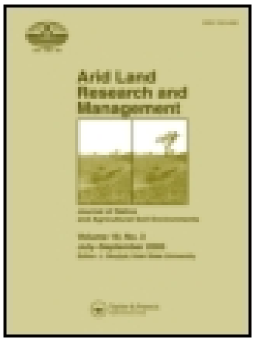

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Evidence on the response of Patagonian forage grasses to the mulching effect of recent tephra deposits in Argentina

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ABSTRACT

In Patagonia, arid and semiarid lands are being affected both by inappropriate management practices, which are leading to degradation, and by volcanic activity, whose effects are still unclear. This study aimed to test whether superficial deposition of volcanic tephra could benefit two of the most prominent Patagonian forage grass species (*Poa ligularis* and *Pappostipa speciosa var. speciosa*). Pots with *P. ligularis* and *P. speciosa* were kept under wet (*W*) and dry (*D*) conditions in the presence (*T*+) or absence (*T*−) of tephra for 105 days, and then were all well-watered. We determined the effects of tephra on soil water retention and conservation, soil moisture content (% v/v), plant growth, stomatal conductance (*gs*), and *gs* recovery capacity. The water regime significantly affected both species performance and *gs*. The presence of tephra increased soil water conservation, soil moisture content in wet conditions, and *P. ligularis gs* in wet conditions, and decreased senescence in dry conditions (9% in *P. ligularis* and 16% in *P. speciosa*). The presence of tephra allowed roots to grow in 8/10 and 2/10 pots in *W* conditions for *P. ligularis* and *P. speciosa*, respectively, and in only 1/10 pots in *D* conditions, only for *P. ligularis*. Tephra was also associated with *gs* recovery after dry conditions. *Poa ligularis* was more positively affected by tephra than *P. speciosa*, probably because *P. ligularis* has higher phenotypic plasticity. The positive effects of tephra may increase the resilience and resistance of *P. speciosa* and *P. ligularis* to periods of water shortage.

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Introduction

The degradation of arid and semiarid regions of the world has been precipitated by a lack of appropriate management practices, coupled with extreme, stochastic climatic events (Millennium Ecosystem Assessment 2005; Gibson 2009). Throughout the degradation process, the vegetation cover is reduced, thus favoring soil erosion and leading to degraded states with little or no chance of recovery (Gibson 2009). In these systems, the vegetation

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recovery is strongly limited by the rangeland management and the capacity of the soil to retain and store water, which depends on several factors such as the soil texture and porosity, depth, and organic matter content (López 2011; Linstädter and Baumann 2013). Soil restoration by means of addition of new material could modify the soil hydrological properties and so abiotic extreme events such as volcanic eruptions may alter the water storage capacity of the soil through tephra deposition over vast areas (Hernández-Moreno, Tejedor, and Jiménez 2007; Le Pennec et al. 2012). In some cases, tephra deposits have been shown to produce a "mulching effect," protecting the soil from water loss through a reduction in evaporation and an increase in infiltration due to its grain size, porosity, and deposit thickness (Hernández-Moreno, Tejedor, and Jiménez 2007; Ayris and Delmelle 2012). The use of tephra as mulch has long been documented and has been shown to increase water use efficiency and yields in arid and semiarid regions (Tejedor, Jiménez, and Díaz 2002; Hernández-Moreno, Tejedor, and Jiménez 2007; Pérez 2009). Thus, it is possible to consider tephra deposition as a soil recovery agent, but it is not known whether Patagonian steppe plant species may benefit from it.

In Argentina, the NW Patagonian steppe region consists of arid and semiarid lands which have suffered serious degradation processes (Del Valle, Elissalde, and Gagliardini 1998; León et al. 1998). The main economic activity in the region is extensive sheep farming on natural pastures, and the high stocking rates historically applied to these systems have led them to different degraded states (Golluscio, Deregibus, and Paruelo 1998). Plant cover reduction (principally in forage species), aeolian erosion caused by strong winds, and a scarce precipitation regime have all resulted in the degradation of the steppe (Paruelo et al. 1998; López et al. 2013). The degraded steppe has lost its water retention capacity, which reduces its chance of recovery (Chartier, Rostagno, and Pazos 2011). In addition, the western Patagonian steppe regions closer to Los Andes mountains have historically been affected by volcanic eruptions, which have sculpted the landscape (Stern 2004). In June 2011, as a product of the eruption of the Puyehue-Cordón Caulle Volcanic Complex (40°34′56″S, 72°06′39.5″W), a surface area of 19,700,000 ha in Río Negro province (northern Patagonia) was covered with a layer of tephra ranging from 0.2 to 30 cm in thickness, depending on the proximity to the volcano (Gaitán et al. 2011). Tephra deposits in the steppe region were between 3 and 5 cm thick and were formed by sand and silt particle sizes with high silica content, no fertilizing properties, but high water retention capacity (Cremona, Ferrari, and López 2011). In spite of the relatively frequent tephra deposition during the last century, approximately six times (SERNAGEOMIN 2015), a minimal amount is known regarding its effect on soil water availability and steppe plants (Ghermandi and González 2012; Ghermandi et al. 2015).

The vegetation of NW Patagonia is composed mainly of perennial tussock grasses and shrubs, whose spatial distribution depends on rainfall, temperature regime, and grazing (Paruelo et al. 1998). When there is minimal or no grazing pressure, *Poa ligularis* (Nees ap. Steud) dominates the grass stratum; whereas, when grazing increases, *Pappostipa speciosa var. speciosa* (Trin. et Rupr.) dominates. This occurs because, among other differences, the latter is less preferred by sheep and is more tolerant to conditions of low water availability (Leva, Aguiar, and Oesterheld 2009; Couso and Fernández 2012) (Table 1). Low water availability alters the plant water status and triggers the initial plant response to drought through stomatal closure, which usually reduces photosynthesis, diminishing carbon fixation and growth (Flexas et al. 2004). Stomatal conductance (g_s)

Table 1. Principal comparative characteristics of the two species studied, *Poa ligularis* and *Pappostipa speciosa*.

	P. ligularis	*P. speciosa var. speciosa*	Source
Physiognomy	Tussock grass 15–45 cm tall Perennial	Tussock grass 30–60 cm tall Perennial	Correa 1978
Distribution	Arid & semiarid Patagonia (*Monte and Patagonia Phytogeographical Province*)	Arid & semiarid Patagonia (*Monte and Patagonia Phytogeographical Province*)	León et al. 1998
Physiology	Acquisitive/mesophytic traits (high relative growth rate and potential for resource capture)	Conservative/xerophytic traits (low relative growth rate, high potential for resource conservation)	Díaz et al. 2004
Above/belowground allocation rate	Higher	Lower	Couso and Fernández 2012
Phenotypic plasticity *(in performance traits)*	Higher	Lower	Couso and Fernández 2012
Tolerance to water shortage	Lower	Higher	Couso and Fernández 2012
Livestock preference	High (*indicative of good rangeland condition*)	Intermediate (*indicative of regular- bad rangeland condition*)	Bonvissuto et al. 1993

reflects stomatal behavior and has been used as a plant water stress indicator (Flexas and Medrano 2002). Therefore, recording plant g_s in greenhouse conditions allows detecting changes in the water status of plants caused by modifications in the soil water availability due to the presence of tephra. Thus, the effects of tephra on g_s may be reflected in plant growth.

The aim of the present study was to evaluate: 1) the effects of Puyehue tephra deposits on soil water retention and conservation; 2) the effects of tephra on the above- and belowground growth and the potential recovery capacity of two dominant forage species of the Patagonian steppe under contrasting water regimes; and 3) the differences in the responses of each species. To this end, we physically characterized tephra deposits and soil and estimated water availability in pots (soil moisture content), stomatal conductance, vegetative growth, and the recovery capacity of stomatal conductance in *P. ligularis* and *P. speciosa var. speciosa*. We hypothesized that, under the same climatic conditions, tephra deposits increase water retention, soil water availability, stomatal conductance, and plant growth. We also expected different responses from the two species: for *P. ligularis*, we expected higher and positive response under high water availability (wet conditions) and lower response under low water availability (dry conditions); whereas, for *P. speciosa*, we expected higher and positive response under dry conditions.

Materials and methods

Description of the area of interest

The Pilcaniyeu Experimental Field of the National Institute of Agricultural Technology, (INTA) (41° 01′ 42″ S, 70° 35′ 21″ W; 1050 m a.s.l.) is located in NW Patagonia, Argentina. The landscape in the area is characterized by plateaus and low hills with a shrubby-grassland steppe where *Poa ligularis* and *Pappostipa speciosa* dominate the grass stratum, and *Mulinum spinosum* Cav. Pers and *Senecio filaginoides* DC dominate the shrub stratum (León et al. 1998). The Pilcaniyeu Experimental Field has been under different grazing intensities, ranging from 0.8 sheep $h^{-1}y^{-1}$ to 40 year enclosures. For this study, the material was collected from a site with a historical use of 0.3 sheep $h^{-1}y^{-1}$ (moderate grazing). Total vegetation cover varies with the use intensity, but a total cover of 40–50% dominates the area, where shrubs cover 10–20% and grasses 20–30% (Bonvissuto et al. 1993). The mean annual temperature is 7.7°C and the mean annual precipitation is 257 mm, occurring mainly during April–September (70%) (Bustos 2006). Mean potential evapotranspiration is 570 mm and reaches its maximum values during November–March, promoting water deficit during the same time (Bustos 2006. Unpublished data from INTA weather station). Soils are shallow, of contrasting texture, with rocky superficial layer and loamy-rocky sub-superficial layer (Lores et al. 1983). Although the tephra deposits in the area are 1.5 to 5 cm thick (Gaitán et al. 2011), layers up to 30 cm thick have been observed in *Mulinum spinosum* leeward (personal observation).

Material collection and physical properties of the soil and tephra deposits

Plants, tephra, and soil were extracted from the steppe at Pilcaniyeu Experimental Field, and transported to the Bariloche Agricultural Experimental Station of INTA (41°08′00″S, 71°18′37″ W; 893 m a.s.l.). Tephra deposits were collected in December 2011, and plants and soil samples were collected in June 2012. The soil was sieved through a 2-mm mesh at the laboratory.

To assess the physical properties of the soil and tephra deposits, the permanent wilting point (PWP, % v/v), field capacity (FC, % v/v), available water and texture (*sensu* Day 1965; Peters 1965) were estimated for both the soil and tephra deposits. In addition, ten 5-L pots were three-quarters filled with soil and pot capacity was determined (PC, % v/v, *sensu* Passioura 2006). PC and PWP were used to define the wet and dry watering regimes (see the following sections).

Effect of the presence of tephra on soil water conservation

To assess the effects of tephra on soil water conservation, a greenhouse assay was conducted as follows. Fifteen 4.5-L pots were filled with a 4.5-cm-thick layer of the soil brought from the field. In five of these pots, the soil layer was covered with a 2-cm-thick tephra layer, while in other five pots the soil was covered with a 6-cm-thick tephra layer. The remaining five pots were filled with soil only. Then, all pots were saturated with 1 L of water and left without water input for 30 days. The soil moisture content (%v/v) in the soil layer was periodically measured with a Time domain reflectometer (TDR, Trime FM, Eijkelkamp) by inserting the sensor horizontally. Finally, the moisture of the soil layer was compared between treatments.

Effect of the presence of tephra on plants under contrasting water regimes

Forty tussocks of *Poa ligularis* and forty of *Pappostipa speciosa var. speciosa* were transplanted from the field to 10-L pots each (Figure 1). As an indicator of health, we chose plants with at least 70% green biomass and 30 cm in diameter (visually assessed). Pots with plants were kept in greenhouse conditions with a weekly watering regime for one year previous to the beginning of the experiments. Following this, from each pot, a 10-cm diameter tussock containing 90% green biomass was transplanted to a 5-L pot

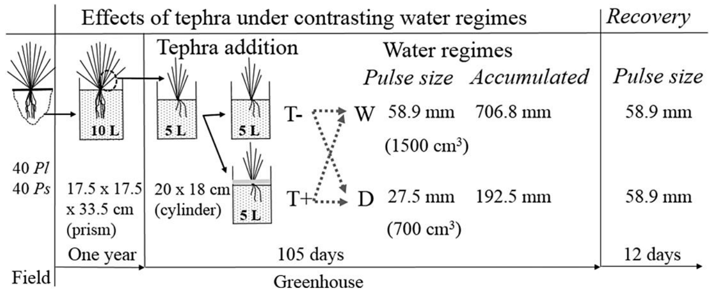

Figure 1. Experimental procedure after plant extraction from the field for *Poa ligularis* (Pl) and *Pappostipa speciosa var. speciosa* (Ps). After plant extraction, each plant was placed in a 10-L pot (length x width x height). To test the effects of tephra under contrasting water regimes, a portion of 10 cm diameter from each plant was placed in a 5-L pot (height x diameter) and a 4-cm tephra layer was randomly added in 20 pots for each species. Water regimes were randomly assigned (wet- W or dry- D). After 105 days, all plants received a final watering pulse to test potential recovery.

three-quarters filled with steppe soil (two-thirds of the pot volume) and irrigated with 1500 cm^3 of water which equals a 58.9 mm pulse. This amount of water was enough to saturate the pot. Four morphologically similar tillers on each plant (two facing north and two facing south) were marked with a metallic colored ring. For each tiller, the number of green leaves was recorded as the initial vegetative values.

Plants of each species (*P. ligularis* and *P. speciosa*) were randomly distributed in two tephra states (absence, *T−*, and presence, *T+*) and two watering regimes (wet, *W*, and dry, *D*). Each treatment had 10 replicates (n = 80). The *T+* treatment consisted of 4 cm of a superficial tephra layer, emulating average tephra deposits on the steppe (Gaitán et al. 2011). The *W* treatment consisted of irrigation pulses with 58.9 mm (1500 cm^3) of water to maintain soil moisture content (% v/v) always above PWP and close to PC (within the water availability range). The moment of watering depended on the decrease in soil moisture, if soil moisture dropped close to PWP, a watering pulse was added. In contrast, in the *D* treatments, soil moisture decreased progressively as the number of days in each deficit period (periods between watering pulses in the *D* treatments) increased, so that values came closer to PWP. This was achieved by alternating watering events of 27.5 mm (700 cm^3) with increasingly long water deficit periods. In this case, the moment of watering depended on the proximity to PWP, increasing the number of days with soil moisture values at PWP. This methodology allowed water to infiltrate the superficial tephra layer and reach the underlying soil, causing gradual water deficit and preventing immediate plant death. One pre-deficit period (period 0) and five deficit periods (1 to 5) were generated with a total length of 105 days from December 2013 to April 2014.

Every 2 days throughout the experiment, soil moisture content (% v/v) was measured with a TDR in five replicates per treatment (n = 40). TDR sensors were inserted vertically into the pot, in the southern side (through the tephra layer), keeping a 5-cm distance from the plant. On the same days, between 10:00 a.m. and 12:00 p.m, g_s (mmol H_2O $m^{-2}s^{-1}$) was recorded with a porometer (SC-1, Decagon Devices Inc., USA) in four fully expanded north-facing leaves in the same plants used for soil moisture content measurements. Measurements were carried out always in the same plants and in random order to avoid any effect related to the time of recording.

Effect of the presence of tephra on the potential recovery capacity of plants

At the end of period 5, a recovery watering pulse of 58.9 mm was applied to all treatments to evaluate g_s recovery capacity in all plants (period 6). Soil moisture content and g_s were also recorded during this period in the aforemention plants.

Finally, at the end of the experiment, 12 days after the recovery watering pulse, we counted the numbers of tillers and green leaves on marked tillers, and the difference with the initial values constituted the vegetative response variables. Then, each plant was divided into the following biomass fractions: a) green aboveground biomass, b) senescent aboveground biomass (yellow), c) roots in tephra, d) superficial roots (up to 5 cm soil depth), and e) deep roots (below 5 cm soil depth). All biomass fractions were oven-dried at 60°C for 7 days. The dry weight of each biomass fraction was then recorded and expressed as a percentage of total plant biomass.

Data analysis

The soil layer moisture values (% v/v) obtained during the water conservation assay for each treatment were fitted applying the model $Y = (Y0 - plateau) * exp(-K*X) + plateau$, where X is time, Y is % v/v, Y0 is the Y value when X is zero, Plateau is the Y value at infinite times and K is the rate constant. The fitting procedure (Motulsky and Christopoulus 2004) was used to compare fitted parameters for the treatments and was performed using the regression analysis in the *Prism 5* software (*GraphPad*, San Diego CA, USA).

For each species, to explain the relation between soil moisture content (% v/v- as x) and plant g_s (as y), we applied the model $y = a + bx^{-1}$ to each level of tephra ($T-$ and $T+$). This model was selected due to its simplicity and best fit (compared to other previously tested models). The fitting procedure (Motulsky and Christopoulus 2004) was used to compare fitted parameters for tephra levels. The adjustment procedure was also performed using the regression analysis in the *Prism 5* software.

For soil moisture content and plant g_s, we first compared the effects of water availability and tephra presence and tested how the species differed by averaging the entire growing season data set through the corresponding factorial model in a completely randomized design throughout the experiment (periods 0 to 5). The error term was adjusted by an autoregressive continuous model due to repeated measurements. This analysis consisted of specific contrast comparisons. Initially, for each species, the effects of water availability and the effects of the presence of tephra within each water availability level were contrasted. Then, species were compared at the same levels of water availability and tephra. Secondly, we repeated the aforementioned contrast comparisons for each deficit period, using in this case for each period, the average value of each plant for the variables soil moisture content and plant gs.

For vegetative response variables, we also compared the effects of water availability and tephra presence and tested how the species differed. In the case of tiller and leaf production, the variables were square root transformed, and the model included a random effect due to subsampling at tiller level. The presence of roots in the tephra layer was only analyzed at a descriptive level.

Data were analyzed using Infostat (Di Rienzo et al. 2015) and *Prism 5* software. An α value of 0.05 was used.

Results

Physical properties of the steppe soil and tephra deposits

Tephra deposits presented a higher mean value of PWP (% v/v) and FC (% v/v) than steppe soil (PWP: 7.3 ± 1.1% and 5.7 ± 1%, FC: 17.4 ± 0.1% and 11.3 ± 1.8%, respectively) and held two-fold higher available water than steppe soil (10.1% vs. 5.5%, respectively). PC (% v/v) was 25 ± 5%. The texture of tephra was finer than that of steppe soil (sandy loam vs loamy sand, respectively). Tephra contained 2.2 ± 0.4% clay, 38.6 ± 7.9% silt, and 54.3 ± 6.1% sand, whereas steppe soil contained 6.7 ± 1.6%, 10.6 ± 1.3%, and 79.3 ± 1.7%, respectively.

Effect of the presence of tephra on soil water conservation

The presence of a tephra layer had a significant effect on soil moisture content. After saturation, the soil in pots covered with tephra layers 2 and 6 cm thick showed less decrease in soil moisture content and reached PWP values approximately 10 days later than the soil without tephra (Figure 2). The models fitted to treatments without ($R^2 = 0.98$) and with tephra differed significantly (*ratio of probabilities tending to infinity*), whereas the models fitted only to treatments with tephra did not differ between the 2 and 6 cm thick layers ($R^2 = 0.96$, *ratio of probabilities* = *6.32*).

Effects of the presence of tephra on plants under contrasting water regimes

The wet water regime (*W*) accumulated a total of 705.8 mm of water (275% of the mean annual precipitation recorded for Pilcaniyeu (Bustos 2006), while the dry regime (*D*) accumulated 192.5 mm (75% or the mean annual precipitation).

The average of the whole growing season showed that the soil moisture mean value for *W* was significantly higher than that for *D*, differing by 8.1% ($p < 0.0001$) and 8.5% ($p < 0.0001$) for *P. ligularis* and *P. speciosa*, respectively (Figure 3). The mean percentage of soil moisture was significantly higher in *W* than in *D* water conditions from period 2 ($p < 0.0001$ for *P. ligularis*; $p < 0.0001$ for *P. speciosa*) to period 5, with $p < 0.0001$ for all

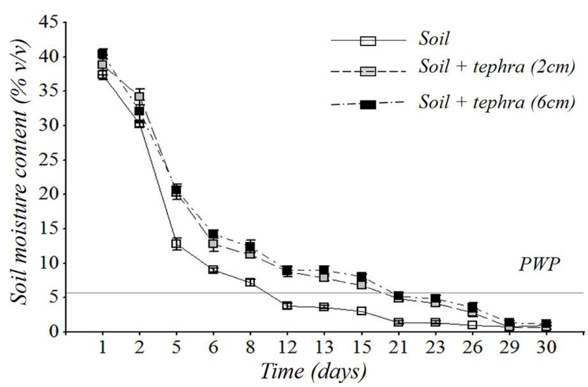

Figure 2. Mean percentage volumetric water content (v/v) and standard error (SE) in soil with and without tephra layer along a 30-day experiment. The horizontal line represents the value of the permanent wilting point (PWP) obtained for this soil.

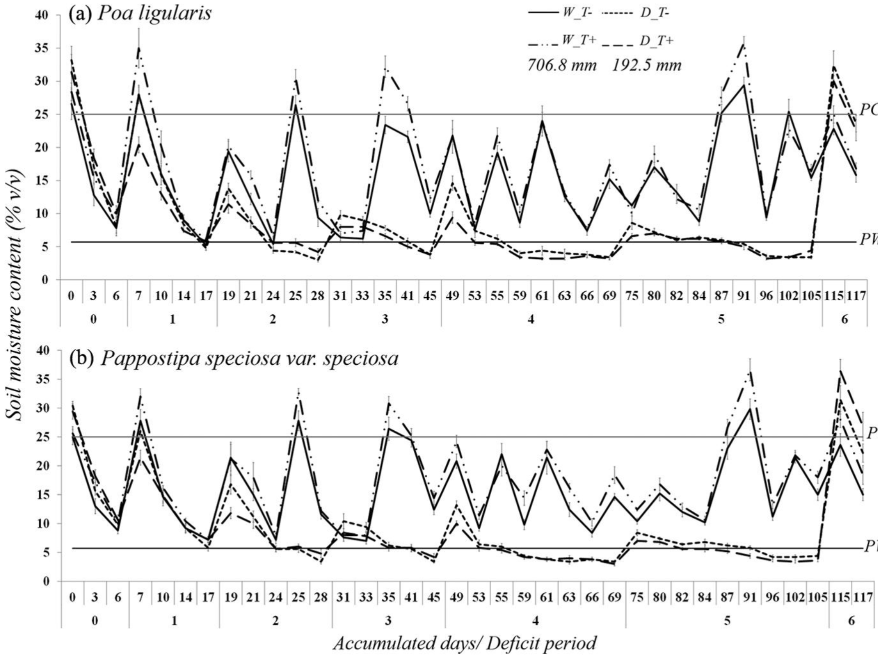

Figure 3. Mean percentage volumetric water content (v/v) and standard error (S.E.) in soil for (a) *Poa ligularis* and (b) *Pappostipa speciosa var. speciosa* in wet (W, 706.8 mm accumulated water) and dry (D, 192.5 mm accumulated water) conditions, and in the absence (T−) and presence (T+) of tephra throughout the experiment. Horizontal lines represent pot capacity (PC- gray, upper) and permanent wilting point (PWP- black, lower) values. The abscissa axis represents the experiment length in days (0-105), the pre-deficit period (0), the deficit periods (1 to 5, inclusive) and the potential recovery period (6).

periods in both species. After the first two periods, all *D* treatments showed average soil moisture values below PC and progressively closer to PWP (Figure 3) up to the final saturation watering (at the beginning of period 6). In the *W* treatments, the average soil moisture was always in the availability range, above PWP, closer to PC and FC (Figure 3). The presence of tephra (*T*+) in *W* conditions was associated with mean soil moisture increases of 2% in *P. ligularis* ($p < 0.0001$) and 2.1% in *P. speciosa* ($p < 0.0001$). No effects of the presence of tephra on the soil moisture content were detected under *D* conditions for either species (Figure 3).

In *P. ligularis*, the presence of tephra was related to higher soil moisture content and g_s relationship (ratio of probabilities tending to infinity), whereas in *P. speciosa*, the presence of tephra was not (ratio of probabilities = 1.28). The R^2 for each model of *P. ligularis* was 0.38 and 0.40 for *T*− and *T*+, respectively (Figure 4a). Estimated curves for each level of *P. speciosa* are shown to visualize their similarity (Figure 4b). For both species, a decrease in g_s was associated with soil moisture values lower than 10%.

Again, the average of the whole growing season showed that both species had significantly higher mean g_s values in *W* than in *D* conditions ($p < 0.0001$), with differences of 102 and 73 mmol $H_2O\ m^{-2}\ s^{-1}$ for *P. ligularis* and *P. speciosa*, respectively. When analyzing these results by deficit periods for both species, these differences were detected from period 2 ($p = 0.0016$ *P. ligularis*, $p < 0.0439$ *P. speciosa*) to period 5, showing decreasing *p* values (Figure 5). Also, the average of the whole growing season showed that

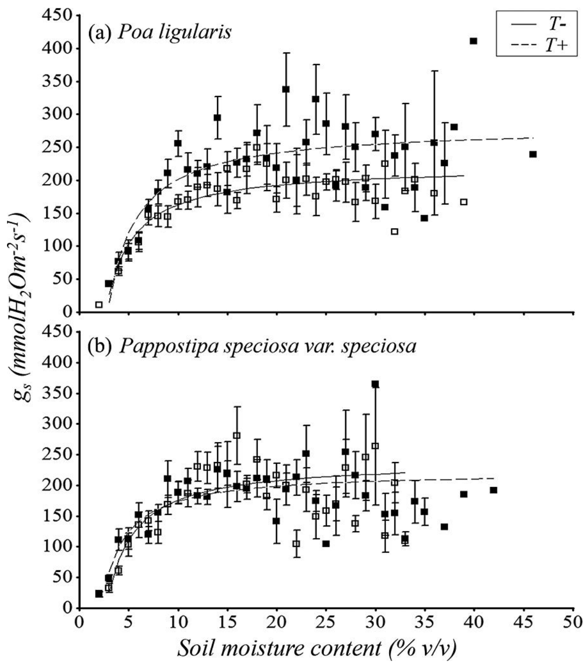

Figure 4. Mean gs values (mmol H_2O m^{-2} s^{-1}) and soil moisture content (%v/v) in plants of (a) *Poa ligularis* and (b) *Pappostipa speciosa var. speciosa* (b). Fitted models for the absence (T−, continuous line) and presence (T+, dashed line) of tephra are shown. Bars indicate SE.

at *W* levels, *P. ligularis* mean g_s was higher in *T*+ than in *T*−, differing by 57.7 mmol H_2O m^{-2} s^{-1} ($p < 0.0001$), which was attributed to differences in periods 2 and 4 ($p = 0.0376$, $p = 0.0061$, respectively) (Figure 5). In *P. speciosa*, no differences due to the presence of tephra were detected when averaging the whole growing season, but by deficit period, in period 2 (under *D*), the mean g_s in *T*+ treatments was 41 mmol H_2O m^{-2} s^{-1} higher than in *T*− treatments ($p = 0.0271$).

Tillering was higher in *W* than in *D* conditions for both species ($p < 0.0001$). *Poa ligularis* produced a mean value of 3.6 ± 0.4 tillers/plant in *W* conditions and a mean value of 1.1 ± 0.1 tillers/plant in *D* conditions, whereas *P. speciosa* produced a mean value of 3.9 ± 0.4 tillers/plant in *W* conditions and a mean value of 1.5 ± 0.2 tillers/plant in *D* conditions. Similarly, leaf production was higher in *W* than in *D* conditions, in both *P. ligularis* ($p < 0.0001$) and *P. speciosa* ($p < 0.0001$). *Poa ligularis* produced a mean value of 16.9 ± 1.5 leaves/tiller in *W* conditions and a mean value of 4.4 ± 0.4 leaves/tiller in *D* conditions, while *P. speciosa* produced a mean value of 22.6 ± 2.22 leaves/tiller in *W* conditions and a mean value of 7.4 ± 0.8 leaves/tiller in *D* conditions. Neither tiller nor leaf production were affected by the presence of tephra in *W* or *D* conditions for either species.

The dry conditions affected senescent and green biomass allocation (Figure 6). The percentage of senescent biomass increased 23.6% in *P. ligularis* ($p < 0.0001$) and 8.2% in *P. speciosa* ($p = 0.0167$), whereas the percentage of green biomass decreased 26.3% in *P. ligularis* ($p < 0.0001$) and 12.1% in *P. speciosa* ($p < 0.0001$). In *W* conditions, the presence of tephra affected senescent and green biomass in *P. ligularis*, reducing senescence by 12.7% ($p = 0.0092$) and increasing green biomass by 10.6% ($p = 0.0073$), whereas in *D* conditions,

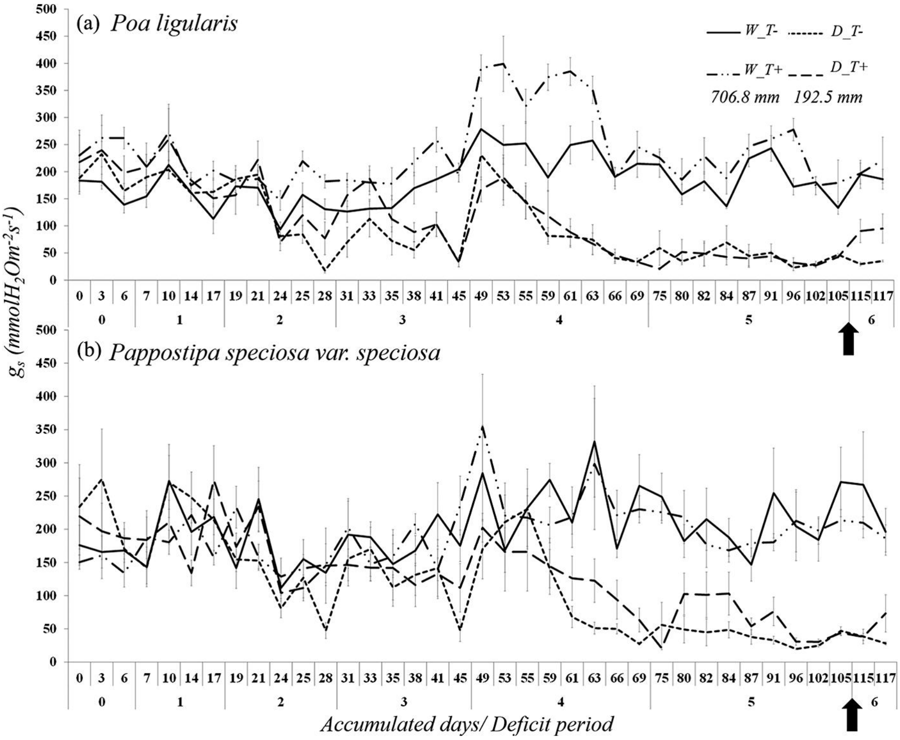

Figure 5. Mean gs values and standard error (SE) in plants of (a) *Poa ligularis* and (b) *Pappostipa speciosa var. speciosa* in wet (W, 706.8 mm accumulated water) and dry (D, 192.5 mm accumulated water) water conditions, in the absence (T−) and presence (T+) of tephra. The abscissa axis represents the experiment length in days (0–117), the pre-deficit period (0), the deficit periods (1 to 5, inclusive) and the potential recovery period (6) with the initial time highlighted by thick black arrows on the x axis.

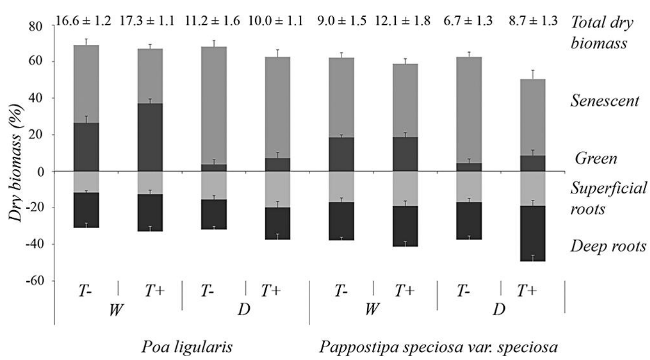

Figure 6. Mean percentage of biomass allocation and standard error (SE) for superficial (up to 5 cm) and deep (below 5 cm) aboveground senescent and green biomass in *Poa ligularis* and *Pappostipa speciosa var. speciosa* in wet (W) and dry (D) water conditions, in the presence (T+) or in the absence of (T−) tephra. Mean total dry biomass and SE (g) values are shown. Roots in the tephra layer were excluded from the graph due to their lower values. Negative values were used for underground traits for easier visualization.

the presence of tephra was associated with 9% and 16% senescent biomass reduction in *P. ligularis* ($p = 0.0628$) and *P. speciosa* ($p = 0.001$), respectively. Green biomass increased in *T+* (3.4% in *P. ligularis* and 4.3% in *P. speciosa*), but the results were not statistically significant (Figure 6).

Neither the dry condition (*D*) nor the presence of tephra (*T+*) affected the superficial or deep root biomass allocation in either species (Figure 6). In *W* conditions, the roots of both species extended into the tephra layer, in eight and two pots for roots of *P. ligularis* and *P. speciosa*, respectively, while in *D* conditions, only *P. ligularis* explored the tephra layer, and only in one pot. *Poa ligularis* produced 0.03 ± 0.02 g under *W* and 0.03 g under *D*, whereas *P. speciosa* produced an average biomass of 0.3 ± 0.05 g only in *W*.

Effect of the presence of tephra on the potential recovery capacity of plants

During the recovery period (period 6) and for each species, the mean g_s value in *D* was lower than that in *W* (*P. ligularis* differed by 137 mmol $H_2O\ m^{-2}\ s^{-1}$ with $p < 0.0001$, and *P. speciosa* differed by 170 mmol $H_2O\ m^{-2}\ s^{-1}$ with $p < 0.0001$, Figure 5). Although in *D* conditions the presence of tephra showed no statistically significant effects, the mean g_s values for the *T+* treatments were almost two-fold higher than those for the *T−* treatments (*P. ligularis* differed by 60 mmol $H_2O\ m^{-2}\ s^{-1}$ and *P. speciosa* differed by 22 mmol $H_2O\ m^{-2}\ s^{-1}$, Figure 5).

Comparisons between species response

Species differed in g_s and senescent and green dry biomass. *Poa ligularis* showed higher mean values than *P. speciosa* in: g_s (a difference of 44 mmol $H_2O\ m^{-2}\ s^{-1}$ in the *W_T+* treatment, Wet level with tephra, $p < 0.0001$), senescent dry biomass (13.5% higher, *D_T+* Dry level with tephra, $p = 0.0058$) and green dry biomass (7.9% higher in *W*, $p = 0.043$). The green dry biomass difference increased by up to 18% in the presence of tephra ($p < 0.0001$). In contrast, *P. speciosa* exceeded *P. ligularis* in deep root dry biomass by 13% in *D_T+* conditions ($p < 0.0004$).

Discussion

In the present study, tephra deposits from Puyehue volcano in the Northern Patagonia steppe presented higher available water than soils, favored water conservation in covered soil, and increased soil moisture by 2% in wet conditions. The latter was related to higher g_s values, decreased senescent biomass, and the growth of roots into this new tephra layer. In addition, the presence of tephra was associated with trends in the g_s recovery of plants previously affected by a dry growing season, with *P. ligularis* more positively affected than *P. speciosa*.

This new fine-textured material differed from the underlying soil texture and favored water conservation in covered soil. Similar effects of the presence of tephra have been reported by Hernández-Moreno, Tejedor, and Jiménez (2007) and Tejedor, Jiménez, and Díaz (2003, 2002). This phenomenon is known as "mulching effect," where the superficial tephra layer interrupts the capillary flow, diminishing the evaporation rate and increasing the soil moisture content (Diaz, Jimenez, and Tejedor 2005; Pérez 2009; Yuan et al. 2009). Although various inorganic materials can be used as "mulch" (Hernández-Moreno, Tejedor, and Jiménez 2007), the higher porosity of tephra may emphasize its water retention and conservation capacity.

The increase in water content caused by the mulching effect of tephra increases plant g_s, decreasing senescence and increasing green biomass, particularly in *P. ligularis*. The increase in water retention of this tephra (Puyehue eruption in 2011) has also been reported in a local field study as a possible cause of the increase in the post-eruption cover of *Poa lanuginosa* Poir. (a perennial and rhizomatous forage grass) in a region of the semi-arid Patagonia (Ghermandi et al. 2015). In other steppe environments in the Northern hemisphere, in a tephra of finer texture (silt loam) from Mount St. Helens, Black and Mack (1986) found an immediate mulching effect as well as several alterations in other parameters of the energy budget, such as an increase in the albedo (reflected solar radiation) and a decrease in the soil surface temperature. This increase in the albedo occurs because the presence of light colored tephra on the soil surface usually affects the soil temperature due to its high silica content, which makes it more light reflective and less absorbent than average soil, promoting a decrease in the underlying soil temperature (Ayris and Delmelle 2012). It is also known that the thermal properties of pumice soils promote an environment with more extreme temperatures near the surface than other common soils (Cochran 1969). The tephra deposited on Patagonian steppes is light colored and has high silica content (Cremona, Ferrari, and López 2011). Thus, we expect alterations in the energy budget. In this sense, Ghermandi et al. (2015) mentioned these alterations as potentially responsible for the reduction in the post-eruption seed bank of steppe plants. To understand the effects of tephra on the energy budget in field conditions, specific studies are required.

The effects of the presence of tephra on soil moisture content were detectable in high water availability conditions but not in dry conditions. Nevertheless, the decrease in senescent biomass detected in both species and the higher plant stomatal conductance observed on days 28 (both species), 45 (only in *P. speciosa*) and at the end of deficit period 4 (Figure 5) may indicate higher soil moisture due to the presence of tephra under dry conditions. The more marked g_s recovery trends (period 6) recorded only on plants with tephra (within dry conditions) may also be indicative of beneficial effects of the presence of tephra. The lack of notorious changes in soil moisture content under dry conditions may be attributable to the fact that evaporation losses occur at high and constant rates when soil moisture is high, but when soil moisture is low, losses by evaporation occur at decreasing rates because water is forced to move as vapor (Diaz, Jimenez, and Tejedor 2005; Yuan et al. 2009). Thus, small changes could have been undetectable during the dry periods. Further studies may consider soil gravimetric water content measurements, which can provide contrastable values with TDR in case small variations in moisture were not detected.

Regarding the differences in species response, in the presence of tephra, *P. ligularis* showed higher stomatal conductance, higher green dry biomass and lower senescence than *P. speciosa*. In the absence of tephra, the difference in green dry biomass between species was smaller. In dry conditions, the presence of tephra favored *P. speciosa* deep root growth. Here, *P. ligularis* demonstrated its higher phenotypic plasticity, higher growth rate and higher potential resource acquisition, while *P. speciosa* exhibited lower growth rate and higher biomass allocation to roots (Table 1). Thus, if these differences, plus the species capacity for root growth in tephra and the stomatal conductance recovery trends detected, are indicative of a concrete response, tephra may promote an increase in species resilience to water shortage periods or capitalize in years with high water availability, increasing growth, plant cover and/or productivity.

Tephra deposits on Patagonian steppe soils combined with abundant rain pulses and proper management practices may trigger positive state transitions which are unlikely to occur under non-tephra conditions, and which lead to vegetation recovery in degraded steppe regions (Westoby, Walker, and Noy-Meir 1989; Paruelo and Golluscio 1994). Patagonian degraded steppe thresholds are associated with soil loss by erosion and water balance alterations, with the consequent loss of key species such as *P. ligularis* (Bonvissuto et al. 1993; López 2011). Therefore, if the species response to the presence of tephra in field conditions is similar to that observed in the present study, we expect to observe the recovery of the *P. ligularis* population first (because of its higher phenotypic plasticity) and that of *P. speciosa* second. We also expect an increase in the stability of the soil-tephra complex due to root growth, with a consequent increase in the resistance to erosion, which may help the system to overcome limiting abiotic thresholds (Briske, Fuhlendorf, and Smeins 2005; López 2011; Bardgett, Mommer, and De Vries 2014).

Although more complex studies should be carried out to reveal the long-term effects of these phenomena in natural ecosystems, it is encouraging to think that tephra deposits generate favorable water conditions that may promote the recovery of vegetation in degraded steppe systems.

Conclusions

It was concluded that the presence of tephra in the soil may favor the recovery of degraded lands, especially in rainy years. The results showed that tephra has more available water than the steppe soil, and that, under greenhouse conditions, the tephra layer has a mulching effect on the steppe soil, which does not differ between 2- and 6-cm-thick layers. In greenhouse conditions, the main Patagonian forage grasses benefited from the presence of a 4-cm-thick tephra layer.

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