PHYTOSOCIOLOGICAL AND EDAPHYC ASPECTS OF THE INVASION BY *CLEISTOGENES SEROTINA* (L.) Keng IN THE KISKUNSÁG NATIONAL PARK

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Abstract. In the recent decades Cleistogenes serotina, a perennial grass native to Hungary has become a successful invader in the open sand grasslands of the Great Hungarian Plain. The aim of the present study is to detect if there is any relation between the different community types, soil properties and the dominance of the invader. Plant cover as well as seven soil parameters (soil water, organic matter and carbonate content, pH, nitrate, available potassium and phosphate concentration) were studied in a transect of 139 0.5×0.5 m quadrats on a slope of a sand hill in the Kiskunság National Park, Hungary.

Three distinct vegetation types were detected: Cleistogenes-dominated type, Fumana procumbens-dominated open perennial grassland type, and Secale-dominated open annual grassland type. The invader-dominated type was in many aspects — low cover of spring annuals and criptogams, high pH, low nutrient concentration — more similar to the Fumana-type (which is close to the original natural vegetation of the habitat) than to the Secale-type (which is considered a degraded vegetation type). In the Cleistogenes-dominated quadrats soil water content was higher than in the other two types, and a slight increment in the cover of the subordinate annuals was also detected as compared to the Fumana-dominated vegetation.

Keywords: invasion success, open sand grassland, degraded and natural vegetation, soil conditions, transect,

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Introduction

One of the successful invaders of the seminatural open sand grasslands in the "Duna-Tisza köze" region (Danube-Tisza Interfluve) is the perennial grass Cleistogenes serotina. Although this species is a native member of the Hungarian flora, it was first recorded from the Great Hungarian Plain only in the middle of the 20th century from two localities, but recently the species has been found in more and more sites (Soó 1973, 1980, Szujkó-Lacza and Kováts 1993, Tölgyesi 1980, Molnár et al. 1999). In the recent decade Cleistogenes has occupied huge areas of high conservational value in some parts of the Kiskunság National Park (Bagi 1997a, Molnár et al. 1999). This vegetation process might considerably alter the endemic open sand grassland vegetation of the region (Bagi 1997a).

In order to make good predictions about the further spread of an invasive plant and about the future changes in the invaded vegetation it is necessary to identify the community types and abiotic conditions that the invader prefers. The preferences of Cleistogenes serotina in terms of spread rate in resistant and susceptible plant associations has already been investigated at a relatively broad scale by Bagi (1997a), and he found varying success in different community types. The aim of our study is to detect how the preference and success of the species in terms of relative dominance is related to different gradients in vegetation composition and soil properties at a fine scale and what are the characteristics of the invader-dominated patches as compared to the disturbed and the seminatural vegetation types of the habitat.

Materials and methods

Research area

Our examinations were carried out in the first two weeks of August in 1996 on the slope of a sand hill in territory IV of Kiskunság National Park near Fülöpháza (20 kilometres west of the city of Kecskemét) in the "Duna-Tisza köze" region in Hungary.

The climate of the area is of moderate continental type. The mean annual temperature is $10-11^{\circ}\text{C}$ with $-1.5-2^{\circ}\text{C}$ in January and $21-22^{\circ}\text{C}$ in July. The mean annual precipitation is about 550 mm with a maximum in June and November. The number of sunny hours is about 2050 (Iványosi 1979, Borhidi 1993). The water balance is negative, which was extremely expressed in the drought period between 1985 and 1995 (Iványosi 1994).

The historical data show that the main land use form in the latest centuries was grazing which led to the reactivation of sand dunes in the 18th century or before. After the afforestation efforts that culminated in the 20th century and the changes in land use management the sand immobilization began. In the study area intensive grazing went on until the middle of the 20th century, therefore the sand grasslands of the area represent an early phase of the revegetation processes and the immobilization of sand (Magyar 1960, Biró and Molnár 1998).

The sand dunes of the area consist of basic wind-blown sand of Danubian origin (Járai-Komlódi 1966, 1969, Babos 1958). The soil of the sand hills is a very poor basic skeleton soil, without expressed soil profile differentiation. The clay and colloid fraction is extremely low, the humus content is less than 1 per cent. The calcium-carbonate content is considerable, the pH measured in distilled water is around or above eight. The concentration of nutrients is very low. The soils of the depressions have slightly higher humus fraction and lower reaction (Bagi 1997a, Szabolcs 1979, Várallyai 1993).

The vegetation of the study area was mapped in 1990 (Bagi unpublished). Most of the area is covered by different types — Festuca vaginata, Fumana procumbens, Stipa capillata and borysthenica, Salix repens ssp. rosmarinifolia dominated types — of the open perennial sand grassland, with patches of the open annual sand grassland dominated by Secale sylvestre and Bromus tectorum. According to the latest concept of sand vegetation dynamics (Fekete 1992) the Festuca vaginata grassland is the — permanent — natural pioneer plant association on bare sand, while the Bromus tectorum—Secale sylvestre type, which was earlier thought to precede

the perennial grassland in natural succession (Hargitai 1940, Zsolt 1943, Magyar 1933), develops where degradation — mainly grazing, trampling, ploughing, drying — destroys the original vegetation and nutrients accumulate in the soil (Bagi 1997b, Molnár 1999, Borhidi 1999). In spite of its pioneer character, the open perennial grassland is very rich in rare and specialist species, the number of endemic species (including the dominant grass Festuca vaginata) is especially high. The transformation of the annual open sand grassland into a perennial grassland is a slow and uncertain process (Bagi 1990).

The different types of the perennial sand grassland reflect the heterogeneity of the sand dunes: The extremely open Fumana procumbens dominated vegetation is found in dry, steep, south facing slopes where sand is still in motion. In the depressions where ground water is close the meadow-like Salix repens ssp. rosmarinifolia type is found. The habitats of the Festuca vaginata and Stipa capillata and Stipa borysthenica dominated vegetation are less easy to describe, but the latter tends to be more closed and develops on drier soil less disturbed by the wind (Biró and Molnár 1998, Hargitai 1940, Magyar 1933).

In the research area Cleistogenes serotina was first found in the end of the 1970's by G. Fekete. During the last decade the species has shown rapid invasion into the Festuca vaginata, Fumana procumbens, Stipa capillata and S. borysthenica dominated types (the latter two are more frequent) of the open perennial grassland, while the degraded Secale sylvestre and Bromus tectorum dominated vegetation has proved to be more resistant. In the invaded vegetation Cleistogenes was evaluated to be a facies-forming species up to 28 per cents absolute cover in 10×10 m quadrats. Using the above scale no significant relationship was found between the dominance of Cleistogenes serotina and the soil parameters (Bagi 1997a).

Study species

Cleistogenes serotina, a perennial grass is a native member of the Hungarian flora. The geographical range of the species in Europe shows submediterranean characteristics: the northest limits of its area are in Austria, the Czech Republic and Slovakia. Cleistogenes can also be found in the east: in the Ukraine, in the region of the Krim and in the Caucasus (Hegi 1935). According to the literature the Hungarian populations belong to the serotina subspecies (Soó 1973).

The original habitats of the species in Hungary are dry mountain grasslands on south-facing slopes. In closed limestone or dolomite grasslands

Cleistogenes is often dominant or co-dominant (Soó 1973). The ecological indicator values used in Hungary show that Cleistogenes serotina frequents relatively dry, warm, nutrient-poor, calciferous sites (Borhidi 1995, Simon et al. 1992, Zólyomi et al. 1967). Soó in addition mentions that the species lives on skeleton or silt soils with moderate or poor humus fraction developing on limestone or dolomite, occasionally on andesite (Soó 1973, 1980).

Vegetation sampling

In order to describe spatial gradients in vegetation and soil we used the transect method. The transect was laid on the slope of a south-south-east facing sand hill, running from the top to the bottom with a 10 m long break in the middle which divided the transect in two sections consisting of 70 and 69 0.5×0.5 m quadrats, respectively. The starting point of the transect lies 6.5 metres higher than the end. Thus, the first section represents the higher, the second section represents the lower parts of the slope. The gradient of the slope is uniformly steep in the first section, while the second section gradually flattens out.

Plant cover was collected from 0.5×0.5 m quadrats, the arrangement of which enables to join them into 1 m² quadrats overlapping by one quarter with each other. Thus the axis of the transect is the diagonal of the consecutive 1 m² quadrats.

The per cent absolute cover of living plants, the dead parts of the vernal aspect, and the criptogams was estimated in each 0.5×0.5 m quadrats. The data might be biassed in the case of the species of the vernal aspect, the cover of which was estimated from the dry stalks except from *Poa bulbosa* (cover of the bulbs). The abundance of *Medicago minima* was estimated on the basis of the number of fruits. The latter species was omitted from the mathematical analyses in which the same type of input data was required for each species.

Soil analysis

Soil samples were taken from the centre of every 1 m² quadrats from the top 5 centimetres of the soil. The samples were collected two days after vegetation sampling, one day after rain. Each soil sample was put into plastic bags, and weighed one day later. After that the samples were dried out at 60 °C and weighed again. Soil humidity is expressed as the percentage weight difference of the collected and the dried soil. Organic matter was determined with dichromatic method with photometric evaluation. CaCO₃ content was measured by calcimeter of

SCHLEIBER. Soil reaction was determined from a 1:2.5 water suspension with an electric pH meter. Available phosphate and potassium were extracted from the soil by ammonium-lactate. Phosphate was determined with ammonium-molibdenate by colorimetry, potassium content was determined by flame photometry. Avaliable nitrate was measured from a 1:5 water suspension with phenol-disulphonic-acid by colorimetry (Ballenegger 1953). All measurements were performed in one replicate.

Mathematical evaluation

The ordination of the species was performed by nonmetric multidimensional scaling (NMDS) on the basis of the cover in the 0.5×0.5 m quadrats, while the vegetation was examined by principal components analysis (PCA) of the cover in the overlapping 1×1 m quadrats (the 0.5×0.5 m quadrats yield the same result, but in that case the interpretation is more complicated). The calculation of the ordination was based on a correlation matrix in both cases, the number of dimensions was three.

Correlations between soil parameters and relative elevation were estimated using Spearman's rank order correlation coefficient R_s. The difference of the soil parameters among groups of quadrats separated by the PCA analysis were tested using the Kruskal-Wallis test, pairwise comparisions between groups were calculated by Dunn's method (Zar 1984). For the calculation of the statistical analyses and ordinations we used Statistica for Windows program package (Statsoft Inc. 1995).

Results

The vegetation of the whole transect consists of 24 phanerogamous plant species. At the time of the sampling 15 of them had living aboveground parts. The vernal aspect was represented by 10 species. Only *Medicago minima* was present in both groups (abundant in the vernal aspect, but having merely one living specimen). Half of the species was present in less than 5 per cents of the primary 0.5×0.5 m sampling units. The cryptogams were represented by one moss species (*Tortula ruralis*) and three lichens (Table 1).

The abundant species quite well define the vegetation types along the transect (Fig. 1): Fumana procumbens is the dominant species in the first part of the first and second section of the transect (1-12, 23-28). Stipa borysthenica achieves its greatest cover values in the first part of the second section of the transect (24-34), while Secale sylvestre becomes gradually the most abundant in the second part (30-

Table 1. Species list for the two sections of the transect. The number of occurences are given for the 0.5×0.5 m quadrats as well as the median of the per cent cover data for the quadrats where the species was present. Where the species was present only in one quadrat, the cover value is given in parentheses.

SPECIES	CODE		NUMBER OF COVER OCCURENCES MEDIAN			
		Sect.	Sect.	Total	Sect.	Sect.
		1	2		1	2
Living plants						
Cleistogenes serotina (L.) Keng	CLES	67_	43	110	10	8
Stipa borysthenica Klokov	STIB	51	50	101	3	6
Fumana procumbens (Dun.) Gren. et Godr.	FUMP	43	16	59	10	9
Festuca vaginata W. et Kit.	FESV	4	1	5	4.5	(15)
Alyssum tortuosum W. et Kit.	ALYT	7	0	7	1	0
Salsola kali L.	SALK	2	10	12	11.5	10
Polygonum arenarium W. et Kit.	POLA	10	1	11	3.5	(2)
Bothriochloa ischaemum (L.) Keng	BOTI	1	0	1	(1)	0
Alkanna tinctoria (L.) Tausch	ALKT	2	4	6	0.75	5
Stipa capillata L.	STIC	3	1	4	8	(3)
Koeleria glauca (Schkuhr) DC	KOEG	4	2	6	3	6.25
Euphorbia segueriana Necker	EUPS	3	0	3	1	0
Corispermum nitidum Kit.	CORN	0	1	1	0	(2)
Conyza canadensis (L.) Cronq	CONC	1	14	15	(1)	2
Vernal aspect						
Medicago minima (L.) Grufbg.	MEDM	9	50	59	_	-
Poa bulbosa L.	POAB	54	13	67	15	5
Buglossoides arvensis (L.) I. M. Johnst.	LITA	39	69	108	2	5
Arenaria serpyllifolia L.	ARES	29	56	85	1	2
Minuartia verna (L.) Hiern.	MINV	4	0	4	1.5	0
Silene conica L.	SILC	4	26	30	1	4
Cerastium semidecandrum L.	CERS	2	1	3	1.5	(1)
Alyssum turcestanicum Regel et Schmalh	ALYD	1	1	2	(0.5)	(0.5)
Secale sylvestre Host	SECS	0	65	65	0	10
Bromus squarrosus L.	BROS	. 0	43	43	0.	3
Cryptogams						
Tortula ruralis (Hedw.) Gaertn. et al.	TORR	51	79	130	1	15
Cladonia convoluta (Lam.) P. Cout.	CLAC	69	70	139	1	1
Parmelia pokornyi (Koerb.) Szat.	PARR	49	69	118	3	1
Collema crispum (Huds.) Web.	COLC	30	14	44	0.5	0.5

45), with other degradation-indicating species like *Bromus tectorum*, the moss *Tortula ruralis* and the adventive *Conyza canadensis*.

The invader Cleistogenes serotina is present in almost all quadrats except those at the end of the transect, where degradative species predominate (Fig. 1). The species shows two marked peaks: the greatest cover is found at the second part of the first section (10–19), while a much smaller peak is found in the second section (35–39).

Small subordinate annuals like Buglossoides arvensis, Arenaria serpyllifolia, Medicago minima though achieve their maximal abundance in the company of Secale sylvestre have a smaller peak in the first section (10–21) where Cleistogenes predominates. The ephemerous perennial Poa

bulbosa displays a peculiar trend: its greatest abundances in the first section almost overlap with the peak of Cleistogenes serotina. This species is not present in the second section except from some quadrats where the cover of Secale sylvestre shows local minimum (Fig. 1).

The PCA ordination of the 46 quadrats (Fig. 2) reveals three consistent groups, which can be corresponded to the *Fumana*- (Fig. 2: A-group, 1-13, 24-26), *Secale*- (Fig. 2: C-group, 31-46) and the *Cleistogenes*-dominated (Fig. 2: B-group, 14-23) types. Both sections of the transect start from the *Fumana*-dominated type. The transition towards the *Cleistogenes*-dominated group is relatively sharp in the ordination space while there is a continous transition towards the *Secale*-dominated type (Fig. 2).

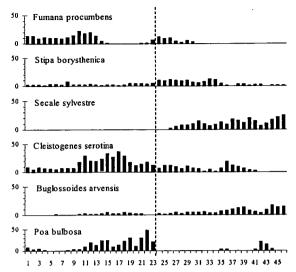


Fig. 1. The per cent cover of some representative species along the transect in the 1×1 m quadrats. The two sections are separated by the broken line.

Nonmetric multidimensional scaling of the species evaluating the 0.5×0.5 m quadrats is performed for all quadrats (Fig 3a) and also separately for the two sections (Fig. 3b and 3c) of the transect, as the representatives of two different vegetation transitions according to the PCA results. Most of the vernal annuals form a consistent group together with the moss Tortula ruralis and the invasive annual Conyza canadensis, while Fumana procumbens and Cleistogenes serotina are at the opposite end of the first axis when the whole transect (Fig. 3a) or the second section (Fig. 3c) is analyzed.

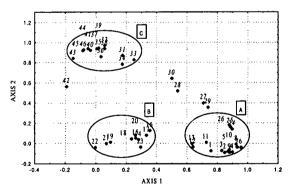


Fig. 2. PCA ordination of the 1×1 m quadrats along the transect on the basis of the cover of the phanerogamous plants. The per cent variance represented by the first two axes are 40.62 and 28.90, respectively. The serial number of the quadrats belonging to the second section are written in italics. A: Fumana-type, B: Cleistogenes-type, C: Secale-type.

Evaluating the first section Cleistogenes serotina and Fumana procumbens form two opposite poles along the first dimension. The position of cryptogams and the small therophytes like the vernal serpyllifolia, Buglossoides Arenaria and the Medicago minima. summer annual Polygonum arenarium show in the ordination space that these species are more abundant in the Cleistogenes-dominated quadrats (Fig. 3b).

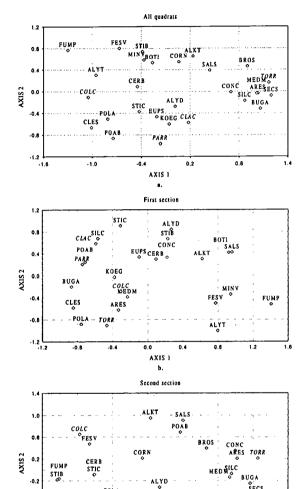


Fig. 3. The NMDS ordination of the species on the basis of the cover in the 0.5×0.5 m quadrats in the whole transect (a.), and separately for the first (b.) and the second section (c.) of the transect. STRESS = 0.1446 and 0.1674 and 0.1405 respectively. For the abbrevations see Table 1. The codes of the cryptogams are written in italics.

-0.2

-0.€

CLES

-1.0

CLAC

0.2 AXIS I

KOÉG

The values of the measured soil parameters along the transect are seen in Fig. 4. Three of the soil parameters are significantly correlated with relative elevation (carbonate content: $R_s = 0.589$, p < 0.001;

Table 2. The sum and the average of ranks for seven soil parameters in the three groups of quadrats separated by PCA analysis (see Fig. 2) and the results of the Kruskal-Wallis test. The groups of quadrats are marked A, B and C as in Fig. 2. The soil parameters are: WAT: soil water content, HUM: soil organic matter content, PH: soil pH, CARB: soil carbonate content, P: soil phosphate content, K: soil potassium content, N: soil nitrate content. The significance values for the H statistic are: *: p < 0.05; **: p < 0.01; ***: p < 0.001; ns: p > 0.05.

	A (n = 16)		B (n = 10)		C (n = 15)		Н	
	Sum Rank	Aver Rank	Sum Rank	Aver Rank	Sum Rank	Aver Rank		
WAT	252	15.750	326	32.600	283	18.867	12.927**	
HUM	277	17.313	225.5	22.550	358.5	23.900	2.566 ns	
PH	404.5	25.250	254	25.400	202.5	13.500	9.303**	
CARB	479	29.938	183.5	18.350	198.5	13.233	15.716***	
P	193.5	12.094	190	19.000	477.5	31.833	21.400***	
K	331.5	20.719	254.5	25.450	275	18.333	2.142 ns	
N	215	13.438	165.5	16.550	480.5	32.033	20.499***	

Table 3. The difference between the rank averages of the three groups separated by PCA analysis (see Fig. 2) and the results of the Dunn's test for the soil parameters that yield significant result in the Kruskal-Wallis test (cf. Table 3.). The groups of quadrats are marked A, B and C as in Fig. 2. For the abbrevations see Table 3. The significance values for the Q statistic are: *: p < 0.05; **: p < 0.01; ***: p < 0.001; ns: p > 0.05.

	A vs. B		A vs. C		B vs. C	
	Diff Ranks	Q	Diff Ranks	Q	Diff Ranks	Q
WAT	16.850	3.489**	3.117	0.725 ns	13.733	2.808*
PH	0.150	0.031 ns	11.750	2.735*	11.900	2.438*
CARB	15.588	2.402*	16.704	3.883***	5.117	1.047 ns
P	6.906	1.430 ns	19.740	4.586***	12.833	2.625*
N	3.113	0.645 ns	18.596	4.323***	15.483	3.168**

phosphate content: $R_s = -0.666$, p < 0.001; nitrate content: $R_s = 0.645$, p < 0.001). The correlations suggest that soil phosphate and nitrate tend to accumulate at the bottom, while carbonate concentration is higher at the top of the slope.

The consistent groups of quadrats separated by PCA were analyzed for differences in their soil properties. The Kruskal-Wallis test shows that the three vegetation types do not differ significantly in their soil organic matter and potassium content (Table 2). The pairwise comparisions reveal that the most marked differences are between the soils of the Fumana-dominated and the the Secale-dominated groups. The soils of the Cleistogenes- and the Fumana-dominated types have significantly different water and carbonate content, while the difference between the soils of the Cleistogenes- and the Secale-dominated group is the nitrate, phosphate, and water content and soil reaction (Table 3).

Discussion

The analysis of the transect detected three quite distinct vegetation types. Two of them, the Fumana procumbens-Stipa borysthenica-dominated quadrats at the top and the middle of the slope represent the original seminatural perennial grassland type while the Secale sylvestre-dominated quadrats with high

moss cover, at the bottom of the slope, represent the degraded annual grassland type of the habitat. The soil of the latter type has higher nutrient concentration, lower pH and carbonate content. The invader Cleistogenes serotina is present in both types with relatively low cover, though it seems to be less successful where the representatives of the degraded annual type predominate at the end of the transect. Interestingly, at the bottom of the slope, where Cleistogenes disappears there are practically no summer green plants except Stipa borysthenica at very low densities and another invasive species Conyza canadensis.

The third type, the Cleistogenes serotina-dominated quadrats are also found at the higher part of the slope. In this type Fumana disappears, and the cover of the small subordinate annuals and cryptogams is slightly higher than in the Fumana-dominated quadrats but is lower than in the Secale-type. The soil conditions are more similar to the Fumana-dominated type (low nitrate and phosphate concentration and high soil pH) although carbonate concentration is lower. As the main difference we measured the highest water content of the top soil in the Cleistogenes-type.

Our results agree with the conclusions of Bagi (1997a) who detected the highest spread rate in the Fumana- and Stipa-dominated vegetation, and slow

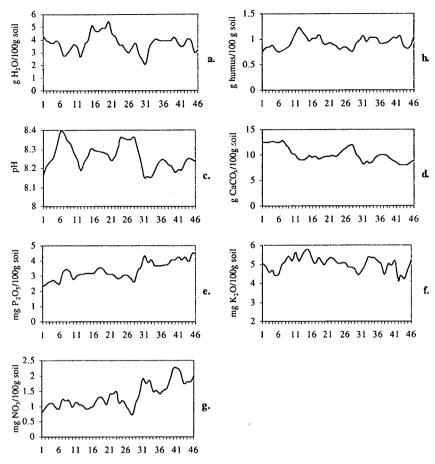


Fig. 4. The distribution of the soil parameters (represented as sliding average) along the transect: (a): actual water content, (b): organic matter content, (c): pH in distilled water, (d): carbonate content, (e): available phosphate content, (f): available potassium content, (g): nitrate content.

spread in the Secale-Bromus-dominated type. The soil conditions of Cleistogenes-dominated type detected by our transect suggest that the invader is most successful in terms of dominance in patches that are similar to the habitat of the Fumana-type except from the slightly more favourable water conditions. Other studies have proved that water is one of the the most important limiting factors in these communities (Kovács-Láng and Szabó 1973, Szabó 1975), but it should be mentioned that our results are founded on one measurement and refer only to the top five centimetres of the soil, which is not comparable to the actual root depth of many species (Magyar 1933, Simon and Batanouny 1970), therefore care should be taken when our data are concerned.

The studies on invasions traditionally emphasize that exogenously disturbed habitats are more prone to invasions (Fox and Fox 1986, Usher 1988, Drake

et al. 1989, Hobbs and Huenneke 1992, Beerling 1995). Although this phenomenon in many cases seems trivial, the interpretation that relates invader success to disturbance status or degradation of the target community in our case is not relevant. The invasion process of Cleistogenes serotina has apparently not been mediated by exogenous disturbance at the relatively intact parts of the strictly protected study area since it was first detected. Nonetheless, the perturbation of the soil probably promoted colonization inside some sites, mainly along the roads (Bagi 1997a). Interestingly the two invasive species that are present in our transect show different behaviour: the focal species of our study, Cleistogenes serotina seems to be more successful in the natural, nutrient-poor open perennial grassland type while Conyza canadensis is found in the degraded open annual grassland type where relatively more nutrients accumulate.

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