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Resource capture and utilization in intercropping: water

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ABSTRACT

The capture and utilization of water by sole and intercrops are compared by decomposing crop production/unit area into uptake/unit area (capture) and production/unit uptake (utilization efficiency). Data are from published studies. Comparisons are made by contrasting data from the intercrops against weighted means from the sole crops, with weights based on the proportion of each species in the intercrop. Water capture by intercrops differs from water capture by sole crops only slightly (usually between −6 and +7%). Water-utilization efficiency by intercrops, however, greatly exceeds water-utilization efficiency by sole crops, often by more than 18% and by as much as 99%. Four mechanisms that may account for the consistent increases in water-utilization efficiency by intercrops are postulated on the basis of crop water relations theory but empirical data from intercropping studies are not adequate to test them. The water-utilization efficiency response by intercrops to increased levels of seasonably available water differs from the response by sole crops. Variation in plant density often affects water-utilization efficiency.

INTRODUCTION

During the past two decades, yield increases from intercropping have been observed in a substantial number of studies in semi-arid and monsoonal environments. On the basis of these and other studies, intercropping has been advocated to increase crop productivity and to improve yield stability in environments where water stress occurs frequently.

Two intercropping strategies have been described which are relevant for the discussion on water capture and utilization by crops (Willey, 1979). In the first strategy, a primary crop component, intended to yield near its full potential, is planted at optimum plant density. A secondary component is planted at a density often lower than its optimum and is harvested either much

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earlier or later than the primary species. In this strategy, competition from the secondary crop against the primary one is weak or the primary crop can recover from it. This first strategy is typical in monsoonal or semi-arid environments where the late-maturing crop will deplete most of the available soil water as it grows into the early dry season. In the second strategy, the component crops have a greater degree of concurrent growth (but seldom are completely concurrent). Both species usually are planted in time to avoid late-season water deficit. When adjusted for proportional crop area, planting densities usually are somewhat greater than those optimal for sole crops. Often, the expected yield of each species is below that of a sole crop. The boundary between these two strategies is not well defined; therefore, a continuum exists between them.

THE AGGREGATE PROCESSES OF CAPTURE AND UTILIZATION

Water capture and utilization are examined by decomposing crop production (dry weight/unit area) into two aggregate processes:

Dry weight/unit area = (unit mass of water uptake/unit area)*

(dry weight/unit mass of water uptake)

Water capture or use (WU) is the first of these processes and water-utilization efficiency (WUE) is the second process.

The analytical approach to examination of resource capture and use has similarities to those used by van Keulen and van Heemst (1982) and Trenbath (1986). However, yield and uptake data for each intercrop component are not required as in Trenbath's analytical method. Moreover, the less complex approach is adequate for our purposes.

In field research, WU has commonly been defined as the ET (evapotranspiration) component of a water balance:

$$P+I=S_{init}-S_{fin}+R+D+ET$$

where P (rain), I (irrigation), S_{init} (initial stored soil water) and S_{fin} (final stored soil water) are always measured. Runoff (R) and D (drainage) are occasionally measured or, with valid reason, regarded as zero. The ET component is estimated by difference. When determined this way, it appears to be a widely accepted as well as a valid measure of WU. All water balance components are reported in units of depth.

We define the pool from which WU is captured as seasonally available water (SAW). Using P, I, S_{init} and R from the equation above, and S_{low}, which is the content at the lower bound of plant-available soil water, $SAW=P+I+S_{init}-S_{low}-R$. The concept is similar to "effective rainfall" and, except for the adjustment for runoff, is the same as that used by Singh and Russell (1981). Seasonally available water is equal to $WU+S_{fin}-S_{low}$ and, thus, it is the sum of WU and the quantity of unused available water at harvest. Therefore, the proportion captured will depend on the lower bound estimate. The significance of that estimate is evident when WU/SAW is rewritten as $WU/(WU+S_{fin}-S_{low})$. If S_{low} is unrealistically small, WU/SAW cannot approach 100%.

To calculate changes in water capture by intercrops relative to capture by sole crops, we defined the following:

$$\Delta WU=[WU_{ic}/(P_aWU_{sa}+P_bWU_{sb})]-1 \quad (1)$$

where the subscript ic indicates the intercrop of crops C_a and C_b, sa indicates sole crop C_a and sb indicates sole crop C_b. The proportion of C_a in the intercrop (P_a) is determined as $P_a=A/(A+B)$, where A is the density of C_a in the intercrop relative to its sole-crop density; B is analogously defined for C_b. The same procedure is used to calculate P_b for C_b. $P_a+P_b=1$. Thus the denominator in Eq. 1 is a weighted sum of sole-crop WU. The water use change, ΔWU, is discussed in its percentage form.

To calculate changes in water-use efficiency, we defined the following:

$$\Delta WUE=\{[Y_{ic}/WU_{ic}]/[(P_aY_{sa}/WU_{sa})+(P_bY_{sb}/WU_{sb})]\}-1 \quad (2)$$

where the Y is yield and the remaining subscripts and terms are defined as for Eq. 1.

COMPARISONS OF WU BY SOLE AND INTERCROPS

In the 10 studies summarized in Table 1, WU by intercrops ranged from 125 to 585 mm. The wide WU range is attributable primarily to water availability differences. For example, rainfall during Rees' (1986a) experiments ranged from 84 to 140 mm whereas during Natarajan and Willey's (1980a) experiment it was 575 mm. In Kushwaha and De's (1987) study, WU was low because crops were grown in northern India during the winter when evaporative demand was low. Hulugalle and Lal (1986) reported on one experiment in a season that received 225 mm rainfall and another in a season that received 559 mm. Wide ranges between and within studies were expected because many factors, including SAW, influence WU.

Regardless of the wide range of conditions, WU by intercrops differed from WU by sole crops by only −6 to +7% in all but two studies. In addition to the 10 studies in Table 1, two other studies reported data that permitted only approximate ΔWU determinations. The approximated ΔWU of both these studies were in the range of those in Table 1. In experiments on irrigated wheat

TABLE 1

Water use (WU) and water-use efficiency (WUE) by intercrops and ΔWU and ΔWUE of intercrops relative to WU and WUE by sole crops

Reference	WU (mm)	ΔWU (%)	WUE (kg/mm)	ΔWUE (%)	Species	Concurrency[1] (%)	Crop proportion[2]	Yield measure
Rees (1986a,b)[3]	125 to 198	−2 to 6	0.6 to 2.9	−25 to 0	Sorghum+cowpea	70	93:22[4]	Grain
	129 to 204	1 to 7	0.2 to 2.2	−42 to 3			100:133[5]	
Singh et al. (1988)[6]	517 to 571	6 to 7	8.0 to 13.0	−8 to 55	Pearl millet+cowpea	100	100:100	Dry matter
Morris et al. (1990)[7]	177 to 271	2 to 5	12.0 to 12.6	25 to 53	Sorghum+cowpea	71	50:50	Grain
Hulugalle and Lal (1986)[8]	248 to 554	−5 to 0	1.6 to 4.2	4 to 99	Maize+cowpea	100	50:50, 50:30	Grain
Kushwaha and De (19887)[9]	199 to 222	−6 to 0	9.8 to 16.4	4 to 39	Mustard+chickpea	86	33:67, 67:33	Grain
Suwanarit et al. (1984)[10]	362	4	20.5	78	Maize+mungbean	74	100:100	Dry matter
Natarajan and Willey (1980a,b)[11]	585 (168)	15	8.3	38	Pigeon pea+sorghum	50	100:100	Grain
Reddy and Willey (1981)[12]	406	15	21.4	18	Pearl millet+groundnut	78	75:25	Dry matter
Singh (1985)[13]	210 to 435	5 to 6	6.7 to 7.1	17 to 31	Pearl millet+cluster bean	not indicated	100:30, 100:60	Grain
	263 to 474	0 to 5	7.3 to 7.6	22 to 33				

[1] Percent of time that the earlier-harvested species was in the field with the later-harvested species.

[2] Crop proportions relative to respective sole crop plant densities.

[3] Botswana; very dry; narrow uptake range (125 to 200 mm); 4 expts. in 2 years on 2 soils.

[4] 1.5-m rows.

[5] 0.75-m rows.

[6] India; no difference for within row vs. alternative rows; 2 years.

[7] Philippines; post-wet season rice fields; 2 years.

[8] Nigeria, shallow gravelly soil; 1 dry and 1 wet season.

[9] India; no difference between the two replacement series; 2 years.

[10] Thailand; wet season with abundant rainfall; 1 year.

[11] India; means over populations; value in parenthesis is WU of the intercrop after sorghum harvest; 1 year.

[12] India; wet-season rainfall about 50% above average; 1 year.

[13] India; values in the second row are from treatments receiving a single 70-mm irrigation; 2 years.

(*Triticum aestivum*)+mustard (*Brassica juncea*) and wheat+chickpea (*Cicer arietinum*), ΔWU ranged from 3 to 7% (Mandal et al., 1986). In the second study, ΔWU for intercropped wheat+mustard was −3% when determined on the basis of WU of the sole wheat crop (Sinha et al., 1985). Water use by sole mustard was not reported but other studies indicate that it would have not been more than 15% lower than that of wheat.

Two small exceptions to nearly equal WU by intercrop and sole crops were reported. In the first of these (Reddy and Willey, 1981), WU by sole pearl millet (*Pennisetum glaucum*) was 18% less than that by sole groundnut (*Arachis hypogaea*) and 25% less than that by the intercrop. The leaf area index of sole pearl millet exceeded 2 for only about 20 days of the 82-day crop. In the intercrop, however, pearl millet vegetative development complemented that of groundnut and the combined leaf area index exceeded 2 for about 50 days of the 105-day intercrop. The investigators attributed differences among treatments to differences in evaporation from the soil.

In the second exception (Natarajan and Willey, 1980a,b), the WU difference was nil when it was determined at harvest of the early-maturing species (sorghum, *Sorghum bicolor*) but was 15% when total WU by the late-maturing species (pigeon pea) was used in the calculation. Pigeon pea used water remaining in the profile and from late-season rains which would otherwise be lost by evaporation after harvest of the first crop. At sorghum harvest, sole pigeon pea had used 430 mm, sole sorghum used 434 mm and the intercrop used 417 mm. During the 10 weeks after sorghum harvest, intercropped pigeon pea used 168 mm and sole pigeon pea used 154 mm.

In the studies by Morris et al. (1990) and Kushwaha and De (1987) listed in Table 1, water balances were adjusted for water lost from the fallow plots created by harvest of the earlier-maturing sole crop. Kushwaha and De added fallow period rainfall to the water balance and Morris et al. added evaporation losses from the soil during the fallow period to the balance. These water balance adjustments appear justified because when a dry season is in progress, the potential is nil for using residual water by crops other than those established before rains cease. Had Morris et al. not adjusted for water losses after harvest of the first crop, mean ΔWU for their study would be 18%, not 4%. Without the adjustment in Kushwaha and De's study, it would be 2%, not −4%.

After considering the exceptions and taking note of reasons for computing WU differently for intercrops composed of species with contrasting maturities, it is apparent that ΔWU is usually near zero for most intercrop combinations. Had WU by sole sorghum in the Natarajan and Willey (1980a,b) study been adjusted for water loss following harvest of the early-maturing species, the exceptions would even be fewer.

Although evidence for similarities among WU from sole and intercrops is abundant, a study by Jena and Misra (1988) suggests that differences may be large when species contrast in root distributions as pigeon pea and rice (*Oryza sativa*) do. They reported WU during brief dry periods that occurred two months after planting. During these periods, WU by sole rice was 2.8 mm/day, by sole pigeon pea was 7.9 mm/day, and by the intercrop was 4.2 mm/day. Sole pigeon pea removed an average 2.5 mm water/day from below the 1-m plane whereas an average 1.4 mm water/day drained through it under the sole rice crop. Under the intercrop, average drainage through the 1-m plane occurred at the same rate as that under rice in one year. Barely perceptible upward fluxes (6% of the flux under pigeon pea) were observed in the other year. Reasons for low WU by intercrops when pigeon pea was planted at full density were not offered but it is probable that vigorous early rice growth suppressed pigeon pea development. Intercropped pigeon pea grain yields were reduced only 11% by competition with rice which is consistent with this conjecture. It is probable that the suppressed pigeon pea used water removed from deep in the profile after rice harvest to expand vegetative growth as well as to maintain leaf water potential during reproductive growth. Had a season-long water balance been recorded, WU by rice probably would have been substantially less than those of sole pigeon pea and the intercrop because of drainage losses under rice.

Management factors and WU

If WU by intercrops and sole crops are nearly equal, interactions between management factors and cropping method (i.e., management factor × (intercrop vs sole crop) interactions) should occur only for exceptional cases. Several studies support this statement but data are sparse. Singh et al.'s (1988) study suggested none for degree of intimacy (alternate rows of each species vs species mixed within rows) and Natarajan and Willey's (1980a,b), Rees' (1986b) and Kushwaha and De's (1987) none for plant density variation. Moreover, Singh (1985), Mandal et al. (1986) and Singh et al. (1988) did not report a significant interaction with cropping method with irrigation although yield did respond to irrigation in two of the three studies.

A similar conclusion regarding interactions can be drawn for intercrops composed of similar combinations of species, especially when changes are limited to secondary species in the crops combinations. Support for this statement is found in a study of pearl millet intercropped with soybean (*Glycine max*) or with cowpea (*Vigna unguiculata*) (Singh et al., 1988) and in a study of pigeon pea intercropped with mungbean (*Vigna radiata*) or with cowpea (Hegde and Saraf, 1979). In the latter study, however, when blackgram (*Vigna mungo*), a species that matured 15 to 18 days later than mungbean and cowpea, was used, only 20 mm more water was removed from the 0.45 to 0.90 m depth. The studies by Singh et al. (1988) and Hegde and Saraf (1979) suggest that secondary species effects on WU will be small, except when the characteristics of alternatives contrast significantly as in the rice and pigeon pea study by Jena and Misra (1988).

Seasonally available water and WU

Intercropping is advocated for environments where water stress is likely to occur. In most of the cases reviewed, however, WU by sole and intercrops differed only slightly, especially when growth was largely concurrent. Therefore, WU/SAW of sole and intercrops did not differ within studies. However, there were differences among the five studies from which data were available to compute WU/SAW; values ranged from 61 to 100%.

Sparse evidence suggests that WU/SAW decreased as SAW increased. In Singh et al.'s (1988) study, WU/SAW decreased as irrigation increased but an estimated 84% of SAW was used even in the wettest treatment. Water use in the wettest treatment was 47% greater than in the driest. Singh and Russell (1981) compiled detailed water balances for intercropped maize and pigeon pea. During concurrent growth (i.e., during the wet season), capture was 75% in a year when SAW was 573 mm and 58% when it was 868 mm. However, the water available to pigeon pea after maize harvest was similar in both years (293 and 271 mm in the first and second years, respectively), but the corresponding captures by the pigeon pea crop were 82 and 68%. Factors contributing to the difference between capture percentages were not known.

Water use was 60 to 75% of SAW, which is lower than expected for capture of a mobile soil resource, especially in semi-arid environments. The low percentages are probably partly due to the methods used to estimate S_{low}. Even though S_{low} was adjusted for depth in Singh and Russell's (1981) study, significant available water remained between the 0.6- and 1.5-m depths at pigeon pea harvest. In contrast, roots in Hulugalle and Lal's (1986) study were restricted by gravel to a 0.5-m deep profile and root densities throughout the sandy soil were probably sufficient for water removal to highly negative matric potentials and therefore WU/SAW equalled 100%. It is probably unreasonable, however, to expect a single S_{low} estimation method to serve equally well for all soils and all crops.

COMPARISONS OF WUE BY SOLE AND INTERCROPS

Although WUE comparisons among studies summarized in Table 1 are confounded by the measures of production reported in each study (dry-matter yield in some, grain yield in others), the percentage change within a study generally indicated substantially increased WUE due to intercropping. The majority exceeded the 18% reported for a pearl millet+groundnut intercrop which was attributed to a greater fraction of transpiration in ET from the intercrop compared to ET from sole crops (Reddy and Willey, 1981). The negative ΔWUE reported by Rees (1986a,b) and Singh et al. (1988) were exceptions. Rees reported severe plant mortality from water stress. No explanation was given nor was evident to account for the decrease. It was observed in a year when the pearl millet sole-crop dry-matter yield was 6970 kg/ha whereas a positive ΔWUE was observed in a year when it was only 2150 kg/ha. The reason for the large yield difference was not indicated but may be related to a negative response to irrigation as described earlier.

Difference in WUE between studies were large even when similar crop combinations were used (e.g., −42 to +3% by Rees (1986a,b) and 25 to 53% by Morris et al. (1990)). Mean potential ET in Rees' study was 700 mm whereas in the Morris et al. study it was 420 mm.

Mandal et al.'s (1986) graphical data presentation did not permit accurate quantitative WUE estimates and was not included in Table 1. However, the ΔWUE estimated from their wheat+mustard and wheat+chickpea were in general agreement with the percentages shown in Table 1.

Eq. 1 does not indicate how equitably water was shared between components of the intercrop nor does Eq. 2 indicate WUE changes of either component, possibly caused by altered microclimate. Therefore, ΔWU and ΔWUE mask changes that are due to interference by one crop component with another. To determine changes in WU and WUE by each component, estimates of water capture by each are required. However, the methods to separate WU by the intercrops into that used by each component crop are not well developed. None of the reviewed studies, except Trenbath's (1986) for wheat cultivars in mixture, attempted the separation.

Keeping the small differences observed between WU_{ic}, WU_{sa}, and WU_{sb} in mind, the relative yields of crop components data in studies listed in Table 1 and three others (Stewart, 1983; Mason et al., 1986; Natarajan and Willey, 1986) were compared. The comparisons showed that the relative yield of the component that was physically dominating during concurrent growth tended to exceed that of the dominated species. For most intercrops, C_4 cereals were the dominating species and C_3 legumes were the dominated species. Architecture, nitrogen fixation ability and maturity were often confounded with carbon assimilation pathway. When both intercrop components were C_3 species or both were C_4 species, with few exceptions the taller of the two had larger relative yields (Mason et al., 1986; Natarajan and Willey, 1986; Kushwaha and De, 1987). Shading by tall species can have a pronounced effect on photosynthesis of intercropped short plants (Trenbath, 1986). Less well appreciated is the depressing effect of even moderate shade on nitrogen fixation by legumes (Eriksen and Whitney, 1984). The degree of water stress complicates interpretation because it can alter the rankings of relative yields (Stewart, 1983; Natarajan and Willey, 1986). The studies hint at a number of mechanisms that might contribute to the large ΔWUE observed for some intercrop combinations.

Planting geometry and WUE

The effects of plant density, row spacing, intimacy and crop proportion on WUE have been inconsistent. In Kushwaha and De's (1987) study, conducted during a season favoring chickpea yields, WUE by the chickpea sole crop responded to plant density. Water-use efficiency by the intercrop also responded positively to chickpea density (a 15% ΔWUE increase as density increased from 7.5 to 30.0 plants/m^2). In neither year, however, did WUE by the intercrop respond to mustard plant density. Natarajan and Willey's (1980a,b) study showed that variation of either sorghum or pigeon pea plant densities affected intercrop WUE through effects on pigeon pea yield. As noted, Rees (1986b) attributed large negative WUE changes in his study to severe terminal water stress brought on by early water extraction from a limited supply. The ΔWUE for crops in 0.75-m rows was more negative than for those planted in wider rows at a fraction of the plant density. Singh et al.'s (1988) study exhibited no substantial intimacy effect (species in alternate rows vs mixed within a row) on WUE. Singh's (1985) and Hulugalle and Lal's (1986) studies exhibited only small intimacy effects on WUE. Crop proportion also affected WUE, at least in some years (Natarajan and Willey, 1986; Kushwaha and De, 1987).

Seasonally available water and WUE

The sole vs intercrop × SAW interaction is of more interest to agriculturalists than are simple WUE trends with SAW. An understanding of factors contributing to positive or negative ΔWUE in response to SAW would help with the specification of conditions in which intercrops, including selection of component species, should be considered as alternatives to sole crops.

Although no individual study reported WU for sole and intercrops from a wide SAW range, data from two intercropping studies offer insight into responses of intercrops as well as sole crops to SAW. Stewart (1983) estimated water response functions for grain yields of maize and bean (*Phaseolus vulgaris*) sole and intercrops from a linesource sprinkler experiment conducted in a semi-arid environment. Responses were segmented lines: sole bean response to water was linear to about 250 mm after which it plateaued; sole maize response was zero to about 100 mm after which it was linear for the remaining range. Individual intercrop component responses were lower than those of the sole crop (14.6 vs 16.3 kg grain yield/mm applied water for maize and 2.7 vs 10.4 kg grain yield/mm applied water for beans).

According to Stewart (1983), yield responses to ET would follow the same patterns as responses to applied water as shown by studies of the same species in a similar environment. Therefore estimated changes in kg grain yield/mm applied water for intercrops relative to sole crops would be correlated with ΔWUE. When calculated from Stewart's (1983) response equations, intercrop yield changes were −49% for 235 mm of applied water, −1% for 335 mm, 17% for 435 mm and 30% for 535 mm. For this particular crop combination, the intercrop yield response to water exceeded that by the sole crops, apparently because when water applications were small, the intercrops drew down soil water reserves to low levels so that water was deficient during reproductive growth. In this regard, Stewart's data agree with Rees' (1986b) speculation that had the SAW range in the latter's study been larger, WUE of the intercrops would have increased relative to those of the sole crops as SAW increased (i.e., a sole vs intercrop×WUE interaction would have been observed).

Like Stewart (1983), Natarajan and Willey (1986) used a linesource sprinkler to study sole and intercrop responses to SAW. The irrigation+rainfall range was 297 to 584 mm. Crops were sorghum, pearl millet and groundnut, with intercrops arranged in replacement series. Sole sorghum grain yields were most responsive to water and pearl millet grain yields least responsive. Moreover, responses of all sole crops as well as intercrops were essentially linear over the water treatment range. Table 2 shows kg grain yield/mm water and, analogous to ΔWUE, percentage change in kg yield/mm water by the intercrops relative to kg yield/mm water of the component sole crops. Yield/mm water applied for each intercrop (and the sole crops as well) increased as available water increased. However, change of intercrop yield/mm water relative to sole-crop yield/mm varied with crop combination. For the sorghum+groundnut intercrop (33:67 proportion), efficiency relative to that of the sole crops increased as water availability decreased. In intercrops in which pearl millet was one component, changes were not as large nor did percentages follow a consistently increasing or decreasing trend in response to water. One intercrop (pearl millet+groundnut) permitted comparisons among three crop proportions (50:50, 33:67, 25:75). At the lowest water application, WUE and ΔWUE by the intercrops increased and then decreased as pearl millet proportion decreased.

TABLE 2

Grain yield/mm water applied and percentage increase by intercrops composed of sorghum (S), groundnut (G) and millet (M) over sole crops (data source: Natarajan and Willey, 1986)

Water applied mm	Intercrop combination									
	SGG[1]		SM[1]		MG[1]		MGG[1]		MGGG[1]	
	kg/mm	%[2]	kg/mm	%	kg/mm	%	kg/mm	%	kg/mm	%
584	8.2	26	7.9	12	6.3	27	–	–	–	–
420	6.1	94	6.9	35	5.7	57	–	–	–	–
297	4.0	140	4.0	4	3.7	57	5.4	71	4.2	44

[1] SGG=a sorghum:groundnut interceop with a 33:67 proportion; SM=a sorghum:millet intercrop with a 50:50 proportion; MG, MGG, and MGGG=millet:groundnut intercrop with 50:50, 33:67 and 25:75 proportions, respectively.

[2] %=percent change relative to kg grain/mm water applied to component sole crops. See text for detailed description.

Mechanisms contributing to increased WUE

The discussion of WU and WUE data has shown that the benefit of intercropping can in most cases be attributed to increased WUE, not to greater WU. If WUE of intercrops frequently exceed those of sole crops then the mechanisms that influence water and carbon dioxide fluxes may account for the advantages. There are several ways by which intercropping may enhance WUE. Direct empirical observations are not available, but water balance theory suggests four logical insights.

First, intercrops may capture a larger portion of ET as transpiration than sole crops do. Gains in WUE have been frequently observed in agronomic studies on sole crops due to improved crop management, for example, increased nutrient availability or greater plant density (Fischer and Turner, 1978). In these cases it is unlikely that WUE, defined as mg CO_2 assimilated/g H_2O transpired, has significantly increased. Rather, most of the gains are due to an increase in transpiration as a fraction of evapotranspiration (T/ET) because expanded plant cover reduces soil evaporation, particularly during early vegetative development. The analogy with intercropping is clear, since intercrop combinations usually have a total plant density exceeding that of either sole crop and the early-season leaf area indices of intercrops are generally greater, a higher proportion of light is intercepted by the canopy. As noted, Reddy and Willey (1981) estimated that increased WUE by a pearl millet+groundnut intercrop was entirely accounted for by greater T/ET.

The interception of more light by intercrops, especially during the vegetative development phase with a canopy composed of species contrasting in architecture, was also cited by others as a factor contributing to higher WUE (Natarajan and Willey, 1980b; Kushwaha and De, 1987). In these cases it was also linked to the general notion that a lower portion of ET from an intercrop was lost by direct evaporation during early vegetative development. Under extreme water stress, however, enhanced early canopy development can result in negative effects on WUE. Rees (1986b) found that the enlarged vegetative cover from intercropping increased early growth but depleted water reserves more quickly in very dry conditions, exacerbating water stress during reproductive development and depressing WUE. Hulugalle and Lal (1986) reported that water stress reduced vegetative development of cowpea, and thereby reduced ground cover in intercrop treatments.

Second, a crop component with an inherently greater WUE may capture a large portion of WU_{ic} and in so doing, increase its contribution to Y_{ic}, thereby increasing ΔWUE calculated from Eq. 2. As noted earlier, comparisons showed that relative yields of the physically dominating species tended to be larger than those of the dominated species. In most studies, the dominating crops were C_4 species with high WUE and the dominated were C_3 species with low WUE, but these characteristics were often confounded with architecture (above and below ground), N fixation ability, and maturity. A crop component that combines a physically dominating architecture that interferes with growth of the dominated species, captures a large SAW share, and possesses an inherently greater WUE, should increase overall ΔWUE of the intercrop.

Third, the intercrop environment, composed of two crops of differing stature and growth dynamics, may create characteristics that convey favorable direct effects on transpiration efficiency (i.e, biomass produced per unit water transpired). An examination of the physical parameters indicates that WUE is driven by the following relationship at the leaf level:

$$\mathrm{WUE} = (360/\text{delta-e})\,[(r_a + r_s)/(r_a + r_s + r_i)] \qquad (3)$$

where WUE is in units of mg CO_2/g H_20, delta-e is the leaf-to-air water vapor concentration deficit, r_a, r_s, and r_i are the boundary layer, stomatal and leaf internal resistances to diffusion, respectively, and the CO_2 concentration at the chloroplast is assumed to be zero. Discussion at the leaf level is relevant in that both theory and measurements suggest that extrapolation to the canopy level is straightforward (Fischer and Turner, 1978).

Intercropping a taller-statured crop with one of shorter stature may significantly affect most of the variables in Eq. 3. The equation shows that the air vapor saturation deficit has a dominant effect on WUE. The windbreak condition produced by the taller canopy component tends to elevate relative humidity in the vicinity of the shorter crop component and the partial shade effect tends to reduce air temperature (IRRI, 1978, pp. 110–112); these both tend to reduce delta-e. Radiant energy loads on the dominated crop are reduced but this crop is usually a C_3 species with low light-saturated photosynthetic rates. Stomatal resistance increases in the dominated species in the intercrop, particularly with moisture stress (Chastain and Grabe, 1989). Water-use efficiency tends always to increase as the stomatal resistance (r_s) increases, particularly in C_3 species (Jones, 1976).

Fourth, WUE in the dominant crop is favored by the reduced boundary layer (r_a) of its open canopy (Jones, 1976). This effect is evident in studies of canopies composed of plants varying in height, in which air movement penetrates more thoroughly than in canopies of plants of uniform heights. Intercrop canopies are typically rough due to differences in plant height and architecture among the component crops.

The definitive contribution of the four mechanisms impinging upon enhanced WUE in intercrops cannot be established on the basis of current empirical evidence. There is a reasonable basis to assume that increased T/ET is largely responsible for the phenomenon in some cases. But ΔWUE can exceed 50% (Table 1) and it is not likely that enhanced T/ET alone would account for differences of this magnitude.

CONCLUSIONS AND RESEARCH NEEDS

The four following points are evident from the preceding review of water capture and utilization studies.

1. With respect to WU, the difference between intercrops and sole crops was usually near zero. This appears to be especially true for intercrops in which growth is largely concurrent, although an exception was noted (Reddy and Willey, 1981). For intercrops with short growth concurrencies, as in pigeon pea+sorghum, the WU advantage was due to continued water uptake by the component that remained after the other crop was harvested.
2. Because WU differences between intercrops and sole crops were small, potentials for an intercrop vs sole-crop interaction with environment and management factors were small as well. No evidence to support major interactions was found in reports of investigations in which the effects of species, intimacy, irrigation, soils, and plant density were examined.
3. Whereas WU differences between intercrops and sole crops were near zero, WUE differences (ΔWUE) were usually positive and often substantial when water was not severely limiting. Four mechanisms may account for these large positive observations. Limited evidence also showed that ΔWUE tends to become negative when seasonally available water is low.
4. While interactions between sole vs intercropping and seasonally available water were evident on WUE, sole vs intercropping × management practice interactions were less common and small when they did occur. Among three planting geometry factors (plant density, intimacy and crop proportion), evidence for plant density effects on WUE was most compelling but all factors require further study in conjunction with investigations of the four processes outlined as potential mechanisms contributing to increased WUE.

Three general areas are suggested for future research on water capture and utilization by intercrops.

1. The minor effect that intercropping has on WU and the major effect it has on WUE have been documented. Research to quantify the effects of mechanisms postulated as responsible for positive ΔWUE is needed. To examine the mechanisms, determinations of parameters such as delta-e, r_a, r_s, and r_i, light interception, and leaf area indices must be obtained. The apparatus to make the required determinations is available in institutions equipped to conduct field crop physiology studies. The utility of the studies would be enhanced if measurements were made on intercrops at two or three levels of water stress. To estimate water capture and utilization changes attributable to the superior competitiveness of a crop species, a method such as

that used by Trenbath (1986) to estimate the portion of total WU transpired by each of two wheat cultivars in a mixed crop, needs to be developed for general application.

2. Planting geometry affects WUE but the effects have not been fully quantified for a range of intercrop combinations and environmental conditions. Studies to quantify the effects should not be limited to collection of yield and water use data; the postulated mechanisms should be examined by investigations parallel to those suggested in No. 1.
3. In semi-arid regions, where SAW is highly irregular, the mean productivity of an intercrop across years should exceed that of component species but more critically, the intercrop response to diminished SAW should be less than that of the component species. Investigations are needed to identify the characteristics that intercrop components must possess for the practice to maintain its advantage in years when SAW falls below normal.

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