

Water relations and leaf growth rate of three *Agropyron* genotypes under water stress

MARÍA G. GARCÍA, CARLOS A. BUSO, PABLO POLCI, NORBERTO L. GARCÍA GIROU, AND VIVIANA ECHENIQUE

Departamento de Agronomía y CERZOS (CONICET), Universidad Nacional del Sur. (8000) Bahía Blanca, Argentina.

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ABSTRACT: The effects of water stress on leaf water relations and growth are reported for three perennial tussock grass genotypes under glasshouse conditions. Studies were performed in genotypes El Palmar INTA and Selección Anguil of *Agropyron scabrifolium* (Döell) Parodi, and El Vizcachero of *A. elongatum* (Host) Beauv. *Agropyron scabrifolium* El Palmar INTA is native to a region with warm-temperate and humid climate without a dry season, and an average annual precipitation of 900 mm. *Agropyron scabrifolium* Selección Anguil comes from a region with a sub-humid, dry to semiarid climate and a mean annual precipitation of 600 mm. *Agropyron elongatum* is a widespread forage in semiarid Argentina with well-known water stress resistance. A mild water stress treatment was imposed slowly; plants reached a minimum pre-dawn leaf water potential of about -1.83 MPa by day 21 after watering was withheld. In all genotypes, water stress led to a reduction of leaf growth. There was a tendency for a greater epicuticular wax accumulation on water-stressed plants of *A. scabrifolium* Selección Anguil and *A. elongatum* than on those of *A. scabrifolium* El Palmar INTA. This may have contributed to obtain greater turgor pressures and relative water contents in the first two than in the later genotype. In turn, this may have contributed to determine smaller leaf growth rate reductions in *A. scabrifolium* Selección Anguil and *A. elongatum* than in *A. scabrifolium* El Palmar INTA under water stress. This study demonstrated variation in water stress resistance between genotypes in *A. scabrifolium*, and between *A. scabrifolium* Selección Anguil and *A. elongatum* versus *A. scabrifolium* El Palmar INTA, which was related to their differential responses in water relations.

Introduction

Water potential and its components are generally considered a reliable measurement of the water status of plant tissue (Brown, 1995). By the mid eightys, relative water content was proposed as a better indicator of water status than water potential (Sinclair and Ludlow, 1985). This is because relative water content, through its relation to cell volume, may more closely reflect the balance between water supply to the leaf and transpira-

tion rate. Measurements of total leaf water potential, leaf osmotic potential and relative water content relate directly or indirectly to plant response to water stress (Brown, 1995). All of these are, in theory, potential water stress resistance screening criteria (Matin *et al.*, 1989).

The importance of plant water for the maintenance of turgidity required for plant growth is widely recognized. Many workers (e.g., Levitt, 1972; Brown, 1995) have shown that water stress-resistant plants have smaller water deficit per unit decrease in leaf water potential than more water-stress susceptible plants. Work of Carter and Patterson (1985) on *Glycine max* and Schonfeld *et al.* (1988) on *Triticum aestivum* indicated that cultivars with higher relative water content are more water stress resistant.

Many workers have suggested that total water po-

Address correspondence to: Dr. Carlos A. Busso. Dpto. de Agronomía, Universidad Nacional del Sur, Altos del Palihue. (8000) Bahía Blanca, Buenos Aires, ARGENTINA.
Fax: (+54- 291) 459 5127. E-mail: cebusso@criba.edu.ar
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tential of plant tissue may differentiate between water stress-resistant and -susceptible cultivars. More water stress-resistant lines of *Glycine max* (L.) Merr (Cortes and Sinclair, 1986), *Hordeum vulgare* L. (Hanson *et al.*, 1977; Matin *et al.*, 1989) and *Oryza sativa* L. (Novero *et al.*, 1985) have been shown to maintain higher total leaf water potentials. Genotypic total water potential variation in large populations of plants has been obtained by Sammons *et al.* (1978) in *Glycine max*, Blum (1974) in *Sorghum bicolor* (L.) Moench, and Quarrie and Jones (1979) in *Triticum aestivum*. These studies concluded that higher total leaf water potentials in specific cultivars within the populations indicated increased water stress resistance. Additionally, various physiological indices have been used in the past to differentiate genotype response to water stress. For example, Quarrie and Jones (1979) reported genotypic differences in *Triticum aestivum* L. leaves in the rate of water potential decrease.

It is well known that water deficit in plants can induce a lowering of osmotic potential in some species and cultivars which contributes to cell turgor maintenance at low leaf water potentials (Brown, 1995). Maintenance of turgor pressure helps the plant in maintaining stomatal opening, photosynthesis, and more water uptake from the soil (Brown, 1995). Genotypic differences in turgor maintenance have been reported on several grasses such as wheat (Morgan, 1977; Fischer and Sanchez, 1979), sorghum (Ackerson *et al.*, 1980) and pearl millet (Henson *et al.*, 1982).

Agropyron scabrifolium (Döell) Parodi is a perennial tussock grass native to the northeast and central Argentina growing mainly close to water courses. This species has also established successfully in the semiarid region of this country showing resistance to water stress conditions (Kade and Cardielo, 1983). Although this species can then show resistance to water stress, the mechanisms underlying this response are not well understood. In central Argentina, it has replaced to some extent to *Agropyron elongatum* (Host) Beauv., another common perennial, water-resistant, less palatable forage grass in this region (García *et al.*, 1992). Although water stress resistance make these species valuable forages in arid and semiarid regions of Argentina (Covas and Ballari, 1969), research is limited on their water stress resistance and physiological responses to water stress.

We sought to determine the effects of water stress during the vegetative stage of development on leaf water relations and leaf growth rates in two genotypes of *A. scabrifolium* coming from regions with different ecological characteristics, and in one genotype of *A.*

elongatum. Leaf water and osmotic potentials, turgor pressure, and relative water content, and their relationship to leaf growth, were measured in an attempt to differentiate genotypes differing in apparent water stress resistance.

Materials and Methods

Experimental procedures

Studies were performed in genotypes El Palmar INTA and Selección Anguil of *A. scabrifolium*, and El Vizcachero of *A. elongatum*. *Agropyron scabrifolium* El Palmar INTA is native to a region with warm-temperate and humid climate without a dry season, and an average annual precipitation of 900 mm. *Agropyron scabrifolium* Selección Anguil comes from a region with a sub-humid, dry to semiarid climate and a mean annual precipitation of 600 mm. *Agropyron elongatum* is a widespread forage in semiarid Argentina with well-known water stress resistance.

Seeds of the three *Agropyron* genotypes were sown during mid-summer (6 February) in 10 l pots filled with soil under glasshouse conditions with natural sunlight and photoperiod. Plants were kept under these conditions during the study. Seeding was carried out at a time when commercial seeding usually takes place under field conditions. Thinning was thereafter conducted leaving 12 plants on each pot. Two water treatments were imposed on a total of 96 pots (50% irrigated, 50% water-stressed): irrigated plants were maintained near field capacity by irrigating daily during the experiment while water was withheld from water-stressed plants from day 120 to day 141 after sowing. Four pots (replicates) were randomly assigned to each genotype and water treatment combination, and different pot sets were sampled 3, 14, 17 and 21 days after withholding water. When pots were sampled more than once, determinations were effected on different plants. On each pot, 9 to 12 plants were destructively sampled for determining plant-water relation parameters while another group of 3 plants was used for conducting leaf growth measurements. These later measurements, however, were conducted only on those pots assigned to the last sampling date. Glasshouse temperatures during the measurement period ranged between 15 and 18°C by day and between 10 and 12°C by night.

The development of water stress was monitored by measuring pre-dawn leaf water and osmotic potentials, and relative water content of youngest, fully expanded

leaves. These measurements were conducted using 4 replicate leaves, one per pot, on each genotype and water treatment. Leaf water potentials were measured by the pressure chamber technique following Turner (1981). Leaf osmotic potentials were measured thereafter on the same leaves after freezing in liquid nitrogen and measuring osmotic potential in the expressed sap using a vapour pressure osmometer (Wescor model 5500, USA). Osmotic potentials, which were not corrected for the dilution from apoplastic water, were calculated according to the following formula: osmotic potential (J kg^{-1}) = $-RCT$, where R is the gas constant ($\text{J K}^{-1} \text{mol}^{-1}$), T the absolute temperature ($^{\circ}\text{K}$) and C the osmotic concentration (mol kg^{-1}); values of osmotic potential were multiplied by 0.001 to obtain this parameter in MPa. Turgor pressures were calculated as the difference between leaf water and osmotic potentials (Turner, 1981). Measurements of leaf relative water content were effected following Turner (1981).

At the beginning of the study, one tiller on each of 3 plants per pot was permanently marked using a wire loop at its base; 4 replicates were used per genotype and water treatment. The leaf apex of the youngest expanding leaf on each selected tiller was daily marked using a water-proof pen; daily growth was calculated as the distance between two adjacent points (Cutler *et al.*,

1980). Leaf growth rates were calculated by dividing the amount of new leaf length produced during any period by the number of days of that period.

At the last sampling date, three to four wholly expanded leaves were taken from each of four replicate pots per genotype and water treatment. Total leaf area was determined on those leaves used for wax extraction. This was accomplished by weighing leaf heliographic copies and then relating this weight to that of known surface areas. Leaves were immersed in chloroform during 15 sec. The resulting solutions were then filtered using filter paper Whatman N° 43 and evaporated to near dryness in a chamber with nitrogen to prevent oxidation of organic compounds. Wax content was determined following Ebercon *et al.* (1977). In addition, wax was extracted from 30 leaves of *A. scabrifolium* and 40 leaves of *A. elongatum* to obtain a calibration curve; details of this procedure are given by García *et al.* (1992). Wax content will be expressed in g cm^{-2} leaf area.

Statistical analysis

A completely randomized block experimental design was used in this study. Plant water relation variables were analyzed using three-way (2 water levels x 3

TABLE 1.

Three-way analysis of variance examining the effects of water level, plant genotype and harvest date on total leaf and osmotic potentials, turgor pressure and relative water content for *Agropyron scabrifolium* cv Selección Anguil, *A. scabrifolium* cv El Palmar INTA and *A. elongatum*. Data are presented in Figs 1 and 2.

Source	df	Potential		Pressure Mean Squares	Relative water content
		Osmotic	Total		
Blocks	3	1,198	8.45	6,004	38,748
Main Effects					
Water level	1	138.597***	814.277***	280.992***	1483.408***
Genotype	2	14.761**	92.226***	35.175***	272.287***
Date	7	13.188***	139.994***	84.953***	400.311***
Interaction					
Water level x genotype	2	15.754**	50.498***	9.859*	201.793**
Water level x date	7	27.135***	88.092***	24.866***	371.426***
Genotype x date	14	5.588**	4,652	3,437	31,394
Water level x genotype x date	14	3,233	4,562	2,612	38,183
Error	141	2,205	4,856	2,832	28,417
Total	191				

*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$

genotypes x 8 sampling dates) ANOVA. Differences in leaf growth rate between irrigated and water-stressed plants (3 genotypes x 12 sampling dates) or the wax data (2 water levels x 3 genotypes) were analyzed using two-way ANOVA. Student-Newman-Keuls test was utilized for mean separation when F tests were significant at the 0.05 level. Linear regression analysis was used to investigate relationships between leaf water potential, osmotic potential, turgor pressure or relative water content following Neter and Wasserman (1974).

Results and Discussion

Plant water relations

Genotype and date interacted significantly ($P < 0.05$) with water level when studying leaf water and osmotic potentials, turgor pressure and relative water content (Table 1). By day 12 after watering was withheld, the predawn leaf water potential was lower ($P < 0.05$) than at previous sampling dates and reached the lowest ($P < 0.05$) value by the end of the study in the water-stressed plants of the three genotypes (mean \pm 1 s.e.; *A. scabrifolium* El Palmar INTA = -1.83 ± 0.15 MPa, *A. scabrifolium* Selección Anguil = -1.23 ± 0.33 MPa, *A. elongatum* = -1.34 ± 0.18 MPa; Fig. 1). In agreement with other reports (e.g., Sobrado, 1986), this degree of water deficit was considered mild and slowly achieved.

When predawn leaf water potential of water-stressed plants was taken as the average of all values from day 1 to the end of measurements, it was lower ($P < 0.05$) in *A. scabrifolium* El Palmar INTA (mean = -0.89 MPa) than in *A. scabrifolium* Selección Anguil (mean = -0.56 MPa) and *A. elongatum* (mean = -0.51 MPa). Several authors have reported that more water stress resistant crop plants can maintain higher total leaf water potentials than those susceptible (Hanson *et al.*, 1977; Quarrie and Jones, 1979; Cortes and Sinclair, 1986; Matin *et al.*, 1989). From 9 to 13 days after withholding water, predawn leaf water potentials in water-stressed plants decreased from -0.28 ± 0.01 to -0.83 ± 0.14 MPa in *A. scabrifolium* Selección Anguil, -0.36 ± 0.04 to -1.49 ± 0.25 MPa in *A. scabrifolium* El Palmar INTA and -0.21 ± 0.02 to -0.74 ± 0.20 MPa in *A. elongatum* (Fig. 1). At the same time, predawn leaf osmotic potentials in these plants only followed concomitant decreases in leaf water potentials by days 12-13 in *A. scabrifolium* Selección Anguil, and days 11-13 in *A. scabrifolium* El Palmar INTA and *A. elongatum* (Fig. 1). This determined reductions in turgor pressure in all three genotypes, although they were greater

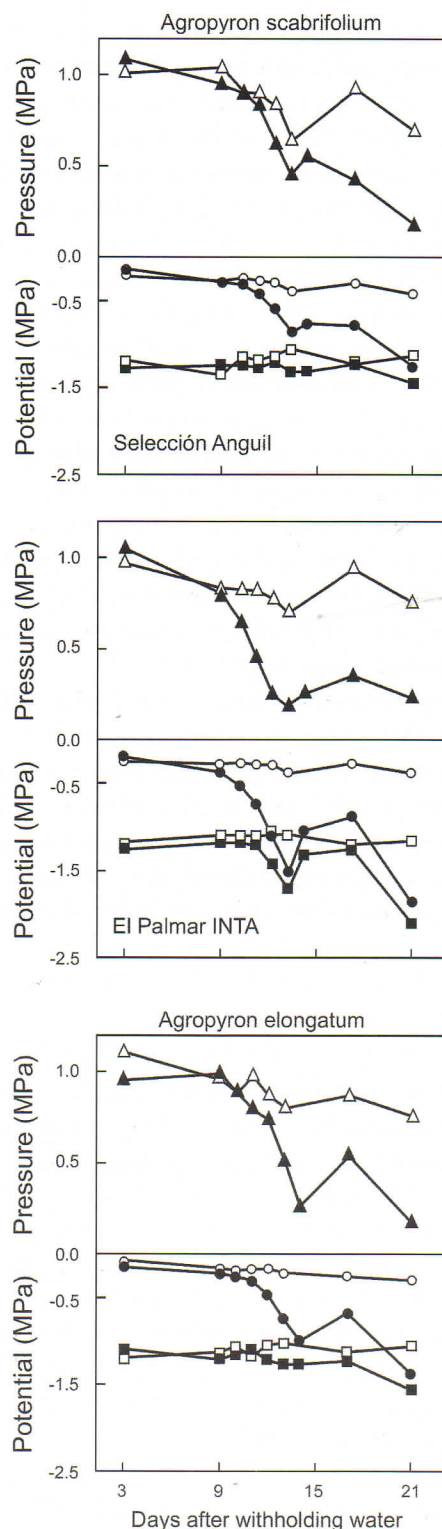


FIGURE 1. Predawn turgor pressure (▲, water stress; △, irrigation), and osmotic (■, water stress; □, irrigation) and water (●, water stress; ○, irrigation) potentials in genotypes Selección Anguil and El Palmar INTA of *A. scabrifolium* and *A. elongatum* under increasing water stress and under irrigated conditions. Each symbol is the average of $n=4$.

in *A. scabrifolium* El Palmar INTA than in *A. scabrifolium* Selección Anguil or *A. elongatum* because its earlier and greater decreases in leaf water potentials were not accompanied with parallel decreases in leaf osmotic potentials (Fig. 1). In fact, predawn leaf osmotic potentials on water-stressed plants of *A. scabrifolium* Selección Anguil and *A. elongatum* were only significantly lower ($P < 0.05$) by 21 days after withholding water (mean = -1.47 MPa) than at previous sampling dates (mean = -1.20 MPa). Maximum rates of decline in predawn leaf water potential, osmotic potential or turgor pressure were -0.28, -0.13 or 0.15 MPa d⁻¹, respectively, from 9 to 13 days after withholding water in all three genotypes. Similar rates of decline for leaf and osmotic potentials, and turgor pressures, have been found in other studies after exposing grass plants to water stress (Westgate and Boyer, 1985; McCree, 1986; García Girou and Curvetto, 1988).

After 17 days of withholding water, and except by day 14 in *A. elongatum*, *A. scabrifolium* Selección Anguil and *A. elongatum* maintained turgor pressures greater than 0.43 MPa (Fig. 1). Turgor pressures in *A. scabrifolium* El Palmar INTA, however, only ranged from 0.19 ± 0.13 to 0.36 ± 0.12 MPa between 12-21 days after water was withheld (Fig. 1), and they were lower ($P < 0.05$) in this genotype (mean = 0.50 MPa) than in *A. scabrifolium* Selección Anguil (mean = 0.69 MPa) and *A. elongatum* (mean = 0.70 MPa). Turgor pressures were also lower ($P < 0.05$) in *A. scabrifolium* El Palmar INTA (mean = 0.83 MPa) than in *A. elongatum* (mean = 0.91 MPa) on controls but differences were not as great as those on water-stressed plants. Predawn leaf water potentials also decreased ($P < 0.05$) in unstressed plants of the *Agropyron* genotypes after 13 days of withholding water but they ranged on average from -0.16 to -0.33 MPa (Fig. 1); mean values for this parameter in these plants, however, were lower ($P < 0.05$) in *A. scabrifolium* El Palmar INTA and *A. scabrifolium* Selección Anguil (-0.27 MPa in both genotypes) than in *A. elongatum* (-0.18 MPa). Mean pre-dawn leaf osmotic potentials were about -1.11 MPa in control plants of the three genotypes during the entire experiment.

Leaf relative water content was similar ($P > 0.05$) among genotypes on control plants (mean = 98.8%) and it declined slightly but significantly ($P < 0.05$) from 10 (mean = 99.43%) to 21 days (mean = 98.31%) after study initiation in these plants (Fig. 2). Declines in relative water content were also significant ($P < 0.05$) but much more pronounced on water-stressed plants of the three genotypes, and values ranged from 99.05 to 75.44% after 3 to 21 days of withholding water, respectively (Fig. 2). Relative water contents on water-stressed plants, how-

ever, were lower ($P < 0.05$) in *A. scabrifolium* El Palmar INTA (mean = 88.69%) than in *A. scabrifolium* Selección Anguil (95.70%) and *A. elongatum* (94.91%) (Fig. 2). Matin *et al.* (1989) found that relative water contents were usually significantly higher in the water stress resistant cultivars than on those susceptible of *Hordeum vulgare* after the development of enough plant stress. These results agree with Kirkham *et al.* (1980),

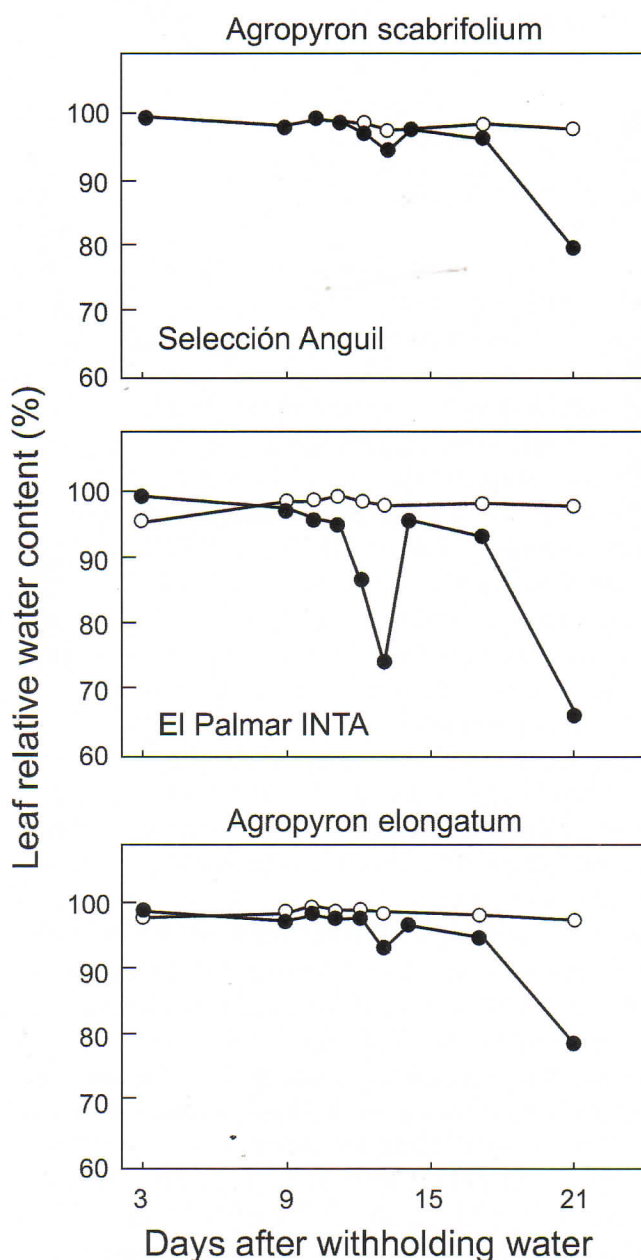


FIGURE 2. Leaf relative water content in genotypes Selección Anguil and El Palmar INTA of *A. scabrifolium* and *A. elongatum* under increasing water stress (●) and under irrigated (○) conditions. Each symbol is the average of n=4.

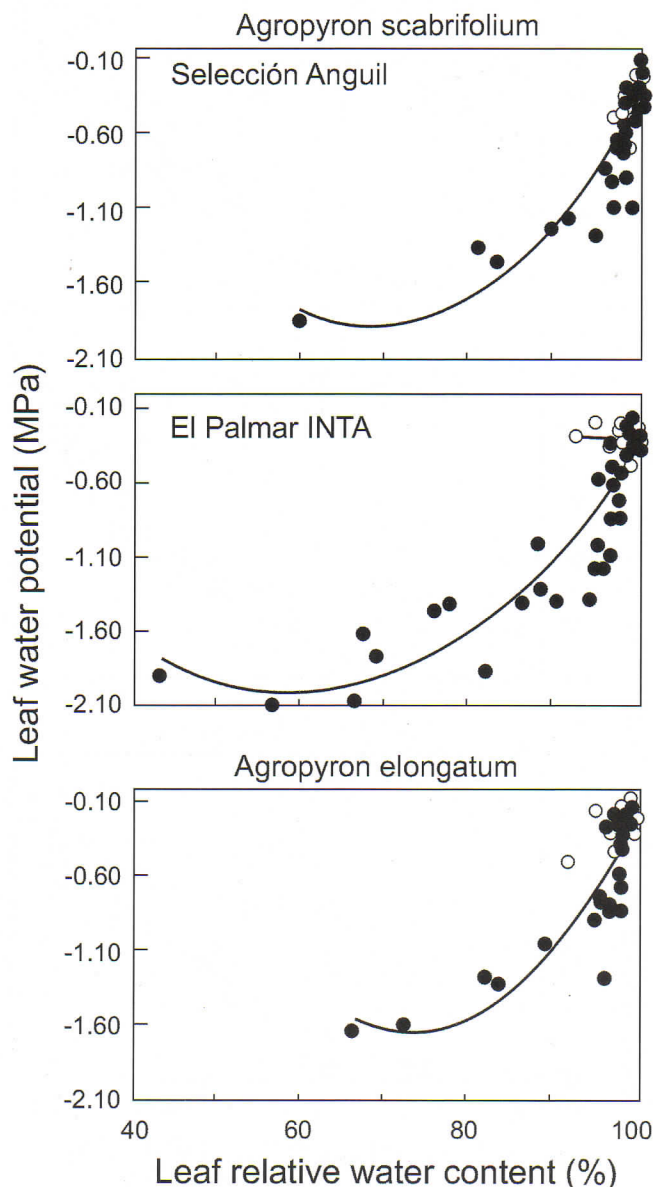


FIGURE 3. Relationship of relative water content (x) to total water potential (y) on leaves of water-stressed (●) or irrigated (○) plants of *A. scabrifolium* cv Selección Anguil (water-stressed, $y = 5.390 - 0.214x + 0.002x^2$, $R^2 = 0.80$, $P < 0.001$; irrigated, $y = -7.25 + 0.071x$, $R^2 = 0.31$, $P = 0.001$), *A. scabrifolium* cv El Palmar INTA (water-stressed, $y = 1.270 - 0.112x + 0.001x^2$, $R^2 = 0.83$, $P < 0.001$; irrigated, $y = -0.056 - 0.002x$, $R^2 = 0$, $P > 0.8$) or *A. elongatum* (water-stressed, $y = 9.418 - 0.300x + 0.002x^2$, $R^2 = 0.71$, $P < 0.01$; irrigated, $y = -1.69 + 0.015x$, $R^2 = 0.5$, $P > 0.2$). Linear regressions were fitted to the data when the curvature effect coefficient was not significant. Symbols are individual data points.

Clarke and McCraig (1982), Carter and Patterson (1985) and Schonfeld *et al.* (1988), who found that cultivars believed to be more water stress resistant usually maintained higher leaf relative water contents under stress.

The trends of pre-dawn leaf water potentials versus relative water content were different for control and water-stressed plants of the *Agropyron* genotypes (Fig. 3): decreases in predawn leaf water potentials per unit decrease in relative water content were larger on water-stressed than on control plants. Similar results have been reported in other cultivated plants under water stress (Jones and Turner, 1978, 1980). These adjustments in the relationship between water potential and water content are determined by the interactions between osmotic concentration and wall elasticity (Tyree and Jarvis, 1982). Decreases in relative water content per unit decrease in total leaf water potential were similar ($P > 0.05$) on water-stressed plants of the three genotypes (Fig. 3). Water stress-resistant plants have been shown to have smaller water deficit per unit decrease in leaf water potential than more water stress-susceptible plants (e.g. Levitt, 1972; Carter and Patterson, 1985), which suggests a similar resistance to water stress in both genotypes of *A. scabrifolium* and in *A. elongatum*. The relationship between osmotic potential and relative water content was also similar ($P > 0.05$) among genotypes (Fig. 4).

Within each genotype, regression lines of the relationship between turgor pressure and total leaf water potential were similar ($P > 0.05$) between water-stressed and control plants (Fig. 5). However, leaf turgor pressures tended to be higher in water-stressed than in control plants when leaf water potentials declined (Fig. 5), which suggests the ability of turgor maintenance in the face of declining leaf water potentials.

Leaf epicuticular wax

Wax content was not significantly different ($P > 0.05$) among genotypes or water level treatments (Fig. 6). However, it was similar on water-stressed and irrigated plants of *A. scabrifolium* El Palmar INTA, but more than 50% greater on water-stressed than on irrigated plants in *A. scabrifolium* Selección Anguil and *A. elongatum* (Fig. 6). Increases of epicuticular wax production as a result of water stress have been shown in other *Agropyron* species (Jefferson *et al.*, 1989). Brown (1995) reported that leaf cuticular waxes possibly lead to reduced cuticular loss of water when stomata are closed, and generally are felt to increase water conservation during water stress periods. Thus, although not significantly different ($P > 0.05$), the tendency to a

greater epicuticular wax content in *A. scabrifolium* Selección Anguil and *A. elongatum* than in *A. scabrifolium* El Palmar INTA may have contributed to determine greater turgor pressures in the first two than in the later genotype.

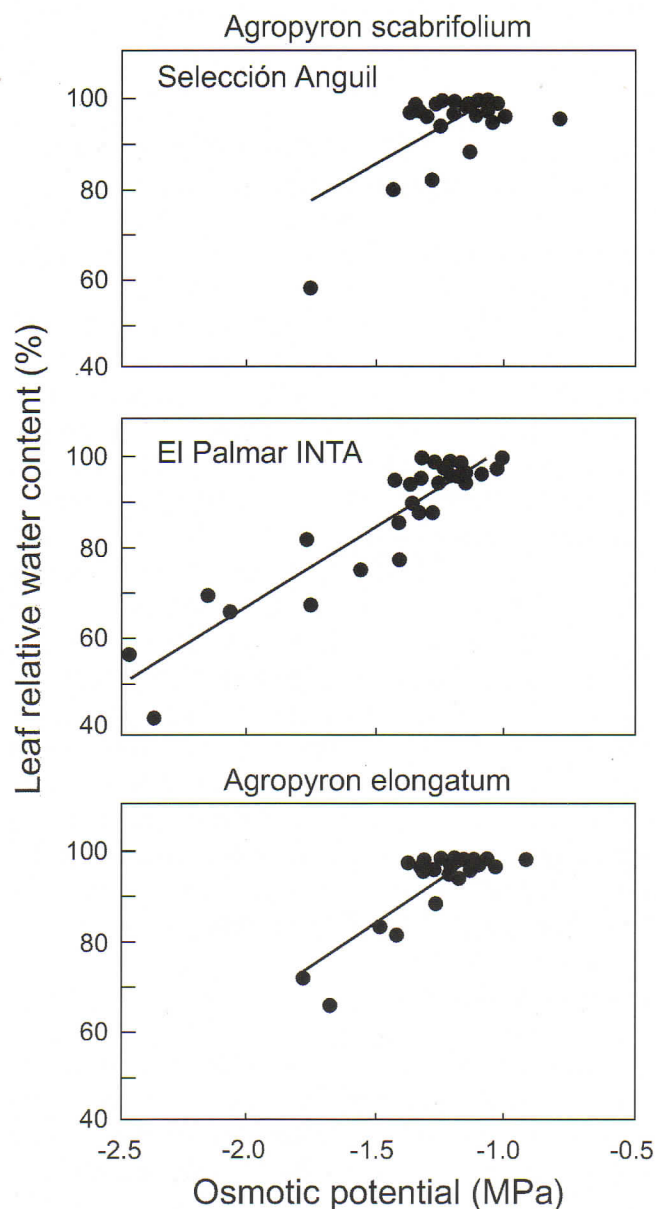


FIGURE 4. Relationship of osmotic potential (x) to relative water content (y) on leaves of water-stressed plants of *A. scabrifolium* cv Selección Anguil ($y=15.2-0.444x$, $R^2=0.54$, $P<0.001$), *A. scabrifolium* cv El Palmar INTA ($y=13.8-0.352x$, $R^2=0.87$, $P<0.001$) or *A. elongatum* ($y=14.2-0.379x$, $R^2=0.71$, $P<0.001$). Symbols are individual data points.

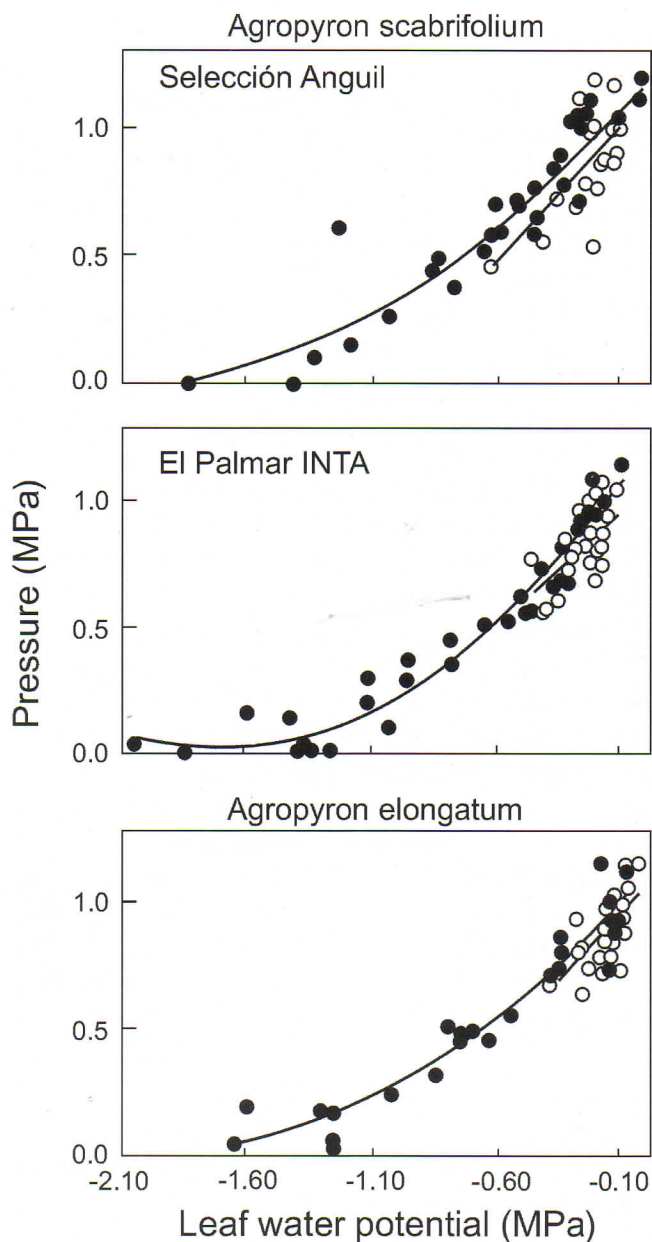


FIGURE 5. Relationship of total water potential (x) to turgor pressure (y) on leaves of water-stressed (●) or irrigated (○) plants of *A. scabrifolium* cv Selección Anguil (water-stressed, $y=1.264+0.125x+0.003x^2$, $R^2=0.94$, $P<0.01$; irrigated, $y=1.18+0.109x$, $R^2=0.38$, $P<0.001$), *A. scabrifolium* cv El Palmar INTA (water-stressed, $y=1.331+0.169x+0.006x^2$, $R^2=0.90$, $P<0.001$; irrigated, $y=1.09+0.092x$, $R^2=0.32$, $P<0.001$) or *A. elongatum* (water-stressed, $y=1.162+0.115x+0.0031x^2$, $R^2=0.93$, $P<0.001$; irrigated, $y=1.11+0.111x$, $R^2=0.40$, $P<0.001$). Linear regressions were fitted to the data when the curvature effect coefficient was not significant. Symbols are individual data points.

Plant growth

Rates of leaf growth decreased in both water levels for all genotypes during the study period (Fig. 7). Leaf growth rates were always smaller in water-stressed than in irrigated plants of the three *Agropyron* genotypes (Fig. 7). Reduction of leaf growth because of water stress is well known in grasses (e.g., Brown, 1995), and it has been observed in other *Agropyron* species (Busso and Richards, 1995). Reductions in leaf growth because of water stress were greater ($P < 0.05$) during days 9 to 13 after withholding water when compared to values at the beginning and end of the study period (Fig. 7). The smallest ($P < 0.05$) differences in leaf growth rate between water-stressed and irrigated plants were observed in *A. elongatum* (mean = 0.27 cm d^{-1}) in comparison to *A. scabrifolium* Selección Anguil (mean = 0.62 cm d^{-1}) and *A. scabrifolium* El Palmar INTA (mean = 0.76 cm d^{-1}) (Fig. 7). These differences tended to be the greatest in *A. scabrifolium* El Palmar INTA, although they were not significantly different ($P > 0.05$) from those in *A. scabrifolium* Selección Anguil.

Based on the greater leaf growth reductions in *A. scabrifolium* El Palmar INTA than in *A. scabrifolium* Selección Anguil and *A. elongatum* in response to water stress, *A. scabrifolium* Selección Anguil and *A. elongatum* appeared more water stress resistant than *A. scabrifolium* El Palmar INTA. *Agropyron scabrifolium* Selección Anguil and *A. elongatum* maintained greater

turgor pressures, relative water contents and leaf water potentials than *A. scabrifolium* El Palmar INTA after withholding irrigation. It appeared to be a tendency for a greater epicuticular wax accumulation on the leaf surfaces of *A. scabrifolium* Selección Anguil and *A. elongatum* than on those of *A. scabrifolium* El Palmar INTA. Greater values for these parameters in *A. scabrifolium* Selección Anguil and *A. elongatum* may

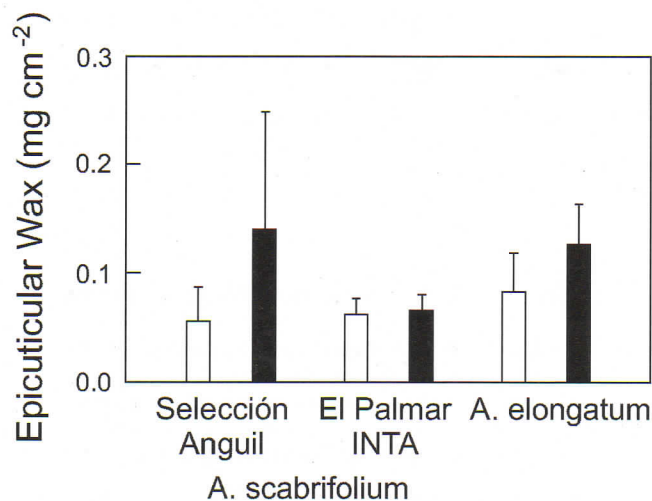


FIGURE 6. Epicuticular wax content on leaves of water-stressed (■) or irrigated (□) plants of *A. scabrifolium* cv Selección Anguil, *A. scabrifolium* cv El Palmar INTA or *A. elongatum* at the end of the study. Each histogram is the mean of $n=4$. Vertical bars represent one s.e.m.

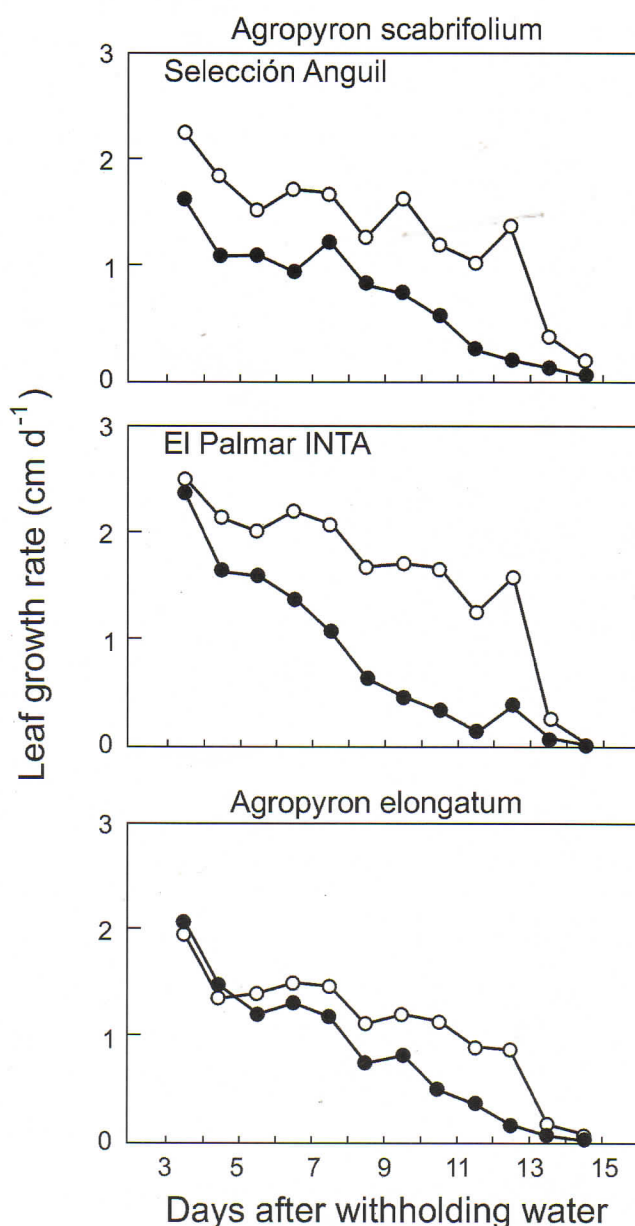


FIGURE 7. Leaf growth rate on water-stressed (●) or irrigated (○) plants of *A. scabrifolium* cv Selección Anguil, *A. scabrifolium* cv El Palmar INTA or *A. elongatum* at different times after withholding water. Each symbol is the mean of $n=4$.

contribute to explain their smaller leaf growth reductions under water stress. Similar relative water content per unit decrease in total leaf water potential; however, did not suggest differences on water stress resistance in

these genotypes. More research is then needed to determine whether differences in resistance to water stress exist or not among genotypes of *A. scabrifolium* and *A. elongatum*.

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