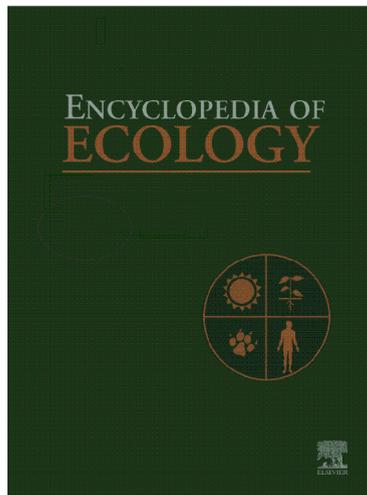


Provided for non-commercial research and educational use.  
Not for reproduction, distribution or commercial use.

This article was originally published in the *Encyclopedia of Ecology*, Volumes 1-5 published by Elsevier, and the attached copy is provided by Elsevier for the author's benefit and for the benefit of the author's institution, for non-commercial research and educational use including without limitation use in instruction at your institution, sending it to specific colleagues who you know, and providing a copy to your institution's administrator.



All other uses, reproduction and distribution, including without limitation commercial reprints, selling or licensing copies or access, or posting on open internet sites, your personal or institution's website or repository, are prohibited. For exceptions, permission may be sought for such use through Elsevier's permissions site at:

<http://www.elsevier.com/locate/permissionusematerial>

S Irmak. Evapotranspiration, Origin of. In Sven Erik Jørgensen and Brian D. Fath (Editor-in-Chief), *Ecological Processes*. Vol. [2] of *Encyclopedia of Ecology*, 5 vols. pp. [1432-1438] Oxford: Elsevier.

eukaryotes. These protists have within their endoplasmic reticulum an endosymbiont resembling a eukaryote. This endosymbiont possesses its own plasma membrane and ribosomes (which are both similar to those of eukaryotes) as well as the remnant of a nucleus containing its own DNA (a nucleomorph), and finally plastids. Thus, these organisms have four sets of DNA: mitochondrial, plastid, nuclear, and nucleomorph. Some protists may even contain plastids from tertiary endocytosis.

### Other Possible Symbiotic Events

Christian de Duve proposed that peroxisomes (which contain enzymes for oxidative reactions) may also have originated as endosymbionts; however, because of their single layer membranes, lack of DNA, and the recent observation that peroxisomes can be formed from the endoplasmic reticulum, it is now generally accepted that they arose endogenously.

Lynn Margulis proposed in 1967 that along with mitochondria and plastids, the eukaryotic flagella was

also the result of symbiosis (see the section entitled 'Origin of eukaryotes'). However, this fell largely out of favor when flagella were found not to possess DNA, and subsequently that spirochetes are rather dissimilar to eukaryotic flagella.

See also: Evolutionary Ecology: Overview; Fitness.

### Further Reading

- Brown JR and Doolittle WF (1997) Archea and the prokaryote-to-eukaryote transition. *Microbiology and Molecular Biology Reviews* 61: 456–502.
- Emelyanov VV (2003) Mitochondrial connection to the origin of the eukaryotic cell. *European Journal of Biochemistry* 270(8): 1599–1618.
- Gupta RS and Golding GB (1996) The origin of the eukaryotic cell. *Trends in Biochemical Sciences* 21: 166–171.
- Katz LA (1998) Changing perspectives on the origin of eukaryotes. *Trends in Ecology and Evolution* 13: 493–497.
- Katz LA (1999) The tangled web: Gene genealogies and the origin of eukaryotes. *American Naturalist* 154: S137–S145.
- Roger AJ (1999) Reconstructing early events in eukaryotic evolution. *American Naturalist* 154: S146–S153.

## Evapotranspiration

S Irmak, University of Nebraska–Lincoln, Lincoln, NE, USA

© 2008 Elsevier B.V. All rights reserved.

### Introduction

The Hydrologic Cycle and ET  
ET Terminology

### Crop Coefficient Concept Further Reading

### Introduction

Water is one of the most important limited natural resources. Declining water resources and water quality problems have resulted in dramatic increase in the need for water-conserving methodologies on a field, watershed, and regional scale and this makes efficient use of freshwater resources an obligation of each user. During the 30-year period from 1950 to 1980, the actual level of per capita water supply decreased significantly in many countries due to population increases. It has been projected that in early year 2000 considerably low water availability per capita is anticipated in many regions of the world. As water becomes increasingly scarce and the need becomes more pressing, newer and more complete methods of measuring and evaluating techniques of handling water resources are necessary. In terms of agricultural production, approximately 17% of the cropped area of the world

is irrigated and contributes more than one-third of the total world food production. In the United States, about 12% of the cropped area is irrigated and contributes about 25% of the total value of the United States crops. In the United States and around the world, irrigated agriculture uses most of the water withdrawals from the surface and groundwater supplies. Thus, accurate quantification of plant water use (evapotranspiration) is crucial for better management and allocation of water resources.

The process known as evapotranspiration (ET) is of great importance in many disciplines. Accurate quantification of ET in agroecosystems is critical for better planning, managing, and efficient use of water resources, especially in arid or semiarid environments where lack of precipitation usually limits plant growth and yield and negatively affects ecological balances. Quantification of ET is also crucial in water allocation, irrigation management, evaluating the effects of changing land use on water

yield, environmental assessment, and development of best management practices to protect surface and groundwater quality.

ET can be defined as the loss of water from the ground, lake or pond, and vegetative surfaces to the atmosphere through vaporization of liquid water. In agroecosystems, ET is the sum of two terms: (1) transpiration, which is water entering plant roots and used to build plant tissue or being passed through leaves of the plant into the atmosphere in the vapor form, and (2) evaporation which is water evaporating from soil and water surfaces, or from the surfaces of plant leaves. Evaporation from buildings, streets, parking lots, etc., after a rain event also contributes to the total ET in the hydrologic cycle.

Evaporation and transpiration processes occur simultaneously and there is no easy method to separate these two processes. Evaporation in the field can take place from crop canopies, from the soil surface, or from a free water surface. When the soil surface is bare, evaporation will take place from the soil directly. In the absence of vegetation, and when the soil surface is subject to radiation and wind effects, evaporation can result in considerable loss of water in both irrigated and nonirrigated agriculture, and other ecological landscapes. In the semiarid and arid western regions of the United States, evaporation can be as high as 40% of the total ET.

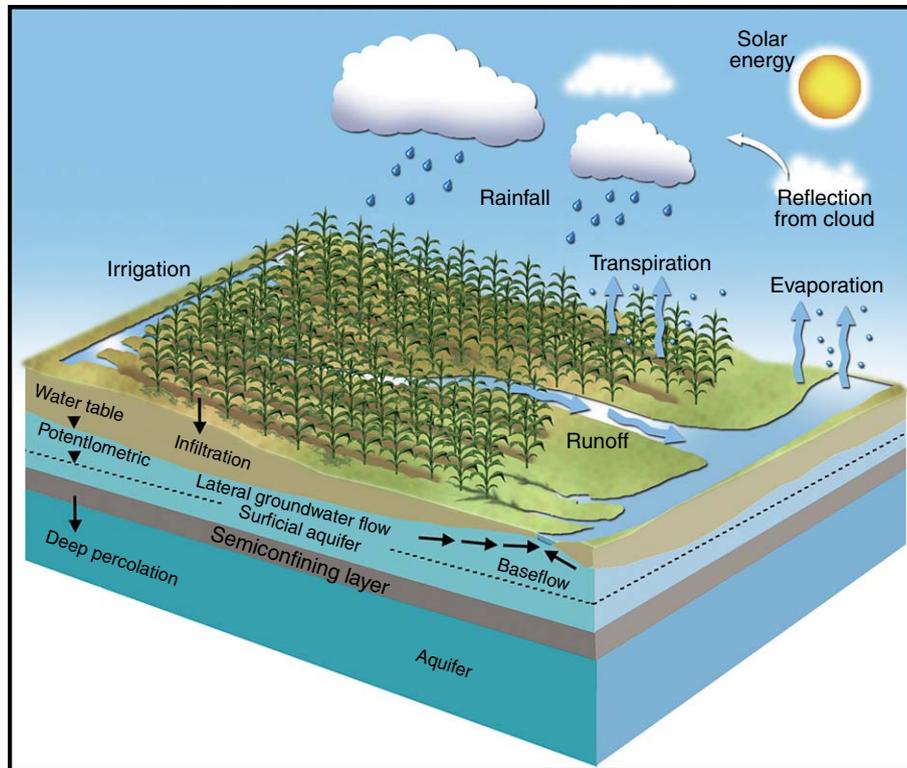
Transpiration increases with increasing leaf area until complete closure of the canopy occurs. For agricultural crops such maximum transpiration is usually attained at a leaf area index (LAI) of about 3–3.5. In the transpiration process, stomata opening and closure depends on water uptake rate which in turn depends on the density and distribution of roots and their effectiveness to uptake water and nutrients from the soil. Stomata would close when roots cannot uptake water from soil with sufficient rate to keep up with the transpiration. In irrigated agroecosystems, the goal should be decreasing the evaporation component of the total ET for optimum crop production because yield and transpiration are strongly related and evaporation does not have any contribution to the crop growth and yield. Thus, the evaporation falls into the 'unbeneficial water use' category.

The ET rate and amount for different vegetation surfaces (i.e., agronomical crops, which are mostly 'annual crops' vs. trees and shrubs, which are mostly 'perennials') show significant variation from one location to another and are strong functions of climatic, soil conditions, and management practices. For example, the seasonal crop ET for corn (maize, *Zea mays*) can range from 500 to 800 mm depending on climate. The ET for typical alfalfa (*Medicago sativa*) plant can range from 800 to 1600 mm per growing period depending on climate and length of growing period. For a tropical plant such as banana (*Musa* spp.), this value is between 1200 mm in the humid tropics and 2200 mm in the dry tropics. Water requirement of

trees can also show wide variations depending on climate, soil type, and root structures. For example, an orange tree (*Citrus aurantium*) can use as much as between 900 and 1200 mm of water per year whereas olive tree (*Olea europaea*) can use only between 400 and 600 mm of water per year. The expected water use of natural vegetations can also show significant variation. For example, the seasonal water use of cattail (*Typha*) can range from only 890 mm to as much as 2500 mm. Water use for foxtail (*Lycopodium clavatum*) is about 140 mm and for pine tree (*Pinus*) water use can range from 480 to 1190 mm. Water use of different natural vegetation and agronomical plants are important and necessary for accurate determination of hydrologic balance components.

## The Hydrologic Cycle and ET

ET is a major component of the hydrologic cycle. A major proportion of the total precipitation falling on the land surface is returned to the atmosphere by ET. As a global average, 57% of the annual precipitation falling over the land is returned to the atmosphere by ET. ET amounts to about 70% of the annual precipitation of the United States, and more than 90% of the precipitation in the arid and semiarid areas of the western United States. Different components of a typical hydrologic cycle are illustrated in [Figure 1](#). The hydrologic cycle can be defined as the pathways of water as it moves in its various phases through the atmosphere, to the Earth, over and through the land, to the ocean, and back to the atmosphere. During this cycle, which has no beginning or end, water molecules may assume various states, returning to a hydrologic pathway as new chemical compounds that are mixed with various solid and liquid substances. In the cycle, water evaporates from the oceans, ponds, rivers, and various land surface to become part of the atmosphere; water vapor is transported and lifted in the atmosphere until it condenses and precipitates on the land or oceans. Precipitated water may be intercepted by vegetation, become overland flow over the ground surface, infiltrate into the ground, flow through the soil as subsurface flow, or discharge into streams as surface runoff. In a given watershed, discharge of water is primarily from groundwater withdrawals for irrigation, ET where the water table is near land surface, overland flow (runoff), and seepage to streams and springs where the water table intersects the land surface. Recharge of water is primarily from precipitation; other sources of recharge are irrigation return flow and seepage from streams, canals, and reservoirs. Large amounts of the intercepted water and surface runoff return to the atmosphere through evaporation. Infiltrated water may percolate to deeper soil layers to recharge groundwater, and later emerge in springs, or as seepage into streams, to form



**Figure 1** The hydrologic cycle showing different components of the hydrological process.

surface flow. Finally, this water may flow to the larger rivers and, eventually, to the sea and/or evaporate into the atmosphere. Throughout this cycle, water is usually subject to evaporation of one kind. Types of vegetation, management and land use, and climatic conditions significantly affect ET, and therefore determine the amount of water lost through ET from a watershed.

In agroecosystems, it is important to have a water balance to protect the sustainability and productivity of the agroecosystems. Water-level declines may result in increased costs for groundwater withdrawals because of increased pumping lift and decreased well yields. Water-level declines also can affect groundwater availability, surface water flow, and near-stream habitat (riparian) areas, and other ecological systems. Therefore developing efficient and effective management strategies is crucial for protecting sustainability of efficient use of water resources, protecting habitat and environment, and preventing ground and surface water degradation.

## ET Terminology

### Potential ET ( $ET_p$ )

Many methods have been developed for direct and indirect measurement of ET. The water loss (evaporative losses) from different surfaces such as turf, bare soil, and

water was originally measured in large tanks (lysimeters). The term 'lysimeter' was derived from the Greek words 'lysis' and 'metron' meaning dissolving and measuring, respectively. The term is applicable to any device utilized that measures the rate, amount, and composition of percolation of water through soil. In a simple term, the lysimeter can be defined as large containers packed with soil located in the field to represent field and environmental conditions, with bare soil or vegetated surfaces (field crops, trees, shrubs, grass, etc.) for measuring the ET of plants or evaporation from bare soil through a mass-balance approach. Lysimeters are expensive and labor-intensive tools to measure evaporation or ET. Thus, other meteorological approaches have been developed over the years to simplify the measurements of ET. One of the commonly used methodologies to determine ET will be discussed later.

The original ET equation was based on evaporation from free water surface as measured with lysimeters. The definition of potential ET that emerged from an earlier work implied a maximum value of ET when there was adequate amount of water to be transpired or evaporated. Formally, potential ET has been defined as "the evaporation from an extended surface of short green crop which fully shade the ground, exerts little or negligible resistance to the flow of water and is always supplied with water." Potential ET cannot exceed free

water evaporation under the same weather conditions. However, in the definition of potential ET, the condition of nonlimiting supply of water is never achieved because the resistance of water flow through plants and soil has a finite value greater than zero. Another problem with this definition is the phrase 'short green crop'. The short green crop has been defined as 8–15 cm tall grass cover, but it has also been defined as a 30–50 cm tall crop of alfalfa. It is important to distinguish between the short green vegetations because the ET rates from well-watered agricultural crops may be as much as 10–30% greater than that occurring from short green grass. This dichotomy in the definition of a 'short green crop' has led to the use of the term 'reference crop ET' ( $ET_{ref}$ ). To eliminate the confusion, in late 1970s and early 1980s, engineers and practitioners introduced and started using the 'reference ET' concept rather than 'potential ET'. The use of the term 'potential ET' is diminishing rapidly and the term 'reference ET' has been gaining significant acceptance by the water resources community.

### Reference Evapotranspiration ( $ET_{ref}$ )

The reference ET ( $ET_{ref}$ ) concept was introduced by irrigation engineers and researchers to avoid the confusions that existed in the definition of potential ET. By adopting a reference crop (grass or alfalfa), it became easier and more practical to select consistent crop coefficients and to make reliable actual crop ET estimates in new areas. Introduction of the reference ET concept also helped to enhance the transferability of the crop coefficients from one location to another. Two reference crops have been used to represent the reference ET: grass and alfalfa.

### Grass Reference Evapotranspiration ( $ET_0$ )

Grass reference ET is defined as "the rate of ET from a hypothetical reference crop with an assumed crop height of 0.08–0.12 m, a fixed surface resistance of  $70 \text{ s m}^{-1}$ , and an albedo of 0.23, closely resembling the ET from an extensive surface of green grass of uniform height, actively growing, well-watered, and completely shading the ground." In the grass reference ET definition, the grass is specifically defined as the reference crop and this crop is assumed to be free of water stress and diseases.

### Alfalfa Reference Evapotranspiration ( $ET_r$ )

Alfalfa reference ET is defined as the ET rate from an extensive, uniform surface of dense, actively growing alfalfa, 0.30–0.50 m tall and not short of soil water. In the

literature, the terms 'reference ET' and 'reference crop ET' have been used interchangeably and they both represent the same ET rate from a short, green alfalfa or grass surface. Unlike the potential ET definition, in the alfalfa reference ET definition, an alfalfa crop is specifically noted as the reference crop.

One of the other important differences between potential and reference ET is that the weather data collection site is well defined in the reference ET definition. It is important to note in the reference ET definition that the climate data that are used to estimate reference ET need to be collected in a well-watered and has certain characteristic (reference) environment. Therefore, based on the definition, the weather data for the reference ET estimations should be collected in a well-irrigated and well-maintained grass or alfalfa field. The irrigated grass area of the weather data collection site should be fairly large (e.g., at least 4 ha) to have enough fetch distance between the instrumentation to measure the climatic variables and the edge of the field because the quality of the weather data will ultimately affect the final estimated reference ET value. Enough fetch distance allows the air to travel on the reference crop surface and represent the aerodynamic, humidity, and temperature characteristics of the reference crop before it is sampled at the weather station. In a hot, dry month the average air temperature may be as much as 5–6 °C higher in a dryland (non-irrigated) area than for a nearby well-irrigated area. The differences in the air temperature will also affect the relative humidity and vapor pressure deficit values, and these differences will ultimately cause differences in the reference ET calculated using the weather data collected from the two sites (dry vs. well-irrigated).

### Determination of Crop ET (Plant Water Use) in Agroecosystems Using Climate Variables

In irrigated agroecosystems, a large part of the irrigation water applied to agricultural lands is consumed by evaporation and transpiration. In practice, in field measurements, it is hard to separate evaporation from transpiration, and the two processes are usually considered as one component. Crop ET can be measured directly using precision weighing lysimeters, Eddy correlation system, Bowen ratio energy balance system, atmometers, including evaporation pans, soil water balance by measuring soil water status continuously, etc. However, because direct measurement of crop ET ( $ET_c$ ) is difficult, time consuming, and costly, the most common procedure is to estimate  $ET_c$  using climatic data. Currently, most commonly practiced way of estimating the crop ET rate (or crop water use rate) for a specific crop or vegetation surface requires first calculating

reference ET ( $ET_{ref}$ ) and then applying the crop coefficients ( $K_c$ ) to estimate actual crop ET ( $ET_c$ ) as

$$ET_c = ET_{ref} \times K_c \quad [1]$$

where  $ET_c$  is the crop ET (crop water use) in units of water depth (inches  $d^{-1}$ ,  $cm d^{-1}$ , or  $mm d^{-1}$ ),  $ET_{ref}$  ( $ET_o$  or  $ET_r$ ) is the reference ET in unit of water depth (inches  $d^{-1}$ ,  $cm d^{-1}$ , or  $mm d^{-1}$ ) as calculated from the basic weather variables (solar radiation, air temperature, wind speed, and relative humidity) measured with a weather station in reference conditions.

Although the first equation by Penman for potential ET, ( $ET_p$ ), was introduced almost 60 years ago; it still provides fundamental principles for the calculation and/or modification of ET models today. Numerous methods have been introduced for computing  $ET_{ref}$  causing confusion among users, decision- and policymakers as to which method to select for  $ET_{ref}$  estimation. Recently, the American Society of Civil Engineers (ASCE) Evapotranspiration in Irrigation and Hydrology Committee established a Task Committee on 'Standardization of Reference Evapotranspiration Calculation'. Based on extensive research and data analyses and comparison of lysimeter-measured reference ET across various climates and Task Committee experience, the Task Committee recommended the use of the ASCE-Penman-Monteith (PM) method as the representation for reference ET. A reduced form of the ASCE-PM was used as the basis for 'standardized'  $ET_{ref}$  computation. Equation parameters differ for hourly and 24-h data. Coefficients and parameters for a taller, rougher crop surface (0.5 m tall, like alfalfa) were also developed. The ASCE standardized  $ET_{ref}$  equation based on a surface resistance of  $50 s m^{-1}$  during daytime and  $200 s m^{-1}$  during nighttime provided the best agreement with the full form of the ASCE-PM method applied on a daily basis. The advantages of adapting a specific procedure as a standardized method are (1) it provides commonality to computing  $ET_{ref}$ , and (2) the use of a standardized method enhances the transferability of crop coefficients.

The standardized ASCE-PM equation is intended to simplify and clarify the application of the method and associated equations for computing aerodynamic and bulk surface resistance ( $r_a$  and  $r_s$ , respectively). Equations were

combined into a single expression for both grass and alfalfa reference surfaces and for a 24-h or an hourly time step by varying coefficients. Computation of standardized short grass  $ET_o$  with a 24-h time step uses a grass height of 0.12 m and an  $r_s$  value of  $70 s m^{-1}$ , which is the same as for the FAO56-PM equation. For hourly time steps,  $r_s$  is set to  $50 s m^{-1}$  for daytime hours and to  $200 s m^{-1}$  for nighttime hours. The standardized ASCE-PM equation is

$$ET_{ref} = \frac{0.408 \Delta (R_n - G) + \gamma (C_n / (T + 273)) U_2 (e_s - e_a)}{[\Delta + \gamma (1 + C_d U_2)]} \quad [2]$$

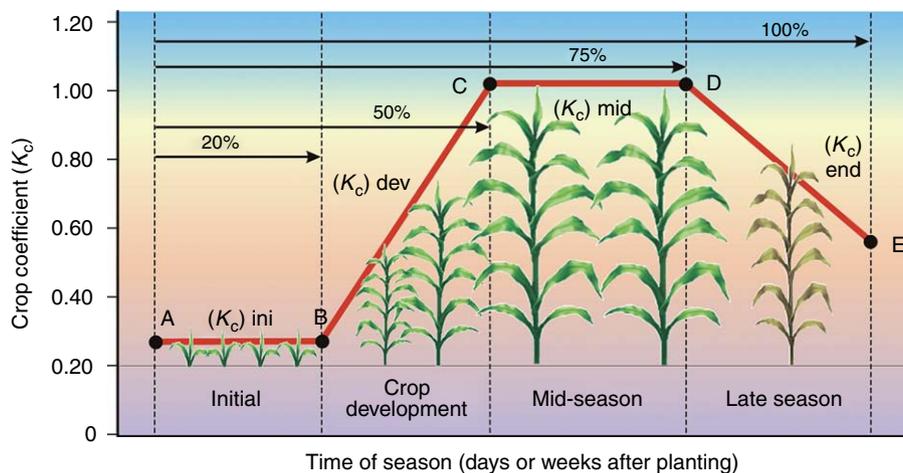
where  $ET_{ref}$  is the standardized reference ET ( $mm d^{-1}$  or  $mm h^{-1}$ ),  $\Delta$  is the slope of saturation vapor pressure versus air temperature curve ( $kPa ^\circ C^{-1}$ ),  $R_n$  is the calculated net radiation at the crop surface ( $MJ m^{-2} d^{-1}$  for 24-h time steps or  $MJ m^{-2} h^{-1}$  for hourly time steps),  $G$  is the heat flux density at the soil surface (zero for 24-h time steps or  $MJ m^{-2} h^{-1}$  for hourly time steps),  $T$  is the mean daily or hourly air temperature at 1.5–2.5 m height ( $^\circ C$ ),  $U_2$  is the mean daily or hourly wind speed at 2 m height ( $m s^{-1}$ ),  $e_s$  is the saturation vapor pressure ( $kPa$ ),  $e_a$  is the actual vapor pressure ( $kPa$ ),  $e_s - e_a$  is the vapor pressure deficit ( $kPa$ ),  $\gamma$  is the psychrometric constant ( $kPa ^\circ C^{-1}$ ),  $C_n$  is the numerator constant that changes with reference surface and calculation time step ( $C_n = 900 ^\circ C mm s^3 Mg^{-1} d^{-1}$  for 24-h time steps, and  $C_n = 37 ^\circ C mm s^3 Mg^{-1} h^{-1}$  for hourly time steps for the grass reference surface),  $C_d$  is the denominator constant that changes with reference surface and calculation time step ( $C_d = 0.34 s m^{-1}$  for 24-h time steps,  $C_d = 0.24 s m^{-1}$  for hourly time steps during daytime, and  $C_d = 0.96 s m^{-1}$  for hourly nighttime for the grass reference surface), and 0.408 is the coefficient having units of  $m^2 mm MJ^{-1}$ . The values of  $C_n$  and  $C_d$  for the grass and alfalfa reference surfaces for daily and hourly time steps are given in **Table 1**.

### Crop Coefficient Concept

The  $K_c$  is the crop coefficient for a given crop and is usually determined experimentally. The  $K_c$  values represent the integrated effects of changes in leaf area, plant

**Table 1** Values for  $C_n$  and  $C_d$  in eqn [2]

Time step	Grass reference ( $ET_o$ )		Alfalfa reference ( $ET_r$ )		Units for $ET_o$ and $ET_r$	Units for $R_n$ and $G$
	$C_n$	$C_d$	$C_n$	$C_d$		
Daily	900	0.34	1600	0.38	$mm d^{-1}$	$MJ m^{-2} d^{-1}$
Hourly during daytime	37	0.24	66	0.25	$mm h^{-1}$	$MJ m^{-2} h^{-1}$
Hourly during nighttime	37	0.96	66	1.7	$mm h^{-1}$	$MJ m^{-2} h^{-1}$



**Figure 2** Schematic representation of increase and decrease in crop coefficient based on different plant development stages.

height, crop characteristics, irrigation method, rate of crop development, crop planting date, degree of canopy cover, canopy resistance, soil and climate conditions, and management practices. Each crop will have a set of specific crop coefficient and will predict different water use for different crops for different growth stages. An example of a  $K_c$  curve as a function of days or weeks after planting for a plant for initial, development, mid-season, and end-season stages is given in [Figure 2](#).

In general, crop growth stages can be divided into four main growth stages: initial, crop development, mid-season, and late season. The length of each of these stages depends on the climate, latitude, elevation, planting date, crop type, and cultural practices. Local field observations are best for determining the growth stage of the crop and adjust the empirical  $K_c$  values accordingly. Early in the growing season, during the crop germination and establishment stage, most of the ET occurs as evaporation from the soil surface. As the crop canopy develops and covers the soil surface, evaporation from the soil surface decreases and transpiration component of the ET increases.

Early in the season when plant is small, the water-use rate and  $K_c$  value are also small ( $K_c$  initial stage) and the crop ET rate increases as the plant develops ([Figure 2](#)). For agronomical plants, the crop ET rate is at the maximum level when plant is fully developed ( $K_c$  mid-season). The ET rate decreases again when plant completes development and reaches physiological maturity towards the end of the season ( $K_c$  end season).

For perennial crops a similar pattern can occur as the plant starts to develop canopy area, grow new shoots, and develop fruit. The percentage of leaf area, soil water status, and climatic conditions will drive the rate of crop (ET) at a given growth stage. Usually, the maximum canopy cover coincides with the time of year when the solar radiation and temperature are at their peak values

(usually mid-season) and the maximum ET therefore occurs during that period. The  $K_c$  values for many different crops have been published in numerous literatures.

## Acknowledgments

This article is a contribution of the University of Nebraska-Lincoln Extension, Journal Series No. 1037. The author expresses his appreciation to Sheila Smith, illustrator in the Department of Biological Systems Engineering at the University of Nebraska-Lincoln, for her excellent technical assistance in [Figures 1 and 2](#).

See also: Soil Erosion by Water; Water Availability; Water Cycle; Water Cycle Management.

## Further Reading

- Aboukhaled A, Alfaro A, and Smith M (1982) *Lysimeters*. FAO Irrigation and Drainage Paper No. 39, 68pp. Rome, Italy: FAO.
- Allen RG, Pereira LS, Raes D, and Smith M (1998) *Crop Evapotranspiration. Guidelines for Computing Crop Water Requirements*. FAO Irrigation and Drainage Paper No. 56, 300pp. Rome, Italy: FAO.
- ASCE-EWRI (2005) The ASCE standardized reference evapotranspiration equation. In: Allen RG, Walter IA, Elliot RL, et al. (eds.) *Environmental and Water Resources Institute (EWRI) of the American Society of Civil Engineers, ASCE, Standardization of Reference Evapotranspiration Task Committee Final Report*, 213pp. Reston, VA: American Society of Civil Engineers (ASCE).
- Burman RD, Cuenca RH, and Weiss A (1983) Techniques for estimating irrigation water requirements. In: Hillel D (ed.) *Advances in Irrigation*, vol. 2. Orlando, FL: Academic Press.
- Doorenbos J and Pruitt WO (1977) Guidelines for predicting crop water requirements. *Irrigation and Drainage Paper No. 24*, 2nd edn, 144pp. Rome, Italy: FAO.
- Doorenbos J and Kassam AH (1979) *Yield Response to Water*. *Irrigation and Drainage Paper No. 33*, 193pp. Rome, Italy: FAO.
- Field WP (1990) World irrigation. *Irrigation and Drainage Systems* 4(2): 91–107.

- Hatfield JL and Fuchs M (1990) Evapotranspiration models. In: Hoffman GJ, Howell TA, and Solomon KH. (eds.) *Management of Farm Irrigation Systems*, pp. 33–59. St. Joseph, Michigan: American Society of Agricultural Engineers (ASAE).
- Irmak S, Howell TA, Allen RG, Payero JO, and Martin DL (2005) Standardized ASCE-Penman-Monteith: Impact of sum-of-hourly vs. 24-hr-timestep computations at Reference Weather Station Sites. *Transactions of the ASABE* 48(3): 1063–1077.
- Itenfisu D, Elliot RL, Allen RG, and Walter IA (2003) Comparison of reference evapotranspiration calculations as part of the ASCE standardization effort. *Journal of the Irrigation and Drainage Engineering ASCE* 129(6): 440–448.
- Johns EL (1989) Water Use by Naturally Occurring Vegetation Including an Annotated Bibliography. *ASCE Task Committee on Water Requirements of Natural Vegetation Committee on Irrigation Water Requirements*, 216pp. New York, NY: American Society of Civil Engineers (ASCE).
- Mays LW (1996) *Water Resources Handbook*. New York: McGraw-Hill.
- Penman HL (1948) Natural evaporation from open water, bare soil and grass. *Proceedings of the Royal Society of London A* 193: 120–146.
- Rosenberg NJ, Blad BL, and Verma SB (1983) *Microclimate: The Biological Environment*, 2nd edn. New York: Wiley.
- Shiklomanov I (1993) World fresh water resources. In: Gleick P (ed.) *Water in Crisis*, ch. 2, pp. 13–24. Oxford, New York: Oxford University Press.
- United States Department of Agriculture (1982) *Food-From Farm Table. 1982 Yearbook of Agriculture*, US. Washington, DC: Government Printing Office.

**Evenness Indices** See Coastal and Estuarine Environments

## Evolution of Defense Strategies

**B Schulze**, University of Basel, Basel, Switzerland

**D Spiteller**, Max Planck Institute for Chemical Ecology, Jena, Germany

© 2008 Elsevier B.V. All rights reserved.

**Introduction**  
**Counterdefense Strategies**

**Conclusions**  
**Further Reading**

### Introduction

Despite their extremely powerful defense mechanisms, many organisms still have to face attack from organisms that evolved efficient counterdefense strategies. Thus, even very well defended organisms are often victims of some specialist attackers. For instance, the marine anemones (*Palythoa* and *Zoanthus*) being protected with the highly toxic palytoxin ( $LD_{50}$  10 ng kg<sup>-1</sup>) (see Defense Strategies of Marine and Aquatic Organisms) are consumed by the fish *Alutera scripta* indicating that some species obviously have gained a counterdefense mechanism which renders them resistant against this toxin.

As general counterdefense mechanism toxins can be avoided, excreted, detoxified, or the attacking organisms are adapted to the poison. This article presents some examples for the different strategies how organisms cope with the defensive arsenal of their victims.

### Counterdefense Strategies

#### Behavioral Adaptations

Specialized behavior allows bypassing the defensive system of the attacked organism. Thus, for example, thorns

or spines do not deter all enemies because some are insensitive enough or have special techniques to ignore this type of defense.

Among herbivores some specialists prepare plant leaves before they start feeding by cutting the leaf veins or trenches in the leaf. Then they feed distant from the cuts. This ensures both a better food quality and safe feeding for the herbivore because the flow of resin, which can trap the insects or may expose them to toxic secondary metabolites in the fluid, is prevented. This specialized behavior is widespread among different insects, for example, caterpillars and beetles, indicating that it may have been acquired during evolution independently. Alternatively, some herbivores carefully concentrate their feeding between the leaf veins in order to avoid damage to plant organs that contain toxic secretions.

Similarly, herbivores feeding on plants, which contain poisonous coumarin derivatives, have developed a behavioral adaptation protecting them from the toxicity of these compounds. Coumarin derivatives are phototoxic molecules which are activated by UV-light and subsequently damage DNA molecules. Some insects have developed a so-called leaf-rolling behavior which shields them from direct sunlight during feeding. This technique