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Ecophysiology of the polyploid shrub *Atriplex canescens* (Chenopodiaceae) growing *in situ* in the northern Chihuahuan Desert*

R. S. Senock†, J. R. Barrow, R. P. Gibbens & C. H. Herbel

Jornada Experimental Range, Agricultural Research Service, U.S. Department of Agriculture, P.O. Box 30003 — Department 3JER, New Mexico State University, Las Cruces, NM 88003-0003, U.S.A.

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Diurnal profiles of gas exchange, leaf temperature, and stem xylem pressure potentials were measured at three field sites where plants representative of diploid ($2n = 18$), tetraploid ($2n = 36$) or hexaploid ($2n = 54$) cytotypes of fourwing saltbush (*Atriplex canescens*) occurred together in various combinations. Results indicated that differences among cytotypes in leaf morphology were related to differences in leaf temperatures, net photosynthesis, leaf conductances, and internal CO_2 concentrations. Mean area per leaf for diploids was 0·228 cm^2, for tetraploids 0·427 cm^2, and for hexaploids 0·613 cm^2. Leaf temperatures of diploids were consistently 1–5°C higher than the other cytotypes. In contrast, leaf temperatures of hexaploids were at or below ambient levels while leaf temperatures of tetraploids were intermediate to the other cytotypes. Photosynthetic rates of diploids decreased rapidly when leaf temperatures approached 37°C, and 63% of the variation of photosynthesis was accounted for by leaf temperatures. Increasing internal CO_2 levels in diploids indicated internal limitations to CO_2 uptake in the mesophyll were responsible for depressed photosynthesis. In contrast, photosynthesis of tetraploids and hexaploids was largely unaffected by leaf temperatures. Higher leaf temperatures in diploids were also translated into higher conductances and lower water-use efficiency (WUE) than the other cytotypes. Tetraploids and hexaploids had higher WUE that were related to either lower conductances, increased photosynthesis, or a combination of reduced conductances and higher photosynthesis. The intermediate leaf form and physiology of tetraploids may represent a compromise to diploids and hexaploids.

Introduction

Polyploid genotypes contribute to the successful establishment of a plant species in the range of environmental conditions that exist across its geographical range (Hayman, 1960; Gottlieb, 1981). The effects of polyploidy have been related to biochemical differences in cellular constituents such as enzyme production, concentration and diversity (Roose & Gottlieb, 1980; Gottlieb, 1981). Physical differences in anatomical and structural charac-

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† Current address: Agronomy Department, Kansas State University, Manhattan, KS, U.S.A.

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teristics such as leaf shape and size, stomata size and density, and number of chloroplasts have also been documented in polyploid species (Byrne *et al.*, 1981). Furthermore, these differences have been shown to affect photosynthesis (Randall *et al.*, 1977) and transpiration (Setter *et al.*, 1978). Physiological studies of polyploid species have largely focused on C_3 species and one C_4 grass (Warner *et al.*, 1987), with the majority of studies conducted under laboratory or greenhouse conditions.

Fourwing saltbush [*Atriplex canescens* (Pursh) Nuttall] is the most widespread species of perennial *Atriplex* in North America. *A. canescens* is a C_4 (Syvertsen *et al.*, 1976) evergreen, drought-resistant shrub found throughout the western U.S.A., Canada and Mexico. It is co-dominant in portions of the creosotebush (*Larrea tridentata*)-dominated desert in the south-west, and in the shrub communities of the Colorado Plateau (Wagner & Aldon, 1978). Polyploidy appears to provide most of the inheritable variation that allows it to occupy a wide range of habitats (Stutz & Sanderson, 1979).

Populations of *A. canescens* throughout its range have been identified according to chromosome number. These include the diploid ($2n = 18$), tetraploid ($2n = 36$), hexaploid ($2n = 54$), and twelveploid ($2n = 104$). Tetraploids are the most widely distributed cytotype, with the other ploidy-level populations being isolated enclaves within the overall geographical range. Heritable variation is provided by hybridisation with other *Atriplex* species, and gene exchange between ploidy levels (Stutz & Sanderson, 1979).

In addition to the distinctive geographical distribution of the various genetic populations, the effect of polyploidy within the species of *A. canescens* has also resulted in pronounced morphological and ecological differences among the cytotypes. In the northern portion of the Chihuahuan Desert that extends into southern New Mexico, distinct differences in leaf length and width exist among the cytotypes (Dunford, 1985). Differences in canopy structures are also readily apparent among the plants in the region, with a low-growing form 100–150 cm high contrasting with a form of 2 m or more in height (Wooton & Standley, 1915). Distribution of the three cytotypes appears to vary according to soil type, and is considered to reflect rather specific ecological adaptations (Dunford, 1984). Diploid and tetraploid plants inhabit sandy soils, while the hexaploid occurs on the heavier clay loam fluvial-plain soils.

Physiologically, differences in leaf nitrate reductase activity and total reduced nitrogen were found among the three cytotypes in greenhouse plants (Sisson & Throneberry, 1986). Other physiological differences reported among cytotypes involve flavonoid constituents (Sanderson & Stutz, 1983) and dosage effects for the enzyme peroxidase (McArthur *et al.*, 1986).

Given the distinct geographical, ecological and morphological differences apparent within the species *A. canescens* in the southern New Mexico region, the objective of this research was to determine the variation in gas exchange and water relations of plants of various ploidy levels growing under natural conditions in the field.

Materials and methods

Site selection and plant material

The study was conducted in the Rio Grande Valley near Las Cruces, New Mexico during the months of August, September and October 1987, in a region characterised by cool, dry winters and hot, wet summers (Sisson, 1983). Average annual precipitation is 230 mm. Field sites were determined by the occurrence of plants representative of the diploid ($2n = 18$), tetraploid ($2n = 36$) or hexaploid ($2n = 54$) cytotypes of *A. canescens* growing in close proximity with each other. Such occurrences were very rare and only three sites were located in time for the study. Plants were identified by leaf morphology as well as by edaphic characteristics of the site, which permitted cytotypes to be readily identified (Dunford, 1984). Site 1 had one staminate plant each of the diploid and hexaploid

Table 1. *Physical and chemical properties of study sites near Las Cruces, New Mexico*

Site	pH	Organic matter (%)	TKN (p.p.m.)	Texture
1	8·02	0·53	278	Sand
2	8·04	0·16	103	Sand
3	7·71	0·66	350	Sand loam

cytotypes growing on a disturbed elevated embankment within the Rio Grande flood plain. Site 2 had two staminate plants each of all three cytotypes and was an arroyo drainage area on the edge of the flood plain. Site 3 had three staminate plants each of the diploid and tetraploid cytotypes growing on a site typical of the surrounding rangelands in the Jornada Basin. Composite soil core samples (0–20 cm depth) were collected from each site and analysed for texture (pipette method), pH, organic matter content and total Kjeldahl nitrogen, according to standard procedures (USDA, 1972). The pH values showed all sites (Table 1) to be calcareous as is typical of the soils in the region (Maker *et al.*, 1974). Organic matter and total nitrogen were comparable at sites 1 (278 p.p.m.) and 3 (350 p.p.m.), and were adequate to provide for favourable plant growth. At a soil water potential of $-1{\cdot}5$ MPa, the sandy loam texture of site 3 increased nearly two-fold the moisture-retention potential of the soil (5·8% H_2O) over that of the other sites (2·6% H_2O). Site 2, the arroyo drainage area, with substantially lower organic matter content (0·16%), low total nitrogen (103 p.p.m.) and low water-retention capacity of the sandy soil, provided the least favourable conditions for plant growth.

Field procedures

Diurnal measurements were made in the morning (0800–1100h), midday (1200–1300h) and afternoon (1400–1700h) periods on two sample dates at each site to determine temporal differences. Days chosen (26 August; 12, 23, 28 September; 2, 5 October) were dictated by weather conditions and most were virtually cloudless allowing maximum incident solar radiation.

Apparent photosynthetic rate, stomatal conductance to water vapour, internal CO_2 concentration, leaf temperature, and ambient temperature were measured simultaneously using the LI-COR 6000 portable photosynthetic system (LI-COR, Inc., Lincoln, NE) and a 250 cm^3 leaf cuvette. Photosynthetic water-use efficiency (WUE) was defined as the ratio of photosynthesis to leaf conductance. The terminal portion (4–5 cm) of a shoot grown in 1987 was inserted in the chamber and marked to permit the same section to be used in subsequent measurements. Measurements were made of the same shoot throughout the day, except when the shoot appeared damaged, in which case a replacement was chosen. Shoots selected occurred on the south side at the top of the canopy. Individual shoot measurements are the mean of 10 readings at 3 s intervals. Values reported are based on projected leaf areas (one-sided) of the shoots as measured with the LI-COR (Model LI-3000) area meter. Preliminary work indicated the contribution of stem material to total shoot photosynthesis was negligible. Number of plants per ploidy level per site varied from one to three while three–seven shoots per plant were used during a measurement period.

Plant water status was evaluated by stem xylem pressure potentials measured with a pressure bomb (Waring & Cleary, 1967) on three shoots collected from the plant canopy area adjacent to those used in the gas exchange measurements. Incident photosynthetic photon flux density (PPFD, 400–700 nm) was measured at half-hour intervals throughout the day using a LI-COR (Model LI-185) photometer.

Surface area per leaf (one-sided) for the different cytotypes was determined with data obtained from the shoots used in the gas exchange measurements. Mean area per leaf on a shoot was found by dividing the total leaf area of a shoot by the number of leaves on the shoot. Overall cytotype means for a site were then calculated from plant means based on individual shoot values.

For purposes of statistical analysis, treatments were defined by site × ploidy-level combinations giving seven treatment groups. This was done because each ploidy level did not occur at each site. Site, day, and plant variations were thus included in the defined treatments. Using the assumption that genetically related differences among the cytotypes should be consistent across sites, sampling dates, and plants, defining treatments this way allowed all the diurnal measurements of gas exchange activity to be used in the comparisons. The resulting analysis of variance model was a two-fold nested design with factors group, plant within group and stem within plant group as sub-sampling terms. The term plant within group was used as the error term to test treatment groups. Contrast statements were then used for cytotype means comparisons using a GLM (General Linear Model) procedure in SAS (SAS Institute, 1985). Relationships between various gas exchange parameters and abiotic conditions were examined using standard correlation procedures (SAS Institute, 1985). Differences among cytotypes in the slopes of the relationships were tested for statistical significance. Differences among cytotypes in surface area per leaf were performed within sites using *t*-tests and across sites using the previously defined treatment groups.

Results

Environmental conditions

Soil moisture conditions during the study period were dominated by a single large precipitation event (75 mm) over the entire valley in mid-August before the study began. Few significant rainfall events occurred in the region before or after that date. Diurnal patterns of xylem water potentials at sites 1 and 3 were very similar between cytotypes, and generally ranged from -2 MPa in the morning periods to -4 MPa in the afternoon periods (data not presented). At site 2, diurnal xylem water potentials were lower and reached almost -5 MPa during the afternoon hours. Although plants for all cytotypes at site 2 were apparently under greater water stress than the other sites, the magnitude of the differences in water potentials among cytotypes did not appear to substantially affect comparative differences in gas exchange among cytotypes on any date at any site. Statistical comparison of the diurnal patterns of xylem water potentials across sites, sample dates and plants indicated that differences among cytotypes were not significantly different ($p > 0{\cdot}56$).

PPFD at solar noon on the first sample date on 26 August reached 2200 μmol m^{-2} s^{-1} and decreased to 1850 μmol m^{-2} s^{-1} at solar noon on the last sample date on 5 October (Fig. 1). With all sample dates being virtually cloudless, the diurnal fluctuations of solar irradiance exhibited the typical patterns of steadily increasing irradiance levels until the solar noon maximum followed by steadily decreasing irradiance levels through the late afternoon. Maximum daytime air temperatures ranged from 33 to 38°C during the study period.

Diurnal patterns of gas exchange and leaf temperatures

Comparative diurnal patterns of photosynthesis among cytotypes were consistent across days within sites, but varied among sites. Photosynthesis of hexaploids at site 1 and site 2 was nearly 50% greater than diploids through most of the day on each date [Figs 2(a) and 3(a)]. In comparison to the relatively small diurnal variation of hexaploids, photosynthesis

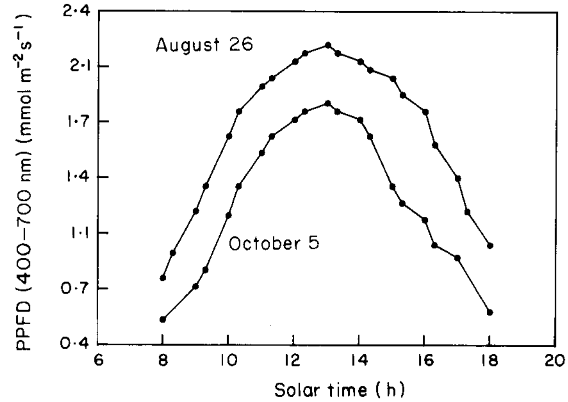

Figure 1. Diurnal patterns of solar irradiance (PPFD, photosynthetic photon flux density 400–700 nm) on 26 August and 5 October 1987 near Las Cruces, New Mexico, U.S.A.

of diploids declined steadily from the morning to the early afternoon hours at both sites. At site 3, photosynthesis of diploid and tetraploid plants was similar within and between days, with the diurnal pattern being a slow continual decrease from 20 μmol m^{-2} s^{-1} in the morning to 10 μmol m^{-2} s^{-1} in the afternoon hours [Fig. 4(a)].

Patterns and rates of leaf conductance to water vapour were site-dependent and varied slightly between days within sites. Rates of conductance for the diploids at site 1 [Fig. 2(b)] showed substantial diurnal variation decreasing from a high of 1·5 m^{-2} s^{-1} in the morning to 0·5 m^{-2} s^{-1} in the afternoon hours, with a somewhat smaller range of variation for the hexaploids. At site 2, leaf conductance varied slightly among cytotypes [Fig. 3(b)] and followed similar diurnal decreases of nearly 50% on both days. Diurnal patterns of conductances at site 3 [Fig. 4(b)] differed between days, with diploids being consistently greater than tetraploids on either day. In no instances, however, was the magnitude of the diurnal fluctuations in conductances reflected in the diurnal patterns of photosynthesis and indicated little stomatal limitations on photosynthesis for any cytotype at any site on any date.

In most instances water-use efficiency (WUE) for all cytotypes remained relatively steady through the day for all cytotypes on all dates indicating compensating fluctuations in photosynthesis and leaf conductance. Comparative diurnal patterns of WUE were consistent across sites and dates with diploids always lower than the other cytotypes. At site 1, hexaploids had higher WUE than diploids that was due to both reduced conductance and higher photosynthesis [Fig. 2(c)]. At site 2, WUE of both tetraploids and hexaploids were largely due to greater photosynthesis as there were only small differences in conductance among cytotypes [Fig. 3(c)]. At site 3, tetraploids had greater WUE that was due entirely to lower conductance as photosynthesis of diploids was similar to or greater than tetraploids [Fig. 4(c)].

Diurnal patterns of internal CO_2 concentration were very consistent across days within sites and distinct differences were readily apparent among cytotypes on all sample dates. On both dates at sites 1 and 2, internal CO_2 of diploids showed a steady increase through the day while internal CO_2 of the other cytotypes present steadily decreased [Figs 2(d) and 3(d)]. Although internal CO_2 of both cytotypes at site 3 remained relatively steady through the day and showed similar fluctuations, internal CO_2 of diploids was consistently greater than tetraploids on both dates [Fig. 4(d)].

Diurnal patterns of leaf temperatures showed distinct differences among cytotypes at all sites on all sample days. At site 1 on the first day when maximum ambient air temperature was 35°C, leaf temperatures of diploid leaves were 2–5°C higher than the hexaploids, which maintained leaf temperatures near ambient [Fig. 2(e)]. On the second day at site 1

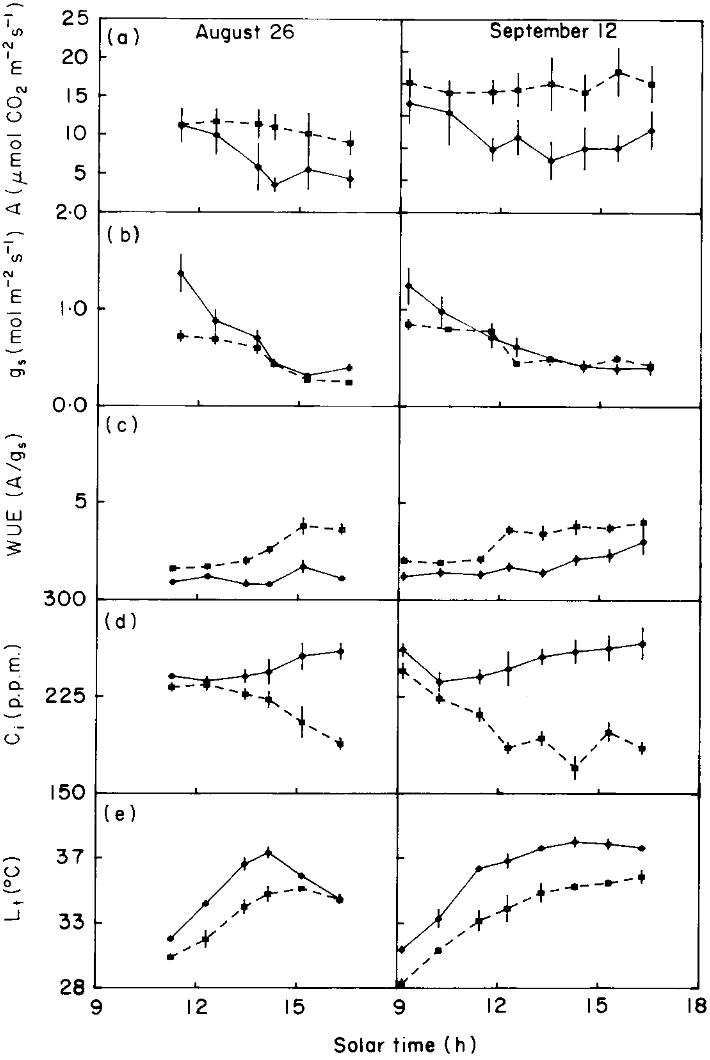

Figure 2. Site 1—(a) diurnal patterns of net photosynthesis, (b) stomatal conductance to water vapour (g_S), (c) water-use efficiency (WUE) × 10^3, (d) internal CO$_2$ concentration (C_i), and (e) leaf temperature (L_t), for one staminate plant each of diploids (2*n*) (——) and hexaploids (6*n*) (– – –) of *Atriplex canescens* growing on a disturbed elevated embankment within the Rio Grande flood plain of southern New Mexico. Plotted values are means (±S.E.) of five–seven shoots per plant.

when maximum air temperature reached 38°C leaf temperatures of the hexaploids were consistently 1°C below ambient. Similarly, leaf temperatures of diploids at site 2 on both days (maximum ambient temperature = 37°C) were consistently 3–4°C above leaf temperatures of the hexaploids, which again remained close to ambient [Fig. 3(e)]. Leaf temperatures for the tetraploids at site 2 were above ambient and intermediate to the diploids and hexaploids. Although leaf temperatures for both cytotypes at site 3 were above ambient (maximum temperature = 33°C), leaf temperatures of diploids were consistently 1–2°C greater than tetraploids through the day on both sample dates [Fig. 4(e)].

Statistical comparison of the diurnal patterns of physiological activity across sites,

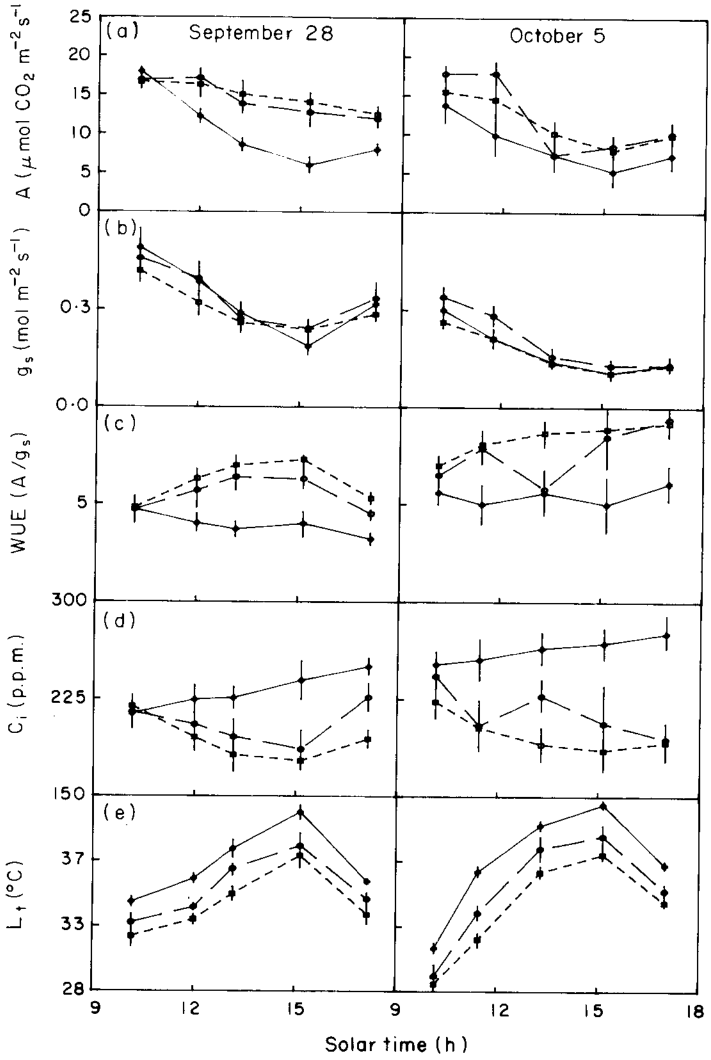

Figure 3. Site 2—(a) diurnal patterns of net photosynthesis, (b) stomatal conductance to water vapour (g_S), (c) water-use efficiency (WUE) × 10^3, (d) internal CO_2 concentration (C_i), and (e) leaf temperature (L_t), for two staminate plants each of diploids (2*n*) (———), tetraploids (4*n*) (— — — —) and hexaploids (6*n*) (- - - -) of *Atriplex canescens* growing in an arroyo drainage area on the edge of the Rio Grande flood plain in southern New Mexico. Plotted values are means (±S.E.) of three–five shoots per plant.

sample dates and plants indicated that differences among cytotypes in photosynthesis were not significant ($p > 0{\cdot}32$) while differences among cytotypes in leaf conductance, internal CO_2, and leaf temperatures were significant ($p < 0{\cdot}05$) and differences in WUE were highly significant ($p < 0{\cdot}01$).

Correlation analysis among gas exchange parameters for any cytotype at any site indicated only a small proportion of the variability in photosynthesis was accounted for by either leaf conductance or internal CO_2 concentration (maximum $r = 0{\cdot}32$, photosynthesis vs. conductance, diploids, site 3). Within and across sites, however, photosynthesis was negatively correlated with leaf temperatures and for the diploids leaf temperatures

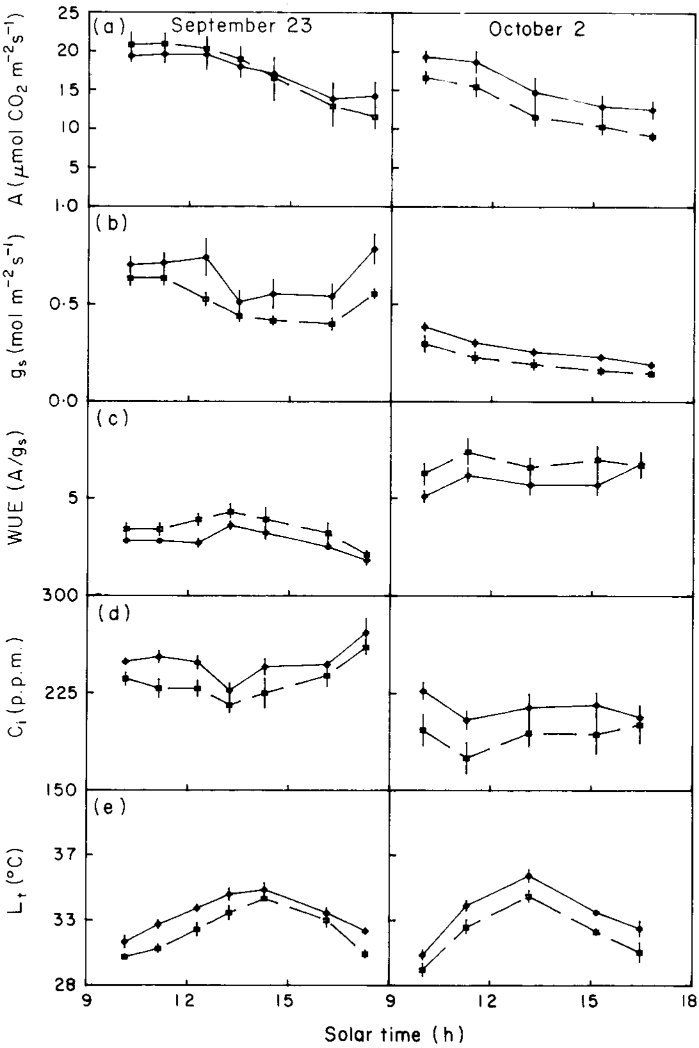

Figure 4. Site 3—(a) diurnal patterns of net photosynthesis, (b) stomatal conductance to water vapour (g_s), (c) water-use efficiency (WUE) × 10^3, (d) internal CO_2 concentration (C_i), and (e) leaf temperature (L_t), for three staminate plants each of diploids (2*n*) (——) and tetraploids (4*n*) (— —) of *Atriplex canescens* growing in the Jornada Basin of southern New Mexico. Plotted values are means (±S.E.) of three–five shoots per plant.

accounted for 63% of the variability in photosynthesis (Fig. 5). The correlation between photosynthesis and leaf temperature was lower for the tetraploids ($r = 0{\cdot}41$) and only a minimal relationship between photosynthesis and leaf temperature was apparent for the hexaploids ($r = -0{\cdot}22$). The slopes of the regression lines among cytotypes were significantly different ($p < 0{\cdot}01$) with the diploids showing a much greater decrease in photosynthesis as leaf temperature increased than either the tetraploids or hexaploids.

Morphological attributes

Mean area per leaf of the terminal portion of the shoots used in the gas exchange measurements for the different cytotypes at each site are presented in Table 2. Diploid

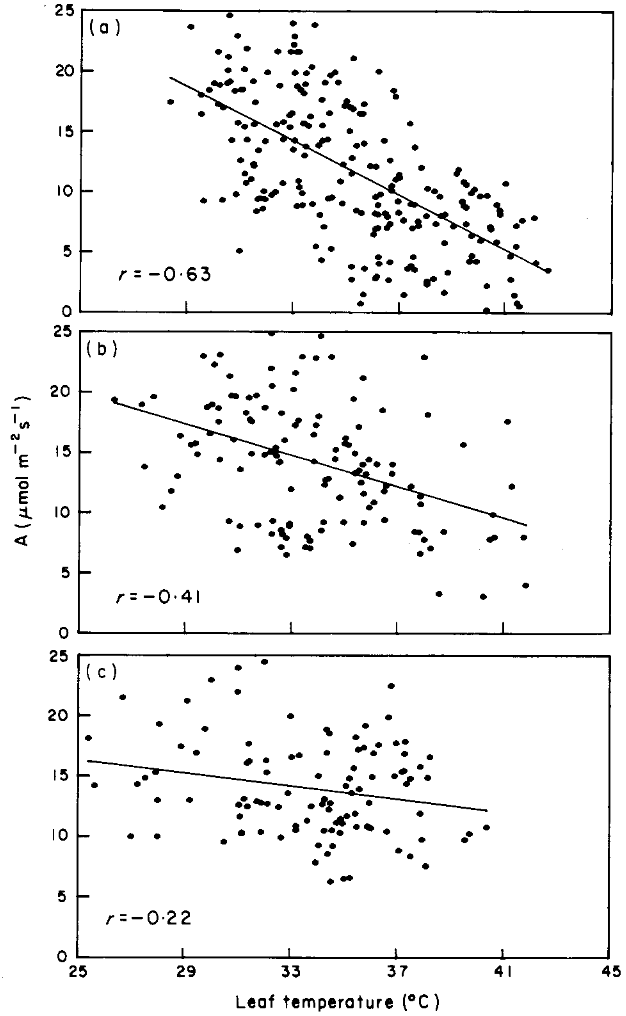

Figure 5. Correlation between net photosynthesis and leaf temperature across study sites and sample dates for (a) diploids (2*n*), (b) tetraploids (4*n*) and (c) hexaploids (6*n*) of *Atriplex canescens* in southern New Mexico.

Table 2. *Mean (±S.D.) area (cm^2) per leaf by cytotype and site. Diploid (2n), tetraploid (4n), hexaploid (6n). All differences among cytotypes within sites were significant (p < 0·001) according to t-tests*

	Cytotype		
Site	2*n*	4*n*	6*n*
1	0·120 ± 0·031 (14)*	—	0·585 ± 0·062 (14)
2	0·241 ± 0·063 (18)	0·411 ± 0·043 (18)	0·640 ± 0·086 (18)
3	0·285 ± 0·045 (16)	0·443 ± 0·047 (16)	—

* Number of shoots used to calculate means.

leaves were consistently the smallest across all sites, averaging only half as much area as tetraploids and only a third the area of hexaploid leaves. According to *t*-tests all differences in mean area per leaf among cytotypes within sites were significantly different ($p < 0{\cdot}001$). The statistical test for data combined across sites indicated significant ($p < 0{\cdot}05$) differences between the overall means of the diploids (0·215 cm^2), tetraploids (0·427 cm^2) and hexaploids (0·613 cm^2).

Discussion

Polyploid differences among the three cytotypes of *A. canescens* occurring in the Rio Grande Valley may represent adaptations in terms of gas exchange and plant water relations. Although widely separated and varying field sites (Table 1) with different combinations of cytotypes present had to be used in the study, diurnal patterns of gas exchange and leaf temperatures were consistent enough within and among sites to support several conclusions.

Despite comparative differences in the diurnal profiles of photosynthesis among all cytotypes not being statistically different across all sites and dates, the trend was for hexaploids to have higher photosynthesis than diploids at the sites where they did occur together. The variation in photosynthesis of tetraploids at site 3 likely contributed to the overall cytotype differences being non-significant. Differences in photosynthetic capacity among ploidy levels at the cellular level have been reported for other polyploid species (Joseph *et al.*, 1981; Molin *et al.*, 1982; Warner *et al.*, 1987). However, in the present study, cytotype differences in photosynthesis were not consistently expressed at the higher functional level of an individual shoot for this species under field conditions. Distinguishing between genetic and site-dependent differences in photosynthesis among the cytotypes of *A. canescens* may require experiments conducted under more controlled conditions.

The differences in photosynthesis among cytotypes that did occur may be partly attributable to the differences in leaf temperatures observed among cytotypes at all sites and sample dates. Leaf temperatures for diploids were typically 1–5°C higher than leaf temperatures for the other cytotypes. The relationship between leaf temperature and photosynthesis was particularly evident for the diploid cytotype (Fig. 5). When leaf temperature reached approximately 37°C, photosynthesis decreased rapidly (Figs 2 and 3). Photosynthesis of diploids was apparently not inhibited when leaf temperatures ($\leq$35°C) were only slightly lower (Fig. 4).

High leaf temperatures in shrub species have often been shown to depress photosynthesis once a critical threshold is exceeded (Bjorkman *et al.*, 1980; Tenhunen *et al.*, 1984). Leaf temperatures above the thermal optimum for photosynthesis in *A. lentiformis* increased the mesophyll limitation to CO_2 uptake by decreasing ribulose diphosphate carboxylase activity (Percy, 1977). The increasing internal CO_2 of diploids at sites 1 and 2 despite decreasing leaf conductance would indicate that internal limitations to CO_2 uptake in the mesophyll, rather than changes in conductance were responsible for depressing photosynthesis once leaf temperature reached a critical level.

In contrast to the diploids, photosynthesis of tetraploids or hexaploids did not appear to be affected in any instance by leaf temperatures. Although the possibility exists that there may be consistent differences among cytotypes in leaf nitrogen content (Sisson & Throneberry, 1986) or different optimum temperatures for carboxylation enzyme activities, the data from this study suggest that tetraploids and hexaploids are able to continue photosynthesis at rates greater than diploids because leaf temperatures remain below a critical threshold. Desert and coastal plants of *A. lentiformis* differ primarily in their capacity to acclimate to high temperatures rather than in genetically fixed temperature responses (Percy, 1976).

Leaf temperature is basically a function of absorbed and re-radiated energy, convective heat loss and latent heat exchange (Gates, 1965), all of which can be altered by leaf dimensions, surface characteristics and orientation (Gates *et al.*, 1968). The measured leaf areas of the cytotypes in this study place them in the two smallest size classes as defined by Raunkiaer (1934). Diploids (0·228 cm^2) fall in the leptophyll category while the tetraploids (0·427 cm^2) and hexaploids (0·613 cm^2) are in the nanophyll category. Although the overall range of leaf areas measured in this study are extremely small, the differences among cytotypes in leaf area may be sufficient to generate differences in leaf temperatures. Higher heat transfer coefficients are characteristic of smaller leaf sizes (0·1–1·0 cm width) and leaf temperatures will often remain close to or slightly above air temperatures (Gates, 1980; Smith & Geller, 1980). Perhaps more importantly, field observations suggest differences in reflectance and orientation also exist among the cytotypes in the Rio Grande Valley (M. Dunford, pers. comm.). Although not measured directly in this study, hexaploid leaves appear to have greater pubescence and lie nearly parallel to the stem. The diploid leaves have less pubescence and protrude at a much greater angle from the stem. Several studies of *Atriplex* species (Sinclair & Thomas, 1970; Mooney *et al.*, 1977) and other desert shrub species (Ehlerginer *et al.*, 1976) have shown the energy balance of leaves is altered by pubescence and leaf angle. Decreased leaf absorptance can result in leaf temperature differences of 5–10°C in desert shrub species (Ehlerginer & Mooney, 1978; Smith, 1978).

The differences in leaf size would also be related to the differences in leaf conductance among cytotypes. Boundary layer conductances as a function of wind speeds are considerably greater for 0·5 cm wide leaves than for even slightly larger (1 cm wide) leaves (Osmond *et al.*, 1980). Just as important would be the differences in leaf dimensions. The long linear dimensions of the diploid leaf form a geometrical surface statistically different from the shorter and wider obovate hexaploid leaves with the tetraploids exhibiting a large variation between the diploids and hexaploids (Dunford, 1985). These differences in geometrical leaf configurations among cytotypes result in different characteristic dimensions parallel to the wind flow that ultimately would affect leaf conductances by alterations in the boundary layer (Taylor, 1975). The pattern of segregation among the three cytotypes in terms of leaf area (hexaploid > tetraploid > diploid) and leaf temperatures (diploid > tetraploid > hexaploid) when considered in relation to conductance (diploid > tetraploid > hexaploid) are in close agreement with simulated interactive effects of leaf properties and environmental conditions (Smith & Geller, 1980). Results of the simulation showed the largest reductions in transpiration and leaf temperature occur in the smallest leaf size classes with the lowest absorptance values.

Differences in leaf conductances among cytotypes can also be related to differences in leaf temperatures. Vapour pressure density deficits are directly determined (exponentially) by leaf temperatures and the higher temperatures for the diploids would increase the gradient between leaf and air, thereby increasing the potential for greater water loss. The differences in conductances resulted in the lowest WUE values for the diploids even when, in one instance, they had comparable rates of photosynthesis (Fig. 3). In contrast, the tetraploids and hexaploids had higher WUEs that were related to either lower conductances, higher photosynthetic rates or a combination of reduced conductances and higher photosynthesis.

Data from this study indicate that leaf morphological differences among the cytotypes are related to leaf temperatures and the physiological processes of photosynthesis and leaf conductance. Considering that differences among cytotypes in distribution also exist, there remains the question of ecological implications and functional significance. The distinct distribution of the cytotypes is not random, and it has been hypothesized that adaptations to soil differences are primarily responsible (Dunford, 1984).

The decreased conductances and subsequent increased WUE of the hexaploids, when taken into consideration with the moisture-retention properties of the clay soils in the flood plain where hexaploids are largely limited, would support this hypothesis. Although water-holding capacity of clay soils is greater than sandy soils, the greater adsorptive properties of clays limit the amount of water available to plants. Increased water conservation by hexaploids through alterations in leaf morphology may simply be a response to edaphic conditions. The distribution pattern of *Artemisia tridentata* and *A. arbuscula* in southern Idaho is determined primarily by the poorer aeration conditions associated with clay soils (Fosberg & Hironaka, 1963). In contrast to the hexaploids, the greater expenditure of water by diploids would tend to limit their distribution in arid regions where water is often the limiting resource. The intermediate leaf form and physiological functioning of the tetraploids may represent the optimal compromise, permitting a wider distribution across the variable habitats of the surrounding arid region.

Intraspecific variation of *Atriplex* species from contrasting environments helped form the basis for the original concept of ecotypic variation (Turesson, 1922). Differences and distinct segregation among cytotypes of *A. canescens* over a limited geographical region, in apparent response to edaphic conditions, provides further evidence for the concept of ecotypic differentiation and the functional significance of differing leaf morphologies. The wide range of morphological and ecotypic variation within a single plant species indicates a high degree of adaptability within the genus *Atriplex*.

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