

Leaf growth dynamics in four plant species of the Patagonian Monte, Argentina

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Abstract Studying plant responses to environmental variables is an elemental key to understand the functioning of arid ecosystems. We selected four dominant species of the two main life forms. The species selected were two evergreen shrubs: *Larrea divaricata* and *Chuquiraga avellanadae* and two perennial grasses: *Nassella tenuis* and *Pappostipa speciosa*. We registered leaf/shoot growth, leaf production and environmental variables (precipitation, air temperature, and volumetric soil water content at two depths) during summer-autumn and winter-spring periods. Multiple regressions were used to test the predictive power of the environmental variables. During the summer-autumn period, the strongest predictors of leaf/shoot growth and leaf production were the soil water content of the upper layer and air temperature while during the winter-spring period, the strongest predictor was air temperature. In conclusion, we found that the leaf/shoot growth and leaf production were associated with current environmental conditions, specially to soil water content and air temperature.

Keywords Air temperature · Arid zones · Precipitation · Root system · Soil water content

Introduction

Studying plant responses to climatic variables is an elemental key to understand the functioning of terrestrial ecosystems (Akpo 1997). An understanding of the responses of growth to precipitation and other climatic variables is critical for linking water pulse use to community dynamics (Snyder et al. 2004). In arid zones, precipitation is the major abiotic factor limiting plant growth (Noy Meir 1973). However, some authors highlighted that the duration of the growing period in some species was relatively independent of precipitation (Díaz and Grana-dillo 2005; Myers et al. 1998). Moreover, the availability of water in soil is more intimately related to foliage than precipitation (Ghazanfar 1997; Olivares and Squeo 1999; Peñuelas et al. 2004; Shackleton 1999). Nevertheless, other climatic variables such as air temperature and photoperiod have also been recognized as factors that could influence growth (Abd El-Ghani 1997; Pavón and Briones 2001). Furthermore, considering that global climate change leads to global warming and also may result in changes in precipitation distribution and pattern it is important to understand how foliage are related to climatic variables (Cheng et al. 2006; Easterling et al. 2000).

Plants vary widely in their phenological behavior according to morphological traits related to resource acquisition and conservation (Bertiller et al. 1991). In the Patagonian Monte, previous phenological studies highlighted that besides the peak of growth in spring there was another peak during late summer, depending on the year (Bisigato and López Laphitz 2009; Campanella 2009). Since leaf dynamics of species provides knowledge on the availability of forage resource, it is of main importance for livestock management knowing how leaf dynamics is related to environmental variables. We assessed leaf/shoot

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growth and leaf production in coexisting species during winter-spring and summer-autumn periods, and we also analyzed the environmental variables related to them.

Methods

Study site and species selected

The study was undertaken in La Esperanza Wildlife Refuge (42°7'43.92"S; 64°57'40.99"W), located in northeastern Chubut Province, Argentina. The average annual precipitation across the area is 200 mm. Soils are a complex of Typic Petrocalcids-Typic Haplocalcids (Soil Survey Staff 1999) with a fractured calcium carbonate layer from 0.45 to 1 m below the soil surface (del Valle 1998). Soil texture types (USDA) are sandy or loamy sand (Rossi and Ares 2012) and volumetric soil moisture at field capacity is c.a. 25 % (Bisigato and Bertiller 1999; Rostagno et al. 1991). The vegetation is a tall shrubland covering 40–60 % of the soil surface, characteristic of the southern Monte (León et al. 1998) (Fig. 1).

We selected four dominant species of the two main life forms. The species selected were two evergreen shrubs: *Larrea divaricata* Cav. and *Chuquiraga avellanadae* L. and two perennial grasses: *Nassella tenuis* (Phil.) Barkworth and *Pappostipa speciosa* (Trin. & Rupr.) Romasch.

Climatic conditions

We registered daily precipitation, maximum and minimum air temperature, and volumetric soil water content (10HS moisture capacitance/frequency domain sensor, Decagon Devices with an accuracy of ± 2 %) at two depths (5 and



Fig. 1 The tall shrubland vegetation characteristic of the southern Monte

30 cm) with an automatic data recorder (21X Micrologger, Campbell Scientific) located at the study site.

Leaf/shoot growth and new leaf production

We randomly selected ten isolated plants of each focal species. Measurements were carried out during summer-autumn (January 5–May 4, 2010) and winter-spring periods (June 29–December 14, 2010). We registered shoot growth and the number of new leaves in three randomly selected terminal branches per plant ($n = 10$ plants per species) of *L. divaricata* and *C. avellanadae*. The terminal branches selected were tagged immediately below the apical bud. In the case of grasses (*N. tenuis* and *P. speciosa*), we randomly selected three tillers per tussock ($n = 10$ tussocks per species) and registered leaf growth and the number of new leaves per tiller. Summer-autumn measurements were carried out at 3, 7, 10, 14, 21, 52 and 120 days after January 5, 2010 while winter-spring measurements were carried out at 8, 16, 30, 51, 65, 90, 129 and 168 days after June 29, 2010.

Statistical analysis

We assessed the significance of differences in leaf/shoot growth and leaf production per shoot/tiller among species by ANOVA of repeated measures. In this analysis, we included species as fixed factor and dates as repeated measures within each plant or tussock. Linear correlation analyses between explanatory variables (climatic variables) were carried out. We used forward stepwise multiple regression analysis and principal component analyses to describe relationships between leaf/shoot growth, leaf production, and climatic variables. Climatic variables included cumulative rain, average volumetric soil water content at two depths and mean air temperature between sampling dates. All statistical analyses were performed with the SPSS package and the level of significance was $\alpha = 0.05$ throughout the study.

Results

Precipitation and soil water content

Total precipitation was 154.98 mm during the study year (January–December 2010), the largest precipitation event occurred at the end of summer and smaller events occurred evenly distributed in the rest of the year. The soil water content was higher at 5 cm than at 30 cm depth for the two growth periods (Fig. 2). During the summer-autumn period, there was a negative correlation between soil water content at 5 cm depth and air temperature while during

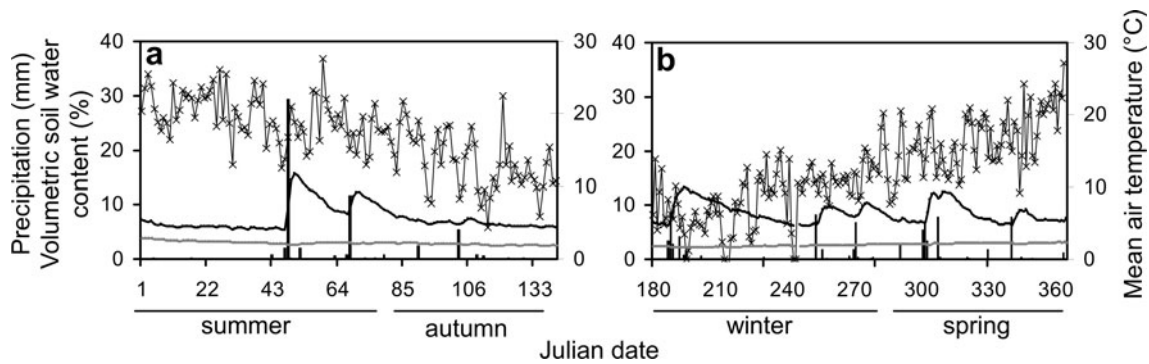


Fig. 2 Precipitation (mm) events (*bars*), daily volumetric soil water content (%) at 5 cm (*black line*) and 30 cm (*grey line*) depth and daily mean air temperature (*cross*) during summer-autumn (**a**) and winter-spring periods (**b**)

Table 1 Spearman correlation matrix between climatic variables in the two periods of growth

	PP	SWC5	SWC30	TEMP
Summer-autumn period				
PP	1.000			
SWC5	0.955**	1.000		
SWC30	-0.839*	-0.800*	1.000	
TEMP	-0.729	-0.855*	0.575	1.000
Winter-spring period				
PP	1.000			
SWC5	-0.208	1.000		
SWC30	0.536	-0.450	1.000	
TEMP	0.571	-0.486	0.989**	1.000

For summer-autumn period N = 7 and for winter-spring period N = 8 (**P* < 0.05, ***P* < 0.01)

PP precipitation, SWC5 volumetric soil water content at 5 cm depth, SWC30 volumetric soil water content at 30 cm depth, TEMP mean air temperature

winter-spring period there was a positive correlation between soil water content at 30 cm depth and air temperature (Table 1). Taking into account that we found no evidence of soil water recharge at 30 cm depth (Fig. 2) and that the fluctuation in volumetric soil water content at 30 cm depth was lower than the sensor accuracy, we attribute the high correlation between temperature and SWC30 to the influence of temperature on capacitance/frequency domain sensors. Because of that, SWC30 was excluded from the subsequent stepwise analysis.

Leaf/shoot growth and new leaf production

Chuquiraga avellanadae did not display new growth during the study period. We found significant differences in leaf/shoot growth in both growth period among species (summer-autumn: $F_{2,27} = 50.51, P < 0.0001$; winter-spring: $F_{2,27} = 44.60, P < 0.0001$), dates (summer-autumn:

$F_{1,27} = 31.22, P < 0.0001$; winter-spring: $F_{1,27} = 46.56, P < 0.0001$) and we found a significant effect of species × date interaction (summer-autumn: $F_{2,27} = 15.32, P < 0.0001$; winter-spring: $F_{2,27} = 14.93, P < 0.0001$) (Fig. 3a, b). Leaf/shoot growth and new leaf production in *Larrea divaricata*, *N. tenuis* and *P. speciosa* mostly occurred during spring and late summer-autumn. Leaf/shoot growth was higher in *P. speciosa* than in *N. tenuis* and *L. divaricata*, in both growth periods.

The number of new leaves per shoot/tiller also differed significantly among species (summer-autumn: $F_{2,27} = 54.35, P < 0.0001$; winter-spring: $F_{2,27} = 68.61, P < 0.0001$), dates (summer-autumn: $F_{1,27} = 21.43, P < 0.0001$; winter-spring: $F_{1,27} = 38.98, P < 0.0001$) and we found a significant species × date interaction (summer-autumn: $F_{2,27} = 6.32, P < 0.0001$; winter-spring: $F_{2,27} = 20.56, P < 0.0001$) in both growth periods (Fig. 3c, d). New leaf production was higher in *N. tenuis* during summer-autumn while during winter-spring was higher in *L. divaricata*. *N. tenuis* was the earliest and *L. divaricata* the latest in the onset of production of new leaves.

Relationships among growth measurements and climatic variables

During the summer-autumn growth period, soil water content in the upper layer (5 cm depth) was the strongest predictor of the leaf/shoot growth and the number of new leaves per shoot/tiller (Table 2). Also, air temperature was found to be a strongest predictor of the both latter plant attributes. Air temperature was negatively associated with shoot growth in *L. divaricata* and the number of new leaves per tiller in *P. speciosa* (Fig. 4a). This was in relation to the negative interaction found between soil water content at 5 cm depth and air temperature, during summer-autumn period (Table 1). In contrast, during winter-spring period air temperature was the strongest predictor of the leaf/shoot

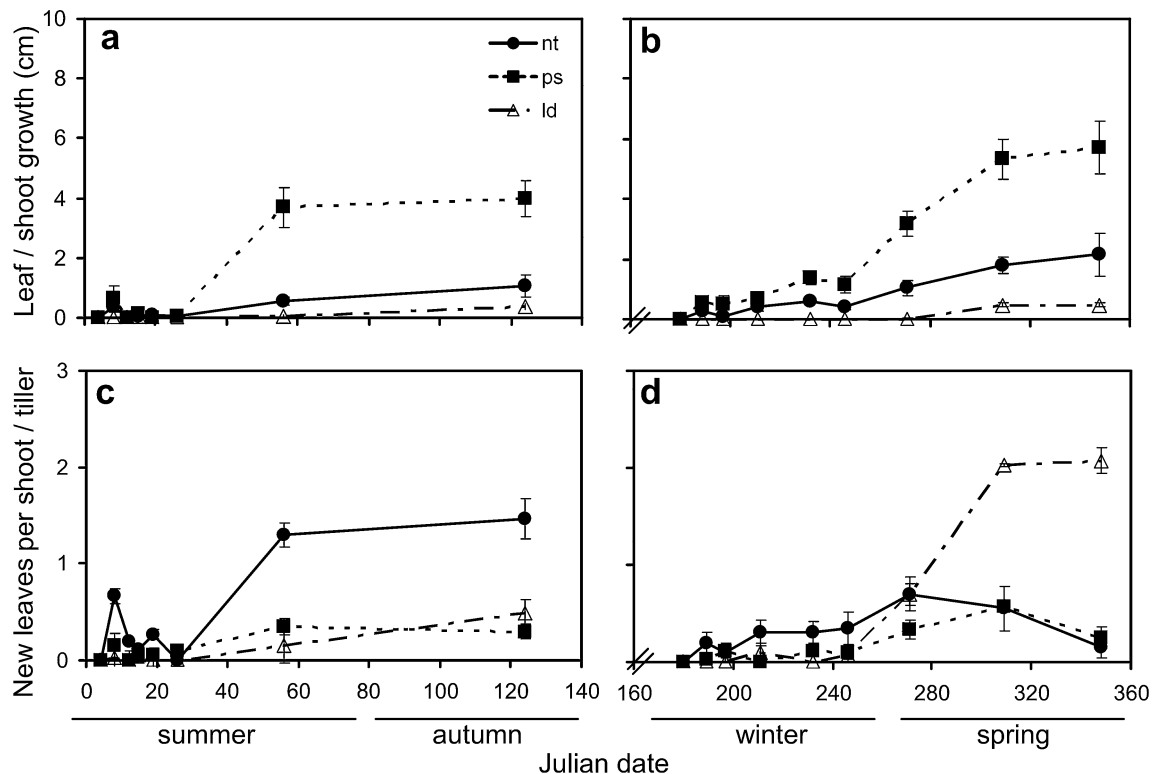


Fig. 3 Dynamics of leaf/shoot growth (a, b) and new leaf production (c, d) during summer-autumn and winter-spring of *Nassella tenuis* -nt- (filled circle and dark line), *Pappostipa speciosa* -ps- (filled square and dotted line) and *Larrea divaricata* -ld- (open triangle and

dashed line). Symbols are means and bars are standard errors. *C. avellaneda* did not show new growth during the studied periods (January 4–May 5 2010 and June 29–December 14 2010)

growth and the new leaves per shoot/tiller (Table 2). Air temperature was positively associated with leaf/shoot growth and new leaves per shoot/tiller (Fig. 4b).

Discussion

In water-limited environments, plant growth is constrained mostly to periods with high water availability (Ghazanfar 1997; Olivares and Squeo 1999; Peñuelas et al. 2004; Shackleton 1999). We found that leafing and growth processes in the studied plants were not directly controlled by precipitation but they were related to the current soil water content among other climatic variables. Jolly and Running (2004) emphasized that precipitation is a direct driver of the water balance in ecosystems, but it alone does not control the amount of water available for plants. Similarly, other studies showed a strong dependence of leaf extension and shoot elongation on the current water status in soil (Busso and Richards 1993; Haase et al. 1999; Otieno et al. 2005; Pugnaire et al. 1996) or close relationships between net photosynthesis and stomatal conductance and soil moisture in the upper soil layer (Montaña et al. 1995).

In three of the four species selected, growth was related to the water content in the upper soil layer (5 cm depth) in

summer-autumn, independently from growth forms. In the same way, species belonging to different functional types in a cold desert ecosystem also used the same water sources (Schwinning et al. 2005a, b). Accordingly, these results would suggest that almost all desert plants are “drinking from the same cup” (Hunter 1989; Reynolds et al. 2004) and that grasses and shrubs could be potential competitors for water soil resources (Montaña et al. 1995). However, some differences in the onset of leaf emergence and leaf/shoot growth among the studied species could indicate the existence of species-specific thresholds related to functional and structural constraints (Ogle et al. 2004) and provide evidence for temporal functional asynchrony among coexisting species (Chesson et al. 2004).

The differences between the two evergreen shrubs, *L. divaricata* and *C. avellaneda*, could be associated with differences in the rooting depth and the spatial pattern of water content during the study period. Throughout the study period the water content in the upper soil was higher than at 30 cm depth. The total precipitation during the studied year was 154.98 mm, less than the long-term average (200 mm) and was characterized by pulses smaller than 11 mm with only a single relatively large event of 30 mm at the end of summer. Previous studies in the Patagonian Monte reported refilling of deep soil layers

Table 2 Relationships between leaf/shoot growth and new leaves per shoot/tiller, and climatic variables for the three species in the two growth periods

	Strongest predictors	r^2	P
Summer-autumn period			
(a) Leaf/shoot growth			
<i>Larrea divaricata</i>	–TEMP	0.65	0.03
<i>Pappostipa speciosa</i>	SWC5	0.99	<0.0001
<i>Nassella tenuis</i>	SWC5, PP	0.99	<0.0001
(b) New leaves per shoot/tiller			
<i>Larrea divaricata</i>	SWC5	0.95	<0.0001
<i>Pappostipa speciosa</i>	–TEMP	0.75	0.01
<i>Nassella tenuis</i>	SWC5	0.92	0.001
Winter-spring period			
(a) Leaf/shoot growth			
<i>Larrea divaricata</i>	TEMP	0.76	0.007
<i>Pappostipa speciosa</i>	TEMP	0.85	0.001
<i>Nassella tenuis</i>	TEMP	0.85	0.001
(b) New leaves per shoot/tiller			
<i>Larrea divaricata</i>	TEMP, SWC5	0.95	0.001
<i>Pappostipa speciosa</i>	PP	0.68	0.01
<i>Nassella tenuis</i>	ns	ns	ns

Acronyms of climatic variables like in Table 1. A negative sign in the strongest predictor column indicates a negative relationship. For summer-autumn period N = 7 and for winter-spring period N = 8 ns indicates no significant model

after large precipitation events during winter and showed strong differences in water content among years (Bisigato and López Laphitz 2009; Coronato and Bertiller 1997). Moreover, Wierenga et al. (1987) and Reynolds et al. (1999) reported no soil recharge at 30 cm and below in some dry years in the Chihuahuan Desert. This could have benefited leaf/shoot growth of *L. divaricata* with a dimorphic root system (Rodríguez et al. 2007). Instead *C. avellaneda* with deep roots (Bertiller et al. 1991) using water preferentially below 30 cm depth could have experienced water limitation for leaf/shoot growth in comparison with the other species. In arid environments, precipitation events of approximately 10–20 mm could considerably enhance soil water content only in the upper soil profile (Bisigato and López Laphitz 2009; Coronato and Bertiller 1997; Reynolds et al. 2004).

These findings are consistent with the experimental evidence suggesting that an increment in the number of large precipitation events would favor shrub growth while small precipitation events would tend to promote grass development (Bates et al. 2006; Fay et al. 2002; Gao and Reynolds 2003; Knapp et al. 2002; Sala et al. 1982). Despite that *C. avellaneda* did not produce new growth during the period of study, this species has xerophytic leaf attributes

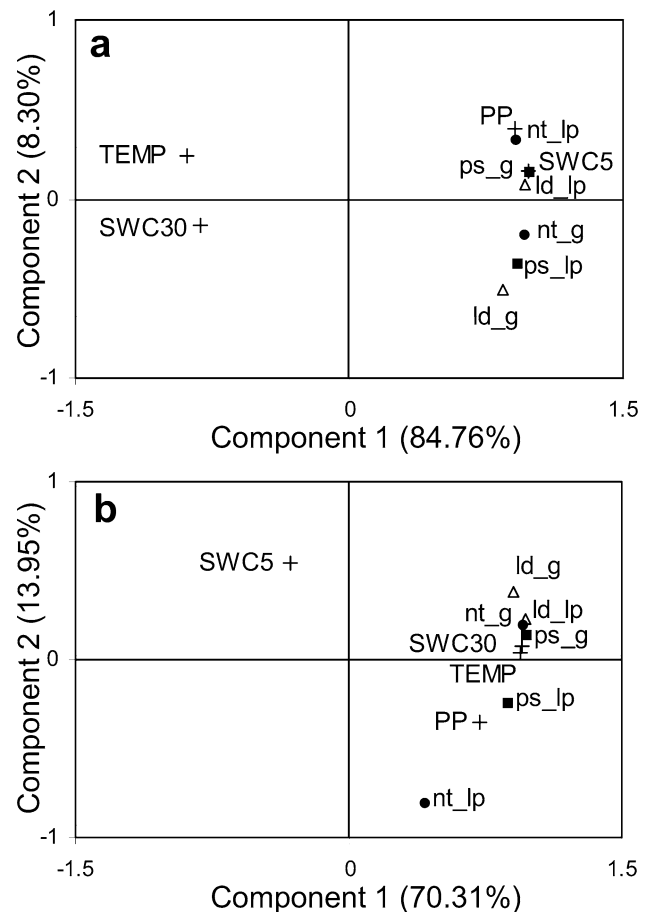


Fig. 4 Principal component analyses showing relationships among leaf/shoot growth (_g) and new leaf production (_lp) of *Nassella tenuis* -nt- (filled circle), *Pappostipa speciosa* -ps- (filled square) and *Larrea divaricata* -ld- (open triangle) and environmental variables for (a) summer-autumn and (b) winter-spring periods. Environmental variables acronyms like in Table 1. Symbols represent mean values

(Campanella and Bertiller 2011) that contribute to overcome extending hot and dry periods (Wright et al. 2004). Because temporal and spatial variation in water availability could modify competitive interactions among plants in desert ecosystems (Briones et al. 1998) it is important to perform long term research. Thus, additional studies will be required to get a better understanding of growth pattern of the species studied with above average precipitation and/or with high number of large precipitation events.

We found that air temperature was also related to leaf/shoot growth and leaf production. In accordance, a study that simulated phenological characteristics of two dominant grass species in a semi-arid steppe ecosystem highlighted the importance of develop a water-heat-based phenological model (Yuan et al. 2007). Air temperature affects plant growth due to changes in photosynthetic rate, CO₂ losses by respiration, and enhanced photorespiration (Prieto et al. 2009). This is in agreement with other works showing a high sensitivity of leaf extension and growth of

semi-arid grasses to temperature fluctuations (Busso and Richards 1993; Pugnaire et al. 1996). Additionally, other study showed that the differences in leaf dynamics between 2 years were more related to differences in air temperature and air humidity than to precipitation inputs (Schwinning et al. 2005a). As well, other works revealed that the initiation of spring growth was more related to soil temperature than to precipitation or soil moisture (Chew and Chew 1965; Reynolds et al. 1999). Similarly, Peñuelas et al. (2007) showed that, at the stand level, temperature and soil moisture of the preceding months determined the annual biomass production. Thus, Schwinning et al. (2005b) highlighted that primary productivity in deserts is not a direct response to precipitation.

In conclusion, we found that the leaf/shoot growth and leaf production were affected by current environmental conditions. Leaf/shoot growth and leaf production were not a direct response to precipitation, but were strongly related to soil water content and air temperature. Our research suggests that any change in water availability and temperature due to global warming could have consequences on species-specific plant responses in leaf/shoot growth and leaf production. This study also highlighted the importance of soil water dynamics of the different layers as well as root depth in controlling leaf dynamics of arid plants. However, since our study lacks of soil water content replication these issues should be validated in future studies.

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