

Fallen fruits stimulate decomposition of leaf litter of dominant species in NW Patagonia shrublands

Manuel de Paz, Miriam E. Gobbi & Estela Raffaele

Plant and Soil

An International Journal on Plant-Soil Relationships

ISSN 0032-079X

Plant Soil

DOI 10.1007/s11104-018-3590-0



Your article is protected by copyright and all rights are held exclusively by Springer International Publishing AG, part of Springer Nature. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your article, please use the accepted manuscript version for posting on your own website. You may further deposit the accepted manuscript version in any repository, provided it is only made publicly available 12 months after official publication or later and provided acknowledgement is given to the original source of publication and a link is inserted to the published article on Springer's website. The link must be accompanied by the following text: "The final publication is available at link.springer.com".

Fallen fruits stimulate decomposition of leaf litter of dominant species in NW Patagonia shrublands

 Manuel de Paz  · Miriam E. Gobbi · Estela Raffaele

 Received: 12 June 2017 / Accepted: 1 February 2018
 © Springer International Publishing AG, part of Springer Nature 2018

Abstract

Background and aims Leaf-litter decomposition rate (k_L) regulates nutrient dynamics and is affected at microsite level by species traits, soil biota and microclimate conditions. Fallen fruits form part of the litter and some, particularly fleshy fruits, contain large quantities of nutrients and sugar. We estimated the amount of fruit fall to litter, and evaluated the effect of its decomposition and sugar content on k_L in dominant species of NW Patagonia shrublands.

Methods We selected six woody species, four with fleshy and two with dry fruit. We followed 224 decomposition bags with leaf or leaf+fruit throughout 1 year. Fruit-litter and fruit sugar content were also measured.

Results and conclusions Fleshy fruit decomposition rate was associated with changes in k_L , while no effects of dry fruit on k_L were registered. We found that three of the fleshy fruits (*R. cucullatum*, *R. rubiginosa* and *S. patagonicus*) had a positive influence on k_L due to their sugar content. In contrast, *Berberis microphylla* fruit had a negative effect on k_L , probably due to the

presence of antimicrobial substances in the fruit. Considering the abundance of these species and their copious fruit production, the fleshy fruits could play an important role in determining soil fertility.

Keywords Litter quality · Dry fruit · Fleshy fruit · Sugar · Fruit production

Introduction

Litter decomposition rate (k) regulates nutrient dynamics, and is affected by the functional traits of the species involved (e.g. chemical and physical characteristics of leaf litter). At microsite level several environmental and biological factors are involved, including soil biota and microclimate conditions (e.g. Santos et al. 1984, Austin and Vivanco 2006; Pérez Harguindeguy et al. 2008, de Paz et al. 2017). Also, favorable conditions for soil microbiota could increase litter decomposition (high temperature and humidity, labile organic matter, high quality of litter, e.g. Wardle et al. 2002). In this sense, fallen fruits form part of the litter but constitute a material which is very different to leaf litter, with higher humidity levels, different physical properties, and in some cases, with larger amounts of N, P and sugar, particularly if the fruits are fleshy (Sandhu et al. 1990, Muoghalu et al. 1993, León-Rico et al. 2003, Damascos et al. 2008, Janick and Paull 2008, Rathore 2009). These nutrient inputs, mainly N and P, and high sugar concentration, are key elements that could significantly stimulate microbial activity and litter decomposition (e.g., Wardle et al. 2002; Ekblad and

 Responsible Editor: Harry Olde Venterink

 M. de Paz (✉) · E. Raffaele
 Laboratorio Ecotono, INIBIOMA (Universidad Nacional del Comahue-CONICET), Quintral 1250, 8400 Bariloche, Argentina
 e-mail: manoldpz@yahoo.com.ar
 e-mail: depazm@comahue-conicet.gob.ar

 M. E. Gobbi
 Departamento de Biología, CRUB, Universidad Nacional del Comahue e INIBIOMA (Universidad Nacional del Comahue-CONICET), Quintral 1250, 8400 Bariloche, Argentina

Nordgren 2002, Hamer and Marschner 2005; Kuzyakov et al. 2007; Ohm et al. 2007). In addition, fleshy fruits promote wetter micro-environmental conditions, and this could be particularly important for microorganisms, constituting a safe site, especially in regions with a dry climate during the growing season. The presence of fruits in litter was registered in temperate forest (Gosz et al. 1972 and Palacios-Bianchi 2002), tropical forest (Muoghalu et al. 1993, Fournier and de Castro 1973, León –Rico 2003), the Amazon jungle (Patricia and Morellato 1992 and Chale 1996), and Mediterranean forest (Santa-Regina and Gallardo 1986). Surprisingly few studies have considered the effect of fallen fruit on litter decomposition and soil fertility (e.g. Sandhu et al. 1990, Dean et al. 1999, León –Rico et al. 2003). Dean et al. (1999) found that trees with fleshy fruit create “fertility islands” beneath them by providing nutrients and labile organic matter (sugar). Furthermore, additional nutrient input was contributed to the soil below the canopy of these trees, from the feces of dispersers and micro-fauna attracted to the fruits (Dean et al. 1999).

In Andean forests and shrublands, the fruit production of woody and sub-shrub species (Arena et al. 2003, Paritsis et al. 2006, de Paz and Raffaele 2013) and the concentrations of nutrients and sugars in fruit have been reported for some of the shrubland species (Damascos et al. 2008, Arena and Curvetto 2008, Arena et al. 2012). In these shrublands, dominant woody species with fleshy fruits represent approximately 47% of the total community (Aizen and Ezcurra 1998) and the fruit production of these species increases after fire (Paritsis et al. 2006; de Paz and Raffaele 2013). However, the importance of these fruits to the shrubland soil nutrient dynamics has yet to be studied.

In a previous study in the same shrublands in NW Patagonia, we found no direct relationship between soil fertility and the nutrient contribution of leaf litter produced by woody nurse species to the soil beneath them (de Paz et al. 2017), some of these woody species being the subject of study in the present work. For example, the high content of nitrogen and carbon under the canopy of *Rosa rubiginosa* L. (exotic) is surprising, since this species produces litter with relatively low concentrations of these elements. These results suggest that other sources of organic matter (roots, branches and fruits) are more important than leaves to soil nutrient content (Wardle and Bardgett 2004, Hobbie 1992), and/or decomposition changes produced by the presence of fruit litter could explain these inconsistencies,

principally in dominant fleshy-fruit species with high fruit production (e.g. *R. rubiginosa* and *Schinus patagonicus* (Phil.) I. M. Jonnst., (de Paz et al. 2017).

The main objective of the current study is to examine the effects of fleshy and dry fruits of different woody species on k_L . In this paper we study fruit production, fall, fruit sugar content, and the effects of these factors on leaf decomposition rates in six dominant species of post-fire shrublands in NW Patagonia.

Methods

Study area

The study area is located in Nahuel Huapi National Park, in northwest Patagonia, Argentina. We selected four similar sites located in the ecotone between the humid Andean forests and the steppe (41°12'47 to 41°11'58 S and 71° 3'58.09" to 71°26'13.09" O). The sites were located at a distance of less than 5 km apart. The study area is characterized by 800–900 mm mean annual precipitation and 6 °C mean annual temperature. Soils are andisols with a low degree of development, characterized by a high capacity to stabilize organic matter, store water, buffer pH and retain P (Mazzarino et al. 1998; Diehl et al. 2003). The dominant vegetation in this transition area is shrubland. Rain occurs during autumn and winter (March–September) in this region, and vegetation growth is associated with the dry season (Veblen et al. 1992). Shrublands are highly diverse compared to the surrounding areas; however, soils usually have low nutrient concentrations (de Paz 2014). Within this setting, fires create a vegetation structure of shrub islands that vary in size and account for 50% of plant cover in a bare soil matrix (Cavallero et al. 2013). Considering the characteristics of these post-fire shrublands, the importance of plant-plant facilitation in this environment (de Paz 2014), and the increase in fruit production after fire (Paritsis et al. 2006), it would be interesting to study the implications of fruit decomposition for nutrient dynamics below woody nurse species, for different types of fruit (fleshy and dry). The vegetation is dominated by the woody species *Nothofagus antarctica* (G.Forst.) Oerst., *S. patagonicus*, *Discaria articulata* (Phil.) Miers, *Berberis microphylla* (Phil.) Miers (synonym of *Berberis buxifolia* Lam.), *Lomatia hirsuta* (Lam) Diels ex J.F. Macbr., *R. rubiginosa* and *R. cucullatum*, all of which are nurse species. The sub-

shrub *A. splendens* is another important pioneer species. Herbaceous cover is poor and associated with below-shrub canopy microsites, and is mainly represented by *Stipa* spp., *Hordeum* spp., *Festuca* spp., and *Poa* spp.

Experimental design

In order to fulfill our aim, we compare the fruit fall, fruit sugar content and decomposition rates of leaf litter with and without fruit presence for the dominant six shrubland species selected. Five woody and one semi-woody species were selected for this study: four fleshy fruit species (*Berberis microphylla*, *R. cucullatum*, *R. rubiginosa*, and *S. patagonicus*), and two dry fruit species (*A. splendens* and *L. hirsuta*). We selected five individuals per species as a sampling unit and analyzed as a replication. For each species, the individuals selected were growing in similar micro-topographical conditions (e.g. slope, exposure), were similar in size, and where possible, isolated from other individuals.

Fruit, litter, and decomposition rates (k)

We estimated the presence of fruit in litter as percentage fruit production minus the rates of predation before fruit fall, since the detection of fruit in litter tramps is underestimated (de Paz et al. 2013). Mean fruit production per plant was estimated from the average number of fruits from ten branches multiplied by the number of branches carrying fruit. Fruit mass per individual was estimated by multiplying the average number of fruits per plant by the average mass of each fruit. To estimate rates of fruit predation, six branches with fruit were marked in each individual, three of which were wrapped in tulle mesh. Predation of fruit was calculated as the difference between the percentage of missing fruit on the branches without tulle and the percentage of fallen fruit inside the tulle mesh on each sampling date. Fruit drop to litter was calculated as the weight of fruit produced per plant less the weight equivalent to the percentage of fruit predation. Monitoring was performed every 15 days during the period of maximum fruit production for each species from November 2010 to March 2011. Using these values, the contribution of fruit to the soil was estimated per hectare per species, weighted by species. Sugar content in fruit was measured in ten fruits per species, using a refractometer (measurement unit ° Bx = Brix = percentage of sucrose in 100 g of liquid). Refraction was measured for the

fleshy fruit juice and various water solutions of dry fruits (1:100, 1:10, and 1:1 g fruit: g water). Since this determination was made for fresh fruit, it was performed at different times for each species throughout the growing season, depending on fruit stock.

Leaf decomposition of the 6 study species was evaluated with and without the presence of fruit in the field. Senescent leaves were collected in square traps of 40 × 40 cm, with a plastic base of 1-mm mesh, under five individuals for each woody species, located five to fifteen centimeters above the soil. In the case of *A. splendens* (semi-shrub species) we removed the senescent leaves manually one year before collecting the litter, since its senescent leaves remain attached to the plant. Thus, we ensured that the collected litter for this species was produced by plants within our study period. Additionally, fruits were collected directly from the tulle bags and all the collected material was stove dried in labs at 60 °C for 72 h. The litterbag method of Bockock et al. (1960) was used to calculate decomposition rates. We used nylon mesh bags with a mesh size of 1 mm. This mesh is a standard size, and includes micro fauna but excludes meso and macrofauna. The bags were prepared with either senescent leaves (single bags) or senescent leaves plus fruit (mixed bags), in order to assess differences produced by fruit in litter decomposition. Two grams dry weight of recently fallen senescent leaves were put in each of the single bags and the mixed bags. In the latter, the amount of fruit added to the bag was determined according to the proportion of fallen fruit in litter for each species (fruit weight per area/leaf litter per area). These values ranged from 0.03 g in *R. cucullatum* to 2.7 g in *S. patagonicus*. Bag size was adapted in accordance with the leaf size of each species, in order to maintain similar density of leaves for all species. The bags were placed in the field below the canopy of each corresponding species in early spring (the end of September) and were protected with small metal cages to prevent predation by rodents and birds. This assay comprised 120 single decomposition bags ($n = 20$ per species) and 104 mixed bags ($n = 20$ per species, except in species with a limited amount of litter: *B. microphylla* and *R. cucullatum* with $n = 12$, per species). Removal of litter bags from the field (5 simple bags and 3 or 5 mixed per species per season), extractions, were performed seasonally every three months (0, 90, 180, 270 and 360 days; Steubing et al. 2001) and the remaining organic material (ROM) was stove dried at 60 °C for 72 h for dry weight estimation. Leaves and fruit in the mixed bags

were independently weighed at the beginning and end of the assay to allow independent ROM and k estimations. In spring of 2010 we measured the initial organic matter (OM) of litter bags for each species so as to homogenize incubation conditions (Pearse et al. 2013).

Data analysis

The decomposition rate (k) for each species was estimated by nonlinear regression (negative exponential model with intercept fixed in initial mass) of the difference between the initial weight and the ROM in each seasonal extraction. The ROM was expressed as a percentage of the initial OM. The analyses were performed separately for each species, and litter separately (k_L) from fruit (k_F) in the mixed bags. To evaluate the effect of the fruit on litter decomposition, the overlap of the confidence intervals (95%, performed with the t student test), for k_L of single and mixed bags was compared within species. The weight of fallen fruit was estimated as follows:

$$W_{FF} = W_{TF} - W_{PF}$$

where W_{FF} is the weight of the fallen fruit, W_{TF} is the total weight of fruit produced by a certain species and W_{PF} is the weight of the predated fruit, estimated from the predation rate. The differences in W_{TF} , W_{PF} , and W_{FF} of dry or fleshy fruit between groups of species and between species of the same group were evaluated using ANOVA nested model, with the kind factor nested in the Functional Group factor (Zar 1996; Gelman 2007). Level of significance was set at $\alpha = 0.05$.

All analysis was performed using nlme R package (Pinheiro et al. 2012). Homoscedasticity and normality were tested with Levene and Kolmogorov-Smirnoff test, respectively (Zar 1996).

Results

Effect of fruit on litter decomposition rates

Average annual fruit production across all species was 74.0 ± 23.0 g per plant. Fleshy fruit species produced significantly higher weight than dry fruit species (135.0 ± 48.0 and 22.0 ± 7.0 g per plant, respectively; $F_{1, 44} = 12.2$, $p < 0.01$). Additionally, differences within each type of fruit were also registered ($F_{6, 44} = 6.34$, $p > 0.01$). In fleshy fruit species,

the highest production per plant was observed for *S. patagonicus* and *R. rubiginosa* whereas *B. microphylla* and *R. cucullatum* had the lowest yield (Table 1). Of the dry fruit species, *L. hirsuta* and *A. splendens* had the highest production per plant, while *D. articulata* and *D. juncea* had the lowest (Table 1).

In general, the total fruit removal recorded was low ($3.4 \pm 0.7\%$), with lower values in dry fruit species and higher in fleshy fruit species ($F_{1,37} = 6.04$, $p < 0.01$, Table 1). These results represent 6.6-fold more weight of fleshy fruit per plant falling to litter than dry fruit ($F_{1,37} = 20.9$, $p < 0.01$, Table 1). No fruit remains on the tree; all fruit finally falls or is predated. Species cover, senesced matter and total mass of fruit supplied to the litter per plant per hectare are shown in Table 1.

Total sugar content of the fleshy fruit species varied significantly between species. *Berberis microphylla* and *R. rubiginosa* had the highest sugar concentration (45.1 ± 0.5 °Bx y 42.1 ± 2.1 °Bx; Table 1). These species were followed by *R. cucullatum* (28.2 ± 1.6 °Bx) and *S. patagonicus* (6.2 ± 0.6 °Bx). In dry fruit species (*A. splendens* and *L. hirsuta*) total sugar content in all tested dilutions was lower than the detection limit of the refractometer.

Leaf litter decomposition rate was significantly higher in mixed bags with fleshy fruits than in single litter bags (1.3-fold for *R. rubiginosa*, 3.7-fold for *R. cucullatum* and 1.2-fold for *S. patagonicus*), although this tendency was not followed by *B. microphylla*, which had a negative effect on k_L (decreased the rate by 62.0%, Fig. 1). *Berberis microphylla* was the richest in sugar content and the most predated of the four fleshy fruit species. Moreover, fleshy fruit k_F in the mixed bags was higher than k_L for all species (Fig. 1). No persistent fruit biomass was detected for *R. cucullatum* or *B. microphylla* after one year, while only 51.7% and 12.0% of the initial mass remained in the bags for *R. rubiginosa* and *S. patagonicus*. In dry fruit species, no difference was found between k_L in simple and mixed bags (Fig. 1); fruit biomass persistence was higher for these species (*A. splendens* 66.5% and *L. hirsuta* 77.5%) and k_F was lower than for fleshy fruits (Fig. 1).

In summary, dry fruit sugar content was below the detection limit and its presence had no effect on k_L . Three fleshy fruit species significantly increased k_L in the presence of fruit, with moderate fruit sugar concentrations and high k_F . In contrast, the fruit litter of *B. microphylla*, the richest in fruit sugar, had the opposite effect on k_L (Fig. 1).

Table 1 Fruit production, fallen fruit (fruit production minus depreddation weighted for plant cover), Fruit sugar content (°Brix) and Senesced matter weight (kg ha⁻¹) per year for dominant species, and cover in the study area. Plant cover and senesced

matter was taken from de Paz et al. (2013). Plant cover (mean ± SD) is expressed as a percentage of total area. Total plant cover is 50% of study site and 8.7% of the study site is covered by other species presented in this table; the remaining 50% is bare soil

Species	Fruit production (g per plant)	Fruit predation (%)	Fallen fruit (kg ha ⁻¹)	Fruit sugar Bx	Senescent matter year ⁻¹ (kg ha ⁻¹)	Plant cover (%)
<i>Fleshy fruit</i>	135.0 ± 48.0 ^A	10.4 ± 5.8 ^A	161.1 ± 41.1 ^A			
<i>B. microphylla</i>	1.9 ± 0.4 ^c	20.0 ± 5.2 ^a	0.468 ^c	45.0 ± 0.5	14.5	2.4 ± 3.7
<i>M. boaria</i>			*		136.9	1.7 ± 3.8
<i>R. rubiginosa</i>	268.0 ± 42.0 ^a	0.0 ± 0.1 ^c	86.703 ^b	42.1 ± 2.1	5.4	3.2 ± 9.6
<i>R. cucullatum</i>	10 ± 0.01 ^b	21.1 ± 5.1 ^d	0.001 ^d	28.2 ± 1.6	1.2	0.1 ± 0.3
<i>S. patagonicus</i>	326 ± 172 ^a	0.8 ± 0.1 ^b	219.011 ^{ab}	6.2 ± 0.6	15.8	5.8 ± 7.1
<i>Dry fruit</i>	22.0 ± 7.0 ^B	0.9 ± 0.28 ^B	24.5 ± 10.1 ^B			
<i>A. splendens</i>	32.0 ± 17.0 ^a	2.2 ± 0.1 ^a	9.769 ^a	0.0 ± 0.0	120.3	3.0 ± 5.3
<i>D. articulata</i>	8.7 ± 7.9 ^b	0.0 ± 0.1 ^c	5.156 ^b		1.5	5.9 ± 9.5
<i>D. juncea</i>	2.7 ± 1.2 ^b	0.0 ± 0.1 ^c	0.695 ^c		2.4	2.5 ± 7.1
<i>L. hirsuta</i>	44.0 ± 17 ^a	1.4 ± 0.1 ^b	7.252 ^{ab}	0.0 ± 0.0	12.5	6.7 ± 13.9
<i>N. antarctica</i>			*		120.6	10.0 ± 13.4

Senescent matter year-1: leaf litter + branches. *Species without fruit production in the study year

Homoscedasticity and normality: Kolmogorov-Smirnoff (K) and Levene (F_L) tests were passed: Fruit production K = 0.19: p = 0.06 and F_L = 0.56: p = 0.55; Fruit predation (%) K = 0.2: p = 0.6, F_L = 4.4: p = 0.06; Fallen fruit K = 0.21: p = 0.06, F_L = 0.35: p = 0.55). Different uppercase and lowercase letters indicate significant differences between and within functional groups, respectively (p < 0.05, 95% c.i.)

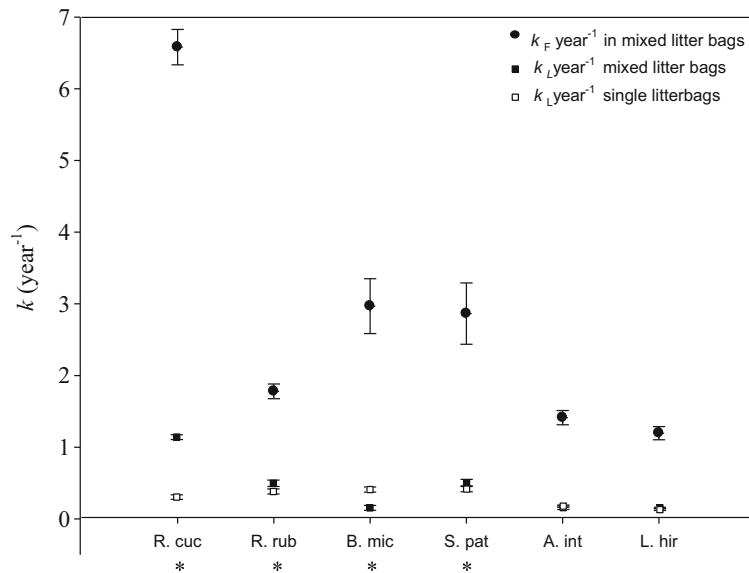


Fig. 1 Left axis: litter decomposition rates (k_L) in single and mixed bags, and fruit decomposition rates (k_F) in the mixed bags (expressed individually). Right axis: sugar content in °Brix (expressed as g in 100 g of juice or water solution) of two deciduous fleshy fruit species, *Ribes cucullatum* (R.cuc), *Rosa rubiginosa* (R. rub) and four evergreen, two of fleshy fruit,

Berberis microphylla (B. mic) and *Schinus patagonicus* (S. pat) and two of dry fruit, *Acaena splendens* (A. int) and *Lomatia hirsuta* (L.hir). Significant differences between single and mixed bags were tested by using 95% interval confidence performed with the t student test and they are marked with * (asterisk) under the species name

Discussion

Effect of fruit on leaf litter decomposition rates

The results obtained here showed the important role played by certain fruit species in litter nutrient dynamics in Patagonian shrublands. For two fleshy fruit species, *R. rubiginosa* and *S. patagonicus*, fruit mass was significantly higher than the senescent material produced throughout the year (Table 1). In this regard, the presence of fleshy fruit from these species was associated with an increment in k_L , while no differences were registered in the mixed bags with dry fruit. We attributed the positive influence on k_L observed for the three fleshy species (*R. cucullatum*, *R. rubiginosa* and *S. patagonicus*) to their moderate sugar content. Several studies demonstrated that when sugar was added to soil, microbial growth was stimulated, with the consequent acceleration of litter decomposition (Ekblad and Nordgren 2002; Ohm et al. 2007; Hamer and Marschner 2005 and Kuzyakov et al. 2007). Moreover, the magnitude of the effect seemed to be related to k_F rather than to the absolute sugar content, thus indicating that other factors such as fruit moisture or micronutrient content may play a role in determining the value of k_L , except in *B. microphylla*, as discussed in the next paragraph. In addition, respiratory rate, an indicator of microbial activity, is closely correlated with litter decomposition in NW Patagonian shrublands (de Paz 2014). Micronutrients detected in fruits of *R. rubiginosa*, *B. microphylla* and *R. magellanicum* (Damascos et al. 2008) were described as enhancers of litter decomposition rate in tropical forests (Kaspari et al. 2008). Furthermore, the non-significant effect on k_L registered for *A. splendens* and *L. hirsuta* was likewise attributed to their low, non-detectable sugar content. Dry fruits from these species do not supply litter with fruit sugar, which could be a labile carbon source consumed by microbiota (Kuzyakov et al. 2007).

Litter decomposition rates in mixed bags with *B. microphylla* fruits have the lowest k_L values, regardless of the abundant fruit production and high sugar content of this species. Similar fruit production and sugar content has previously been described for different species of *Berberis* (Arena et al. 2003, 2008, 2011, 2013, Rosales Laguna and Arias Arroyo 2015). A possible cause could be the presence of allelopathic substances which inhibit the growth of other plants and

microorganisms living in the same or a nearby habitat (Rice 2012). The negative effects of *Berberis* fruits on leaf litter decomposition could be due to the presence of berberine and other alkaloids in the fruit, with antimicrobial properties (Araya Rojas 2006; Meza Van Der Molen 2008, among others). A complementary explanation is based on observation by Neuvonen and Suomela (1990) and Hagvar and Kjondal (1981). In their work, dilute sulfuric and nitric acids were supplied to the litter to simulate the effect of acid rain, and hindered leaf litter decomposition was observed. *Berberis* spp. fruits are also characterized by their high citric acid content (e.g. Arena et al. 2013) and could have the same effect on litter decomposition. However, the soil beneath this species has the highest pH within the community studied (de Paz et al. 2017). Similarly, the other fleshy fruit species, like *Ribes* spp. (Romero Rodriguez et al. 1992), *Rosa rubiginosa* (Adamczak et al. 2012) and *Schinus* spp. (Queires et al. 2006), also had similar organic acid and had no negative effect on decomposition. It is possible that these acid substances do not interfere with decomposition or that the positive effect of fruit decomposition conceals them. Therefore, further research is needed to confirm whether *Berberis microphylla* fruits have a strong negative impact on litter nutrient dynamics and decomposition processes, as a result of its high abundance in these shrublands (de Paz 2014).

The presence of *S. patagonicus* and *R. rubiginosa* could contribute to the creation of “fertility islands” with high values of available nutrients and reserves of labile organic carbon in the soil (Dean et al. 1999; León-Rico 2003) due to the high production of litter and fruit falling into the litter (Table 1), and the positive effect of fruits on k_L (Fig. 1). In a previous work, in the same study sites and growth season, these two species were among the species with the highest proportion of fruits in senescent material per year (15.7% *S. patagonicus*, de Paz et al. 2013, and 7.3% in *R. rubiginosa*, personal observation). These proportions, and even more so the data in the present work (see Table 1), were higher than other environments like north temperate forest (2.8%, Gosz et al. 1972), southern hemisphere temperate forest (8.9%, Palacios-Bianchi 2002), tropical forest (1.3%, Muoghalu et al. 1993, and 2.0%, Fournier and de Castro 1973), the Amazon jungle (5.7%, Patricia and Morellato 1992 and 24.8%, Chale 1996), and Mediterranean forest (1.5%, Santa-Regina and Gallardo 1986). The present

results are more accurate than the results found in de Paz et al. (2013), due to the high level of predation in the traps used in this prior work. Moreover, this effect could be important on a community scale because of the abundance of *S. patagonicus* and *R. rubiginosa* in the studied shrublands (the fourth and the fifth most abundant woody species, respectively, Table 1). Indeed, the fruit effect on k_L could explain certain inconsistencies observed in the previous work (de Paz et al. 2017) regarding litter nutrient input to soil, and soil fertility. In earlier work we observed contradictions such as the high content of nitrogen and carbon under the canopy of *R. rubiginosa*, since this species produces litter with a relatively low concentration of these elements, or the similarity in organic matter content in soils under *A. splendens* and *R. cucullatum*, when they have quantitative and qualitative differences with regard to leaf production (de Paz et al. 2017). Our present results showed the influence of fleshy fruits on the acceleration of litter decomposition, and the important biomass input to litter of some dominant woody species in the form of fallen fruit. An alternative or complementary hypothesis to test in future studies could be that the influence of feces of disperser animals and the associated micro and mesofauna attracted by these species fruits could be similar or higher than in other environments (Dean et al. 1999).

Conclusions

Fleshy fruits play an important role in litter decomposition, unlike the dry fruits of Patagonian shrublands. This fruit effect on leaf litter decomposition is related to the sugar and nutrient content and/or decomposition rate of the fruits, and the antimicrobial substances present in *Berberis spp.* fruits.

The impact of mixed litter and the presence of fleshy fruit of other species on litter decomposition rates at a community level should be addressed in further studies, in order to better understand the magnitude of the effect of fruit on the nutrient cycle, on a large scale.

Acknowledgments This study was funded by Universidad Nacional del Comahue (B103), MINCyT (*PROEVO 40-B-189*), CONICET (PIP-5066), MAGyP (PIA10118) and YPF (4 × 4 Ford Ranger donation). Thanks are due to M. Carruitero, L. Aput, and C. Tur for field assistance and to Dr. Marcelo Barrera and Dr. Juan Cabrera for reviewing the manuscript.

References

- Adamczak A, Buchwald W, Zieliński J, Mielcarek S (2012) Flavonoid and organic acid content in rose hips (*Rosa L.*, sect. *Caninae* dc. Em. Christ.) *Acta Biol Cracov Ser Bot* 54(1):105–112
- Aizen MA, Ezcurra C (1998) High incidence of plant-animal mutualism in the woody flora of the temperate forest of Southern South America: biogeographical origin and present ecological significance. *Ecol Austral* 8:217–236
- Araya Rojas, M (2006) Estudio químico de *Berberis colletioides* Lechl. Departamento de Química. Punta Arenas (Chile), Universidad Nacional de Magallanes. Tesis de grado: 66
- Arena ME, Vater G, Peri P (2003) Fruit production of *Berberis buxifolia* Lam. in Tierra del Fuego. *HortScience* 38(2):200–202
- Arena ME, Curvetto N (2008) *Berberis buxifolia* fruiting: Kinetic growth behavior and evolution of chemical properties during the fruiting period and different growing seasons. *Sci Hortic* 118(2):120–127
- Arena ME, Giordani E, Radice S (2011) Flowering, fruiting and leaf and seed variability in *Berberis buxifolia*, a native Patagonian fruit species. In: Marin L, Kovac D (eds) *Native species: identification, conservation and restoration*. Nova Sciences Publishers, New York
- Arena ME, Postemsky P, Curvetto NR (2012) Accumulation patterns of phenolic compounds during fruit growth and ripening of *Berberis buxifolia*, a native Patagonian species. *N Z J Bot* 50:15–28
- Arena ME, Zuleta A, Dynner L, Constenla D, Ceci L, Curvetto N (2013) *Berberis buxifolia* fruit growth and ripening: evolution in sugar and organic acid contents. *Sci Hortic* 158:52–58
- Austin AT, Vivanco L (2006) Plant litter decomposition in a semi-arid ecosystem controlled by photodegradation. *Nature* 442: 555–558
- Bocock KL, Gilbert O, Capstick CK, Twinn DC, Waid JS, Woodman MJ (1960) Changes in leaf litter when placed on the surface of soils with contrasting humus types. *Eur J Soil Sci* 11(1):1–9
- Cavallero L, Raffaele E, Aizen MA (2013) Birds as mediators of passive restoration during early post-fire recovery. *Biol Conserv* 158:342–350
- Chale FMM (1996) Litter production in an *Avicennia germinans* (L.) stearn forest in Guyana, South America. *Hydrobiologia* 330:47–53
- Damascos M, Arribere M, Svriz M, Bran D (2008) Fruit mineral contents of six wild species of the north andean Patagonia, Argentina. *Biol Trace Elem Res* 125:72–80
- de Paz M 2014. Heterogeneidad de micrositios, dinámica de nutrientes y facilitación en especies leñosas de los matorrales del NO de la Patagonia. Tesis Doctoral. Directora: Dra. Estela Raffaele (CONICET). Codirectora: Dra. Miriam Gobbi (CRUB). Centro Regional Universitario Bariloche, Universidad Nacional del Comahue
- de Paz M, Gobbi ME, Raffaele E (2013) Mantillo de las especies leñosas de matorrales del NO de la Patagonia: abundancia, composición, estructura y heterogeneidad. *Boletín de la Sociedad Argentina de Botánica* 48:525–541
- de Paz M, Gobbi ME, Raffaele E, Buamscha MG (2017) Litter decomposition of woody species in shrublands of NW Patagonia: how much do functional groups and microsite

- conditions influence decomposition? *Plant Ecol* 218: 699–710
- de Paz M, Raffaele E (2013) Cattle change plant reproductive phenology, promoting community changes in a post-fire *Nothofagus* forest in northern Patagonia, Argentina. *J Plant Ecol* 6:459–467
- Dean WRJ, Milton SJ, Jeltsch F (1999) Large trees, fertile islands, and birds in arid savanna. *J Arid Environ* 41:61–78
- Diehl P, Mazzarino MJ, Funes F, Fontenla S, Gobbi ME, Ferrari J (2003) Nutrient conservation strategies in native Andean-Patagonian forests. *J Veg Sci* 14:63–70
- Ekblad A, Nordgren A (2002) Is growth of soil microorganisms in boreal forests limited by carbon or nitrogen availability? *Plant Soil* 242:115–122
- Fournier LA, de Castro LC (1973) Producción y descomposición del mantillo en un bosque secundario húmedo de premontano. *Rev Biol Trop* 21:59–67
- Gelman A (2007) Data analysis using regression and multilevel/hierarchical models. Cambridge University Press, Cambridge, England
- Gosz JR, Likens GE, Bormann FH (1972) Nutrient content of litter fall on the Hubbard Brook experimental forest, New Hampshire. *Ecology* 53:769–784
- Hagvar, S, & Kjondal, BR (1981) Decomposition of birch leaves: dry weight loss, chemical changes, and effects of artificial acid rain. *Pedobiologia*
- Hamer U, Marschner B (2005) Priming effects in soils after combined and repeated substrate additions. *Geoderma* 128:38–51
- Hobbie SE (1992) Effects of plant species on nutrient cycling. *Trends Ecol Evol* 7:336–339
- Janick J, Paull RE (2008) The encyclopedia of fruit and nuts. CABI, London
- Kaspari M, García MN, Harms KE, Santana M, Wright SJ, Yavitt JB (2008) Multiple nutrients limit litterfall and decomposition in a tropical forest. *Ecol Lett* 11:35–43
- Kuzyakov Y, Hill PW, Jones DL (2007) Root exudate components change litter decomposition in a simulated rhizosphere depending on temperature. *Plant Soil* 290:293–305
- León-Rico R (2003) PARTE III. Los procesos en el suelo: la descomposición. Efecto de la descomposición, frugivoría, remoción de frutos y semillas de especies arbóreas en los patrones de descomposición. En Naranjo-García, E (2003) *Ecología del suelo en la selva tropical húmeda de México*. UNAM.
- Mazzarino MJ, Bertiller MB, Schlichter TM, Gobbi ME (1998) Nutrient cycling in Patagonian ecosystems. *Ecologia Austral* 8:167–181
- Van Der Molen KIM (2008) Química y actividad biológica de *Berberis rotundifolia*. Facultad de Ciencias Escuela de Química y Farmacia. Universidad Austral de Chile, Valdivia, p 89
- Muoghalu JI, Akanni SO, Eretan OO (1993) Litter fall and nutrient dynamics in a Nigerian rain forest seven years after a ground fire. *J Veg Sci* 4:323–328
- Neuvonen S, Suomela J (1990) The effect of simulated acid rain on pine needle and birch leaf litter decomposition. *J Appl Ecol* 27(3):857–872
- Ohm H, Hamer U, Marschner B (2007) Priming effects in soil size fractions of a podzolBs horizon after addition of fructose and alanine. *J Plant Nutr Soil Sci* 17:551–559
- Palacios-Bianchi P (2002) Producción y descomposición de hojarasca en un bosque maulino fragmentado. *Biología Ambiental* (en línea) <http://www.mantruc.com/pilar/seminario-palacios-bianchi2002.pdf>
- Paritsis J, Raffaele E, Veblen TT (2006) Vegetation disturbance by fire affects plant reproductive phenology in a shrubland community in northwestern Patagonia, Argentina. *N Z J Ecol* 30: 387–395
- Patricia L, Morellato C (1992) Nutrient cycling in two south-east Brazilian forests. I Litterfall and litter standing crop. *J Trop Ecol* 8:205–215
- Pearse IS, Cobb RC, Karban R (2013) The phenology substrate match hypothesis explains decomposition rates of evergreen and deciduous oak leaves. *J Ecol* 102:28–35
- Pérez Harguindeguy N, Blundo C, Gurruch D, Díaz S, Cuevas E (2008) More than the sum of its parts? Assessing litter heterogeneity effects on the decomposition of litter mixtures through leaf chemistry. *Plant Soil* 303:151–159
- Pinheiro J, Bates D, DebRoy S, Sarkar D, R-Development-Core-Team (2012) nlme: Linear and nonlinear mixed effects models. R package version 3.1-96. R Foundation for Statistical Computing, Vienna.
- Queires LCS, Fauvel-Lafève F, Terry S, De la Taille A, Kouyoumdjian JC, Chopin DK, Crepin M (2006) Polyphenols purified from the Brazilian aroeira plant (*Schinus terebinthifolius*, Raddi) induce apoptotic and autophagic cell death of DU145 cells. *Anticancer Res* 26(1A):379–387
- Rathore M (2009) Nutrient content of important fruit trees from arid zone of Rajasthan. *J Horticult For* 1:103–108
- Rice EL (2012) Allelopathy. Academic press, UK
- Romero Rodriguez MA, Vazquez Oderiz ML, Lopez Hernandez J, Lozano JS (1992) Determination of vitamin C and organic acids in various fruits by HPLC. *J Chromatogr Sci* 30(11):433–437
- Rosales Laguna, DD and Arias Arroyo G (2015) Vitamina C y parámetros fisicoquímicos durante la maduración de *Berberis lobbiana* "Untusha" Rev. Soc. Quím. Perú[online]., vol. 81, n. 1 [citado 2016-04-11], pp. 63–75. http://www.scielo.org.pe/scielo.php?script=sci_arttext&pid=S1810-634X2015000100008&lng=es&nrm=iso.
- Sandhu J, Sinha M, Ambashit RS (1990) Nitrogen release from decomposing litter of *Leucaena leucocephala* in the dry tropics. *Soil Biol Biochem* 22:859–863
- Santos PF, Elkins NZ, Steinberger Y, Whitford WG (1984) A comparison of surface and buried *Larrea tridentata* leaf litter decomposition in North American hot deserts. *Ecology*:278–284
- Santa Regina, I. & Gallardo, J.F (1985) Producción de hojarasca en tres bosques de la Sierra de Béjar (Salamanca). *Mediterránea Ser Biol* 8: 89-101
- Steubing L, Godoy R, Alberdi M (2001) Métodos de ecología vegetal. Editorial Universitaria S.A, Santiago de Chile
- Veblen TT, Kitzberger T, Lara A (1992) Disturbance and forest dynamics along a transect from Andean rain forest to Patagonian shrubland. *J Veg Sci* 3:507–520
- Wardle DA, Bonner KI, Barker GM (2002) Linkages between plant litter decomposition, litter quality, and vegetation responses to herbivores. *Funct Ecol* 16:585–595
- Wardle DA, Bardgett RD (2004) Human-induced changes in large herbivorous mammal density: the consequences for decomposers. *Front Ecol Environ* 2:145–153
- Zar JH (1996) Biostatistical analysis. Prentice-Hall, Inc., New Jersey, USA, p 663