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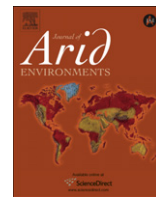
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## Short Communication

Photosynthetic response to different light intensities, water status and leaf age of two *Berberis* species (Berberidaceae) of Patagonian steppe, ArgentinaP.L. Peri<sup>a,\*</sup>, M. Arena<sup>b</sup>, G. Martínez Pastur<sup>b</sup>, M.V. Lencinas<sup>b</sup><sup>a</sup>Universidad Nacional de la Patagonia Austral-Instituto Nacional de Tecnología Agropecuaria-Consejo Nacional de Investigaciones Científicas y Técnicas (UNPA-INTA-CONICET), cc 332 (CP 9400) Río Gallegos, Santa Cruz, Argentina<sup>b</sup>Centro Austral de Investigaciones Científicas (CADIC-CONICET) Ushuaia, Tierra del Fuego, Argentina

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## ABSTRACT

Net photosynthetic rate ( $A$ ) and stomatal conductance ( $g_s$ ) from leaves of *Berberis buxifolia* and *Berberis heterophylla* saplings were measured under different conditions of radiation and water availability and for leaves of different ages. Comparative studies of basic physiological performance would give insight how these shrubs survive and grow under this austral extreme ecosystem. *B. buxifolia* had higher  $A$  values than *B. heterophylla* for all light intensities measured. Values of  $g_s$  for both *Berberis* species also declined as light intensity decreased. There was a negative relationship between  $A$  and water stress expressed as pre-dawn leaf water potential ( $\psi_{lp}$ ) where the reduction in  $g_s$  was the main factor that reduced  $A$  in both species. Also,  $A$  and  $g_s$  of *Berberis* plants increased rapidly during the first days after leaf unfolding, reached a maximum value when the leaf was completely expanded, and then declined. These results could be used to estimate the responses of saplings to environmental conditions under the dynamic of natural stands in this austral extreme ecosystem and for restoration plans.

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## 1. Introduction

*Berberis buxifolia* Lam. and *Berberis heterophylla* Juss. (Berberidaceae) are two thorny shrubs native to Southern Patagonia (Argentina). The phenology, growth and fruit production of *Berberis* plants has been previously reported in natural populations where new leaf emergence and full flower occur in early and mid-spring, respectively (Arena et al., 2003). Their edible purple fruits are eaten either raw or made into marmalade, jams and infusions. These fruits are now considered as an alternative source of essential organic and inorganic nutrients, alkaloids (berberines) and also considered for their nutraceutical properties as functional foods that give additional health benefits and tinctorial applications (Arena and Curvetto, 2008).

The understanding of ecophysiological traits such as photosynthesis provides important information of how ecosystems may respond to climate variability. In the Patagonian steppe ecosystem, water is the main factor controlling plant physiological processes and growth (Jobbágy and Sala, 2000). Comparison of ecophysiological performance between *Berberis* shrub species may indicate differences in plant tolerance and acclimation to drought and light conditions.

Leaf photosynthesis of shrubs can be influenced by many plant factors such as leaf age, leaf position and mutual shading, as well as environmental factors such as light, temperature, and water and nutrient availability (Field and Mooney, 1983). Plant establishment and growth of these *Berberis* species are strongly coupled to soil water availability due to root competition between saplings and the presence of established vegetation. While *B. heterophylla* grows mainly on drier sites of the Patagonian steppe, *B. buxifolia* often grows in better soil water availability conditions such as in coastal scrub, *Nothofagus* forest margins and clearings, moister areas in grass steppe, and along streams and rivers (Correa, 1984; Moore, 1983). In this context, plant response to soil water status may play an important role in the distribution of these species.

When considering the environmental physiology of shrubs, solar radiation is of special importance due to its role as a source of energy that drives the biological production of dry matter (Peri and Lasagno, 2006) and consequently fruit yield. In field environments plants can experience frequent fluctuations in irradiance from full sun to shade caused by shading within canopy (Knapp and Smith, 1987). However, the physiological adaptability of leaves to different light conditions within the canopy for *Berberis* plants has received little attention.

In addition, species with extended lifespan, such as *B. buxifolia* and *B. heterophylla*, has advantages for carbon balance and

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nutrient-use efficiency in limited resource environment (Reich et al., 1991). However, photosynthetic capacity of a leaf generally decline after full expansion (Kitajima et al., 2002), caused by a redistribution of nitrogen to other plant parts, a decrease in  $g_s$  and chlorophyll content, or changes in anatomical structures during the ageing process (Field and Mooney, 1983; Xie and Luo, 2003). Information related to photosynthetic capacity during ageing of leaves is necessary to estimate the long-term carbon budget of the whole shrub canopy. However, there are no antecedents focused on leaf age of *Berberis* shrubs influencing photosynthesis. Therefore, investigation of leaf photosynthetic responses to both light and water availability, and leaf ageing will reveal the potential for abiotic and plant regulation of *Berberis* saplings regeneration and ecology. In this study, the focus is on *Berberis* saplings where plants experience sunlight fluctuations and different soil water conditions similar to those likely to be experienced in the native steppe ecosystem. Therefore, the aim was to evaluate the effect of light intensity, water stress and leaf age on net photosynthesis and stomatal conductance of individual leaves of the two major *Berberis* species in these austral extreme ecosystems.

## 2. Materials and methods

Four-year-old saplings (mean height of  $400 \pm 11$  mm) of *B. buxifolia* from an area located near Ushuaia, Tierra del Fuego ( $54^\circ 48' S$ ,  $68^\circ 19' W$ ) and *B. heterophylla* from El Calafate area, Santa Cruz ( $50^\circ 19' S$ ,  $72^\circ 23' W$ ) were grown in a nursery located in San Carlos de Bariloche ( $41^\circ 08' S$  and  $71^\circ 19' W$ ). Saplings were grown in 4-L pots containing a mix of peat (50%), coarse sand (10%) and clay-loam soil (40%). The mean monthly temperature during the growing seasons (September–April) ranged from  $6.1^\circ C$  to  $16.2^\circ C$  with a mean maximum monthly temperature of  $23.2^\circ C$ . The N content of leaves determined using the micro-Kjeldahl technique after net photosynthesis measurements was  $16.2 \pm 2.6$  and  $12.8 \pm 1.8$  mg N g<sup>-1</sup> for *B. buxifolia* and *B. heterophylla*, respectively. Samples were dried in a forced draft oven at  $65^\circ C$  for 48 h and grounded in a mill containing a 1 mm stainless steel screen. The leaf area and dry weight values of individual leaves were used in the calculation of the specific leaf area (SLA). The SLA was  $7.2 \pm 0.4$  and  $5.6 \pm 0.7$  m<sup>2</sup> kg<sup>-1</sup> DM for *B. buxifolia* and *B. heterophylla*, respectively.

Net photosynthesis ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) and  $g_s$  to water vapour ( $\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$ ) were measured simultaneously in an open infrared gas analysis system (IRGAs) with the “LiCor 6200 Portable Photosynthesis System” instrument (Lincoln, Nebraska, USA). Measurements were taken at midday  $\pm 1$  h on sunny days during several days in December 2002–January 2003 and on sunlit leaves of the upper canopy level of samplings.

Pre-dawn leaf water potential ( $\psi_{lp}$ ) was measured on the same day as photosynthesis measurements. Values for  $\psi_{lp}$  were obtained from a random sample of the youngest fully expanded leaves with a pressure chamber (Model 1002, PMS Instrument Co., Corvallis, Oregon, USA).

### 2.1. A and $g_s$ responses to light intensity

Forty well-irrigated whole saplings of each species were exposed for 60 min for each of eight light intensities: 20, 150, 250, 500, 750, 1000, 1500 and 2200 (full sun condition)  $\mu\text{mol m}^{-2} \text{ s}^{-1}$  PPFD before measurements of instantaneous photosynthetic and stomatal conductance ( $g_s$ ) responses to light intensity when a steady-state was reached. The light intensities were chosen to cover the range of light conditions that leaves can experience by shading within the canopy of *Berberis* plants growing in the field (Peri and Lasagno, 2006). The experiment was arranged in

a completely randomised single-sapling plot design, and each treatment (light intensity) contained five plants of each species. Different black shade clothes which covered a  $2.3 \times 1.8$  m area supported horizontally on a vertically adjustable metal frame were used to provide shading. Light intensity was monitored with quantum sensors installed above and below the shade source and recorded every 5 min. The photosynthesis rate and  $g_s$  were measured on a random sample of the youngest fully expanded intact sunlit leaves located on top of the main stem of each sapling. All measurements were taken when water (pre-dawn leaf water potential  $-0.01$  to  $-0.12$  MPa) and temperature ( $18$ – $23^\circ C$ ) were not limiting.

### 2.2. A and $g_s$ responses to water status

Twenty plants of each species were selected for measurements of instantaneous photosynthetic rate and  $g_s$  responses to water stress. The experiment was set up with two water availability treatments in a completely randomised single-sapling plot design ( $n = 10$ ). The treatments were: (i) well-watered saplings where soil water content was maintained near field capacity throughout the experiment (pre-dawn leaf water potential  $-0.01$  to  $-0.12$  MPa), and (ii) saplings which were left unwatered until negative net photosynthesis values occurred. The aim of this experiment was to cover the water status range that plants can experience in the Patagonian steppe where the precipitation/potential evapotranspiration ratio, on an annual basis, ranged between 0.06 and 0.20 (Paruelo and Sala, 1995). The photosynthesis rate and  $g_s$  were measured on a random sample of the youngest fully expanded intact sunlit leaves when temperature ( $18$ – $23^\circ C$ ) was not limiting and in full sun conditions ( $1600$ – $2000 \mu\text{mol m}^{-2} \text{ s}^{-1}$  PPFD).

### 2.3. A and $g_s$ responses to leaf age

Another twenty-five plants of each species were selected for measurements of instantaneous photosynthetic rate and  $g_s$  responses to leaf age. The experiment was arranged in a completely randomised single-sapling plot design, and each treatment (leaf age) contained five plants of each species. Leaves on main branch of each sapling were tagged for leaf age measurements. Leaf age was determined as the number of days after the leaflet unfolded. Leaf photosynthesis and  $g_s$  were measured at different ages (5, 15, 30, 45 and 60 days after the leaflet unfolded) on a random sample of intact sunlit leaves located on top of the main stem avoiding shading of older leaves. All measurements were taken when temperature ( $18$ – $23^\circ C$ ) and water (pre-dawn leaf water potential  $-0.01$  to  $-0.12$  MPa) were not limiting and in full sun conditions ( $1700$ – $2000 \mu\text{mol m}^{-2} \text{ s}^{-1}$  PPFD).

Immediately after photosynthesis measurements, each leaf was harvested to measure its area. Then, leaf samples were oven-dried to determine N content on area basis ( $N_a$ ) by using the micro-Kjeldahl technique. From these, photosynthetic nitrogen use efficiency ( $A/N_a$ ) was calculated.

### 2.4. Data analysis

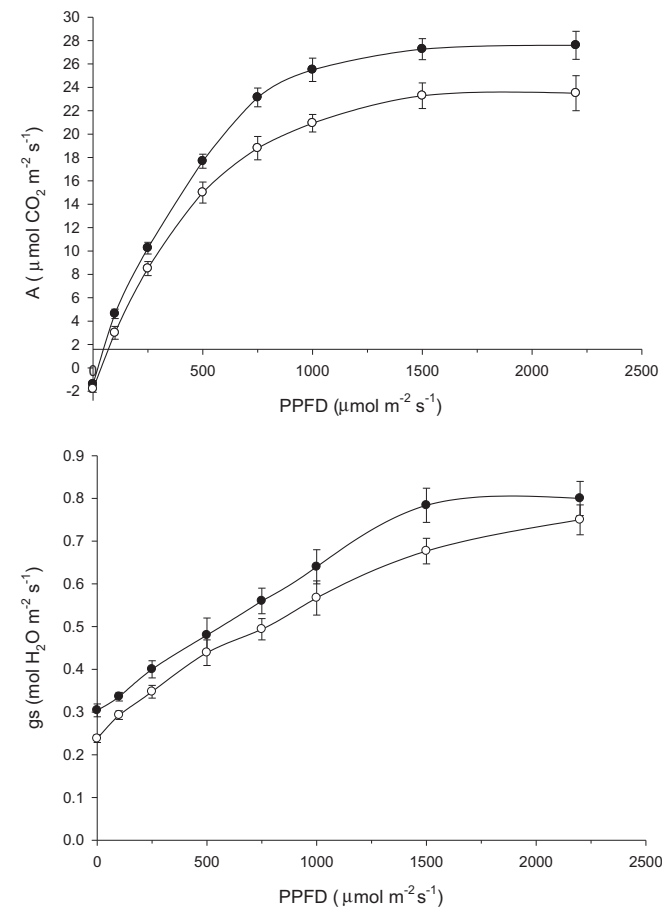
Overall, 200 photosynthesis and  $g_s$  measurements were taken. Of these: 80 were used to quantify the responses to light intensity, 70 for the responses to water stress, and 50 for the leaf age response. Statistical analyses were carried out using the Genstat statistical package (GENSTAT 5 1997). Standard error of means (s.e.m.) was used to evaluate least significant differences (Lsd) at the 0.05 probability level for mean separation of the studied variables.

### 3. Results

#### 3.1. Net photosynthetic rate (A) and stomatal conductance (gs) responses to light intensities

The photosynthetic rate of individual *Berberis* leaves decreased as a function of PPFD from high to low light intensities (Fig. 1). *B. buxifolia* had higher A values ( $p < 0.01$ ) than *B. heterophylla* for most of light intensities measured. The maximum A values were 27.6 and 23.5  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  saturated at 1500  $\mu\text{mol m}^{-2} \text{ s}^{-1}$  PPFD for *B. buxifolia* and *B. heterophylla*, respectively. From this, as shade increased net photosynthesis decreased ( $p < 0.01$ ). For example, from 1500 to 100  $\mu\text{mol m}^{-2} \text{ s}^{-1}$  PPFD, A decreased from its maximum value to 4.6 and 3.1  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  for *B. buxifolia* and *B. heterophylla*, respectively. The light compensation point for *B. buxifolia* was lower (25  $\mu\text{mol m}^{-2} \text{ s}^{-1}$  PPFD) compared with *B. heterophylla* with a mean value of 66  $\mu\text{mol m}^{-2} \text{ s}^{-1}$  PPFD. The photosynthetic efficiency also showed differences between species being 0.021 and 0.016  $\mu\text{mol CO}_2 \mu\text{mol PPFD}^{-1}$  for *B. buxifolia* and *B. heterophylla*, respectively.

Values of  $g_s$  for both *Berberis* species also declined ( $p < 0.01$ ) as light intensity decreased (Fig. 1). The maximum  $g_s$  values were 0.79 and 0.73  $\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$  at high light intensities (1500–2200  $\mu\text{mol m}^{-2} \text{ s}^{-1}$  PPFD) for *B. buxifolia* and *B. heterophylla*, respectively. From this, the rate of  $g_s$  decline was similar between species (0.0005  $\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1} / \mu\text{mol m}^{-2} \text{ s}^{-1}$  PPFD). There was

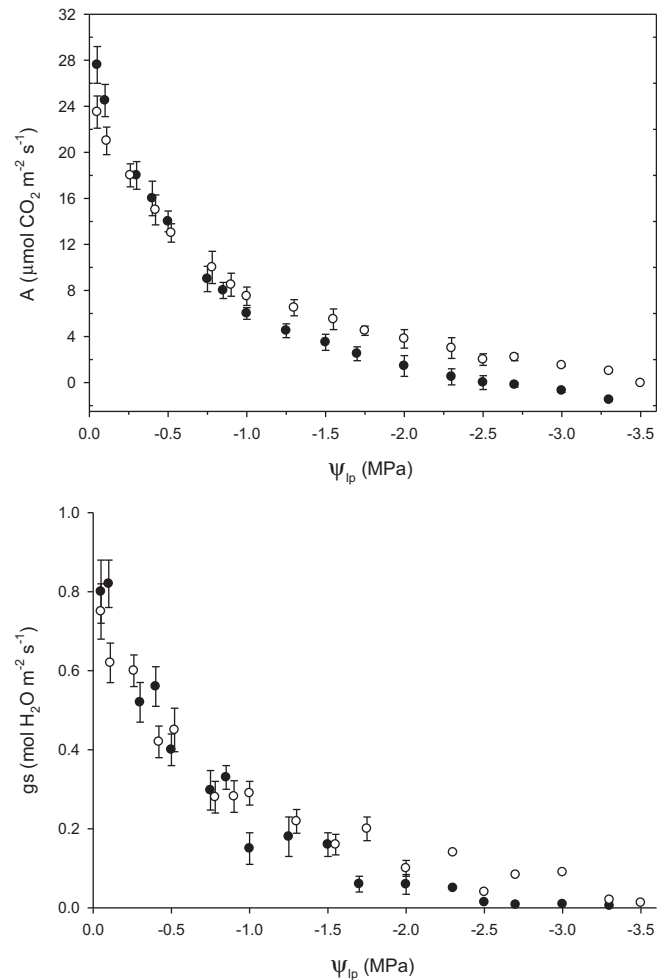


**Fig. 1.** Net photosynthesis rate (A) and stomatal conductance ( $g_s$ ) measured at different light intensities (photosynthetic photon flux density, PPFD) for *Berberis buxifolia* (●) and *Berberis heterophylla* (○) leaves. Bars indicate standard error of the mean (s.e.m.).

a positive relationship between A and  $g_s$  in response to different light intensities (data not shown). However, values of  $g_s$  close to 0.2–0.3  $\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$  were related to negative values of A.

#### 3.2. A and $g_s$ responses to water stress

Values of  $\psi_{lp}$  ranged from –0.05 MPa to –3.3 and –3.5 MPa for *B. buxifolia* and *B. heterophylla*, respectively. There was a negative relationship between A and  $\psi_{lp}$  and between  $g_s$  and  $\psi_{lp}$  (Fig. 2). The maximum value of A of 27.5  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  and 0.79  $\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$  of  $g_s$  for *B. buxifolia* were measured at –0.05 MPa. From this point, A decreased at the rate of 1.14  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  per 0.1 MPa of  $\psi_{lp}$  and  $g_s$  at the rate of 0.032  $\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$  per 0.1 MPa (Fig. 2) as water stress increased down to –2.5 MPa. In contrast, *B. heterophylla* showed lower ( $p < 0.01$ ) values of A and  $g_s$  under no limiting conditions (irrigated plants) compared with *B. buxifolia*, but declined smoothly as water stress increased. Thus, the maximum value of A for *B. heterophylla* of 23.4  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  at –0.05 MPa decreased at the rate of 0.69  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  per 0.1 MPa of  $\psi_{lp}$  down to –3.4 MPa (Fig. 2). Similarly, the maximum value of  $g_s$  of 0.73  $\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$  declined at the rate of 0.022  $\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$  per 0.1 MPa (Fig. 2). Then, A reached a negative value from –2.6 MPa for *B. buxifolia* and from –3.4 MPa for *B. heterophylla*.



**Fig. 2.** Response of leaf net photosynthesis rate (A) and stomatal conductance ( $g_s$ ) to water stress expressed as pre-dawn leaf water potential ( $\psi_{lp}$ ) for *Berberis buxifolia* (●) and *Berberis heterophylla* (○) measured under non-limiting temperature and PPFD conditions. Bars indicate standard error of the mean (s.e.m.).

Least squares regression analysis showed a positive linear relationship between  $g_s$  and  $A$  for changes in  $\psi_{lp}$  with a coefficient for the slope of 0.97 for both *Berberis* species (data not shown). The negative ordinate axis intercept values showed that values of  $g_s$  close to zero were related to negative values of  $A$ .

### 3.3. $A$ and $g_s$ responses to leaf age

Net photosynthesis and  $g_s$  of *Berberis* plants increased ( $p < 0.01$ ) rapidly during the first 30 days after leaf unfolding (Table 1). Net photosynthesis and  $g_s$  reached a maximum value when the leaf was completely expanded (at 30 days for *B. buxifolia* and 45 days for *B. heterophylla*), and then declined. Photosynthetic nitrogen use efficiency ( $A/N_a$ ) increased ( $p < 0.01$ ) until full expansion and then decreased with leaf age in both species, being slightly more steeply in *B. heterophylla* than *B. buxifolia* after 60 days from the date on which the leaf unfolded (Table 1).

## 4. Discussion

The photosynthetic rate of individual leaves of both *Berberis* species decreased as a function of the PPFD from high to low light intensities level (Fig. 1). This was consistent with data found by Xu et al. (2007) who reported for *Berberis thunbergii* an increment in the rate of net photosynthesis from 1.8–2.1 to 13.4  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  at 40 and 608 PPFD  $\mu\text{mol m}^{-2} \text{ s}^{-1}$ , respectively. *B. buxifolia* had a higher net photosynthesis than *B. heterophylla* over the range of PPFD (Fig. 1). These maximum values of  $A$  for *B. buxifolia* can be due to a higher N investment in different proteins related to photosynthesis such as RuBisCO activity and light harvesting complex (Field and Mooney, 1986) which is consistent with higher leaf N concentration. The minimum value of  $A$  for plants of both species exposed at 100  $\mu\text{mol m}^{-2} \text{ s}^{-1}$  PPFD was around 95% lower than those exposed at full sunlight conditions (Fig. 1). A reduction in  $g_s$  occurred under low light and this would explain the differences in the rate of decrease in  $A$  (Tinoco-Ojanguren and Percy, 1993). However, the rate of  $g_s$  limitation occurred slower than the  $A$  reduction rate, and  $A$  reached negative values when leaf stomata still appear partially opened (values of  $g_s$  close to 0.2–0.3  $\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$ ). This indicates that factors other than stomatal closure, such as biochemical limitations, caused the reduction in  $A$  under shade conditions.

The rate of decrease in  $A$  under different shade intensities could be used as physiological indicators to define shade-tolerant species from a physiological perspective. Thus, species with a slow decrease in  $A$  when exposed to shade, a lower light compensation point and a higher photosynthetic efficiency, would be classified as

more shade-tolerant because they would increase the carbon photosynthetic gain. Thus, *B. buxifolia* was more 'shade-tolerant' from a physiological perspective compared to *B. heterophylla*. In a shrub plant, light distribution will therefore affect whole plant carbon gain by affecting the PPFD available for individual leaves within the canopy. Peri and Lasagno (2006) reported that the light transmission patterns within a *Berberis* canopy determined an increase of mean light transmittance from 1% at 0.12 m height from soil level to over 80% at 1.0 m height. However, understanding the ecological significance of photosynthesis as a function of PPFD requires an integrated knowledge of foliar anatomy, the morphology and architecture (branch and leaf angles) of mature *Berberis* shrubs that affects light interception capacity and therefore whole-canopy photosynthesis level.

There was a negative relationship between  $A$  and the water status of the plants expressed as pre-dawn leaf water potential ( $\psi_{lp}$ ). Effects of water stress on  $A$  can be caused by stomatal and non-stomatal factors. In the present study, the reduction in stomatal conductance to water vapour was the main factor that reduced  $A$  in both species (Fig. 2). Chaves (1991) confirmed that moderate water deficit stress reduces photosynthesis primarily by inducing stomatal closure. This stomatal behaviour confirms that both species had shown a drought avoidance response to water stress rather than a stress tolerance response through osmotic adjustments. However,  $g_s$  does not respond to changes in leaf water potential until a critical threshold level is reached. In the present study, this was confirmed when  $A$  reached a negative value from  $-2.6 \text{ MPa}$  for *B. buxifolia* and from  $-3.4 \text{ MPa}$  for *B. heterophylla* with positive values of  $g_s$ . This indicated that total respiration was higher than photosynthesis under severe water stress and highlights that non-stomatal factors were limiting  $A$ . The better response to water stress of *B. heterophylla* compared with *B. buxifolia* can be attributed to a less responsiveness stomatal closure (Fig. 2) and also to a lower value of SLA which is related to a greater concentration of structural constituents (abundant sclerenchyma and bigger vascular bundles) and thicker cuticle (Landberg and Gower, 1997).

Net photosynthesis and  $g_s$  of both *Berberis* species increased rapidly reaching a peak when the leaf was completely expanded, and then declined as the leaf ages. Stomatal conductance has been one cause of changes in  $A$  with leaf age. Several studies have shown that the decline in  $A$  with leaf age is associated with a reduction in  $g_s$  (Lin and Ehleringer, 1982; Xie and Luo, 2003). The increase of  $A$  for full expanded leaves has been attributed to biochemical changes such as an increase in the total number and the production of fully developed chloroplasts (Leech and Baker, 1983). Reductions in  $A$  as leaves age have been associated to reductions in both total leaf chlorophyll content, enzymes concentration involved in photosynthetic reactions and chloroplast membrane composition (Lin and Ehleringer, 1982). In the present work, photosynthetic nitrogen use efficiency ( $A/N_a$ ) increased until full expansion and then decreased with leaf age in both species, and this may contributed to the changes of photosynthetic capacity with leaf age. The decrease in  $A/N_a$  with leaf age has been observed previously (Field and Mooney, 1983; Kitajima et al., 2002).

The relationship between  $A$  and  $\psi_{lp}$  and between  $g_s$  and  $\psi_{lp}$  are physiological variables that can assist to understand the ecological and geographical distribution of shrub species. In Patagonia, precipitation (and therefore soil water availability) is one of the main factors that affect net primary production, and determine the spatial pattern of vegetation and the distribution of life forms at regional level (Jobbágy and Sala, 2000). Bertiller et al. (2006) reported that the shifting of species and life forms across a humidity gradient in Patagonia was related to a shifting in leaf traits related to carbon fixation. In this context, *B. heterophylla*

**Table 1**

The effect of leaf age on net photosynthesis rate ( $A$ ), stomatal conductance ( $g_s$ ) and photosynthetic nitrogen use efficiency ( $A/N_a$ ) of *Berberis buxifolia* and *B. heterophylla*. Leaf age was determined as the number of days from the date on which the leaflet unfolded. Between brackets standard error of means (s.e.m.) are presented.

Species	Age of leaf (day)	$A$ ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ )	$g_s$ ( $\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$ )	$A/N_a$ ( $\mu\text{mol CO}_2 \text{ g N}^{-1} \text{ s}^{-1}$ )
<i>B. buxifolia</i>	5	1.2 (0.12)	0.28 (0.03)	13.8 (1.44)
	15	9.4 (0.85)	0.55 (0.06)	15.1 (1.64)
	30	27.5 (1.82)	0.75 (0.08)	17.1 (1.82)
	45	20.1 (1.24)	0.54 (0.04)	11.2 (1.13)
	60	14.2 (1.02)	0.35 (0.03)	9.2 (1.01)
<i>B. heterophylla</i>	5	0.8 (0.09)	0.18 (0.02)	14.6 (1.33)
	15	12.3 (0.15)	0.25 (0.03)	15.5 (1.44)
	30	20.5 (0.16)	0.61 (0.07)	16.9 (1.81)
	45	23.6 (0.25)	0.65 (0.07)	18.4 (1.46)
	60	18.1 (0.14)	0.42 (0.05)	12.7 (0.09)

showed to be more adapted to water stress than *B. buxifolia* from photosynthesis performance and because showed higher SLA which is related to leaf thickness, thick cell walls and wax deposits characteristic traits of species living in regions with water shortage. Thus, the results highlighted that *B. heterophylla* may have competitive advantages to grow in harsh conditions (dry sites) compared with *B. buxifolia*. However, *B. buxifolia* showed higher values of  $A$  and  $g_s$  under no limiting water conditions and under shade being a specie with better competitive ability to grow on more moist soil sites or as an understorey specie growing in forest floor. These features are consistent with the natural spatial distribution of these species in Patagonian, where *B. heterophylla* grows mainly on drier sites of the Patagonian steppe and *B. buxifolia* often grows in better soil water availability conditions and in *Nothofagus* forest margins and clearings (Moore, 1983).

Finally, results from the present study can assist active restoration plans with native species in large degraded areas of Patagonia to restore environmental services ( $CO_2$  fixation, clear water, biodiversity, landscape, and recreation). The response of  $A$  to water status from the present work can be used to estimate the response of *B. buxifolia* and *B. heterophylla* saplings related to the degraded sites suitable to be restored. However,  $\psi_{lp}$  is a state variable which is difficult to obtain from field measurement. A solution to this practical limitation would be the use of a water basis model which predicts plant water potential based on the masses of water in soil, root and shoot, and processes of rainfall, drainage and evapotranspiration.

We conclude that *B. buxifolia* has a higher net photosynthesis than *B. heterophylla* over the range of PPFD when water is no limiting indicating that *B. buxifolia* saplings can grow better with denser canopies. The relationship between  $A$  and  $\psi_{lp}$  and between  $g_s$  and  $\psi_{lp}$  are physiological variables that can assist to understand the ecological and geographical distribution of *Berberis* shrub land. The photosynthetic characteristics of *Berberis* leaves found in this manuscript related to light, water stress and leaf age could be used to estimate the responses of saplings to environmental conditions under the dynamic of natural stands and for restoration plans. However, future studies may include the effect of any potential interactions between light, water stress and leaf age on net photosynthesis for *B. buxifolia* and *B. heterophylla* leaves.

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