Response of Two *Salix* L. Species to Water Deficit[1]

Olena P. Zhivotovsky[2] and Yulia A. Kuzovkina[3]
Department of Plant Science, University of Connecticut, Storrs, CT 06269-4067

Abstract

Physiological responses and growth of two *Salix* species — *S. miyabeana* and *S. cinerea* — were compared during one and two drought cycles. Photosynthetic rate (A_{sat}), stomatal conductance (g_s), and transpiration (E) were determined for each species. The highest total biomass and root:shoot ratio were recorded for *S. cinerea*. After two drought cycles, *S. cinerea* had significantly higher A_{sat} at wilting and recovery stages compared to *S. miyabeana*. In addition, after two drought cycles, the stem water potential and water use efficiency were higher in *S. cinerea* than in *S. miyabeana*. Based on the results obtained in this study, *S. cinerea* is more drought tolerant than *S. miyabeana*.

Index words: willow, drought, photosynthetic rate, water use efficiency, WUE.

Species used in this study: *Salix cinerea, Salix miyabeana.*

Significance to the Nursery Industry

Many willows are utilized for landscaping purposes as well as for various environmental applications including erosion control, protective structures (windbreaks and snowfences), phytoremediation and biomass production. Broad genetic variation is available within the genus *Salix*, and its species express varying degrees of stress tolerances. Nurserymen and horticulturists can select varieties with improved resistance to site specific environmental stresses, including drought, to increase plant survival in a landscape and optimize the efficiency of each installation. This study compared two willows for their tolerance to drought based on a screening test which included two drought episodes. Our research shows that a fast-growing clone 'SX67' of *S. miyabeana* selected for biomass production is less adapted to drought stress than a clone of *S. cinerea* collected from native habitats based on lower total biomass, root:shoot ratio, photosynthetic rate, stem water potential and water use efficiency.

Introduction

In the last decade, *Salix* species have received considerable attention due to their potential for environmental applications and for biomass production. Willows are currently being used in ecotechnological projects designed to reduce environmental degradation and to promote horticultural value (1, 28). Their rapid growth rate, low nutrient requirements, resistance to many pollutants, and varying degrees of stress tolerance make willows ideal candidates for environmental applications (13). Research in the past decade has demonstrated that *Salix* species have the potential for uptake and accumulation of heavy metals from contaminated sites (11, 12). However, their usefulness in many sites may be limited under conditions of water stress resulting from sloping topography, low

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[2] Former Graduate Student.

[3] Assistant Professor and Corresponding Author. jkuzovkina@uconn.edu

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water-holding capacity of the soil, limited precipitation, and high temperature.

The majority of *Salix* species are mesophytes and hydrophytes, characterized by high transpiration rates and vulnerability to xylem cavitation under conditions of water stress (25, 31). However, drought tolerance of willows differs widely between species (9); there are indications that some varieties possess desirable drought resistance traits which may make them suitable for specific environmental applications (13).

Plants can resist drought through avoidance and/or tolerance mechanisms (19, 20, 26, 27). Drought avoidance involves efficient stomatal regulation, reduction of light absorbance through the rolling of leaves (4), and/or decreasing the canopy leaf area by the shedding of shoots and leaves (3), while drought tolerance involves processes at the cellular level including osmotic adjustment (22). In order to select or breed plant species with improved water use efficiency and drought resistance, it is important to evaluate the physiological responses of these species to water deficit (18, 30, 32).

Changes in plant growth, photosynthetic rate, stomatal conductance, osmotic adjustment and increase in water use efficiency are useful parameters of the consequences of water deficit (16, 17, 21). Resistance and acclimation to drought have been documented for only few *Salix* species (9, 31, 32). These studies showed considerable variation in the water use efficiency, stomatal conductance, stem water potential, osmoregulation, and growth of the studied species. Considering the potential usefulness of *Salix* species in environmental projects and the limitations that may be imposed on willows by drought, it is worthwhile to identify species with drought-resistant traits.

The objectives of this study were to characterize the physiological responses and growth of two willow species when exposed to one or two drought cycles, and to determine which species will better withstand drought stress.

Materials and Methods

Greenhouse temperature was between 20 and 25C (68 and 77F) with natural photoperiod. On cloudy days, ambient light was supplemented with high-pressure 400W sodium lamps (P.L. Light Systems, Beamsville, ON, Canada) and averaged 500 $\mu mol\cdot m^{-2}\cdot s^{-1}$ at the plant height (16-hour photoperiod). Pots were arranged in randomized complete block design with six treatments (two clones and three drought treatments) and four replications.

Two species of *Salix* with different morphological characteristics — *S. miyabeana* and *S. cinerea* — were used in the experiment. Each species was represented by one clone. *Salix cinerea* (clone I.D. '2007-10') was collected from native habitats in Storrs, CT, and a fast-growing biomass clone 'SX67' of *S. miyabeana* was purchased from Double A Willow, Fredonia, NY. Uniform 20 cm (7.9 in) cuttings were rooted in pots filled with soilless potting substrate Metro Mix-360 (O. M. Scotts, Marysville, OH) under mist. After 3 weeks, the cuttings were transplanted to 4 liter (1 gal) plastic pots containing a 1:1 (v/v) mixture of Metro Mix 360 and vermiculite. Plants were fertilized once a week with 240 ppm N (20-20-20 Peters Professional, O. M. Scotts, Marysville, OH) and irrigated daily to full saturation using drip irrigation connected to each pot until the beginning of the drought treatments. After 3 weeks of growth the following treatments were applied: control (no drought); drought followed by recovery; and two cycles of drought followed by recovery. The drought treatments were imposed by removing the irrigation tubes from the pots. The drought period lasted for 6 days (time between full turgor and the beginning of first leaf wilting); plants were then allowed to recover for 4 days, with daily irrigation. At the end of the experiment, plants were harvested, including dry detached leaves, and separated into roots and shoots (aboveground tissue). The roots of each plant were thoroughly washed. All harvested tissues, were cut into small pieces and dried in the oven for 48 hours at 70C (158F). Dry weight (DW) was then recorded.

Gas exchange and water relations. Photosynthetic rate (A_{sat}) measured as leaf gas exchange at saturation point, stomatal conductance (g_s), and transpiration (E) were recorded on the youngest fully expanded leaves between 1100 and 1230 h daily during the drought and recovery periods using a portable open gas exchange system with an infrared CO_2 analyzer and a red-blue light source (Li-Cor 6400 XT; Li-Cor, Inc., Lincoln, NE). The measurements were taken in random order among treatments. The A_{sat}, g_s and E of two willows were compared at full saturation, at wilting point, and at the end of recovery. The timing for daily measurements was based on a diagonal response for the two species.

A constant CO_2 concentration of 400 $\mu mol\cdot mol^{-1}$ was set in the leaf chamber. The temperature of the gas exchange cuvette block was set to 25C (77F). Immediately before taking measurements, the red-blue light-emitting diode (LED) light source in the system's cuvette was set to the incident photosynthetic flux individually for each species, based on its previously determined photosynthetic response saturation point. For *S. miyabeana* the light irradiance was 1500 $\mu mol\cdot m^{-2}\cdot s^{-1}$ (139.35 $\mu mol\cdot ft^{-2}\cdot s^{-1}$) and for *S. cinerea*, 2000 $\mu mol\cdot m^{-2}\cdot s^{-1}$ (185.80 $\mu mol\cdot ft^{-2}\cdot s^{-1}$). To maximize the accuracy of A_{sat}, the light response curve was repeated during the experiment every week. The measurements were recorded after the photosynthetic rate and stomatal conductance had stabilized (50 to 70 seconds). The time required to make measurements of all plants ranged from 60 to 90 min.

Stem water potential (Ψ_w) was determined on three out of seven plants from each species and treatment using a pressure chamber (PMS Instrument Company, Albany, OR) and was measured at dusk. Stem water potential was measured at full saturation, at the wilting point, and at the end of recovery at the same time of the day and random order among species and treatments. Intrinsic water use efficiency (WUE), which quantifies the amount of carbon assimilated per unit leaf area per unit time at per unit cost of water, was determined as $A_{sat} \div g$ (5). This measurement allows direct comparison of the intrinsic physiological capabilities of individual plants, and avoids the effects of environmental conditions.

Statistical analysis. Statistical analysis was performed using SAS software (version 9.2, SAS Institute, Cary, NC). The MIXED procedure for analysis of variance was used to determine statistical differences ($P < 0.05$) among treatments and species. The data were tested for homogeneity of variance and normality. The data for WUE were rank transformed to meet the assumptions. A repeated measures analysis model was used for drought and recovery effects on A_{sat}, g_s, and E. Comparisons were made between treatments and species at the beginning of the treatments, and at the wilting and recovery stages. The means of dry weight (DW), stem (Ψ_w), and WUE were separated using the Tukey-Kramer test after rejecting H_o of equal means. Relationships between variables were determined using a linear regression fit in Sigma Plot (version 11.0, Systat Software Inc., San Jose, CA).

Results and Discussion

Visual symptoms. At the end of each drought cycle, the leaves of both willow species lost their glossy appearance and became dull. The laminas of *S. cinerea* remained perpendicular to the branch and rolled inwards, whereas blades of *S. miyabeana* drooped and curled (Fig. 1). After two drought cycles, willows had a tendency to abscise their leaves. These symptoms are the dehydration avoidance mechanisms associated with drought stress. Rolling up leaves reduces light absorbance, minimizing water loss by closing stomata (4). Deciduous plants may abscise their leaves if the stress becomes severe and then re-foliate when the water supply is restored.

Plant growth. There was no treatment effect on the root dry weight for *S. miyabeana*; however, after two drought cycles, the root dry weight of *S. cinerea* was less than the control (Table 1). *Salix cinerea* had significantly higher root dry weight in the control and single drought treatments [16.1 and 7.8 g (0.57 and 0.28 oz), respectively] than *S. miyabeana* [4.1 and 2.3 g (0.15 and 0.8 oz)], possibly because *S. miyabeana* allocated more carbon resources to the shoots (the studied clone 'SX67' had been previously selected for high aboveground biomass production), while *S. cinerea* moved more carbon to the roots for use as food storage reserves. The dry weight of roots in *S. cinerea* decreased significantly after one drought cycle compared to controls. Root growth inhibition under water deficit is the result of inhibition of the division and the elongation growth of the cells (14). The rates of these two independent processes are plant specific and depend on the severity of drought, where cell elongation is more sensitive than cell division (6, 10, 23).

Table 1. Average dry weight and root:shoot ratio of two *Salix* species exposed to 0, 1, or 2 drought cycles (n = 4). Means within each column followed by the same letter do not differ significantly, according to the Tukey-Kramer test (P < 0.05).

Species	Drought cycles	Dry weight (g)			Root/shoot ratio
		Root	Shoot	Total	
S. cinerea	0	16.1a	29.6a	45.7a	0.5a
	1	7.8b	24.4ab	32.2b	0.3b
	2	4.8bc	18.8bc	23.6bcd	0.3bc
S. miyabeana	0	4.1c	23.1ab	27.0b	0.2cd
	1	2.3c	15.7c	17.9cd	0.1d
	2	1.8c	13.1c	14.9d	0.1d

The shoot dry weight of the two willow species did not differ in the control treatment. No decrease in shoot dry weight of *S. cinerea* was observed between the control and a single drought cycle or between one and two drought cycles. However, in *S. miyabeana*, the shoot dry weight in either one or two drought cycles decreased compared to the control. When exposed to one drought cycle, the shoot dry weight of *S. cinerea* was considerably higher than that of *S. miyabeana*, indicating that *S. cinerea* was less sensitive to water limitation. Similar results were previously recorded under drought conditions where the fast growing hybrid willow had 25% less than willow clone collected from native habitats (29). There is evidence that plants that have a high growth rate under optimum environmental conditions will conserve water and nutrients less efficiently and plants that grow slowly due to resource limitations have developed specific mechanisms to adapt to those conditions and survive (2).

S. cinera S. miyabeana

Fig. 1. *Salix cinerea* and *S. miyabeana* at the wilting stage after two drought cycles.

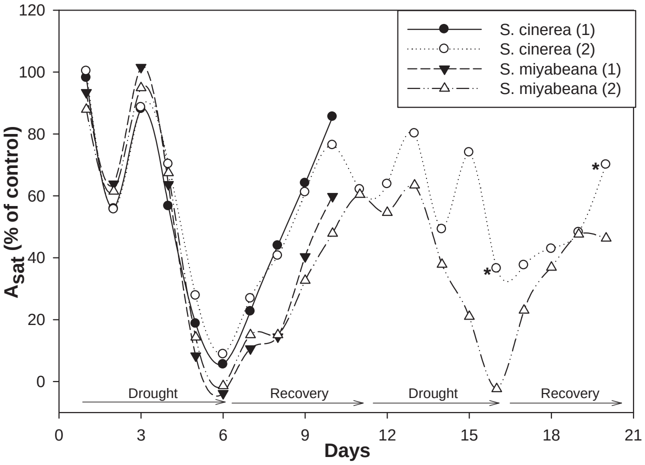

Fig. 2. CO_2 assimilation rate (A_{sat}) of *S. cinerea* and *S. miyabeana* during drought and recovery cycles as a percentage of control. One drought cycle (1), and two drought cycles (2) for each species. Values are means of four replications. Asterisks indicate significant differences (P ≤ 0.05) between species and treatments at wilting stage and full recovery.

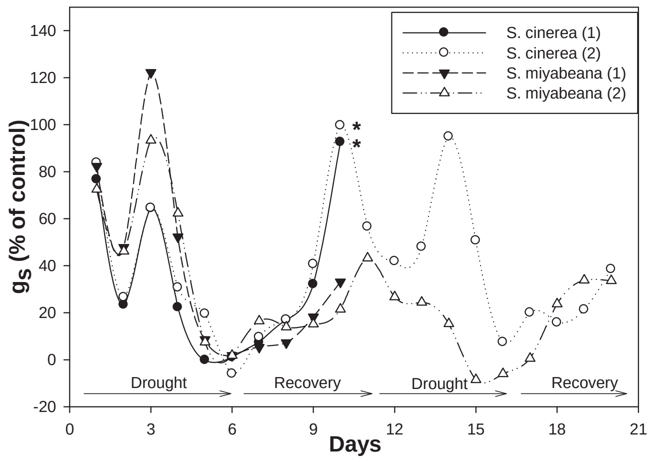

Fig. 3. Stomatal conductance (g_s) of *S. cinerea* and *S. miyabeana* during drought and recovery cycles as a percentage of control. One drought cycle (1), and two drought cycles (2) for each species. Values are means of four replications. Asterisks indicate significant differences ($P \leq 0.05$) between species and treatments at wilting stage and full recovery.

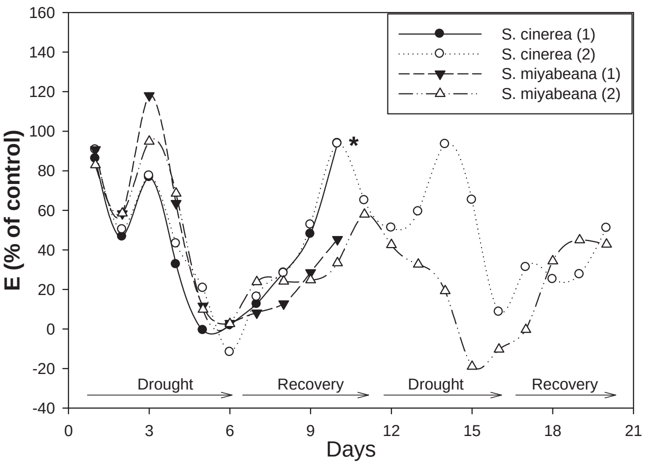

Fig. 4. Transpiration (E) of *S. cinerea* and *S. miyabeana* during drought and recovery cycles as a percentage of control. One drought cycle (1), and two drought cycles (2) for each species. Values are means of four replications. Asterisks indicate significant differences ($P \leq 0.05$) between species and treatments at wilting stage and full recovery.

Compared to the control, the total dry weight of both *S. cinerea* and *S. miyabeana* decreased after one drought cycle. Yet, no significant difference in the total dry weight was recorded between one or two drought cycles for either species. Higher root:shoot ratio was recorded for *S. cinerea* compared to *S. miyabeana*, suggesting resistance to drought in *S. cinerea*. Higher root:shoot ratio has been observed in other drought tolerant species (24).

Gas exchange. At the beginning of each drought cycle, A_{sat}, g_s, and E for both species were similar. At the wilting stage, the photosynthetic rate dropped dramatically in both species, mainly due to stomata closure and the resulting decline in intercellular CO_2. However, no significant differences in A_{sat} in the two drought treatments were observed between species either during or after a single drought cycle (Fig. 2). After two drought cycles at wilting stage, the A_{sat} of *S. cinerea* was 36% higher than *S. miyabeana* ($P \leq 0.05$). The photosynthetic rate of *S. cinerea* in the recovery following the second drought treatment was higher than that of *S. miyabeana* (70 and 46% of the control, respectively), showing its greater ability to recover.

No difference in stomatal conductance (g_s) between the two species was observed at the wilting stage after one or two drought cycles (Fig. 3). However, in the recovery stage following the first drought treatment, there were differences in g_s between the species: in *S. cinerea,* g_s was 99.7 and 93% of the control, whereas the g_s in *S. miyabeana*, it was only 34 and 22% of the control. After two drought cycles, no differences in g_s were found between the two species in either the wilting or the recovery stages. Nevertheless, in *S. cinerea*, the stomata were still open , while the stomata in *S. miyabeana* were closed. Under water deficit, the inhibition of photosynthesis may be due to lower CO_2 diffusion across the leaf mesophyll (8). During periods of water deficit, plant species that exhibit greater drought resistance often have higher photosynthetic rates than drought-sensitive plants (15). These observations suggest that *S. cinerea* is adapted to repeated drought cycles commonly found in the natural environment.

Greater sensitivity of *S. miyabeana* to water deficit may be due to its higher nutrient requirements, as water stress can influence the nutrient level in plants (29).

Differences in transpiration rate (E) were recorded only with two drought cycles, at first recovery. *Salix cinerea* had a significantly higher transpiration rate (expressed as a percentage of the control) compared to *S. miyabeana* (95 and 33%, respectively) (Fig. 4).

Water relations. The soil-water wilting limit parameter was previously used to evaluate drought resistance in *Salix* species (31). In our study we did not find any differences in soil-water limit between the two species (data not shown).

No difference of the stem water potential (Ψ_w) was observed between species or treatments at starting and recovery stages (Table 2). However, at the wilting stage after one drought cycle, *S. miyabeana* had less negative Ψ_w than *S. cinerea* (–1.31 MPa and –1.63 MPa, respectively). By contrast, the Ψ_w of *S. cinerea* (–1.53 MPa) was less negative than in *S. miyabeana* (–2.07 MPa) at the wilting stage of the second drought cycle. After the second drought cycle, the Ψ_w in *S. miyabeana* became more negative than in *S. cinerea,* indicating its sensitivity to water deficit.

Table 2. Stem water potential (MPa) for two willows exposed to different drought treatments measured at wilt and recovery stages (n = 4). Means within each column followed by the same letter do not differ significantly, according to the Tukey- Kramer test ($P < 0.05$).

Species	Drought cycles	Stage		
		Start	Wilt	Recovery
S. cinerea	1	−0.70a	−1.63b	−0.18a
	2	−0.70a	−1.53b	−0.57a
S. miyabeana	1	−0.65a	−1.31a	−0.71a
	2	−0.65a	−2.07c	−0.57a

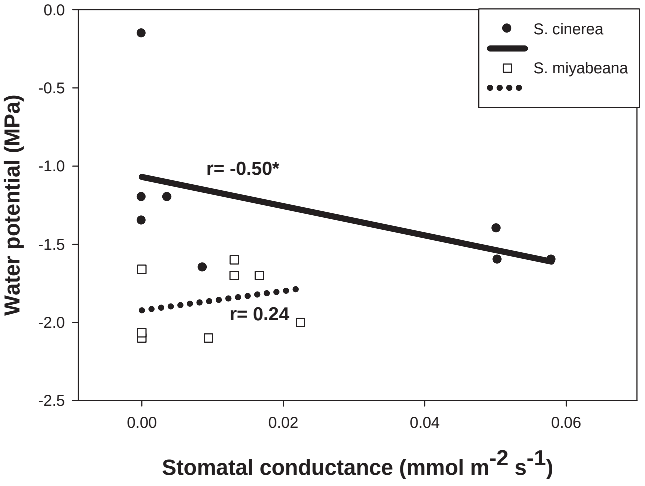

Fig. 5. **Leaf water potential in relation to stomatal conductance for *S. cinerea* (solid line) and *S. miyabeana* (dotted line) at the wilting stage in two drought cycles. Negative values of g_s were replaced by zero (stomatal conductance rate was below the resolution of the instrument). Values of all replications. Asterisk indicates a significant ($P \leq 0.05$) correlation coefficient.**

No correlation was found between A_{sat} and Ψ_w in this experiment (data not shown) There was a negative correlation between g_s and Ψ_w in *S. cinerea,* in which Ψ_w decreased linearly; however, no response was observed in *S. miyabeana* (Fig. 5). The negative correlation between stem Ψ_w and stomatal conductance (g_s) found in *S. cinerea* suggests that stomatal opening controls Ψ_w. We found a negative correlation between Ψ_w and E in *S. cinerea* at the wilting stage in two drought cycles, indicating that the leaf water potential decreased with increased transpiration (Fig. 6). Willows tend to have a high E rate, which is an important prerequisite for a plant to be used in environmental applications (13); however it may negatively affect the Ψ_w of the plant.

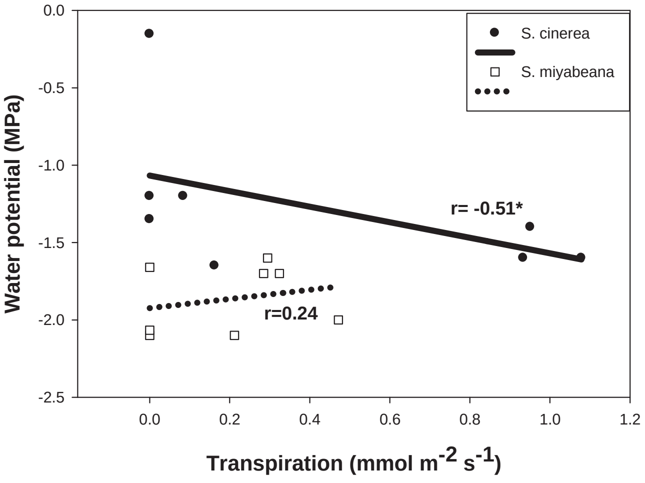

Fig. 6. **Leaf water potential in relation to leaf transpiration for *S. cinerea* (solid line) and *S. miyabeana* (dotted line) at the wilting stage in two drought cycles. Negative values of E were replaced by zero (transpiration rate was below the resolution of the instrument). Values of all replications. Asterisk indicates a significant ($P \leq 0.05$) correlation coefficient.**

Table 3. **Water use efficiency (WUE) for two willows exposed to different drought treatments. Means within each column followed by the same letter do not differ significantly according to the Tukey-Kramer test ($P < 0.05$). Data were rank transformed prior to analysis. The data is presented with the original means and rank transformed lettering.**

Species	Drought cycles	WUE (mmol CO_2·mmol H_2O m^{-2} s^{-1})
S. cinerea	0	0.04ab
	1	0.32ab
	2	18.76a
S. miyabeana	0	0.05a
	1	0.0b
	2	0.01b

There was no correlation between leaf Ψ_w and transpiration in *S. miyabeana*. The water use efficiency was the same for both species in the control and plants exposed to a single drought cycle; however, with two drought cycles, *S. cinerea* had significantly higher WUE than *S. miyabeana* (Table 3).

Physiological acclimation to drought tends to be reflected in an increase in WUE (7). During drought, plants that use water more efficiently will grow more rapidly; thus, increased WUE would be expected to result in higher plant productivity (33). In our study, after two drought cycles *S. cinerea* had significantly higher intrinsic WUE than *S. miyabeana*, and it had significantly higher shoot dry weight and total plant dry weight.

In conclusion, we found differences in plant physiological responses and growth between two willows. The results obtained in this study indicate that studied clone of *S. cinerea* collected form a native habitat was more drought resistant than biomass clone 'SX67' of *S. miyabeana* based on higher root:shoot ratio. After two drought cycles *S. cinerea* had significantly higher A_{sat} at wilting and recovery stages compared to *S. miyabeana*. In addition, after two drought cycles, the stem Ψ_w and water use efficiency were higher in *S. cinerea* than in *S. miyabeana*.

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