

La Semilla



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1993 - 1995 ANNUAL REPORT

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**TUCSON PLANT MATERIALS
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1990 COWANIA MEXICANA ADVANCED EVALUATION
(Project Number: 04A9002H)
1995 - FINAL REPORT

by
Mark Pater

Abstract:

In 1983, the *Cowania mexicana* initial evaluation planting (IEP) was installed at the Tucson Plant Materials Center (TPMC) to evaluate the potential of this species for use as a component in seed mixes for various revegetation projects as well as its potential use as a low water use landscape plant. Three accessions were selected in 1989 out of this IEP for further evaluations. However, due to a limited genetic base for this developed cliffrose population, the project has been removed from the TPMC evaluation process.

KEY WORDS: *Cowania mexicana*, cliffrose, drought resistant, actinorhizal, germination.

Introduction:

The cliffrose (*Cowania mexicana* D. Don var. *stansburiana* [Torr.] Jeps.) advanced evaluation project originally began with the 1983 *Cowania mexicana* IEP. This IEP was initiated to evaluate this species' potential use as a component in seeding mixes for use in reseeding depleted range sites, critical areas, mine reclamation sites as well as provide improved wildlife habitat and winter forage for areas located in Major Land Resource Areas (MLRA) 29, 35, 39, 40 and 41. The shrubs in the IEP were evaluated for emergence, survival, vigor, height and width, and flowering periods. Each accession was evaluated individually in the process of trying to determine which ones were the superior performers.

Three accessions of *Cowania mexicana* were selected in 1989 for advanced evaluation. These accessions were: 9018061, 9026143 and 9026144. Accessions 9026143 and 9026144 were selected for their very good vigor, a nicely rounded growth form (desirable landscape characteristic), longer flowering period and superior seed production. Collection 9018061 demonstrated long leader growth and more desirable ground cover characteristics: lower branches spread laterally over the ground. This collection also flowers 4-6 weeks earlier than the other accessions and the flower set is very dense and uniform over the whole plant.

In 1991, accessions 9026143 and 9026144 were combined into a single lot and assigned accession number 9058832. Both accessions are very similar in appearance and

phenology. These two collections were originally gathered from two sites which are located very close to one another near Winona, Arizona.

Description:

Cowania mexicana is a many-branched, leafy, spreading, evergreen, native shrub. It usually grows to a height of 1 to 3.5 meters. Under favorable conditions it can grow up to 7.5 meters in height. Benson and Darrow (1981) describe this species as having twigs with some straight, spreading hairs, not woolly or woolly only around the leaf axils, with stalked glands; bark reddish-brown; leaves all pinnately 3-5 parted into linear lobes, the margins and upper surfaces with conspicuous, sticky, glandular dots; pecicels, floral tubes, and calyces with stalked glands; petals 6-9 mm long, 4-6 mm broad; fruits with tails (persistent styles) 3-5 cm long. Chromosome numbers are listed as $2n= 18$ (Baker et al. 1984).

The fruit is described as an achene with a persistent feathery style, borne in clusters of 4-10 on a flat disk. The first and usually best crop of fruits (under natural conditions) ripens from the middle of July through August. Fruits maturing from later flowers may be dispersed from August through October. These late fruits are usually of poor quality and are not worth harvesting (Young & Young 1992).

All three accessions which were selected from the 1983 *Cowania* IEP were collected from areas in northern Arizona:

9018061: Collected by Dave Matthews on 06/01/80; southeast of Snowflake; Sec.28, T12N, R23E.

9026143: Collected by Barry Wallace on 10/01/80; 0.75 mi. west of Winona on I-40; SW of the NW 1/4 of Sec.14, T21N, R9E.

9016144: Collected by Barry Wallace on 10/01/80; Winona exit on I-40; NW of the SE 1/4 of Sec.14, T21N, R9E.

Discussion:

Cowania mexicana occurs naturally in the upper Mojavean and Arizona deserts, the Desert Grassland, and the Southwestern Woodlands at 1,067 to 2,438 meters (3,500-8,000 ft) in elevation. California in the Death Valley region and in the Clark and Providence mountains in the Mojave desert; southern Nevada; southern and eastern Utah from the Arches National Park southward; Arizona throughout the Colorado Plateau and from the Hualapai Mountains, Mohave County, southeastward below the Mogollon Rim to Santa Cruz and Cochise counties; New Mexico on the San Juan River drainage and

west of the Rio Grande; southern Colorado; Sonora and Chihuahua (Benson & Darrow 1981).

This species grows on thin, rocky soils of both igneous and sedimentary origin. It thrives in the juniper-pinyon zone, particularly in calcareous soils and on immature limestone rocklands. *Cowania mexicana* is also found at the edge of the salt desert and on southern exposures in the mountain shrub and ponderosa pine types. It is strongly drought resistant after fully established; less so in the seedling stages. It thrives fully in sunlight but exhibits fair shade tolerance, especially in the seedling stage. Some variation in frost sensitivity of seedlings is to be expected from the southern and low altitude strains, also in vigor when introduced from habitats differing much from the planting site. It is generally killed by wildfire; old one-stemmed specimens readily killed by chaining, dozing, or severing of the main trunk. Quite tolerant of winter browsing; removal of 65% of current twig growth stimulates flowering and reproduction but browsing more than 80% causes plants to deteriorate. It is competitive beyond the seedling stage and suitable for inclusion in seeding mixtures for exposed rocky slopes within its climatic tolerances¹.

The leaf margins roll in slightly which is a characteristic associated with a plant's increased ability to survive dry conditions.

Where abundant, cliffrose is an important and valuable browse for deer, cattle and sheep, the chief utilization period being in winter. It is little used by deer, cattle, or sheep during spring and summer if other succulent forage is plentiful. The branches of this shrub are brittle and under abusive grazing are liable to be broken and severely damaged. Proper browsing stimulates lateral bud growth which results in the production of a greater number of leafy shoots and more forage than where the plant is protected (USDA 1937).

Many species of woody perennials that are native to the shrub-dominated vegetation of the western U.S. fix nitrogen when infected with the appropriate actinomycete microsymbiont (Klemmedson 1979). *Cowania* is an important actinorhizal genus (Righetti and Munns 1980) and interest in this system has increased as its value in the revegetation of deteriorated wildlife habitats and rehabilitation of nitrogen-deficient disturbed areas has become apparent. Cliffrose can pioneer on semi-arid plains, foothills and mountain slopes, and has been successfully utilized in revegetation efforts (McArthur et al. 1974; Righetti et al. 1986).

Young and Young (1992) provide the most current information in regard to pregermination treatment. They state that without pregermination treatment, seeds of cliffrose have exhibited limited germination. When germination was tested at 55 constant or alternating temperatures ranging from 0 through 40 °C, the mean germination of optima (defined as not significantly lower than the maximum observed germination and its confidence level at the 0.01 level of probability) was 13% (Young and Evans 1981). Soaking seeds of cliffrose in a 3% solution of thiourea increased mean optimal

¹Clinton Wasser. 1982. *Ecology and Culture of Selected Species Useful in Revegetating Disturbed Lands in the West*. U.S. Fish and Wildlife Service, Dept. of the Interior, Washington, D.C.

germination to 66%. However the use of this very toxic chemical is not recommended because it is suspected to cause cancer in laboratory animals. Prechilling cliffrose seeds for 2 weeks at 5 °C produced mean optimal germination of 55%. The incubation temperatures that most frequently supported optimum germination were 10/20, 10/25, 10/30, and 15/25 °C.

When propagating *Cowania* plants from seed, a one-month moist and cool period (35 °F-41 °F) enhances seed germination. Stem propagation can easily be accomplished by basally treating 3-4 inch, semi-hardwood terminal stems with 0.8% indolebutyric acid (Borland 1988).

Tucson PMC personnel have propagated numerous plants from seed in the TPMC greenhouses without the one-month moist and cool period and germination has resulted in approximately 80%. This propagation process was begun in early March while temperatures were still relatively cool and a mist system was used to keep the soil moist. Germination response time was 10 days.

Young and Young (1992) also state that cliffrose has been successfully direct seeded on rangelands in Utah. Seeds were drilled or broadcast in the fall on sites that had the competing vegetation reduced and some seedbed preparation had been performed. The seed was planted at a rate of approximately 5.5 kg ha⁻¹. Container-grown and bare rootstock of cliffrose have been successfully transplanted into rangeland sites. Alexander et al. (1974) suggested transplanting relatively young seedlings. Young and Young (1992) report to have had excellent results with 12- to 18-month old, container-grown stock that was fully hardened off when transplanted.

Conclusions:

This project has been discontinued. Because cliffrose is a cross-pollinated species and the genetic component for this population has been derived from three individual collections, TPMC personnel have determined the genetic base for this population to be too narrow. This narrow genetic base could very likely lead to establishment, production and performance problems in the future. It should also be noted that from an economic standpoint, commercial seed producers can harvest seed from natural stands more efficiently than producing seed in a cultivated seed orchard.

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1990 *ERIOGONUM WRIGHTII* ADVANCED EVALUATION
(Project Number: 04A9001L)
1995 - FINAL REPORT

by
Mark Pater

Abstract:

In 1983, the *Eriogonum* species initial evaluation planting (IEP) was installed at the Tucson Plant Materials Center (TPMC) to evaluate and identify potentially superior ecotypes for uses in various revegetation projects. One accession, shrubby buckwheat, was selected in 1990 out of this IEP for further evaluations. However, due to a limited genetic base for this shrubby buckwheat population, the project has been removed from the TPMC evaluation process.

KEY WORDS: *Eriogonum wrightii*, shrubby buckwheat,

Introduction:

Eriogonum wrightii, 9034580, was selected in 1990 out of the 1983 *Eriogonum* spp. IEP (Initial Evaluation Planting) for its good overall performance and superior ability to produce viable seed. The 1983 *Eriogonum* spp. IEP (Project Number: 04I383H) was initiated to try and identify a superior ecotype(s) for potential uses in various revegetation projects. Improved cultivars of drought tolerant shrubs are desired for use in Major Land Resource Areas (MLRA's) 35,40, and 41. The *Eriogonum* species in the IEP were evaluated for emergence, survival, vigor, height and width, and seed production capabilities.

Description

Eriogonum wrightii (shrubby buckwheat) is a native, white-tomentose, leafy perennial growing up to 60 cm in height, remaining woody near the base. It flowers June-September, peduncles seminaked, solitary or irregularly 2-3-forked, slender, ascending, tomentose; involucre loosely spicate, sessile, 2-3 mm (1/12-1/8 in) long, teeth rigid and acute; petals absent; sepaloid segments of the perianth 6 2-3 mm (1/12-1/8 in) long, glabrous, white or pink; stamens 9; styles 3, stigmas capitate, ovary 1-celled. The fruit is a solitary achene, erect, scabrous, base acute, 3-angled. The leaves are mostly on the lower half of the plant, scattered, alternate or clustered, oval to oblong or linear to lanceolate, apex acute, base tapering, margin entire, less than 2.5 cm (1 in) long, both surfaces densely white-tomentose above and beneath. The stems are erect and slender, woody toward the base, tomentose above, bark reddish brown, thin-scaly (Vines 1976).

Discussion

Eriogonum wrightii can be found growing naturally at elevations from 760 to 2,195 m (2,500-7,000 ft) on dry hills, valleys, and alluvial fans in the Arizona Desert, the Desert Grassland, the Great Plains Grassland, and the Southwestern Woodland and Chaparral. In southern Utah on the San Juan and Colorado river drainages; almost throughout Arizona, except in the lower desert elevations; western and central New Mexico on the San Juan, Gila, and Rio Grande drainages; TransPecos Texas and the Great Plains Grassland; Baja California and Sonora to San Luis Potosi (Benson & Darrow 1981).

This species is highly important as both a browse plant for deer and livestock as well as a bee plant for honey production (Benson & Darrow 1981)

To date the most efficient harvesting methods are either hand-harvesting or utilization of the Shop-Vac vacuum cleaner. The best seed processing procedure has been to first work the seed through the Westrup Brush Machine followed by using the Office Clipper (dual-screen air separator).

Although no germination tests have been performed on the seed, germination rates during the plant propagation process for the seed increase planting have been 75-90+% germination within the first 24 hours from planting.

Conclusions:

This project has been discontinued. Because shrubby buckwheat is a cross-pollinated species and the genetic base for this population has been derived from a single accession which originally consisted of less than three individuals, TPMC personnel have determined the genetic base for this population to be too narrow. This narrow genetic base could very likely lead to establishment, production and performance problems in the future. It should also be noted that from an economic standpoint, commercial seed producers can harvest seed from natural stands more efficiently than producing seed in a cultivated seed orchard.

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1989 SPOROBOLUS FLEXUOSUS
(Project Number: 04I0211)
1995 - FINAL REPORT

by
Mark Pater

Abstract:

In 1989, 80 accessions of *Sporobolus flexuosus* (mesa dropseed) were installed at the Tucson Plant Materials Center (TPMC) to evaluate the potential of this species for use as a component in revegetation projects in southeastern Arizona. This project failed in the initial evaluation planting (IEP) phase of the evaluation process. Tucson PMC personnel still feel that this species merits continued evaluations.

KEY WORDS: *Sporobolus flexuosus*, mesa dropseed, native.

Introduction:

This IEP consisted of 80 accessions. *Sporobolus flexuosus* is a native, perennial, warm-season bunchgrass. It is found on dry or moist, open, sandy or gravelly soils, mostly at 2,500 - 5,500 feet in elevation. *Sporobolus flexuosus* was being evaluated for its potential use in rangeland erosion control, providing vegetative cover on abandoned cropland and other large areas where the vegetation has been disturbed or removed, as well as to provide vegetative diversity in these problem areas. Its natural adaptive range includes MLRA's 30, 35, 39, 40 and 41. Each accession was evaluated for emergence, survival, vigor, foliage and seed production.

Objectives:

The objective of this IEP was to assemble, evaluate, develop and cooperatively release a superior ecotype of *Sporobolus flexuosus* for use in range improvement and critical area stabilization.

Procedure:

The assembly for the 1989 *Sporobolus flexuosus* IEP was completed in November 1988. In February 1989, seed from each accession was planted into 1.5" x 8" conetainers with a 1:1:1 mixture of peat moss, vermiculite, perlite and sand. After sufficient seedling growth (90-120 days) the plants were placed in the lathhouse for a hardening off period prior to transplanting into the field.

The plants for this IEP were planted by hand into Field 4, Borders 13 and 14 at the Tucson PMC. The soils are Comoro fine sandy loam. Prior to planting, the border was rotovated, harrowed, cultipacked and pre-irrigated.

For statistical purposes, the assembly utilized a randomized complete block design with four replications per accession. Each accession was replicated four times with five plants per accession per replication. The IEP plot encompassed all of Borders 13 and 14 (0.56 acres). Guard rows of *Bouteloua curtipendula* and *Bouteloua gracilis* were planted along the outside rows to reduce edge effects. All plants were irrigated to ensure establishment. Evaluation data was to be collected quarterly and summarized in the yearly TPMC Technical Report.

In 1992 TPMC personnel decided to improve the selection process for this assembly by reestablishing this IEP using a Convergent-Divergent Improvement (CDI) process. A procedure for cross-pollinated plants as outlined by Lonquist et al. (1979) was to be followed. This procedure is based on a system involving the collection of separate units of germplasm (accessions) from a broad area within the species' natural range of adaptation. This is then followed by bulking of seed and then dispersal (divergence) to a set of evaluation sites located within the species' natural range of adaptation. Following equal intensity mass selection at each evaluation site, samples of the harvested seed will be returned (convergence) to the Tucson PMC for intermating prior to divergence to the set planting sites for continued selection.

If it is determined that *Sporobolus flexuosus* is a self-pollinated species, a mass selection procedure will be used to develop a population with a broad genetic base. Following mass selection and bulking of seed at the Tucson PMC, equal amounts of the bulked material will be planted at various off-center evaluation sites located within the species' natural range of adaptation. As with the convergent-divergent system, equal intensity mass selection will be conducted at each evaluation site and the harvested seed will be returned to the Tucson PMC to form a breeder's block.

Results and Discussion:

1990 Evaluations

Evaluation data for 1990 was summarized in the 1991 TPMC Technical Report². Five accessions appeared to be superior based on above average vigor and production. These were: 9027977, 9029731, 9023304, 9029731 and 9055828

1991 Evaluations

Evaluation data for 1991 was marginal. Seven accessions were shown to be superior in vigor however nine other accessions were shown to be superior in terms of % survival (↓90%).

² Frank Archuleta. 1991. 1989 *Sporobolus flexuosus* IEP - 04I021L. 1991 Report. USDA-SCS Tucson Plant Materials Center Ann. Tech. Report. p.12

1992 Evaluations

In 1992 all of the collection sites for the accessions assembled for this evaluation were to be plotted on a map in order to determine the range of collection within the species' natural range of adaptation. This map was to aid in the development of a genetically broad-based population.

For the CDI selection method to be employed, live plants from the original IEP planting were to be used for the initial composite planting (CO). Three plants from each of the 80 accessions in the IEP were to be placed in square planting configuration using a completely randomized block design. Prior to transplanting, the IEP block was to be mowed to a 6-8" height and irrigated. The individual plants in the CO block were to be planted on a 3x3 foot spacing. The CO planting was to be flood irrigated and managed to ensure optimal seed production.

At harvest, equal amounts of seed were to be harvested from all plants and bulked. Plants from this seed were to be propagated at the Tucson PMC and groups of 160 plants were to be planted out in 10x16 square-configured grids at off-center locations within the species' natural range of adaptation. A minimum combined total of 100 live plants selected from each off-center location were to be returned to the Tucson PMC where a new composite planting would be formed for the next cycle of the selection process. If Tucson PMC personnel were to decide that the selections to date were sufficient, the new composite planting would serve as a breeder's block.

If a modified mass selection technique was to be utilized, live plants from the IEP planting would be used to form the initial mass selection composite planting (MA). Three plants from each of the 80 original accessions in the IEP planting were to be planted into a square planting configuration using a completely randomized block design. This would have resulted in a total of 240 plants being installed into the MA planting.

Prior to transplanting, the IEP block was to be mowed to a 6-8" height and irrigated. The individual plants in the MA planting were to be planted on a 3x3 foot spacing. The MA planting was to be flood irrigated and managed to ensure optimum seed production. At harvest, seed from the MA planting was to be bulked and equal amounts would be planted at various off-center sites located within the species' natural range of adaptation. Off-center evaluations would primarily focus on emergence and seedling establishment. Following adequate off-center evaluations the MA block could be designated as a breeder's block.

None of these procedures were completed and the project has been discontinued. Tucson PMC personnel feel that *Sporobolus flexuosus* is an excellent candidate to be included in the PMC evaluation program. This species has excellent potential for future use as a soil stabilizing plant in southeastern Arizona.

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1977 TETRACHNE DREGEI ADVANCED EVALUATION
(Project Number: 04A810G)
1995 - FINAL REPORT

by
Mark Pater

Abstract:

In 1977, *Tetrachne dregei* (Karoograss) was included as part of the Warm- and Cool-Season Grass initial evaluation planting (IEP) which was installed at the Tucson Plant Materials Center (TPMC). This IEP was initiated to identify potentially superior grass species which could be utilized for either range improvement plantings, site stabilization projects or mine reclamation work in MLRA's 30, 35 and 40. One Karoograss accession was selected in 1981 out of this IEP for further evaluations. Tucson PMC personnel observed potentially undesirable growth characteristics by this species and it was decided to remove Karoograss from the testing program.

KEY WORDS: *Tetrachne dregei*, Karoograss, introduced.

Introduction:

Karoograss (P.I. 330683) was selected in 1981 out of the 1977 Warm- and Cool-Season Grass IEP which was installed at the TPMC. This IEP was initiated in order to evaluate various grass species for their potential use in rangeland improvement, critical area stabilization, mine reclamation and pasture and hayland plantings.

History:

The 1977 Warm- and Cool-Season Grass IEP was initiated to evaluate various grasses to be used in range improvement, critical area stabilization, and mine reclamation in MLRA's 30, 35 and 40. MLRA 30 contains some of the harshest sites in Arizona in terms of annual rainfall (76-178 mm) and temperatures (>49 °C during summer months). The grasses in this trial were evaluated for vigor, forage production, size, and ability to spread. Each accession was evaluated individually to be able to select the superior accessions, which in turn will be increased and evaluated further. This initial evaluation project lasted from 1977-1981.³

Karoograss is an introduced, warm-season species originating from South Africa.

³James A. Briggs. 1981. 1977 Warm- and Cool-Season Grass IEP - 04I904T and 04I905T. 1981 Report. USDA-SCS Tucson Plant Materials Center Ann. Tech. Report. p.7

P.I. 330683 arrived at the Tucson PMC, from Israel through the National Plant Materials Center (Beltsville, MD) on January 29, 1977. Literature searches at the National Agricultural Library and the University of Arizona Science Library did not reveal much information on Karoograss. This species is found growing primarily in South Africa at intermediate elevations within annual precipitation zones of 381 to 635 mm (15-25 inches). P.I. 330683 had shown itself to be drought resistant in the 1977 Warm- and Cool-Season Grass IEP. It was also noted to have maintained excellent to fair vigor from 1977-1981 and had produced a good amount of forage. This accession was very comparable to P.I. 354922, also from Israel. However, P.I. 330683 produced more forage in both spring and summer clipping evaluations.⁴ Complete 1981 data for all *Tetrachne dregei* accessions is shown in Table 1.

Status:

From 1982 until 1993, this species was not evaluated extensively. In June, 1993 a seed increase block was installed in Field 4, Border 15. This accession was noted to exhibit a slightly stoloniferous growth habit. It was also noted that this accession did not go fully dormant during the winter months and that it began to green up in the late winter period. These observations led TPMC personnel to believe that this species may tend to outcompete and dominate off-center planting sites by making use of available soil moisture and nutrients before the indigenous species began their growing cycle. These observations along with a lack of demand by customers for non-native grass species helped TPMC personnel to decide to drop this species from the TPMC testing program. It should be noted that this accession may show promise for use as an irrigated pasture grass.

⁴James A. Briggs. 1981. 1977 Warm- and Cool-Season Grass IEP - 04I904T and 04I905T. 1981 Report. USDA-SCS Tucson Plant Materials Center Ann. Tech. Report. p.10.

Table 3

Tetrachne dregei
1981 Data for All Accessions⁵

Accession No.	P.I. No.	Origin	Vigor ⁶		Forage (grams/3.2 ft ²)	Remarks
			April	July		
14408	198603	S. Africa	-	-	-	Dead, 1979
15286	209829	S. Africa	7	5	82.5	
17121	300137		7	5	55.5	
17854		Hawaii	3	4	101.5	
19094	330683	Israel	5	5	88.5	Selected for increase
19095	354922	Israel	5	5	94.5	
19096	365059	S. Africa	-	-	-	Dead, 1978

⁵James A. Briggs. 1981. 1977 Warm- and Cool-Season Grass IEP - 04I904T and 04I905T. 1981 Report. USDA-SCS Tucson Plant Materials Center Ann. Tech. Report. p.16

⁶Ratings: 1= Excellent; 3= Good; 5= Average; 7= Poor; 9= Very Poor

REGISTRATION AND RELEASE OF 'STEVAN' PLAINS BRISTLEGRASS 1995 - FINAL REPORT

by
Mark Pater

'STEVAN' PLAINS BRISTLEGRASS [*Setaria leucopila* (Scribn. & Merrill) K. Schum.] (Reg. no. CV-173, P.I. 552568) was released by the USDA-SCS, USDA-ARS, and the University of Arizona Agricultural Experiment Station April 1, 1994. The cultivar will be used as an erosion control plant in southeastern Arizona, southwestern and southeastern New Mexico, and western Texas.

Stevan plains bristlegrass is an apomictic, C_4 , native, perennial, warm-season bunchgrass (Emery 1957).

Stevan is the product of a testing program to develop a superior population of plains bristlegrass that was conducted at the Tucson Plant Materials Center (TPMC). Stevan plains bristlegrass is a population of 13 accessions that were selected from an initial evaluation study conducted at the TPMC from 1975 through 1979. Open-pollinated seed produced in 1979 from these accessions was bulked to form Stevan. Stevan was included in plantings on the Santa Rita Experimental Range from 1982 through 1986 (Briggs 1982, Munda and Pater 1989). The Stevan population exhibited good germination and establishment in years having normal amounts of precipitation (200-300 mm yr⁻¹). In 1993 Stevan was included in a planting in Avra Valley, Arizona. The purpose of this planting was to evaluate seedling emergence and establishment from planting depths of 1.25, 2.5, and 3.75 cm. Stevan exhibited a higher seedling emergence percentage and average number of seedlings per 0.3 m at the 3.75 cm planting depth. However, this was not significantly higher ($P < 0.05$) than emergence and establishment from the 1.25 and 2.5 cm planting depths. Stevan exhibited significantly higher emergence percentage ($P < 0.05$) over a commercially available population of plains bristlegrass.

Stevan was selected primarily for use in revegetation of eroded rangelands, retired croplands, critical areas (i.e. highway construction sites), and to provide a degree of forage for wildlife and livestock use. In arid climates soil surface moisture is a limiting factor in germination and seedling establishment. Stevan plains bristlegrass is an excellent candidate for revegetation use because of its ability to emerge and establish from greater seeding depths than many other grass species. It is recommended that Stevan be utilized as part of a seeding mixture comprising roughly 20-30% of the total mix. However, the percent composition can vary depending on the seeding objective.

Seed propagation of Stevan is restricted to two generations of increase from breeder seed, and one each of foundation and certified. Breeder and foundation seed will be maintained by the USDA-SCS, Tucson Plant Materials Center, 3241 N. Romero Rd., Tucson, AZ 85705. Limited quantities of foundation seed will be available for commercial production in 1994.

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1990 *BOTHRIOCHLOA ISCHAEMUM* ADVANCED EVALUATION
(Project Number: 04A9001L)
1995 - FINAL REPORT

by
Mark Pater

Abstract:

***Bothriochloa ischaemum* (Yellow bluestem), P.I. 237110, was initially selected for its superior performance in the 1975 Critical Area and Range Improvement Grass IEP⁷. In 1983 this accession was included in the 1983 Yellow Bluestem Intercenter Strain Trial (Project Number: 04R006H). In 1989, *Bothriochloa ischaemum*, P.I. 237110, was selected for advanced evaluation for its superior forage production, drought tolerance, vigor, early grownup and robust appearance. Studies on this species were concluded in 1993. This accession was not released for commercial production.**

KEY WORDS: *Bothriochloa ischaemum*, yellow bluestem, introduced,.

Introduction:

Bothriochloa ischaemum (L.) Keng is an introduced, warm-season, C₄, tufted, perennial bunchgrass with slender, strictly erect or decumbent culms, these becoming somewhat stoloniferous or rhizomatous under close grazing or cutting. Culms mostly 30-50 cm tall but occasionally over 100 cm long when decumbent or trailing at base; Culm nodes bearded with short hairs, glabrate in age; sheaths glabrous; ligule a short, truncate membrane, usually 1 mm or less long; blades linear-attenuate, mostly 2-4 mm broad and 4-20 cm long, the uppermost greatly reduced, usually sparsely hispid with long papilla-based hairs, at least in vicinity of ligule; inflorescence well exerted above uppermost leaf, mostly 4-10 cm long and with 2-(1-)8 primary branches 3-9 cm long, these infrequently rebranched; branches slender, terete below the spikelets; internodes of branch rachis and pedicels ciliate on margins, at least the terminal internodes and pedicels with a narrow medial groove. Sessile spikelets 3-4.5 mm long, narrowly ovate; first glume never with a glandular pit or depression, usually scabrous on margins and hispid on back below middle, the apex acute; lemma awn geniculate and twisted, mostly 1-1.5 mm long; pediceled spikelet staminate, awnless, about as long as sessile one but usually narrower; first glume glabrous or hairy below middle.⁸

Bothriochloa ischaemum, P.I. 237110, was evaluated for its use in providing vegetative cover on abandoned cropland and critically disturbed areas. Another potential use considered this species as a warm-season, irrigated pasture grass. P.I. 237110 performs well at elevations below 1,200 m (3,900 ft) within rainfall zones of 200-355 mm (8-14

⁷Patrick T. Williams. 1979. 1975 Critical Area and Range Improvement Grass IEP. Final Summary. USDA-SCS, Tucson Plant Materials Center Ann. Tech. Report. p.6-23.

⁸F.W. Gould. 1975. The Grasses of Texas. Texas A&M Univ. Press, College Station, TX. p.602-604.

inches). Potential soils to which this cultivar is adapted to includes loamy sand, loamy fine sand, sandy loam, loam, sandy clay loam, clay loam and silt loam.

History:

In August 1989, a large-scale seed production block was established in Field, Borders 18 & 19 at the Tucson Plant Materials Center (Tucson PMC). Seed harvests were conducted in the late spring and late fall using the Flail-Vac seed harvester.

Tucson PMC personnel also comparatively evaluated *Bothriochloa ischaemum*, P.I. 237110 and 'Ganada'. Evaluation factors included: germination rates under various osmotic potentials, seedling vigor at various osmotic potentials, tolerance to drought-like conditions, water use efficiency, stomate densities, leaf surface areas, specific leaf weights, apparent photosynthetic rates, and dark respiration rates.

Results and Discussion:

This accession will not be released for commercial production due to a lack of interest by customers for introduced species. Yellow bluestem has been and is currently being studied extensively for use as a pasture grass in the southern Great Plains region of the U.S. The following report summarizes the final evaluations conducted with this accession.

mm broad and 4-20 cm long, the uppermost greatly reduced, usually sparsely hispid with long papilla-based hairs, at least in vicinity of ligule; inflorescence well exerted above uppermost leaf, mostly 4-10 cm long and with 2-(1-)8 primary branches 3-9 cm long, these infrequently rebranched; branches slender, terete below the spikelets; internodes of branch rachis and pedicels ciliate on margins, at least the terminal internodes and pedicels with a narrow medial groove. Sessile spikelets 3-4.5 mm long, narrowly ovate; first glume never with a glandular pit or depression, usually scabrous on margins and hispid on back below middle, the apex acute; lemma awn geniculate and twisted, mostly 1-1.5 mm long; pediceled spikelet staminate, awnless, about as long as sessile one but usually narrower; first glume glabrous or hairy below middle.⁹

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⁹ F.W. Gould. 1975. The Grasses of Texas. Texas A&M Univ. Press, College Station, TX. p.602-604.

A PHYSIOLOGICAL COMPARISON OF TWO YELLOW BLUESTEMS

(*Bothriochloa ischaemum* [L.] Keng.)

by

Mark Pater

ABSTRACT

Yellow bluestem (*Bothriochloa ischaemum* (L.) Keng.) cultivars are used in conservation plantings in New Mexico, Texas and Oklahoma. The recommended cultivar in southern Arizona is Ganada. However, a population from Saudi Arabia, P.I. 237110, may be better adapted to the Sonoran Desert environment. This study was conducted to determine why P.I. 237110 may be better adapted to this environment than Ganada. Morphological and physiological characteristics of P.I. 237110 and Ganada were compared in five experiments. Evaluations revealed significant differences in combined stomate densities on both leaf surfaces, leaf surface area, and water use efficiency but not in apparent photosynthesis or dark respiration. Combined average stomate density was significantly lower for P.I. 237110 than Ganada (107 vs. 136 stomates mm⁻²). P.I. 237110 had a significantly higher leaf surface area (40.5 cm²) than Ganada (25.3 cm²). Apparent photosynthetic rates were not significantly different between the populations (Ganada: 12 μmol m⁻² s⁻¹ and P.I. 237110: 10 μmol m⁻² s⁻¹). Dark respiration rates for Ganada were not significantly different (1.4 μmol m⁻² s⁻¹) from those of P.I. 237110 (1.9 μmol m⁻² s⁻¹). P.I. 237110 required 88.9 g of water per 1 g of dry matter than Ganada which required 52.3 g of water.

INTRODUCTION

Yellow bluestem (*Bothriochloa ischaemum* [L.] Keng.), sometimes classified within the "Old World Bluestems" (OWB), is an apomictic, C₄, warm-season, perennial bunchgrass that has been introduced into North America (Dalrymple 1990). The culms are noticeably pale yellow, with dark nodes, leaves are mostly basal, slightly scabrous above with scattered long hairs more prominent near the base of the blade, and foliage color is generally light green. The typical inflorescence consists of several unbranched racemes arranged subdigitally on an axis distinctly shorter than the longest raceme. Individual plants tend to form large, saucer-shaped clumps with the stems curving up from the periphery (Gould 1975).

The Old World Bluestems have been commercially available in the U.S.A. since the 1930's when Caucasian bluestem (*Bothriochloa caucasica* [Trin.] C.E. Hub.) came into use. These species (Caucasian and Yellow bluestem) were originally introduced into Texas and southwestern Oklahoma from Eurasia and North Africa, primarily for use as

pasture grasses (Dewald et al. 1988). Since the introduction of yellow bluestem, several varieties have been extensively tested, developed and made commercially available for pasture and conservation uses.

U.S.D.A. Soil Conservation Service (SCS) personnel at the Tucson Plant Materials Center (TPMC) began evaluating yellow bluestem in the mid-1970's for its potential use in reseeding degraded rangelands, retired farmlands, critical areas, and as a warm-season, irrigated pasture species (Pater 1992). In light of the growing concern for the use of native species for reseeding rangeland, the focus for yellow bluestem shifted primarily towards its use as a low water use, irrigated pasture grass, as well as for reseeding retired farmland, highway construction sites, critical areas and mine spoils. Currently, one of the best adapted, commercially available cultivars of yellow bluestem for use in Arizona is 'Ganada'. This cultivar was originally collected in Turkestan in 1934, and released for commercial production from the Los Lunas Plant Materials Center, New Mexico in 1979 (Anonymous 1979).

An evaluation of 13 Old World yellow bluestem accessions was initiated at the TPMC in September of 1983. Evaluation criteria included vigor, size, yield, and tolerance to drought and cold in mature, single plants. One accession, P.I. 237110, quickly proved to be the superior performer in vigor, biomass production, spring green-up, and tolerance to drought-like conditions.

P.I. 237110 was originally collected from the Al Khars region in Saudi Arabia in the spring of 1952. It was first selected as the superior performer in the 1975 Critical Area and Range Improvement Grass Initial Evaluation Planting at the TPMC in 1979. P.I. 237110 was also evaluated in revegetation trials on abandoned cropland southwest of Tucson from 1987-1989. In comparison with a variety of native and introduced grass species, P.I. 237110 was one of the few perennial bunchgrass species to become effectively established (Munda and Pater. 1989).

The superior performance of P.I. 237110 over the commercially available Ganada, suggested that P.I. 237110 was better adapted to the southwestern desert climate. The objective of this experiment was to determine what physiological or morphological differences might explain the large differences in performance between Ganada and P.I. 237110. The objectives of this study were achieved by comparing the variation in stomate densities on both surfaces of leaf blades as well as the leaf sheath, and evaluating specific leaf weights, apparent photosynthetic rate, dark respiration rate, and water use efficiency (WUE) of Ganada and P.I. 237110.

LITERATURE REVIEW

Leaf Anatomy

Gould and Shaw (1983) describe the leaf of a grass plant as consisting of a basal sheath, which tightly enfolds the culm, and a flattened blade or lamina. A membranous or hairy ligule is commonly present on the adaxial surface at the apex of the sheath. Projections of tissue called auricles may be developed laterally at the apex of the sheath or at the base of the blade. Both the sheath and the blade conduct the normal leaf

functions of photosynthesis and respiration. They also play an important role in supporting and protecting the developing shoot.

Gould and Shaw (1983) also state that the sheath typically has the general shape of a hollow cylinder that is split down one side. The margins of the sheath commonly overlap, both at the point of attachment and for all or most of the length of the sheath. In *Glyceria*, *Bromus*, *Festuca*, and other genera, the margins of the sheath are completely or incompletely united (connate) from the base upward (Gould and Shaw 1983). The nerves of the sheath are usually numerous and relatively uniform in development. However, frequently, there is a distinct midrib. Such grasses as *Andropogon virginicus* L., *Muhlenbergia emersleyi* Vasey., *Poa compressa* L., and many species of *Chloris* that have flattened culms, also have sharply keeled and laterally compressed leaf sheaths.

Gould and Shaw (1983) define the ligule as usually a thin, white or brownish membrane, but in some grasses, especially those of the Chloridoideae, it consists of a fringe of hairs or is absent. The Mexican grass *Muhlenbergia macroura* Hitchc. (*Epicampes macroura* Benth.) has a broad, firm ligule 2 to 4 cm long. *Sorghastrum nutans* (L.) Nash. has a stiff, brownish ligule that is usually divided into a rounded central lobe and two stiff, pointed lateral projections. The latter have been referred to as sheath auricles (Hitchcock 1951). In *Leptoloma cognatum* (Schult.) Chase there is a gradual transition from sheath to ligule on either side of the blade attachment. The green lateral nerves of the sheath extend upward into the marginal portions of the ligule. A particular type of ligule is usually consistent for all species of a genus. However in *Panicum* there are both membranous and hairy ligules, and in some species the ligule is absent.

The leaf blade, is typically linear or lanceolate, with parallel nerves and entire, smooth or scabrous margins. Blade size and shape vary within wide limits (Gould and Shaw 1983). The blades of *Monanthochloë littoralis* Engelm. are infrequently over 1 cm long. At the other extreme, the blades of the bamboo *Neurolepis nobilis* Mun. reach 4.5 m in length and 30 cm in width (Arber 1934). Grasses of the humid tropics tend to have large, often ovate or oblong blades. In contrast, grasses of semiarid regions commonly have narrow, linear blades that are often involute to better withstand drought. Aciculate blades are extremely narrow and permanently involute to the extent that the internal structure is altered. Variation in nervation of the leaf blade is somewhat greater than in the sheath. Broad, flat blades, such as in *Sorghastrum halepense* (L.) Pers. and *Zea mays* L., have a large, strongly developed midnerve. Narrow blades that become involute usually have uniformly developed nerves and lack a prominent midnerve.

Leaf development and final morphology depend on genotype, ontogenetic position, and on growth environment. All features of leaf structure and physiology, including size, shape, cell size, trichome density, stomatal distribution, and photosynthetic capacities are sensitive to the growth environment and contribute to a plant's adaptability. Although a given set of characters may be adaptive in the natural situation, they may be of little or no advantage when introduced into new environments (Baker et al. 1985).

Generally, grass leaves contain three types of tissue elements: epidermis, mesophyll, and vascular tissues (Fahn 1967). Booth (1964) states that in seed plants, the epidermis reaches its highest degree of specialization in the Gramineae with the possible exception of the Cyperaceae. The epidermis provides a wide variety of characters that are

readily visible and certain features that may be used as an indication of comparative chromosomal numbers. Booth (1964) also noted that leaves located at different levels on a plant may exhibit variation, and that plants grown in different habitats may also vary.

The epidermis is usually one cell layer thick (Esau 1976). and the epidermis of most grasses is made up of cells of two distinct sizes (Booth 1964). The cells with long, vertical axes (long axis parallel to the length of the leaf) are termed "long cells", and those that are noticeably shorter in length are termed "short cells" (Booth 1964). The long cells form the most distinct pattern of the leaf epidermis. The cells located within the longitudinal line between the stomata are often somewhat different from the other long cells and are referred to as interstomatal cells in order to separate them from cells not associated with the stomata (Booth 1964). Short cells occur in rows parallel to the long axis of the leaf blade either singly or in pairs, depending on the species. They may be only in the costal zone (epidermal tissue located over leaf veins), only in the intercostal zone (epidermal tissue located between leaf veins) or present in both zones. In some species they may be entirely absent. They are easily identified by their shorter length when compared with other cells of the epidermis (Booth 1964). All unicellular and multicellular appendages of the epidermis are designated by the term "trichome" (Fahn 1967). The epidermal appendages of the grasses are diverse in form and structure. They are represented mainly by macro-hairs, micro-hairs, prickles, and papillae (Booth 1964).

Stomata in grass leaves are confined to the intercostal regions where they may form one or more well-defined longitudinal rows. The number of rows of stomata in the intercostal zone will vary across species. Variation may also be found among the leaves on a single plant or even within a single leaf (Booth 1964). Esau (1976) defined stomata as apertures in the epidermis, each curbed by two guard cells. By changing their shape, guard cells control the size of the stomatal opening. The guard cells are generally kidney shaped in surface view. Esau (1976) also stated that an outstanding characteristic of stomata is the unevenly thickened walls of the guard cells that appears to be related to the changes in shape and volume which occur in the guard cells due to fluctuations in turgor pressure.

The ground tissue of the leaf that is enclosed within the epidermis is called the "mesophyll" (from the Greek words *mesos*, in the middle, and *phyllon*, leaf). The mesophyll is usually specialized as a photosynthetic tissue and consists of living lacunose parenchyma containing chloroplasts (Esau 1976). It occupies the space not occupied by sclerenchyma and vascular bundles, and is readily identified by its translucency, or by a green color, in which case it is designated as chlorenchyma. The cells are of a variety of shapes, but do not follow the common pattern of being divided into palisade and spongy parenchyma seen in dicotyledonous plants. The shape of the chlorenchyma cells is highly variable among different grass species. Some species are noted for their uniformity of cell shape, while other species exhibit cell shapes that are highly irregular in outline and frequency (Booth 1964).

The vascular tissues of grass leaves are arranged in vascular bundles, mostly in a single row in the mesophyll. Vascular bundles are usually associated with mechanical tissues (xylem and phloem) and produce the characteristic venation of grasses that is usually apparent from visual examination as well as from sectioned leaves. The term vein

is applied to a vascular bundle or a group of closely associated bundles that usually produce an easily visible configuration (Booth 1964).

Fahn (1967) described two types of bundle sheaths that are distinguished in grasses. In the subfamily Panicoideae (with the exception of certain species of *Panicum*) the sheath consists of a single layer of thin-walled cells that contain chloroplasts. In the subfamily Pooideae, the sheath consists of two layers of cells. The inner layer, which apparently develops from the procambium, consists of living, thick-walled, chloroplast-free cells that are elongated parallel to the veins, while the cells of the outer layer are thin-walled and mostly contain chloroplasts. On the small veins the inner layer may be present only on the side of the phloem.

Esau (1976) described the bulliform cells as large, thin-walled, highly vacuolated cells that occur in almost all monocotyledonous orders. Bulliform cells either cover the entire upper surface of the leaf blade or are restricted to grooves between the veins. Bulliform cells may occur on both sides of the leaf and are not restricted to the epidermis but are sometimes accompanied by similar cells in the subjacent mesophyll. Bulliform cells contain much water and are completely or nearly devoid of chloroplasts. Their cell wall consists of cellulose and pectic substances, and the outermost wall contains cutin and is covered by cuticle (Fahn 1967).

The principal function attributed to the bulliform cells is the rolling or folding of the leaf. The term "motor cells" is sometimes also used for these cells (Esau 1976). The position of the bulliform cells, associated with their usually thin walls and large water-filled vacuoles seems to indicate the possibility of change in turgor playing an important role in the folding or rolling of the leaves. It has been found that in some grasses the bulliform cells are rigid as a result of silicon accumulation and hence are unable to change shape (Booth 1964). Shields (1951) stated that involution of the leaves, which is especially common in grasses, is a characteristic brought about by the action of the bulliform cells and/or other epidermal and mesophyll elements which may be parenchymatous or sclerenchymatous. Booth (1964) further explained that bulliform cells have proven to be useful for taxonomic purposes, the following being some of the characters most commonly used: (1) Cell uniformity: bulliform cells regular vs. irregular (irregular mixing of small and large cells); (2) Number of cells: the cells are counted in transverse sections of leaves; (3) Size of cells: size is determined as a ratio of bulliform cell length and width to regular epidermal cell dimensions. Because of the variation in size of the bulliform cells, it is often necessary to select the largest cells; (4) Position of strands: position is given in reference to vascular bundles or furrows; (5) Pattern outline: this is the form or outline of the bulliform strand as it appears in the leaf cross-section; and (6) Cell shapes, thickness of cell walls, and extension of the bulliform cells into the mesophyll.

Cutter (1971) stated that all grasses belonging to the Chloridoid-Eragrostoid and Panicoid divisions of the Gramineae have low CO₂ compensation values. These grasses all have certain anatomical features in common, namely specialized bundle sheath cells in the leaves. Some of these grasses, which have the C₄-dicarboxylic acid (Hatch-Slack) photosynthetic pathway, are capable of lowering the concentration of CO₂ in a closed system to less than 5 ppm, and are therefore said to show low CO₂ compensation values (Downton and Tregunna 1968). Most plants have higher compensation values, being

capable of lowering the concentration to only about 50 ppm, and they produce CO₂ in the light by a process known as photorespiration (Cutter 1971).

Stomate Density

In higher plants, stomates are the regulators of gas exchange, principally carbon dioxide (CO₂), and water vapor. The stomatal pore is formed between two guard cells which are specialized cells of the epidermis. The two basic forms of guard cells are the elliptical (kidney-shaped) type and the graminaceous (dumbbell-shaped) type. The guard cells alter in turgor and volume during stomatal movements. This alteration in shape is a result of differential wall thickening and elasticity. Stomatal aperture is influenced by changes in guard cell solute levels that are regulated by the metabolism of organic compounds within the guard cells resulting in the import and export of osmotically active (mainly inorganic) substances from neighboring cells (Weyers and Meidner 1990).

Carbon dioxide enters the plant primarily through the stomates. As the stomates open to receive CO₂, water vapor is released at the same time. When a plant is growing under favorable conditions with an adequate supply of water, the exchange of water vapor for CO₂ is not detrimental to the plant. The loss of water through the stomates creates the pressure gradient that allows more water and dissolved solutes to be drawn up from the roots through the plant (Raven et al. 1981). However when water is not readily available in the soil, water vapor lost through transpiration cannot be as easily replaced and water deficits within the plant can quickly develop (Sundberg 1985). This problem may be particularly severe in arid environments and xerophytic plants have consequently evolved a variety of physiological and morphological features to minimize water loss. The cells of many desert plants are simply able to withstand reduced water content without injury (Levitt 1980). Other desert plants have long taproots that allow them to reach available moisture located deep within the soil while others have extensively-branched shallow root systems which are efficient at making use of whatever minimal precipitation may occur. A large number of xerophytic plants lose their leaves, or even whole shoots as conditions become drier (Levitt 1980).

Over many years it has been recognized that certain modifications of stomates are characteristic of plants adapted to arid environments. The stomates of many xerophytes occur at the surface of the leaf or stem or they may be sunken beneath the epidermal surface. Likewise, the density and size of stomates have been implied as being xeromorphic adaptations. However, the literature dealing with this issue is full of contradictions (Sundberg 1985). Sundberg (1985) explained that Haberlandt (1884) claimed that stomatal densities are relatively low in desert plants. With fewer stomates per unit surface area there would be potentially less transpiration. In the same year, Volkens (1884) stated that there is no correlation between the density of stomates and the xeric environment. In later studies Volkens (1887) and Maximov (1929) claimed that desert plants may actually have higher stomatal densities which would allow for increased rates of transpiration that in turn would produce evaporative cooling of leaf surfaces. Both sides of the issue have continued to be discussed in recent plant physiology textbooks. Hall (1976), Bidwell (1979), and Ting (1982) expressed that stomatal density

is decreased in plants adapted to arid environments while Devlin and Witham (1983) and Noggle and Fritz (1983) argued that densities are increased in xerophytic plants.

Quarrie and Jones (1977) stated that stomatal density tends to increase with irradiance during growth. A similar increase is often, but not always, apparent with water stress. The variable response arises because of two conflicting effects: a general decrease in cell size with water stress and a decreased stomatal index (stomata as a proportion of total epidermal cells). Although water stress does not often affect the ratio of adaxial to abaxial stomatal density (Grace and Russell 1977; Quarrie and Jones 1977), there are several reports of this ratio increasing with irradiance during growth (Gay and Hurd 1975; Ticha 1982).

Willmer (1983) stated that in addition to large differences in stomatal density, size and distribution over the leaf surfaces, there are major genetic differences in both stomatal density and size between species by at least an order of magnitude. Some species are hypostomatous with stomata only on the lower (abaxial) leaf surface. Others are amphistomatous (similar numbers on each leaf surface), and others are intermediate between these extremes (Baker et al. 1985).

Strobel and Sundberg (1984) suggested that xerophytic plants evolved different stomatal strategies to deal with water stress. They associated high stomatal densities with non-succulent xerophytes and stated that average stomatal densities for non-succulent plants were 165 mm^{-2} . According to Sundberg (1985), in contrast to succulents, the stomatal densities of non-succulent xerophytes fall mostly within the typical range of more mesophytic plants and actually include some of the highest stomatal densities recorded. He also stated that many non-succulent xerophytes have high rates of transpiration that often increase with increasing levels of evaporative demand. The apparent evolutionary advantage here is the ability to reduce tissue temperature by evaporative cooling and avoid a buildup of heat in the tissues. Levitt (1980) has shown that evaporative cooling due to high rates of transpiration can actually reduce internal tissue temperatures to below that of the surrounding air.

Sundberg (1985) also explained that studies by Ting and Szarek (1975) showed that maximum gas exchange occurs in leaves with many small stomates as opposed to a few, relatively large stomates. Although an individual small stomate will be less efficient at allowing gas exchange per unit pore area than an individual large stomate, more small stomates may be packed into a unit leaf area which allows for higher total transpiration and hence a greater evaporative cooling capacity.

Studies by Dobrenz et al. (1969)¹⁰ on alkali sacaton (*Sporobolus airoides* Torr.) demonstrated that plants with higher stomate densities exhibited a lower resistance to gas and water vapor movement into and out of the leaf. For example, ecotype AC-13 had an abaxial stomate density of approximately $136 \text{ stomates mm}^{-2}$ and a diffusive resistance of 3.26 s cm^{-1} , while ecotype CO-40, with an abaxial stomate density of approximately $157 \text{ stomates mm}^{-2}$ had a diffusive resistance of 5.37 s cm^{-1} .

Another study by Dobrenz et al. (1969), was undertaken to determine the stomate density of a wide range of blue panic grass (*Panicum antidotale* Retz.) genotypes, and the association between stomate density, drought tolerance and water use efficiency. In this

¹⁰A.K. Dobrenz, Jerry Cox, Bruce Munda, and Dave Robinson. 1990. Stomate density and physiological measurements of leaves of *Alkali sacaton* (unpublished).

comparative evaluation of six blue panic grass clones, those that were drought tolerant as seedlings had a lower stomate density than the drought susceptible clones and no relationship was found between stomate density and water use efficiency. This study also showed that stomate density varied with leaf position and age. The younger leaves at the top of the flowering culm had a significantly lower stomate density than leaves from the middle or the base of the culm. Data averaged over the six clones also showed the abaxial surface of the leaves to have a significantly higher stomate density than the adaxial leaf surface.

Photosynthesis and Dark Respiration

Ultimately the most important physiological factor affecting plant productivity is the photosynthetic process. Calvin and Bassham (1962) described a pathway for CO₂ fixation in which CO₂ was incorporated into a 6-carbon compound and rapidly converted to a 3-carbon compound, 3-phosphoglyceric acid (3PGA). This pathway, also known as the C₃ pathway (or Calvin cycle), was considered to be the major photosynthetic mechanism for carbon (C) fixation. However, Hatch and Slack (1966) later characterized a form of CO₂ fixation in which CO₂ was first incorporated in 4-carbon compounds (aspartic, malic, or oxalocetic acid) prior to transfer to sugars by way of 3-phosphoglycerate. The proposed mechanism involved the operation of two interrelated metabolic cycles. Downton (1970) described carbon fixation into C₄-dicarboxylic acids in mesophyll cells and the subsequent incorporation into the Calvin cycle located in the bundle sheath cells. These plants possessing the 4-carbon pathway (C₄ plants) were generally found to be of tropical origin and more efficient in fixing CO₂. They were also found to produce three times more dry matter than C₃ plants, especially in relatively sunny, warm, dry climates (Black 1971).

Black (1971) explained that a variety of characteristics differentiate plants that have the C₄ photosynthetic pathway from those with the C₃ photosynthetic pathway. In C₄ plants compared to C₃ plants: net photosynthetic rate is two to three times greater; CO₂ compensation points are lower; bundle sheath cells contain chloroplasts and starch; discrimination against ¹³C compounds is lower; and CO₂ fixation initially yields 4-C acids as opposed to 3-C acids.

Waller and Lewis (1979) described how leaf anatomy also provides an easily distinguished difference between C₃ and C₄ plants. Plants with the C₃ photosynthetic pathway do not have well defined parenchymatic bundle sheaths and starch grains are found mainly within the mesophyll (Bisalputra et al. 1969) while C₄ plants generally have well developed parenchymatic bundle sheaths containing high concentrations of chloroplasts and starch. Bundle sheath cells utilize the C₃ photosynthetic process, however, they are surrounded by mesophyll cells containing chloroplasts utilizing the C₄ photosynthetic process which fix and then supply C for the C₃ pathway. Stern (1991) stated that the C₄ pathway provides CO₂ to the Calvin cycle more efficiently than the C₃ pathway thereby reducing of photorespiration. The presence of two active photosynthetic

carboxylases and their associated enzymes in the same leaf of a C₄ plant appears to result in a higher attraction for more rapid uptake of CO₂. The close proximity of starch formation to the vascular bundles should also make photosynthate translocation more efficient (Waller and Lewis 1979).

Black (1971) explained that C₄ plants exhibit continued increases in CO₂ uptake as light intensity increases to nearly full sunlight (approximately 1.5 to 1.8 langley), while C₃ plants are saturated at 0.2 to 0.4 langley. Maximum CO₂ assimilation on a leaf area basis at normal atmospheric concentrations of CO₂ ranges from 50 to 80 mg CO₂ dm⁻² hr⁻¹ for C₄ plants, but only 15 to 35 mg CO₂ dm⁻² hr⁻¹ for C₃ plants. Optimum temperatures for CO₂ uptake by C₄ plants were reported to be between 30 and 40 °C with uptake decreasing rapidly below 15 to 20 °C. In comparison with C₃ plants, the optimum temperatures ranged from 10 to 25 °C with usually a sharp decrease in CO₂ uptake at temperatures above 25 °C.

Björkman (1976) summarized that the function of the C₄ photosynthetic pathway is to concentrate CO₂ in the bundle sheath cells, permitting the Calvin cycle to operate at more favorable concentrations of this rate-limiting substrate. This provides a more efficient mechanism for CO₂ fixation at low CO₂ concentrations in the intercellular spaces than does the C₃ photosynthetic pathway. Therefore, the advantage of the C₄ photosynthetic pathway is maximized when photosynthesis is operating at high light intensities and temperatures, and especially when stomatal conductance to gas exchange is low. The C₄ pathway is an important adaptive mechanism in hot and dry environments, but it does not necessarily provide a significant adaptive advantage in cool, moist environments (Björkman et al. 1974).

Gifford (1974) compared the carbon dioxide exchange rates (CER) between C₃ and C₄ plants and reported that values for maximum CER in C₄ grasses ranged from 53 to 64 μmol m⁻² s⁻¹. Similarly, Evans and Wardlaw (1976) reported rates for C₄ cereals of 55 to 64 μmol m⁻² s⁻¹. Apparently the highest rate reported for any plant was 67 μmol m⁻² s⁻¹ in big galleta [*Hilaria rigida* (Thurb.) Benth.] which is a perennial C₄ species native to the deserts of the southwestern U.S. (Nobel 1980).

Water Use Efficiency

Two essential but opposing requirements are needed for plant growth. First the plant requires rapid gas exchange with the atmosphere for the assimilation of CO₂ and the production of dry matter. However, maintenance of a high level of humidity within the leaf requires minimal gas exchange with the atmosphere. By the same token, the requirement for maximum absorption of solar radiation to operate the assimilation process conflicts with the requirement not to increase the energy available for latent heat exchange -- the heat source for plant water loss to the atmosphere (Stanhill 1986).

The quantity of water a plant requires for the production of a unit weight of dry matter (exclusive of the roots) was termed its "water requirement" by Briggs and Shantz (1914). The ratio between transpired water and the dry weight produced varies between

different species when grown under the same conditions and may vary within the same species under different environments (McGinnies and Arnold 1939). Water use efficiency (WUE) is defined as the amount of water required by a plant to produce one unit of dry matter. Stanhill (1986) stated that although it is the plant's biological processes that determine the ratio of transpiration to dry matter production, these are strongly and differentially affected by the physical environment, in particular, by the vapor pressure deficit of the atmosphere during daylight hours. This relationship is such that the transpiration ratio increases markedly with atmospheric demand, making plant water loss less productive in those situations when transpiration is highest.

Water Use in Rangeland Plants

Water that is available for plant growth is one of the most limiting factors on rangelands throughout the world. Plants that are efficient in terms of water use may have a competitive advantage over less efficient plants especially during periods of moisture stress. In general, C_4 plants require about half as much water as do C_3 plants to produce one unit of dry matter (Black 1971). The water use efficiency values of 28 species of Arizona range plants and five crop plants were determined under varying climatic conditions from 1931 through 1936 at the Desert Grassland Station on the Santa Rita Experimental Range (approximately 48 km south of Tucson.). Such a comprehensive evaluation of water use in Arizona range plants of this scale has not been conducted since that time. The native species included six groups of plants; (1) perennial grasses of the desert grassland, (2) perennial grasses of the plains grassland, (3) southern tall grasses, (4) winter annuals, (5) summer annuals, and (6) xerophytic trees and shrubs.

In this study it was determined that as a group perennial grasses were fairly uniform in WUE throughout the year. There was less difference between species of different geographical groups than there was of species within the same geographical groups. Summer annuals had lower total WUE values than the winter annuals. However, winter annuals were at least as efficient in the use of water as the perennial grasses. As a group the summer annuals had lower WUE values than the perennial grasses.

The perennial grasses showed wide variation in WUE values under different climatic conditions. There was also wide diversity within each species as well as considerable variation between species (Table 1). In the fall-winter-spring period the most water use efficient grasses were tanglehead, smooth three-awn, and hairy grama. The least efficient were feather grass, and side-oats grama.

Miller and Hunt (1966) reviewed research conducted to measure the WUE of most crop plants with emphasis placed on grasses. They found no significant correlation between WUE and drought tolerance of rangeland grasses. Keller (1953) discovered significant differences in WUE among genotypes of orchardgrass (*Dactylis glomerata* L.). He determined that the variability expressed in WUE may provide a mechanism for developing more water-efficient strains. Hunt (1962) studied variation in the WUE among two genotypes of *Elymus junceus* Fisch. and *Agropyron intermedium* (Host) Beauv. He found significant differences in WUE between species as well as among genotypes within species. He concluded that this trait was highly heritable and that selection should result in more efficient water use.

WUE studies were conducted by Wright and Dobrenz (1970b) on five selections of Boer lovegrass (*Eragrostis curvula* Nees.) in greenhouse and growth chamber

Table 1. Mean water use efficiency (WUE) values for Arizona range plants as determined by McGinnies and Arnold (1939).

Common Name	Scientific Name	Growth Form*	Mean WUE (g g ⁻¹)
Blue grama	<i>Bouteloua eriopoda</i> Torr.	WSP	387
Hairy grama	<i>Bouteloua hirsuta</i> Lag.	WSP	412
Rothrock grama	<i>Bouteloua rothrockii</i> Vasey	WSP	418
Curly mesquite	<i>Hilaria belangeri</i> (Steud.) Nash.	WSP	427
Tanglehead	<i>Heteropogon contortus</i> (L.) Beauv. Ex. Roem and J.A. Schultes	WSP	448
Arizona cottontop	<i>Digitaria californica</i> Henr. [<i>Trichachne californica</i> (Benth.) Chase]	WSP	457
Slender grama	<i>Bouteloua filiformis</i> (Fourn.) Griffiths	WSP	474

Table 1. (cont'd.)

Common Name	Scientific Name	Growth Form*	Mean WUE (g g ⁻¹)
Black grama	<i>Bouteloua gracilis</i> (H.B.K.) Lag.	WSP	476
Poverty three-awn	<i>Aristida divaricata</i> Humb. Bonpl.	WSP	534
Sideoats grama	<i>Bouteloua curtipendula</i> (Michx.) Torr.	WSP	550
Smooth three-awn	<i>Aristida glabrata</i> (Vasey) Hitch.	WSP	576
Feather grass	<i>Andropogon saccharoides</i> Swartz.	WSP	707
Six-weeks needle grass	<i>Bouteloua aristoides</i> (H.B.K.) Griseb.	SA	331
Caltrop	<i>Kallstroemia grandiflora</i> Torr.	SA	422
Six-weeks threeawn	<i>Aristida adscensionis</i> L.	SA	430

Table 1. (cont'd.)

Common Name	Scientific Name	Growth Form*	Mean WUE (g g ⁻¹)
Boerhaavia	<i>Boerhaavia torreyana</i> (Wats.) Standl.	SA	580
Eight-flowered fescue	<i>Festuca octoflora</i> Walt.	WA	464
Combseed	<i>Pectocarya linearis</i> (Ruiz & Pavon) DC.	WA	594
Lotus	<i>Lotus humistratus</i> Greene.	WA	608
Filaree	<i>Erodium cicutarium</i> (L.) L'Hér.	WA	749
Indian wheat	<i>Plantago insularis</i> Eastw. var. <i>fastigiata</i> Morris.	WA	775
California poppy	<i>Escholtzia mexicana</i> Greene.	WA	897

* Growth Form: WSP= Warm Season Perennial, SA= Summer Annual, WA= Winter Annual

environments. They reported significant differences in WUE among selections within environments. WUE values were reported as being lower for seedlings than mature plants, yet the relative ranking of selections did not change over stages of maturity. Selections with the lowest water use were determined to be the most drought tolerant at the seedling stage. They also observed a significant negative association between seedling WUE and seedling drought tolerance. The same association was shown to exist for seedling drought tolerance and mature-plant WUE.

Wright and Dobrenz (1973) also studied WUE and its associated characteristics in Lehmann lovegrass (*Eragrostis lehmanniana* Nees). They found the two components of WUE, transpired water and dry matter produced, varied significantly among the Lehmann lovegrass lines. Their studies revealed that the lines with the highest production of dry matter transpired the most water. They stated that WUE was not significantly associated with the amount of transpired water but was significantly associated with the production of dry matter. Individual measurements of these two components did not provide an accurate estimate of WUE. However, the WUE values did demonstrate the interrelationship of transpired water and the amount of dry matter produced. This study demonstrated that the most water-use efficient plants produced about twice the amount of total dry matter as the least-efficient plants. The desired performance is a minimum amount of water used for maximum production which translates into superior efficiency of water use.

Additional studies conducted by Wright and Dobrenz (1970a) on blue panicgrass (*Panicum antidotale* Retz.) focused on determining the WUE of this species and relating this to previous studies of blue panicgrass conducted by Wright (1962a, 1962b) which revealed that blue panicgrass showed a relatively high tolerance to soil-moisture stress. In studies by Wright and Dobrenz (1970), soil moisture levels ranged from 15 to 60 cm in depth. WUE and root weight decreased when soil moisture stress increased, while the dry weight of forage was unchanged. Two prominent findings were noted: (1) the most efficient use of water and the highest level of forage production were achieved when plants were clipped at a 30 cm height and when a majority of the seedheads had emerged from the boot ("emergence-maturity stage"); and (2) the emergence-maturity stage gave the highest forage and protein yield, which along with the 30-cm clipping height was the superior management for efficient use of water.

Coyne and Bradford (1985) hypothesized that differences in morphology and geographical origin of two accessions of eastern gamagrass [*Tripsacum dactyloides* (L.) L.] might result in differences in photosynthesis and WUE that could be exploited in a plant improvement program. This study showed that eastern gamagrass has comparatively high photosynthetic rates and WUE when soil water is not limiting. It was also stated that the differences in the measured physiological parameters between the two gamagrass strains suggests that potential exists for germplasm enhancement with respect to maintaining optimum performance in variable environments.

Coyne and Bradford (1985) also stated that the efficiency with which a plant fixes C in relation to water loss is a function of the manner in which the CO₂ pathway is partitioned into its component conductances. Species having the C₄ photosynthetic pathway are generally considered to be more water use efficient than C₃ species because the C₄ species have a higher ratio of residual conductance (g'_r) to stomatal conductance

(g'_s) (Rawson et al. 1983). In the gamagrass studies it was found that the CO_2 pathway was partitioned to minimize water loss because g'_r was greater than g'_s . It was also shown that increasing vapor pressure deficit (VPD) tended to enhance the partitioning of the stomatal conductance to g'_r at the expense of g'_s since stomates are more sensitive to VPD than are the reactions associated with g'_r .

MATERIALS AND METHODS

Plant Materials

In June of 1990 10 plants of each bluestem population (P.I. 237110 and Ganada) were propagated from seed in 0.8-L plastic pots in the Tucson PMC greenhouse. Seed of Ganada was received from the Los Lunas Plant Materials Center and seed of P.I. 237110 was harvested at the Tucson Plant Materials Center. Sixty-five grams of perlite was placed in the bottom of each pot to allow for good drainage, on top of which was placed 200 g of commercial potting mix. Daytime temperatures in the greenhouse were maintained between 32 and 35 °C and nighttime temperatures were maintained between 24 and 27 °C. The plants were watered twice a day (morning and afternoon) with an automatic overhead mist system. No artificial lighting was used, however, the greenhouse was covered with shade cloth that reduced the natural sunlight entering the greenhouse by approximately 50%. These potted plants were used for all of the following experiments except the WUE experiments. All experiments were organized in a completely randomized design and were analyzed by analysis of variance. Probability values of $P \leq 0.05$ were used in statistical analyses for all experiments.

Leaf Peels for Determining Stomate Densities

In November 1990 stomate densities of leaves from both yellow bluestem populations were determined by taking leaf impressions from five randomly selected plants of each population on leaves located in the lower, middle, and upper portions of the plant canopies. Cellulose acetate was applied to the adaxial and abaxial leaf surfaces as well as the sheaths. After allowing the cellulose acetate to dry it was removed with a pair of tweezers and mounted onto microscope slides. The leaf peels were then viewed under a microscope at 450X where the surface area viewed was 0.15 mm² per microscope field. Stomata in three separate fields were counted for each slide and stomate density averages for each population were calculated.

Measurements of Apparent Photosynthesis Under Full Sunlight

Photosynthetic rates were measured using two specially constructed, air-tight, plexiglass chambers that allowed atmospheric gases to circulate within a closed system. This method is similar to one described by Clegg and Sullivan (1978). One of the chambers was equipped with a battery-powered fan that facilitated the movement of gases within the closed system. This chamber was called the "circulation chamber". This

chamber was attached to a second chamber with two small hoses made of surgical tubing (Fig. 1). This second chamber was called the "leaf chamber." To measure apparent photosynthetic rates, a single leaf was carefully inserted through the length of the leaf chamber. Both ends of the leaf chamber were then sealed shut using a pliable clay material that allowed for an air-tight seal.

The circulation chamber was fitted with two rubber septa (plugs) through which a needle and syringe, with their plungers depressed, is placed. At the onset of the process (at 0-time), after the fan circulated the gases within the system for 1 minute, a 6 ml sample was taken by pulling back the plunger of the first syringe. This first sample was then removed from the circulation chamber and

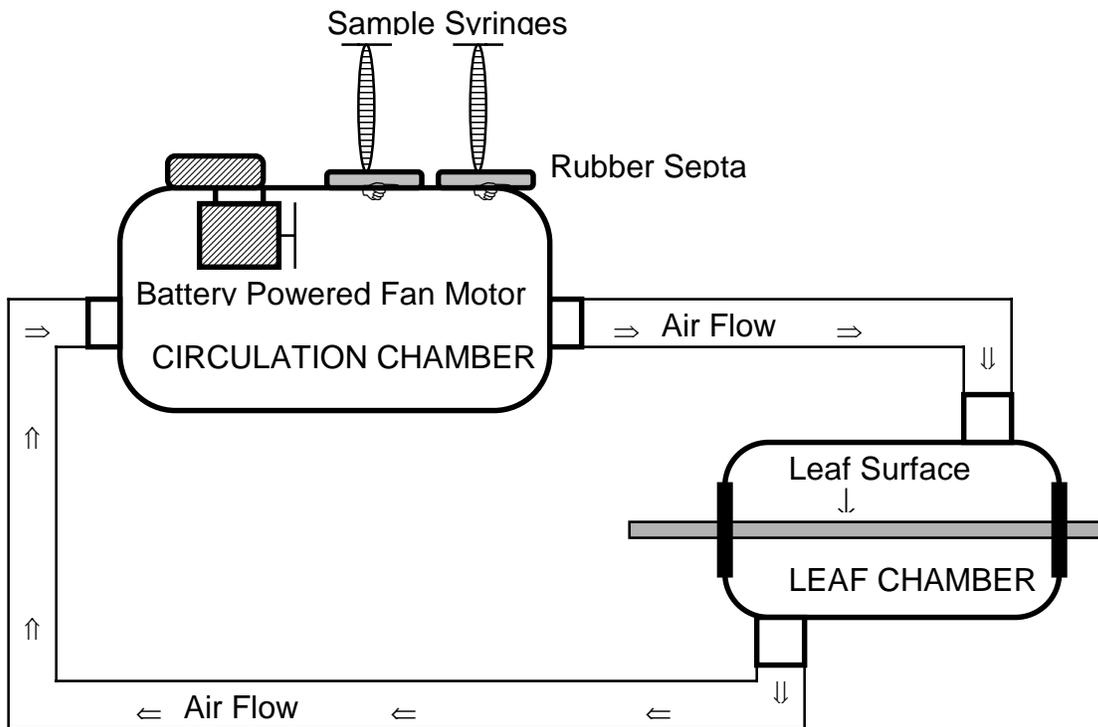


Fig. 1: Diagram of the closed CO₂ measurement system using the syringe technique to obtain CO₂ samples in the field.

the needle immediately inserted in a rubber stopper to prevent the sample from being contaminated with outside gases. After the gases circulated within the system for 2 minutes, a second 6 ml sample was taken.

Ten sample measurements were taken from five potted plants of each population at the TPMC from 11:00-11:45 am under full sunlight. The samples in the syringes were then taken to the lab for measurement of CO₂ concentration differences between each pair of samples for each plant. The CO₂ concentration differences in each pair of syringes was measured using a Beckman model 865 infrared gas analyzer. Five ml of the gas within each pair of syringes was individually injected into a nitrogen gas carrier flowing at 1 L per minute through the analyzer (Fig. 2) and the peak output was measured with a microvolt meter. The system was calibrated with standard gases of known CO₂ concentration. The differences in CO₂ concentrations between the first and second syringes taken from each leaf was a measure of CO₂ uptake.

Laboratory Measurements of Apparent Photosynthesis and Dark Respiration

Five potted plants of each population which were used in the previous experiment were taken to the lab to measure apparent photosynthesis and dark respiration. Prior to obtaining any measurements, each plant was first placed under a light bank (2000 $\mu\text{Ein m}^{-2} \text{s}^{-1}$) for 5 minutes. This presumably allowed the plants' photosynthetic mechanisms to reach a steady optimum rate. Each plant was then placed in an airtight photosynthetic chamber and illuminated with 2000 $\mu\text{Ein m}^{-2} \text{s}^{-1}$ photosynthetically active radiation (PAR) with approximately 0.035% CO₂ concentration flowing through closed system. It should be noted that with

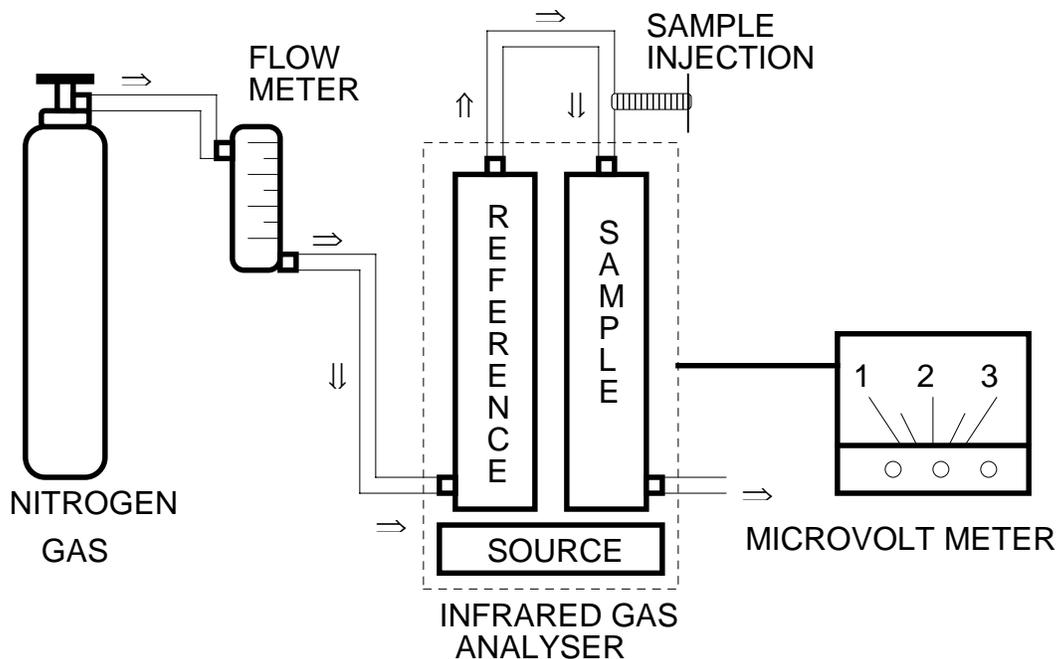


Fig. 2 : Diagram of the CO₂ measurement system in the laboratory.

To measure dark respiration, the light bank was turned off and the airtight plant chamber was covered with a black cloth. The increase in CO₂ concentration within the atmosphere of the closed system was analyzed and recorded for 1 minute. Apparent photosynthesis was calculated from the initial slope of decreased CO₂ concentration recorded. Dark respiration was calculated from the steady state slope of CO₂ increase recorded within the closed system. Gas fluxes were expressed as $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$.

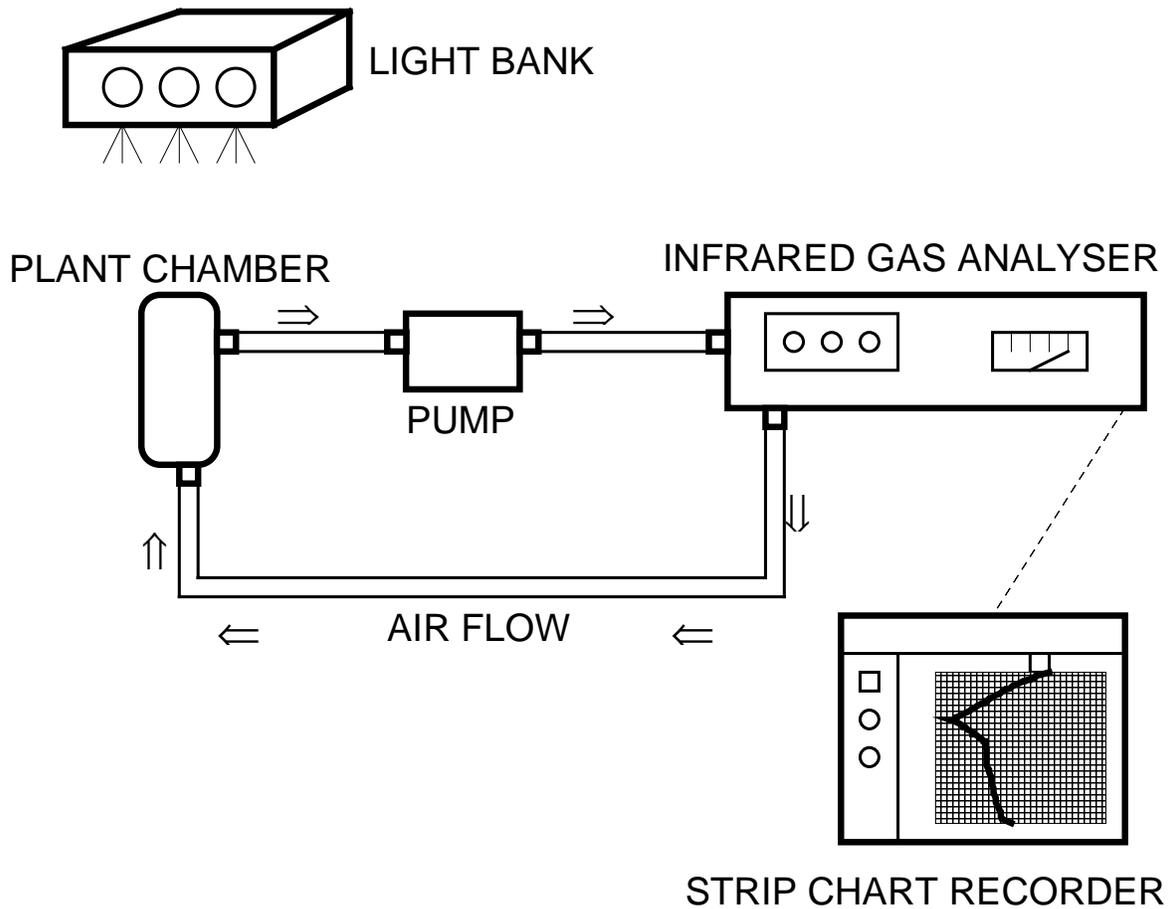


Fig. 3: Diagram of a closed CO₂ exchange system used to measure apparent photosynthesis and dark respiration.

Measuring Leaf Surface Areas

Leaf areas were determined following the gas exchange experiments using a light-sensitive automatic area meter. Leaf samples were obtained by removing all of the leaf and sheath material from the plants that were used in the gas exchange experiments. Leaf samples were placed on the Licor Leaf Area Meter where after passing through a beam of light the machine displays the surface area in cm^2 . Leaf sample measurements were averaged on a plant by plant basis for each cultivar to obtain the mean leaf surface area. Leaf and sheath samples were then dried for 24 hours at 60°C and weighed. Specific leaf weights (SLW) were calculated by dividing the leaf surface area measurements into the dry weight measurements and expressed as mg cm^{-2} .

Measuring Water Use Efficiency

Ten plants of each population were grown in pots in the greenhouse at the Tucson PMC. These plants are separate from those used in the previous experiments. Each plant was grown in a 0.8-L plastic pot containing 750 grams of commercial potting mix. The plants were initially propagated from seedlings grown in containers and after 6 months of growth were transplanted into 0.8-L plastic pots and maintained in the Tucson PMC greenhouse. Daytime temperatures in the greenhouse were maintained between 32 and 35°C and nighttime temperatures were maintained between 24 and 27°C . The plants were watered twice a day (morning and afternoon) with an automatic overhead mist system. No artificial lighting was used, however, the greenhouse was covered with shade cloth which reduced the natural sunlight entering the greenhouse by approximately 50%.

At the beginning of this experiment each plant was initially trimmed back to a 5 cm height above the lip of the pot. The potting soil was covered with styrofoam to reduce evaporative water loss from the soil surface (Dobrenz et al. 1968). The drain holes at the base of each plastic pot were plugged with a rubber stopper to prevent water loss via soil drainage. Each pot was then watered while placed on a scale and brought to a weight of 2,000 g. This was determined to be the "base" weight for each plant. The soil moisture content at the 2,000 g "base weight" was at a point just above field capacity. Every Monday, Wednesday and Friday morning for 4 weeks each plant was weighed to determine water loss and re-watered until it reached the "base" weight of 2,000 g. The amount of water required to bring each pot back up to its "base" weight was recorded. At the end of the experiment each plant was clipped back to its original height. The clipped material for each plant was separated into leaves and culms and placed into marked sample bags. This clipped material was taken to the lab and dried for 24 hr at 80°C and weighed. The weight of the dried material for each plant within each population was then divided by the SLW (mg cm^{-2}) for each respective plant. This permitted approximation of the total leaf area for each plant. This area was then divided by the amount of water used at the last reading for each plant, to obtain the amount of water transpired per cm^2 for a 72 hour period. WUE was determined for each plant by dividing total amount of dry matter produced into the total amount of water used.

Leaf Anatomy

Leaf samples of P.I. 237110 were collected and preserved in formalin acetic acid and alcohol. The tissue was dehydrated with alcohol and imbedded in paraffin (Berlyn and Mischke 1977). Sections were then cut 15 μm thick and stained with saffranin. The leaf cross section and stomate photographs were obtained using a microscope-mounted Polaroid camera at 450 X. Visual observations without measurements were made of the cross sections. Photographs of Ganada could not be created for comparison due to a lack of plant materials from which to obtain samples.

RESULTS AND DISCUSSION

Stomate Densities

Average stomate densities for the two populations were significantly different. P.I. 237110 averaged 107 and Ganada averaged 136 stomates mm^{-2} (Fig. 4.). These measurements represent an average over all plants that were examined in each population. Stomate densities for both populations were significantly higher in the lower and middle sections of the plant canopy than in the upper sections of the canopy. Both populations also showed significantly higher stomate densities on the abaxial leaf surface (183 stomates mm^{-2}) in comparison with the adaxial side of the leaves (60 stomates mm^{-2}) (Fig. 5.).

Studies by Dobrenz et al. (1969) of six clones of blue panicgrass revealed an average of 114 stomates mm^{-2} on the adaxial leaf surfaces and 122 stomates mm^{-2} on the abaxial leaf surfaces. When the data obtained from the six clones were averaged, the abaxial surface of the leaves had a significantly higher stomate density than the adaxial surface. These authors also concluded that seedling drought tolerant clones had a lower stomate density than drought susceptible clones.

Research by Cox et al. (1990) revealed that the stomate density among alkali sacaton populations ranged from 70 stomates mm^{-2} for plants collected near Casa Grande, Arizona to 319 stomates mm^{-2} for TX-III which was collected near Alpine, Texas. This study also concluded that alkali sacaton plants with a higher stomate density had a lower resistance to gas and water vapor movement in and out of the leaf.

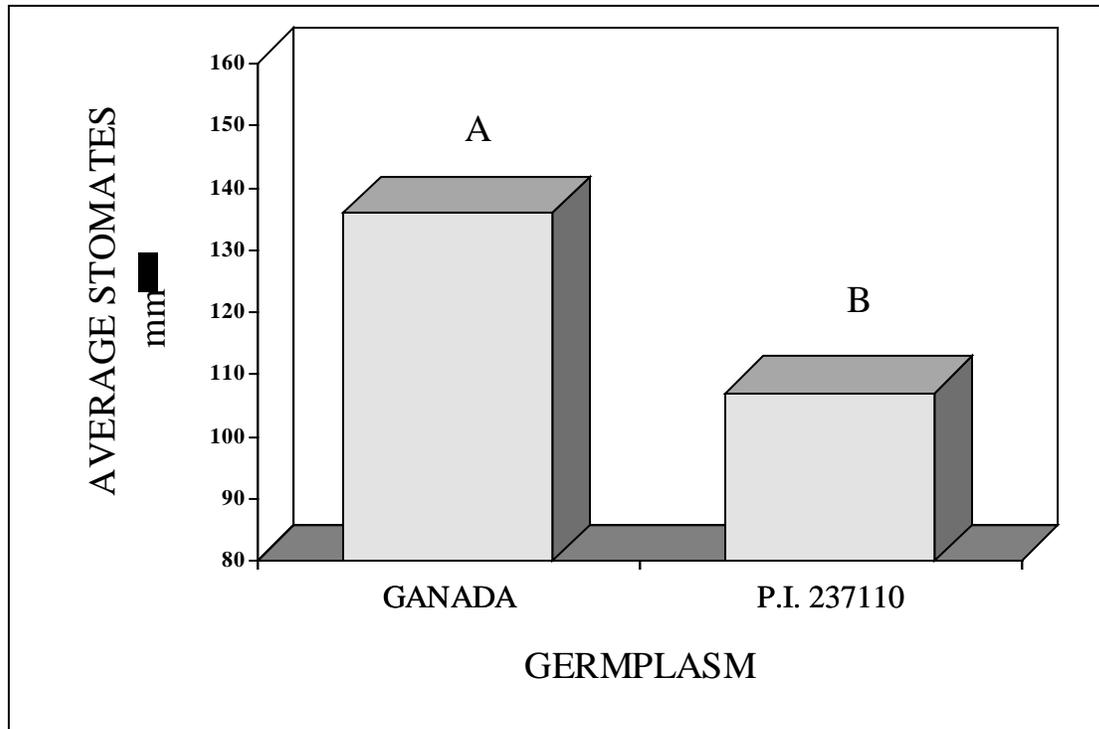


Fig. 4: Average stomates mm⁻² (adaxial and abaxial surfaces) for Ganada and P.I. 237110 yellow bluestem. Means with different letters are significantly different at the 0.05 level.

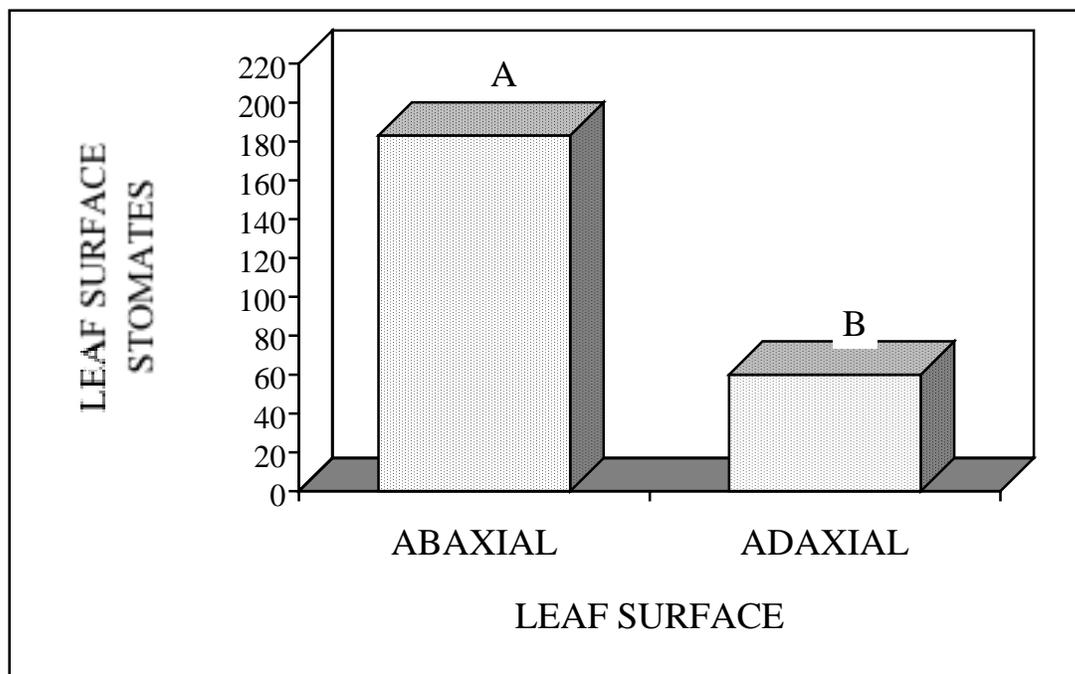


Fig. 5: Average number of leaf surface stomates mm⁻² for Ganada and P.I. 237110 yellow bluestem. Means with different letters are significantly different at the 0.05 level.

Dobrenz et al. (1969) concluded that stomatal densities in blue panicgrass were different across all populations with the lower canopy leaf having higher stomatal density. It was also stated that the abaxial leaf surface had significantly more stomates than the adaxial surface. This difference in stomatal numbers between the two leaf surfaces was also observed with P.I. 237110 and Ganada. Sundberg (1985) concluded that higher densities of smaller stomates on the leaf surfaces of non-succulent, xerophytic plants is an adaptation that allows for higher daytime transpiration rates resulting in lower tissue temperatures. Although no leaf temperature data were obtained, P.I. 237110 has a significantly lower stomate density than Ganada which may suggest that the leaf tissue in P.I. 237110 can better withstand higher daytime temperatures.

Stomate densities on the sheaths of both plant populations were determined to be significantly different. Ganada showed 111 stomates mm^{-2} and P.I. 237110 had 92 stomates mm^{-2} (Fig. 6). These differences were not surprising due to Ganada having significantly higher stomate densities on the leaves. The higher stomate densities on the sheaths of the Ganada population may also contribute to a lower tolerance to drought. No studies dealing with stomate densities on the sheaths of grass species could be located.

P.I. 237110 has an SLW of 2.66 mg cm^{-2} compared to an SLW for Ganada of 2.92 mg cm^{-2} (Fig. 7). Plants with a higher SLW have been shown to exhibit higher photosynthetic rates (Nelson and Schweitzer 1988).

Leaf Area

Total leaf area for P.I. 237110 was much greater at 40.5 cm^2 than for Ganada which was measured to be 25.3 cm^2 (Fig. 8). In studies with winter wheat (*Triticum*

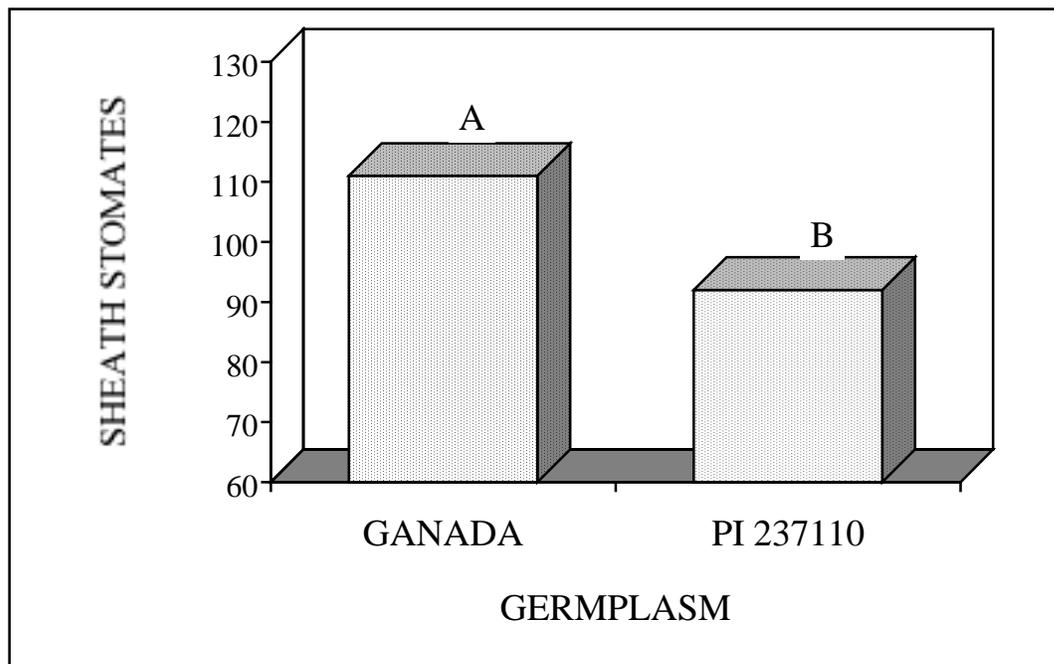


Fig. 6: Stomates mm^{-2} on the leaf sheaths of Ganada and P.I. 237110 yellow bluestem. Means with different letters are significantly different at the 0.05 level.

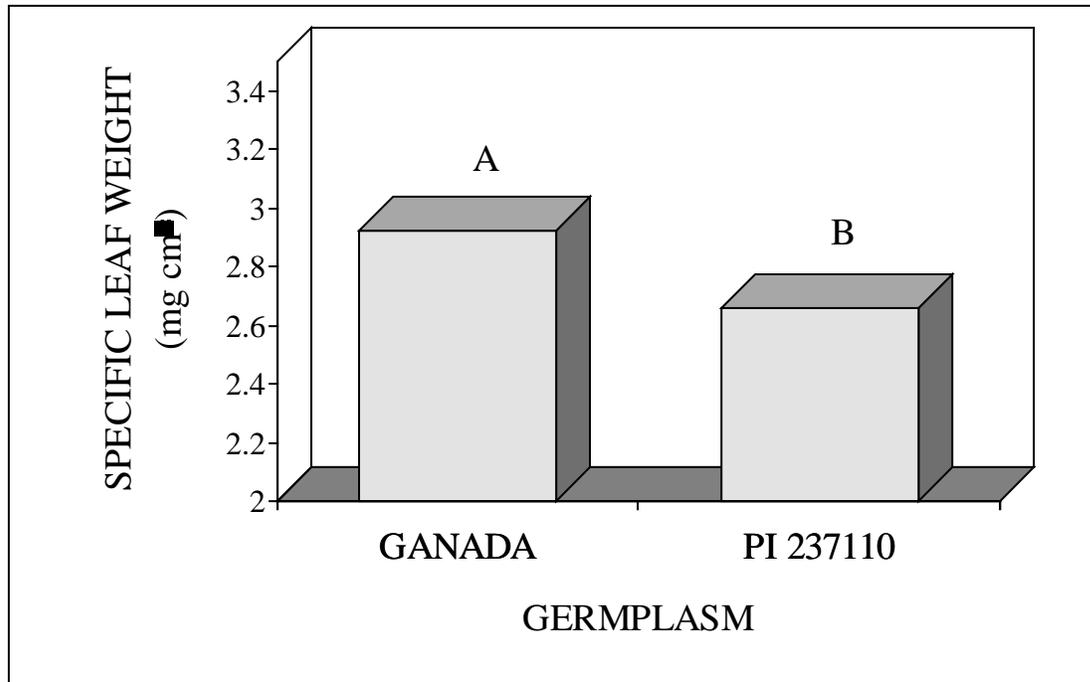


Fig. 7: Specific leaf weight (mg cm⁻²) for Ganada and P.I. 237110 yellow bluestem. Means with different letters are significantly different at the 0.05 level.

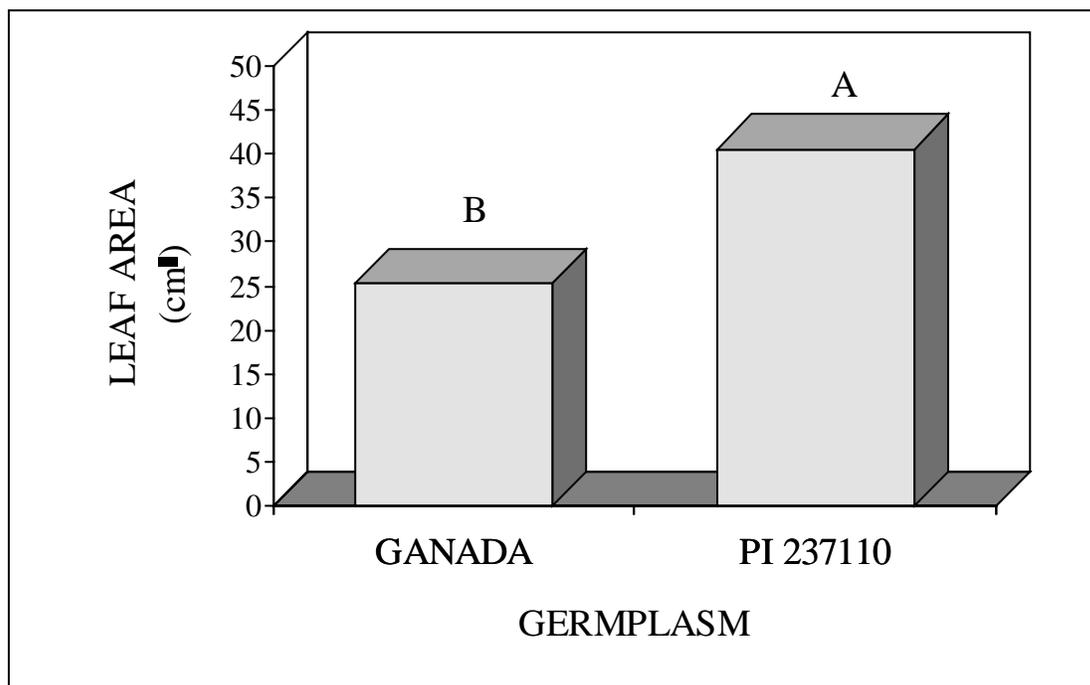


Fig. 8: Leaf surface area (cm²) for whole plants of Ganada and P.I. 237110 yellow bluestem. Means with different letters are significantly different at the 0.05 level.

aestivum L.) Martin and Kiyomoto (1992) stated that biomass (Aase 1978) and canopy production (Puckridge 1971) are highly correlated with leaf area. Genotypic differences in flag leaf area and duration have also been correlated with differences in yield in winter wheat (Fischer et al. 1981; Rawson et al. 1983).

Apparent Photosynthesis

When apparent photosynthesis was measured in the field at the TPMC, no significant differences were observed between Ganada ($12\mu\text{mol m}^{-2} \text{s}^{-1}$) and P.I. 237110 ($10\mu\text{mol m}^{-2} \text{s}^{-1}$) (Fig. 9). When measuring apparent photosynthetic rates in the lab, there was also no significant difference between these two populations, Ganada exhibited a rate of $3.3\mu\text{mol m}^{-2} \text{s}^{-1}$ and P.I. 237110 showed a rate of $3.1\mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 10).

Lower photosynthetic rates were measured in the lab than in the field because in the field a single leaf was measured under full sunlight. In the lab we measured apparent photosynthetic rates of a whole plant under a light bank that produced $2000\mu\text{Ein m}^{-2} \text{s}^{-1}$ at the top of the plant canopy and $500\mu\text{Ein m}^{-2} \text{s}^{-1}$ at the base of the plant due to shading from the plant canopy.

The lower rates in the lab may also have been the result of lower overall light intensity due to fluorescent lighting and lower air temperature as compared to the full sunlight intensity and outside air temperature when the photosynthetic rate samples were taken at the TPMC. No data were taken on light intensity and air temperature in the lab.

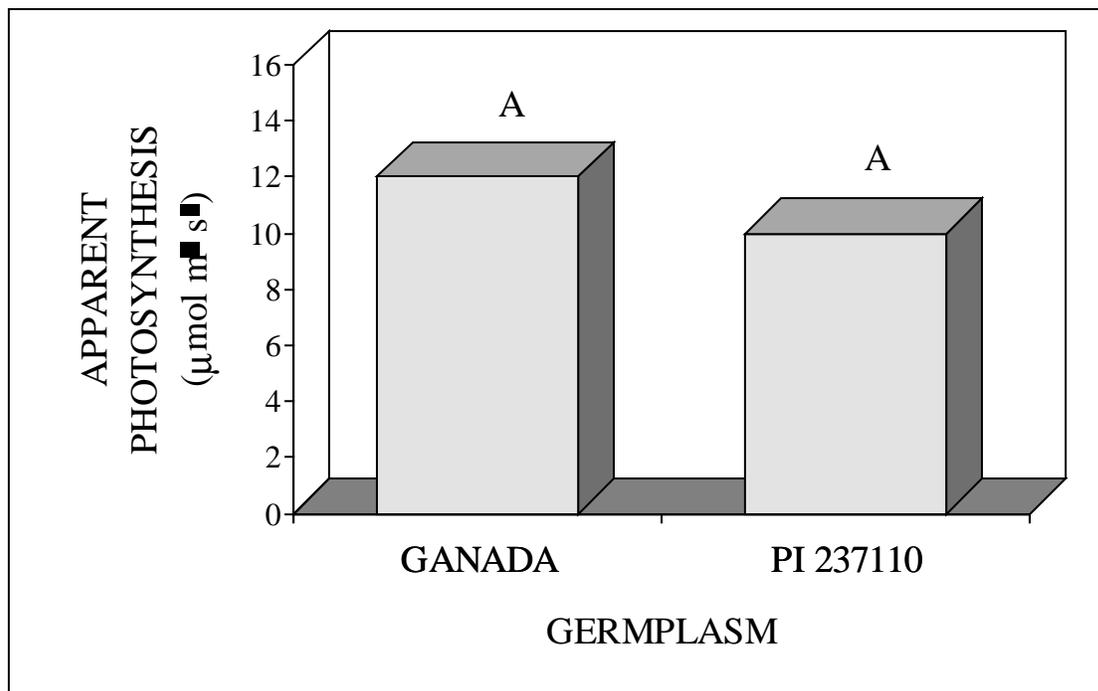


Fig. 9: Apparent photosynthesis ($\mu\text{mol m}^{-2} \text{s}^{-1}$) of Ganada and P.I. 237110 in full sunlight at the Tucson Plant Materials Center (11:00 - 11:45 am, January 1992). Means with the same letters are not significantly different at the 0.05 level.

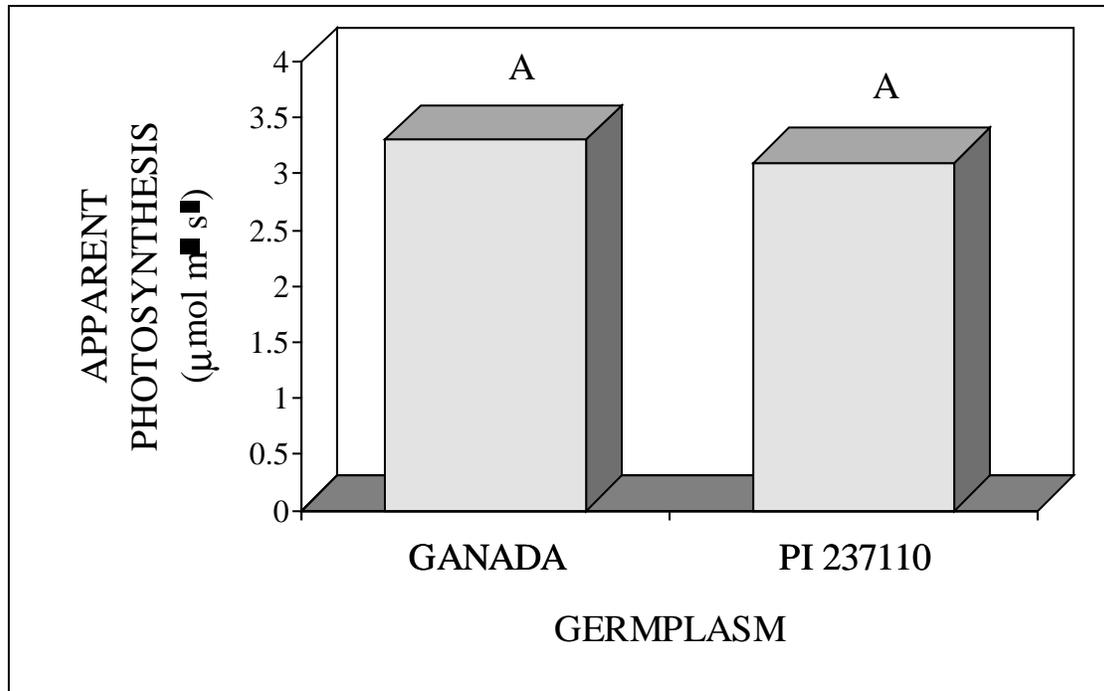


Fig. 10: Apparent photosynthesis ($\mu\text{mol m}^{-2} \text{s}^{-1}$) of Ganada and P.I. 237110 in the lab (cool air temperatures, artificial lighting). Means with the same letters are not significantly different at the 0.05 level.

Studies conducted with 13 cultivars of alkali sacaton that differed in stomate density Cox et al. (1990) revealed transpiration rates ranging from $7 \mu\text{g cm}^{-2} \text{s}^{-1}$ up to $15 \mu\text{g cm}^{-2} \text{s}^{-1}$. However their data did not support reports by Dobrenz et al. (1969) and Miskin et al. (1972) that grasses with fewer stomates had lower transpiration rates. This was due to the fact that Cox et al. were limited in their ability to accurately measure stomate densities because of the severely corrugated adaxial leaf surfaces, therefore only abaxial stomate densities were presented. This prevented an accurate comparison with the studies by Dobrenz et al. (1969) and Miskin et al. (1972) where stomate densities were determined for both leaf surfaces.

Castonguay and Markhart (1992) stated that the coordination of gas exchange and chloroplast activity are important for plant performance in water-limited environments. Together they allow growth to proceed while minimizing dehydration. Stomatal closure is a primary effect of moderate water stress and the observed decrease in photosynthetic rates under moisture-limited conditions is often mainly due to a reduction in CO_2 partial pressure inside the leaf (Chaves 1991; Vassey et al. 1991).

Although no significant differences in photosynthetic rate were observed between the two yellow bluestem populations, it appears that based on plant performance in terms of total dry matter production alone, P.I. 237110 may better coordinate gas exchange and

photosynthesis resulting in increased plant growth over Ganada. Although no leaf temperature data were collected, Ganada may transpire more in order to maintain cooler leaf temperatures. P.I. 237110 may also have the ability to direct more resources into tissue growth and production if it is able to withstand higher leaf temperatures.

Dark Respiration

Dark respiration rate measurements in the lab showed no significant differences between the two varieties (P.I. 237110, $1.9 \mu\text{mol m}^{-2} \text{s}^{-1}$ and Ganada, $1.4 \mu\text{mol m}^{-2} \text{s}^{-1}$) (Fig. 11). Baker et al. (1985) stated that estimates of the proportion of the dark respiration that is inhibited by light suggest that large fluctuations in the ability of light to inhibit respiratory activity occur during leaf development. The high cytosolic ATP/ADP ratio that is generated by photosynthetic activity of the thylakoids when a leaf is exposed to light is thought to inhibit mitochondrial respiratory activity.

Water Use Efficiency

The calculated WUE rates for each population were 89 g of water required to produce 1 gram of dry matter for P.I. 237110 and 52 g for Ganada (Fig. 12). In the study conducted by Wright and Dobrenz (1973), the calculated WUE rates for the six lines of Lehmann's lovegrass ranged from 135 to 178 units of water required to produce one unit of dry matter. The lower WUE rates in the experiments with the yellow bluestem populations may be due to the use of smaller pots; 0.8-L pots for the yellow bluestem versus 4.2-L pots for the Lehmann's lovegrass experiments. The smaller pots may have restricted root growth in the yellow bluestem plants as well as reduce the amount of water for transpiration. This reduction in the amount of available water may have lowered the rate of transpiration in the yellow bluestem plants which in turn may have reduced the WUE values.

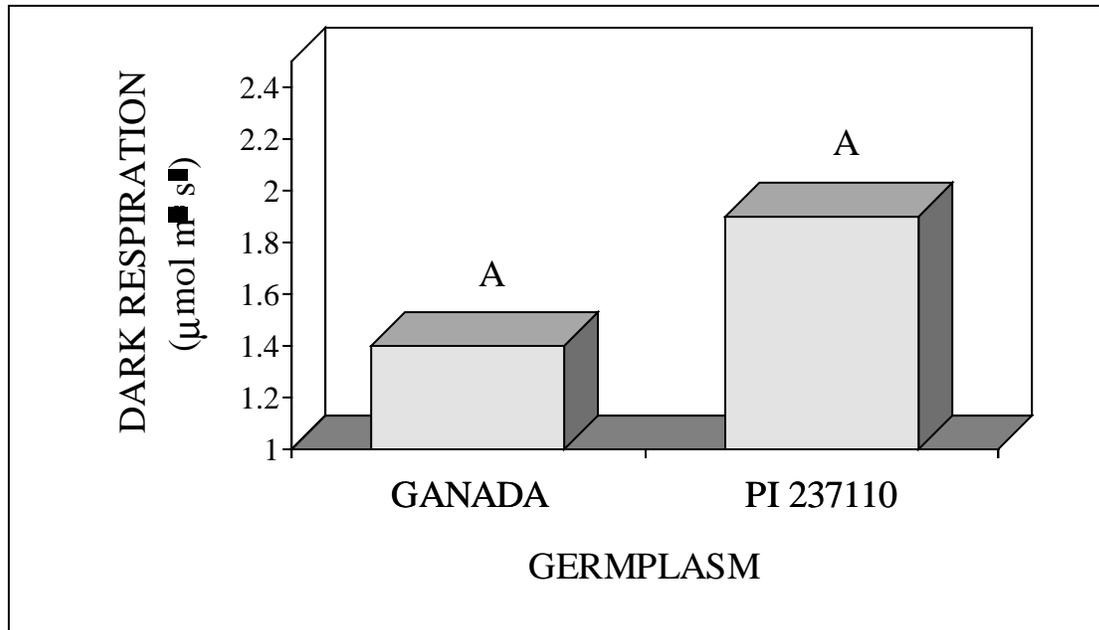


Fig. 11: Dark respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$) for Ganada and P.I. 237110 yellow bluestem. Means with the same letters are not significantly different at the 0.05 level.

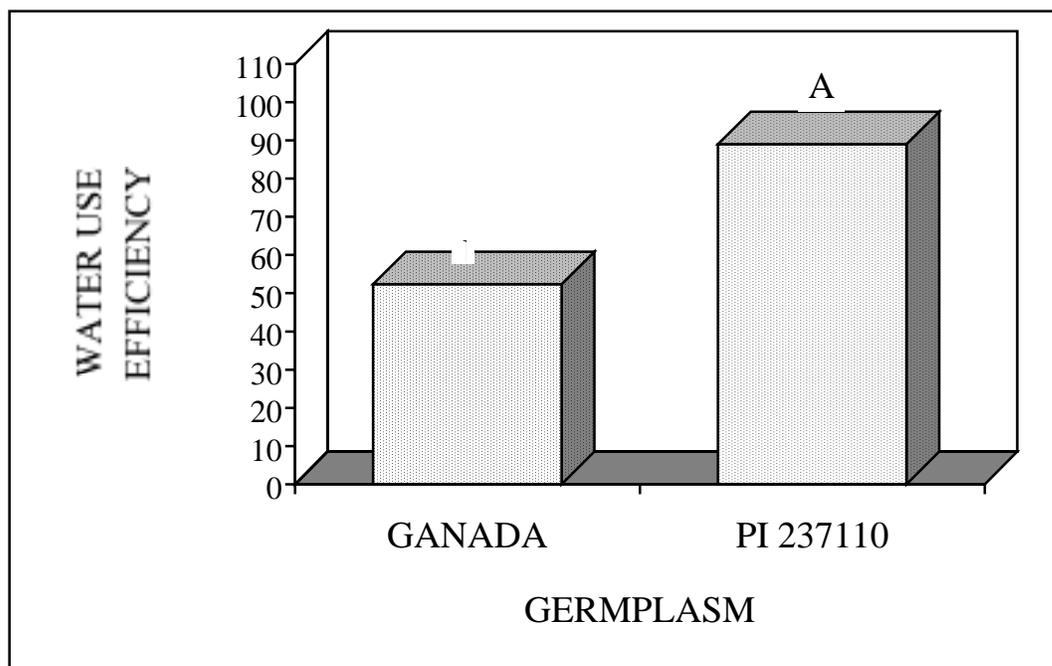


Fig. 12: Water use efficiency (g g^{-1}) of Ganada and P.I. 237110 yellow bluestem. Means with different letters are significantly different at the 0.05 level.

The average amount of transpired water for each population over the 24-day evaluation period was 3,179 g of water for P.I. 237110 and 1,794 g for Ganada. The transpiration rates over a 72 hour period for each population were 42.8 mg cm^{-2} of leaf area for P.I. 237110 and 29.9 mg cm^{-2} for Ganada (Fig. 13). Average daily water use was also significantly different between these two varieties with P.I. 237110 showing a

significantly higher water use than Ganada (Fig. 14). This may be due to P.I. 237110's increased leaf area and higher total dry matter production. McGinnies and Arnold (1939) stated that for any given species, the WUE will vary more or less with changes in external factors, and that a plant should have the lowest WUE under optimum growing conditions. If this is true, it should follow that a comparatively low WUE for a given species should indicate an approach toward optimum growth conditions, while a relatively high WUE would indicate less favorable conditions. A single determination of the WUE of a species considered by itself is no indication of the adaptability of that species to the environment. Furthermore, while a single WUE determination may not indicate the adaptability of a species to various environments, a series of

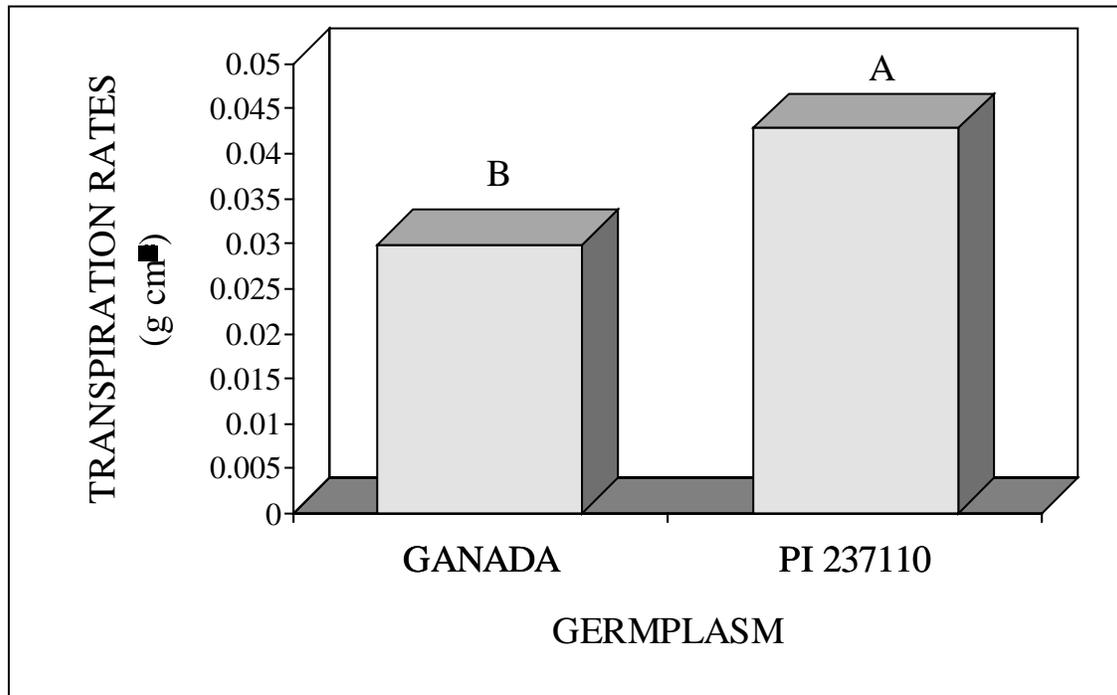


Figure 13: Transpiration rates for 72 hr period (g cm⁻²) for Ganada and P.I. 237110 yellow bluestem. Means with different letters are significantly different at the 0.05 level.

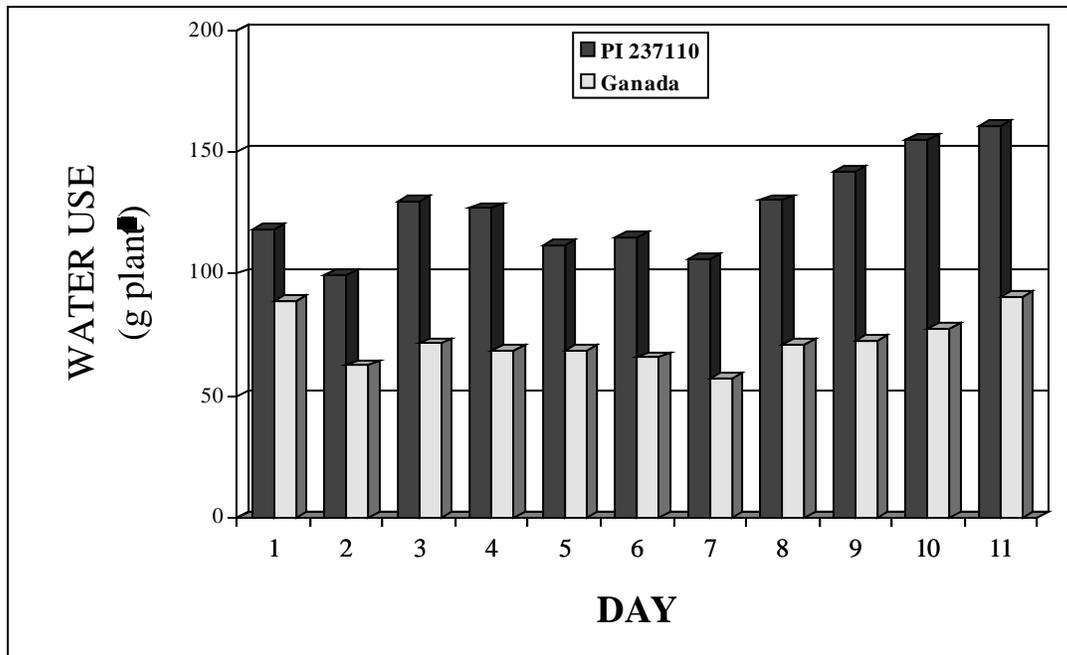


Fig. 14. Average daily water use measurements for Ganada and P.I. 237110 (Day 1= June 8, 1992).

WUE determinations should help to determine that species' range of distribution.

P.I. 237110 apparently took greater advantage of available moisture in photosynthetic processes which resulted in greater dry matter production than Ganada. Ganada appears to utilize the available water for increased transpiration in order to maintain cooler tissue temperatures.

Leaf Anatomy

In a leaf cross section photograph of P.I. 237110, the bulliform cells appear very prominently. According to Mauseth (1988), these cells may act as points of flexure: if they are turgid and swollen, the leaf is open and flat, but if they lose water and become flaccid the leaf folds, minimizing its exposed surface area. Shields (1951) reported that such movements may involve other cells as well as the bulliform cells. It may be that the primary function of bulliform cells is the opening of the leaf as it expands from the sheath node. The bundle sheath cells in the photograph are characteristically large for a C₄ species and contain chloroplasts. The radially aligned chlorenchyma cells (mesophyll cells) around the bundles are also characteristic of a C₄ species (Kranz anatomy). Mauseth (1988) describes how the mesophyll cells in C₄ plants use a different enzyme to take up CO₂ very efficiently, as compared to C₃ plants, and use it to manufacture oxaloacetic acid. OAA is transported to the bundle sheath cells where it is broken down,

releasing the CO₂ again. Because the CO₂ is collected throughout the leaf and then released in just one layer of cells, it achieves a

Fig. 15. Leaf cross section of P.I. 237110 yellow bluestem (450 X). Bundle Sheath Cell (BS), Vascular Bundle (VB), Bulliform Cells (B), Xylem (X), and Phloem (P). very high concentration in the bundle sheath. The chloroplasts of the bundle sheath cells can pick up the CO₂ because it is high in concentration, and RuBP carboxylase can work efficiently.

The difference in stomate densities between the adaxial and abaxial leaf surfaces of P.I. 237110 can also be seen. Stomates are found on virtually all green parts of a plant, especially the leaves and culms. On the leaves, they are typically more abundant on the abaxial surface. Grasses typically have dumbbell-shaped guard cells. This results from the fact that the elongated guard cells are thin walled on the ends and have thick walls along the middle. As the cells absorb water the ends swell but the middle remains narrow. The middle regions of the two guard cells are pushed apart by the enlarged ends, opening the stomatal pore. When the guard cells lose water, the ends shrink and the mid regions move together, and the pore is then closed. The dumbbell shape is present only when the guard cells are turgid (Mauseth 1988).

SUMMARY

Five experiments were conducted to compare the physiological and morphological differences between Ganada and P.I. 237110 yellow bluestem. P.I. 237110 yellow bluestem is currently being evaluated at the Tucson PMC for its potential use as a conservation plant in the lower deserts of the southwestern United States. Ganada yellow bluestem is a commercially available cultivar that was released by the Los Lunas, New Mexico PMC in 1979. Stomate densities for both populations were measured on both leaf surfaces as well as the leaf sheaths. Photosynthetic rates were measured outside under full sunlight, as well as in a laboratory setting under simulated sunlight conditions ($2,000 \mu\text{Ein m}^{-2} \text{s}^{-1}$). Dark respiration was measured in the laboratory under controlled conditions. WUE values were obtained using containerized plants grown in a greenhouse at the TPMC.

The average stomate densities for both populations were significantly higher in Ganada on both leaf surfaces than in P.I. 237110. Both populations revealed significantly higher stomate densities on the abaxial leaf surface than the adaxial leaf surface. Stomate densities for both populations were higher on the leaves in the lower and middle portions of the plant canopy than in the upper plant canopy. Lower stomate densities in the upper plant canopy may help reduce water loss from transpiration due to higher air temperatures and light intensities as compared to those in the middle and lower plant canopy. The observed stomate densities on the sheaths of both plant populations were significantly different with Ganada having more stomates than P.I. 237110. Specific leaf weight was also significantly higher for Ganada than P.I. 237110.

Field and laboratory measurements of photosynthesis did not reveal any significant differences between the two populations. The dark respiration rates obtained in the laboratory were also not significantly different between the two populations.

The WUE experiment showed significant differences between P.I. 237110 and Ganada (Ganada required 52 units of water to produce a unit of dry matter while P.I. 237110 required 89 units). These differences were most likely due to P.I. 237110 having a significantly higher total leaf surface area which in return results in a higher number of stomates per plant. The difference in WUE values may also be explained by considering the original collection sites for these two populations. Ganada originated in Turkestan (presently Turkmenistan) which is characterized as having a cold desert climate (Trewartha and Horn 1980). P.I. 237110 was originally collected in Saudi Arabia from the Al Khars region which has a much hotter desert climate during the growing season (Trewartha and Horn 1980). Ganada also originates from an area of a more northerly latitude and therefore may be more adapted to shorter daylengths as well as a cooler climate. From a strictly geographical standpoint P.I. 237110 appears to be better adapted to Sonoran desert climate than Ganada. Ganada performs better than P.I. 237110 at elevations above 1,065 m and in areas with cooler summer temperatures such as central and northern New Mexico and southeastern Colorado (Anonymous 1979).

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LOWER COLORADO RIVER REVEGETATION PROJECT
Bureau of Reclamation - Natural Resources Conservation Service
Reimbursable Project
1995 - FINAL REPORT

by
Mark Pater

Abstract:

Germination experiments were conducted on five genotypes of honey mesquite (*Prosopis juliflora*), four genotypes of screwbean mesquite (*Prosopis pubescens*) and 27 genotypes of quailbush (*Atriplex lentiformis*). Rooting experiments were conducted on ten cottonwood genotypes (*Populus fremontii*) and four willow genotypes (*Salix gooddingii*). Five treatment levels were developed for the germination and rooting experiments and consisted of the following salt concentrations (NaCl): 0 mmhos cm⁻¹ (control), 5 mmhos cm⁻¹, 10 mmhos cm⁻¹, 20 mmhos cm⁻¹ and 40 mmhos cm⁻¹. The objective of this project was to evaluate various genotypes of these native shrub and tree species which are indigenous to the Lower Colorado River and assess their performance at the five salt concentrations. The focus of these experiments was to determine whether any of the genotypes in each species group exhibited any tolerance to the saline conditions that might be encountered along the Lower Colorado River.

KEY WORDS: honey mesquite, screwbean mesquite, quailbush, cottonwood, willow, salt concentration, germination, biomass production, salt tolerance.

Introduction

Arizona has lost nearly 90% of its lowland riparian areas in the last 100 years according to Pinkney (1992), regional riparian ecosystems along the Colorado River have been reduced to less than 10% of their original area. This has spurred numerous studies and revegetation attempts. Southwestern riparian ecosystems are particularly sensitive to overuse because they are subjected to a wide variation in annual precipitation. They also have a relatively simple species composition in comparison to more mesic riparian areas, giving each species in the southwestern riparian areas a proportionately larger impact on the whole ecosystem. Restoration of deteriorated riparian areas is often complex and difficult (DeBano and Schmidt 1989; Brock 1984).

This report discusses the background of benefits and uses of riparian areas, factors affecting these areas, current knowledge and methods that have been used for revegetation, and factors influencing revegetation attempts. The purpose of this project was to determine whether any genotypes of the species being evaluated exhibited any tolerance to various saline conditions which may be encountered along the Lower

Colorado River. The results may provide some information that is needed to effectively restore and manage riparian ecosystems adjacent to the Colorado River. The results of this study may also provide information pertaining to source locations of adapted native plant material for use in riparian restoration and reclamation activities along the Lower Colorado River.

Literature Review

The USDA, Natural Resources Conservation Service (NRCS) General Manual (1991) defines riparian areas as ecosystems that occur along water courses or water bodies. They are distinctly different from the surrounding lands because of unique soil and vegetation characteristics that are strongly influenced by free water in the soil. Riparian ecosystems occupy the transitional area between terrestrial and aquatic ecosystems. Typical examples would include floodplains, streambanks, and lakeshores.

The Bureau of Land Management (BLM) (1990) defines a riparian area as land directly influenced by permanent water either on the surface or as free subsurface water within the rooting zone of dependent vegetation. A riparian area has vegetation or physical characteristics that reflect permanent water influence. Lake shores and stream banks are typical riparian areas. Excluded are such sites as ephemeral streams or washes that do not exhibit the presence of vegetation dependent upon free water in the soil.

Anderson and Ohmart (1985) offer a similar definition: “A riparian association of any kind is one which occurs in or adjacent to drainageways and/or their floodplains and which is further characterized by species and/or life-forms different from that of the immediately surrounding non-riparian climax.”

Riparian Area Benefits:

The previous definitions of riparian areas indicate that one of the key aspects of riparian areas is the relatively abundant supply of water. As human populations have grown and agricultural lands expanded in the southwestern United States, the need for and scarcity of water has caused many of the current water-related problems and the decline of riparian areas. Some of the benefits of riparian areas are more obvious, such as increased and diverse wildlife populations, aesthetic and recreational opportunities, and erosion control. Other less obvious benefits of well-vegetated riparian areas, which are equally or perhaps more important, may include reduced flood peaks by resistance to flow and storage of floodwaters; providing key recharge points for renewing groundwater; providing travel corridors for wildlife; cooling of water temperatures through shading by riparian vegetation which also reduces evaporation and provides aquatic wildlife with habitat; increasing length of time of streamflow, in some cases to perennial flow; livestock use for forage, shade, shelter and water; and providing repositories for sediment and acting as a nutrient sink for surrounding watersheds (BLM 1991; DeBano and Schmidt 1989; Anderson and Ohmart 1985; Elmore and Beschta 1987).

Factors Detrimental to Riparian Areas:

Considering the previously mentioned benefits, working to prevent further degradation of riparian areas would appear to be a highly advantageous proposition. However, the problems associated with the decline of these areas are complex and require long-term commitments by many people and agencies in order to begin to address the damage.

Stevens (1989) states that riparian systems are the most biologically productive and the most poorly managed terrestrial habitats in the American Southwest. A major factor that is detrimental to riparian areas is groundwater pumping and the subsequent lowering of the water tables. According to a water-use study of phreatophytic species by Busch and Smith (1992), the lowering of riparian water tables appears to have diminished the source of shallow soil moisture supply and may be a causal factor in the increasing impoverishment of the lower Colorado River floodplain vegetation with respect to its formerly dominant trees, i.e., cottonwood (*Populus fremontii* S. Wats.) and willow (*Salix gooddingii* Ball). Water diversion and channeling also have detrimental effects. For example, channel migration and sediment deposition are important to the reproductive biology of cottonwood. Damming and regulation of water flow has caused various detrimental effects including increased salinity. Overgrazing may seriously reduce seedling and sapling regrowth. Competition by the non-native salt cedar (*Tamarix chinensis* Lour.) with native species has become more intense as riparian conditions change. *Tamarix* is more tolerant to drought, inundation, higher salinity levels, fire, and it flowers earlier and longer than native shrub and tree species. Non-maintenance of the watershed is also affecting these areas. Reduction of waterflow due to agricultural and other uses, excessive flooding, recreational overuse, commercial and residential development, off-road vehicle use, increase in fire frequency, and water and air pollution are additional factors presently threatening riparian areas (Stromberg 1990; Reichenbacher 1984; Elmore and Beschta 1987; Brock 1984; Munda, personal comm. 1993; Busch and Smith 1993; Stevens 1989).

Riparian Area Ecology:

According to Stromberg (1990), in mixed broadleaf riparian forests, the streamside zone is generally dominated by cottonwoods and willows, and the terrace (or upland) zone supports mesquite (*Prosopis* spp.), hackberry (*Celtis reticulata* Torr.) or walnut (*Juglans major* [Torr.] L. Benson). These zones are most distinct at lower elevations, due to sharper environmental gradients between riparian and upland zones. Stromberg also states that the seeding characteristics of the streamside plants are the result of small, wind-dispersed seed (secondarily water dispersed) that have a rapid growth rate. This adapts the group for a functional role as pioneering species. In contrast, the upland group has fewer but larger seeds per plant, a slower growth rate, and utilizes animal as well as abiotic factors for seed dispersal. These features are more characteristic of a stable environment. All of the streamside group have an Arctotertiary origin, whereas the upland trees either have a Neotropical origin (e.g. *Prosopis* spp.) or are primarily restricted to warm temperate or tropical Arctotertiary refuges. This group also tends to have germination and other processes stimulated by warmer temperatures and a lower

moisture requirement versus the vernal orientation of the streamside group. This coincides with increased stream flow generated by upper elevation snowmelt, which recharges water regimes along streams and rivers and acts in seed dispersal. The effect of controlled stream flow on regeneration of seed can be viewed as detrimental.

Controlled stream flow through damming has been shown to affect riparian soil quality by coarsening soil texture, leaching nutrients, hydraulic and eolian erosion, desiccation, and the non-renewal of sediment deposits. It also increases pH levels (Stevens 1989).

Clonal species colonize sand beaches more rapidly than species that reproduced primarily by seed. The reduction of seasonal flooding resulting from dam construction and controlled stream flow has reduced clonal species colonization. This decreases the overall genetic diversity of a clonal community, since clones are genetically identical to the parent plant, while seedlings are not. Seedling density was significantly greater in relatively rare deposits of silt as compared to sand or other substrates (Stevens 1989).

According to Brock (1984), riparian forests are considered by many to be relics of pluvial periods in the Southwest when glaciation was active in the northern latitudes. He describes four stages of gallery forest formation: 1) seedling nursery-bar stands, 2) adolescent nursery-bar stands, 3) sub-mature stands, and 4) mature stands. Seedling establishment in raw recent deposits (usually silt) either in the main channel or in the overflow side channels. As seedlings develop towards adolescence, debris and sediments allow building of stands during light or moderate floods. This process successively builds the soil and raises the soil surface which increases the resistance of the tree stands to flood damage. This process results in the true riparian community occurring on slightly raised terraces. The nursery area may emerge over time and appear to be a single stand of mature trees.

Reichenbacher (1984) presents a slightly different point of view. He states that channel migration and sediment deposition from the stream are what allows the growth to reach maturity. From this point of view, the concave banks that have established vegetation are gradually undercut by the stream, and sediment is deposited on convex banks. Since the sediment is usually silt, which is the preferred germination medium for *Salix* and *Populus*, and if there is no blockage of light by the overstory, the conditions for germination of the seed are good. Also, *Salix* is not as highly tolerant of flooding as are many swamp trees, indicating that growth to maturity is only possible when lateral migration of the stream leaves the trees well above the level of prolonged submergence.

Elevation may be a significant factor in analysis for all community types if riparian vegetation. For example, according to Szaro (1990), Goodding willows form almost pure stands on lower elevation sites ($546 \pm 76\text{m}$) along the lower Colorado and Gila rivers, codominates with Fremont cottonwood at the mid-elevation sites ($1,036 \pm 171\text{m}$) and is only a minor component at higher elevation cottonwood sites ($1,264 \pm 162\text{m}$) in the Southwest. Stream gradient and direction are also important, but at a more limited and local level. Brock (1984) slightly contradicts this observation by stating that the

dominant trees at lower elevations are Fremont cottonwood and Goodding willow. Also, there are a fairly large proportion of cottonwoods mixed in with willows at elevations as low as 122 m in areas along the Lower Colorado River (K. Bade, personal comm. 1993). The focus of this review is on the lower elevation vegetation along the Lower Colorado River. In this area, the plants of interest in the upland zone are *Prosopis juliflora* var. *Torreyana* L. Benson (honey mesquite), *P. Pubescens* Benth. (screwbean mesquite) and *Atriplex lentiformis* (Torr.) Wats. (Quailbush), rather than the higher elevation hackberry or walnut. These plants, along with the streamside cottonwoods and willows, were found to support the largest and most diverse wildlife populations. In comparison, *Tamarix chinensis* (salt cedar), an invasive, non-native species, has invaded large areas formerly occupied by cottonwoods and willows and has been found to have minimal value to wildlife (Anderson and Ohmart 1985).

The Problem of *Tamarix*:

It is commonly agreed that salt cedar is very difficult to eradicate and can reseed or resprout readily. Salt cedar is a non-native plant that is less useful to wildlife and utilizes more water than native vegetation, and competes aggressively with native vegetation. One large salt cedar plant can transpire about 757 liters of water per day (Duncan 1992). Native plant species, such as quailbush, honey mesquite, and blue palo verde (*Cercidium floridum* Benth), all use and transpire less water per unit of occupied space than does salt cedar (Anderson and Ohmart 1985).

According to Don Alam, district conservationist for the USDA Natural Resources Conservation Service (NRCS) in Artesia, NM, an estimated 1 million acres have been overrun by this plant in California, Arizona, Texas and parts of Oklahoma, Colorado, Utah and Nevada. The spread of salt cedar began when it was imported from North Africa and the Middle East in the early 1800's. A disturbing drop in groundwater levels was associated with this plant by the 1940's. In the Colorado River Basin, salt cedar consumes more than 700 billion liters of water annually (DeBano and Schmidt 1989; Duncan 1992). Salt cedar actually dries up natural wetlands according to Alam. It also produces more than 500,000 seeds per plant per season and has proven itself to be highly invasive.

Mature salt cedar plants can tolerate heat, high salinity, drought and can even be submerged for more than 70 days and still survive. Early attempts at control by burning only stimulated growth, root plowing knocked out less than half of the plants at average cost of \$700 per acre, and plowing increased erosion and destroyed other vegetation in the area (Duncan 1992).

Herbicides may be the only effective control of salt cedar. One herbicide has recently proven itself to be particularly useful. ARSENAL, a systemic herbicide produced by American Cyanamid, works by inhibiting a vital plant enzyme and has been successfully used by several researchers. There is little effect on non-plant species because it is specific to plant metabolism, and it is effective at small application rates. On one test site

where this herbicide was used on salt cedar, water levels were deeper than six meters below the surface when the herbicide testing began. Two years later, after controlling the stands and leaving dead trees, the water table returned to the surface for the first time in 20 years (Duncan 1992).

Some researchers have found that willow seed can inhibit salt cedar germination, but there are not enough willow seedlings versus salt cedar seedlings under natural conditions. These same researchers also found that willow can invade salt cedar stands given the proper release conditions from the dams. However, current release procedures have produced increased selection against species with low adaptive abilities to vary the proportion of root to shoot growth depending on environmental conditions (Stevens 1989).

According to Briggs and Munda (1992), salt cedar suppression appears possible with close and uniform cottonwood pole plantings that allows the cottonwood to shade out the salt cedar. They further observed that canopy closure could be expected in two years following the initial pole plantings.

Accompanying the invasion of salt cedar in the low elevation riparian areas of the southwestern U.S. is an apparent increase in the frequency of fire in these areas. Between 1981 and 1990, 166 individual fire incidents burned more than 11,800 ha (27%) of woody riparian vegetation in the Lower Colorado River floodplain. This may be due to the accumulation of highly resinous duff (partially decayed organic matter) under the salt cedar plants. In a comparison of willow and salt cedar, the duff accumulation was greater under salt cedar where a depth of up to 150 cm of material was found. The depth of willow duff rarely accumulated to the point of exceeding one centimeter. Also, the soils under salt cedar plants were found to be virtually hydrophobic (Stevens 1989).

Soil analyses indicated that concentrations of most nutrients increased following a fire, but that alluvium salinity also increased. These changes may favor salt cedar at the expense of native vegetation, and fires appear to have been infrequent in riparian ecosystems prior to salt cedar invasion. Also, fire is currently uncommon in riparian systems where salt cedar has not invaded. Salt cedar has been shown to resprout profusely following fire, and this is one reason why it has been able to rapidly colonize riparian areas. Efficient post-fire resprouting mechanisms appear to be lacking in willows and cottonwoods (Busch and Smith 1993).

It may be possible for cottonwoods and willows, which can resprout from roots, to have an advantage in terms of fire tolerance. Root sprouting is sometimes observed in cottonwood and often in willows having a basal diameter greater than 20 cm (Briggs and Munda 1992). Willows tend to survive fires better than cottonwoods according to these authors and root sprouting may be the mechanism that allows them to do so. Stromberg (1990) states that most riparian species recover from fire by resprouting, but he does not specify whether from stumps or roots.

Wildlife in Riparian Areas:

Anderson and Ohmart (1985) made the prediction that enhancement of avian and rodent populations is most likely to be achieved if cottonwood and willow trees are present. These tree species attract, or are correlated with vegetational factors that attract, the greatest density and diversity of insectivorous birds. If frugiverous birds are included, then mistletoe needs to be present. Since mistletoe grows best on honey mesquite, this tree needs to be included in the riparian vegetation as well. Doves were also associated with honey mesquite. Gambel's quail and small grainivorous birds, as well as certain rodents, were associated with shrubs, and detailed studies showed that quailbush was an excellent shrub.

Water Conservation:

Removal of riparian vegetation and channeling was practiced into the 1960's to conserve water. Based on calculations done at the time, this seemed a reasonable procedure, since riparian vegetation transpired water and impeded transport of flood water (Brock 1984). What was not realized during this period was that through a complex series of events, riparian vegetation can sometimes raise the water table and increase available water. This can occur because woody species provide local channel stability and resistance to channel erosion, this allows other species (sedges, rushes, grasses, and forbs) to become established. As vegetation becomes established, channels typically begin to aggrade (i.e., channel elevation will increase as sediment is deposited within and along the banks of the channel). As this continues, water tables rise (Elmore and Beschta 1987).

Water Quality:

Our increasing awareness of the risks of chemical contamination magnifies another benefit of riparian vegetation. Riparian vegetation serves as an active sink for nutrients, organic matter and contaminants. Streamside vegetation traps both sediments and chemicals generated on agricultural lands in the watershed before they can be transported to nearby stream channels. This can be particularly important in managing downstream nitrate contamination. Riparian forest and wetland ecosystems in the watersheds of Lake Tahoe were found capable of removing 99% of the incoming nitrate nitrogen (DeBano and Schmidt 1989).

A study by Lowrance et al. (1984) showed that waterborne inputs exceeded streamflow outputs for all elements. In this study, located in an agricultural area in Georgia, the percent of nutrient retention in the riparian system varied from 6% for potassium to 68% for nitrogen. It was also shown that denitrification was one of the important methods of nitrogen removal in riparian systems. Soils of riparian areas present ideal conditions for denitrification: high organic matter, seasonal waterlogging, and large inputs of nitrate in subsurface flow. The conclusion of this study was that removal of the riparian forest would tend to contribute higher nutrient loads in streams and lower water quality through loss of nutrient uptake and storage by woody vegetation. It was further concluded that maintenance of riparian ecosystems is essential to avoid degradation of water quality due to increased nutrient loss from agricultural watersheds.

Salinity:

The Colorado River has been increasing in salinity in the years since the river was dammed, and is projected to continue to increase, but at lower rates (U.S. Dept. of the Interior 1989). This does not bode well for the salt-sensitive native plants in riparian zones.

Salt tolerance is known to differ with ontogeny, so the tolerance of a particular species may differ at each of its physiological stages of development, such as germination, seedling growth, vegetative growth, flowering and fruiting. Barley, sugar beet and cotton, for instance, are among the most salt tolerant agricultural crops, but each is relatively sensitive during either germination or early seedling growth. The level of tolerance at one growth stage cannot be assumed to be the same level of tolerance at any other (Shannon 1984; Maas 1986).

Allen et al. (1994) discuss the potential for developing salt tolerance in forest tree species. They discuss three major points: 1) evidence exists that demonstrates considerable intraspecific variation in salt tolerance in many species; 2) evidence associated with differences in the ability to exclude Na^+ and Cl^- from leaves are important factors underlying intraspecific differences in tolerance; 3) progress towards improving salt tolerance of forest trees.

A number of studies cited by Allen et al. (1994) have been conducted to measure salt tolerance in woody perennial plant species. Compared with annual crop and horticultural species, there is very little literature relating to intraspecific variation in salt tolerance of forest trees. Van der Moezel et al. (1989) found that the highest intraspecific variability in salt tolerance occurred in the species that were least tolerant overall. This may suggest that progress in the development of salt tolerant genotypes may be possible in species traditionally thought to have a low salt tolerance (Allen et al. 1994).

Allen et al. (1994) state that the mechanisms of salt tolerance may be divided into two broad categories: 1) avoidance and 2) tissue tolerance. Greenway and Munns (1980) explain that avoidance refers to the ability to keep salt ions away from parts of the plant where they may cause damage. This may be achieved by passive exclusion of ions because of selective membrane permeability, active extrusion or dilution through the development of succulent tissue. Tissue tolerance refers to situations where salt ions accumulate in tissues, and their presence is accommodated by some means, usually by compartmentation in vacuoles and corresponding osmoregulation in the cytoplasm.

According to Allen et al. (1994), a large amount of evidence has been collected that demonstrates the elaborate, multigenic control of response to salinity (Dvorack et al. 1992). The complex pattern of inheritance to salt tolerance in trees is supported by studies done on Citrus (Cooper and Gorton 1952; Furr and Ream 1969; Sykes 1992). It was also stated that genes with major effects on salt tolerance can be found and that salt

tolerance is amenable to breeding (Abel 1969; Newman and Antcliff 1984). Allen et al. (1994) report that no significant progress in the identification of major genes controlling salt tolerance has been made for forest tree species, however the authors concluded that the most probable and immediate improvement in salt tolerance in trees can be accomplished through intensive screening and selection, specifically in cases where large numbers of individuals have been exposed to saline conditions.

Allocational Plasticity:

Seedlings of species exhibiting strong allocational plasticity (e.g. *Tamarix*, *Salix exigua*, *Baccharis sarthroides*, *B. salicifolia*, *Tessaria* and *Phragmites australis*) were significantly more common than species that were less capable of altering allocation between roots and above-ground growth (e.g. *Populus fremontii*, *Salix gooddingii*, *Fraxinus pennsylvanica* and *Prosopis glandulosa*). Relative allocation to roots in all species decreased as limiting nutrient availability increased, but the degree of this varied. Selection against species with low phenotypic plasticity has increased whereas clonal and phenotypically plastic species have a selective advantage (Stevens 1989).

The preferential allocation of resources to shoots or roots appears to be an adaptive response to soil condition changes. Since the soils of the pre-dam era were generally much higher in fertility than the post-dam soils, allocational plasticity was not as crucial before the river was dammed (Stevens 1989).

An example of change in soils tested by Stevens (1989) along the Colorado river in the Grand Canyon, showed the pre-dam amounts of K^+ , Mg^{2+} and Ca^{2+} as 213.7, 229.6 and 1,695.0 $\mu\text{g/g}$ respectively, while post-dam amounts were 19.3, 75.7 and 666.7 $\mu\text{g/g}$ respectively. In addition, the pre-dam soil had a total base cation level of 18.5 and 3.7 $\mu\text{g/g}$ for NO_3^- and PO_4^{3-} respectively, while the post-dam amounts were 7.2 and 2.7 $\mu\text{g/g}$ respectively. Another significant change was noted in the percentages of sand and silt. Pre-dam sand content was 89% and silt+clay was 11%. Post-dam sand content was 97% and silt+clay was noted as being three percent. This change in texture influences infiltration rates and nutrient levels as well as water holding capacities.

Stevens (1989) stated that seedling density is significantly greater in the relatively rare silt deposits, compared to sand or other substrates. He also noted that seedling germination, growth and survival were limited by moisture and nutrient availability, and moisture interactions with substrate particle size.

Materials and Methods

The primary objective for the target species in this project is to determine which genotypes, if any, are more tolerant to saline conditions. Soil samples taken from various collection sites revealed soil salinity levels ranging from nonsaline (<2 ds/m) to strongly saline (>16 ds/m). Experiments for this project tried to determine whether genotypes collected from sites classified as moderately or strongly saline would exhibit higher tolerances to salt concentrations than genotypes collected from sites classified as nonsaline or very slightly saline. Individual genotypes that exhibit a higher level of tolerance to saline conditions may prove themselves useful for revegetation projects on moderate to strongly saline sites along the Lower Colorado River. The collection sites for these genotypes can easily be identified at the time of seed collection and recorded using standard legal descriptions (Township, Range, Section) for future reference.

Target Species for this Project:

Atriplex lentiformis (Torr.) Wats. - Quailbush

An erect, rapid-growing shrub forming a rounded or globular outline, reaching a height of approximately 3.05 m where the water table is high. It is found at elevations up to 1,219 m in moist or dry saline soil types from along the Colorado River in southwestern Arizona, southeastern California, northern Sonora, Mexico, north to southern Utah and Nevada (Kearny and Peebles 1960).

Prosopis juliflora (Swartz) DC - Honey mesquite

A large shrub or small tree reaching a height of 9 m or more with crooked branches and a rounded crown. Trunk dividing into branches a short distance above the ground. Root system radially spreading and deep (Vines 1976). Found growing at elevations of 1,524 m and lower, mainly along water streams where the water table is relatively high, from southern Kansas to southeastern California and Mexico (Kearny and Peebles 1960).

Prosopis pubescens Benth. - Screwbean mesquite

A small, thorny tree with short leaves and unique fruits. It looks like honey mesquite, but with both leaves and fruits only 2.54-5.08 cm long. Not so generally abundant as honey mesquite. Found growing at elevations of 1,219 m and lower (Kearny and Peebles 1960). Distribution, southwestern North America, Baja California, and northern Mexico (Simpson 1977).

Populus fremontii Wats. - Fremont cottonwood

Dioecious, deciduous tree attaining a height of 15-30 m, the trunk diameter may reach 1.2 m (Kearny and Peebles 1960). The stout, spreading or pendulous branches form a broad, open crown. Conspicuous along streams throughout the state except in higher mountains. Found at elevations from sea level to 2,134 m, southwestern New Mexico, Colorado, Arizona, Utah, Nevada, and California; in Mexico in Lower California and Sonora (Vines 1976).

Salix gooddingii Ball - Gooding willow

Dioecious, deciduous tree attaining a height of 13.5 m and a trunk diameter of 75 cm. In Arizona it is found growing with cottonwood along the lower courses of the Colorado and Gila rivers. Found growing at elevations up to 2,134 m but usually much lower. The typical form, with pubescent ovaries and young capsules, is restricted mainly to the Colorado River Valley, the trees in other parts of Arizona belonging mostly to var. *varibilis* Ball (Kearny and Peebles 1960).

Germination experiments were conducted on the quailbush, honey mesquite and screwbean mesquite genotypes. Five salt concentrations were utilized for these experiments: 0 mmhos cm⁻¹ (Control), 5 mmhos cm⁻¹, 10 mmhos cm⁻¹, 20 mmhos cm⁻¹ and 40 mmhos cm⁻¹ NaCl.

Twenty-seven quailbush genotypes were evaluated in this experiment (Table 1). Seed for this experiment. Seed was harvested from various locations along the Lower Colorado River during the months of November and December in 1993. The harvested material was cleaned at the Tucson PMC and stored in a VWR Scientific general purpose laboratory refrigerator. The experiment with these genotypes was initiated on January 30, 1995. Seed packets with 100 seeds per packet per genotype were organized and separated for each treatment level. Salt concentrations were prepared using distilled water using a Gyrotherm agitator to ensure thorough dissolution. Approximately four ml of solution was administered to each petri dish. Each petri dish was lined with Whatman No. 1 filter paper (bottom only) and the dishes were then placed into plastic Ziploc bags along with wet sponges to maintain humidity within the plastic bags. The temperature settings for this experiment were set at 8 hours at 25 °C/12 hours at 12 °C. The light bank in the germinator was turned off. Germination data was collected every Monday, Wednesday and Friday mornings. A seed was considered to have germinated and was removed from the dish when the radicle was ≥2mm in length. Seeds that developed fungal growth were removed and considered nonviable.

Five honey mesquite and four screwbean mesquite genotypes were evaluated in this experiment (Table 2). Seed for these experiments was harvested from various locations along the Lower Colorado River during the months of August and September, 1994. The harvested material was cleaned at the Tucson PMC and stored in a VWR Scientific general purpose laboratory refrigerator. Seeds were scarified during the cleaning process while using the Westrup brush machine. The experiments for both species was initiated on January 30, 1995. Seed packets with 100 seeds per packet per genotype were organized and separated according to each treatment level.

Due to fungal growth on the mesquite seeds during preliminary germination tests, the seed surfaces of the honey and screwbean mesquite genotypes were sterilized. A technique described by Dodds and Roberts (1986) was followed. This method required soaking the mesquite seeds in an aqueous solution of sodium hypochlorite (NaOCl) for

Table 1

Collection Site Descriptions for Quailbush Genotypes

Sample I.D.	Collection Location
Q1	T8S, R24W, SE, SE, SW, NW Sec. 33 (Yuma West Quad.)
Q2	T9S, R24W, SW, SE, NW Sec. 18 (Grays Well NE Quad.)
Q3	T9S, R24W, NE, SW, NE Sec. 18 (Grays Well NE Quad.)
Q4	T16S, R22E, SW, NE, NE Sec. 36 (Yuma East Quad.)
Q5	T16S, R23E, SW, NE, NW Sec. 31 (Yuma East Quad.)
Q6	T7S, R23E, SW, SW, SE, SE Sec. 3 (Bard, AZ-CA Quad.)
Q7	T16S, R22W, NE, SW, SW Sec. 9 (Yuma East Quad.)
Q8	T16S, R22W, NW, NW, NW Sec. 16 (Yuma East Quad.)
Q9	T7S, R22W, SW, SW, NW, SW Sec. 14 (Laguna Dam, AZ-CA Quad.)
Q10	T1S, R23W, NW, NW, NW Sec. 31 (Cibola, AZ Quad.)
Q11	T1S, R23W, NE, NE, SW Sec. 31 (Cibola, AZ Quad.)
Q12	T10S, R24W, NW, NE, SE Sec. 14 (Cibola, AZ Quad.)
Q13	T9S, R24W, NE, NE, SE Sec. 36 (Cibola, AZ Quad.)
Q14	T14S, R22W, NE, SW, NE Sec. 13 (Imperial Reservoir, AZ-CA Quad.)
Q15	T14S, R21W, SE, NE, NW Sec. 18 (Imperial Reservoir, AZ-CA Quad.)
Q101	CRIT, <1 mile north of Agnes Wilson Bridge (California side)
Q102	CRIT, 0.6 miles south of Agnes Wilson Bridge (California side)
Q103	CRIT, 0.4 miles north of Agnes Wilson Bridge (Arizona side)
Q104	CRIT, 0.1 miles south of Agnes Wilson Bridge (Arizona side)
Q105	T7N, R22W, SE, NW, NW Sec. 13 (Big Maria Mtns. NE, AZ-CA Quad.)
Q106	T7N, R23E, NW, NE, SW, SE Sec. 14 (Big Maria Mtns. NE, AZ-CA Quad.)
Q107	CRIT, mile marker 1 on Postum Road
Q108	CRIT, mile marker 4 on Postum Road
Q109	Havasu National Wildlife Refuge, 0.5 miles southeast of refuge boundary
Q110	Havasu National Wildlife Refuge, 1.3 miles southeast of refuge boundary
Q111	Havasu National Wildlife Refuge, 0.1 miles north of south dike
Q112	Havasu National Wildlife Refuge, Junction of Arizona 95 and Pintail Slough Road

Table 2.

**Collection Site Descriptions and Soil Sample Analyses for Honey and Screwbean
Mesquite Seed**
(Collections made in August and September, 1994)

Sample I.D./ Sample Depth	Collection Location	Texture	pH*	ds/m
HM 894-1	T17N, R23E, NW, SE Sec. 31 (Bard, AZ-CA Quad.)			
0-12"		LS	7.6	<1
12-24"		S	7.8	<1
24-36"		CS	7.8	<1
HM 894-2	T8S, R23E, NW, SE Sec. 23 (Yuma East, AZ-CA Quad.)			
0-12"		SL	7.8	6.0
12-24"		SL	8.0	<1
HM 994-1	T1S, R24W, NE, NE, SE, NE Sec. 35 (Cibola, AZ-CA Quad.)			
0-12"		SiCL	8.6	23.0
12-24"		SiCL	8.2	15.0
24-36"		FSL	8.2	4.4
36-48"		FSL	8.6	4.4
HM 994-2	T1S, R24W, NE, NE, SW, SW Sec. 30 (Cibola, AZ-CA Quad.)			
0-12"		SL	8.0	<1
12-24"		SL	8.2	<1
24-36"		SL	7.8	<1
36-48"		SL	8.2	<1
HM 994-3	T1S, R24W, SW, SE, NE, NW Sec. 30 (Cibola, AZ-CA Quad.)			
0-12"		FSL	8.6	4.0
12-24"		FSL	8.6	3.0
24-36"		FSL	8.6	3.0
36-48"		SL	8.0	<1

* pH Range	Description	EC (ds/m)	Description
<4.5	Extremely acid	<2	Nonsaline
4.5 - 5.0	Very strongly acid	2 - 4	Very slightly saline
5.1 - 5.5	Strongly acid	4 - 8	Slightly saline
5.6 - 6.0	Moderately acid	8 - 16	Moderately saline
6.1 - 6.5	Slightly acid	>16	Strongly saline
6.6 - 7.3	Neutral		
7.4 - 7.8	Slightly alkaline		
7.9 - 8.4	Moderately alkaline		
8.5 - 9.0	Strongly alkaline		
>9.0	Very strongly alkaline		

Table 2 (continued)

**Collection Site Descriptions and Soil Sample Analyses for Honey and Screwbean
Mesquite Seed**
(Collections made in August and September, 1994)

Sample I.D./ Sample Depth	Collection Location	Texture	pH*	ds/m
SB 894-1	T8S, R22W, SW, SW Sec. 17 (Yuma East, AZ-CA Quad.)			
0-12"		FLS	8.5	<1
12-24"		FLS	7.6	<1
24-36"		FLS	7.8	<1
36-48"		FLS	7.6	<1
SB 894-2	T8S, R23E, NW, SE Sec. 23 (Yuma East, AZ-CA Quad.)			
0-12"		FSL	7.8	<1
12-24"		FSL	7.6	<1
24-36"		FLS	7.6	<1
36-48"		FLS	7.6	<1
SB 894-3	T7S, R22W, SW, SW Sec. 13 (Laguna Dam, AZ-CA Quad.)			
0-12"		GrCoSL	8.2	17.5
12-24"		SCL	8.6	9.0
24-36"		SCL	8.8	10.5
SB 994-1	T1S, R24W, SW, NE, NE, SE Sec. 14 (Cibola, AZ-CA Quad.)			
0-12"		FSL	8.2	<1
12-24"		FSL	8.0	<1
24-36"		SL	8.6	4.0

* pH Range	Description	EC (ds/m)	Description
<4.5	Extremely acid	<2	Nonsaline
4.5 - 5.0	Very strongly acid	2 - 4	Very slightly saline
5.1 - 5.5	Strongly acid	4 - 8	Slightly saline
5.6 - 6.0	Moderately acid	8 - 16	Moderately saline
6.1 - 6.5	Slightly acid	>16	Strongly saline
6.6 - 7.3	Neutral		
7.4 - 7.8	Slightly alkaline		
7.9 - 8.4	Moderately alkaline		
8.5 - 9.0	Strongly alkaline		
>9.0	Very strongly alkaline		

10 minutes (1 part bleach:9 parts distilled water) followed by a thorough rinsing with distilled water. The seed was then dried in an oven for 60 minutes at 64 °C.

In preparation, clear, plastic petri dishes, 100 X 15 mm, were clearly labeled (genotype, salt concentration treatment, date) and lined with Whatman No. 1 filter paper (bottom only). Each petri dish represented a given genotype and treatment level. Five hundred seeds from each genotype were separated into five packets, resulting in 100 seeds per packet. Each packet was emptied into its respective dish (treatment level). Each dish was then wetted with either the control solution or one of the four salt concentration solutions. A sufficient amount of solution was applied to each petri dish as to thoroughly wet the seed. Excess solution was drained from each dish.

Each group of five petri dishes per genotype were then placed into Ziploc plastic bags along with a moist sponge to maintain humidity. The collective bags were then placed into the germinator. The temperature settings for the mesquite experiment in the germinator were set at 12 hours at 30 °C/12 hours at 25 °C. The light bank was not turned on in order to minimize fungal growth. Germination data was collected each Monday, Wednesday, and Friday mornings. A seed was considered to have germinated and was removed from the dish when the radicle was ≥ 2 mm in length. Seeds that developed fungal growth were removed and considered nonviable.

Rooting experiments were conducted with ten cottonwood genotypes and four willow genotypes (Table 3). Again, five salt concentration levels were used for these experiments: 0 mmhos cm^{-1} (Control), 5 mmhos cm^{-1} , 10 mmhos cm^{-1} , 20 mmhos cm^{-1} and 40 mmhos cm^{-1} NaCl. The genotypes for the rooting experiments were initially harvested as pole cuttings from various locations along the Lower Colorado River. The pole cuttings were harvested during April and May of 1993. The poles were transported to the Tucson PMC and planted into Field 6 where they were flood irrigated on a regular basis to ensure optimum growth.

The rooting experiments were initiated on February 17, 1995. Five Rubbermaid, 68.2 liter containers were set up for this experiment, one container per treatment. At the onset of each replication, pole cuttings were harvested from the trees in Field 6 and brought into the Tucson PMC laboratory. Four containers were filled with 37.85 liters of salt concentration solution and one container received 37.85 liters of distilled water (Control). Three cuttings from each genotype were clearly labeled and banded loosely together. The lids for the Rubbermaid containers had 4.45 cm diameter holes cut into them for each group of three cuttings. After all groups of poles had been placed into each container with the lids firmly attached, the openings were then sealed with cotton to prevent light from entering the containers as well as to reduce evaporation. An aerator was also placed into each container to prevent stagnation and to keep oxygen levels within the solutions at optimum levels.

Table 3

Cottonwood and Willow Genotype Collection Locations

Sample I.D.	Collection Location
C-2	Lake Mead delta
C-3	T10S, R24W, SW, NE, NE Sec. 14 (Cibola, AZ-CA Quad.)
C-4	T9S, R21E, SE, SE, SE Sec. 25 (Cibola, AZ-CA Quad.)
C-5	T7N, R22W, SE, NW, NW Sec. 13 (Big Maria Mtns. NE, AZ-CA Quad.)
C-6	T11N, R17W, NW, NW SE, NE Sec. 29 (Monkeys Head Quad.)
C-12	T9S, R24W, NW, NW Sec. 19 (Grays Well NE, Quad.)
C-16	T10S, R25W, SE, NW, SW Sec. 2 (Gadsden Quad.)
C-22	T11N, R16W, SE, NW, SW, NE Sec. 31 (Castaneda Hills SW, AZ Quad.)
C-26	T11N, R16W, SE, NE, SE, NW Sec. 31 (Castaneda Hills SW, AZ Quad.)
C-30	T11N, R16W, NW, NE, SE, NW Sec. 31 (Castaneda Hills SW, AZ Quad.)
W-1	Lake Mead (Pierce Ferry)
W-4	Lake Mead delta
W-5	Lake Mead delta
W-10	Lake Mead delta

Following a 28-day observation period, all root and green leaf and stem tissue from each pole was stripped from the cuttings. The individual root samples from each genotype was placed in labeled envelopes. These samples were then dried in a laboratory oven for 24 hours at 60 °C and weighed. The dry weight for each observation was recorded and statistical comparisons made on the amount of biomass produced between genotype and treatments.

Results and Discussion

Experiments evaluating salt tolerance levels pertaining to the species in our experiments have also been performed by the Desert Research Institute (DRI) at the University of Nevada (Jackson et al. 1990). Researchers at DRI set up their experiments using the following salt concentration levels: 0 mg l⁻¹ (Control), 1,500 mg l⁻¹ (2.34 mmhos cm⁻¹), 6,000 mg l⁻¹ (9.38 mmhos cm⁻¹), 18,000 mg l⁻¹ (28.13 mmhos cm⁻¹), 36,000 mg l⁻¹ (56.25 mmhos cm⁻¹) and 60,000 mg l⁻¹ (93.75 mmhos cm⁻¹). Summaries of their results follow the results of each species in the Tucson PMC experiments.

Germination Experiments - Quailbush Genotypes:

Mean germination at the control level was significantly higher than at the other four treatment levels. The mean germination percentage for all quailbush genotypes at the control level was 75% versus 70.1% at 5 mmhos cm⁻¹, 54.1% at 10 mmhos cm⁻¹, 19% at 20 mmhos cm⁻¹, and 0.9% at 40 mmhos cm⁻¹.

Twenty-four genotypes exhibited mean germination percentages greater than 50% at the control level. Twenty-three genotypes exhibited mean germination percentages greater than 50% at the 5 mmhos cm⁻¹ treatment level. At the 10 mmhos cm⁻¹ treatment level, 16 genotypes exhibited mean germination percentages greater than 50%. Mean germination percentages at the 20 mmhos cm⁻¹ treatment level showed a marked decrease with only 2 genotypes having greater than 40% germination. At the 40 mmhos cm⁻¹ treatment level, only one genotype exhibited a significantly higher mean germination percentage than the other 26. However, the mean germination percentage for this genotype was only 10.2%.

In summary, the results of this experiment showed that the 27 quailbush genotypes germinated best (>50%) at salt concentrations up to 10 mmhos cm⁻¹. Mean germination percentages dropped off drastically at the 20 and 40 mmhos cm⁻¹ treatment levels (19% and 0.9% respectively).

Results of the DRI experiments on quailbush are summarized as follows: Quailbush can grow under a range of salt concentration levels but growth responses were noticeably decreased at the 56.25 and 93.75 mmhos cm⁻¹ treatment levels. Germination results revealed germination only to occur in the three lowest salt concentration treatment levels, and less than 25% germination at each level (Jackson et al. 1990).

Germination Experiments - Honey Mesquite Genotypes:

No significant differences were found among the five honey mesquite genotypes at the control treatment level. The mean germination percentage for all genotypes at the control treatment level was 83%.

At the 5 mmhos cm^{-1} treatment level, one genotype exhibited a significantly lower mean germination percentage at 75.4%. The mean germination percentage for all genotypes at this treatment level was 83%, the highest mean percentage was 91% for the HM 894-2 genotype. Two genotypes exhibited significantly higher mean germination percentages at the 10 mmhos cm^{-1} treatment level, 86.8% for genotype HM 894-2 and 85.4% for genotype HM 994-1.

At the 20 mmhos cm^{-1} treatment level, the highest mean germination percentage was exhibited by genotype HM 894-1 at 66.6%. This genotype was significantly higher than the two genotypes which had the lowest mean percent germination at 49% (HM 994-2) and 45.8% (HM 894-2). Genotypes HM 994-1 and HM 994-3 did not exhibit any significant difference in comparison with the other three genotypes.

There were no significant differences in the mean germination percentage between any of the genotypes at the 40 mmhos cm^{-1} treatment level. The highest mean percentage being 7.8% (HM 894-1) and the lowest mean percentage of 3.4% (HM 994-2).

In summary, the results of the honey mesquite experiment showed that the five honey mesquite genotypes germinated best (>50%) at all treatment levels except at 40 mmhos cm^{-1} . Mean germination percentages for the five treatment levels were: 83% (control), 84.6% (5 mmhos cm^{-1}), 78.2% (10 mmhos cm^{-1}), 57.4% (20 mmhos cm^{-1}) and 5.7% (40 mmhos cm^{-1}). Soil salinity concentrations derived from the soil samples taken at the honey mesquite collection sites do not appear to have a direct correlation to the observed germination percentages in these experiments. The collection site for genotype HM 994-1 exhibited the highest soil salinity readings in comparison with the other four collection sites (Table 2). However, this genotype did not exhibit significantly greater germination percentages in comparison with the other four genotypes. The soil analysis data from the other four collection sites revealed readings ranging from nonsaline to very slightly saline.

Results of the DRI experiments on honey mesquite are summarized as follows: Germination results revealed 100% germination up to and including the 28.13 mmhos cm^{-1} treatment level. There was no germination at the 56.25 and 93.75 mmhos cm^{-1} treatment levels (Jackson et al. 1990).

Germination Experiments - Screwbean Mesquite Genotypes:

Mean percent germination at the control treatment level showed one genotype having significantly lower germination with 17.2% (SB 894-1) than the genotype with the highest mean percent germination, SB 994-1 at 43.2%. The other two genotypes were not

significantly different from either the genotype with the highest or lowest mean percent germination.

The mean germination percentage for all genotypes at the control level was 29.4%. Similar differences were also exhibited by the same genotypes at the 5 mmhos cm^{-1} treatment level. The mean germination percentage for all genotypes at this treatment level was 27.1%. Genotype SB 994-1 again exhibited the highest mean percent germination, 37.4%, which was only significantly different from genotype SB 894-1 with 17% germination.

At the 10 mmhos cm^{-1} treatment level, the mean germination percentage for all genotypes was 24.2%. Genotypes SB 894-2 and SB 994-1 exhibited significantly higher mean germination percentages, 32.8% for both, versus genotypes SB 894-3 at 16.6% and SB 894-1 at 14.4%. At the 20 mmhos cm^{-1} treatment level, genotype SB 894-2 exhibited a significantly higher mean germination percentage at 28.4% versus 10.6% for genotype SB 894-1 and 3.2% for genotype SB 894-3. This was not a significantly higher mean germination percentage than what was exhibited by genotype SB 994-1 at 21.6%.

The mean germination percentages for all genotypes at the 40 mmhos cm^{-1} treatment level dropped to 4%. Genotype SB 894-2 again exhibited a significantly higher mean germination percentage at 9.4% versus 1% for SB 894-3 and 0.2% for SB 894-1. It was not significantly different from genotype SB 994-1 which exhibited 5.2% germination.

In summary, the results of the screwbean mesquite experiment show lower mean germination percentages in comparison with the honey mesquite genotypes. Mean germination percentages at each treatment level are 29.4% (control), 27.1% (5 mmhos cm^{-1}), 24.2% (10 mmhos cm^{-1}), 16% (20 mmhos cm^{-1}) and 4% (40 mmhos cm^{-1}). None of the genotypes exhibited a significantly greater germination percentage over another at the control and 5 mmhos cm^{-1} treatment levels. However, at the 10, 20 and 40 mmhos cm^{-1} treatment levels, genotype SB 894-2 did exhibit a significantly greater germination percentage over genotypes SB 894-1 and SB 894-3.

Soil salinity concentrations derived from soil samples taken at the collection sites did not appear to have a direct correlation to the germination percentages observed in these experiments. The collection site for genotype SB 894-3 was determined to have the highest soil salinity readings versus the other three collection sites (Table 2). However, this genotype did not exhibit significantly greater germination percentages in the laboratory experiments. In contrast, the collection site for SB 894-2 revealed nonsaline soil conditions and this genotype consistently exhibited higher mean germination percentages over SB 894-3 at all treatment levels. The low mean germination percentages for all genotypes may be attributed to hard seed or experimental error.

Results of the DRI experiments on screwbean mesquite are summarized as follows: Germination results revealed nearly 100% germination at the control, 2.34 and 9.38 mmhos cm^{-1} treatment levels. At the 28.13 mmhos cm^{-1} treatment level, partial radicle

elongation was exhibited by no cotyledon emergence. Radicle length was approximately 75% shorter in this group than fully developed radicles (Jackson et al. 1990).

Honey Mesquite - Screwbean Mesquite Comparisons:

Mean germination percentages for all honey and screwbean mesquite genotypes over all treatment levels reveal significantly higher mean germination percentages for the honey mesquite genotypes over the screwbean mesquite genotypes. Observing each treatment level individually revealed the honey mesquite genotypes to exhibit significantly higher mean germination percentages than the screwbean mesquite genotypes up to the 20 mmhos cm^{-1} treatment level. At the 40 mmhos cm^{-1} treatment level, one screwbean mesquite genotype exhibited a significantly lower mean germination percentage (SB 894-1, 0.2%) than all other genotypes in comparison.

Rooting Experiments - Cottonwood Genotypes:

Mean dry weights (mg) of leaf and root material for all cottonwood genotypes were collected up to the 10 mmhos cm^{-1} treatment level. The 20 and 40 mmhos cm^{-1} treatment levels did not yield any measurable amounts. Mean dry weight amounts of leaf and root biomass were calculated for each treatment level. Leaf dry weights generally greatly exceeded root dry weights. At the control level, there were no significant differences between genotypes in terms of mean leaf biomass production or mean root biomass production.

At the 5 mmhos cm^{-1} treatment level, three genotypes exhibited significantly lower mean leaf dry weights versus all other genotypes: C-2 40 mg; C-26 65 mg; C-30 44.3 mg. The largest mean leaf biomass production was exhibited by genotype C-4 at 704 mg. The highest mean root dry weight was exhibited by genotype C-4 at 46.8 mg.

At the 10 mmhos cm^{-1} treatment level, there were no significant differences between any of the genotypes in terms of leaf or root biomass production. The two genotypes exhibiting the highest mean leaf biomass production were C-3 (161 mg) and C-4 (153.3 mg). The same two genotypes also exhibited the highest mean root biomass production with 10 mg for genotype C-4 and 8.3 mg for genotype C-3.

In summary, mean leaf biomass production greatly exceeded mean root biomass production at all treatment levels. Predictably, as the salt concentrations increased, biomass production decreased. Mean leaf and root biomass production over all genotypes was significantly greatest at the control level (Leaves: 502.4 mg, Roots: 30.6 mg). Production at the 5 mmhos cm^{-1} treatment level was significantly greater (Leaves: 272.7 mg, Roots: 19.8 mg) than all other treatment levels except at the control treatment level. The 10 mmhos cm^{-1} treatment level yielded a mean of 71.7 mg for leaves and 3.9 mg for roots. The 20 and 40 mmhos cm^{-1} treatment levels yielded no measurable amounts of biomass.

Results of the DRI experiments on cottonwood are summarized as follows: There was almost 100% mortality at the 56.25 and 93.75 mmhos cm^{-1} treatment levels after 30 days and in the 28.13 mmhos cm^{-1} treatment level after day 60. The only surviving plants at day 120 were in the control and 2.34 mmhos cm^{-1} treatment levels (Jackson et al. 1990).

Rooting Experiments - Willow Genotypes:

Mean dry weights (mg) of leaf and root material for all willow genotypes were collected up to the 20 mmhos cm^{-1} treatment level. The 40 mmhos cm^{-1} treatment level did not yield any measurable amounts. Mean dry weight amounts of leaf and root biomass were calculated for each treatment level. Leaf dry weights generally greatly exceeded root dry weights. At the control level, there were no significant differences between genotypes in terms of leaf biomass production or mean root biomass production.

Mean leaf and root biomass production at the 5 mmhos cm^{-1} treatment level revealed no clear, significant differences between the four genotypes. Genotype W-1 (540 mg) produced mean leaf biomass amounts which were only significantly higher than genotypes W-4 (211.8 mg) and W-5 (206 mg) but not significantly greater than genotype W-6 (284.3 mg). Genotype W-1 also produced the highest mean amount of root biomass (130 mg) but this was only significantly greater than genotype W-10 which produced 24 mg.

Results at the 10 mmhos cm^{-1} treatment level showed no significant differences between all genotypes in terms of mean leaf biomass production and mean root biomass production. Genotype W-4 produced the highest mean leaf biomass with 173.3 mg and genotype W-10 the lowest with 65 mg. The highest mean root biomass was produced by genotype W-1 with 29.3 mg and the lowest mean root biomass was produced by genotype W-10 with 0 mg.

There were no significant differences at the 20 mmhos cm^{-1} treatment level between all genotypes in terms of mean leaf biomass production and mean root biomass production. The highest mean leaf biomass amount was produced by genotype W-4 with 69.3 mg. The highest mean root biomass quantity was produced by genotype W-1 with 5 mg.

In summary, mean leaf biomass production greatly exceeded mean root biomass production at all treatment levels. Predictably, as salt concentrations increased, biomass production decreased. Mean leaf and root biomass production over all genotypes was significantly greatest at the control level (Leaves: 576 mg, Roots: 142 mg). Production at the 5 mmhos cm^{-1} treatment level was significantly greater than all other treatment levels except the control treatment (Leaves: 311 mg, Roots: 69 mg). There were no significant differences in total mean biomass production at the 10, 20 and 40 mmhos cm^{-1} treatment levels. No measurable amounts of leaf or root biomass were produced by any genotypes at the 40 mmhos cm^{-1} treatment level.

Results of the DRI experiments on willow are summarized as follows: Shoot and root biomass responses indicate that *Salix* is intolerant of salinity in concentrations greater than 2.34 mmhos cm⁻¹. However, after 60 days shoot length responses in the control and 9.38 mmhos cm⁻¹ treatment levels were similar, but the 9.38 mmhos cm⁻¹ had 80% mortality during this time (Jackson et al., 1990).

Cottonwood - Willow Comparisons:

In comparison, mean leaf biomass production for all cottonwood and willow genotypes at the control treatment level revealed no significant differences. However, mean root biomass production for all genotypes at the control level revealed two willow genotypes as producing significantly greater mean amounts of root biomass. Genotype W-5 produced a mean of 190 mg and genotype W-10 produced a mean of 170 mg.

At the 5 mmhos cm⁻¹ treatment level one cottonwood genotype produced a significantly greater mean leaf biomass (C-4 704 mg) than the majority of all other genotypes. However, mean root biomass production at the 5 mmhos cm⁻¹ treatment level revealed one willow genotype to have produced a significantly higher mean amount of root material (W-1 130 mg) over the majority of all other genotypes in comparison. No significant differences were revealed between any of the genotypes in terms of mean leaf biomass production at the 10 mmhos cm⁻¹ treatment level. Mean root biomass production at this treatment level decreased to a large degree. Genotype W-1 produced a mean root biomass amount of 29.3 mg but this was not significantly different in comparison with the majority of all other genotypes.

Mean leaf biomass production at the 20 mmhos cm⁻¹ treatment level revealed genotype W-4 (69.3 mg) to be significantly higher than the majority of all other genotypes in comparison. Mean root biomass production for all cottonwood and willow genotypes at this treatment level revealed genotypes W-1 (5 mg) and W-5 (3.3 mg) to have produced higher mean amounts of root biomass than all other genotypes in comparison. However, these are not significantly different from all other genotypes in comparison which produced no measurable amounts of root biomass.

Summary

The objective of this project was to evaluate various genotypes of five native shrub and tree species collected from along the Lower Colorado River and assess their performance at five salt concentrations. The primary goal of these experiments was to determine whether any of the genotypes in each species group exhibit any tolerance to the saline conditions that might be encountered along the Lower Colorado River. Species examined in this project included quailbush (*Atriplex lentiformis*), honey mesquite (*Prosopis juliflora*), screwbean mesquite (*Prosopis pubescens*), cottonwood (*Populus fremontii*) and willow (*Salix gooddingii*).

Soil samples were collected from each of the harvest sites for the mesquite genotypes. These samples were then evaluated for texture, pH and salinity. This information was used to determine whether genotypes collected from highly saline sites would exhibit significantly higher germination percentages at higher salt concentrations than genotypes collected from non- or low-saline sites.

Germination experiments were conducted on five genotypes of honey mesquite, four genotypes of screwbean mesquite and 27 genotypes of quailbush. Rooting experiments were conducted on ten cottonwood genotypes and four willow genotypes. The five treatment levels developed for the germination and rooting experiments consisted of the following salt concentrations (NaCl): 0 mmhos cm^{-1} (control), 5 mmhos cm^{-1} , 10 mmhos cm^{-1} , 20 mmhos cm^{-1} and 40 mmhos cm^{-1} .

Mean germination percentage for all quailbush genotypes in the control treatment was 75%. Mean germination percentages for quailbush in the other four treatments were: 70% at 5 mmhos cm^{-1} , 54% at 10 mmhos cm^{-1} , 19% at 20 mmhos cm^{-1} and 1% at 40 mmhos cm^{-1} . As expected, mean germination percentages declined with increasing salt concentrations. None of the quailbush genotypes exhibited a consistently higher mean germination percentage than any of the other genotypes over all of the salt concentration levels.

Mean germination percentage for all honey mesquite genotypes in the control treatment was 83%. Mean germination percentage in the 5 mmhos cm^{-1} treatment was slightly higher, 84.6%, but not significantly so. Mean germination percentages for the honey mesquite genotypes in the other three treatments were: 78% at 10 mmhos cm^{-1} , 57% at 20 mmhos cm^{-1} and 6% at 40 mmhos cm^{-1} . Again, as salt concentrations increased, mean germination percentages decreased. This decrease was significantly greater in the 20 and 40 mmhos cm^{-1} treatments than at the control, 5 and 10 mmhos cm^{-1} treatments. None of the honey mesquite genotypes exhibited a consistently higher mean germination percentage than any of the other genotypes across all salt concentration levels.

Germination experiments conducted on screwbean mesquite genotypes revealed that mean germination percentages decreased as salt concentrations increased. This decrease was significantly greater in the 20 and 40 mmhos cm^{-1} treatments in comparison with the control, 5 and 10 mmhos cm^{-1} treatments. Mean germination percentage for all screwbean mesquite genotypes in the control treatment was 29%. Mean germination percentages for all screwbean mesquite genotypes in the other four treatments were: 27% at 5 mmhos cm^{-1} , 24% at 10 mmhos cm^{-1} , 16% at 20 mmhos cm^{-1} and 4% at 40 mmhos cm^{-1} . None of the screwbean mesquite genotypes exhibited a consistently higher mean germination percentage than any other genotypes across all salt concentration levels.

Soil salinity data from samples taken at each collection site was not correlated to the observed germination percentages in either the honey or screwbean mesquite experiments.

Rooting experiments conducted on the cottonwood genotypes revealed that as salt concentration levels increased, mean leaf and root biomass production decreased significantly. None of the cottonwood genotypes exhibited consistently higher mean biomass production than any of the other genotypes across all treatment levels. Mean leaf biomass production for all genotypes in the control treatment was 502 mg per genotype. Mean leaf biomass production for all cottonwood genotypes at the other four treatment levels were: 273 mg at 5 mmhos cm^{-1} , 72 mg at 10 mmhos cm^{-1} and 0 mg at the 20 and 40 mmhos cm^{-1} treatment levels. Mean root biomass production for all cottonwood genotypes in the control treatment was 31 mg per genotype. Mean root biomass production at the other four treatment levels were: 20 mg at 5 mmhos cm^{-1} , 4 mg at 10 mmhos cm^{-1} and 0 mg at 20 and 40 mmhos cm^{-1} .

Rooting experiments conducted on the willow genotypes also revealed that as salt concentration levels increased, mean leaf and root biomass production decreased significantly. None of the willow genotypes exhibited consistently significantly higher mean biomass production than any of the other willow genotypes across all treatment levels. Mean leaf biomass production for all willow genotypes in the control treatment was 576 mg per genotype. Mean leaf biomass production for all willow genotypes at the other four treatment levels were 311 mg at 5 mmhos cm^{-1} , 100 mg at 10 mmhos cm^{-1} , 26 mg at 20 mmhos cm^{-1} and 0 mg at 40 mmhos cm^{-1} . Mean root biomass production for all willow genotypes in the control treatment was 142 mg per genotype. Mean root biomass production for all willow genotypes at the other four treatment levels were 69 mg at 5 mmhos cm^{-1} , 10 mg at 10 mmhos cm^{-1} , 2 mg at 20 mmhos cm^{-1} and 0 mg at 40 mmhos cm^{-1} .

None of the genotypes in any of the germination experiments proved to be more salt tolerant over any of the other genotypes in each respective species group. As expected, as salinity levels increased, germination percentages decreased. None of the observed germination percentages in the mesquite experiments appeared to be correlated to the soil salinity data from each collection site.

All experiments for this project were conducted under controlled, laboratory conditions at the Tucson PMC. These results may not relate directly to field conditions where environmental factors fluctuate widely. Soil salinity concentration levels along the Lower Colorado River may vary throughout the year depending on streamflow and climatic conditions such as annual precipitation. Therefore, soil data collected for this project most likely does not reflect accurate soil conditions.

Better results pertaining to the quailbush, honey mesquite and screwbean mesquite genotypes may be obtained by replicating these experiments using seed harvested over a three to five year period. This may provide adequate baseline data that can be used to set up field experiments. The cottonwood and willow genotype experiments should also be replicated over time in order to better observe the performance of each genotype within each treatment level.

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