

Centaurea Species: the Forb That Won the West

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Abstract: Grasslands of the western United States and Canada are being converted to ecosystems that resemble "old fields," dominated in terms of percent cover or biomass by forb species. In particular, five species of the genus *Centaurea* (star thistle, diffuse, spotted, squarrose, and Russian knapweed) have invaded millions of hectares of western United States and Canadian grasslands. *Centaurea* species are fundamentally different from the preexisting dominant species and may exploit changes in resource availability to become established. We suspect that they then maintain dominance by preventing resources from returning to levels that favor the native species. Increased atmospheric nitrogen deposition, reduced fire frequency, and, possibly, direct and indirect fertilization resulting from cattle grazing appear to have reduced the historically strong nitrogen limitation to which native species of western grasslands are adapted. We suggest that the success of *Centaurea* species in dominating grasslands is explained by their ability to compete successfully for the new limiting resource or resources. Our preliminary evidence suggests that phosphorus limitation or a colimitation of phosphorus and water best explains the current dominance patterns.

Especies de *Centaurea*: la Hierba que Conquistó el Oeste

Resumen: Los pastizales del oeste de Estados Unidos y Canadá están siendo convertidos en ecosistemas que asemejan "campos viejos", dominados por especies herbáceas en términos porcentuales de cobertura o biomasa. En particular, cinco especies del género *Centaurea* (*centaura estrella*, *difusa*, *manchada*, *escamosa* y *Rusa*) han invadido millones de hectáreas de pastizales del oeste de Estados Unidos y Canadá. Las especies de *Centaurea* son fundamentalmente diferentes a las especies dominantes preexistentes y pueden explotar cambios en la disponibilidad de recursos para establecerse. Sospechamos que luego mantienen su dominancia previniendo que los recursos retornen a niveles en los que favorecen a especies nativas. El incremento en la deposición de nitrógeno atmosférico, la reducción en la frecuencia de fuego y, posiblemente, la fertilización directa e indirecta resultante de la actividad ganadera parecen haber reducido la limitación histórica de nitrógeno a la que se adaptan las especies nativas de pastizales del oeste. Sugerimos que el éxito de las especies de *Centaurea* dominantes en pastizales se explica por su habilidad de competir exitosamente por el(los) nuevo(s) recurso(s) limitante(s). Nuestra evidencia preliminar sugiere que la limitación de fósforo o una colimitación de fósforo y agua explican mejor los patrones de dominancia actual.

Introduction

Multiple factors have been proposed as the ecological mechanisms responsible for the invasion of natural communities by nonindigenous plants (Lonsdale 1999). Ecologists are able to provide after-the-fact explanations for in-

vasions, but predicting which species will be invasive and which ecosystems are particularly invulnerable remains difficult (Williamson 1999). Plant invasions have been addressed in two general contexts in the ecological and conservation literature: factors regulating the number of nonindigenous species invading natural systems and mechanisms by which specific invaders achieve dominance in specific ecosystems. The latter focuses on the extent of resource preemption by invaders rather than the presence, absence, or number of invaders. Indeed, the factors

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Paper submitted June 7, 2000; revised manuscript accepted February 28, 2001.

that affect the number of nonindigenous species that can invade an ecosystem may well be different from the factors that control dominance of nonindigenous invaders.

We focused on the second issue and attempted an after-the-fact explanation of a regional phenomenon. Specifically, we asked why many grasslands of the western United States and Canada are being converted to ecosystems that resemble "old fields," dominated in terms of percent cover or biomass by nonwoody herbaceous species (forbs). In particular, five species of the genus *Centaurea* (star thistle [*C. solstitialis*], diffuse [*C. diffusa*], spotted [*C. maculosa*], squarrose [*C. virgata*], and Russian [*C. repens*] knapweed) have invaded millions of hectares of both C₃- and C₄-dominated North American grasslands (Sheley & Petroff 1999). Based on county and state lists, the genus *Centaurea* is the most abundant noxious weed in the western United States (Skinner et al. 2000). The area estimated to be invaded by *Centaurea* species is larger than that occupied by other nonindigenous plant genera capable of dominating and persisting as dominants in grassland ecosystems. Our question focuses on the success of a single genus, but the mechanisms we discuss may be applicable to other forbs, such as leafy spurge (*Euphorbia esula*), that have also dominated substantial areas of former grasslands in the western United States and Canada.

Based on the literature, two general mechanisms by which large-scale resource preemption by an invasive species occurs seem plausible. First, the nonindigenous species is an ecologically equivalent species adapted to the climate and the exact suite of resources provided by the native ecosystem, and it has a competitive advantage over the native species. The species may have genetic traits that allow it to deplete a resource more rapidly or to a lower level than the native species does (i.e., winner of resource limitation competition; sensu Tilman 1985). The nonindigenous species might have greater net reproductive capacity than native species, through, for example, evasion of species-specific predators or parasites that reduce its relative competitive ability or net reproductive output in its native range.

A second general explanation for large-scale resource preemption is that the nonindigenous species functions fundamentally differently from preexisting species and has the ability to modify resource availability in ways that subsequently exclude the native species. Species with these characteristics may simply exploit changes in resource availability, such as increased nutrient availability following disturbance, to become established, and then maintain dominance by preventing the resources from returning to levels that favor the native species.

Consistent with the second general explanation, we suggest that a change in the ratio of resources available over a large part of the United States and Canada has allowed *Centaurea* species to invade. Subsequently, the *Centaurea* species may have altered resource availabil-

ity and competitive hierarchies in grasslands in ways such that they benefit and dominate. In particular, we suspect that region-wide nitrogen (N) fertilization has changed the suite of traits that make a competitor successful. Increased atmospheric N deposition, reduced fire frequency, and, possibly, direct and indirect fertilization that results from cattle grazing have reduced the historically strong N limitation to which species of western grasslands were adapted (Hooper & Johnson 1999). With greater N availability, slow-growing perennial grasses with low N requirements may no longer have a distinct competitive advantage over fast-growing, short-lived species with high N requirements (Chapin et al. 1986).

If *Centaurea* species function as early seral, fast-growing, high-N-demanding species (Story et al. 1989), then they are probably favored regionally by the greater N availability. *Centaurea* species may perpetuate the high N availability through positive feedback mechanisms. For example, early successional species, including many weedy forbs, allocate less carbon to belowground structure, reduce carbon storage in soil, reduce root and litter ratios of carbon (C) to N, and increase N mineralization and mineral N leaching (Wedin & Tilman 1996). The net effect is to increase N availability in soils relative to that of more mature soils in which most of the total N is immobilized in accumulated organic matter.

The ability of *Centaurea* species to dominate the grasslands they invade is not explained fully by the presence of more N, however. Abundant N should allow establishment of the many early successional native species that dominate transiently following disturbance. Numerous other nonindigenous weedy species favored by higher N availability also should be competing for dominance. Instead, *Centaurea* species dominate. We suspect the ability of *Centaurea* species to dominate invaded grasslands is explained by their ability to compete successfully for the "new" limiting resource or resources. Our preliminary evidence suggests that phosphorus (P) or a colimitation of P and water best explains current dominance patterns.

Historical Nitrogen Limitation

Historically, western grassland ecosystems may have resisted invasion by nonindigenous species because nonindigenous species were not successful competitors for N in N-poor environments. Most, and perhaps all, of the western grasslands of the United States and Canada were N limited or N and water colimited (e.g., Vitousek & Howarth 1991; Hooper & Johnson 1999). The N limitation resulted primarily from high fire frequency, but it was enhanced by the growth characteristics and efficient use of N by the dominant grasses (e.g., Seastedt et al. 1991; Wedin & Tilman 1996). Over the last 100–150 years, European settlement and subsequent urbanization of areas for-

merly dominated by grasslands have resulted in changes in the historical range of variability of disturbances.

Fire suppression, chronic grazing, and increased atmospheric deposition of N have increased N availability in soils (Day & Detling 1990; Holland & Detling 1990; Ojima et al. 1990; Seastedt et al. 1991; Riggan et al. 1994; Steinauer & Collins 1995; Blair 1997; McNaughton et al. 1997; Fenn et al. 1998; Baron et al. 2000). After 20 years of fire suppression in mesic grasslands, N limitation, as measured by enhanced productivity with the addition of N, has largely been eliminated (Seastedt et al. 1991). In many areas of the western United States and Canada, fire has been suppressed for over a century (Houghton et al. 1999; Miller & Rose 1999; Soulé & Knapp 1999).

In mixed-grass and tallgrass prairies, chronic grazing by cattle has replaced infrequent grazing by bison. Chronic grazing often enhances the availability of inorganic N (Day & Detling 1990; Holland & Detling 1990; Steinauer & Collins 1995; McNaughton et al. 1997). In particular, livestock grazing can result in patches of bare, disturbed soils and patches of N-rich soils, and the destruction of soil organic matter that can accompany overgrazing can generate a substantial amount of inorganic N (Belsky & Gelbard 2000).

Finally, atmospheric N deposition has increased substantially in most industrial nations (Vitousek et al. 1997), particularly in the Colorado Front Range (Williams et al. 1996; Baron et al. 2000). Feedlots throughout the western United States create localized plumes of ammonia gas that can fertilize adjacent areas (Baron et al. 2000). Although much of the western United States is not exposed to the high levels of N deposition that plague the eastern United States and Europe, even low levels of anthropogenic N input may be sufficient to cause measurable changes in ecosystem properties (Baron et al. 2000). The effect of even the small increases in N deposition, combined with fire suppression, may cause significant changes in ecosystems adapted to frequent fires that maintained low N.

The magnitude of the increases of available N in soils resulting from anthropogenic sources is unknown for much of the grassland of North America. But contributions to N enrichment from fire suppression, cattle grazing, and atmospheric deposition are cumulative, and N enrichment is predictable in terms of its effects on dominant species. Increases in both available N and CO₂ favor early seral species and C₃ species over late-successional and C₄ species (Hobbs & Huenneke 1992; Wedin & Tilman 1996; Dukes & Mooney 1999). In tallgrass prairie, fire suppression and N fertilization caused a shift from dominance by C₄ grasses to dominance by C₃ species (Seastedt et al. 1991; Collins et al. 1998). The cumulative effects of 12 years of N deposition on Minnesota grasslands included decreased species diversity and carbon storage, reduced root and litter C:N ratios, increased N mineralization and mineral N leaching loss, and shifts in

composition from C₄ to C₃ dominance (Wedin & Tilman 1996). In naturally low-nutrient serpentine grasslands, increased nutrient availability alone (without physical disturbance) favored the invasion and persistence of nonindigenous species and caused a greater increase in aboveground biomass than in belowground biomass (Huenneke et al. 1990). Twenty years after experimental fertilization in the shortgrass steppe of Colorado, *Kochia scoparia*, a nonindigenous forb, persisted and maintained more rapid N cycling than in surrounding native shortgrass prairie (Milchunas et al. 1995; Vinton & Burke 1995).

Multiple Resource Limitation

Increased N availability and interruption of soil succession could explain the reduced competitiveness of native perennials, but existing data do not support the hypothesis that *Centaurea* species are better competitors for N or that they benefit directly from added inorganic N. If increased N availability and superior acquisition of N explained *Centaurea* dominance, then reduction of available N should reduce the dominance of *Centaurea* relative to perennial species that use N more efficiently. Reever-Morghan and Seastedt (1999) found that 3 years of organic carbon additions to mixed-grass prairie containing both western wheatgrass (*Agropyron smithii*) and diffuse knapweed (*C. diffusa*) significantly reduced total plant biomass but did not reduce the relative biomass of *C. diffusa* or significantly increase the relative biomass of *A. smithii*. There was no evidence that *C. diffusa* was a better competitor for N. In a similar experiment, we found that addition of C to a C₄ grassland invaded by *C. diffusa* decreased available N concentrations, labile P concentrations, and the growth of both *C. diffusa* and buffalograss (*Buchloe dactyloides*) (unpublished data). Carbon addition probably immobilized the N and P in microbial biomass. Our data suggest that the reduction in total plant biomass with C addition (in our preliminary study and in that of Reever-Morghan & Seastedt [1999]) resulted from the reduction of the absolute abundance of both elements rather than from a shift in the N:P ratio.

In a greenhouse study of competitive interactions in soils with a range of added N, Lindquist et al. (1996) found that spotted knapweed (*C. maculosa*) was not a better competitor for N than bluebunch wheatgrass (*Agropyron spicatum*) or Idaho fescue (*Festuca idahoensis*). The growth of the native grasses was neither increased nor suppressed in the presence of *C. maculosa*, regardless of the amount of N added. Similarly, in a fertilization study conducted in a mixed-grass prairie invaded by *C. diffusa*, flowering *C. diffusa* individuals did not respond significantly to added N (mean plant biomass 10.3 g in control plots vs. 12.9 g in N-treated plots; Fig. 1) (T. R. Seastedt, unpublished data). Nitrogen additions

did not significantly increase plot productivity, although non-*Centaurea* plant biomass did exhibit a slight but nonsignificant increase (114 g/m² in controls vs. 138 g/m² in N-treated plots). These results are consistent with the contention that native prairie species are no longer strongly limited by N.

Changes in N limitation may have shifted many North American grasslands from a system in which the dominant species were limited by a common single resource (N) to a system in which P, water, or other resources differentially limit species. The species that is able to sequester the next most limiting nutrient should become dominant. In the fertilization study in the mixed-grass prairie invaded by *C. diffusa* (T. R. Seastedt, unpublished data), *C. diffusa* responded strongly to P additions (Fig. 1). Average biomass of flowering individuals was 57.2 g/m² (6.2 g per individual) in controls versus 84.2 g/m² (17.6 g per individual) in plots with added P ($p < 0.01$ for transformed, per-plant weights). In contrast, non-*Centaurea* vegetation showed no significant response to P (129.7 g/m² in control plots vs. 118.6 g/m² in plots with added P). These results suggest that *C. diffusa* is limited P rather than N and either that the non-*Centaurea* biomass is not limited by P or that *C. diffusa* is a better competitor for P. Although individual species in a community may be limited by a resource other than the one that limits the dominant species, the response of the dominant species will largely determine the entire community's response (Vitousek et al. 1998). No previous North America grassland studies have shown the dominant species, and therefore the community, to be limited by P.

Several studies suggest that *Centaurea* species are strong competitors for limiting resources. Callaway and Aschehoug (2000) showed that *C. diffusa* is a better competitor

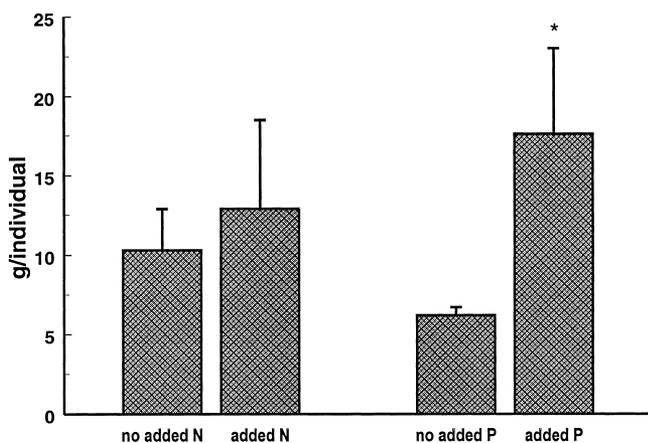


Figure 1. Mean (+1 SE) biomass of flowering *Centaurea diffusa* individuals in control plots and plots fertilized with nitrogen (as ammonium sulfate, 10 g/m²) or phosphorus (as superphosphate, 1 g/m²). Asterisk indicates significant difference at $p < 0.05$.

for P than the native North American grasses *Festuca idahoensis*, *Koeleria cristata*, and *Pseudoroegneria spicata*, but that *C. diffusa* is not a better competitor for P than three Eurasian grasses of similar morphology and size to the North American grasses tested. Harvey and Nowierski (1989) found that potassium, N, and P concentrations were 44%, 62%, and 88% lower on soils from a site infested with *C. maculosa* than from a site dominated by grasses. They speculated that *C. maculosa* might convert P to a form not readily available to competitors, but they did not quantify the forms of soil P. Similarly, in a comparison of patches dominated by *C. diffusa* and *B. dactyloides*, a native C₄ grass, we found that labile P concentrations are significantly lower in soils under *C. diffusa* patches than in soils under *B. dactyloides* patches (unpublished data). Concentrations and forms of P in the soils before invasion are unknown, so it is not clear whether the measured differences predated invasion in either case. If not, the depletions suggest that *Centaurea* may compete strongly for P. Jacobs and Sheley (1999) describe niche partitioning between *A. spicatum* and *C. maculosa*. Although they do not elucidate the specific mechanism, their results suggest that *Centaurea* species acquire soil resources that are not accessible to competitors.

In an environment in which N is abundant, no species may now be capable of reducing N to levels where it effectively limits the growth of other species. But if *C. diffusa* has traits that allow it to reduce available P in soils, it could eventually reduce P to levels that affect native plant growth. This scenario is plausible only in a system in which N is no longer limiting and native species no longer have an advantage.

Species Traits

Competitive dominance occurs, and occurs more rapidly, when one species is distinctly different from the other species. Numerous *Centaurea* species traits allow a distinctly different response to seasonal environmental variability from that of native grasses. For example, *C. diffusa* can operate as an annual, biennial, or triennial (Thompson & Stout 1991), depending on resource availability, and seeds can germinate nearly continuously throughout the growing season (Sheley & Larson 1996). The continuous seed rain and seedling emergence of *C. diffusa* may allow it to occupy all available safe sites, avoid intraspecific competition for limiting resources, and develop a hierarchy of age classes within the population (Sheley & Larson 1996). Flexibility in the timing of germination and flowering enhances the ability of *C. diffusa* to exploit a variable environment, which is important in a semiarid region where available moisture may limit seedling survival or flowering (Berube & Myers 1982; Thompson & Stout 1991). The ability to germinate in autumn or early in the growing season allows preemption of available resources.

Centaurea species also differ from native species in terms of plant architecture and biomass allocation, which has implications for resource availability and nutrient cycling. *C. diffusa* and other *Centaurea* species have tap roots and can exploit deeper nutrient and water sources than native fibrous-rooted species. Although this might benefit a successional invader, once deep water is removed and not replaced by annual precipitation, the deep-root strategy must be of neutral or negative value.

In vitro experiments have shown that cnicin, a sesquiterpene lactone produced by both *C. diffusa* and *C. maculosa*, can be allelopathic. Extracts of cnicin from *C. maculosa* leaves and roots reduce the germination and seedling growth in several species (Muir & Majak 1983; Kelsey & Locken 1987). Cnicin is also reported to be antimicrobial (Cavallito & Bailey 1949). Callaway and Aschehoug (2000) provide evidence that *C. diffusa* negatively affects the growth of native North American grasses and demonstrate that activated carbon additions to test soils reduce the negative effect. Activated carbon has a high affinity for organic substances and is believed to reduce the negative effects of allelopathic exudates (Callaway & Aschehoug 2000). Activated carbon can also affect the soil microbial community and nutrient cycling (Wardle et al. 1998; Pietikainen et al. 2000). Therefore, chemicals released by *C. diffusa* may suppress growth of native species by direct phytotoxicity or by restricting nutrient availability via changes in soil microbial activity.

These biological traits alone do not confer great competitive advantage to *Centaurea* species in their eastern European and western Asian homelands. We suspect that a different resource ratio in western grasslands of the United States and Canada and particularly a ratio different from the range of ratios that occurred over the last century, allows species with traits more suited to the new environmental conditions to establish and dominate. Species have not evolved to be invasive; rather, invasiveness results when a species encounters habitats in which its particular suite of traits confers competitive advantage over the native dominants (Callaway & Aschehoug 2000; Sher & Hyatt 1999). This dominance of *Centaurea* species may be transient; their dispersal ability may simply allow them to be the first in a suite of competitors better adapted to the new resource ratio. We suspect, however, that the young soils of much of the western United States and Canada, and particularly the volcanic soils of the Pacific Northwest, provide a fertile habitat for a species with high phosphorus demands.

Conclusions: Proposed Regional Cause for a Regional Problem

Species of the genus *Centaurea* and other weedy forbs are able to exploit local natural disturbances, such as

soils exposed by gophers (e.g., *Thomomys* sp.), prairie dogs (*Cynomys* sp.), or other mammals. Historically, disturbances such as these that enhanced N availability were spatially and temporally discrete. Current human disturbances similarly enhance N availability, but at a regional scale. We suspect that the region-wide increase in N availability has given *Centaurea* species opportunities to invade anthropogenically disturbed areas at a regional scale. Where N no longer limits community productivity, some other resource must. The limiting resource for *Centaurea* species appears to be P, and *Centaurea* species appear to be good competitors for P.

The degree of anthropogenically enhanced N availability probably differs across the various western North American grassland ecosystems, and the effects probably differ spatially depending on the anthropogenic loadings and the initial degree of N limitation in the ecosystem. For example, responses to chronic grazing differ across grassland ecosystems. Smith and Knapp (1999) reported increased native and exotic species richness in tallgrass prairie with increased grazing. Although the effect of the removal of the dominant species by grazers is difficult to separate from the fertilization effect of grazing, the result nonetheless supports the hypothesis that disturbances that alter competitive hierarchies and allow resource availability greater than historical levels increase invasibility. Based on a review of the scientific literature, Belsky and Gelbard (2000) concluded that livestock grazing is a major cause of nonindigenous species invasions and that nutrient enhancement caused by urine deposition and patchy disturbances favors nitrophilous weeds in particular. Shortgrass prairies evolved under heavy grazing pressure, however, and lack of grazing is a greater disturbance than chronic grazing (Milchunas et al. 1989). In shortgrass prairie, Kotanen et al. (1998) found that invasive species are few and dominance by them is low. These studies both indicate grazing in shortgrass prairie maintains the dominance of the native C_4 grasses. Where the historical disturbance regime, and presumably available nutrient ratios, have been maintained, exotic species have been unable to attain dominance over native species. But even in shortgrass prairie, exotic species will dominate where resource levels are raised artificially (Milchunas et al. 1995; Vinton & Burke 1995).

Stohlgren et al. (1999) reported that 73% of the cover by exotic species in the central grasslands could be explained by a regression equation including cover of native species and percentage of clay in the soil. The regression suggests that when native species are abundant, exotic species are not, and that indices of high resource availability (e.g., clay content, which is positively correlated with soil moisture and cation exchange capacity) are positively correlated with cover by exotic species. The relationship between soil characteristics and cover by exotic species supports our contention that the high (and increasing) nutrient status of North American grass-

land soils provides a region-wide explanation for increased cover by *Centaurea* species. Similarly, Smith and Knapp (1999; 2001) found greater native and exotic species richness in unburned plots than in annually burned plots, which suggests that both native and exotic species respond to greater resource availability. Although exotic species have not become dominant in tallgrass prairie, the greater exotic species richness in higher-nutrient unburned prairie does support the hypothesis that artificially enhanced nutrient levels resulting from fire suppression affect community structure, nutrient limitation, and competitive hierarchies. If an exotic species is present and able to differentially exploit newly available resources, it may then become the new community dominant.

Our preliminary data suggest that *Centaurea* species may be better competitors for P than native species and may create a P limitation in invaded grassland soils. We suspect that this combination of plant traits and environmental conditions explains the dominance of *Centaurea*. These speculations, in combination with speculations regarding differential resource limitations for *Centaurea* and native vegetation, lead to two hypotheses. First, re-establishment of N limitation is critical if the traditional species composition of invaded sites is to be restored. Second, because the productivity of *Centaurea* species seems to be related to P availability, reduction of P availability should be a useful management technique for reducing *Centaurea* abundance. Phosphorus availability can be reduced with various calcium amendments (Zhu & Alva 1994; Bastin et al. 1999); but if *Centaurea* species do control P availability, then further limiting the availability of this element could have even larger negative results on competitor species. In any case, we hypothesize that manipulation of soil resource availability with traditional techniques such as fire and new techniques such as carbon, calcium, or iron additions can affect the dominance of invasive species such as *Centaurea*.

The conversion of western grasslands of the United States and Canada to forb meadows implies major changes in regional soil biogeochemical properties. In restoration projects, managers of native North American grasslands must consider the soil biogeochemical landscape as well as current and historical disturbance regimes and their effect on nutrient availability and nutrient ratios. If the historically limiting nutrient that structured grassland communities and interspecific competitive relationships is now no longer limiting, then traditional weed-control techniques are unlikely to restore native community composition over the long term.

Acknowledgments

We thank J. Bock for comments on a draft manuscript, K. N. Suding for discussions that inspired this effort, and

Boulder County Commissioners for providing the motivation and the site for our *Centaurea diffusa* research.

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