Letter Code System of Nomenclature for *Puccinia graminis* f. sp. *avenae*

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ABSTRACT

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Current systems that describe the virulence phenotype in *Puccinia graminis* f. sp. *avenae* lack a systematic approach for the naming of races or to provide easily made comparisons of virulence among races. A new nomenclature system that simply and systematically characterizes virulence in *P. graminis* f. sp. *avenae* is described. The new system has the distinct advantage of providing easily seen relationships among races in contrast to previous nomenclature systems. This allows for easier interpretation of virulence relationships in the oat stem rust population and provides a large amount of virulence information with a minimum of written characters. This system uses single-gene differential lines with the resistance genes *Pg1*, *Pg2*, *Pg3*, *Pg4*, *Pg6*, *Pg8*, *Pg9*, *Pg10*, *Pg12*, *Pg13*, *Pg15*, and *Pg16*, grouped into three subsets of four lines in sequential *Pg* gene order. By grouping in sequential gene number order, the relationship of the new system to the “standard” system is easily seen. Each race is designated by a three-letter code, based on the seedling reaction (low or high) on 12 differential lines. The letter code nomenclature system is open ended and can be updated easily as new differential genes are identified. This system simply and precisely describes the virulence phenotypes of isolates of *P. graminis* f. sp. *avenae*, and allows for easily made comparisons of virulence of isolates collected over time and across geographical locations worldwide.

Several nomenclature systems to describe virulence in *Puccinia graminis* f. sp. *avenae* Erikss. & Henning have been developed; however, currently, there is no adequate system that simply describes the virulence phenotypes of isolates of *P. graminis* f. sp. *avenae* or provides easily made comparisons of virulence of isolates from different geographical areas. Physiologic specialization in *P. graminis* f. sp. *avenae* first was described by Stakman et al. in 1923 using the varieties Victory, White Tartar, and Monarch to describe four races of oat stem rust (20). In 1925, Bailey described five races of *P. graminis* f. sp. *avenae*, using White Tartar (=White Russian), Richland, and Jostrain (3). Levine and Smith added races 6 to 10 in 1937, and Newton and Johnson added races 11 to 13 in 1944, using the same three differential

varieties (11,16). These first 13 races were used as the standard for describing physiologic specialization in *P. graminis* f. sp. *avenae*.

Subsequent to the description of the 13 “standard” races, additional genes conferring resistance to *P. graminis* f. sp. *avenae* were found and are described in Table 1. Genes originally were designated by using a letter (e.g., gene A) but currently are designated by number (e.g., *Pg2*) using a standardized gene nomenclature system (19). Deviations from standard races were described as subraces, adding letters to standard race numbers to identify additional races. In 1965, Green (7) devised a virulence formula nomenclature system for Canada (C-races) using genes from the differential varieties Richland, Rodney, Minrus, Jostrain, CI 4023, and CI 5844-1. In 1970, Stewart and Roberts published the first proposed international system for identifying races of *P. graminis* f. sp. *avenae*, using the same six differential varieties as Green (7) and the diploid oat line Saia to describe the “standard” races, numerous subraces, C-races, and exotic races from several countries, with a total of 97 races identified (21).

The development of backcross-derived lines (Rodney 0 background) with a single gene (*Pg* gene) for oat stem rust resistance led to the development of the North

American (NA) nomenclature system in 1979 (14), which currently is used to characterize virulence in *P. graminis* f. sp. *avenae* in Canada and the United States. In contrast, virulence in *P. graminis* f. sp. *avenae* in Australia currently is characterized using a modified Stewart and Roberts system (2). Because there is a lack of continuity across the various nomenclature systems and there appears to be no systematic approach in the naming of races (other than by order of discovery), we describe a new nomenclature similar to existing cereal rust nomenclature systems (4,12,17) that simply and precisely identifies the virulence phenotype (race) of isolates of *P. graminis* f. sp. *avenae*. This system will provide a method to easily and accurately compare virulence of isolates collected over time and across geographical areas.

THE LETTER CODE RACE NOMENCLATURE SYSTEM

Currently, there are 17 numbered *Pg* genes identified, plus the *Pg-a* complex. Genes *Pg5* and *Pg7* are repetitive of genes *Pg4* and *Pg6*, respectively, and are of no use as differential lines (13). Genes *Pg11* and *Pg17* are expressed only at the adult plant stage and would not be useful as differential lines at the seedling stage (10,15). Gene *Pg14* is ineffective to numerous North American and exotic isolates tested thus far (T. Fetch, unpublished data) and is not noted for its resistance (13); thus, it is not included in the differential set. All other numbered genes are useful in characterizing virulence and are included in the differential sets.

The differential lines for the new nomenclature system are listed in Table 2. Most (*Pg1*, *Pg2*, *Pg3*, *Pg8*, *Pg9*, *Pg13*, *Pg15*, and *Pg16*) are in a Rodney 0 (CI 9317, no known *Pg* resistance gene) background as described by Martens et al. (14). Comparisons of infection type (IT) between original sources of resistance to their Rodney 0-derived lines were made with several races using previously reported methods (5), and the results are presented in Table 3. IT of infected seedlings was determined using a 0-to-4 scale, where ITs of 0, 1, and 2, or combinations thereof, are classified as low ITs and indicative of resistance, whereas ITs of 3 or

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4 are high ITs and indicative of susceptibility (3). Because expression of several *Pg* genes is affected by incubation temperature (6,14), all comparisons were conducted in a growth chamber at 19°C with a 16-h photoperiod and light intensity of 180 to 220 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$. Under these incubation conditions, all genes will express their low ITs to avirulent races of *P. graminis* f. sp. *avenae*, which is easily discernable from a susceptible (IT 34 or 4) reaction. For a given *Pg* gene, the observed ITs between the original source and the corresponding Rodney line were comparable (Table 3). However, it was found that several *Pg* gene sources and their Rodney 0 derivatives acquired from the United States Department of Agriculture–Agricultural Research Service (USDA-ARS) National Small Grains Collection (NSGC) in Aberdeen, ID were mixed for ITs. Therefore, differential lines in the Rodney 0 background were reselected for the correct phenotype and increased for seed that is available for race identification of *P. graminis* f. sp. *avenae*.

The letter code nomenclature utilizes 12 single-gene *Pg* differential lines, using three subsets of four lines organized into a hexadecimal system that has 16 possible combinations of low (L) or high (H) reaction for each letter (Table 4). This is adapted from the existing nomenclature systems used for other cereal rusts (4,12,17). The advantage of the letter code system is a simple, short, and accurate description of virulence phenotype across most of the described resistance genes, which enables utilization of this system regardless of when and where isolates have been collected. In contrast, comparisons of virulence of isolates identified using the “standard”, C number, and NA formula system were difficult and imprecise (8),

due to the lack of a systematic approach in numbering of races and to addition of differential lines that occurred over time. Because the order of genes in the new system is sequential, it is relatively easy to make comparisons to the “standard” system originally described (e.g., race 1 = B_ or C_ races, race 2 = D_ races, race 6 group = TG_ or TD_ races, race 7 group = N_ or P_ races, race 8 = J_ races, and race 11 group = G_ or H_ races). Additionally, virulence of isolates collected worldwide cannot currently be compared, because differential sets are not uniform and different nomenclature systems are utilized. The letter code system is flexible in that, as new *Pg* genes are characterized, they can be added as additional subsets and letters appended accordingly. Data on supplemental lines can be added to the letter code using a plus (+) sign (e.g., race TGL+ *Pg-a*). In addition, the letter code system is suitable for international use because it

incorporates almost all *Pg* genes to characterize virulence in *P. graminis* f. sp. *avenae*. Virulence information previously reported in North America is presented in Table 5 using the new letter code, NA number designation (14), and avirulence or virulence formula systems. Each NA race reported previously corresponded to a unique letter-code race designation following this system.

The new system uses three seedling *Pg* genes (*Pg6*, *Pg10*, and *Pg12*) that have not been used previously to characterize *P. graminis* f. sp. *avenae*. Gene *Pg6* (from CI 6956) and the resistance gene in the diploid line Saia (which is used in the Stewart and Roberts nomenclature) appear to be identical (18). Although *Pg6* has not yet been transferred into a hexaploid background, it has been shown to be useful in differentiating isolates of stem rust at the Winnipeg Rust laboratory. In testing of 23 common North American races stored at

Table 2. Differential lines used for characterizing virulence in *Puccinia graminis* f. sp. *avenae*^a

<i>Pg</i> gene	CI no.	CN no.	RL no.	IT at 20°C ^b	Source of resistance
<i>Pg1</i>	9318	58243	899	11+	White Russian, CI 551
<i>Pg2</i>	9319	58244	815	;1	Hajira, CI 1001
<i>Pg3</i>	2660	58245	...	;1 to X-	Jostrain, CI 2660
<i>Pg4</i>	6661	56534	2123	;1-	Hajira, CI 1001
<i>Pg6</i>	6956	56818	...	0;1-	CD 3820, CI 6956
<i>Pg8</i>	9321	58246	903	12-	Hajira, CI 8111
<i>Pg9</i>	9322	58247	879	11+	CI 6792
<i>Pg10</i>	8457	58055	...	23n	Illinois Hulless, CI 2824
<i>Pg12</i>	8250	64102	...	;1	Kyto, CI 8250
<i>Pg13</i>	9212	28959	618	11+	<i>Avena sterilis</i> , PI 324798
<i>Pg15</i>	9351	58276	997	11+	<i>A. sterilis</i> , CAV 1830
<i>Pg16</i>	9352	58277	882	12-	<i>A. barbata</i> , D203
<i>Pg-a</i>	...	1947	996	0;1-	Omega, CI 9139

^a CI is the Cereal Introduction number (United States Department of Agriculture–Agricultural Research Service, Aberdeen, ID), CN is the Canadian Number (Plant Genetic Resources Collection, Saskatoon, SK, Canada), and RL is the Rust Lab accession number (Cereal Rust Lab, Winnipeg, MB, Canada).

^b Infection types (ITs) are based on a 0-to-4 scale (3).

Table 1. Background information for resistance genes to *Puccinia graminis* f. sp. *avenae*

<i>Pg</i> gene	Letter ^a	Year	Origin	Source	<i>Avena</i> sp.	CI number	Temperature ^b
1	D	1925	Russia	White Russian	<i>sativa</i>	551	None
1	D	1938	Russia	Minrus	<i>sativa</i>	2144	None
2	A	1925	Russia	Richland	<i>sativa</i>	787	None
3	E	1925	USA	Sevnothree	<i>sativa</i>	3251	21°C
3	E	1925	France	Jostrain	<i>sativa</i>	2660	21°C
4	B	1954	South Africa	Hajira	<i>sativa</i>	1001	26°C
5	C	1954	South Africa	Hajira	<i>sativa</i>	4019	...
6	...	1956	Uruguay	CD 3820	<i>strigosa</i>	6956	None
7	...	1956	Uruguay	CD 3820	<i>strigosa</i>	6956	...
8	F	1959	North Africa	Hajira	<i>sativa</i>	8111	27°C
9	H	1965	Argentina	Sante Fe selection	<i>sativa</i>	5844-1	25°C
10	G	1965	USA	Illinois Hulless	<i>nuda</i>	2824	None
11	...	1968	Rhodesia	Burt	<i>sativa</i>	3034	Adult ^c
12	...	1968	Yugoslavia	Kyto	<i>sativa</i>	8250	25°C
13	M	1970	Tunisia	CW490-2	<i>sterilis</i>	PI 324798	27°C
14	N	1972	Wales	Milford	<i>sativa</i>	5039	...
15	...	1980	Turkey	CAV 1830	<i>sterilis</i>	9351	26°C
16	R	1979	Israel	D-203	<i>barbata</i>	9125	25°C
17	...	1990	Spain	IB 3056	<i>sterilis</i>	...	Adult
<i>Pg-a</i>	X	1981	USA	Omega	hybrid	9139	26°C

^a Genes originally were designated by letter, then changed later to a *Pg* gene number (17).

^b Incubation of lines at or above this temperature renders ineffective the expression of resistance (6). For genes *Pg1*, *Pg2*, *Pg6*, and *Pg10*, there is no effect of incubation temperature up to 30°C.

^c CI 3034 also has been reported to possess the seedling gene *Pg1* (11).

the Winnipeg Rust Laboratory, only NA1 and NA70 have been found to be virulent on *Pg6* (T. Fetch and Zegeye, *unpublished data*); thus, most North American races were presumed to be avirulent to *Pg6* in Table 5. In contrast, virulence to Saia (= *Pg6*) is observed frequently in isolates of *P. graminis* f. sp. *avenae* in Australia (2).

Gene *Pg10* (from CI 2824) has not been used in previous nomenclature systems due to temperature sensitivity (14). Studies at Winnipeg indicate that the reaction of *Pg10* is intermediate (IT = 23N) at low (15 to 21°C) temperatures, but becomes more resistant (12+N) at elevated (>24°C) temperatures (6). Although *Pg10* exhibits an intermediate resistance reaction (IT = 23n), the distinct necrosis associated with its resistance response is unique to this gene (9) and is easily discernable from a susceptible (IT = 3 or 4) reaction. Virulence to *Pg10* has not been observed in North America among several thousand isolates tested at Winnipeg and St. Paul rust laboratories, but virulence to *Pg10* has been found from an isolate obtained from New Zealand (T. Fetch, *unpublished data*).

Gene *Pg12* has not been used previously in nomenclature systems, but the related *Pg-a* complex was used by Martens et al. (14) in the NA nomenclature. Gene *Pg12* is included in the new differential set in lieu of the *Pg-a* complex because (i) it is a single gene, (ii) no differential response (high versus low) between *Pg12* and *Pg-a* has been found among several thousand isolates tested simultaneously on the two lines, and (iii) allelism tests of F₂ progeny from crosses between the *Pg12* source

'Kyto' (CI 8250) and *Pg-a* source 'Omega' (CI 9139) found no susceptible segregants among 4495 F₂ plants (T. Fetch, *unpublished data*). Thus, the low seedling IT observed on the *Pg-a* complex apparently is conditioned by the gene *Pg12* and may be modified by an additional unknown recessive gene. This is in contrast to previously published data that reported that *Pg12* is not involved in the *Pg-a* response (1). The *Pg-a* complex was included in Table 2 as a supplementary line because of historical use, but is not intended as a differential line in this nomenclature system.

The letter code nomenclature system presented here is simple, precise, and describes the virulence spectrum of races of *P. graminis* f. sp. *avenae* on most known seedling resistance genes in oat. This system will be useful in enabling rust workers to uniformly characterize *P. graminis* f. sp. *avenae* isolates for discussion on virulence dynamics and population studies. Limited seed for all differential lines is available from the authors, and also from seed depositories in Plant Gene Resources Canada (PGRC, Saskatoon, SK) and USDA-ARS NSGC in Aberdeen, ID.

Table 4. Letter code designations for races of *Puccinia graminis* f. sp. *avenae* using 12 differential single *Pg*-gene lines in three ordered subsets of four lines each

Letter code	Subset	Classification of infection types (ITs) ^a				
	1	<i>Pg1</i>	<i>Pg2</i>	<i>Pg3</i>	<i>Pg4</i>	
	2	<i>Pg6</i>	<i>Pg8</i>	<i>Pg9</i>	<i>Pg10</i>	
	3	<i>Pg12</i>	<i>Pg13</i>	<i>Pg15</i>	<i>Pg16</i>	
B	...	L	L	L	L	L
C	...	L	L	L	L	H
D	...	L	L	H	L	L
F	...	L	L	H	H	H
G	...	L	H	L	L	L
H	...	L	H	L	L	H
J	...	L	H	H	L	L
K	...	L	H	H	H	H
L	...	H	L	L	L	L
M	...	H	L	L	L	H
N	...	H	L	H	L	L
P	...	H	L	H	H	H
Q	...	H	H	L	L	L
R	...	H	H	L	H	H
S	...	H	H	H	L	L
T	...	H	H	H	H	H

^a Classification of infection types: L = low/resistant (ITs of 0, ;, 1, and 2, or combination thereof) and H = high/susceptible (ITs of 3, 4, or combination thereof) (17).

Table 3. Infection type (IT) comparison of oat lines with original sources of *Pg* gene resistance and equivalent Rodney 0-derived lines to races of *Puccinia graminis* f. sp. *avenae*

Pg gene	CI no. ^b	Genetic background	IT at 20°C ^a				
			NA1	NA8	NA16	NA20	NA55
<i>Pg1</i>	551	White Russian	2 [±]	12 ⁻	3 ⁺ 4	3 ⁺ 4	34n
	9318	Rodney 0	12 ⁻	1 [±]	3 ⁺ 4	4	3 ⁺ n
<i>Pg2</i>	787	Richland	;1	;1 ⁻	;1	4	34n
	9319	Rodney 0	;1	;1	;1	4	34n
<i>Pg3</i>	2660	Jostrain	X ⁻	X ⁼	4	0;	X ⁼
	9320	Rodney 0	X ⁻	X ⁻	4	0;	X ⁼
<i>Pg4</i>	1001	Hajira	;1	33 ⁺	;1	4	34n
	6661	Rodney	;1 ⁻	33 ⁺	;1	4	34n
<i>Pg8</i>	8111	Hajira	;1	;1 ⁺	34	11 ⁺	;1
	9321	Rodney 0	1 ⁻	1 [±]	3 ⁺ 4	12 ⁻	;1
<i>Pg9</i>	5844-1	Sante Fe select	11 ⁺	4	;1	4	34n
	9322	Rodney 0	12	4	;1 ⁺	4	3 ⁺ 4
<i>Pg10</i>	2824	Illinois Hullless	3 [±] N	23 ⁺ N	24N	23 ⁺ N	13 ⁻ N
	8457	X-1588	13N	12 ⁺ N	23N	12 ⁺ N	22 ⁺ n
<i>Pg13</i>	2647	<i>A. sterilis</i>	;1	34	;1	;1	;1
	9212	Rodney 0	;1 ⁻	34	;1 ⁻	;1	;1
<i>Pg15</i>	1830	<i>A. sterilis</i>	34	34	;1	34	34
	9351	Rodney 0	34	34	;1	34	23 ⁺
<i>Pg16</i>	D203	<i>A. barbata</i>	1 ⁻	;1 ⁻	1 ⁻	;1 ⁻	34
	9352	Rodney 0	11 ⁻	;1	11 ⁻	;1	34

^a ITs are based on a 0-to-4 scale where ITs of 0, ;, 1, and 2 are indicative of a resistant (low) response and ITs of 3 or 4 of a susceptible (high) response (3). Symbols + and - indicate slightly larger and smaller pustule sizes, respectively. North American (NA) races use the nomenclature of Martens et al. (14).

^b CI is the Cereal Introduction number (United States Department of Agriculture-Agricultural Research Service, Aberdeen, ID).

Table 5. Key to races of *Puccinia graminis* f. sp. *avenae* using the letter code nomenclature, North American (NA) nomenclature, and avirulence/virulence formula system^a

Code	Race	Eff/ineff Pg genes	Code	Race	Eff/ineff Pg genes	Code	Race	Eff/ineff Pg genes
BDB	NA38	1,2,3,4,8,13,15,16,a/9	KBD	NA11	1,8,9,13,16,a/2,3,4,15	RBD	NA19	3,8,9,13,16,a/1,2,4,15
BDD	NA2	1,2,3,4,8,13,16,a/9,15	KDD	NA12	1,8,13,16,a/2,3,4,9,15	RDD	NA20	3,8,13,16,a/1,2,4,9,15
BDJ	NA3	1,2,3,4,8,16,a/9,13,15	KDJ	NA32	1,8,16,a/2,3,4,9,13,15	RDF	NA58	3,8,13,a/1,2,4,9,15,16
BLD	NA1	1,2,3,4,8,9,13,16,a/15	KJD	NA13	1,13,16,a/2,3,4,8,9,15	RDJ	NA54	3,8,16,a/1,2,4,9,13,15
CDJ	NA4	1,2,3,8,16,a/4,9,13,15	LDD	NA65	2,3,4,8,13,16,a/1,9,15	RGB	NA21	3,9,13,15,16,a/1,2,4,8
CLD	NA70	1,2,3,8,9,13,16,a/4,15	LGB	NA14	2,3,4,9,13,15,16,a/1,8	RGD	NA77	3,9,13,16,a/1,2,4,8,15
DBB	NA39	1,2,4,8,9,13,15,16,a/3	MDD	NA71	2,3,8,13,16,a/1,4,9,15	RJB	NA51	3,13,15,16,a/1,2,4,8,9
DBD	NA5	1,2,4,8,9,13,16,a/3,15	MGB	NA44	2,3,9,13,15,16,a/1,4,8	RJD	NA72	3,13,16,a/1,2,4,8,9,15
DDD	NA6	1,2,4,8,13,16,a/3,9,15	NBB	NA15	2,4,8,9,13,15,16,a/1,3	RJJ	NA75	3,16,a/1,2,4,8,9,13,15
DDJ	NA7	1,2,4,8,16,a/3,9,13,15	NDB	NA45	2,4,8,13,15,16,a/1,3,9	SBD	NA22	4,8,9,13,16,a/1,2,3,15
DJD	NA53	1,2,4,13,16,a/3,8,9,15	NDD	NA35	2,4,8,13,16,a/1,3,9,15	SDD	NA61	4,8,13,16,a/1,2,3,9,15
FBD	NA56	1,2,8,9,13,16,a/3,4,15	NDJ	NA47	2,4,8,16,a/1,3,9,13,15	SGB	NA23	4,9,13,15,16,a/1,2,3,8
FDD	NA74	1,2,8,13,16,a/3,4,9,15	NDL	NA46	2,4,8,13,15,16/1,3,9,a	SGD	NA63	4,9,13,16,a/1,2,3,8,15
FDJ	NA8	1,2,8,16,a/3,4,9,13,15	NGB	NA16	2,4,9,13,15,16,a/1,3,8	TBD	NA24	8,9,13,16,a/1,2,3,4,15
GBD	NA59	1,3,4,8,9,13,16,a/2,15	NGD	NA18	2,4,9,13,16,a/1,3,8,15	TDB	NA52	8,13,15,16,a/1,2,3,4,9
GDD	NA64	1,3,4,8,9,13,16,a/2,9,15	NGL	NA17	2,4,9,13,15,16,a/1,3,8,a	TDD	NA25	8,13,16,a/1,2,3,4,8,15
GDJ	NA34	1,3,4,8,16,a/2,9,13,15	NJB	NA48	2,4,13,15,16,a/1,3,8,9	TDF	NA55	8,13,a/1,2,3,4,9,15,16
HBD	NA69	1,3,8,9,13,16,a/2,4,15	PBD	NA57	2,8,9,13,16,a/1,3,4,15	TDJ	NA26	8,16,a/1,2,3,4,9,13,15
HDB	NA40	1,3,8,13,15,16,a/2,4,9	PBG	NA66	2,8,9,15,16,a/1,3,4,13	TGB	NA27	9,13,15,16,a/1,2,3,4,8
HDD	NA9	1,3,8,13,16,a/2,4,9,15	PDB	NA49	2,8,13,15,16,a/1,3,4,9	TGD	NA29	9,13,16,a/1,2,3,4,8,15
HDJ	NA31	1,3,8,16,a/2,4,9,13,15	PDD	NA36	2,8,13,16,a/1,3,4,9,15	TGL	NA28	9,13,15,16/1,2,3,4,8,a
JBD	NA10	1,4,8,9,13,16,a/2,3,15	PDJ	NA37	2,8,16,a/1,3,4,9,13,15	TJB	NA68	13,15,16,a/1,2,3,4,8,9
JDB	NA41	1,4,8,13,15,16,a/2,3,9	QBB	NA73	3,4,8,9,13,15,16,a/1,2	TJD	NA30	13,16,a/1,2,3,4,8,9,15
JDD	NA33	1,4,8,13,16,a/2,3,9,15	QBD	NA60	3,4,8,9,13,16,a/1,2,15	TJG	NA76	15,16,a/1,2,3,4,8,9,13
JDJ	NA42	1,4,8,16,a/2,3,9,13,15	QDD	NA62	3,4,8,13,16,a/1,2,9,15	TJJ	NA67	16,a/1,2,3,4,8,9,13,15
KBB	NA43	1,8,9,13,15,16,a/2,3,4	QGB	NA50	3,4,9,13,15,16,a/1,2,8			

^a Code = letter code, Race = NA race, and Eff/ineff = effective/ineffective. The letter code system infers that reaction to *Pg12* is identical to *Pg-a*, all NA races are avirulent to *Pg10*, and only races NA1 and NA70 are virulent to *Pg6*.

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