Reducing Water Stress through Ecological Approaches and Crop Characteristics

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Abstract

With the increasing shortage in water supply, maximization of water use efficiency is critical for maintaining sufficient food supply for the steadily growing population in dryland areas. Plants have evolved a variety of ecological strategies, and morphological and physiological traits that allow them to survive in water-limited environments. This paper highlights the importance of some ecological approaches and major crop characteristics in reducing water stress in dryland farming. A deep root system with a high root length density in deep soil layers is useful for extracting water held deep in the soil profile. Intercropping offers a substantial scope for spatial and temporal complementarities of water use especially when the crops involved differ appreciably in their rooting pattern and maturity duration. Fallow, conservation tillage and mulching are examples of soil moisture conservation practices that improve water use efficiency through the increase of water infiltration and soil moisture storage, and reduction of runoff and evaporation. In crop plants, several drought resistance mechanisms and their putative traits have been identified. Important among them are drought escape via appropriate phenology, and dehydration avoidance and tolerance through various root and shoot characteristics. Identification of the moisture environments in drought-prone areas in terms of the amount, duration and timing of rainfall is crucial for utilizing suitable drought resistance mechanisms and implementing appropriate soil moisture conservation practices.

Introduction

About 47% of the earth consists of drylands where the potential evapotranspiration is higher than precipitation. It is inhabited by approximately 20% of the world population. Serious water shortages are developing in arid, semi-arid and dry subhumid areas, where rainfall ranges from 0 to 800 mm with a fluctuation rate between 25 and 100% (Inanaga, 1998).

Rainfed crop production is subject to frequent fluctuations in precipitation and failing rains often result in drought and food deficit. Drought is generally defined as a period or periods during the life of the crop in which the supply of water is too low to meet the evapotranspiration (ET) demand to the extent that the loss in yield is becoming economically unacceptable (Bunting and Kassam, 1988). The great challenge for the coming decades will be to increase food production to secure food for the steadily growing world population, particularly in countries with limited water and land resources.

In drylands, the traditional cropping systems have evolved in such a way as to minimize drought risks, while the genetic characteristics of the local landraces are adapted to maintain minimum production levels under erratic rainfall conditions. Hence, yields and water use efficiency of the local landraces may remain low even during periods of ample precipitation. Crop water use needs to be optimized through a more effective use

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and conservation of rainwater, and by measures to increase crop production.

This paper highlights the major ecological approaches and crop characteristics that can be useful in reducing the effect of water stress in dryland farming.

Reducing water stress through ecological approaches

Water is the most limiting factor to plant growth and ecosystem productivity in arid and semi-arid areas, and it affects considerably species and vegetation distribution. Plants have evolved ecological strategies and a variety of morphological and physiological traits that allow them to complete their life cycles and persist in water-limited environments. The most common mechanisms by which plants can adapt to drought are drought escape, recovery, avoidance and tolerance (Fukai and Cooper, 1995). Diverse rooting profiles may limit competitive interactions among perennial plants in arid and semi-arid environments and may be one explanation for species coexistence (Fowler, 1986). At spatial level, neighboring plants may aggravate water stress by interfering with water uptake or they may alleviate water stress by ameliorating the microclimate. The mechanism proposed for the negative interaction is that one individual uses water more rapidly or more efficiently than others. Positive effects have been attributed to the amelioration of the microclimate and nocturnal transport of soil moisture from deep to shallow layers. The shade provided by the canopy of one individual also reduces the evaporative demand and, hence, water stress on individuals beneath the canopy.

Deep rooting, intercropping, fallow, conservation tillage and mulching are different examples of ecological approaches to cope with limited water in dry environments.

Deep rooting

Deeply rooted woody perennials can overcome periods of insufficient or absence of rainfall by using groundwater or water stored deep in the soil from previous rains (Weltzin and McPherson, 1997). However, development and maintenance of an extensive root system is costly from the viewpoint of energy and may decrease the yield potential. While shallow-rooted plants are very effective in capturing moisture from growing season precipitation, they regularly experience wide fluctuations in soil moisture that limit photosynthesis. On the other hand, deep rooting has been reported to be associated with the improved performance of sorghum and wheat under water stress conditions (Wright and Smith, 1983). Root depth in cereals is generally associated with a small number of main thick axes. Such a fibrous root system is often seen in upland rice, which has a deeper root system than lowland rice. Yoshida and Hasegawa (1982) observed large variations among rice lines in root length density (RLD) and concluded that lines with a high RLD below 30 cm have deeper roots. The ratio of deep-root to shoot was used as an index for drought resistance as there was a positive correlation between this ratio and field evaluation of drought resistance (Fig. 1). Limited tillering in rice has also been found to be associated with deep rooting. Although a direct relationship between RLD and water extraction is rarely demonstrated, Lilley and Fukai (1994) showed that variation in water extraction among four rice cultivars was directly related to variation in RLD, and that the water extraction rate increased with increased RLD (Fig. 2).

Rice lines with long roots tend to show a high leaf water potential and delayed leaf senescence that may result in larger grain yield under drought (Mambani and Lal, 1983). Although rice cultivars with the greatest root length performed better than others under mild stress conditions, there was no direct relationship between the RLD and grain yield when there was only one period of prolonged drought (Fukai and Cooper, 1995). It is likely that the advantages of lines with large root systems would be greater under intermittent stress.

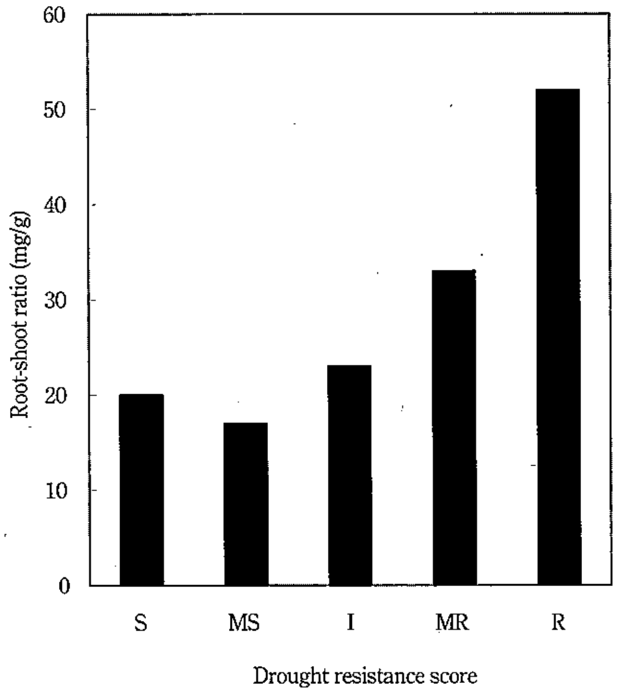

Fig. 1 **Relationship between root-shoot ratio and drought resistance score in rice lines (where S= susceptible, MS= moderately susceptible, I= intermediate, MR= moderately resistant, R= resistant)(Adapted from Yoshida and Hasegawa, 1982).**

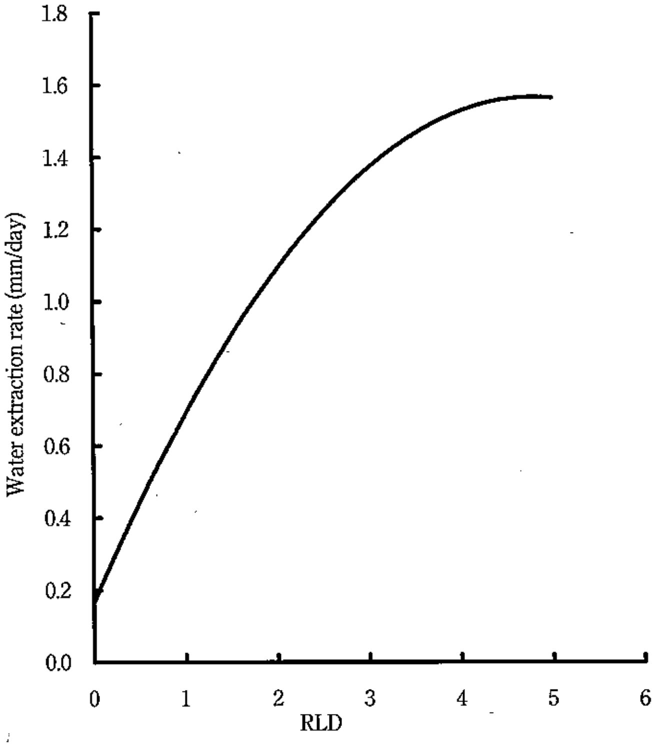

Fig. 2 **Relationship between water extraction rate and root length density (RLD) in four rice cultivars (Adapted from Lilley and Fukai, 1994).**

In certain soils, a hardpan can limit deep root growth and the capacity for hardpan penetration by roots becomes a critical factor in drought resistance. The factors, which may support axial root force and hardpan penetration, have not yet been elucidated.

Intercropping

Diversification of farming is an old but an effective approach to reduce the risk associated with farming in unpredictable environments. Intercropping is a traditional and successful approach to crop diversification on a single piece of land, where two or more crops are grown together in various possible configurations. Intercropping, agroforestry, and mixed and relay cropping offer substantial scope for spatial and temporal complementarities of water use. However, this is likely to be limited unless the species involved differ appreciably in their rooting pattern or maturity duration. The former permits at least partial exploitation of different soil layers, while the latter allows continued extraction of moisture following harvest of the shorter duration component. Total water use by intercrops is often slightly different from that by sole crops, particularly when water losses from land left bare after harvest of the shorter duration component, are taken into account (Morris and Garrity, 1993). Substantial improvements in water use may also occur when species with complementary root distributions are used. In rice/pigeonpea intercropping system (Jena and Misra, 1988), roots of rice were able to deplete water only to a depth of 60 cm, while the deep roots of the sole pigeonpea crop and intercrops were able to extract more water from the lower layers of the soil profile to meet the higher ET demand (Table 1).

Table 1 Components of soil water balance for sole crops of rice and pigeonpea, and intercrops grown in two different row arrangements

	Soil water depletion (cm)				ET	Grain yield
	Soil depth (cm)				(cm d^{-1})	(kg ha^{-1})
	0-30	30-60	60-105	0-105		
Rice (R)	0.75	0.39	0.09	1.23	0.19	625
Pigeonpea (PP)	0.87	0.42	0.45	1.74	0.86	862
R + PP (1: 2)	0.87	0.51	0.45	1.83	0.45	450 + 850
R + PP (2: 5)	0.66	0.48	0.59	1.73	0.27	410 + 737
SE (mean)					0.107	8.7

Adapted from Jena and Misra, 1988.

Intercropping may increase the proportion of available water used for transpiration because the presence of a C4 cereal results in more rapid canopy development and reduced soil evaporation. However, this potential benefit must be offset against the risk of water depletion prior to maturity. Finally, intercropping may confer microclimatic benefits including partial shade and reduced evaporative demand on the shorter components, mostly C3 species with a relatively low photosynthetic light saturation point. In such circumstances, partial shade may not affect assimilation appreciably.

Fallow, conservation tillage and mulching

Increasing storage of soil moisture by fallow system with or without conservation tillage is a standard practice in dryland farming. The main benefit of the fallow is the increase of water availability through storage of water in the absence of crop growth. Other benefits include improved soil nutrient availability and eradication of certain soil-borne pests. The work conducted in Israel by Bonfil *et al.* (1999) has shown that wheat grain yield and WUE can be increased in arid zones with annual precipitation of less than 200 mm through the use of a wheat-fallow rotation system that is managed by no-tillage (Table 2). However, fallow also has disadvantages such as increased soil erosion, loss of organic matter and under-utilization of land.

Conservation tillage involves the principle of minimized tillage operations to conserve the soil structure and maintain a ground cover by mulch, such as stubble. These practices reduce water runoff and increase water infiltration. Mulching is likely to decrease soil and water erosion, increase the content of organic matter in soil, reduce evaporation and increase soil water content. Unger (1978) reported that 8- and 12- t/ha wheat straw mulch treatments increased the amount of available soil water at planting, WUE and sorghum grain yield by about or more than two-fold (Table 3). In another study, Amir and Sinclair (1996) reported substantial increases in grain yield and WUE due to mulching and fallowing in the drought years of 1989-90 and 1993-94 (Table 4). While the benefits of conservation tillage are well documented, it has also been noted that crop residues under this system may promote the occurrence of certain crop diseases and outbreaks of insect pests.

In compacted soils where hardpan is a problem, deep tillage has been found to be very useful in improving soil moisture storage and increasing grain yield. In a compacted sandy clay soil in Sudan, Omer and Elamin (1997) reported remarkable increases in soil water storage and grain yield of sorghum due to chisel plowing as compared to the no-till and other tillage systems (Table 5).

Table 2 Effect of tillage and crop rotation on wheat grain yield and water use efficiency

Year	Rain (mm)	Crop rotation †	Tillage ‡ system	Grain yield (kg ha^{-1})	WUE # (kg ha^{-1} mm^{-1})
1994	163	WF	CT	2130 b	10.4
	163	CW	CT	930 c	6.5
	163	CW	NT	2770 a	18.5
S. E.					0.48
1996	215	WF	CT	650 c	3.0
	215	WF	NT	1060 a	5.2
	215	CW	CT	710 c	3.6
	215	CW	NT	840 b	4.3
S. E.					0.25
1997	150	WF	CT	1250 b	7.8
	150	WF	NT	2080 a	12.4
	150	CW	CT	530 d	4.0
	150	CW	NT	930 c	6.5
S. E.					0.37

†WF, wheat after fallow; CW, continuous wheat.
‡CT, conventional tillage; NT, no tillage.
#WUE, water use efficiency = grain yield / available water (precipitation + available soil water at sowing).
Within years, means followed by the same letter are not significantly different according to DMRT.
Adapted from Bonfil *et al.*, 1999.

Table 3 Effect of straw mulch rates on soil water content at planting, water use efficiency (WUE), and sorghum grain yield

Mulch rate (t ha^{-1})	Soil water content at planting† (mm)	WUE ‡ (kg ha^{-1} mm^{-1})	Grain yield (kg ha^{-1})
0	123^{c}	5.56	1780^{c}
1	159^{b}	7.30	2410^{b}
2	157^{b}	7.37	2600^{b}
4	172^{b}	8.35	2980^{b}
8	205^{a}	10.08	3680^{a}
12	214^{a}	11.50	3990^{a}

† Determined to a 1.8-m depth.

‡ Values based on average yields and average total growing season water use.

Means within the same column followed by the same letter are not significantly different at the 5% level according to DMRT.

Data are averages of three years (1973-74, 1974-75 and 1975-76).

Adapted from Unger, 1978.

Table 4 Effect of crop rotation and mulching on wheat grain yield, water use efficiency (WUE) and ratio of transpiration to evapotranspiration (T/ET)

Year	Seasonal rainfall (mm)	Manage - ment†	Grain yield (kg ha^{-1})	WUE (kg ha^{-1} mm^{-1})	T/ET (kg ha^{-1} mm^{-1})
1989-90	243	CW	1200	4.9	0.24
	243	CW + SM	2510	10.3	0.37
	243	FW	2450	10.0	0.31
	243	FW + SM	3140	12.9	0.41
LSD (0.05)			660		
1993-94	163	CW	930	5.7	0.31
	163	CW + SM	2820	17.3	0.76
	163	FW	2210	13.6	0.64
	163	FW + SM	3110	19.0	0.75
LSD (0.05)			1080		

†CW, continuous wheat; FW, wheat after fallow; SM, straw mulch (4,000 kg of standing stems and flat straw residues).

Adapted from Amir and Sinclair, 1996.

Reducing water stress through crop characteristics

Several plant traits affect crop water use efficiency through various aspects such as timing of crop development, efficiency of roots to extract water, effective transpiration and ability of plant to withstand stress. The most useful traits in reducing water stress are listed in Table 6 and briefly discussed below:

Table 5 Effect of tillage system on soil water storage and sorghum grain yield in a compacted sandy clay soil in western Sudan during 1992-1995 growing seasons

Tillage system	Mean soil water storage† (cm)	Grain yield (kg ha^{-1}) 1992-93	1993-94	1994-95	Mean
Chisel	7.27	1284	1835	1226	1448
Broadbed and furrow	5.95	551	1260	716	842
Ridge-furrow	5.45	1217	398	490	701
No-till	3.80	307	250	341	299
LSD (0.05)					489

† Mean of three years.

Adapted from Omer and Elamin, 1997.

Table 6 Major plant traits, their resistance mechanisms and suitability in terminal and intermittent drought stress environments

Trait	Resistance mechanism	Timing of drought stress
Phenological		
Early maturity	Escape	Terminal
Developmental plasticity	Escape, recovery	Terminal, intermittent
Morphological		
Deep-root	Escape, avoidance	Terminal, intermittent
Cuticular wax	Tolerance, avoidance	Terminal, intermittent
Erect leaf	Tolerance	Terminal, intermittent
Reduced leaf area	Tolerance	Terminal, intermittent
Stay-green	Tolerance, recovery	Terminal, intermittent
Physiological		
Osmotic adjustment	Tolerance	Terminal, intermittent
Stomatal conductance	Tolerance	Terminal, intermittent

Phenological traits

Phenology is the timing of major developmental events in the life of crop from germination to seed formation. These events are mainly affected by photoperiod and temperature and to a lesser degree by water availability. Mild water deficit accelerated flowering of wheat by a few days but not that of sunflower (Turner, 1982). Variation in the response to photoperiod can be utilized to optimize the growth of a crop to a period of favorable water supply. Such adjustment has been found to be possible in sorghum and rice (O'Toole and Chang, 1979), where flowering and grain filling of cultivars coincided with the wet season. However, the most notable progress has been achieved by lessening the sensitivity of crops to photoperiod and by shortening the growing season. Cultivars with short growing duration and fast development usually avoid late water shortage. Nevertheless, in cases of adequate water supply, early maturing varieties often give lower yields than late maturing ones. Therefore, flexibility in development should be considered in breeding early maturing cultivars for drought-prone areas in such a way that the cultivar will be able to extend its growing period if further water becomes available. This flexibility provides efficient use of water for seed development, ensures some reproductive turnover even in extremely dry years, and enables crop to maintain high yields when rains become more abundant.

Morphological traits

Roots: An extensive root system is desirable for efficient water extraction in different crops. Its significance in reducing water stress has been highlighted previously.

Leaf area: Reduction in leaf growth under water stress is a major mechanism by which plants reduce their water requirement. Narrow leaves in wheat and super-okra leaf type in cotton are considered to be water stress-adaptive traits (Blum, 1982). Total leaf area can also be adjusted during water stress through shedding of old leaves. Many of the drought-deciduous desert plants drop their leaves during drought and sprout new ones after rain. The associated effect of reduced leaf area on crop productivity is controversial and should be of little significance as productivity under water stress is expected to be below the potential (Blum, 1982).

Leaf angle and orientation: Leaf orientation affects the energy load on the leaf and consequently the leaf water status. Upright narrow leaves should be selected as a drought-adaptive trait instead of wide lax leaves. Variation in leaf angles and orientation under water stress was reported in legumes and cereals (Blum, 1982). In addition, leaf rolling under drought stress has been reported as a resistance trait in rice and sorghum.

Cuticular wax: It forms a barrier between the plant and its environment. Thick cuticular wax reduces the energy load on leaves and, hence is very effective in limiting water loss from aerial parts of the plant. The thickness of the cuticle varies with species, genotype and environment. Genetic variation in the thickness of cuticular wax was observed in maize, oats, rice and sorghum. Drought susceptibility in wheat was found to be associated with a low waxiness (Fischer and Wood, 1979).

Retention of green leaves: Stay-green trait is often used as selection criterion for drought resistance in crop plants on the assumption that genotypes possessing this trait produce a higher yield than others in a dry environment. Such genotypes also show a greater potential for drought recovery. Stay-green under water stress has been reported in sorghum, rice and other crops (Fukai and Cooper 1995; Crasta *et al.*, 1999).

Physiological traits

Osmotic adjustment: Osmotic adjustment affects the maintenance of plant tissue turgor under water stress. It allows further reduction in water potential against the ET demand before the wilting-point is reached. Osmotic adjustment is mostly due to increases in the concentrations of a variety of common solutes, including organic acids, sugars and ions. Progress in water stress needs to be sufficiently slow for solute accumulation and, hence, the value of osmotic adjustment as a drought resistance mechanism is limited in plants exposed to prolonged water deficit. Osmotic adjustment occurs both in leaves and roots. It can enhance the turgor of root meristems, and maintain root growth under conditions of soil water depletion. Osmotic adjustment reduces the rate of leaf senescence and enhances both dehydration avoidance and tolerance. Genetic variations in osmotic adjustment were observed in sorghum, wheat and other crops (Blum, 1982). However, the use of osmotic adjustment to improve crop performance in drought-prone areas is yet to be realized.

Stomatal conductance: The ability of stomata to regulate water loss provides an important mechanism for reducing water loss during drought. There is a genetic variation in the relationship between stomatal conductance and leaf water potential. Maintenance of dehydration avoidance through stomatal closure results in a negative effect on crop productivity through reduced CO_2 exchange. However, studies on sorghum and wheat indicated that maintenance of dehydration avoidance is possibly due to osmotic adjustment of stomata under stress (Ludlow, 1980). Reduced stomatal conductance through various characters such as frequency, length and behavior of stomata increases WUE. Stomatal responses to leaf dehydration vary widely within and between species. In drought-tolerant cowpea and cassava, stomata are unusually responsive to water deficit, and stomatal conductance and transpiration decrease so much that the leaf water potential may remain constant during drought.

Conclusions

* Agrometeorological work targeting the various moisture environments of the drought-prone areas in terms of the amount, duration and timing of rainfall is needed so that the most appropriate approaches for reducing water stress can be devised.

* Intercropping offers substantial scope for spatial and temporal complementarities of water use, especially when the crops involved differ appreciably in their rooting pattern or duration.

* Fallow, conservation tillage and mulching are examples of ecological approaches for soil moisture conservation that improve WUE through the increase of water infiltration and soil water storage, and reduction of runoff and evaporation.

* In crop plants, several drought resistance mechanisms and their putative traits have been identified. Important among them are drought escape via appropriate phenology, root characteristics, specific dehydration avoidance and tolerance mechanisms. A deep root system with high RLD in deep soil layers is useful for extracting water held deep in the soil profile.

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