Food Quality, Larval Consumption, and Growth of *Klapopteryx kuscheli* (Plecoptera: Austroperlidae) from a South Andes Stream

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ABSTRACT

The effect of food quality, measured as leaf resistance and carbon:nitrogen ratio, on the consumption and growth of the plecopteran *Klapopteryx kuscheli* was analyzed through an *in situ* experiment. Leaves from seven different tree species were used in feeding trials with intermediate sized *K. kuscheli* larvae. We used leaves from both deciduous and evergreen species, which exhibited a wide range in C:N ratio as well as leaf resistance. After 30 days, leaf consumption and larval growth were estimated for each of the 119 experimental units. Results showed that *K. kuscheli* was unable to consume tough leaves (leaf resistance higher than 300 g mm^{-2}). Among deciduous species, consumption was proportional to C:N ratio showing a compensatory strategy on leaves with higher C:N ratio. Nevertheless, consumption rate did not compensate for growth as ingestion was inversely related to food quality. Native deciduous plant species were of low quality for larval growth and efficient food conversion, and this may have ecological implications for both secondary production and life cycle length in detritivore-shredders inhabiting Andean low-order canopied streams.

INTRODUCTION

Food consumption and body growth in aquatic insects is especially affected by the quality of ingested food (Williams and Feltmate 1994). Although total amount of food is hardly ever limiting for aquatic detritivores in natural ecosystems, high quality food can often be limited in time or space (Anderson and Sedell 1979, Petersen et al. 1989), and food quality is known to affect larval development (Sweeney 1984). Organic matter of plant origin, and especially detritus, is considered of low quality because much of its energy is trapped in refractory compounds such as cellulose or lignin that are difficult to digest (Anderson and Cargill 1987, Chapman 1998) or even leaf structure (e.g. cuticle thickness) that may avoid access. In addition, such material often contains polyphenols and tannins that can diminish instream decay rate (Triska and Sedell 1976, Campbell and Fuchshuber 1995) as well as palatability and digestibility for consumers (Suberkropp 1992, Chapman 1998). However, microbial activity that converts detritus into microbial biomass is an important process in conditioning leaves for shredder activity (Bärlocher 1981) and may be a key in increasing food quality of litter (Bärlocher 1985, Arsuffi and Suberkropp 1986). In addition to the intrinsic features of the litter, the enzymatic capabilities of the guts of different consumers may differ greatly among species (Chapman 1998). Therefore, since the quality of a specific litter can vary from one consumer species to another (Maltby 1996) it is difficult to predict the consumption and growth of particular organisms based on specific available food. For example, some studies found that body growth was positively related to N content of food (Iversen 1974, Friberg and Jacobsen 1999) while others did not (Garden and Davies 1988). In this sense, land management can affect the quality of litter input to low order streams, increasing or decreasing quality, and these changes can modify both the rate at which the litter is consumed by shredders and the secondary production of their populations.

In the Patagonian Andes, low-order streams run through deciduous forests composed mainly of *Nothofagus pumilio* (Poepp. et Endl.) Krasser and *N. antarctica* (Forst.) Oerst. Downstream, these systems flow through forests of the evergreen *N. dombeyi* (Mirb.)

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Blume. The deciduous trees are responsible for much of the leaf litter input to these streams where shredders, particularly larvae of Plecoptera, participate in leaf litter decay (Albariño 1997, Albariño and Balseiro 1998, Albariño 2000). However, in the last five decades, exotic plants have been introduced for forestry (pine plantations) and ornamental purposes. As a result, natural litter inputs to these streams have been altered and changes in food availability and quality for shredders may be occurring.

In this study we experimentally tested the leaf quality of seven plant species as food for larvae of *Klapopteryx kuscheli*, a common shredder in low order Andean Patagonian streams (Albariño 2000). We measured consumption and body growth of *K. kuscheli* larvae on leaf litter of both native and exotic, deciduous and evergreen plants that exhibit a wide range of C:N ratios and leaf resistance. We hypothesized that those leaves with higher C:N ratio and lower leaf resistance would be the most consumed food items. Also we hypothesized that those leaves of higher quality (i.e., with both the lowest C:N ratio and leaf resistance) would yield the highest growth and gross growth efficiency.

METHODS AND MATERIALS

Leaf collection

The leaves used in this study belong to seven different species, of which four are native (*Ribes magellanicum* Poir., *Nothofagus antarctica*, *N. pumilio*, *N. dombeyi*), and three are exotic (*Alnus glutinosa* L., *Pinus ponderosa* Douglas, and *Pseudotsuga menziesii* (Mirb.) Franco). Native species were selected due to their ecological importance in terms of abundance and distribution. Pine trees were tested because they are relevant as exotic items in terms of land uses. *A. glutinosa* is common in urban and suburban areas of Bariloche as an ornamental. We included alder for comparison because its leaves are known to be of high quality for detritivores (i.e., high N content, low C:N ratio, low leaf resistance, and apparently absence of chemical deterrents). Fresh leaves were manually picked from the plants. Those of native species were collected in the surroundings of the stream where the macroinvertebrates were collected, while those of exotic species were collected from trees at the Universidad del Comahue fish farm (Centro de Salmonicultura) where the experiments were carried out. Only undamaged leaves were selected. In the laboratory, a leaf litter fresh mass-dry mass regression was established for each species in order to avoid drying the leaves before using them in the experiments.

Litter quality

The C:N ratio and the leaf resistance were used as indicators of litter quality. These two parameters were measured for each leaf species on day 15 (t_{15}) when macroinvertebrates were added to treatment units, and on day 45 (t_{45}) when the experiment ended.

Carbon content was estimated as 50% of ash free dry mass (AFDM) of leaf material (Golueke 1991). Leaves were dried at 105 ^{0}C for 48 h, and the dry mass was measured to the nearest 0.01 mg. Each sample was then ashed at 550 ^{0}C, and AFDM was obtained as the difference between dry mass (DM) and ash mass.

Nitrogen content was obtained using the Kjeldahl method (APHA 1989) at the Laboratory of Soils of INTA Bariloche and it was expressed as percentage of dry mass.

Leaf resistance was defined as the pressure needed to penetrate a leaf of a given species, and was expressed as g mm^{-2}. Resistance was quantified following Graça et al. (1993) as the mass required to push a steel rod (0.885 mm diameter) through a leaf maintained between two Plexiglas holders. Thirty resistance measurements were performed for each time period (t_{15} and t_{45}) for each of the species. The rod was placed at least 3 mm from main or secondary veins. On needles, the rod was placed in the center of the needle.

Macroinvertebrate collection and acclimation

Larvae of *Klapopteryx kuscheli* were collected with a Surber sampler from an unnamed tributary of Ñireco stream at 1000 m a.s.l. (41^0 13' S, 71^0 22' O), a first order stream flowing

through a *Nothofagus pumilio* forest. Only individuals of intermediate size (body length: 17.6 ± 0.1 mm, body DM: 6.5 ± 0.3 mg; mean $\pm$ s.e.) were selected for experimentation. Individuals were acclimated for 24 h in a laboratory container at 11°C. Because of the narrow body length range of experimental larvae, body dry mass was estimated using a dry mass – body length (BL) regression equation. Dry mass was obtained by drying organisms for 24 h at 60 °C and weighing to the nearest 0.01 mg. Body length was measured to the nearest 0.01 mm from the anterior margin of labrum to the posterior margin of the last abdominal tergite. The regression was:

DM (mg) = 1.91 BL (mm) - 27.16   (r^2adj. = 0.84, n = 20).

Experimental design

Experiments were carried out at the Centro de Salmonicultura in an experimental channel, which was a 400 x 40 x 40 cm fiberglass trough fed with Arroyo Gutierrez stream water. Temperature during the experiment was 10.8 °C and conductivity was 58 μS cm^{-1}. Water was maintained at a depth of 35 cm with a discharge of 17 L min^{-1}. Experimental units consisted of cylindrical plastic chambers of 10 cm length and 5.8 cm diameter. Both ends were covered with a net of 1mm mesh.

Each treatment chamber contained 600 mg of leaves from one plant species, and one larva of *K. kuscheli*. Each leaf species treatment was replicated five times. On May 10, 1998 (t_0), experimental units were immersed in the channel for leaf conditioning, and larvae were added to the chambers on May 25 (t_{15}). All treatment chambers were removed from the channel on day 45 when the experiment was ended.

Controls consisted of chambers with 600 mg DM of leaves from one of the plant species but no larvae. On 10 May, 1998, 12 control chambers of each species were placed in the experimental channel. Of these, two were used to measure leaf resistance and C:N ratio at days 15 and 45. Therefore, 119 units were placed on May 10 in the experimental channel of which 84 were controls (35 initial controls, 35 final controls and 14 for litter quality analysis) and 35 were treatments. On day 15, five replicates of each species (initial controls) were collected and leaf mass was measured, the other five replicates of final controls and treatments were collected at the end of the experiment on day 45.

As macroinvertebrates were added on day 15 (t_{15}), the dry mass of treatment units was corrected using the mean decay of controls from t_0 to t_{15}. Differences between controls and treatments on day 45 were assumed to be net larval consumption. Comparisons between controls and treatments and, comparisons between treatments were tested using the *t* test. Leaf resistance and C:N ratios were tested for statistical differences within treatments using ANOVA. Because no difference was obtained for independent variables, data from t_{15} and t_{45} for each treatment were pooled and tested again. Leaf resistance values were log-transformed to achieve normality. When significant differences were found, a multiple comparison *a posteriori* Student-Newman-Keuls test was performed.

Larval growth was obtained as the difference in dry mass between t_{45} and t_{15} for each larva. Both net larval consumption and gross growth were expressed as mg DM *per* initial larval DM *per* day (i.e., relative consumption /growth rates: mg mg^{-1} d^{-1}). The efficiency of conversion of ingested food (ECI; Arsuffi and Suberkropp 1986) was estimated as the percentage ratio between growth and consumption: G/C *100, where G is larval growth in mg DM and C is leaf consumption in mg DM.

RESULTS

Significant differences in C:N ratios were demonstrated among species (ANOVA, P<0.05), but no differences were observed between dates within each species. Leaves from deciduous *Alnus glutinosa* had the lowest C:N ratio (20:1), while the coniferous *Pseudotsuga menziesii* had the highest (53:1) (Table 1). Using the multiple comparison test (S-N-K), the species were ordered according to this ratio into five significantly different

(P<0.05) groups: *P. menziesii* > *P. ponderosa* > *N. dombeyi* > *R. magellanicum, N. antarctica, N. pumilio* > *A. glutinosa*. In this sequence, the native South Andes species formed two groups in the middle of the distribution. One was constituted by the evergreen *N. dombeyi*, while the three deciduous made up the other one.

Leaf resistance showed significant differences among species (ANOVA, P<0.001) but not between dates within species (ANOVA, P>0.05), although some species showed a reduction of leaf resistance with time. The multiple comparison test showed again that the species were grouped according to leaf resistance. There were three significantly different (P<0.05) groups: *P. ponderosa* > *N. dombeyi, P. menziesii* > *N. antarctica, N. pumilio, R. magellanicum, A. glutinosa*. The *P. ponderosa* needles had the highest leaf resistance with 1146.4 g mm^{-2}, and *A. glutinosa* leaf was the lowest with 58.8 g mm^{-2} (Table 1). Once more, native species were in two different groups, where the evergreen *N. dombeyi* had significantly higher resistance than those of deciduous plants. All deciduous species were grouped together.

The two features representing different food quality parameters for shredders, showed similar patterns. Higher values of C:N ratio and leaf resistance were found in evergreen species (*N. dombeyi, P. menziesii, P. ponderosa*), while the deciduous ones (*A. glutinosa, N. antarctica, N. pumilio, R. magellanicum*) showed lower values for both variables (Table 1).

During the 30 day experiment, larvae in seven of the 35 treatment chambers died. These experimental units, three of which were the *P. ponderosa* treatment, were not considered in the analysis. At the end of the experiment, deciduous leaves showed signs of larval feeding, whereas those of evergreen did not. In the four treatments where leaves were consumed, leaf resistance was less than 150 g mm^{-2}, while those with a leaf resistance higher than 300 g mm^{-2} were not consumed (Fig. 1).

Leaf consumption varied among species from nearly zero, in the evergreens *N. dombeyi, P. ponderosa*, and *P. menziesii* , to 0.374 mg mg^{-1} d^{-1} (mean consumption rate) for *R. magellanicum* (Table 2). Among deciduous species, consumption was significant and positively correlated with the C:N ratio but not with leaf resistance (Fig. 1). The difference in dry weight between controls and treatments, considered as larval net consumption, was

Table 1. C:N ratio and leaf resistance from leaves of the seven species used in the experiment.

Leaf species	C:N ratio		Leaf Resistance (g mm^{-2})	
	mean	s.e.	mean	s.e.
Alnus glutinosa	17.5	1.5	58.8	8.5
Nothofagus antarctica	27.7	1.7	119.3	5.8
Nothofagus dombeyi	36.6	1.2	423.2	16.7
Nothofagus pumilio	25.3	1.2	84.2	35.1
Pinus ponderosa	45.7	2.1	1146.5	124.4
Pseudotsuga menziesii	53.3	3.9	373.5	12.2
Ribes magellanicum	30.2	0.3	78.8	32.2

significant (*t* test, P<0.05) in the native deciduous *R. magellanicum* and *N. pumilio*, while there were no significant differences in *N. antarctica*, in the exotic deciduous *A. glutinosa*, or any of the evergreen trees. However, the decay due to feeding was relatively high in *N. antarctica*, with 0.341 mg mg^{-1} d^{-1} during the experiment. Also, the larval consumption on *A. glutinosa* (0.070 mg mg^{-1} d^{-1}) was much higher than any of the evergreen leaves, where the mean decay was virtually zero. The absence of significant differences between control and *N. antarctica*, and control and *A. glutinosa*, is probably due to high variability within replicates that resulted in high error values, and not to the lack of feeding (*t* test, P>0.05).

Larval growth was observed only in those treatments where leaves were consumed (Table 2, Fig. 1). In three cases (*A. glutinosa*, *N. antarctica*, and *N. pumilio*) the differences between initial DM and final DM were significant (*t* test, P<0.05). Larvae that fed on *R. magellanicum* leaves showed no significant growth, although it was the most highly consumed species. The larvae of the *N. dombeyi* treatment grew very little (0.002 mg mg^{-1} d^{-1}) as did those of the *R. magellanicum* treatment (0.007 mg mg^{-1} d^{-1}). When fed on the conifers *P. menziesii* and *P. ponderosa*, larvae did not grow, and 40% of them died (4 of 10). Maximum growth was observed for larvae fed on *A. glutinosa*. Growth rate decreased with
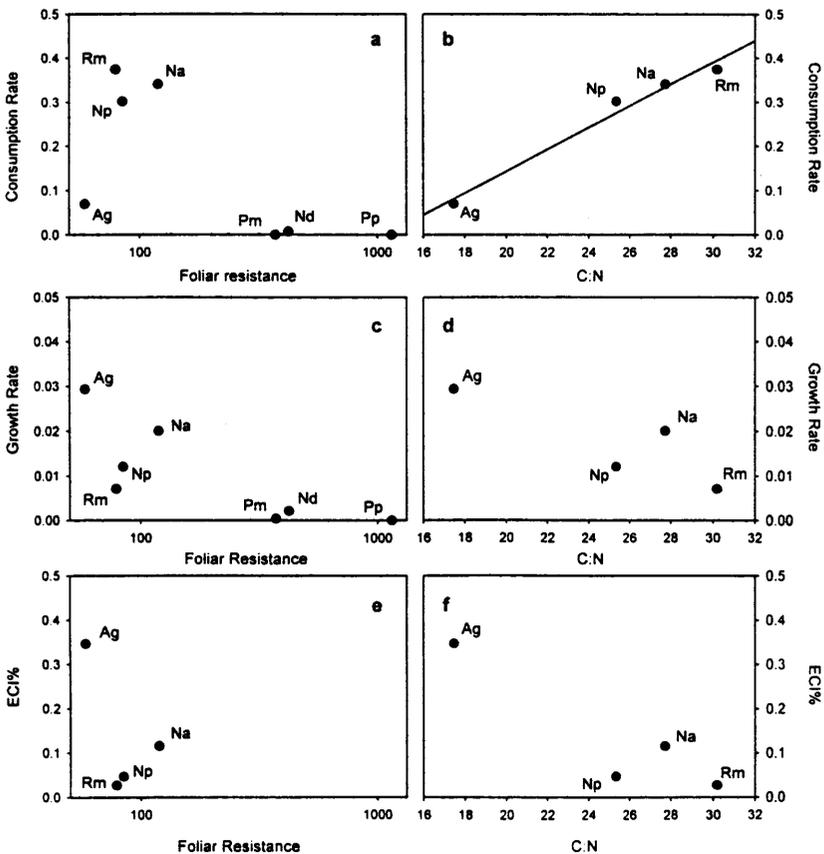

Figure 1. Consumption (mg mg^{-1} d^{-1}) and growth rates (mg mg^{-1} d^{-1}) and Efficiency of Conversion of Ingested food for *Klapopteryx kuscheli* fed on different leaf litter. Linear regression (P<0.01) is shown. **Ag**: *Alnus glutinosa*, **Na**: *Nothofagus antarctica*, **Nd**: *N. dombeyi*, **Np**: *N. pumilio*, **Pp**: *Pinus ponderosa*. **Pm**: *Pseudotsuga menziesii* and **Rm**: *Ribes magellanicum*.

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Table 2. Consumption and growth rates and efficiency of conversion of ingested food (ECI%) of *Klapopteryx kuscheli* during the experiment (mean ± s.e.). ECI% not estimated for species with negative rates.

Leaf species	Consumption (mg mg^{-1} d^{-1})	Growth (mg mg^{-1} d^{-1})	ECI%
Alnus glutinosa	0.070±0.043	0.029±0.019	34.61±9.66
Nothofagus antarctica	0.341±0.157	0.020±0.003	11.49±3.98
Nothofagus dombeyi	0.008±0.013	0.002±0.002	---
Nothofagus pumilio	0.302±0.055	0.012±0.001	4.67±1.18
Pinus ponderosa	0.000±0.032	0.000±0.002	---
Pseudotsuga menziesii	0.000±0.151	0.000±0.003	---
Ribes magellanicum	0.374±0.073	0.007±0.003	2.73±1.12

increasing C:N ratio throughout deciduous leaves, but the relationship was not significant. Within consumed leaves, the highest values of larval growth were associated with the lowest consumption rates, but no significant relationship was found (Fig. 2).

Klapopteryx kuscheli's consumption and growth in treatments with evergreen leaves were extremely low, almost zero in treatments with exotic conifers, and very low for the evergreen native *N. dombeyi* (Table 2). The conversion of ingested food to body tissue (ECI%) was calculated for the deciduous leaf species set in which there occurred both larval consumption and growth. The quality of food measured as ECI% against leaf resistance did not show a clear trend (Fig. 1) but it tended to decrease with increasing C:N ratio, although there was no significant relationship.
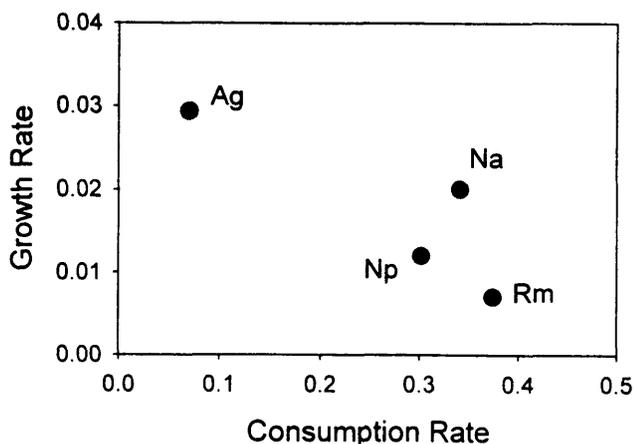

Figure 2. Growth (mg mg^{-1} d^{-1}) of *Klapopteryx kuscheli* larvae as function of leaf litter consumption. **Ag**: *Alnus glutinosa*, **Na**: *Nothofagus antarctica*, **Nd**: *N. dombeyi*, **Np**: *N. pumilio*, **Pp**: *Pinus ponderosa*, **Pm**: *Pseudotsuga menziesii* and **Rm**: *Ribes magellanicum*.

DISCUSSION

The results obtained in our experiment with *K. kuscheli* showed that this shredder was not able to exploit leaf litter with a leaf resistance over 300 g mm^{-2}. When only one food item is offered, attempted feeding should occur even on non-preferred litter species. However, physical features such as size, for collectors, or toughness, for shredders, can limit consumption (Cummins and Merritt 1996) and this was the case in our experiments. The softening of leaf tissues in water is related to time, and tough leaves would require longer immersion periods to be both conditioned and available for shredders (Petersen and Cummins 1974). In spite of that, needles may not be adequate for shredders even when conditioned. For example, needles of *Pseudosuga menziesii* conditioned for five months in the laboratory did not result in body growth for the trichopteran *Lepidostoma unicolor* (Banks) (Grafius and Anderson 1980). In addition, feeding preference experiments on six food items showed that conditioned needles of the Sitka spruce *Picea sitchensis* (Bong.) Carr. were the least consumed item by the amphipod *Gammarus pulex* L. and the trichopteran *Sericostoma personatum* Spence (Friberg and Jacobsen 1994). On the other hand, leaves with resistance less than 150 g mm^{-2}, all from deciduous species, were successfully eaten by *K. kuscheli* during our experiment. Among these, we observed a positive relationship between consumption and C:N ratio. We had hypothesized that those leaves with higher C:N ratio and lower toughness would be more consumed. In part, larvae would tend to feed on more low quality food to satisfy larval nutritional requirements (Iversen 1974, Cummins and Klug 1979) but also on food easy to chew (low toughness) in a cost/benefit balance. In our experiments, larval consumption tended to increase with leaf resistance, but no significant relationship was found, showing that in the range of soft leafy food only C:N ratio governed the consumption. In addition, the expected effect of leaf resistance on larval responses was masked by the lack of statistical difference in toughness between consumed leaves.

Scriber and Slansky (1981) suggested that consumption rate of low quality food could decrease in order to increase retention time in the gut and thus increase assimilation. This homeostatic strategy is used by the elmid *Lara avara* LeConte to gain nutrients from a woody low quality diet (Anderson and Cargill 1987). The response of *K. kuscheli* to low quality food was to increase consumption and not to increase retention. When multiple-choice food experiment were conducted, larvae of *S. personatum* (Trichoptera) tended to prefer and consume faster those items with better quality in a selective response for high nitrogen content (Friberg and Jacobsen 1994). In contrast, no-choice experiments (only one food item) showed that those larvae consumed more quantity of those items with lower N content in a compensatory response, although this behavior was not enough to compensate for body growth. The exotic *Alnus glutinosa*, considered a high quality food item for aquatic macroinvertebrates (Iversen 1974, Grafius and Anderson 1980, Jacobsen and Friberg 1995), showed the lowest consumption by *K. kuscheli*. On the other hand, the shrubby *R. magellanicum* with a higher C:N ratio was the most consumed item, and *N. pumilio* with intermediate values of C:N ratio, also showed intermediate values of consumption.

Food quality has a direct effect on larval growth, and *K. kuscheli* larvae did not grow when tough leaves were offered as food. In treatments with deciduous leaves, larval growth was related to the amount of available nitrogen. Litter with high proportion of nitrogen (e.g., *A. glutinosa)* resulted in a higher conversion of ingested food to body mass, measured as larval growth. In contrast, *N. pumilio* or *R. magellanicum* (lower N content) were more consumed, but growth rates were lower. If the consumer requires an element in a higher proportion than that in the food, the assimilation rates of the non-limiting element will be lowered in order to preserve the internal elemental relationship (Hessen 1997). If *K. kuscheli* has a higher N requirement than that in the leaf litter, then carbon will be no longer the limiting element, and so it would require a larger amount of food to complete its growth. Thus, if an organism is not limited by food quantity (as in this experiment) but the food is of

low quality, and the strategy is to compensate for the poor food quality by increasing consumption, then the maximal body growth would be determined by its processing capability - the ingestion rate, gut capacity and digestion-egestion rates - (Scriber and Slansky 1981). This was shown in treatments with *R. magellanicum* and *N. pumilio* where larval consumption of those leaves, offered in excess, was high but did not compensate for the low nutritious food to achieve similar body growth when compared with *A. glutinosa*. *K. kuscheli* had to consume four times more *N. antarctica* than *A. glutinosa* to achieve 70% of its growth. The C:N ratio of *N. antarctica* was 60% higher than that of *A. glutinosa*, and according to our experiments, it can be hypothesized that *K. kuscheli* varies its carbon ingestion and assimilation to the content of limiting elements such as nitrogen. The ECI% showed a similar trend with growth rate being inversely related to C:N ratio, but the ECI% on *A. glutinosa* was notably higher than that of the native species as reflected by its significant lowest C:N ratio.

Our study showed that the principal limiting condition for *K. kuscheli* is leaf resistance. Leaf resistance was a pre-ingestion barrier to resource accessibility. Among soft leaves, quality was determined by nitrogen content. The facts that the native deciduous plant species offered to *K. kuscheli* in this study produced relatively high consumption (*R. magellanicum*, *N. antarctica*, *N. pumilio*) and relatively low growth (*R. magellanicum*, *N. pumilio*) are likely to have ecological importance both on particulate organic matter dynamics and macroinvertebrate secondary production. The south mountain beech, *N. pumilio*, is the main source of allochthonous input for 1st and 2nd order streams, on an annual basis (R. Albariño, personal observation), because it forms pure stands composing the upper belt of Andean-patagonian forest (Hildebrand-Vogel et al. 1990). In spite of its slow decay rate (Albariño 1997, Albariño and Balseiro 1998), and its relatively low food quality, it can influence secondary production of streams in the area. However, replacement of *N. pumilio* by exotic conifers could produce great changes in shredder dynamics, because of strong differences in leaf litter features of those species. Although it has been shown that pine needles may be consumed by aquatic invertebrates and they can produce body mass increment and/or loss in body fat content (Friberg and Jacobsen, 1999), it is clear that very long conditioning time would be needed. Thus, pine detritus entering a stream as the main food source may alter shredder life cycles. For example, population species normally univoltine have been reported to be semivoltine in low quality-food resource habitats (Brittain 1974, 1978). In addition, the longer leaf litter-conditioning time may increase the probability of downstream loading. Thus, pine needles may be more prone to exportation than *in situ* processing. Since the replacement of native woodland by pine plantations is expected to increase in the Andean area (Schlichter and Laclau 1998), field studies are needed to evaluate how such practices might influence both the community assemblage and secondary production of aquatic invertebrates in Andean headwater streams.

ACKNOWLEDGEMENTS

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