Crayfish process leaf litter in tropical streams even when shredding insects are common

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Abstract. Comparisons of leaf-litter processing in streams suggest that tropical streams have fewer leaf shredders than temperate streams and that insect shredders might be replaced by other taxa such as Crustacea in tropical systems. Australian wet-tropical streams have abundant insect shredders, and also abundant crayfish, which may contribute to litter processing. We monitored litter input and retention in a Queensland rainforest stream to determine availability of litter in different seasons, and we conducted experiments to test the hypothesis that crayfish were important contributors to litter processing. Litter fall peaked in the late dry season and litter accumulated steadily in pools, whereas in riffles, the standing crop was maintained at a threshold level. All accumulated litter was washed from the stream during a flood. The crayfish, Cherax cairnsensis, readily fed on leaves. Its processing rate was related negatively to leaf toughness and positively to leaf nitrogen content. The crayfish assimilated up to 28.5% of the material processed at 24°C, and none at 11°C. These results confirm that there are alternatives to insect shredders in tropical streams, even when insect shredders are abundant.

Additional keywords: allochthonous material, Cherax, decomposition, litter processing, rainforest stream, shredder.

Introduction

Forested headwater stream communities in temperate areas depend on allochthonous detritus inputs from the adjacent terrestrial vegetation (Benfield and Webster 1985; Cummins et al. 1989). However, there is some controversy regarding the relative importance of allochthonous v. authochthonous energy sources in tropical headwater streams (Cheshire et al. 2005; Lau et al. 2009). Whereas some tropical streams have a numerically and functionally important insect shredder guild similar to that of temperate streams (e.g. in peninsular Malaysia; Yule et al. 2009), others are fuelled by primary production, with little contribution of litter to shredding (e.g. in Hong Kong; Lau et al. 2008). In some cases, stream insect shredders are scarce and they are functionally replaced by other taxa – e.g. snails, semi-terrestrial cockroaches, crabs or crayfish (Dobson 2004; Yule et al. 2009). Crayfish are often a conspicuous component of tropical stream communities, yet little has been reported about their contribution to litter breakdown in tropical streams (but see Rosemond et al. 1998). However, they are known to greatly promote litter breakdown in some temperate streams (Usio 2000) and detritus is reported to be their primary food source in many aquatic ecosystems, including streams (Lorman and Magnuson 1978; Growns and Richardson 1988). Recent literature suggests that litter breakdown rates are affected by shredder and litter species diversity, and by the identity of the species involved (Jonsson and Malmqvist 2003a; Bastian et al. 2008). The role of insect shredders in Australian tropical streams is well known (Nolen and Pearson 1993; Bastian et al. 2007), but not that of the crayfish Cherax cairnsensis Riek (Parastacidae), which is a prominent member of the fauna (Boyero et al. 2006).

The aim of the present study was to determine whether crayfish were an alternative litter processor to insects in a tropical stream and, therefore, whether they were an alternative source of fine particulate matter in the detritus-dominated food web (Cheshire et al. 2005). We hypothesised that (1) suitable litter is available across seasons, potentially allowing year-round contributions to the food web, (2) crayfish have no role in litter processing and (3) if a role were to be demonstrated, it would not be influenced by temperature, leaf identity and/or leaf quality (level of conditioning and toughness).

Materials and methods

Study site

The site for the field study was a 400-m reach of Birthday Creek (19°00′S, 146°11′E), commencing 200 m from the stream source. The site is at an elevation of 860 m asl and 80 km north of Townsville, north-eastern Queensland. The climate is tropical and seasonal, with most rain usually falling between December and March. Tropical storms (cyclones) occur unpredictably during the wet season (not every year) and cause severe floods. During the present study, water temperatures ranged from 11.0°C (July) to 21.5°C (February). Stream width was 2.5–4.0 m and the rainforest canopy was unbroken at the site (further details are given in Nolen and Pearson 1992).
Litter fall and standing crop

To test the hypothesis that litter was available across seasons, litter fall was collected monthly from 15 vertical litter traps placed in the riparian vegetation (see Benson and Pearson 1993). Lateral litter input and blow-in were minimal at this site (Benson and Pearson 1993). The standing crop of coarse litter (CPOM 4-1 mm) on the streambed was measured monthly in 10 random 0.25-m² quadrats (five in pools and five in riffles). Litter was wet-weighed in the field to 0.1 g with a Pesola spring balance (Pesola AG, Baar, Switzerland) and returned to the stream. Wood and leaf material were separated before weighing; however, only data on the leaf fraction are presented here. Litter dry weight was estimated from an unweighted least-squares linear regression of litter wet weight vs. oven-dry weight of 1-month’s samples. Raw data were used in the regression because the residuals were normally distributed.

Litter-processing experiments

To test the hypothesis that leaf identity did not affect processing rates by crayfish, leaves from four species of rainforest trees from the riparian zone of Birthday Creek were used in leaf-breakdown experiments. Leaves were chosen partly on the basis of their predominance in stream leaf packs (R. W. Davies, University of Calgary, pers. comm.) and partly to coincide with other studies of leaf processing in Birthday Creek (Nolen and Pearson 1993). The leaf species were from the tree species Apodytes brachystylis Mueller (Icacinaceae), Cryptocarya densiflora Blume (Lauraceae) and Cryptocarya leucophylla Pearson 1993). The remaining leaf material was oven-dried at 65°C for at least 24 h and weighed to the nearest 0.01 g. The amount of leaf material processed was then determined. Treatment values were adjusted for control effects before determining the amount of material processed. All results are expressed as the amount of leaf material processed per gram of crayfish bodyweight.

Experiment 1: processing of leaves of different species and degrees of conditioning by C. cairnsensis

This experiment was conducted to test the hypothesis that leaf species and condition (immersion period) have no effect on the quantity of leaf processed. All combinations of leaf species and condition (2, 4 and 10 weeks’ immersion) were used. The experiment was conducted in three consecutive 11-day phases, one per conditioning time. Each treatment contained a 3-g bundle of each leaf species (12 g total) and one crayfish. This allowed crayfish to choose between four species, all of which had been subjected to the same conditioning period. Ten replicates and five controls were used. For the purposes of analysis, it was assumed that the trends observed were due to effects of species and condition and that time had no effect, because the temperature remained constant (T2.0°C) for the duration of the experiment and the same animals were used each time.

Data were analysed with a split-plot ANOVA (Snedecor and Cochran 1980), with leaf condition (i.e. conditioning period – fixed factor) as the main plot and crayfish mass (random factor) as the subplot. Leaf species identity was a fixed factor. The choice of leaf species to be used in subsequent experiments was based on the results of this experiment. Raw data were used as the assumptions of the ANOVA were met.

We performed a further trial to validate the results of Experiment 1, because the preference for leaves of all conditions was not determined concurrently. Leaves of A. brachystylis (the most preferred species in Experiment 1) were conditioned by placing them in the artificial streams at different times and removing them at the same time so that the crayfish could choose among all conditions of this species. Twelve replicates and six controls were used. Leaves were labelled with Dymo tags (http://global.dymo.com/enAU/Home/default.html). The 12 treatment tanks comprised six with animals from the previous experiment and six with animals collected from the stream immediately before running the experiment. This allowed us to determine whether the prior acclimation of the animals to laboratory conditions had any effect on their performance in previous experiments. The experiment was conducted at 24°C over 4 days. Data were analysed with a two-way ANOVA; again, the untransformed data met the assumptions of the analysis.

Experiment 2: effect of temperature on processing rate, production of fine particulate organic matter and assimilation efficiency of C. cairnsensis

This experiment was conducted to test the hypothesis that temperature has no effect on litter processing and assimilation between Experiments 1 and 2, they were fed on mixed conditioned leaves from Birthday Creek.

Experiments were monitored daily and qualitative observations were recorded along with maximum/minimum water temperatures for each 24-h period. After each experiment, the remaining leaf material was oven-dried at 65°C for at least 24 h and weighed to the nearest 0.01 g. The amount of leaf material processed was then determined. Treatment values were adjusted for control effects before determining the amount of material processed. All results are expressed as the amount of leaf material processed per gram of crayfish bodyweight.

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Experiment 2: effect of temperature on processing rate, production of fine particulate organic matter and assimilation efficiency of C. cairnsensis

This experiment was conducted to test the hypothesis that temperature has no effect on litter processing and assimilation
by crayfish. Trials were run at 18°C and 24°C, temperatures reflecting the minimum and maximum typically measured in Birthday Creek. A. brachystylis, conditioned for 10 weeks, was used because this leaf species showed maximum processing rates in Experiment 1. Approximately 3.0 g of leaf material was wet-weighed, and then placed in each tank with one crayfish. Control tanks included leaf material but no crayfish.

Crayfish in the 18°C treatment were acclimated by lowering the temperature by 3°C every 3 days. During this period, animals were not fed so that any fine organic matter collected at the end of the experiment resulted from processing of the experimental leaves. At the beginning of each experiment, all tanks were cleaned thoroughly and filtered fresh water was added to the tanks.

Five replicates and three controls were used in each treatment. The experiment was terminated after 6 days because animals at 24°C had processed most of the leaf material. Remaining intact leaf material was removed and the water was sieved through 1-mm and 63-mm screens to separate fragmentary coarse particulate organic matter (CPOM) and fine particulate organic matter (FPOM), which were then vacuum-filtered on to pre-weighed Whatman qualitative (No. 1) filter papers. All material was then oven-dried at 65°C for 24 h and weighed to the nearest 0.01 g. The amount of leaf processed and CPOM and FPOM produced were then determined. Adopting the terminology from Bird and Kaushik (1985), assimilation was defined as follows:

$$\text{Mean assimilation efficiency } = \frac{\text{mass processed } - \text{fragmentary mass remaining}}{\text{mass processed}} \times 100$$

where mass processed is the amount of leaf material that has been processed and fragmentary mass remaining is the sum of faecal material, CPOM and fragmentary CPOM. Assimilation estimates may be exaggerated because of the possibility of losses owing to microbial respiration and dissolution of organic material, especially at the higher temperature. Data were analysed with one-way ANOVA; data met the assumptions of the analysis.

Leaf properties

Toughness of each leaf species at each conditioning time was determined with a penetrometer (Graça and Zimmer 2005) and the results were expressed as the mass required to penetrate 1 mm² of leaf surface. Two measurements were taken from each of four individual leaves of each species–condition combination. Data were analysed with a two-way ANOVA, with level of conditioning and leaf species as the two fixed factors; data met the assumptions of the analysis.

Nitrogen content of each leaf species at each conditioning time was similarly determined for (1) fresh green leaves from five trees of each species to give an indication of the amount of within-species variation and (2) senescent leaves of known age that were collected from sheets placed on the forest floor. Senescent M. salicina leaves were not found during this period, so were not available for analysis of nitrogen content.

Results

Litter fall and standing crop

Total litter fall over 8 months comprised (by weight) 75% leaf, 13.5% small wood, 8.6% reproductive material and 2% miscellaneous plant debris. The peak in total litter fall occurred in the late dry season (October–November) and consisted of 94.2% leaf material (Fig. 1a). A secondary peak in the total litter fall in March was caused by the increased fall of wood resulting from Cyclone Ivor. At this time, wood constituted 39.4% of the total litter fall and leaves constituted 45.6%. Following Cyclone Ivor, a predominance of fresh green litter was noted in leaf fall and much new growth was observed in the riparian vegetation.

The equation to describe the relationship between wet and oven-dry weight of CPOM was as follows:

$$\text{Dry weight } \frac{1}{4} 0.2032 \times \text{ wet weight} - 1.7865$$

$$\text{R}^2 = 0.9987, P < 0.001$$:

The monthly standing crop of CPOM was similar in riffles and pools until late summer, when an increase in the pools was
Amount of leaf material processed by crayfish (%)

apparent, reaching a peak of 412 g m\(^{-2}\) in March (Fig. 1b). Heavy rains in late March, following Cyclone Ivor, caused flooding, which washed the accumulated litter from the stream.

**Litter-processing experiments**

All leaf types showed significant linear relationships between leaf wet weight and oven-dry weight (Table 1). The amount of variation explained by the equation (\(r^2\)) ranged from 52% to 97%. The relationships were very similar for the two *Cryptocarya* species and similar for *M. salicina* and *A. brachystylis*, and suggested that the *Cryptocarya* species hold less water than do the other species. *C. cairnsensis* shredded leaf material in the following two ways: usually it held the leaf upright between its chelae and used its maxillipeds to tear small pieces from the leaf edge and transfer them to its mouth; alternatively, it held the leaf flat on the substratum with its chelae and used the chelate peripods to tear small pieces from the leaf edge and transfer them to the mouth. Both modes of feeding were observed in the laboratory and in the stream. The maximum variation in water temperatures in the experimental tanks over any 24-h period was 2.0°C.

**Experiment 1: processing of leaves of different species and degrees of conditioning**

There were significant differences in the amount of leaf processed by *C. cairnsensis* among leaf species (\(F_{3,9} = 21.14, P < 0.0001\)) and among leaf conditions (\(F_{2,0} = 10.47, P = 0.0001\)) (Fig. 2). There was a consistent preference for leaves of *A. brachystylis* and, for those species that were consumed (*A. brachystylis* and *M. salicina*), there was a preference for maximally conditioned leaves. A pairwise comparison of means by the least significant difference method showed processing of *A. brachystylis* to be significantly higher than that of *M. salicina*. Both species were processed in significantly greater amounts than *Cryptocarya leucophylla* or *C. densiflora*. There was no significant difference between the amounts processed of the *Cryptocarya* species (\(t_{1,27} = 2.052, P = 0.05\)). The negative processing values for *C. leucophylla* and *C. densiflora* probably resulted from leaf weight gain owing to microbial growth, as typically occurs during leaf processing (e.g. Pearson and Tobin 1989).

Leaves conditioned for 2 and 4 weeks were not processed in significantly different amounts from each other; however, they were processed significantly less than leaves conditioned for 10 weeks (\(t_{1,18} = 2.101, P < 0.05\)). A significant interaction between the leaf condition and species (\(F_{2,6} = 11.53, P < 0.0001\)) reflects the absence of processing at any condition for

![Fig. 2](image-url)
newly collected crayfish and those that had been acclimated to the experimental conditions. All leaf material processed was converted to fine or fragmentary coarse particulate matter. In contrast, animals at 11°C were less active than animals at 24°C (F1,4 = 0.009, P = 0.75). Correspondingly, the amount of FPOM produced was significantly higher at 24°C (F1,4 = 0.0001). This FPOM consisted of faecal material and fine fragments resulting from the mechanical action of the mouthparts. The shredding activity of the crayfish also produced significantly more fragmentary CPOM at 24°C than at 11°C (F1,4 = 0.0001). Crayfish in the 11°C treatment assimilated no material over the duration of the experiment. All leaf material processed was converted to fine or fragmentary coarse particulate matter. In contrast, animals at 24°C assimilated up to 28.5% of the material they processed and converted 71.5% to fine or fragmentary CPOM.

**Leaf properties**

There was a significant difference in leaf toughness among species (F2,4 = 50.91, P = 0.0001) (Fig. 4). C. densiflora was consistently tougher than all other species whereas A. brachystylis was the least tough of all species at all conditioning times. Differences in the toughness of leaves among the different conditioning treatments were significant (F2,4 = 11.33, P = 0.0001). The decline in toughness owing to conditioning from 2 to 4 weeks was more pronounced than that between 4 weeks and 10 weeks. The lack of an interaction effect (F2,6 = 0.75, P = 0.6144) indicates that condition acts independently of species to affect the toughness of the leaf, and that species has an effect on toughness regardless of the condition of the leaf.

Nitrogen content of leaves ranged from 1.45% (2-week-conditioned C. densiflora) to 2.72% (10-week-conditioned M. salicina) (Fig. 5). Unconditioned green leaves (time zero) of all species had a higher nitrogen content than leaves conditioned for 2 weeks. After the initial leaching of nitrogen from fresh green leaves, there was an increase corresponding to continued conditioning in the stream. The increase was somewhat delayed in C. leucophylla and C. densiflora, suggesting that microbial colonisation of these species was slower. These two species had very similar nitrogen levels. Differences in nitrogen content among species were significant (F1,3 = 17.64, P = 0.0022), as were differences in variously conditioned leaves (F1,3 = 6.82, P = 0.0285). Green leaves from different trees within a species showed no variation in nitrogen content: for A. brachystylis, F1,4 = 0.67, P = 0.626; for M. salicina, F1,4 = 0.80, P = 0.585; for C. leucophylla, F1,4 = 0.25, P = 0.859; and for C. densiflora, F1,4 = 1.64, P = 0.321. There was a significant negative correlation between the amount of each leaf type processed by the crayfish and the toughness of the leaf type (r² = 0.6296, P = 0.0282) (cf. Figs 2, 4). A. brachystylis was the least tough and most preferred at all conditions. M. salicina was tougher and processed less than A. brachystylis. The two species of Cryptocarya were toughest overall and were not processed. Nitrogen content of C. densiflora and C. leucophylla did not increase.
between immersion for 2 weeks and that for 4 weeks, unlike it did for A. brachystylis and M. salicina (Fig. 5).

The amount of leaf processed was positively correlated with the nitrogen content of the leaf type (r = 0.6607, P < 0.0193) (cf. Figs 2, 5). A. brachystylis leaves contained less nitrogen than did M. salicina leaves. The nitrogen contents of C. leucophylla and C. densiflora were lower again, although similar to each other. Nitrogen content was shown to decrease initially from fresh leaves and increase again after conditioning (Fig. 5). A. brachystylis leaves contained less nitrogen than did M. salicina leaves. The nitrogen contents of C. leucophylla and C. densiflora were lower again, although similar to each other. Nitrogen content was shown to decrease initially from fresh leaves and increase again after conditioning (Fig. 5).

The equation that describes the relationship between nitrogen content (%N), toughness (g per 3 mm²) and processing (g per gram bodyweight) is as follows:

\[
\text{Amount processed} = 0.73 \times 80.96 \times \%N - 69.23 \times 10^{-3} \times \text{toughness}.
\]

Discussion

Litter dynamics

Retention of litter in streams provides the critical link between input and storage, which allows utilisation of this energy source by the stream community (Speaker et al. 1984). Litter fall at Birthday Creek reached a peak in the late dry season (spring/early summer) and accumulation in the stream was similar to the long-term trend over 3 years (Benson and Pearson 1993) and to accumulation in Yuccabine Creek, another Queensland rainforest stream (Pearson et al. 1989). Wet-season spates affected litter accumulation, with cyclonic floods flushing all litter from the stream, as normally occurs (Pearson 2005).

Cyclonic activity defoliates trees and initiates a period of leaf flush (newly expanded leaves) (Hopkins and Graham 1987). This period is immediately followed by several months of minimal litter fall (Fig. 3) in which a large proportion of the leaf fall is likely to be fresh. Standing crop was not measured after March; however, other observations have shown that litter gradually builds up in both riffles and pools (Pearson 2005). During this period, the standing crop in riffles may exceed that in pools for a short period, because green leaf litter does not sink in the pools but instead is trapped at the head of riffles.

Processing by crayfish

The results of Experiment 1 indicated a clear preference of C. cairnsensis for well-conditioned leaves; however, regardless of condition, A. brachystylis was preferred over other species. Two effects of conditioning which may act independently to influence the choice are the increase in nitrogen content and the reduction in leaf toughness. Nitrogen is a vital nutrient for animal metabolism and is often a limiting factor (Mattson 1980). Toughness can be regarded as an indicator of the tendency for a leaf to be shredded, and results from a combination of leaf characters such as cuticle thickness, presence of wax, degree of sclerotisation, moisture content and venation density. Coley (1983) found that over 70% of the variation in rates of herbivory could be explained by leaf properties such as pubescence, toughness, water content, protein, fibre and phenolic contents. Of these, toughness was the factor most highly correlated with leaf herbivory.

The results of the present study suggest that, regardless of the nutrient quality of the leaf, there are morphological and behavioural restrictions to processing by crayfish. Thus, the crayfish may be incapable of physically breaking down the tough leaf material, given the morphology of their mouthparts, or a lack of suitable enzymes for digestion may inhibit the utilisation of the leaf material. However, although the inability to break down structural polysaccharides has been reported as widespread among freshwater crayfish (Musgrove 1988), more recent literature has suggested that Cherax species have appropriate cellulose and hemicellulase enzymes (e.g. Byrne et al. 1999; Davison and Blaxter 2005) and are believed to be capable of substantial cellulose and hemicellulose digestion, without the need for symbiotic microorganisms (Jones and DeSilva 1997; Byrne et al. 1999). In the present study, leaf material was not processed when microbial conditioning had not occurred, as evidenced by the lack of increase in nitrogen content after 4 weeks of immersion in stream water. This may simply reflect the preference for more nutrient-rich conditioned leaves rather than an inability to digest leaf material.

An alternative explanation for the leaf preferences is the existence of a factor such as a high level of condensed tannins, which may override the apparent palatability in terms of nitrogen content. Ferns have relatively high levels of such defensive compounds compared with higher vascular plants (B. Jackes, James Cook University, pers. comm.), which may explain why A. brachystylis was preferred over the fern M. salicina, despite the higher nitrogen content of the latter species.

In general, assimilation efficiencies for detritus are low, with means ranging from 6 to 35% (Berrie 1976). Musgrove (1988) found that P. zealandicus had an assimilation efficiency of 0.69.
12–28% when fed on Elodea leaves. C. cairnsensis assimilated up to 28% of the processed leaf material at 24°C, whereas it assimilated none at 11°C. This result, and the finding that only very small amounts of leaf material were processed at 11°C, suggests that the contribution of C. cairnsensis to litter processing in winter will be negligible, although stream temperature does not normally remain as low as 11°C for extended periods (R. G. Pearson, unpubl. data). However, the contribution of C. cairnsensis to litter breakdown in the summer can be important. The population density of C. cairnsensis in Birthday Creek was estimated to be 0.5 animals per m², using mark–recapture and random benthic sampling techniques (J. F. Coughlan, unpubl. data). Given the breakdown rates determined in the present study, it is estimated that 1% of the detritus entering Birthday Creek is processed by the crayfish. Although this might suggest that food is not limiting for this species, except following floods, it is not known how much of the litter fall is useful (i.e. palatable and nutritious); for example, of the common litter species tested here, the Cryptocaria species are apparently unavailable to the crayfish.

**Trophic dynamics**

These results raise interesting questions about the trophic basis of production for C. cairnsensis. Processing rates should be highest in summer (Experiment 2), which is the time when peak litter fall occurs. However, cyclonic and/or monsoonal activity, which is characteristic of the summer months in the tropics, results in heavy rains that flush much of the litter from the stream, as occurred after Cyclone Ivor. Thus, litter that has fallen in October and November will have been subjected to about 4 months of stream conditioning before being washed out. For some species, this may be ample time for leaves to be suitably conditioned, whereas species that appear resistant to microbial colonisation may require longer (e.g. members of the genus Cryptocarya). For this reason, the flush of green litter fall, which is a feature associated with cyclones (Hopkins and Graham 1987), may be of particular dietary importance to stream shredders during the absence of optimally conditioned litter. However, C. cairnsensis did not process fresh leaves, in contrast to the caddisfly larva Anisocentropus kirramus, which processes, and in some cases actually prefers, fresh green leaves (Nolen and Pearson 1993). The inability of the crayfish to process fresh leaves may be due to their mouthpart morphology or to the presence of high levels of defensive compounds that occur in fresh rainforest tree leaves (Janzen 1974). Thus, in post-cyclone periods, the contribution of alternative food supplies, such as animals, or endogenous reserves, may be important for the crayfish.

**Conclusion**

A diversity of shredders

Our results confirmed that litter processing in tropical streams is not the sole preserve of the shredders expected from temperate systems (such as caddisflies, stoneflies and amphipods). In Australian tropical streams, litter decomposition is effected by microbes (Pearson and Connolly 2000), insects (e.g. Nolen and Pearson 1993; Cheshire et al. 2005) and crayfish. Additionally, recent work has suggested that tadpoles have some role in leaf shredding, especially in combination with insects (Iwai et al. 2009), and that a range of invertebrates such as cockroaches and snails can be involved in this process (Yule et al. 2009). It is important that research on litter decomposition identifies the species involved in processing to quantify breakdown rates properly (Jonsson and Malmqvist 2003a) to identify facilitation and interference effects (Jonsson and Malmqvist 2003b; Bastian et al. 2008; Iwai et al. 2009), and to ensure inclusion of all components of the process. Given the relative sizes of insect and crustacean shredders, and the omnivorous nature of crayfish (Growns and Richardson 1988), it is likely that crayfish interfere not only with insect shredding competitively, but also as predators.

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