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Effects of Soil Type on the Damage Potential of *Meloidogyne incognita* on Soybean[1]

G. L. Windham and K. R. Barker[2]

Abstract: Effects of soil type on the reproduction and damage potential of *Meloidogyne incognita* on soybean, *Glycine max* (L.) Merr., were determined at five locations in North Carolina, including one site where plots with six soil types were established. *M. incognita* reproduced readily on a susceptible soybean cultivar in most soil types, with somewhat limited reproduction in muck soils. The relationship between initial population densities and yield varied among soil types and nematode populations. Yield losses were greatest in sandy and muck soil types, with less nematode damage occurring in the clay soil types. A North Carolina and a Georgia population of *M. incognita* differed greatly in their ability to reproduce on soybean and suppress growth. The North Carolina population had a moderate effect on yield in 1981 and only a slight effect in 1982. In contrast, a Georgia population severely limited soybean growth and yield at lower initial population densities in 1983. Initial population densities of the nematodes and physical and chemical edaphic factors accounted for much of the variation of soybean yield and nematode reproduction.
Key words: *Glycine max*, soybean, *Meloidogyne incognita*, root-knot nematode, population dynamics, soil type, yield.

The southern root-knot nematode, *Meloidogyne incognita* (Kofoid and White) Chitwood, is a major limiting factor in soybean, *Glycine max* (L.) Merr., production in the southern United States (12). Soybean yield losses can be substantial, depending on cultivar susceptibility (11). The general negative relationship between soil infestation levels of *M. incognita* and yield of soybean has been described (10,19). By determining preplant nematode soil population densities, appropriate management tactics—including resistant cultivars, crop rotation, and (or) nematicides (9,14,19)—can be selected. Nematode damage thresholds, although useful in predicting yield loss, may be influenced by cultivar and many environmental factors (4).

Soil type is a primary edaphic factor that may influence the damage potential of *M. incognita* on soybean. Soil type or texture affects nematode movement (17), penetration of roots (23), reproduction (18), general population densities in fields (7,21), and relationship between preplant population densities and crop productivity (20). Limited studies on the effects of soil type on the virulence of *Meloidogyne* spp. on soybean have been conducted (15).

Additional information on the effects of soil type on the reproduction and damage potential of *M. incognita* is necessary to develop more precise predictions of crop losses. The objectives of this research were to determine 1) the effect of soil type on host efficiency of a susceptible soybean cultivar, 2) the damage potential of *M. incognita* on

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[2] Former Graduate Student and Professor, Department of Plant Pathology, North Carolina State University, Raleigh, NC 27695. Present address of senior author: U.S. Department of Agriculture, Agriculture Research Service, Crop Science Research Laboratory, Forage Research Unit, P.O. Box 5367, Mississippi State, MS 39762.
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soybean in different soil types, and 3) the relationship of physical and chemical edaphic factors to soybean yield and *M. incognita* reproduction.

Materials and Methods

Effects of soil type: Experiments were conducted in 80-cm-d fiberglass microplots at Central Crops Research Station (CCRS) near Clayton, North Carolina, from 1981 to 1983. Soils included at this common Fuquay-sand site were Fuquay sand (91% sand, 3% clay, 6% silt, pH 6.1, 0.6% OM), Norfolk loamy sand (84% sand, 4% clay, 12% silt, pH 6.3, 1.4% OM), Portsmouth loamy sand (72% sand, 10% clay, 18% silt, pH 5.9, 2.7% OM), muck (58% sand, 9% clay, 33% silt, pH 5.0, > 30% OM), Cecil sandy clay loam (53% sand, 29% clay, 18% silt, pH 6.7, 2.2% OM), and Cecil sandy clay (48% sand, 39% clay, 13% silt, pH 6.7, 0.9% OM). Plots were fumigated in 1981 and 1983 with 98 g methyl bromide/m^2.

A North Carolina population of *M. incognita* was used at various initial population densities in 1981 and 1982. A Georgia population obtained from Dr. R. S. Hussey of the University of Georgia was used in 1983. The Georgia population was a composite culture of three nematode populations collected from Florida, Georgia, and South Carolina. Inoculum was increased on tomato, *Lycopersicum esculentum* Mill. 'Manapal', in the greenhouse. Eggs were extracted from tomato roots with 0.5% NaOCl (5). Initial population densities (Pi) were 0, 1,250, 5,000, and 20,000 eggs/500 cm^3 soil in 1981 and 0, 625, 2,500, and 10,000 eggs/500 cm^3 in 1982 and 1983. Nematode survival was determined 3 May 1982, and eggs were added to adjust Pi to desired levels. Plots were infested with eggs and planted with the soybean cultivar Lee 68 on 22 May 1981, 12 May 1982, and 10 May 1983. Each plot was infested with 2,000 chlamydospores of *Glomus macrocarpus* Tul. and Tul. in 1981 and 1,000 chlamydospores in 1983. All seeds were inoculated with a commercial source of *Rhizobium japonicum* (Kirchner) Buchanan.

Nematode population densities were determined on 18 August and 3 November 1981, 13 August and 3 November 1982, and 10 August and 10 November 1983. Ten to twelve 2.5-cm-d soil cores were taken 15–20 cm deep from each plot. Nematodes were extracted from 500-cm^3 soil samples by a combination of elutriation and centrifugation (2). Eggs were extracted from egg masses on roots using NaOCl (5).

Acidity, base saturation, cation-exchange capacity (CEC), percentage of organic matter, pH, weight/volume, and levels of exchangeable and extractable anions and cations (calcium, copper, magnesium, manganese, phosphorus, potassium, and zinc) for each soil type were determined each year by the Agronomic Division of the North Carolina Department of Agriculture. Soil moisture was monitored during flowering and pod set in 1983 with a depth moisture gauge (Troxler Electronic Laboratories, Inc., Research Triangle Park, NC 27709).

A randomized complete block design with treatments factorially arranged and replicated five times was conducted. Analysis of variance was performed on all data. Reproduction factors (RF = final population density per initial population density) were determined. Orthogonal contrasts were calculated for comparison of soil types and Pi. Orthogonal contrasts of soil type included muck vs. others; Cecil sandy clay and Cecil sandy clay loam vs. Fuquay sand, Norfolk loamy sand, and Portsmouth loamy sand; Cecil sandy clay vs. Cecil sandy clay loam; Fuquay sand vs. Norfolk loamy sand and Portsmouth loamy sand; and Norfolk loamy sand vs. Portsmouth loamy sand. Regression analyses compared soybean yields with Pi. Numbers of nematodes (X) were converted to $\log_{10}(X + 1)$ for statistical analysis to stabilize variance of the data. Principal component analysis was used to reduce the number of soil texture and soil analysis variables. Maximum R^2 improvement analysis was used to determine the relationship of selected edaphic variables to soybean yield and *M. incognita* reproduction.

Influence of location and soil type: Experiments were conducted using 80-cm-d fiberglass microplots at four locations in North Carolina in 1983. Soil types at the locations included an Appling sandy clay loam (53% sand, 30% clay, 17% silt, pH 6.0, 0.4% OM) at Research Farm Unit 2 near Raleigh, a Goldsboro sandy loam (69% sand, 4% clay, 27% silt, pH 5.6, 0.9% OM) at Border Belt Tobacco Research Station near Whiteville, a Lakeland sand (93%

TABLE 1. Reproduction factors of *Meloidogyne incognita* on soybean as influenced by soil type and initial population densities at Central Crops Research Station, Clayton, North Carolina, 1981–83.

	RF per Pi*								
	1981			1982			1983		
Soil type	1,250	5,000	20,000	625	2,500	10,000	625	2,500	10,000
Cecil sandy clay	27	7	2.0	13	6.0	0.7	27	15	2.1
Cecil sandy clay loam	21	5	1.2	3	0.6	0.4	28	33	0.8
Fuquay sand	100	18	2.8	6	2.6	0.5	132	27	0.3
Muck	39	9	0.7	1	1.1	0.1	121	14	1.3
Norfolk loamy sand	87	19	4.6	12	1.4	0.5	323	58	7.0
Portsmouth loamy sand	59	15	2.1	15	2.8	0.7	188	17	2.2
Orthogonal contrasts†	B	B	A, B, E	NS	C	a	B	E	D, E

* RF (reproduction factor) = final population density/initial population density. Pi = initial population densities (eggs) per 500 cm^3 soil.
† Letters are used to designate differences as determined by orthogonal contrasts: A = muck vs. others. B = Cecil sandy clay and Cecil sandy clay loam vs. Fuquay sand, Norfolk loamy sand, Portsmouth loamy sand. C = Cecil sandy clay vs. Cecil sandy clay loam. D = Fuquay sand vs. Norfolk loamy sand, Portsmouth loamy sand. E = Norfolk loamy sand vs. Portsmouth loamy sand. Capital letters indicate significance at $P = 0.01$; lower case letter indicates significance at $P = 0.05$.

sand, 4% clay, 3% silt, pH 5.8, 0.3% OM) near Grifton, and a muck (71% sand, 7% clay, and 22% silt, pH 4.5, > 10% OM) near Wenona Community. All plots were fumigated with 98 g methyl bromide/m^2. The Georgia *M. incognita* population was used, and egg inoculation procedures were the same as previously described. The Pi were 0, 625, 2,500, and 10,000 eggs/500 cm^3 soil. Plots were infested with *M. incognita* eggs and planted with Lee 68 in the Appling sandy clay loam on 9 May, in the muck and Lakeland sand on 12 May, and in the Goldsboro sandy loam on 19 May. Each plot was infested with 1,000 chlamydospores of *G. macrocarpus.* Seeds were inoculated with *R. japonicum* as indicated in the experiment at CCRS.

Nematode population densities were determined on 17 August and 3 November in the Goldsboro sandy loam, 30 August and 8 November in the muck and Lakeland sand, and 9 September and 18 November in the Appling sandy clay loam. Soil samples were collected and nematodes and eggs were extracted by the same procedures used for samples collected at CCRS.

Treatments were arranged in a randomized complete block design with four replications. All data were subjected to analysis of variance. RF of *M. incognita* for each treatment were determined for each location. Orthogonal contrasts were made for comparison of soil types (locations), Pi, and the determination of interactions. Orthogonal comparisons of soil types included Appling sandy clay loam and muck vs. Goldsboro sandy loam and Lakeland sand, Goldsboro sandy loam vs. Lakeland sand, and Appling sandy clay loam vs. muck.

TABLE 2. Influence of soil type on soybean yield at Central Crops Research Station, Clayton, North Carolina.

	Annual yield (g/plot)		
Soil type	1981	1982	1983
Cecil sandy clay	132	299	70
Cecil sandy clay loam	276	386	104
Fuquay sand	362	267	52
Muck	211	287	54
Norfolk loamy sand	353	342	113
Portsmouth loamy sand	249	349	82
Orthogonal contrasts*	A, B, C, D, E	A, b, C, D	A, C, D, E

Means are averages of 20 observations.
* Letters are used to designate differences as determined by orthogonal contrasts: A = muck vs. others. B = Cecil sandy clay and Cecil sandy clay loam vs. Fuquay sand, Norfolk loamy sand, Portsmouth loamy sand. C = Cecil sandy clay vs. Cecil sandy clay loam. D = Fuquay sand vs. Norfolk loamy sand, Portsmouth loamy sand. E = Norfolk loamy sand vs. Portsmouth loamy sand. Capital letters indicate significance at $P = 0.01$; lower case letter indicates significance at $P = 0.05$.

TABLE 3. Influence of initial population density of *Meloidogyne incognita* on soybean yield at Central Crops Research Station, Clayton, North Carolina.

Inoculum/500 cm^3 soil		Annual yield (g/plot)		
1981	1982–83	1981	1982	1983
0	0 (check)	375	330	185
1,250	625 (low)	281	319	108
5,000	2,500 (medium)	243	315	20
20,000	10,000 (high)	156	315	4
Orthogonal contrasts*		A, B, C	NS	A, B

Means are averages of 30 observations.

* Letters are used to designate differences as determined by orthogonal contrasts: A = check vs. others. B = low vs. medium and high. C = medium vs. high ($P = 0.01$). NS = no significant differences.

Regression analysis was used to compare yield against Pi. Numbers of nematodes (X) were converted to $\log_{10}(X + 1)$ for statistical analysis.

RESULTS AND DISCUSSION

Effects of soil type: Reproduction of *M. incognita* was affected by soil type and Pi (Table 1). Host efficiency differed ($P = 0.05–0.01$) among the six soil types, with higher RF values generally found in the Fuquay, Norfolk, and Portsmouth soils. RF values declined in all soils as Pi increased except in Cecil sandy clay loam in 1983. There was limited reproduction, with little or no increase in nematode numbers, by *M. incognita* in 1982 in the muck. Although the Georgia population reproduced readily in 1983, the virulence of this nematode was the limiting factor of reproduction. Plant death at 2,500 and 10,000 Pi was common.

Soil type had a significant ($P = 0.05–0.01$) effect on soybean yield each year (Table 2). Most orthogonal contrasts of soil types differed each year, except in 1982 when there were no yield differences in Norfolk and Portsmouth soils and in 1983 when there were no yield differences in clay plots. Yields were greatest in 1981 and 1982 when the North Carolina nematode population was used and substantially lower in 1983 when plots were infested with the Georgia population. Plants were subjected to drought stress during flowering and pod set in 1983 which contributed to low yields.

Soybean yields were suppressed by the higher Pi treatments each year (Table 3). However, yields were significantly suppressed ($P = 0.01$) by *M. incognita* only in 1981 and 1983. All contrasts of nematode treatments were significantly different in 1981 and 1983, except the medium vs. high population level in 1983. Yield was only slightly affected by the North Carolina population in 1982 when lower Pi levels were used. The soil type–Pi interaction was highly significant ($P = 0.01$) in 1983.

The relationship between yield and *M. incognita* Pi varied between soil types and years. Regression equations were determined for the relationship between Pi and yield for the 1981 and 1983 data (Table 4). In 1981 there was a linear relationship

TABLE 4. Regression equations of soybean yield (g/plot) as affected by initial population density (Pi) of *Meloidogyne incognita* at Central Crops Research Station, Clayton, North Carolina.

Soil type	Equation 1981	Equation 1983
Cecil clay	$Y = 203.9 + 35.8Pi - 16.3Pi^2$ $R^2 = -0.57 \quad P = 0.01$	$Y = 127.6 + 552.6Pi - 318.4Pi^2 + 23.3Pi^3$ $R^2 = -0.72 \quad P = 0.01$
Cecil loam	$Y = 401.5 - 45.1Pi$ $R^2 = -0.45 \quad P = 0.01$	$Y = 168.2 + 581.7Pi - 327.6Pi^2 + 41.7Pi^3$ $R^2 = -0.71 \quad P = 0.01$
Fuquay	$Y = 472.3 + 72.1Pi - 29.7Pi^2$ $R^2 = -0.50 \quad P = 0.01$	$Y = 166.9 - 45.1Pi$ $R^2 = -0.83 \quad P = 0.01$
Muck	$Y = 314.9 - 37.4Pi$ $R^2 = -0.28 \quad P = 0.01$	$Y = 166.4 - 44.2Pi$ $R^2 = -0.80 \quad P = 0.01$
Norfolk	$Y = 467.1 + 58.9Pi - 26.5Pi^2$ $R^2 = -0.55 \quad P = 0.01$	$Y = 270 + 624.1Pi - 388.1Pi^2 + 53.8Pi^3$ $R^2 = -0.92 \quad P = 0.01$
Portsmouth	$Y = 411.6 - 58.6Pi$ $R^2 = -0.64 \quad P = 0.01$	$Y = 216.6 - 52.7Pi$ $R^2 = -0.78 \quad P = 0.01$

TABLE 6. Reproduction factors of *Meloidogyne incognita* as influenced by soil type and initial population densities at four locations.

Soil type	RF per Pi*		
	625	2,500	10,000
Appling sandy clay loam	111	13.0	0.2
Lakeland sand	91	7.0	0.4
Muck	6	0.6	0.1
Goldsboro sandy loam	92	11.0	0.4
Orthogonal contrasts†	NS	C	NS

Means are averages of five replications.

* RF (reproduction factor) = final population density/initial population density. Pi = initial population densities (eggs) per 500 cm^3 soil.

† Letters are used to designate differences as determined by orthogonal contrasts: C = Appling sandy clay loam vs. muck ($P = 0.01$). NS = no significant differences.

between Pi and yield in the Cecil sandy clay loam, the muck, and the Portsmouth loamy sand. A quadratic model best described the relationship for the Cecil sandy clay, Fuquay sand, and Norfolk loamy sand. In 1983 a linear relationship existed between Pi and yield in the Fuquay sand, muck, and Portsmouth loamy sand with a marked decrease in yield as the Pi increased. A cubic model best fitted the data for the Cecil sandy clay, Cecil sandy clay loam, and Norfolk loamy sand. There was a sharp decrease in yield at 2,500 Pi in these soil types. Lee 68 was more tolerant at low Pi in these soils than in the muck and sandy soils. Soybean yield was enhanced by low Pi in the Norfolk loamy sand and the muck in 1982 and in the Cecil sandy clay in 1983. This type of response has been reported for several nematode species (3,20). When infected with *Meloidogyne javanica* (Treub) Chitwood or *M. incognita*, Lee soybean formed more lateral roots than did healthy plants (6). This response may explain the increased plant growth observed in those soils.

The relationships of Pi and selected physical and chemical edaphic factors with soybean yield and *M. incognita* reproduction were determined (Table 5). By reducing the number of variables using principal component analysis, more meaningful equations were selected using maximum R^2 improvement. Equations accounting for the greatest variation of yield and *M. incognita* reproduction were selected on the basis of R^2 of the regression equation, Mallows (13) C_p value, and the significance level of each

TABLE 5. Regression equations of soybean yield (g/plot) as affected by initial population density of *Meloidogyne incognita*, soil chemical characteristics, and soil texture at Central Crops Research Station, Clayton, North Carolina.

Year	Equation*	
	Soybean yield	*M. incognita* reproduction
1981	$Y = 490.6 - 69.3Pi - 20.2HM + 3.1M - 4.9C$ $R^2 = 0.64$ $P = 0.01$	$Y = 53.7 - 26.8Pi + 0.7SD$ $R^2 = 0.51$ $P = 0.01$
1982	$Y = 202 - 4.8Pi - 90.4A - 2.7C + 19S$ $R^2 = 0.32$ $P = 0.01$	$Y = 108.6 - 3.9Pi - 115.4WV - 5.1CE + 11.5pH - 0.4C$ $R^2 = 0.33$ $P = 0.01$
1983	$Y = 130.4 - 65.2Pi - 28.6A + 0.5P + 7.3S$ $R^2 = 0.71$ $P = 0.01$	$Y = 187.2 - 62.9Pi + 33.1HM - 57.8A + 0.9P$ $R^2 = 0.40$ $P = 0.01$

* A = acidity. C = % clay. CE = cation exchange capacity. HM = % organic matter. M = manganese index. P = phosphorus index. pH = hydrogen-ion concentration. Pi = initial population. S = % silt. SD = % sand. WV = weight/volume.

TABLE 7. Soybean yield as influenced by soil type and initial population densities of *Meloidogyne incognita* at four locations.

Parameter	Yield (g/plot)
Soil type	
Appling sandy clay loam	61
Lakeland sand	12
Muck	95
Goldsboro sandy loam	74
Orthogonal contrasts*	A, B, C
Inoculum/500 cm^3 soil	
0 (check)	175
625 (low)	57
2,500 (medium)	10
10,000 (high)	1
Orthogonal contrasts†	X, Y

Means are averages of 20 observations.

* Letters are used to designate differences as determined by orthogonal contrasts: A = Appling sandy clay loam and muck vs. Goldsboro sandy loam and Lakeland Sand. B = Goldsboro sandy loam vs. Lakeland sand. C = Appling sandy loam vs. muck ($P = 0.01$).

† Letters are used to designate differences as determined by orthogonal contrasts: X = check vs. others. Y = low vs. medium and high ($P = 0.01$).

TABLE 8. Regression equations of soybean yield (g/plot) as affected by initial population density (Pi) of *Meloidogyne incognita* and soil types at four locations in North Carolina.

Soil type	Equation
Appling sandy clay loam	Y = 145.2 − 33.1Pi $R^2 = 0.69$ $P = 0.01$
Goldsboro sandy loam	Y = 235.3 − 63.4Pi $R^2 = 0.83$ $P = 0.01$
Lakeland sand	Y = 44.1 − 12.5Pi $R^2 = 0.73$ $P = 0.01$
Muck	Y = 275.8 − 70.8Pi $R^2 = 0.74$ $P = 0.01$

variable in the equation. Factors accounting for much of the variability in yield included Pi, percentage of organic matter, manganese index, and percentage of clay in 1981; Pi, acidity, percentage of clay, and percentage of silt in 1982; and Pi, acidity, phosphorus index, and percentage of silt in 1983. Factors with the greatest statistical effect on *M. incognita* reproduction were Pi and percentage of sand in 1981; Pi, weight/volume, CEC, pH, and percentage of clay in 1982; and Pi, percentage of organic matter, acidity, and phosphorus index in 1983.

Initial population densities of nematodes accounted for most of the variation of soybean yield in 1981 and 1983. Chemical and physical edaphic factors proved to be equally important in their relationship to crop yield and *M. incognita* reproduction. Percentage of clay and humic matter are important to chemical and biological activity in soil (16). Clay and organic matter affect moisture holding capacity, bulk densities, CEC, and amount and size of pore space. Chemical parameters, such as CEC, may also have a direct effect on nematode chemoreceptors. Manganese and phosphorus may affect the nematode, but they are more likely related to the nutritional needs of soybean. Many of the parameters in regression equations for reproduction may affect nematode reproduction indirectly by influencing root growth.

Influence of soil type and location: Meloidogyne incognita reproduced readily on soybean in the Appling sandy clay loam, Lakeland sand, and Goldsboro sandy loam, with little reproduction in the muck (Table 6). Reproductive rate was inversely proportional to inoculum level at all locations. Low nematode population densities occurring at harvest may be attributed to the high virulence of the Georgia population. Plant death by midseason at 2,500 and 10,000 Pi was common.

Yield varied significantly ($P = 0.01$) among soil types at the four locations (Table 7). All contrasts of soil type (or location) were significant. Highest yields were in the muck and lowest yields in the Lakeland sand. Soil type, along with rainfall and other environmental parameters, probably accounted for much of the variability between locations.

The Georgia population greatly ($P = 0.01$) limited yields at all four locations. Even with the low reproduction at Wenona (muck), nematode numbers were sufficient to suppress yield. Contrasts of the noninfested vs. nematode-infested plots and the low vs. medium and high Pi were significant. There was no difference in yield between the medium and high nematode Pi. The soil type (or location)–Pi interaction was highly significant ($P = 0.01$). The relationship between Pi and yield was best described by a linear model in all soils (Table 8). As the initial population increased, there was a sharp suppression of soybean yield.

Our hypothesis that soil type influenced

M. incognita reproduction and damage potential on soybean was confirmed by these results. Reproduction and yield suppression varied among soil types at CCRS. At the other locations, soil type as well as other environmental factors (i.e., rainfall, soil temperature, etc.) probably contributed to differences in yields. It is not clear whether soil type or an individual edaphic characteristic of a soil type is the most important factor influencing reproduction and the damage potential of *M. incognita*. However, including selected edaphic factors in damage function models should maximize their reliability.

Ferris (4) has suggested that damage functions be developed using nematode numbers, pathogenic ratings for species, and environmental suitability. Pathogenic ratings would have to be adjusted not only between species but also within species. Variability of virulence of *M. incognita* has been reported between races and within races (22,24). The North Carolina and Georgia populations used in this study vary greatly in virulence (24).

Factors accounting for environmental suitability in Ferris's model included soil texture (4). However, in our experiments and other studies (7,8), chemical characteristics of soil were related to root-knot nematode damage and could be used in models. Another factor that should be considered is soil moisture. Data on soil moisture collected during flowering and pod set in 1983 at CCRS was not statistically important, probably because of the limited number of sampling dates and the method used. Other research indicates that adequate soil moisture may increase tolerance to *M. incognita* (1).

Chemical and physical edaphic factors are interrelated. It is difficult to determine which edaphic factors are most important in nematode ecology (16). However, single factors may directly or indirectly influence nematode reproduction and damage potential. Much research is still needed to relate initial soil population densities of nematodes along with environmental factors to crop yield. Models that include nematode numbers and virulence ratings along with selected environmental factors should provide more precise estimates of potential yield losses caused by *M. incognita*.

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