A POTENTIAL FOR WATER-EFFICIENT, C_4 HALOPHYTES IN ARIZONA'S AGRICULTURAL WATER BUDGET

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Introduction

Arizona's underlying water problem is a shortage of renewable supplies to meet demands, resulting in a depletion of groundwater reserves at the current rate of 3.1 x $10^9 m^3 yr^{-1}$ (Water Resources Research Center, 1980). By far, the majority of water (ca. 89%) is consumed by irrigated agriculture in the arid Basin and Range Lowland Province (White and Stulik, 1962).

An additional problem is that saline aquifers underlie the major riverbottom irrigation districts in the state (Figure 1). Unlike the deep supplies of fresh water, the saline aquifers receive recharge from surface flows as well as underground flows from adjacent, higher drainages, and are not undergoing depletion (U.S.G.S., 1978). Unfortunately, the low salt tolerance of most conventional crops severely limits the usefulness of these saline water resources for agriculture (Allison, 1954).

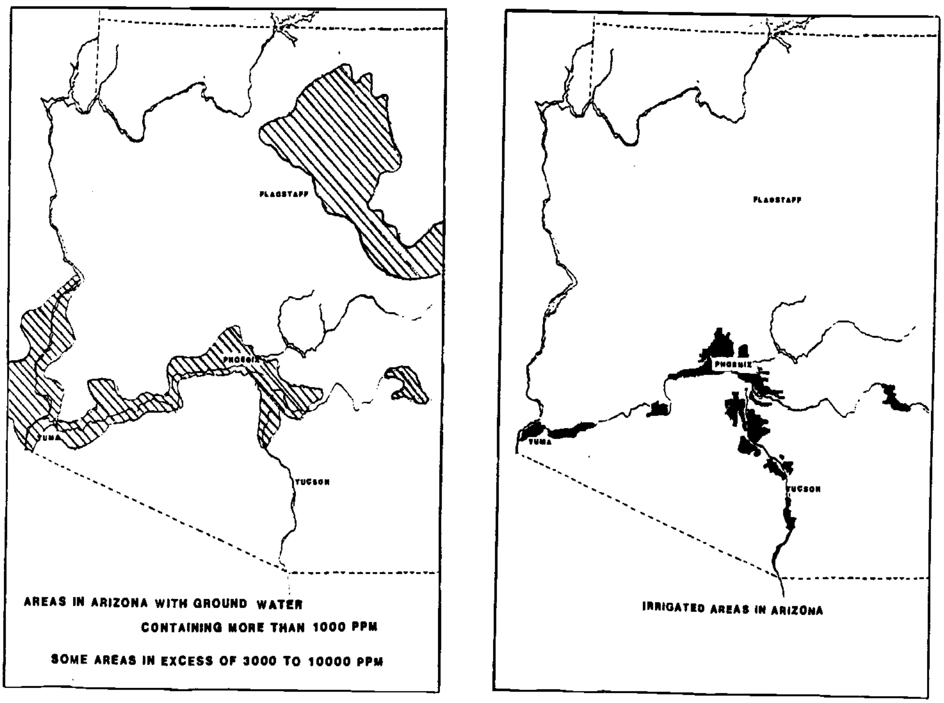

Figure 1. Areas of saline groundwaters (from Kister, 1973) and irrigated areas (from Dept. of Agri. Economics and Agri. Engineering, 1963) in Arizona.

Lowered water tables, salinity problems, and increased competition for available water by growing urban areas have placed the future of Arizona's agriculture in doubt (Webster, 1981). Perhaps the most water-inefficient part of the agricultural sector is forage crop production. Alfalfa, the leading forage crop, is second only to cotton in total acreage (Arizona Crop & Livestock Reporting Service, 1979), and with a consumptive water use of 185 cm yr^{-1} it is by far the thirstiest crop (Erie et al., 1965). Alfalfa is relatively salt-sensitive and requires additional leaching water (above consumptive use) even when grown on water of moderate salinity (Allison, 1954). The total water requirement for alfalfa is as high as 245 cm yr^{-1} in some parts of the state (Advisory Committee on Irrigation Efficiency, 1974).

Forage crops are vital to the state's livestock industry, but their bulky nature requires that they be produced near the point of consumption. A partial solution to Arizona's water problem may be to develop new forage crops to replace alfalfa in the desert irrigation districts. Such crops should have nutritional value equivalent to alfalfa, but at the same time be highly water efficient and salt tolerant, in order to minimize the use of valuable fresh water and take advantage of presently unused saline water resources. Whereas these attributes are absent from conventional forage crops, they exist in the wild flora.

C_4 halophytes are a heterogeneous group of wild plants distributed in salt marshes and inland salt deserts throughout the world. They include grasses as well as broadleaf dicot species, and have been recognized as important constituents of natural rangeland for many years (Jones, 1970). The nutritional value of some species equals alfalfa in terms of protein content (Glenn et al., in press(a); Goodin, 1979). Only in recent years, however, have these exceptionally hardy plants been considered as replacements for alfalfa in arid-zone irrigation districts (Goodin, 1979; Mudie, 1974).

Comparison of C_3 and C_4 Plants

The overwhelming majority of plants contain the C_3 pathway for photosynthesis, in which the first product is a three-carbon compound. This pathway is competitively inhibited by atmospheric levels of oxygen, and operates efficiently only at relatively high levels of carbon dioxide in the leaf. On the other hand, some plants have evolved a C_4 pathway for photosynthesis, in which the first product is a four-carbon organic acid. While the C_3 and C_4 pathways differ in many respects, the most important may be the higher affinity of the C_4 pathway for carbon dioxide, allowing efficent photosynthesis to take place even at very low levels of carbon dioxide in the leaf (Black, 1973). The C_4 pathway is unaffected by atmospheric levels of oxygen.

The C_4 pathway appears to have evolved as a mechanism to ameliorate water stress, whether arising from arid conditions or salts in the water. Carbon dioxide entry into, and water loss from a leaf share the same pathway. Thus, assimilation of carbon and the subsequent conversion into materials that make up the dry weight of a plant, takes place at the expense of water loss. By virtue of their high affinity for carbon dixoide, C_4 plants can keep leaf stomata partially closed to reduce water loss, while still maintaining a high rate of photosynthesis. Under similar conditions of carbon dioxide restriction, C_3 plants actually lose carbon dioxide as a result of photorespiration. On the other hand, in a temperate environment where water is not limiting, stomata can be kept wide open and the C_4 pathway appears to confer no special advantage over the C_3 pathway, and may actually be a liability (Black, 1973).

Numerous studies have confirmed the higher water use efficiency of C_4 plants compared against C_3 plants. Water cost can be defined as the ratio of weight of water lost per weight of dry matter produced (g H_2O/g DW). This transpiration ratio is commonly measured by one of three methods: instantaneous rates of photosynthesis and transpiration are compared for a single leaf; the rate of dry matter accumulation and water usage are compared for potted plants; or dry matter accumulation and total irrigation requirements are compared for field-grown crops. Not surprisingly, the methods yield different results. Instantaneous measurements on single leaves do not take into account water and carbon losses at night and therefore underestimate water usage, whereas field methods do not always correct for water losses due to runoff, deep percolation, and surface evaporation, and therefore generally overestimate actual water consumption by the crop.

The important point, however, is that the superiority of C_4 plants with regard to water use efficiency is maintained at all three levels of measurement (Table 1). The results have been confirmed in numerous studies and hold true over a wide range of environmental conditions. Beginning with the extensive studies of Shantz and Piemeisel (1927), there have been no exceptions found to the general rule that C_4 plants are at least twice as efficient as C_3 plants in water usage (Black, 1973; Vollmer, cited in Szarek, 1979; Caldwell et al., 1977; Dillman, 1931).

Table 1. Transpiration ratio (g H_2O/g DW) for leaves, plants, and fields of C_4 grasses and C_3 legumes (based on data from Ludlow and Wilson, 1972).

	C_4 Grasses	C_3 Legumes	C_3/C_4
Leaf	120	280	2.3
Plant	203	374	1.8
Field	325	700	2.2

C_4 halophytes from the genus *Atriplex* have transpiration ratios ranging from 87 g H_2O/g DW for potted plants (Vollmer, cited in Szarek, 1979), to 232 g H_2O/g DW for field-grown plants (Caldwell et al., 1977). In contrast, the weighted mean water cost for alfalfa over six years in the study by Shantz and Piemeisel (1927) using potted plants, was 814 g H_2O/g DW. A seasonal water cost of 1250 g H_2O/g DW can be dalculated for alfalfa, based on field yields from Arizona, 1977-1979, and water consumption data from Mesa, Arizona (Webster, 1981). In a direct comparison between *Atriplex canescens* and alfalfa in western Texas, Goodin (1979) found that equivalent yields of *Atriplex* were obtained at only 15-25% of the water cost of alfalfa.

It is important to note that not all arid-adapted plants are C_4. C_3 xerophytes that can withstand long periods of severe drought may actually have *high* transpiration ratios when water is available (Maximov, 1929). This applies to arid-adapted plants that have been proposed for desert agriculture, such as jojoba and guayule (Ritchie, 1979). Jojoba, for example, has a transpiration ratio of 1700 g H_2O/g DW, one of the highest ever recorded (McGinnes and Arnold, 1939). These plants probably offer no real water savings under irrigated conditions.

Comparison of Glycophytes and Halophytes

Salinity problems arise in desert irrigation districts because evaporation greatly exceeds precipitation, so salts become concentrated in the soil and groundwaters. Thus, it is not surprising that some of the major areas of saline groundwater correspond to the location of the major irrigation districts in Arizona (Figure 1). Naturally-saline groundwaters also occur in the northeastern corner of the state and in deep aquifers underlying the Safford and Wellton-Mohawk valleys along the Gila River (Kister, 1973 and literature cited therein).

The saline aquifers range in salinity from slightly saline (1,000-3,000 ppm) to saline (above 3,000 ppm), with some wells producing salinities in excess of the salts in seawater (30,000 ppm). Most conventional crops are glycophytes: plants that evolved in the absence of salts and that are sensitive to even low levels of salts in the environment. As a result, water exceeding 1,500 ppm salinity is generally not useful for long-term application in irrigated agriculture (Allison, 1954). In the Safford Irrigation District, farmers rely on good quality water diverted from the surface flow of the Gila for most of their irrigation requirements, and resort to the pumping of shallow "slightly saline" groundwater only when their allotment of surface water is used up (Muller et al., 1973). A deeper artesian aquifer in the valley is not used at all because of salinities in excess of 5,000 ppm. In the Wellton-Mohawk

Irrigation District, irrigation water comes from surface flow diverted from the Colorado River. The shallow aquifer underlying the basin has been deemed unfit for any use due to salinities in excess of 3,000 ppm, and it is pumped from the gound and sent unused into the Gulf of California by lined canal.

Halophytes evolved to survive, and even flourish in salinities up to and exceeding seawater. In addition to the C_4 and CAM pathways for photosynthesis (not present in all halophytes), halophytes have developed specific mechanisms to exclude, compartmentalize, or excrete toxic salts from the growing portions of the plant. Salt tolerance requires expenditures of metabolic energy (O'Leary, 1979), so that even the best adapted halophytes show growth reductions when the salinity of the irrigation water excedds approximately 10,000 ppm (Figure 2). It has been found, however, that the most productive C_4 halophytes, irrigated with 40,000 ppm seawater, produce yields of 850-2270 g DW m^{-2} yr^{-1}, which are equivalent to yields of alfalfa irrigated with fresh water (Glenn et al., in press(b)).

Since the salinities of Arizona's saline aquifers do not generally exceed 10,000 ppm (Kister, 1973), plants adapted to grow on seawater would receive an "energy subsidy" in the form of lower salinity water in Arizona irrigation districts, and could be expected to yield two to three times as high as when irrigated with full strength seawater (O'Leary, 1979) (see Figure 2).

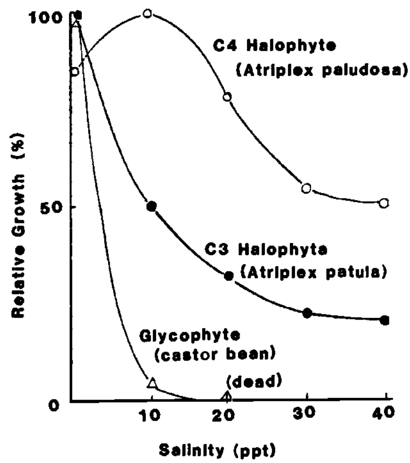

Figure 2. Growth (measured as dry weight) of plants in sand culture with irrigation water of varying salinities. Plants were grown in a greenhouse and irrigated with nutrient solution adjusted to the given salinities with artificial seawater (Instant Ocean). After a three-week adjustment period at each salinity, dry matter increase was measured after eight weeks. Data points are the average of 5-10 plants each.

Conclusion

Halophyte crops are not yet economical due to problems of toxicity and lack of agronomic techniques. Similar problems have been overcome in domesticating our present agricultural crops. On the other hand, it has proven to be quite difficult to alter the core metabolism of plants: efforts to increase productivity by breeding for high rates of photosynthesis have not been successful (O'Leary, 1979); nor have efforts to introduce the C_4 pathway into C_3 plants (Bjorkman et al., 1971). The next logical step is to breed desirable crop characteristics into wild C_4 halophytes that already have the desired attributes of high nutritional content, high water efficiency, and high salt tolerance.

If C_4 plants were to completely replace alfalfa in Arizona's irrigation districts, then a water savings of approximately 740 x 10^6 m^3 yr^{-1} could be achieved, based on an assumed savings of 9.14 x 10^3 m^3 ha^{-1} over an area of 80,900 ha (Arizona Crop & Livestock Reporting Service, 1979). This estimate assumes that only high quality irrigation water would be used. If half of the total irrigation water for such a crop could come from saline resources not presently used for agriculture, the total savings of good quality groundwater would amount to 1.2 x 10^9 m^3 yr^{-1}, or approximately 40% of the current annual overdraft of groundwater in Arizona.

An important question is the extent to which saline water can be used without further damaging soils and aquifer. The position of the U.S.D.A. Salinity Lab is that with proper drainage and a safe disposal site, water of virtually any salinity can be used on normal soils without permanent damage (van Schifgaared, 1981). They encourage the reuse of irrigation and drainage water for successively more salt-tolerant crops including native halophytes, in order to reduce the volume of water that must ultimately be discarded, and to get the maximum beneficial use out of the water.

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