Effect of forest litter depth on seed germination efficacy of *Rhododendron ponticum*

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Abstract
In Ireland one of the most serious invasive alien species which poses threats to local biodiversity is *Rhododendron ponticum* L. Once established on a susceptible site, *R. ponticum* can kill other plant species in the ground vegetation layer and prevent the regeneration of trees and shrubs, thereby also indirectly affecting the local fauna. Forest floor litter negatively impacts on the germination success of many plant species, and both the amount and distribution of forest litter can influence the establishment of invasive alien species. Many land management practices, particularly in forestry, disturb ground cover leading to soil exposure, which may increase the risk of *R. ponticum* invasion. In this study, the effect of forest floor litter on the germination of *R. ponticum* seeds in five different litter types was assessed. The treatments included bare soil; 1 cm, 3 cm and 5 cm depths of broadleaved litter; and 2 cm conifer litter depth. The results showed a clear relationship between litter type and seed germination success with seeds having poorer success rates in deeper forest litter. This study demonstrated that even small decreases in forest litter depth, sufficient to expose bare soil, facilitates *R. ponticum* seedling establishment. These findings will inform guidelines and standard operating procedures for future forest management plans, particularly in areas that are sensitive to *R. ponticum* invasion.

Keywords: *Invasive species control, invasion dynamics, ground disturbance, woodland management*.

Introduction
Rhododendron ponticum L. is native to an area south of the Black Sea (Caucasus, northern Turkey and the southeast corner of Bulgaria). The now naturalised *R. ponticum* was first introduced into Britain in 1763 from southwest Spain (Coats 1963) and was largely used as an ornamental garden plant. Subsequent introductions to these islands have not been well documented and are believed to have originated from the Black Sea area (Cross 1975, Stace 1991). Its suitability as game cover resulted in the species being introduced into many woodland habitats and it has since become an established invasive species throughout Ireland and Britain (Cross 1981, Gritten 1995, Dehnen-Schmutz et al. 2004).

R. ponticum is an extremely successful invasive species in Ireland (Maguire et al. 2008). It has become established in several Annex 1 habitats as listed under the

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EU Habitats Directive[1], including old oak woodland with *Ilex* and *Blechnum*, which is classified as WN1[2] by The Heritage Council (Fossitt 2000). *R. ponticum* now represents one of the greatest conservation problems in relation to the protection of oak woodlands in Ireland (Kelly 2007). It poses a serious threat to the biodiversity of native flora and fauna as it has important competitive advantages over native understory species (Cross 1975, Dehnen-Schmutz and Williamson 2006, Parrott 2013).

Many morphological and ecological characteristics convey an advantage on *R. ponticum* compared with many native species in Ireland, thus allowing it to outcompete native species on many sites in Ireland. Its rapid growth rates and seedling recruitment, compared with competing native species, are a particular advantage for *R. ponticum* (Erfmeier and Bruelheide 2004). The dark undergrowth and toxic leaf litter of *R. ponticum* combine to produce a sterile ground layer which prevents natural regeneration (Edwards 2006) and has negative impacts on the biodiversity potential of the site (Cross 1975). The reduction in native flora species has a knock-on effect on the abundance of native species that rely on native plants for resources such as food and shelter (Cross 1975).

Forest cover in Ireland currently is 10.5%, well below the EU average of 30% (Forest Service 2013). Afforestation in Ireland got underway at the beginning of the 20th century and remained low in Ireland until the end of 1980s when an improved grant system was introduced. The new system focused on encouraging private land owners to invest in forestry with financial incentives to facilitate biodiversity conservation in plantation forests. Plantation forests in Ireland are required to set aside at least 15% of their land cover for biodiversity enhancement, which essentially means that these designated areas must remain fallow. Should *R. ponticum* establish itself in these areas, as well as significantly reducing the biodiversity viability of the immediate area, the potential success of regenerative schemes like the Native Woodland Scheme is threatened. Under the Native Woodland Scheme forest owners are supported, through the awarding of grants, to plant and maintain stands of native Irish trees, predominately oak (*Quercus* spp.) but also ash *(Fraxinus excelsior* L.*)*, Scots pine *(Pinus sylvestris* L.*)*, holly *(Ilex aquifolium* L.*)* and others. However, the acidic soils favoured by these species are ideal for *R. ponticum*. A study conducted by Harris (2011) into the invasion potential of the species in different habitats found that the highest invasion speeds were in evergreen habitats and the highest invasion densities were found in

[1] The Council Directive 92/43/EEC on the Conservation of natural habitats and of wild fauna and flora, more often known as the Habitats Directive, is a European Union directive adopted on 21st May in 1992 in response to the Berne Convention. It is one of the EU's two directives referring to wildlife and nature conservation, the other being the Birds Directive. The aim of the directive is to protect some 220 habitats and approximately 1,000 species which are listed in the directive's Annexes. Annex 1 refers to habitats.

[2] WN1 is the classification for Oak-birch-holly semi-natural woodland.

open habitats; however, deciduous habitats displayed "intermediate invasion potential that is most vulnerable to relatively rapid and dense invasion". Should it establish itself as an understory in these stands, it invariably prevents the natural regeneration of native trees and suppresses ground flora.

A study conducted by Baker (1974) identified the attributes of an "ideal weed", which included fast vegetative growth to reach flowering stage, production of large quantities of seed, vegetative propagation and non-specialized pollination systems and germination requirements. While these characteristics describe the ecophysiology of *R. ponticum*, they are not the only reasons for its successful establishment in Ireland. In its native habitat (Iberia, Bulgaria), *R. ponticum* occurs in small relict populations and is not considered invasive (Mejías et al. 2002). In Turkey and Georgia it is an integral part of the forest flora and its abundance is limited by drought and by vigorous competition. Where a forested area is clear-felled *R. ponticum* spread becomes aggressive, quickly colonizing the disturbed site, in a similar manner as occurs in Ireland.

The continued requirement for *R. ponticum* control in Ireland's native woodlands means that the demand for *R. ponticum* control remains an important management consideration. Despite the clear need for effective *R. ponticum* control strategies, no definitive intervention has been established to date and there is a lack of clear scientific evidence for some commonly implemented management and control strategies (Tyler et al. 2006).

Once they reach maturity, *R. ponticum* plants produce large numbers of small wind-dispersed seeds (Cronk and Fuller 2001). The seeds are non-dormant and germinate quickly after dispersal (following five or six days in favourable conditions). Most dispersed seeds travel 10 m or less, particularly in open habitat, but providing wind speed is sufficient the seeds have the potential to travel 100 m or more (Stephenson et al. 2007). *R. ponticum* seed production has been facilitated in Ireland by native generalist pollinators, mainly bumblebees (*Bombus* spp.) (Stout 2007).

An *R. ponticum* inflorescence can typically produce up to 5,000 seeds and on average a 12-year-old tree can produce up to 1 million seeds per annum. The capsules dehisce during the winter months and early spring, dispensing seeds roughly 0.4-1.0 mm in length and weighing 0.063 mg (Cross 1975, Mejías et al. 2002). The seeds are similar in weight to those of other ericaceous plants and are regarded as some of the smallest seeds in the plant kingdom (Salisbury 1942). They need light to germinate, but low intensities will suffice (Mejías et al. 2002, Erfmeier and Bruelheide 2010). The viability of seeds kept in the dark declines steadily with time and after 160 days no germination occurs (Cross 1981).

Forest litter can affect *R. ponticum*'s establishment by influencing the microclimate (Fowler 1988), nutrient cycling (Proctor et al. 1983), allelopathic interactions (Rai and Tripathi 1984), or via the physical barrier created by the leaves themselves

(Sydes and Grime 1981). Forest litter generally has a negative effect on germination success (Xiong and Nilsson 1999). It can also have varying effects on relative species abundance within a community (Carson and Peterson 1990). There are many reasons for this, including the altering of moisture, light and temperature regimes for competing neighbouring seeds. Litter depth affects germination and subsequent seedling establishment in species that produce small seeds (Xiong and Nilsson 1999). Seeds produced by large-seeded species tend to produce more robust seedlings and are generally less affected by the presence of forest litter (Molofsky and Augspurger 1992, Myster 1994).

Germination of *R. ponticum* seeds can be successful on many different types of substrate and low light levels are the most common limiting factor (Cross 1981, Mejías et al. 2002). In woodlands, disturbance of the ground cover caused by forest management practices, animal grazing or fallen trees, creates gaps in the canopy allowing sufficient light (for germination) to reach the forest floor. As the amount and distribution of forest litter can influence the establishment of *R. ponticum* (Stephenson et al. 2006), the management of forest litter may offer an opportunity to reduce the risk of *R. ponticum* invasion. This scenario is more applicable in susceptible sites such as forests with an existing *R. ponticum* infestation or plantation forests with mature *R. ponticum* plants on neighbouring land.

The aim of this study was to investigate the effect of litter depth on the germination success of *R. ponticum* seeds using seeds collected from plants in an Irish plantation forest. In this study, the germination of *R. ponticum* on forest litter of three different depths and one conifer litter treatment was compared with the germination of *R. ponticum* seeds on bare soil.

Materials and methods

Seed collection and preparation

R. ponticum seeds were collected from two plants located on the edge of a stand of Sitka spruce (*Picea sitchensis* (Bong.) Carr.) in Deerpark, Lismore, Co. Waterford. The stand was planted in 1985 and, as *R. ponticum* in this area is invasive, the plants were no more than 26 years old. One of the shrubs was 2.5 m in height with a crown circumference of 13.4 m and the other was 2.0 m in height and 9.5 m in circumference.

Twenty racemes were collected from each *R. ponticum* plant on January 15th 2012. On average each raceme held 15 seed pods. The following day each seed pod (still attached to its stalk) was separated from its raceme and placed in paper bags. A total of 286 seed pods were harvested from one plant and 306 from the other. The paper bags were stored in a ventilated room under ambient conditions (20 ± 2 °C) for two weeks after harvesting. The seeds used in this study were all from one plant, with the seed from the other one being retained as a backup. Each bag was shaken lightly prior to the removal of the pods to encourage the release of seeds from pods that had naturally opened. The pods were then removed leaving the seeds at the bottom of the paper bag. The seeds were then assigned to 15 batches with each batch containing 1,050 seeds.

Seed viability test

To assess the quality of each batch of seeds, and to ensure that there was no difference in viability between batches, a germination test was carried out in the laboratory. The viability of the seeds was tested using 50 seeds randomly selected from each batch which were sown on filter paper in separate 12 cm Petri dishes and soaked with 8 ml of distilled water (saturation point). The seeds were allowed to germinate in a propagator (Biogreen™ heated propagator) that was kept at a constant 20 °C with a 16-h light cycle (approximate light intensity was 202 μmol s^{-1} m^{-2}). The position of each Petri dish was assigned randomly in the propagator then swapped every three days to mitigate any effect of position on the outcome of the germination test. Distilled water was added as required to ensure that moisture was not a limiting factor in germination success. The number of successfully germinated seeds was monitored for up to eight weeks following sowing.

Germination experiment

The main experiment to test the germination of *R. ponticum* seeds on five different depths of forest litter was carried out in a climate controlled grow-house set at 20 °C ± 4 °C with 16 hours of light per day (approximate light intensity of natural light was 360 μmol s^{-1} m^{-2}). To enhance natural light, high pressure sodium lights were employed when natural light fell below 216 μmol s^{-1} m^{-2}, thus ensuring the minimum illumination value over the experiment was 180 μmol s^{-1} m^{-2} and the maximum value was 240 μmol s^{-1} m^{-2}. Fifteen (5 treatments × 3 replications) 65 L trays (0.45 m^2 base area), with holes drilled in the base to allow for drainage, were used in this experiment. Each tray held 8 cm depth of milled sphagnum peat substrate. Soil pH level was measured in each tray prior to sowing of seeds and ranged between 4.5 and 5.1. Each tray was divided in six equal sub-plots to facilitate the sowing of seeds and subsequent counting of any successfully germinated seeds. Tap water was supplied through the station's irrigation system once daily to ensure that the soil was kept moist throughout the test period.

Five different litter treatments were used in this experiment as described in Table 1. The broadleaf forest litter consisted of a mixture of litter from four common tree species: beech (*Fagus sylvatica* L.), oak (*Quercus* spp.), ash and holly. These were chosen to represent the range of leaf litter most commonly found in Irish broadleaved forests. The conifer needles were obtained from a stand of Sitka spruce. The forest litter was collected two weeks prior to the beginning of the experiment and allowed to dry in a storage area held at 20 °C.

To standardise the amount of litter used across each replicate for each treatment the

Table 1: *Details of the five litter treatments.*

Treatment	Litter type	Litter depth (cm)	Litter mass (g m^{-2})	Exposed soil (%)
1	Bare soil	0	0	100
2	1 cm Broadleaf	1	150	35
3	3 cm Broadleaf	3	210	12
4	5 cm Broadleaf	5	415	0
5	2 cm Conifer	2	398	0

required litter mass per unit area was calculated. The weighed litter was then spread evenly over the tray prior to broadcasting of *R. ponticum* seeds. The litter was spread evenly across the trays to mimic the natural state of forest litter wherein the lower the amount of litter found on the forest floor the higher the area of exposed soil present, so the amount of exposed soil was proportional to the amount of litter used. Different depths of conifer needles were not considered, mainly because this type of litter forms a uniform carpet on the forest floor preventing direct access of the seed's radicle to the soil. Each batch of 1,000 seeds was divided into six equal parts (by weight), which were spread evenly over one of the sub-plots on the garden trays. The position of each tray on the bench was randomised each week. The number of seeds that had germinated in each tray was recorded weekly until germination ceased in all trays at 16 weeks after sowing.

Data analysis

Germination success was calculated as the number of germinated seedlings expressed as a percentage of the total number of seeds sown. As the data from the germination results were non-parametric (and not normally distributed), a Kruskal-Wallis test was used to test for differences among the treatments. Pair-wise comparisons were made between individual treatments using Tukey's wholly significant tests. Weekly germination rates for each treatment were also recorded. Daily rates were then calculated (number of seeds germinated during one week divided by seven days). All results are presented as means and standard errors and data analysis was conducted using Minitab, version 16.

Results

Seed viability test

The mean germination success was 82% ± 0.4% after four weeks for all 15 batches of seeds. The batch with the lowest number of germinated seeds produced 76% germinants while the batch with the highest number of seeds resulted in 90% germinants. The standard errors for the 15 batches overlapped, indicating that batch effects were not significant. No further germination occurred after four weeks.

Germination experiment

The results of the Kuskal-Wallis test showed that treatment effects were significant ($H = 13.5$, $df = 4$, $P < 0.01$). Pair-wise comparisons between the treatments showed that bare soil and the 1 cm broadleaf treatment resulted in higher germination rates, significantly different from the remaining treatments and from each other (all $P < 0.05$) (Table 2). The 2 cm conifer treatment also resulted in a higher germination rate of *R. ponticum* seeds than the 5 cm broadleaf treatment ($P < 0.05$). The remaining comparisons indicated that the 3 cm broadleaf treatment was equally good at suppressing the germination of *R. ponticum* seeds as both the 2 cm conifer and 5 cm broadleaf treatments ($P > 0.05$).

Over half of *R. ponticum* seeds germinated successfully on bare soil (55 ± 2.0%) and seed germination ceased at week eight (Figure 1). The majority of these seeds germinated during weeks four to six (75% ± 0.3%). Seed germination success on 1 cm of broadleaf litter was 21% ± 1.5%. The highest germination occurred during week five (10 ± 1.8 seeds per day). No further germination occurred after week nine.

The germination success rate of *R. ponticum* seeds on 3 cm of broadleaf litter was 2% ± 0.2%. On the trays with 5 cm broadleaf litter fewer than 1% ± 0.1% of seeds germinated successfully. Only 7% ± 0.4% of the seeds broadcast on conifer litter germinated.

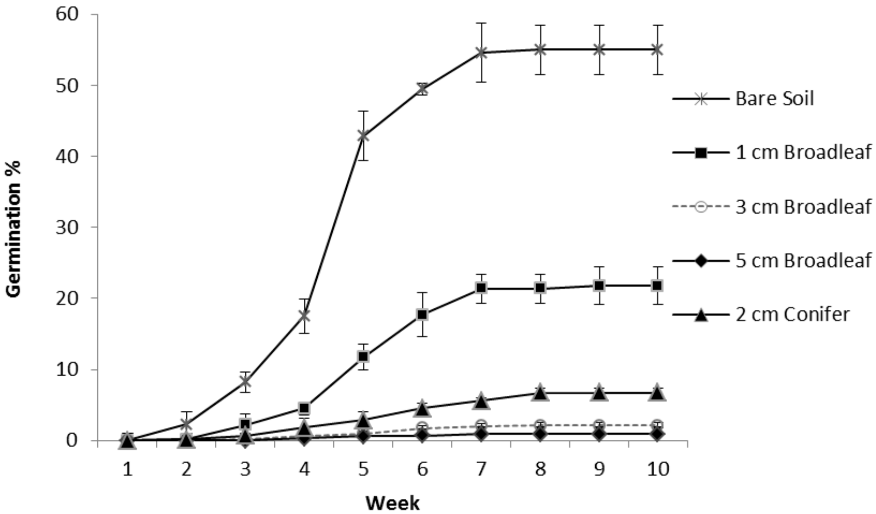

Figure 1: *Mean (± S.E.) cumulative germination rate (percentage of successfully germinated seeds) of R. ponticum seeds in different forest litter treatments over 10 weeks.*

Table 2: *Pair-wise comparisons of the litter treatments (n = 15).*

Comparison	P-value	Comparison	P-value
Bare vs. 1 cm	0.03	1 cm vs. 5 cm	0.02
Bare vs. 3 cm	0.02	1 cm vs. Conifer	0.03
Bare vs. 5 cm	0.01	3 cm vs. 5 cm	0.12
Bare vs. Conifer	0.02	3 cm vs. Conifer	0.06
1 cm vs. 3 cm	0.03	5 cm vs. Conifer	0.02

Discussion

Germination success in the greenhouse was highest on bare soil and lowest on the deepest (5 cm) broadleaf litter indicating that litter depth influences germination. Germination declined as the litter depth increased. While there was an obvious difference between bare soil and the median depth of litter tested (3 cm), there was no significant difference in the germination success between the two deeper litter depths (3 cm and 5 cm). The addition of a litter layer as a measure to control invasive species has not been used widely, perhaps because it can also hinder the establishment of desired species (Sydes and Grime 1981) or provide protection for seeds from predators (Cintra 1997). The manipulation of forest litter depth is not currently part of best practice for *R. ponticum* control in Ireland (Barron 2008, Higgins 2008, Maguire et al. 2008). However, the physiological characteristics of *R. ponticum* seeds (rapid germination and lack of dormancy) makes this species an ideal candidate for a novel control programme involving the modification of forest litter depth (Stephenson et al. 2006). For example, on a clearfell site sensitive to *R. ponticum* invasion, instead of using brash to build windrows, the excess timber could be mulched and used as a litter layer to prevent *R. ponticum* seed germination. However, it should be noted that mulch may display different morphological properties than that of leaf litter, such as a greater ability to retain moisture; more prone to moss growth etc, so it would be prudent to examine *R. ponticum* seed success on mulch in greater detail before recommending this approach as a control measure.

The germination response differed between the litter treatments, with the deeper litter layers perhaps preventing sufficient light reaching seeds that were in contact with soil. However, other seeds may have lacked sufficient vigour to allow the radicle elongate to make contact with the soil surface (Harper et al. 1970). On conifer needle beds in this study just 7% of the seeds germinated and it is likely that none of the resulting seedlings could establish or develop further. The emerging seedling radicles probably degenerated because they could not establish contact with the soil surface. In the case of species that produce small seeds the ability of the seed to germinate is not the only factor in its success in producing a healthy plant (Xiong and Nilsson 1999). A study to determine the maximum length that the radicle of *R. ponticum* seeds achieves before energy reserves become depleted and degeneration commences would be useful.

As *R. ponticum* seeds require adequate access to bare soil, or soils covered in bryophyte carpets (Cross 1981), land disturbance plays a significant factor in the spread and recruitment of this invasive species. The results of this study demonstrate that a reduction in forest litter depth, sufficient to expose bare soil, facilitates *R. ponticum* seedling establishment. Conversely the delicate ephemeral nature of *R. ponticum* seeds means that an increase in forest litter may prevent seed germination. *R. ponticum* seeds are small and delicate, they are non-dormant, germinate quickly and need light to do so (Cross 1981). Once *R. ponticum* seeds have become fully imbibed, seed germination must commence soon afterwards otherwise the seeds will degenerate. For example Mejias (2002) shallowly buried packets of 20 seeds for nine months, but once recovered, none of the seeds germinated on filter paper. Cross (1975) observed that no fully imbibed seeds germinated in the light following storage for 161 days in the dark. Erfmeire and Bruelheide (2005) compared the germination of Irish-sourced seeds against native Spanish and Georgian seeds and found that, while there was no difference in optimum germination temperature or maximum germination rate, the seeds sourced in Ireland germinated more rapidly in response to treatment. These studies reported similar rates of germination as observed in the current study. No seeds germinated after more than eight weeks, suggesting that *R. ponticum* seeds do not retain viability for much longer than this under the conditions evaluated in this study.

Differences in physical properties of litter are likely to result in different light, temperature and moisture conditions for seeds found on a forest floor (Facelli and Pickett 1991). It was beyond the scope of this study to examine the potential effects of light, temperature conditions and moisture availability on the germination of *R. ponticum* seeds. Previous studies have demonstrated the proportional relationship between different litter depths and germination success in small-seeded species (Molofsky and Augspurger 1992, Myster and Pickett 1993, Xiong and Nilsson 1999). In nearly all cases, the greater the depth of the forest litter the less favourable the conditions are for seed germination. The conifer-needle treatment (2 cm layer) had a greater mass than that of the 3 cm broadleaf treatment and resulted in no exposed soil. The conifer needle treatment had a higher germination success rate than that of the 3 cm broadleaf treatment, although bare soil was not exposed. This highlights how a change in litter type can change the dynamics of the litter depth/germination success relationship. It is, however, unlikely that these germinants would establish successfully if the radicle is unable to make contact with the soil surface. It would be useful to examine different depths of conifer needles to simulate the edge of the forest effect where needle depth would be shallower and *R. ponticum* would be more likely to establish.

Using models to estimate colonising potential of an invasive species is an established tool used by ecologists (Bezrukova et al. 2012). According to Stephenson (2006) (and later demonstrated by Harris (2011)) there is substantial potential for the development of spatial population models to predict the colonisation of *R. ponticum* in sensitive habitats. Although many habitat requirements of *R. ponticum* have been described in qualitative terms, quantitative information is important in designing a predictive model in ecology (Guisan and Zimmermann 2000). Quantitative data, such as the data described in this paper, can be integrated into a spatial population model which in turn can aid land managers in designing optimum control strategies against the spread of *R. ponticum*.

Conclusions and recommendations

Despite a good understanding of the nature of the threat posed by invasive species few eradication programs have been a complete success. If the infestation is identified early and all individuals are removed before they have a chance to seed, then eradication can be successful (Mack and Lonsdale 2002). If the infestation is allowed time to establish, then complete eradication is almost impossible. The only available course of action is then containment. Both actions require significant expenditure, the heavier the infestation the greater amount of resources needed to combat it. Many alien species do not have a detrimental effect on native ecosystems, as only a small fraction of them become insidious (Mooney and Cleland 2001). An understanding of why a particular species, compared with another, becomes successful in establishing itself in an unfamiliar habitat is important if an effective control programme is to be developed. As mentioned above, litter depth is not commonly used as a control method for invasive species and forest litter depth is not currently considered as part of a targeted control program for *R. ponticum* in Ireland. However, the physiological characteristics of *R. ponticum* seeds make the species an ideal candidate for a novel control programme involving forest litter depth.

The establishment of *R. ponticum* in an area is often very difficult to reverse. Established colonies of *R. ponticum* will persist indefinitely spreading to their ecological limit, particularly in sensitive ecosystems. Therefore the choice for the landowner is a pre-emptive one; prevention rather than cure. Better awareness and legislation coupled with defined identification and prevention tools will help to prevent new invasions. As *R. ponticum* seeds need adequate access to bare soil (or soils covered in bryophyte carpets) (Cross 1981), land disturbance plays a significant factor in the spread and recruitment of this invasive species. This experiment demonstrates that a small decrease in forest litter depth, enough to expose bare soil will facilitate seedling establishment. Conversely a small increase in forest litter can prevent significant germination. The results of this study should be incorporated into guidelines and standard operating procedures for future forest management plans, particularly in areas which are sensitive to *R. ponticum* invasion.

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