native vegetation appear to be influenced by the frequency of fog occurrence. In certain deserts, in which no rainfall occurs for several years continuously, vegetation may derive its water requirements entirely from fogs or mists.

(5) 3.6 Wind

Wind affects plants in several ways: it effects the exchange processes between plant and the atmosphere, thereby influencing the heat and water balances; and it exerts mechanical effects leading to breakage of plant parts. The sand and dust particles carried by wind may damage plant tissues. Emerging seedlings may be completely covered, or the roots of young plants may be exposed by strong winds. Winds may also cause considerable losses from lodging, breaking of stalks, and shedding of grain.

The physiological effect of wind consists mainly in influencing transpiration and increasing evaporation from the soil. Winds increase transpiration by removing the moist air surrounding the leaves; they decrease transpiration by cooling the leaves. The former effect will be most marked at low levels of radiation and the latter at high levels. Hot, dry winds may also adversely affect photosynthesis, and hence productivity, by causing closure of the stomata even when soil moisture is adequate. Experimental vibration of leaves that produces no visible damage results in increased respiration, diminished photosynthesis and transpiration, and in most cases closure of stomata and marked reduction of plant growth.

Wind damage is accentuated by the abrasive action of wind-borne soil particles, and beyond a threshold value damage tends to be proportional to wind speed and the quantity of soil blown. Armbrust (1972) found that the nitrogen metabolism of injured plants may be affected before visual damage is apparent.

Many comparisons have been made between crop yields in sheltered areas with yields obtained under full exposure to wind. Generally, leeward yield attains a maximum at a point coinciding with maximum protection, with yield tapering off on either side more or less in accordance with the wind profile. The greatest percentage increases in yield are usually where yields are below average, and they may then represent comparatively small additions to total production. Similarly, at a given location percentage yield responses are generally greater in dry years than wet years.

STUDY QUESTIONS

1. Define the following: (a) the environment, (b) functional environment, (c) aerial environment.
2. Define the following: (a) radiation, (b) photosynthetically active radiation, (c) units of light intensity, (d) growth and growth rate.
3. What is photosynthesis? Explain the three partial processes of photosynthesis and their interrelationships.
4. Discuss variables relating to light interception and its utilization by the crop canopy. Discuss its implication for crop growth and yield.
5. Explain environmental effects on photosynthesis and respiration, and the implications they have for dry matter production.
6. Define growth and maintenance respiration. Discuss the effects of light and temperature on crop respiration.
7. Define the following: (a) photoperiod and daylength, (b) long-day plants, (c) short-day plants, (d) day-neutral plants.
8. Describe the influence of temperature on the rate of photosynthesis and respiration.
9. Define the following: (a) transpiration, (b) boundary layer resistance, (c) stomatal resistance, (d) stomatal density.
10. Define the following: (a) potential evapotranspiration, (b) potential soil moisture deficit, (c) maximum potential soil moisture deficit, (d) limiting soil moisture deficit, (e) water-use efficiency, (f) field capacity.
11. Describe the effects of moisture stress on different plant growth processes, and the implications this may have for crop yield.

12. Calculate soil moisture deficit for a month (on a daily basis) using lo meteorological data.
13. Define the following: (a) humidity, (b) relative humidity, (c) vapour pressure deficit, (d) dew, (e) fog.
14. Describe the effects of humidity and wind on crop growth and yield.

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