INTRODUCTION

Approximately four-tenths of the world's land surface is within the arid and semiarid zones as defined by Meigs (99). In both zones water is the major limiting factor to plant productivity. Such is the water limitation that annual net primary produc...
tivity (net dry matter gain above and below ground) ranges from 25 to 400 and 250 to 1000 g m\(^{-2}\) in the arid and semiarid zones, respectively (20, 46, 92, 110), much less than values of up to 3000 g m\(^{-2}\) for vegetation with abundant water (92). These zones are also important world sources of animal and crop production. Grazing of native vegetation is the main means by which man harvests plant production in the arid zone, while grazing of native vegetation and improved pastures and rainfed arable cropping dominate the land use of the semiarid zone. The magnitude of semiarid zone cropping, which has been described in detail by Arnon (4), can be assessed from a recent comprehensive survey of potential world food production (19). By assuming that the semiarid zone comprises those areas in which the calculated ratio of actual crop transpiration to potential crop transpiration (i.e. with unlimited water supply) during the growing season was between 0.2 and 0.5, this survey indicates that 32% of the world's total potential arable land, after unsuitable soils and topography have been excluded, lies in the semiarid zone. The semiarid proportion of present-day arable land is probably higher than this figure. Thus our review will emphasize the productivity of crops and pastures as well as that of natural ecosystems. Joint consideration of natural and agricultural plant communities is also desirable because of the continual interchange of concepts between people studying the two communities, and because many of our cultivated species evolved, and still have relatives in, natural ecosystems of the semiarid zone.

In this review we consider the factors determining plant productivity in arid and semiarid zone communities. While recognizing that salinity, temperature extremes, and low soil nutrient content may limit productivity in some arid and semiarid ecosystems, we will place our emphasis on the water restraint to plant productivity. Although plant responses and adaptation to water shortage have received growing attention from physiologists in recent years (9, 17, 69–71, 87, 88, 91, 146, 152, 161, 162), the relevance of some of the physiological information presented to the productivity of plant communities in the field is not evident. Our review will be concerned explicity with the field community level of organization, and only explores at lower levels those physiological processes which appear to be of major importance for community productivity. As such it complements another review in this series, one in which light limitation of community productivity in water nonlimiting situations was emphasized (94). Furthermore, we give particular attention to genotypically determined differences in strategies for maximizing performance under water-limited conditions. Because of the broad view taken, we draw heavily upon the aforementioned reviews and upon recent reviews of research in natural ecosystems (20, 27, 41, 46–48, 110, 138). Many primary source references are to be found in these reviews.

ENVIRONMENTAL CONTEXT

The definition of arid and semiarid zones by Meigs (99) uses the Thornthwaite moisture index based on mean monthly precipitation and evaporation. Upon this moisture-based classification there can be superimposed divisions according to latitude, temperature, and season when precipitation is likely to occur. As a result, four
major regions of arid and semiarid vegetation are distinguished. The names we shall use for these regions and their approximate features are as follows:

(i) Savanna, latitude 0° to 20°, dry winter, wet summer growing season.
(ii) Transition, latitude 20° to 35°, rain and growth in summer and winter, or at any time of the year.
(iii) Mediterranean, latitude 30° to 40°, dry summer, wet winter and spring growing season.
(iv) Steppe, latitude 40° to 50°, cold winter, spring, and/or summer growing season.

The approximate annual rainfall totals delineating the semiarid zone within each region are 400 to 800 mm (i and ii) and 250 to 500 mm (iii and iv) (99). The transition region, of unfortunate title, is nevertheless of considerable importance, occurring in central Argentina, central and eastern Australia, and southwest United States; the occurrence of the other regions and their plant communities is described elsewhere (e.g. 4, 171).

The pattern of water availability to plants, and the strategies adopted by plants, show unique features in each of the four regions listed. Because of the variability of rainfall between and within years, the best way of summarizing water availability is not through long-term averages, but rather through dynamic models of the soil water balance. Long runs (say 50 years) of precipitation and evaporation data are used to derive probabilistic statements about the availability of water to plants (143). For a given plant community, soil type, and root zone storage, such models calculate the change in soil water each 5 to 10 days based on precipitation, estimated runoff, and evapotranspiration as a function of evaporation, vegetation stage following the onset of growth, and soil water deficit (see Transpiration Modulation).

In the savanna and mediterranean regions, the most relevant information is not simply the mean rainfall, but the variability of the duration of the rainfall-determined growing season. For example, at Katherine, on the wetter edge of Australia's semiarid savanna region (latitude 14°S; annual rainfall 900 mm), in one-tenth of the years the growing season for crops is less than 66% of its mean value of 21 weeks (143). At drier savanna localities the variability is even greater (54, 98). In the mediterranean region, growing season duration may be less variable: at Lock in southern Australia (latitude 33°S; annual rainfall 400 mm) in one-tenth of the years, the duration of the growing season was less than 82% of the mean duration of 26 weeks (J. R. McAlpine, unpublished). Other features of the mediterranean region are that temperatures are low enough to slow growth in winter, and daily evaporation rates are generally low. However, the mediterranean growing season draws to a close when temperature, solar radiation, and evaporation are all rising rapidly, whereas in the savanna region these variables are usually steady as the wet season terminates, and the period of greatest evaporation occurs at the onset of the wet season.

A well-defined wet season does not preclude the possibility of periods of water shortage within the wet season. Estimations of their probable occurrence and duration are possible with soil water budgeting. For example, for a crop like sorghum
at Katherine, a period of water shortage, with available soil water less than 75% of maximum for at least 3 consecutive weeks, can be expected once within each growing season (143). Again the mediterranean region appears less variable, for the probability of such water shortage within any growing season is less than 0.2 at Lock. However, shorter dry spells are common in both regions after the opening rains (false starts) and can have important effects on productivity via reduced or differential establishment of annual pasture species (157, 166). The probability in any year at Lock of false starts after the autumn equinox, when temperatures would favor the germination of most winter annuals, was 0.4.

The transition region has the possibility of growth and nongrowth periods at any time of the year. This calls for great flexibility of response by vegetation, and the presence of winter and summer growing species. Although lower evaporation increases the duration of growth periods for given amounts of precipitation during the winter (54), soil water budgeting suggests that semiarid transition conditions also favor flexible or opportunistic farming strategies (11).

In the steppe region, soil water models have also been developed (5, 23, 35, 131) but do not appear to have been used to summarize patterns of water availability in the above manner. Two unique features of this zone are that some precipitation occurs as snow, and that the growing season usually begins with a substantial amount of available water in the soil being controlled not by water, but by the rise in soil temperature in the spring. Furthermore, high soil water deficits and evaporation rates in the long summer days usually terminate or seriously interrupt the growing season during the summer, but some growth may occur in the autumn.

In all regions, man may increase the water available to his crops by fallowing during preceding wet periods or seasons. Usually only about 20% of precipitation is conserved, but the extra water at seeding can guarantee crop establishment at the optimum seeding date, and may increase the mean and decrease the variability of expected yields (4a). In the mediterranean and especially savanna regions, soil moisture conserved by the end of the wet season can be sufficient for a dry season crop, supplied at times entirely by this stored moisture (4a, 15). Soil moisture budgeting is well suited to predict the gains in crop productivity to be expected from fallowing (5, 11).

PLANT LIFE FORMS AND PRODUCTIVITY MODELS

The life cycle of plants in water-limited environments is usefully summarized in terms of the pulse-reserve model of ecologists (173), in which a pulse of carbon assimilation is triggered by an input of water. This results in the production of a reserve of reduced carbon to maintain the species during the rainless or drought period following the exhaustion of the water, and to facilitate its response to the next input of water sufficient to trigger assimilation.

Most classifications of life forms consider both the synchrony between the input of water and the pulse of assimilation, and the reserve form in which the plants
survive. We shall exclude consideration of lower plants, such as lichens, and only refer to two main groups of higher plants which can be recognized, namely the aridopassive and the aridoactive groups (47). The aridopassive group generally carry no active photosynthetic tissue through the long dry periods which separate wet periods, while the aridoactive plants usually retain photosynthetic tissue and exhibit some, often very limited, photosynthetic activity during the dry period. Figure 1 illustrates the pattern of transpiration that might be expected for these two vegetation types in an arid mediterranean region.

Aridopassive plants tend to have an assimilation pulse closely in phase with the water input. The group includes annual plants, with seeds as their only reserve form, herbaceous perennials with storage organs such as rhizomes, bulbs, etc at or below the soil surface, and the so-called drought deciduous woody perennials. The aridoactive group comprises woody evergreen perennials, which maintain all or at least part of their green tissue during the dry season and are the true xerophytes, and succulents, which have substantial reserves of water in swollen stems and leaves and usually crassulacean acid metabolism (CAM) (see 115).

![Figure 1](image_url)

*Figure 1* Probable annual distribution of daily transpiration for communities of aridopassive (T1) and aridoactive (T2) plants in a semiarid mediterranean region in the northern hemisphere, using typical values of monthly precipitation (P) and daily free water evaporation (E₀) for a given year. The areas under both transpiration curves equals 170 mm, compared to the precipitation total of 260 mm. The broken portion of each transpiration curve indicates periods when soil water limits transpiration.
Distribution of these life forms in natural ecosystems is discussed in many ecological texts (e.g. 171). It suffices here to point to some broad patterns. Annuals contribute most to productivity in the more arid parts of all regions except the steppes, although in very dry years their contribution may be zero (46, 105, 114). Herbaceous perennials, in particular the grasses, often dominate the drier portions of the semiarid zone, especially in the savanna and steppe regions (20). Many semiarid Mediterranean shrubs and shrubs and trees of the savanna region adopt the drought deciduous strategy. Woody evergreens occur in most arid regions, but are strikingly dominant in the sclerophyllous vegetation of semiarid Mediterranean (41, 100) and arid and semiarid transition regions (28, 123, 147). Plants exhibiting CAM tend to be found in arid areas and may be favored by low night temperatures (20, 102, 115).

Domesticated grazing animals in natural ecosystems rely largely on the production of herbaceous annuals and perennials (20) and of some evergreen shrublands (147), while most sown pasture species are annual or perennial grasses or legumes. Furthermore, most crop plants are annuals or weakly perennial. In fact, at least 90% of the total crop production of semiarid regions derives from four cereals, namely: wheat (Triticum spp.), barley (Hordeum spp.), sorghum (Sorghum spp.) and the millets; cotton (Gossypium spp.), oilseeds, and leguminous pulses make up the remainder.

The terms aridoactive and aridopassive highlight life form during the survival phase, but we must emphasize that this phase contributes little directly to productivity when compared to the assimilation phase which is linked to the water input. Simple productivity models have in fact expressed annual or seasonal productivity as a function of total precipitation input (92, 150, 171). More accurate models have recognized that the water loss by the vegetation is the important component of precipitation and have related productivity to total evapotranspiration (1, 5, 61, 73, 92, 150), or for grain crops in particular, to the ratio of actual to potential evapotranspiration (11, 150). Finally, a number of productivity models have used total transpiration, rather than evapotranspiration, as the independent moisture variable (37a, 65).

The use of transpiration ($T$) as the central factor in explaining the influence of water limitation on productivity depends on the recognition of the inevitable association between water loss and CO$_2$ assimilation by terrestrial plants. This approach contrasts with models which attempt primarily to quantify water levels in plants, the amount of time when the plant is "nonstressed," and/or the rate of assimilation as a function of the stress level (e.g. 17a, 22, 98, 128). Central to the former approach is the belief that water use efficiency ($WUE$), meaning the ratio of assimilation to transpiration, is a reasonably predictable function of vegetation and environment. Thus dry matter production ($DM$) over a given period is as follows:

$$DM = T \cdot WUE$$

where $T$ is total transpiration for the period and $WUE$ the mean water use efficiency.

For long growth periods it is important to recognize that total dry matter production is given by the sum of $T \cdot WUE$ over shorter periods (e.g. days, weeks) compris-
ing the long period. Also, over long periods a full understanding of productivity
requires consideration of how each increment of dry matter is allocated to the
various growing sinks (e.g. leaves, roots, seeds, etc). Thus:

\[ DM = f(T, WUE, F) \]  

where \( F \) refers to the allocation or partitioning of assimilate.

We shall adopt the approach represented by Equation 2 to discuss the determina-
tion of water-limited plant productivity. It is essentially that used by van Keulen
(166) in a recent comprehensive effort to model the productivity of annual pastures
in a semiarid mediterranean region. Its usefulness depends on the relative physiolog-
ic independence of the three determinants, \( T, WUE, \) and \( F \), a point to which we
will return in the last section dealing with integration. An additional advantage of
the inclusion of \( F \) in Equation 2 is that it leads logically to the concept of harvest
index, which is the economic yield, for example grain yield or digestible dry matter,
as a proportion of the total above ground dry matter. Harvest index is an important
aspect of yield determination in crops and pastures (4a, 38, 119).

**TRANSPIRATION**

The maximizing on a seasonal or annual basis of the ratio of transpiration to total
water supply is an important consideration for plant communities of arid and
semiarid zones (110, 141), because productivity is proportional to transpiration if
\( WUE \) is constant (Equation 1). The transpiration \( (T) \) of a plant community over
a given time period is as follows:

\[ T = P - R - E_S - \Delta S \]  

where \( P \) is precipitation (rainfall plus snowfall), \( R \) is the net runoff, \( E_s \) is the soil
evaporation, and \( \Delta S \) is the change in soil water in the root zone. The term evapo-
transpiration \( (ET = T + E_s) \) will also be used. Equation 3 ignores movement of
water below the root zone (drainage or, conversely, upward flow from water tables,
etc), interception of fog and mist, dew, evaporation of water intercepted by vegeta-
tion, and foliar absorption of moisture (133). Losses through drainage may be
important in wetter semiarid situations, but the other components ignored are
generally too small to be of any consequence for the productivity of higher plants
in all but exceptional situations.

**Runoff**

The proportion of rainfall available for transpiration is increased by minimizing
runoff and maximizing infiltration of rain into the soil. Despite low rainfall in dry
regions, rainfall intensity is often sufficient to cause runoff, especially with summer
rainfall. This leads to runon elsewhere and an important horizontal redistribution
of water and plant productivity on a microtopographic scale, i.e. within one meter,
as well as mesotopographic one. The latter effect can be seen from the greater density
of vegetation along drainage lines. Microrelief, through the favoring of runoff and
runon, may actually increase the overall plant productivity of annual mediterranean
pastures in dry seasons by reducing soil evaporation and providing more favorable microhabitats for seedling establishment (166). Man has taken advantage of such effects by constructing small watersheds in arid regions (48) and by forming inter-row ridges treated to encourage runoff in row crops such as cotton and sorghum (56). Plants and their litter can substantially reduce runoff by increasing infiltration rates (e.g. 4a, 170), and can trap runon. One example is the natural occurrence of contour-oriented groves of mulga (*Acacia aneura*) in arid central Australia; these groves trap runon from the adjacent intergroves (147).

Another form of water redistribution of particular advantage in arid regions is stem flow in trees and large shrubs adapted to intercept precipitation and channel it down branches to the stem. For example, when rainfall events exceeded 12 mm, stem flow in *Acacia aneura* amounted to 40% of the rain falling on the canopy (142).

**Soil Evaporation**

Soil evaporation \( (E_s) \), representing the loss of water which could have been transpired and hence contributed to productivity, is a major component of Equation 3 in dry regions. This is because the plant cover is usually incomplete, and because a relatively large proportion of the rainfall, especially in the mediterranean zone, comes in light falls. Soil evaporation in plant communities has been reviewed elsewhere (154, 166). When the soil surface is wet, \( E_s \) depends largely upon the radiation reaching the soil surface and hence upon the plant cover or leaf area index \((LAI)\). As the surface dries, the moisture content and water conductivity characteristics, and hence texture, of the uppermost soil layer control \( E_s \) (154). Thus the importance of cover is greatest when the soil surface is wet. For example, in a typical crop of wheat calculations suggest that \( E_s \) falls from 50% of \( ET \) at \( LAI = 1.5 \) to less than 10% at \( LAI = 4 \); however, since \( T \) rises with increased \( LAI \), \( ET \) is largely independent of \( LAI \) when the soil surface is wet (36). Furthermore, at a given \( LAI \), \( T \) was little affected by whether the soil surface was wet (\( E_s \) maximal) or very dry (\( E_s \) zero). The effect of soil texture is such that under intermittent rainfall regimes of dry regions, the cumulative loss due to \( E_s \) is least with coarse textured soil surfaces such as sands and gravels; because of their low water holding capacity, they retain less water in the surface zone subject to most evaporative losses. When rainfall is low, the favoring of productivity by this aspect of such soils has long been recognized (110, 171).

For plant communities over sufficiently long time periods, \( E_s \) can be calculated as part of a soil water budgeting procedure. For example, in a mixed grass prairie in Oklahoma (precipitation = 700 mm, heavy surface texture), the estimated \( E_s \) over one year was about one-half of \( ET \); despite allowance for a reduction of \( E_s \) by the mulch of dead plant material common in such grasslands (131). For shrub steppe communities in the western United States, \( E_s \) estimates range from 23% of \( ET \) [Artemisia tridentata community, precipitation 350 mm (23)] to near 50% of \( ET \) [Atriplex confertifolia, precipitation 250 mm (22)]. At a mediterranean site in Israel (mean annual rainfall 250 mm, fine sandy surface texture), van Keulen (166) calculated that total \( E_s \) averaged 38% of total growing season \( ET \) over 3 years in fertilized annual pastures. The evaporative loss in each year depended very much
on rainfall distribution, ranging from under 30% to over 50%. Moreover, it was predicted that seasonal productivity would increase 40% as a result of reduced $E_t$ losses if the average seasonal rainfall was distributed in half the average number of wet days. Estimates at Akron, Colorado, suggest that $E_t$ losses are also high for unirrigated crops, varying from 30 to 40% of total ET for winter wheat and 20 to 40% for summer sorghum (65).

Despite the importance of $E_t$ in reducing the fraction of precipitation available for transpiration and production by plant communities, the options available to minimize this loss appear to be limited. The horizontal redistribution of water resulting in deeper water infiltration around certain plants has already been mentioned. The rapid establishment of full cover by plants should reduce $E_t$ losses. A high density of active roots in the uppermost layer of soil, competing for water with evaporation, could be a useful mechanism and does seem to be characteristic of some cacti (108, 115, 156). However, there appear to be no measurements, as distinct from estimations, of the proportion of $T$ to $E_t$ losses from the uppermost soil layer. Also, in undisturbed soils, mosses and lichens often cover the soil surface in the wet season (110) and must make use of water that otherwise would have been lost by evaporation.

**Change in Soil Water**

Before considering the importance of the change in soil water, it is useful to point out that, based on soil water potential ($\psi_{soil}$) alone, the available water (i.e. that between $-0.3$ and $-15$ bars) ranges from 70 mm (sand) to 240 mm (silt loam) per meter (133). On the other hand, some prefer to define the maximum storage capacity of the root zone as the difference between the highest and lowest water contents ever measured in the whole profile under the particular community (e.g. 76, 130, 131). On favorable soils this quantity can be as high as 250 mm for sorghum and cotton (15, 130) and higher still for perennials [e.g. 325 mm for *Artemisia tridentata* (23)].

If maximizing transpiration as a fraction of rainfall is a goal for ecosystems in dry regions, then those dominated by perennials, in particular aridoactive species, should continue to transpire into the dry season until there is little soil water available (Figure 1). Change in soil water in the root zone ($\Delta S$ of Equation 3) from before until after the growing season is therefore likely to be small. An exception to this would be steppe communities, since soil water accumulates before the onset of growth in the spring.

It is also likely that the depth of the root zone of perennial communities extends to the greatest depth of the wetting front (7, 23, 35, 110). The depth of wetting in the arid and semiarid zones will depend on soil type and rainfall distribution, but most soil water measurements (22, 23, 35, 123, 149) point to minimal water movement below depths to which perennials could reasonably be expected to root (ranging from 1.5 m in heavy soils to 5 m on sandy soils). Soil water budgeting (e.g. 54, 98) suggests that if the available water storage capacity in the root zone is 100 to 150 mm, this is sufficient to prevent deep drainage losses and maximize water available for transpiration in most situations without fallow periods. Soils with physical or chemical barriers to root penetration may have a lower storage capacity.
than 100 mm, leading to the possibility of drainage and runoff losses, reduced transpiration, and reduced productivity (e.g. 98).

What has been said with respect to root depth does not contradict the observation that there may be available soil water below the root zone in some perennial communities (e.g. 76, 131). This is likely to be water accumulated in exceptionally wet seasons, and of little importance for sustained productivity, but of some importance for the short-term productivity of deeper-rooted introduced species such as alfalfa (*Medicago sativa*) and perhaps of great importance for survival of aridoactive shrubs and trees. In mixed communities, only these last-mentioned plants, plus any perennial grass components, will root deeply; the roots of neighboring ephemerals or drought-deciduous perennials are likely to exploit a shallower portion of the profile (23, 100, 110, 122), while succulents appear to have very shallow roots [no deeper than 15 cm in the barrel cactus *Ferocactus acanthodes* (108)]. Some aridoactive species have been reported to reduce \( \psi_{\text{soil}} \) to as low as \(-100\) bars or more (110). This requires \( \psi_{\text{plant}} \) to be even lower: the phenomenon is, however, only likely to be of importance for survival and not for productivity because the extra water obtained below a more common lower limit for aridopassive species of \(-20\) to \(-40\) bars is small in most soils. Salinity, which is common in arid zone soils, also complicates water extraction at very low \( \psi_{\text{soil}} \) (110).

There are aspects of \( \Delta S \) over a growing season which apply more specifically to annual plant communities, in particular to crops. With the latter, substantial available soil water is often present at sowing as a result of fallowing; an important fraction, and at times all, of the crop's transpiration can be attributed to \( \Delta S \). The situation at the end of the growing season appears to vary. In many cases crops and pastures, like perennial communities, use most or all of the available water in the soil (e.g. 1, 51). In other situations, where the profile has been wet to a considerable depth, as through fallowing, not all this water may be used, and associated with this there can be differences in seasonal \( \Delta S \) between crop species (e.g. 130), cultivars (e.g. 15, 72), and fertilizer levels (4a). These differences probably reflect differences in rooting depth and/or density. More extensive rooting may be associated with greater long-term crop productivity, provided the extra transpiration gained is at the expense of water which otherwise would have been lost to other plants. Annual mediterranean pasture and wheat crops can, on occasions, leave considerable available water in the root zone at maturity because of early maturity and/or rain near maturity, or low soil fertility (61, 166). In the long term, such water is probably lost to the ecosystem via soil evaporation and deep drainage. The increase in underground flow when the natural sclerophyllous vegetation of semiarid mediterranean regions is converted into annual crop and pasture is well known.

**Transpiration Modulation**

We have described factors influencing seasonal transpiration as a fraction of the growing season water input. This fraction, and hence total seasonal transpiration, is largely beyond the control of the vegetation, but plants have a more substantial role in modulating the use of this water throughout the season, with some important
consequences for productivity. We will emphasize the strategies adopted by plants rather than the short-term mechanics of transpiration control, since the latter subject has been reviewed extensively (30, 31, 75, 133).

To discuss transpiration control it is useful to define potential transpiration ($T_p$), i.e. the transpiration of vegetation when the root zone water content is high and stomatal resistances are minimal, and actual transpiration ($T_a$), meaning transpiration when root zone water may be limiting; obviously $T_a \leq T_p$. This definition of $T_p$ does not specify full plant cover as a necessary condition; plant cover is more usually incomplete in dry regions. As an index of the evaporative demand of the environment independent of vegetation type, $E_o$ or free water evaporation is used. Also for simplicity we neglect $E_s$ in this subsection, while recognizing that it will be contributing to the overall water use ($ET$) of the community.

The proportion of solar radiation intercepted by green tissue or, more loosely, the plant cover, is the major determinant of the ratio $T_p/E_o$; at full interception this can be close to or even greater than 1.0 Change in leaf area or cover is also the main means by which most plant communities adjust $T_a/E_o$ on a long-term basis. The reflective properties and aerodynamic roughness of the vegetation can have small effects on $T_p/E_o$, as also can the minimum leaf diffusive resistances to water vapor (i.e. with wet soil and presumably high leaf water potential, $\psi_{leaf}$). The ratio $T_a/T_p$ equals 1.0 in wet soil but falls below 1.0 at some point during soil drying, the major direct cause of this fall being stomatal closing and increased leaf diffusive resistance. In this context stomata close primarily in response to declining $\psi_{leaf}$ (160), although other factors including hormones such as abscisic acid and cytokinins may also be involved (74, 124). In turn, $\psi_{leaf}$ depends on $\psi_{soil}$ in the root zone, resistances to liquid water flow in the rhizosphere, roots, stems, petioles, and leaves, and on the potential atmospheric demand ($E_o$) (30, 75). It is now recognized that the resistances to water flow in the plant can be substantial, in particular in the roots (21, 62, 107, 127), where they can exceed resistances in the soil or rhizosphere at commonly encountered root densities and all but low bulk soil water potentials in most soils ($\leq -8$ to $-10$ bars). Plants, through control of these resistances, can influence $\psi_{leaf}$ at any given $\psi_{soil}$ and given water flux through the plant. This effect, combined with the sensitivity of stomata to $\psi_{leaf}$, provides the major way in which plants control $T_a/T_p$. Other changes in leaves in response to lowered $\psi_{leaf}$, such as increased reflectivity (e.g. 44), leaf rolling (e.g. 128), passive leaf flagging, and active leaf movement (9) will also have small effects on $T_a/T_p$. Considerable attention has been given by both ecologists and crop physiologists to determining the exact form of the relationship of $T_a/T_p$ to $\psi_{soil}$, or more commonly to the fraction of available water left in the root zone (e.g. 76, 129, 133, 149), a question to which we shall return.

The contrasting strategies of aridoactive and aridopassive vegetation for using given total amounts of seasonal transpiration were illustrated in Figure 1. Obviously, over a whole year $T_a < T_p$ and $T_p \leq E_o$, but for productivity it is important to understand these relationships within the growing season. Turning first to the case of aridoactive shrubs and trees in the arid zone, ecologists have emphasized that the transpirational surface reaches a maximum at or soon after the end of the wet season, after which it is reduced substantially as the dry season proceeds, only to
increase again with the onset of the next wet season, unless this latter increase is delayed by winter cold (37, 47, 114, 171). It may be expected that $T_p/E_o$ follows a similar pattern. The decrease in transpirational area during the dry season comes about through the abscission and death of green tissue and the replacement of large leaves with smaller more xeromorphic leaves (23, 37, 47, 113), presumably in response to decreasing $\psi_{\text{plant}}$ (23). At the same time $T_a/T_p$ is likely to fall, and the net effect is that $T_a$ in the dry season is less than the expression “aridoactive” might imply. For example, in the case of each of three shrub species in the Negev, a winter-rainfall desert, at least 90% of the annual transpiration occurred in winter and spring when the rain was received, and about 70% in the months of February, March, and April (47). Summer and autumn transpiration was clearly of little significance to productivity. The heavy investment of some arid shrub communities in new roots each growing season (e.g. 21) also suggests emphasis on extracting soil water as rapidly as $T_p$ demands for as long as possible. Similarly, the ability of stomata of desert shrubs (e.g. 137) and of sclerophylls (e.g. 159) to remain partly open until very low values of $\psi_{\text{leaf}}$ (< - 50 bars) fits this strategy.

In the semiarid zone as distinct from the arid zone, aridoactive shrubs and trees, especially the sclerophyllous vegetation of the Mediterranean zone, do not generally show large seasonal leaf area changes, having a leaf area corresponding to the expectancy of precipitation (100, 148). Also, some measurements suggest that $T_a/T_p$ of sclerophyllous vegetation is especially sensitive to soil water, falling linearly from 1.0 to zero as the fraction of root zone available water falls from 1.0 to zero (e.g. 123, 149). It has been proposed that this is a conservative strategy to avoid the possibility of complete exhaustion of soil water (148). It is not clear, however, whether this behavior is any different from that generally reported for the Californian and Chilean Mediterranean sclerophyllous vegetation, where transpiration appears to proceed at high rates until by midsummer most of the soil water has been used: $\psi_{\text{leaf}}$ falls to moderately low levels (< - 30 bars) before stomata close (100, 122). High minimal leaf resistances (at high $\psi_{\text{leaf}}$) and high cuticular resistances to water loss are other common features of sclerophyllous leaves (27, 41, 122).

Another distinctive group of aridoactive plants are the succulents for which green area also changes little if at all during long dry periods. Nevertheless, their stomata appear to close tightly when $\psi_{\text{leaf}}$ falls below quite high values [e.g. -4 bars in barrel cactus (108)], and cuticular resistance to water loss is extremely high (156). Given this and their shallow roots, it is likely that $T_a/T_p$ approaches zero soon after the surface soil dries and transpiration, and hence assimilation of external CO$_2$, is closely confined to wet periods. At the same time they respond rapidly to rain; for example, full stomatal opening was achieved within 2 days of drought-breaking rain in barrel cactus (108).

Turning to aridopassive vegetation and especially annual crops and pastures, leaf area increases rapidly with the onset of the wet season unless growth is limited by winter cold. If the water input is substantial (e.g. > 100–200 mm), complete cover is approached and $T_p$ is close to $E_o$ (Figure 1). However, as mentioned before, there is the possibility of water deficiency within the expected growing season, plus the
probability that deficiency will terminate the growing season. During both types of
stress, it appears that these plants behave so as to maximize the period during which
\( T_a/T_p \) is equal to 1.0. For example, it has recently been argued that, notwithstanding
the multiplicity of published relationships (e.g. 76, 133), most crops and pastures
appear to show maintenance of \( T_a/T_p \) at 1.0 until the available water fraction of
the root zone falls below 0.3 (129). This is achieved by having high root densities
(e.g. 62, 107), rapid extension of roots into wetter deeper soil (e.g. 130), and a
lowering of the \( \psi_{leaf} \) for stomatal closure (e.g. 81, 82, 161). These plants usually show
sharp stomatal closing at a critical \( \psi_{leaf} \) at which leaf turgor is close to zero (160).
However, with slow drying typical of field situations, extra osmotic solutes accumu­
late in the leaf (osmotic adjustment) so that the critical \( \psi_{leaf} \) for stomatal closing can
be lower than -20 bars in, for example, cotton (82) or sorghum (81). Meaningful
comparisons between genotypes must permit the full expression of osmotic adjust­
ment; such comparisons do point to species differences in the critical \( \psi_{leaf} \) for
stomatal closure (160), but only to small differences among cultivars, at least with
sorghum (66).

In aridopassive plants, \( T_p \) changes during periods of water limitation are usually
not considered explicitly because it is simpler to consider only changes in \( T_e/T_o \).
Nevertheless, it has been pointed out that leaf area reduction (\( T_p \) reduction) is an
important adaptive response to water limitation (9, 87, 162). In early stages of
ontogeny (i.e. before flowering), this arises largely because of the great sensitivity
of leaf area growth to reduced leaf turgor, and hence reduced \( \psi_{leaf} \) (9, 162). As
development proceeds, the stimulation of leaf senescence or leaf abscission or both
by lowered \( \psi_{leaf} \) becomes the major means by which leaf area is reduced (e.g. 50,
52, 162), although recently it has been argued that lowered \( \psi_{leaf} \) stimulates leaf death
rather than leaf senescence, which may in fact be suspended by water deficit (94a).

There has been considerable discussion of the strategies annual plants may adopt
with respect to transpiration control in the face of soil water shortage (e.g. 63, 66).
It can be suggested that the water conservative strategy (sensitive stomata resulting
from a high critical \( \psi_{leaf} \)) may be better for short periods of shortage, for example
within the growing season, because it lessens the reduction in \( \psi_{leaf} \) and resultant
deleterious effects on leaf area or yield processes. Nevertheless, the general pattern
of behavior described seems to be the opposite of a conservative strategy, namely,
transpiration is maintained at the risk of complete soil water exhaustion, very low
\( \psi_{plant} \), and serious damage. This behavior may have been favored by natural selection
in competitive situations (e.g. 25) and may be appropriate for crop plants in the final
phase of their life cycle, since available water in the soil at maturity represents lost
opportunity for photosynthesis. Nevertheless, looking at overall strategies, Passi­
ourea (117, 119) argues for breeding for more water conservative behavior in crop
plants, and suggests that in wheat this may be based on selection for higher resis­
tances in the seminal roots to water flow. With the probable future discovery of more
genotypic differences in the various processes controlling transpiration, opportuni­
ties for crop breeders and physiologists to test these various hypotheses will develop
eventually.
Plant Water Potential and Survival

During very dry periods, the transpiration of aridoactive plants drops to very low levels. It is probably better then to consider plant behavior in terms of survival rather than production, although the amount of tissue which survives these dry periods will of course influence recovery and production when water again becomes available. Even with succulents, which conserve tissue water and carbon very efficiently (115, 156), the level to which $\psi_{\text{leaf}}$ falls appears to govern leaf survival. At the same time, leaves with a small change in water content per bar decrease in $\psi_{\text{leaf}}$, such as relatively inelastic sclerophylls (41), can tolerate very low levels of $\psi_{\text{leaf}}$ (111). On the other hand, it is often stated that continued transpiration and assimilation, albeit at very low levels, and hence root access to some reserves of soil water, are necessary for survival of aridoactive species. Despite this, some sclerophyllous trees can survive several months of negative carbon balance during severe summer drought (e.g. 41), and it is possible that carbon reserves in these plants can substitute for continued assimilation and threatened dessication.

Consideration of survival mechanisms in plants with photosynthetic tissue is also important in the case of seedlings of pasture plants. As pointed out before, short but severe droughts are common after the first germinating rains of the wet season. A water conservative strategy to avoid low $\psi_{\text{plant}}$ appears to be the most important means of increasing the probability of seedling survival (e.g. 157, 174).

WATER USE EFFICIENCY

The second major aspect of plant productivity that we wish to discuss is water use efficiency ($WUE$), considered here initially as the net CO₂ uptake per unit of transpiration (mgCO₂ gH₂O⁻¹), and which can be determined with gas exchange measurements of illuminated photosynthetic tissue. It is appropriate to begin the discussion at the single leaf level because the theory of CO₂ and H₂O exchange at this level is reasonably well understood (31, 32, 58, 80, 116). More importantly, both theory and measurements suggest that relative differences in $WUE$ at the leaf level are reflected largely unchanged at the canopy level and in terms of dry matter gain per unit water lost, as we shall see later. It is interesting to contrast this situation in respect of $WUE$ with that for photosynthetic efficiency, where the great superiority of C₄ plants at the enzyme and leaf level is steadily eroded as one proceeds to the level of canopies and crop growth rates (59).

$WUE$ Determined by Gas Exchange

**SINGLE LEAF**  The important environmental and genotypic influences on $WUE$ are summarized in the following equation:

$$WUE = \Delta c \cdot D_c \left( r_a + r_s / \Delta e \cdot D_e \left( r_a + r_s + r_i \right) \right)$$

where $\Delta c$ and $\Delta e$ are the leaf-to-air concentration differences for CO₂ and water vapor, respectively; $D_c$ and $D_e$ the diffusivities of CO₂ and water vapor, respectively; and $r_a$, $r_s$ and $r_i$ the boundary layer, stomatal, and internal resistances to diffusion,
respectively. Equation 4 assumes that CO₂ and water vapor take identical paths between the leaf cell walls and bulk air, therefore ignoring the cuticular pathway of water loss.

It is sufficient for our purposes to assume that the CO₂ concentration at the chloroplast is zero. This means that the \( r_i \) term of Equation 4 includes photorespiratory effects as well as other apparent and actual internal diffusive resistances to CO₂. As a result, \( \Delta c \) equals the concentration of CO₂ in the atmosphere, 0.58 mg l⁻¹ at 25°C. Assuming \( D_e/D_c \) is 0.6, Equation 4 simplifies to:

\[
WUE = \left( \frac{360}{\Delta e} \right) \frac{(r_o + r_s)}{(r_a + r_s + r_o)}
\]

with \( WUE \) in units of mgCO₂ gH₂O⁻¹ and \( \Delta e \) mg l⁻¹. The intercellular air spaces of the leaf are assumed to be saturated with water vapor at the leaf temperature. It should be pointed out that for reasons intrinsic in the model upon which Equation 4 is based, \( r_s \) and \( r_i \) are not entirely independent (31) and, more significantly, nor are \( \Delta e \) and \( (r_o + r_s) \) independent. This latter complication arises because \( \Delta e \) depends on leaf temperature. Leaf temperature in turn depends on the leaf energy balance, one determinant of which is the influence of \( r_o \) and \( r_s \) on latent and convective heat transfer (31, 58, 80, 116). We shall return to this problem when discussing the influence of changes in \( r_s \) and \( r_o \) on \( WUE \).

The highest \( WUE \) which might be expected under any conditions can be calculated by assuming in Equation 5 that \( r_i \) is zero (ininitely high photosynthetic affinity for CO₂). At a leaf and air temperature of 25°C and an air relative humidity of 50% (air saturation deficit of 12 mg l⁻¹) the \( WUE \) would be 30 mgCO₂ gH₂O⁻¹. In reality, with the exception of plants practicing CAM, \( WUE \) values are usually substantially lower than this.

Of the environmental factors influencing \( WUE \), air saturation deficit through its influence on vapor concentration in the air, and hence \( \Delta e \), has a major effect on \( WUE \). From theory (Equation 5) and measurement (14, 125), \( WUE \) is linearly related to the reciprocal of \( \Delta e \), other things remaining equal, and thus decreases as the saturation deficit increases. Air saturation deficit varies diurnally, from day to day, seasonally and regionally, depending on air temperature and absolute humidity of the air. Midday values encountered by arid and semiarid zone plants may range from 10 mg l⁻¹ to as high as 60 mg l⁻¹ under hot dry conditions. The major influence of air temperature on \( WUE \) operates via its effects on \( \Delta e \); \( \Delta e \) is usually closely coupled to air temperature in the field (137). Thus increased air temperature reduces \( WUE \), unless leaf temperature is markedly suboptimal for photosynthesis as it may be in mediterranean environments in the winter (100).

The importance of another environmental variable, incident irradiance, is seen without recourse to Equation 5. It derives from the fact that transpiration is always positive, showing a relationship which is linear or curvilinear upward with increasing irradiance, because of rising leaf temperature and falling \( r_s \), while net photosynthesis, especially of C₃ species, shows downward curvilinearity with increased irradiance and is negative at zero irradiance. Thus there is an optimum irradiance for maximum incident upon a leaf oriented normal to the sun's rays. Thus leaf orientation at an
appropriate angle to these rays, by reducing the effective incident irradiance, can increase $WUE$ (80, 100). Leaf movements which orient the leaf parallel to the sun's rays, leaf rolling and flagging, erect leaves and needle-like leaves, all common features of dry situations especially once $\psi_{leaf}$ begins to fall, can be considered adaptations to increase $WUE$. Increased reflection of incident radiation would for the same reasons tend to increase $WUE$. Sorghum leaves with normal wax bloom, which increases reflectivity (16), had slightly higher $WUE$ values than bloomless leaves in a study of isogenic lines (24). Furthermore, reflectivity attributable to leaf hairs increases substantially with plant water deficit in the arid-zone species Encelia farinosa (44).

Passing to the influence on $WUE$ of the leaf traits $r_o$, $r_s$, and $r_i$, it is obvious from what has been said that comparisons between genotypes must take place under the same ambient conditions. In addition, we shall see that genotype by environment interactions need to be considered. This complex situation is amenable to theoretical analysis (31, 80, 116). Our limited remarks will be based on analyses (80, 116) in which allowance has been made in the leaf energy balance for long wave thermal emission as well as convective and latent heat exchange.

Beginning with stomatal aperture, theory points to increased $WUE$ as $r_o$ increases, except when the ratio of $r_i$ to $r_o$ is less than a given critical value (80). This latter condition is uncommon, requiring low $r_i$, as in $C_4$ species, high $r_o$ as with large leaves or low wind speeds, and high air temperature. Under conditions of water shortage when $r_i$ is usually higher, $WUE$ should always increase as $r_s$ increases (80). The high minimum $r_s$ values of many aridoactive species (27, 41) should also favor high $WUE$.

Calculations suggest that $WUE$ increases as $r_o$ is reduced, except under conditions of low radiation and high air temperature and saturation deficit (80, 116). Since $r_o$ decreases as leaf size decreases, it has been suggested that a major factor explaining leaf size variation across all plant communities is the need to maximize $WUE$ (116). The decrease in leaf size, and hence $r_o$, as aridity increases is seen to fit this hypothesis, as also would the large size of the photosynthetic organs of many CAM plants when it is considered that a large $r_o$ maximizes $WUE$ for dark assimilation (116). Leaf surface morphology also influences $r_o$; in particular pubescence can increase $r_o$ (80). However, since increased wind speed reduces $r_o$, at normal wind speeds in the field $r_o$ is small relative to $r_s$ and $r_i$ and unlikely to dominate the $WUE$ of exposed leaves.

The above considerations of changes in $r_o$ and $r_o$ assume that $r_i$ remains constant. However, because alterations in $r_o$ and $r_s$ affect leaf temperature (58), in situations where leaf temperature is markedly sub- or supraoptimal for photosynthesis, these temperature changes will influence $r_i$ and modify predicted responses in $WUE$ (100, 116). Change in $r_i$ will have no direct effect on the leaf's energy balance and the result for $WUE$ can be seen by inspection of the ratio $(r_o + r_i)/(r_o + r_s + r_i)$ to which $WUE$ is directly proportional (Equation 5). Various workers (68, 125, 156) have used this dimensionless resistance ratio or, since $r_o$ is usually small, the simpler $r_s/(r_s + r_i)$ (55, 144) as a useful index of genotypic effects on $WUE$. Notwithstanding the need for caution in the situation where $r_i$ changes, as outlined earlier, we shall also refer to this resistance ratio. Decreased $r_i$ increases the ratio and inevitably
increases $WUE$. C₄ plants have high light-saturated photosynthetic rates because their $r_{i}$ values are one-half or less than those of C₃ plants; their $r_{s}$ values are often somewhat greater than those of C₃ plants (40, 59, 95, 125). As a consequence, the resistance ratio of C₄ plants usually ranges from 0.7 to 0.8 while that for C₃ plants ranges from 0.2 to 0.4 (125, 156), and measured $WUE$ of the former group is two- to threefold higher under the same ambient conditions (40, 95, 125, 144). There are exceptions to this pattern, for example, jojoba (*Simmondsia chinensis*), a C₃ aridoactive shrub, showed a resistance ratio of 0.6 in one study (125). Also, since C₄ plants normally occupy warmer habitats than C₃ plants, the $WUE$ advantage of the former under their respective field conditions may not be as great. In addition, the data of Caldwell et al (22) suggest that C₄ plants adapted to cooler regions have higher values of $r_{i}$ and have lost their advantage in terms of $WUE$. It would be interesting to know the resistance ratios of those C₃ desert plants with exceptionally high photosynthetic rates, such as *Camissonia claviformis* (103).

Differences in $WUE$ within the C₃ and C₄ groups have been identified in gas exchange studies with tree species (68), barley lines of different stomatal frequency (101), perennial pasture grasses (55), citrus species (85), and various crop plants (125). With the exception of the citrus study, higher $WUE$ was associated with higher $r_{s}$ rather than lower $r_{i}$, and with lower photosynthetic rates, a situation exemplified by jojoba with a $WUE$ almost twice that of wheat, but a photosynthetic rate of only one-fifth that of wheat (125). Even so, the $WUE$ of jojoba fell well below that of several C₄ species in the same study.

Thus far we have not considered explicitly the response of $WUE$ to declining $\psi_{leaf}$ and possible genotypic differences in response. As already discussed, $r_{i}$ is likely to increase. Although work employing relatively rapid leaf drying suggests that $r_{i}$ may be insensitive to $\psi_{leaf}$ (69, 146), with slower field drying it is probable that $r_{i}$ will also increase (77, 80). The net effect on $WUE$ will depend on relative changes in $r_{s}$ and $r_{i}$, approximately as seen in the resistance ratio. Generally gas exchange measurements show $WUE$ is unchanged (78, 145) or increased (77) by decreased $\psi_{leaf}$, but there are exceptions (77, 140) and there is need for more measurements under drying rates typical of field situations.

Considerations of responses in $WUE$ to dry situations must also include the recent demonstration of a direct effect of air saturation deficit on stomatal aperture, namely, $r_{i}$ increases as saturation deficit increases even though $\psi_{leaf}$ may not decrease (135). Such stomatal responses reduce, but do not eliminate, the decline in $WUE$ to be expected as $\Delta e$ rises (84, 136). Direct stomatal response to humidity has been demonstrated in a number of herbaceous and tree species including arid zone ones (84, 135, 139), but may not be present in all species (125, 139). Differences between species and interactions of the response with environment has been discussed recently (64). Since the response of stomata to air saturation deficit appears to show acclimation, and since many studies have used nonfield-grown material, there is need for more field data before the full ecological significance of the stomatal response to humidity is understood.

So far our discussion of $WUE$ at the leaf level has only considered instantaneous $WUE$. Daily $WUE$ (daytime CO₂ uptake/daytime transpiration) and the important question of how a plant may behave to maximize this is more complex. In the
absence of adjustments in the leaf, theory points to a decline in WUE in the middle of the day largely because of the rise in air saturation deficit and the likely light saturation of photosynthesis. Recently Cowan & Farquhar (32) have calculated the stomatal behavior required to maximize daily WUE. To achieve this, especially in the case of C₃ plants but not necessarily with C₄ plants, rₛ must show a midday increase and an afternoon minimum somewhat higher than the morning minimum. This is in fact the type of diurnal stomatal response often found as water becomes limited (126, 138, 163). To maximize daily WUE, the direct response of stomata to some external condition affecting the rate of transpiration is demanded (32); the humidity response just described fits this requirement. The response is so effective in apricot (Prunus armeniaca) that its daily WUE in the Negev changes little from the mild days of spring to the hot ones of late summer (136), and this appears also to be the case for the sclerophyllous shrub Heteromeles arbutifolia in mediterranean California (100).

Another example of adaptation to the diurnal changes in environmental factors affecting WUE is the behavior of CAM plants, reviewed separately in this volume (115). Typically CAM plants carry out gas exchange at night, when because of lower air saturation deficits and negative absorbed radiation Δₑ is much lower than during the day. Combined with resistance ratios similar to C₄ plants (~0.8) when fixing CO₂ in the dark (156), this means CAM plants can achieve high WUE values, for example, as high as 50 mgCO₂ gH₂O⁻¹ with Agave americana (106). In some CAM plants, night fixation of CO₂ always predominates, while in others water stress appears to induce night fixation of CO₂ and in the absence of stress, they fix most or all of their CO₂ during the day, thereby achieving higher rates of carbon gain but at the expense of high WUE (106). The overall productivity of CAM plants is low, especially when fixing carbon in the CAM mode (115).

Akin to considerations of the diurnal march of WUE are those of its seasonal march. Where water is limited, maximum annual WUE will arise if greater stomatal opening and transpiration is associated with those days and/or months when the environment favors maximum WUE. For example, with Negev desert shrubs transpiration is concentrated in the late winter and early spring when air temperature and humidity is likely to be most favorable for WUE (47).

Canopies Gas exchange theory has been extended to horizontally uniform plant communities such as crops and forests; resultant canopy models have been used to predict canopy WUE (100, 140, 169). With canopies rather than single leaves, some allowance must be made for the fact the effective rₒ is greater because of additional resistances within and above the canopy (80, 144). This means that situations in which an increase in rₛ does not increase WUE may be more common, although those when a reduction in rₒ does not increase WUE are still likely to be rare (80). Because of the difficulties involved, direct tests of these predictions through determination of canopy gas exchange are few. Micrometerological measurements of the maize canopy have shown that WUE increased substantially with increased wind speed and therefore reduced rₛ (93), and decreased with mild soil water stress, presumably as rₛ increased (93, 140). In the study by Sinclair et al (140), the
measured response of canopy WUE to the change in $r_s$ agreed with that predicted from a single leaf model of WUE.

The above-mentioned canopy data was obtained with high LAI values and relatively humid mesic conditions. These may be of limited relevance to communities under drier conditions where smaller LAI would tend to reduce $r_a$ relative to $r_s$ and $r_i$, and horizontal advection could be greater. However, these conditions increase the likelihood that predictions and measurements based on single leaves would be faithfully reflected in differences, particularly genotypic ones, in WUE at the community level.

**WUE Based on Dry Matter Accumulation**

Much information on WUE is available from determinations of dry matter accumulation and transpiration of plants in containers, crops or natural communities, and sampled at intervals of one week to several months. The exact relationship between WUE in terms of $mgDM\ gH_2O^{-1}$ and that expressed as $mgCO_2\ gH_2O^{-1}$, which we have used until now, will depend on the carbon content of dry matter: values from 0.61 to 0.68 $gDM\ gCO_2^{-1}$ are common for most growing plants. Provided dry matter accumulation in roots is included, and losses due to grazing, decomposition, etc are negligible, the only other difference with respect to WUE based on daytime gas exchange arises because of respiratory losses at night and in nonphotosynthetic tissue, and possible night transpirational losses (e.g. 163). WUE based on dry matter accumulation will necessarily be lower as a result. Respiratory losses are in fact a substantial proportion of net daytime photosynthesis (94). These losses can be usefully separated into growth and maintenance components, the quantities of respiration involved being relatively fixed fractions of growth rate and of total dry matter, respectively (121). Major long-term effects of reduced $\psi_{plant}$ on these fractions have not been reported, but the existence of a maintenance component, regardless of the level of net daytime photosynthesis, means that leaf strategies for maximum long-term WUE will be different from those giving maximum daytime WUE (80).

WUE based on dry matter accumulation often suffers from two complications. First, transpiration and soil evaporation may not be separated so that WUE is calculated using evapotranspiration. Second, roots are commonly neglected in measuring dry matter accumulation. Compared to WUE as defined here, these effects may reduce the resultant calculated WUE by as little as 20% in adequately watered annual crops, but in other situations, for example perennial species or containers from which evaporation is not prevented, the reduction could be greater than 50%. Studies where the above complications were absent or of minimal significance were for obvious reasons usually container experiments. Effects upon WUE as determined in these experiments agree with conclusions reached from gas exchange considerations and measurement, especially with regard to the major effect of air saturation deficit and the difference between C3 and C4 plants.

Looking at environmental effects on WUE in container studies, de Wit (37a) showed a strong inverse relationship between WUE and free water evaporation ($E_o$), a relationship which others pointed out probably derives largely from the
effects of air saturation deficit on both WUE and $E_o$ (14). In a careful study of six wheat cultivars planted at monthly intervals in a Mediterranean environment of southern Australia, WUE was also inversely related to $E_o$ (J. F. Warren and W. J. Lill, personal communication). This relationship combined with average monthly $E_o$ predicts the seasonal march of WUE, which varies from as high as 8.5 mgDM gH$_2$O$^{-1}$ in midwinter to only 2.5 mgDM gH$_2$O$^{-1}$ in midsummer. In semiarid Israel, measured fluctuations in container-determined WUE due to seasonal changes in atmospheric conditions agreed closely with predictions from gas exchange theory (166). Further examples of the relationship between WUE and $E_o$ are given later (see Table 1).

Downes (39), regrouping data from many early container experiments, calculated mean WUE values of 1.5 mgDM gH$_2$O$^{-1}$ and 3.3 mgDM gH$_2$O$^{-1}$ for C$_3$ and C$_4$ species, respectively; differences he confirmed with several common crop and pasture species. A more recent comparison of desert shrubs showed a WUE value of 1.4 mgDM gH$_2$O$^{-1}$ for the C$_4$ species Atriplex canescens compared to a mean value of 0.7 mgDM gH$_2$O$^{-1}$ for C$_3$ species, including creosote bush (Larrea tridentata) and mesquite (Prosopis juliflora) (42). In striking contrast to all these values, a CAM plant, pineapple (Ananas comosus), showed a gain of 20 mgDM gH$_2$O$^{-1}$ (83).

Container experiments, on the other hand, suggest that there are not large differences in WUE between plants of the same life form within the C$_3$ and C$_4$ groups (e.g. 42, 166). For example, van Keulen (166) found no difference between several temperate crop species and annual pasture plants native to the semiarid zone. The above-mentioned study with six contrasting wheat cultivars (J. F. Warren and W. J. Lill, personal communication) revealed no significant differences in WUE when WUE was corrected for differences in transpiration pattern and corresponding $E_o$ and root as well as shoot accumulation was considered.

The record of container experiments with respect to the influence of soil and presumably leaf water deficit on WUE is not so clear cut. Some experiments show relatively small changes in WUE (37a), whereas others suggest that WUE increases with increasing soil water limitation until a maximum WUE is reached, beyond which greater limitation lowers WUE (e.g. 42, 43). Earlier we pointed out that the consequences for WUE of lowered leaf water potential will depend on the relative changes in $r_s$ and $r_l$ and probably on the rate of drying. The effects of nutrient deficiency on WUE has also been studied in containers, but effects were generally small (2, 37a). On the other hand, increases in water-limited pasture productivity with nitrogen application (e.g. 20, 166) are indirectly suggestive of WUE increases.

The environment of container experiments may not exactly represent that of field communities, especially with respect to reproducing the canopy microclimate, and also the balance between the growth of various plant parts may change due to reduced interplant competition or reduced soil volume. While such effects may influence the absolute levels of WUE, our discussion of gas exchange would suggest that differences arising from genotypic or other treatment effects should still be valid. This is very important because, for obvious reasons, there are few field studies where measurements of WUE based on dry matter accumulation are relatively free from complications due to the inclusion of soil evaporation or neglect of root dry
matter. One such field study in Kansas compared summer crops of sorghum, a C4 species, and soybean (Glycine max) a C3 species: the former had a WUE approximately three times greater than that of the latter and a peak WUE of 7 mgDM gH2O⁻¹ (155). Very detailed investigations in the high desert of Utah determined an annual average WUE of 4.3 mgDM gH2O⁻¹ for a C4 shrub community (Atriplex confertifolia) and 2.9 mgDM gH2O⁻¹ for an adjacent C3 one (Ceratoides lanata) (22). This result did not contradict gas exchange measurements which showed little difference in WUE at the leaf level: the small WUE advantage of the Atriplex community was apparently due to smaller underground respiratory losses. Ludlow & Wilson (95) quote values of 3 and 1.4 mgDM gH2O⁻¹ for swards of a tropical C4 grass and tropical C3 legume, respectively. These relatively precise community values of WUE and others to be given later (see Table 1) fall within the range of approximate values (1 to 6 mgDM gH2O⁻¹) for desert ecosystems derived simply from the slope of production-precipitation relationships (110).

Agronomists often report that improved management (e.g. fertilization, planting density, etc) and plant breeding have led to substantial gains in water use efficiency in terms of yield of economic product per unit water supplied (4, 4a, 9). However, it is unlikely that WUE as we have defined it (total dry matter per unit transpiration) has increased. Most of the gains reported derive from increases in transpiration as a fraction of water supply, due to greater soil extraction and greater plant cover reducing soil-evaporation, or from increases in harvest index. Even in the case of forage production, claims that efficiency doubled with nitrogen fertilization of semiarid annual pastures (166) could largely reflect savings of soil evaporation.

ASSIMILATE PARTITIONING

Discussion until now has centered around Equation 1, the production of assimilate. The partitioning of each day's assimilate will also in the longer term affect productivity (94, 102) and exert a major influence upon the yield of economic product in the case of crops. By partitioning we refer to the allocation of current assimilate, and at times mobilization of stored assimilate, to metabolic sinks in the plant.

In contrast to the situation with transpiration and water use efficiency, genotype exerts major control over partitioning. Some genotypic effects on partitioning are expressed regardless of environment in which the plant is grown, but appear to be appropriate for the environment to which the plant is adapted, for example, the plant life forms already discussed in relation to dry environments. We shall also be interested in genotypic effects on assimilate allocation which only appear when water is limiting. These two types of adaptation can be considered constitutive and facultative and are synonymous with the concepts of strategy and tactics, respectively, applied by Harper & Ogden (65a) to the allocation of energy and dry weight in plants. Tactical responses will depend on lowered ψplant, but it should be pointed out at the outset that direct effects of ψplant on phloem transport of assimilate are unlikely to be involved since such effects appear to be small (146, 172).

Selection by man has modified the allocation patterns of plants in order to achieve better performance in semiarid monoculture and greater yield of economic product,
i.e. greater seed yield in the case of crops and more digestible dry matter in pastures. Natural selection in mixed plant communities has led to a great diversity of allocation patterns, but it should have favored maximum seed production and harvest index in annual plants (65a), thereby leading to some common ground with at least annual crops.

**Phenology**

Phenology refers to the timing of major developmental events such as germination, floral initiation, flowering, seed maturity, leaf fall, etc. These events, through the control of meristematic sinks, determine the basic temporal framework for partitioning of assimilate and represent a major mechanism by which plants adapt to water-limited environments.

**ANNUALS** The phenology of annuals is such that flowering and seed filling is largely completed during the probable period of available water. Internal control mechanisms including dormancy, germination inhibitors, and sensitivity to temperature, light, and quantity of water prevent seed germination at unfavorable times and in unfavorable habitats (47, 48, 105, 110, 112). Flowering of desert ephemerals may begin soon after germination so that the whole life cycle can be completed within as little as several weeks; nevertheless, if conditions remain favorable, further vegetative growth and flowering may take place (105). While it may seem appropriate that phenology be tied to environment through direct responses to water, with the exception of the obvious need for water for germination, the important environmental stimuli for most other phenological events are temperature and, in particular, photoperiod. Sudden and/or severe early water stress has been shown to delay floral initiation (e.g. 97), but the delay was small and more commonly floral initiation has been found to be insensitive to stress (e.g. 104). Flowering is generally hastened slightly by plant water stress (162), but has also been found to be unaffected in some desert ephemerals (104); in wheat, although accelerated by mild stress, flowering was delayed by severe stress, the delay being approximately equal to the duration of severe stress (3). Photoperiodic control, on the other hand, ensures that the date of flowering is relatively independent of water supply or date of germination. This would seem appropriate since calendar date rather than germination date is the better predictor of the end of the wet season. It means that annual plants of the semiarid savanna region tend to be short-day plants and those of the Mediterranean region long-day plants.

The maturation of seeds and duration of the seed filling phase is largely controlled by factors internal to the seed interacting with environmental temperature. Water stress during seed filling will usually, but not always (104), accelerate seed maturation, but to a lesser extent than the associated acceleration of leaf death (13, 104).

Looking specifically at annual plants subject to selection by man, long-term seed dormancy has largely been eliminated from crop plants, but remains important to ensure persistence in pasture plants. The opportunistic indeterminate strategy seen in many native annuals is also recognized in some crop plants, for example tropical leguminous pulses such as peanut (*Arachis hypogaea*), cowpea (*Vigna unguiculata*), and cotton (18). Natural selection in wild species and in primitive agriculture of the
semiarid zone appears to have favored the indeterminate strategy in some species. Other species are determinate and flowering represents an abrupt and irreversible end to further vegetative growth. Thus for maximum yield, flowering must take place at a given time before the expected end of the supply of available water. For example, in Nigeria the flowering date of locally adapted sorghum cultivars is precisely controlled by subtle sensitivity to photoperiod in order to coincide with the average date of termination of the wet season rains at each location regardless of the sowing date (33). Such sensitivity to photoperiod is usually associated, however, with specific adaptation to small regions. On the other hand, the often spectacular increase in adaptation to drier regions (shorter wet seasons) achieved by modern plant breeders in crops such as wheat, barley, sorghum, and cotton has been closely linked to earlier flowering (63, 161) as a result of the lessening of sensitivity to photoperiod.

PERENNIALS For drought-deciduous perennials the important developmental events of leaf production at the onset of the wet season and leaf fall after its end appear to be controlled by water supply to the plant, although in the mediterranean and steppe zones, where winter temperatures are low, leaf production is often delayed until early spring (6, 37, 122). Also in some savanna species leaf production may precede the onset of rains. With evergreen perennials, leaf production appears to require a substantial pulse of assimilation and hence water (28, 114); for example, leaf production can occur at any time of the year in *Acacia harpophylla* growing in the Australian transition zone (28). Leaf fall, or the switch to a more xeromorphic leaf type in dimorphic shrubs (23, 37, 113), is probably controlled by declining $\psi_{\text{plant}}$ (23, 89, 168).

Seed production in perennials is not critical for survival, and flowering and seed filling often occur at times which do not appear to be the most favorable for assimilation; for example, *Artemisia tridentata*, a shrub of arid steppe regions, flowers in late summer (23, 37) and drought-deciduous perennials of the savanna zone often flower in the dry season (171). For this reason control of flowering by photoperiodism should again predominate, although in coffee (*Coffea arabica*) flowering does appear to require low $\psi_{\text{plant}}$ followed by recovery to high $\psi_{\text{plant}}$ (96), as would occur with the onset of rains after a dry period.

*Photosynthetic Tissue*

The investment of a high proportion of assimilate in new photosynthetic tissue, i.e. a high leaf area to total dry weight or leaf area to leaf weight, maximizes plant growth rate and usually community growth rate when water is not limiting (18, 94, 102). However, under water-limited conditions these ratios are usually lower and other strategies operate. There are two aspects to this: namely, the morphology of photosynthetic organs and the quantity of such organs relative to other tissues.

A multitude of changes in the morphology of leaves and other green organs appear to be correlated with adaptation to increasing aridity and xerophytism (112). Some adaptations which may increase tolerance to low $\psi_{\text{leaf}}$ and increase WUE have been discussed earlier. Here we will concentrate on specific leaf density (leaf weight per unit area), which generally increases with aridity. For example, the
Aridoactive sclerophyllous plants of the Mediterranean zone have specific leaf densities of 1 to 2 gDM dm⁻² (41), compared to values of 0.5 to 1.4 gDM dm⁻² for aridopassive shrubs in the same zone (100), and to values of around 0.4 gDM dm⁻² for aridopassive herbaceous plants (60). Some aridoactive shrubs exhibit leaf dimorphism, producing denser smaller leaves during the dry season (23, 37, 113).

The increased specific leaf density in the sclerophylls results from heavy investment in such nonphotosynthetic components as fibers, vessels, cell walls, sclerenchyma, and the accumulation of silica (48). This strategy appears to favor not only survival but also photosynthetic ability at very low $\psi_{leaf}$; however, it is also associated with low maximal rates of photosynthesis (41, 100, 138, 165).

Amongst the herbaceous plants it is not clear whether there are differences in specific leaf density of adaptive significance. Differences do occur between crop species and cultivars and tend to be positively associated with photosynthetic rate per unit leaf area (86, 120, 158) and therefore possibly WUE. Within the *Triticum* genus and *Brassica* family it has been suggested that the better adaptation to more xeric environments of their more primitive members compared to the more mesophytic cultivated species is associated with smaller, denser (measured as weight of nitrogen per unit leaf area) leaves, having a greater ratio of vascular tissue to photosynthetic tissue and a greater photosynthetic rate (86, 158). Also the response of herbaceous plants to water stress, the xeromorphoses described by Stocker (151), such as the production of smaller denser leaves, could be considered adaptive.

The fact that desert annuals do not have strikingly xeromorphic leaves does not exclude the possibility of other leaf adaptations. For example, summer annuals generally have simple entire leaves and Kranz-type anatomy indicative of $C_4$ photosynthesis, whereas winter annuals generally have highly dissected rosette leaves that lack the Kranz anatomy (105). The rosette form may be an adaptation to increase leaf temperature and enhance growth during the winter, when the availability of soil water is greatest (105).

With regard to the overall allocation of assimilate to leaf growth, this appears to be generally lower with water limitation. Also it should be mentioned that leaf longevity, or conversely the rate of leaf abscission and death, combine with the allocation factor to determine the ratio of total quantity or area of active leaves to biomass at any point in time. Thus hastening of leaf death with decreased $\psi_{plant}$ will lead to further downward adjustment of this ratio. The extent to which carbon and minerals such as nitrogen are translocated out of these leaves before they die is an important aspect of partitioning on which there is little information.

**Roots**

Perennial grasses and shrubs of dry regions generally have root/shoot ratios above 1 and higher than those of humid regions (20, 47, 112), although low temperature may also contribute to this high ratio in the steppe zone (110), and some warm desert shrubs have ratios below 1 (7, 110). Part of the root mass may represent carbon reserve rather than functional absorbing tissue. There are some situations, for example in perennial aridopassive grasses at the beginning of the growing season,
when root reserves should be supplying growing leaves and hence the allocation to roots would be negative. It should also be emphasized that the root/shoot ratio at any point in time not only reflects the proportion of assimilate allocated to roots, but also the rate of death or turnover of roots relative to tops. Both components appear to favor high root/shoot ratios in arid zone perennials. With annual plants of dry regions root/shoot ratios at maturity are lower than the ratios of perennials, presumably because of accumulation of assimilate in seeds in annuals. The ratios range from 0.1 to 1.0 (26, 46, 104, 110, 153, 166) and are not clearly higher than in annuals not native to dry regions (110, 166).

It is commonly observed that the root/shoot ratio increases with lower $\psi_{\text{soil}}$ in annuals from both mesic and arid environments (8, 43, 102, 151, 153) and in arid zone perennials (42). Soil water deficiency can double the root/shoot ratio, increasing the absolute mass of roots in some situations (10, 70). Increased air saturation deficit can also increase the root/shoot ratio (67, 151). In general, it appears that the root/shoot ratio changes so as to maintain $\psi_{\text{plant}}$ within certain limits. Possible mechanisms for the regulation of root/shoot ratios have been discussed elsewhere (49, 70, 74). It is useful to point out here that such responses in the root/shoot ratio can be associated with deeper rooting (10) and hence greater available water in some situations, and that there may be cultivar and species differences in these responses (10, 72). Finally, while more roots may mean more water uptake by the particular plant in a competitive situation, it may not increase total water extraction by the plant community, and in crops it could be disadvantageous (117).

In grasses two types of absorbing roots are produced, the seminal roots and the nodal or adventitious roots. The latter, which require moisture in the surface layer of the soil for initial growth, may be important for establishment and growth in species where the resistance of primary seminal root to water flow is high [e.g. in *Bouteloua gracilis* (174)]. Seminal roots in wheat, on the other hand, may be responsible for a major portion of deep soil water extraction (62), and this fact forms the basis of an aforementioned hypothesis (see Transpiration Modulation) for rationing water use by wheat (117).

**Reproductive Tissues**

In perennials seed production each year is not critical for survival and the production of reproductive tissues is smaller as proportion of total assimilate production than in annuals (102). There are exceptions such as biennials and *Agave* species; for example, *A. deserti* flowers only once, at the end of a lifetime of 10 to 30 years, and floral and seed production depend heavily on carbon and water stored from earlier years (109). The reproductive effort of perennials in any year is very sensitive to water limitation, fluctuating widely from year to year according to the degree of water stress during the growing season (6) or even the preceding growing season. For example, the yield of unirrigated apricots was correlated, via effects on flower bud initiation, with the date at which the soil water was depleted in the previous season (164).

In most annuals, survival depends on viable seed production. It would therefore seem appropriate that annual plants should function so as to maximize the amount
of assimilate going to the seed (65a). As we look at seed yield in annuals in the remainder of this section, it is useful to separate the determination of seed number from that of seed size. Also, differences in seed yield arising from the effects of water deficit on total assimilation need to be distinguished from the effects of deficits on the pattern of assimilate allocation through time. For example, the reduction in seed yield with water limitation is often in proportion to the reduction in total dry matter production (17, 132) or to the reduction in assimilation at ontogenetically important stages for dry matter accumulation in reproductive tissues. Thus, water deficit during seed filling can reduce yield without altering the pattern of assimilate allocation at any point in time.

**SEED NUMBER** The production of floral primordia following floral initiation appears to be sensitive to water stress (146). However, field studies suggest that seed number and crop yield are relatively insensitive to early drought, i.e. drought until approximately halfway to flowering which corresponds to the period of production of floral primordia (53, 73, 134). The main reason for this insensitivity to early water limitation appears to be that annual plants normally produce many more reproductive primordia than can be grown to full size under the competitive conditions of most plant communities. This optimistic strategy is apparently satisfactory because the carbon investment involved in initiating primordia is minimal. Seed number is much more influenced by factors affecting the growth and survival of these primordia, and consequently the influence of water limitation upon these processes is more important.

Assimilate allocation to reproductive organs of annual plants is not substantial until flowering is approached. Because the assimilate available, especially where there is interplant competition as in crops, is insufficient to grow all potential reproductive primordia, some fail. This results in tiller mortality and the production of rudimentary spikelets and florets in, for example, wheat and barley. Water stress accelerates these processes, but from limited information in cereals, the effect probably operates via reduced assimilation because the proportion of total assimilate allocated to reproductive organs is unchanged or may in fact increase with water stress (91a; R. A. Fischer, unpublished). The effect on organ growth may not arise simply because of reduced assimilate supply since labile carbohydrate reserves often increase with water deficit (e.g. 8); direct effects of stress on the growing reproductive sink are probably also involved. The curious substantial increase in female inflorescence growth and survival in maize subsequent to water stress at the time of initiation of the terminal male inflorescence (34) illustrates the complexity of the control of this partitioning.

Although preflowering water limitations appear to be primarily reflected in reduced dry matter accumulation in reproductive tissue, additionally there are effects of water deficits on reproductive efficiency, defined here by the number of flowers, and later seeds, produced per unit of dry matter investment in the inflorescence. Water stress can interfere with microsporogenesis, pollination, and fertilization, and can induce abortion of young seeds or abscission of young fruits (9, 50, 134, 146). Such effects appear to involve direct effects of water stress on the tissues and
processes involved, and would seem to fall into the category of effects on reproductive efficiency. However, few measurements of seed number per unit inflorescence weight have been made. Calculations using unpublished data of the experiments of Fischer (50) show that plant water stress for 3 days, beginning at 22 or at 2 days before ear emergence in wheat, reduced seed number in proportion to the reduction in inflorescence weight, whereas stress beginning 16 and 9 days before ear emergence, characterized by male sterility and drastic reductions in seed number, reduced both inflorescence weight and seeds per unit inflorescence weight. Seed number was relatively insensitive to plant water stress once anthesis had passed.

Comparative data on the sensitivity of reproductive efficiency in different species to water stress are unavailable, but it appears that most, if not all, species show heightened sensitivity around flowering (134). Because of the different mechanisms involved in different types of plants, comparisons between them may be of little value. Even comparisons within species are difficult because of the importance of matching both $\psi_{\text{plant}}$ and the exact stage of inflorescence development. When ten wheat cultivars representing four related species were stressed under controlled conditions at the same stage of development just before ear emergence, effects of a given level of $\psi_{\text{plant}}$ on seed number were not strikingly different between them (R. A. Fischer, unpublished). On the other hand, the spread of inflorescence growth over longer periods of time, as with the indeterminate habit of growth, should reduce the risk of drastic reductions in seed number with short stress periods.

The widespread existence of a critical period during which seed number is particularly sensitive to water limitation may seem, in terms of carbon efficiency, wasteful because carbon is lost when organs are shed. This adjustment of seed number, however, may be a mechanism for ensuring adequate seed size in the cases where flowering occurs toward the end of the wet season. It would seem an appropriate mechanism for those situations in which mild plant water stress at the stage when the seed number is determined provides a reliable index of more severe stress, and hence assimilate limitation, during the subsequent seed-filling phase. Man is unlikely to have selected against such mechanisms, since he also is interested in seed size.

**SEED FILLING** Soon after the seeds begin to fill, they become a strong sink for current assimilate, and a large proportion, at least in determinate annual plants, of total assimilation over the whole seed-filling period goes to the seed (e.g. 13, 79). The other source of seed carbon is assimilate stored in the plant before the onset of seed filling and later transferred to the seed. This source appears to be small in adequately watered cereals (e.g. 13). Water stress during seed filling has its major effect upon current assimilation, both through reductions in assimilatory activity and assimilatory surface (9). As mentioned earlier, the duration of seed filling may also be curtailed. Water stress not only increases the proportion of current assimilate translocated to the seed (13, 79), but also may increase the contribution from assimilate stored prior to seed filling (17, 29, 118): this contribution when expressed relative to total seed yield more clearly increases with water stress (13, 57).

Differences among species in these response patterns to water deficits at seed filling have rarely been examined explicitly. Bidinger (13) compared wheat and
barley crops in the presence and absence of water stress at seed filling and found no differences in the response of assimilatory surface and activity to stress which could not be explained by small differences in the date of anthesis. Also, the absolute contribution to seed yield of assimilate stored prior to anthesis as determined by repeated $^{14}$C canopy labeling was unaffected by water stress or by species, but relative to seed yield the contribution rose from 12% with no water deficit to 22% when there was a deficit during seed filling. One favorable adaptation to water limitation during seed filling appears to be the presence of awns in wheat and barley. For example, in wheat under water stress, the contribution of assimilate to the grains from awns increases relative to that of other sources of assimilate (45). Hsiao et al (71) also suggest that the lack of maintenance of assimilatory activity close to the growing seed may partly explain the greater reduction of yield of maize compared to that of sorghum under water-limited conditions. In maize, dry matter accumulation in the ear comes from assimilation in the middle canopy leaves close to the cob; in sorghum it comes from upper canopy leaves; the former are physiologically older and more likely to die under stress (94a).

*Harvest Index*

The effects of water limitation on seed yield can be summarized usefully by the harvest index ($HI$) in many situations (37a, 119). Where water deficits develop early, or are mild and evenly distributed over the life of the plant, $HI$ is unaffected (37a). On the other hand, if stress is concentrated around flowering or in the seed-filling stage, $HI$ can be reduced substantially (52, 91a, 118, 119, 134). For example, Passioura (118, 119) showed under controlled conditions that $HI$ of several wheat cultivars was linearly related to the percentage of total transpiration occurring in the postanthesis period; $HI$ was maximized if this was 30% or greater. Similar results have been obtained in a study of the striking influence of soil texture on the yield of water-limited wheat (91a), and with other wheat and maize crops (1, 26).

Cultivars differ in $HI$, and increase in $HI$ is the main route by which the yield of various crop species has been improved by plant breeders (38); total dry matter production and hence water use have changed little with this improvement. From studies with numerous wheat, barley, and triticale cultivars, it seems that $HI$ under water-limited conditions is related to $HI$ in the absence of water limitation and is in turn positively associated with yield under water limitation (R. A. Fischer, unpublished). This is probably why modern semidwarf wheats with high $HI$ have usually given superior yields to supposedly drought-resistant, traditional, tall cultivars under rainfed as well as irrigated conditions (90).

**INTEGRATION AND CONCLUSIONS**

In this review we have discussed those factors which we believe are key determinants of plant productivity in dry regions. Table 1 illustrates these determinants in the case of four semiarid plant communities. The weather and plant variables listed are in the order that they have been introduced in the preceding discussion. Needless to say, it was very difficult to find examples in the literature where all of these variables had been measured or estimated simultaneously.
Table 1 needs little explanation except to point out that the variation in WUE between communities is closely related to that which would be expected from the analysis of de Wit (37a) and the container experiments of van Keulen (166). Their results indicate that the product of WUE and $E_0$ was a constant of around 110 to 140 kg ha$^{-1}$ day$^{-1}$ for wheat and many other C$_3$ species (37a, 166), and 207 kg ha$^{-1}$ day$^{-1}$ for a C$_4$ species, sorghum (37a). From Table 1, $WUE \cdot E_0$ in kg ha$^{-1}$

| Site                | Vegetation | Period            | Precipitation, \(P\) (mm) | Change in soil water, \(\Delta S\) (mm) | Evapotranspiration, \(ET\) (mm) | Soil evaporation/evapotranspiration, \(E_d/ET\) | Transpiration, \(T\) (mm) | Free water evaporation, \(E_o\) (mm day$^{-1}$) | Water use efficiency, \(WUE\) (mg DM g H$_2$O$^{-1}$) | Net primary production (g m$^{-2}$) | Root/shoot allocation | Above-ground production (g m$^{-2}$) | Harvest index, \(HI\) | Grain yield (g m$^{-2}$) | Source |
|---------------------|------------|-------------------|---------------------------|----------------------------------------|---------------------------------|--------------------------------------------|------------------------|--------------------------------------------|---------------------------------------------|------------------------|-----------------------|---------------------|-------------------|---------|
| Curlew Valley Utah  | Shrubland  | Oct. 1972 to Sept. 1974 | 258                       | 0                                      | 258                             | 0.53                                       | 123                    | 4.8c                                       | 2.9                                          | 358                    | 3.2                   | 86                  | —                 | 22      |
| Migda Israel        | C. lanata  | 1971 to 1974      | 315                       | 39                                     | 276                             | 0.38                                       | 186                    | 2.2                                        | 5.2                                          | 950                    | 0.38                  | 687                 | —                 | 166     |
| Wagga Wagga         | Annual     | Nov. to May       | 217                       | -83                                    | 300                             | 0.24c                                      | 229                    | 2.4                                        | 5.1                                          | 1,164                  | 0.13d                  | 1,030               | 0.29              | 51,52   |
| New South Wales     | pasture    | June 1962 to Nov. 1962 | 228                       | -106                                   | 335                             | 0.20c                                      | 268                    | 5.5                                        | 4.2                                          | 1,117                  | —                     | 893                 | —                 | 1       |
| Mandan North Dakota | Maize      | May to Oct.       | 217                       | -106                                   | 335                             | 0.20c                                      | 268                    | 5.5                                        | 4.2                                          | 1,117                  | —                     | 893                 | —                 | 1       |

\(a\) Calculated as annual or seasonal means.
\(b\) For the months of greatest transpiration within the period.
\(c\) Our estimates.
\(d\) Taken from other wheat (26) and maize (153) studies.
day$^{-1}$ was 139 (C. lanata), 122 (wheat), 114 (annual mediterranean pasture), and 231 (maize). Also, variation in WUE from season to season in the annual pasture and maize examples of Table 1 was associated inversely with changes in $E_o$. Thus, despite our earlier references to many possible ways in which WUE may be affected by genotype and environment, in the examples of Table 1 the variation in WUE could be attributed largely to the two major influences identified in our discussion, namely $\Delta e$ and the primary carboxylating enzyme in photosynthesis.

Grain yields are shown for the two crop situations in Table 1. It is interesting that the harvest index of the maize crop ranged from 0.12 to 0.34 across the 3 years studied, bearing a close relationship to variation in the fraction of $ET$ occurring after silking. Largely as a result of this $HI$ variation, yield varied fourfold, from 93 to 390 g m$^{-2}$ (1).

The results of Table 1 suggest that primary productivity may not differ greatly between life forms in dry regions, provided allowance is made for differences in transpiration, $E_o$, the initial carboxylating enzymes of photosynthesis, and the root/shoot allocation ratios. Evenari et al (47) concluded that in the arid Negev desert the productivity of life forms as different as lichens and aridoactive shrubs was of the same order of magnitude. Although more data of the type shown in Table 1 is needed, and the lichen-shrub comparison has obvious limitations, it is worthwhile pursuing this point, which essentially means that, other things being equal, WUE on a dry matter basis is not greatly affected by life form and presumably is even more stable within life forms. The first implication of this is that maintenance respiration losses relative to net daytime photosynthesis in life forms such as aridoactive perennials with high phytomass and low relative primary productivities (primary productivity/phytomass) may not be much greater than those in other life forms. This suggestion is supported by some estimations of above and below ground respiration as a percentage of net carbon assimilation by green parts: values for two shrub communities in Utah [20% and 36% (22)] and arid acacia and Atriplex shrublands in Australia [65% and 55%, respectively (147)], differ little from the range of values (20 to 50%) for crops (94) or a value of 49% estimated for a semiarid steppe grassland of Bouteloua gracilis (17a).

The second implication of the suggestion that life forms have similar WUE values is that it tends to contradict the common statement that xerophytes balance their water economy at the expense of reduced productivity (e.g. 47, 138). Insofar as this implies increased WUE at the expense of productivity, it is worth pointing out that in terms of Equation 1, this can only come about if $T$ is lower as a result. While in the short term stomatal closing when $\Delta e$ is unfavorable for high WUE may, for example, lead to an inverse relationship between daily WUE and daily $T$, there seems no reason why maximizing WUE should affect total seasonal or annual $T$.

Also, the implied conflict between water economy and productivity seems to overlook the fact that water not transpired is water lost in terms of productivity. It could be argued that water saved may be important for survival (e.g. 148), but even this seems to disagree with the fact that aridoactive species do not exercise their greatest control over water loss (maximum $r_s$, reduced leaf area, etc) until there is very little water left (see Transpiration Modulation). Such behavior would seem justified be-
cause maximizing $T$ when there is soil water available first reduces losses of water due to competition from adjacent plants and due to soil evaporation (25), and second is conducive to a high $WUE$ insofar as favorable ambient conditions (low $E_o$) are likely to be associated with periods when the soil is wet.

Throughout this review we have referred to strategies and adaptations of plants which seem to favor the maximization of plant productivity in dry regions through either increasing $T$ as a proportion of available water or increasing $WUE$. While it is reasonable to assume that as a result of natural selection in undisturbed ecosystems features of plant life are purposeful in the environment in which the plants are found, it is not necessarily true that maximization of productivity has always been favored (43a). For example, discussion of the preceding paragraph implied that there is conflict between maximization of productivity and maximization of survival. While recognizing that uncertainty as to the exact long-term goals of evolution exists, we suggest that maximization of carbon gain, which in a water-limited environment amounts to maximizing the efficiency with which water is acquired and "traded" for carbon, remains central to other goals, such as stress resistance or survival, which may also have to be satisfied.

Another important aspect of the adaptation question is the need to consider plant traits and functions of possible adaptive significance in the proper time and space perspective (43a). In other words, possible adaptations cannot be examined in isolation from the rest of the plant and community in which the plant exists. The cost to the plant of adaptations might seem to be the respiratory cost of building and maintaining the structure, but that which is foregone as a result of the carbon and mineral investment involved needs also to be considered, i.e. we must consider the opportunity cost as economists would term it. For example, more roots may appear to be advantageous for plants in dry regions, but this is likely to arise at the expense of leaf production. Minimization of $r_i$ by heavy investment in photosynthetic enzymes may seem desirable to maximize $WUE$ in C$_3$ species, but what is the cost to the rest of the plant of the heavy investment of nitrogen in leaves that this necessarily involves? For plants in natural ecosystems the existence of intergenotypic competition will, as already mentioned, modify many strategies. The situation is obviously extremely complex and it will remain difficult to identify convincingly the adaptive significance for productivity of many plant traits in natural ecosystems (43a), although in dry regions the efficient utilization of one environmental resource, water, clearly must take precedence, and there is progress. For example, the field behavior and distribution of CAM plants in the arid zone shows satisfying agreement with what is now known about the structure and function of these plants (115).

This brief discussion of some of the difficulties of determining strategies and adaptations in plant behavior in natural ecosystems has an important bearing upon discussion of these questions in the context of crops and, to a lesser extent, improved pastures. In crops, selection and its goal is determined by man; the general goal is the maximization of yield of economic product, which usually, but not always, coincides with maximization of primary productivity. Also, there is concern not only with the determination of present levels of yield and productivity, but with improving these levels and hence with better adaptations for water-limited environ-
ments. The difficulty mentioned before of looking at adaptations out of context and ignoring the opportunity costs remains, but is not as great with crops, because being monospecific, they are less complicated by effects of competition. Certain major constitutive adaptations are widespread in crop plants, such as the annual herbaceous life form, a high harvest index associated with strong reproductive sinks, large seed size and, for many semiarid situations, earliness associated with a reduced vegetative phase. However, the significance of many other features of crop plants, advanced in the literature as desirable adaptations for water-limited environments or useful in drought resistance, is not well established. The value of awns in wheat and barley in dry situations is probably an exception to this rule. In a way, the situation with respect to crops resembles that of natural ecosystems where life form relationships and some other statistical associations with aridity are recognized, but where within any life form and environment great diversity usually exists (27, 43a). Similarly with crops within the context of general adaptations mentioned above, there seem to be many routes to high dryland productivity. The difference in the case of crops is that it is probable that man has yet to find the best way to obtain the greatest possible productivity in semiarid environments. Also with crop plants it is feasible to test the effect of morphological and physiological traits on productivity through the use of isogenic lines and isogenic populations. However, the research effort in breeding and physiology required is substantial (e.g. 152, pp. 13, 311). Mathematical modeling, in particular dynamic whole community (crop) modeling, has been proposed as a tool in this regard (49, 94, 167), and there is little doubt that such modeling will be easier in the case of monospecific communities such as crops than in most natural ecosystems.

Our attempt here to consider plants both in crops and in natural ecosystems has further implications for the improvement of crop productivity in semiarid regions. First, it has become clear that studies dealing with aridoactive plants during long dry periods when, because of low available soil water, they are basically operating in a survival rather than production mode has little relevance to crop productivity or to the response of crop plants to water shortage within the growing season (161). Yet thinking on drought resistance in crop plants appears to be considerably influenced by the survival strategies seen to operate in the case of aridoactive plants. More benefit may be gained by comparing the crop plants to the group of plants from which most were derived; namely, the herbaceous annuals of the semiarid zone. Evolution of herbaceous annuals in semiarid plant communities may have led, on the one hand, to features which are unsuited to modern agriculture. This could arise because competitiveness is favored in the former situation, or because the environment of modern agriculture (e.g. soil fertility, water supply, temperature, or photoperiod) is different. It is possible that some less obvious of these unsuitable features are still present in modern crop cultivars and that their elimination would further increase agricultural productivity under dry conditions. Possible examples of such undesirable traits have been mentioned: (a) excessive rooting leading to premature exhaustion of soil moisture reserves (117, 119); (b) too great a sensitivity of seed number to lowered $\psi_{\text{plant}}$; (c) unnecessary photoperiodic control of flowering date.
On the other hand, it has been suggested that valuable unexploited adaptations to water limitation exist among annual plants, in particular the progenitors of today's crops, in semiarid natural ecosystems (12, 63). Such adaptations could have been lost if the selection history of the particular crop was dominated by consideration of traits not related to productivity (e.g. grain quality, convenience of harvest, etc) or by use of humid environments. Hall, Foster & Waines (63) have recently pointed to the surprising lack of research on drought resistance mechanisms in the progenitors of modern crop cultivars. The recent discovery of very high rates of C$_3$ photosynthesis in a herbaceous desert annual (103), along with Tsunoda's emphasis upon the importance of high photosynthetic rates for adaptation to xeric environments (86, 158), may point to one useful avenue for improving crop plants for semiarid regions.

While we have been emphasizing the difficulty of knowing the exact adaptive significance of plant traits for performance in dry environments, we do not wish to obscure the fact that the approach to water-limited plant productivity represented in Equations 1 and 2 is an important guide to this problem. Some suggestions for improving dryland crop productivity derive directly from simple considerations of the relationships. For example, the seasonal march of rainfall, evaporation, and likely WUE in a mediterranean climate suggest that it is very difficult to store enough water in the soil to be able to grow a satisfactory summer crop of a C$_3$ plant like sunflower (*Helianthus annuus*), traditionally a summer crop of higher latitudes. For increased sunflower yields in a mediterranean environment it is suggested that research needs to be directed toward cold resistance in order to permit earlier planting in the spring and, among other advantages, growth when WUE is more favorable, rather than toward increased drought resistance (R. W. Downes, personal communication).

Of greater general importance is the fact that the simple model of productivity adopted here provides a sound framework for more detailed modeling of community productivity in dry regions, as exemplified by the work of van Keulen (166, 167). While more environmental and plant variables have been included in van Keulen's model, the objective is still to work with as few variables as are necessary for the precision required, on the assumption that these will be the most important for water-limited productivity (167). Such variables, or key determinants as we termed them earlier, assist in the identification of areas of the ecosystem in which increases in productivity are more likely to be obtained. Moreover, they help identify areas in which more detailed physiological research is likely to be the most useful for improved understanding of productivity at the community level of organization. Authors have lamented the lack of connection between physiological research on the effects of water deficit at the cellular and tissue level and phenomena in the field, such as water influences on productivity or crop yield (71, 146). It has been suggested that bridges between these levels of organization will come from models which start with phenomena at the tissue level of organization and integrate all the observed responses and interactions until the behavior of the whole plant and ultimately the whole community is derived (71). However, the possibilities of success in the short term with this approach seem very limited (43a). It is a truism to
state that the ecosystem, whether natural or agricultural, is much more than the sum of all its component parts. On the other hand, we would emphasize that there are attributes of the whole ecosystem which are much simpler than is suggested by contemplation at a lower level of organization of all of the component parts of the ecosystem. Water-limited productivity is one of these attributes.

Thus the approach used in this review has aided the identification of some areas in which better physiological information would be of great benefit to understanding and perhaps improving the plant productivity of dry regions. These include the ability of roots to compete with evaporation in the surface layers of the soil, and the causes of available water being left in the root zone at maturity under annual communities in apparently water-limited environments. Under the topic of WUE, the effect of slow drying and hence gradual reductions in $\psi_{plant}$ as occur in the field, and the significance of the stomatal response to humidity are important questions. The mechanism by which lowered $\psi_{plant}$ affects root/shoot allocation is unclear and, with regard to stress effects on seed number, the relative roles of reduced assimilate supply and of direct stress effects on reproductive organs requires elucidation. Research on all these questions is particularly lacking in the case of the annual herbaceous plants found in natural ecosystems of dry regions.

In summary, we have attempted to present a simple framework in which plant productivity in arid and semiarid zones can be discussed. The first step is quantification of the physical environment, especially with respect to the total water input and the probability of periods of available soil water. The next step is the determination of the fraction of the total water input which is transpired by vegetation. Soil evaporation represents a major loss of water to plants in dry regions so that total transpiration may only be one-half of water entering the soil (see Table 1). The product of transpiration and the efficiency with which the plants use transpiration to assimilate CO$_2$, the water use efficiency, gives in turn productivity. Ambient humidity and the primary photosynthetic carboxylating enzyme (C$_3$ vs C$_4$) are major factors affecting water use efficiency. In the long term, respiratory losses and allocation of assimilate need also to be considered. Allocation strategies can affect water available for transpiration, for example through root growth, and water use efficiency, for example through leaf form and structure. Plants in dry situations, in particular perennials, invest large amounts of assimilate in below-ground structures so that above-ground productivity may differ substantially from total productivity (see Table 1). Similarly, water limitation can alter considerably the harvest index in crops, meaning the fraction of assimilate allocated to yield organs, and hence modify the relationship between crop yield and total productivity.

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