Identification of Resistance to *Pseudocercospora herpotrichoides* in *Triticum monococcum*

M. M. Cadle and T. D. Murray, Department of Plant Pathology, and S. S. Jones, Department of Crop and Soil Sciences, Washington State University, Pullman 99164-6430

ABSTRACT

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Eyespot is an important disease of wheat in the United States Pacific Northwest. Genes *Pch1*, located on chromosome 7D, and *Pch2*, located on chromosome 7A, are the only known sources of eyespot resistance in hexaploid wheat. A core collection of *Triticum monococcum*, a close relative of the A-genome donor of bread wheat, consisting of 118 accessions from 26 countries was screened for resistance using a β -glucuronidase-transformed strain of the pathogen. Fifty-two (44%) accessions from 15 different countries were resistant. More than half of the accessions collected in Turkey (26 of 42) were resistant. Two accessions were more resistant than resistant cultivars Cappelle Desprez (*Pch2*) and Madsen (*Pch1*). Screening these accessions for the isozyme marker *Ep-A1b*, which is linked with *Pch2* in hexaploid wheat, revealed variation but no association with resistance. These results indicate *T. monococcum* is a new source of resistance to *Pseudocercospora herpotrichoides* that potentially contains more effective resistance to *P. herpotrichoides* than that conferred by either *Pch1* or *Pch2*.

Additional keywords: diversity index, genetic resistance, *Triticum aestivum*

Eyespot, a yield-limiting disease of wheat (*Triticum aestivum* L.) caused by *Pseudocercospora herpotrichoides* (Fron) Deighton (teleomorph = *Tapesia yallundae* Wallwork & Spooner), is capable of causing millions of dollars of damage to the wheat crop in the United States Pacific Northwest (USPNW) in years when it is severe (29). Planting resistant cultivars can save growers the cost of applying a fungicide, and minimize economic losses. Furthermore, strains of the pathogen resistant to commonly used benzimidazole fungicides are widespread, making utilization of disease resistant cultivars increasingly important (21,32,29).

There are four known sources of resistance to eyespot. The most effective resistance gene (*Pch1*) currently in use is derived from *T. ventricosum* Ces. (genomes D^VD^VM^VM^V), a distant wheat relative. This single gene, which is found in wheat line VPM-1, is located on chromosome 7D (14,16). A second, less effective gene, *Pch2*, is found in the cultivar Cappelle Desprez and is located on chromosome 7A (6,25). Although the pedigree of Cappelle Desprez is known (8), the origin of *Pch2* is not known. Two additional diploid wheat

species that confer resistance to eyespot are *Dasyphyrum villosum* (L.) Candargy and *T. tauschii* (Coss.) Schmal. (31,38). Resistance in *D. villosum* is located on chromosome 4V (31); however, the chromosomal location of a resistance gene or genes in *T. tauschii* is unknown.

Pch1 is the only eyespot resistance gene currently used in the USPNW, and cultivars containing this gene are grown on 34% of the total wheat acreage in Washington state (37). In contrast, *Pch2* is not used, primarily because the resistance conferred by this gene is inadequate to prevent yield loss in most years (8,30). Neither *Pch1* nor *Pch2* confer complete resistance when used alone. Combining these genes in a single genotype, finding more effective alleles of these genes, or finding new, more effective genes would be of potential benefit to cultivar development programs.

Wild wheats are sources of disease resistance genes (11,17,19,27), and it is possible to find variation for eyespot resistance among some of the wild populations (38). Einkorn wheats (*T. urartu* Thumanian ex Gandilyan, *T. monococcum* L. subsp. *monococcum* and *T. m. boeoticum* (Boiss.) Hayek) are all wild wheats (genomes AA); however, only *T. urartu* is considered to be the diploid A-genome donor of hexaploid wheat ($2n = 6x = 42$, AABBDD) (12,13,18,26). Unlike many diploid wheat relatives that are considered weeds, *T. monococcum* is cultivated in many parts of Europe and Asia for use as forage, bread making, and in pharmaceuticals. This species is known to contain resistance for other important wheat diseases and pests

such as leaf rust, stripe rust, Karnal bunt, and Russian wheat aphid (28,33). The presence of *Pch2* on chromosome 7A in Cappelle Desprez suggests that the origin of this gene is an A-genome species; however, this is not known with certainty. Consequently, alleles conferring more effective resistance than *Pch2* may exist if variation for this trait occurs among *T. monococcum* accessions.

Resistance to eyespot is associated with morphological and biochemical markers that can be useful in mapping or assessing diversity in wild populations (22,25). *Pch1* is absolutely linked with the *Ep-D1b* band of the endopeptidase enzyme in VPM-1 and cultivars derived from this line. de la Peña et al. (6) speculated that this linkage is due to a nonrecombining fragment of *Ae. ventricosa* chromatin containing *Pch1* inserted adjacent to *Ep-D1b*. It is unknown if the endopeptidase locus is linked with eyespot resistance genes in *Ae. ventricosa* or other wild species, or if the absolute linkage in hexaploid wheat is an artifact of a translocation event. Regardless, breeders have used this close association with eyespot resistance in an application of marker-based selection resulting in the cultivars Hyak and Madsen (1,2). A similar association, although not as tightly linked (about 15% recombination), has been found between *Pch2* and *Ep-A1b* (6). Red coleoptile color has also been associated with both *Pch1* and *Pch2*, although other work has demonstrated that *Pch2* is unlinked to this trait (25,6).

The purpose of this study was to determine if variation for resistance to eyespot exists in *T. monococcum* and, if so, the extent of this variation. Disease reaction was evaluated in a core collection of 118 accessions of *T. monococcum* collected from a wide geographic area. Screening for endopeptidase isozyme composition and coleoptile color were conducted to determine the association of these markers with resistance.

MATERIALS AND METHODS

Germ plasm. A core collection of 118 accessions of *T. monococcum* from 26 countries was selected by H. Bockleman, curator for the United States Department of Agriculture National Small Grains Collection (total *T. monococcum* collection = 235). Known resistant cultivars Cappelle Desprez and Madsen were included in the screening as resistant controls, and Chinese Spring was used as a susceptible control.

Corresponding author: T. D. Murray
E-mail: tim_murray@wsu.edu

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Disease rating. Accessions were grown in a growth chamber in 1:1 (wt/wt) vermiculite:Thatuna silt loam in 5 cm peat pots in plastic flats at 12°C, with 12 h light and 95 to 100% relative humidity (7). Five replicates containing two seeds of each accession were planted. Seedlings were inoculated with a β -glucuronidase (GUS)-

transformed strain of *P. herpotrichoides* at the two-leaf stage as described by de la Peña and Murray (7), and grown under the same conditions for an additional 6 weeks. Disease reaction was evaluated after 6 weeks by measuring fluorescence of infected plant tissue extract after incubation with the GUS substrate 4-methylumbel-

liferyl β -D-galactoside (MUG; 7). Disease was also scored visually on a 1 to 4 disease rating scale (37), where 1 = no symptoms, 2 = lesion on the first leaf sheath, 3 = lesions on the first and second leaf sheaths, and 4 = lesions covering the entire second leaf sheath and penetrating onto the third. Resistance was determined by comparison of *T.*

Table 1. Origin, coleoptile color, endopeptidase banding pattern (Ep), visual, and β -glucuronidase (GUS) disease score means of *Triticum monococcum* core collection

Accession	Cultivar	Origin	Coleoptile ^y	Ep	Disease score means	
					Visual	GUS ^z
CI 002433	Einkorn	Germany	Green	1	3.5	2.1 a
CI 013962		Oregon	Green	2	3.0	1.9 a
CI 013963		Oregon	Green	2	3.0	1.9 a
CI 013964		Oregon	Green	2	2.0	1.7 ab
CI 014520		Canada	Green	7	3.0	1.9 a
CI 017653	Monococcum Mutant 3	Washington	Green	1	2.0	1.6 ab
CI 017655	Monococcum Mutant 6	Washington	Green	1	2.8	1.9 a
CI 017657	Monococcum Mutant 11	Washington	Red	2	3.0	1.9 a
PI 094741	Russian Federation	Ukraine	Green	3	1.0	1.7 ab
PI 094743		Turkey	Green	1	1.3	1.8 ab
PI 119423		Turkey	Red	2	1.0	1.6 ab
PI 119435		Turkey	Red	2	1.5	1.7 ab
PI 167526		Turkey	Red	...	2.8	1.7 ab
PI 167589		Turkey	Red	2	2.8	1.8 ab
PI 167591		Turkey	Red	2	3.0	1.7 ab
PI 167611		Turkey	Red	2	1.8	1.8 ab
PI 167625		Turkey	Red	2	3.3	1.8 ab
PI 167627		Turkey	Red	1	3.5	1.9 a
PI 168803	Double Einkorn	Kansas	Green	1	2.5	1.7 ab
PI 168804		Kansas	Green	1	3.0	2.1 a
PI 168805		Kansas	...	2	2.5	1.9 a
PI 168806		Kansas	Green	1	1.5	1.6 ab
PI 170196		Turkey	Red	...	2.0	1.7 ab
PI 182461		Turkey	Green	4	2.8	2 a
PI 190915		Spain	Green	2	3.5	2 a
PI 190939		Spain	Green	1	3.0	1.8 ab
PI 190940		Spain	Green	1	2.8	1.9 a
PI 190942		Spain	Red	2	1.5	1.6 ab
PI 221393	Einkorn	Yugoslavia	Red	5	2.3	2 a
PI 221416		Yugoslavia	Red	1	3.5	1.8 ab
PI 225164		Greece	Red	2	2.5	1.9 a
PI 237659		Kenya	Red	2	2.5	1.8 ab
PI 264935		Greece	Green	...	2.3	1.9 a
PI 265008		Bosnia/Herzegovina	Red	1	2.8	2.1 a
PI 266844		United Kingdom	Red	1	3.3	2.2 a
PI 272557		Hungary	Red	5	4.0	2.4
PI 272561		Hungary	Red	1	4.0	2.1 a
PI 277130		Uncertain	Red	...	3.0	1.8 ab
PI 277133	V.J. 388	Uncertain	Green	1	2.5	2.3 a
PI 277138		Germany	Red	5	4.0	2.1 a
PI 286068		Poland	Red	7	1.0	1.7 ab
PI 289599		United Kingdom	Red	2	2.3	1.7 ab
PI 289605		United Kingdom	Green	6	4.0	2.5
PI 290508		Hungary	Red	2	2.5	1.9 a
PI 290509		Hungary	Green	1	2.3	1.7 ab
PI 290511		Hungary	Green	2	3.3	1.8 ab
PI 306542		Romania	Green	5	3.5	2 a
PI 306543		Romania	Red	1	3.8	2 a
PI 306547	Blauer Kahler	Romania	Red	1	3.5	2 a
PI 326217		Uncertain	Red	6	4.0	2.5
PI 330551		United Kingdom	Green	1	2.8	1.9 a
PI 343181		Chile	Red	7	1.5	1.7 ab
PI 345133		Yugoslavia	Red	2	3.0	2.3 a
PI 345186		Yugoslavia	Red	2	2.0	1.2 abc
PI 345242		Macedonia	Red	7	2.5	1.9 a
PI 349049		Armenia	Green	6	3.5	2.2 a
PI 352475		Germany	Green	5	4.0	2.5
PI 352483		Spain	Green	2	1.8	1.7 ab

(continued on next page)

^y ... indicates no data.

^z Least significant difference = 0.4, α = 0.05, a = significantly different from Chinese Spring, b = significantly different from Cappelle Desprez, c = significantly different from Madsen.

monococcum log-transformed GUS scores with the controls. To confirm resistance, a second experiment was carried out under the same conditions with 52 accessions determined to be more resistant than Cappelle Desprez in the first experiment. In addition, coleoptile color was noted at emergence in all replicates in each experiment.

Endopeptidase determination. A single seed of each *T. monococcum* accession was sown in vermiculite in 5 cm pots, grown to the one-leaf stage, and placed in a growth chamber (4°C, 12 h light) for 6 weeks for vernalization. One week before removal from the growth chamber, the second youngest leaf of each accession was

collected and placed on ice. Each leaf was passed through a rotary sap extractor with 50 µl buffer (25 mM glycylglycine, pH 7.4) and kept on ice until all samples were processed. A 10× loading dye containing 20% sucrose and 0.25% xylene cyanole was added, and the samples briefly centrifuged prior to loading. Samples were

Table 1. (continued from previous page)

Accession	Cultivar	Origin	Coleoptile ^a	Ep	Disease score means	
					Visual	GUS ^a
PI 352484	JE 28	Yugoslavia	Red	7	3.5	2 a
PI 355517		Turkey	Green	5	4.0	2.4
PI 355519		Iran	Red	2	3.8	2.2 a
PI 355521		Turkey	Red	1	3.3	2.1 a
PI 355522		Germany	Red	2	4.0	2.2 a
PI 355523		Turkey	Red	2	3.0	2 a
PI 355526		Belgium	Green	2	2.8	1.9 a
PI 355529		Belgium	Green	1	3.3	1.9 a
PI 355530		Spain	Red	2	2.8	1.9 a
PI 355531		Belgium	Red	2	1.5	1.6 ab
PI 355536		Italy	Red	1	1.0	1.4 abc
PI 355543		Germany	Green	5	3.0	1.8 ab
PI 355544		Germany	Red	1	2.3	1.8 ab
PI 355547		Austria	Red	1	3.3	2 a
PI 355548		Austria	Red	1	3.0	2 a
PI 355549		Austria	Red	1	3.5	2 a
PI 362610		Macedonia	Red	...	3.0	2.1 a
PI 377666		Yugoslavia	Red	2	3.8	2.1 a
PI 377667		Yugoslavia	Red	2	3.0	1.9 a
PI 377669		Yugoslavia	Green	2	1.8	1.7 ab
PI 377670		Yugoslavia	Green	2	2.3	1.9 a
PI 377671		Yugoslavia	Red	2	3.0	2 a
PI 393496	Einkorn	Israel	Green	1	3.0	1.9 a
PI 418582		Georgia	Green	6	3.8	2.1 a
PI 427927		Iraq	Red	1	3.0	2.1 a
PI 427959		Iraq	Green	7	1.5	1.7 ab
PI 428149		Sweden	Red	2	2.0	2.1 a
PI 428151		Italy	Green	6	4.0	2.3 a
PI 428152		Belgium	Red	2	2.5	1.9 a
PI 428153		California	Green	7	1.5	1.7 ab
PI 428158		United Kingdom	Red	2	3.5	1.9 a
PI 428160		Turkey	Red	2	2.0	1.8 ab
PI 428161		Turkey	Red	7	3.3	1.8 ab
PI 428162		Turkey	Red	2	2.8	1.8 ab
PI 428163		Turkey	Red	2	2.3	1.7 ab
PI 428164		Turkey	Red	2	2.5	1.9 a
PI 428165		Turkey	Red	2	3.0	2.1 a
PI 428166		Turkey	Red	2	3.3	1.9 a
PI 428168		Turkey	Red	6	3.3	2.3 a
PI 428169		Turkey	Red	1	3.0	1.8 ab
PI 428171		Turkey	Red	7	2.5	1.9 a
PI 428172		Turkey	Red	2	2.3	1.7 ab
PI 428173		Turkey	Red	2	3.0	1.7 ab
PI 428175		Turkey	Red	1	2.0	1.7 ab
PI 428176		Turkey	Green	2	2.0	1.8 ab
PI 538721		Turkey	Red	1	3.8	2.1 a
PI 538722		Turkey	Red	2	3.0	1.7 ab
PI 554525		Turkey	Red	...	3.0	2 a
PI 554529		Turkey	Red	...	2.3	1.7 ab
PI 554596		Turkey	Red	2	1.8	1.7 ab
PI 560727		Turkey	Red	1	2.8	2 a
PI 573520		Turkey	Red	7	2.5	2.1 a
PI 573521		Turkey	Red	...	3.8	1.8 ab
PI 573523		Turkey	Red	2	2.5	1.7 ab
PI 573524		Turkey	Red	...	3.5	1.8 ab
PI 573525		Turkey	Red	1	3.5	1.8 ab
PI 573526		Turkey	Red	1	3.8	2 a
PI 573527		Turkey	Red	1	3.3	1.8 ab
PI 573528		Turkey	Red	1	2.8	1.8 ab
PI 573529		Turkey	Red	1	3.5	1.8 ab
Madsen					1.8	1.8
Cappelle Desprez					3.0	2.1
Chinese Spring					3.8	2.7

loaded onto a vertical polyacrylamide gel apparatus using a lithium-borate buffer system (4% stacking gel, 10% running gel, 16 mM boric acid pH 8.3, 3 mM LiOH, 37 mM Tris, 5 mM citric acid) and run at 35 mA/gel constant current for 3.5 h. After running, gels were trimmed to approximately 5 cm above the dye front and placed in staining solution (100 mM Tris-maleate pH 3.7, 38 mM NaOH, 1 mM α -N-benzoyl-DL-arginine- β -naphthylamide-HCl, 0.8 mg/ml Fast Black K salts) in the dark for 1 to 2 h to visualize the endopeptidase bands. Controls were Chinese Spring and Cappelle Desprez.

Statistical analysis. Analysis of variance was conducted on the data from each experiment using SAS statistical analysis software (SAS Institute, Cary, NC). Fisher's least significant difference (LSD, $P = 0.05$) was used to separate means.

RESULTS AND DISCUSSION

Of 118 *T. monococcum* accessions, 114 possessed GUS scores significantly lower than the susceptible check (Chinese Spring), which corresponded to reduced colonization by the fungus. Fifty-two accessions were significantly lower than Cappelle Desprez (mean = 2.1) and 2 were significantly lower than Madsen (mean = 1.8; Table 1). The overall mean of the population, excluding the controls, was 1.9 (Table 2). It should be noted that the potential source species for *Pch2* is, on average, more resistant than the common wheat carrying it.

The second experiment was conducted on the 52 accessions that were more resistant than Cappelle Desprez in the first experiment. This was done to confirm that these lines were resistant and not escapes. All accessions screened in the second experiment were confirmed to be resistant (Fig. 1).

Among countries contributing more than one accession to the collection, the highest frequency of resistant accessions was

Fig. 1. Frequency distributions for (A) the first eyespot resistance experiment, including the entire *Triticum monococcum* core collection, and (B) the second eyespot experiment, containing only accessions classified as resistant by the first experiment. The arrows indicate the log- β -glucuronidase score of Cappelle Desprez in each experiment.

Table 2. Geographic distribution of *Triticum monococcum* endopeptidase isozyme classes and eyespot resistance

Origin	Accessions	Endopeptidase class	Mean	Accessions with GUS ^a activity lower (more resistant) than check	
				Cappelle Desprez	Madsen
Chile	1	7	1.7	1	0
Poland	1	7	1.7	1	0
Russian Federation	1	1	1.8	1	0
Ukraine	1	3	1.7	1	0
Italy	2	1, 6	1.9	1	1
Iraq	3	1, 2, 7	2	1	0
Belgium	4	1, 2	1.9	1	0
Hungary	5	1, 2, 5	2	2	0
United Kingdom	5	1, 2, 6	2	1	0
Germany	6	1, 2, 5	1.9	2	0
Spain	6	1, 2	1.9	3	0
Yugoslavia	10	1, 2, 5, 7	1.8	3	1
USA	11	1, 2, 7	1.8	5	0
Turkey	42	1, 2, 4, 5, 6	1.9	26	0
Others (12 countries)	17	1, 2, 5, 6, 7	2	0	0
Overall	118		1.9	52	2

^a GUS = β -glucuronidase.

among wheats from Turkey. Of 42 accessions from Turkey, 26 (62%) were significantly more resistant than Cappelle Desprez, whereas none was more resistant than Madsen based on GUS scores. Individual accessions from Italy and Yugoslavia had the lowest GUS scores, indicating that they were more resistant. One accession from each of these countries was more resistant than Madsen (Table 2).

No correlation was found between coleoptile color and eyespot resistance. This corresponds with linkage data reported by de la Peña et al. (6). *Rc1*, which conditions red coleoptile color, was found on the short arm of chromosome 7A, whereas *Pch2* is on the long arm. The presence of both genes on the same chromosome may result in the two loci segregating apparently non-independently in populations. However, the loose linkage is of little value in screening for resistance to eyespot.

Seven different endopeptidase banding patterns were identified in the screening population, ranging from 2 to 6 bands per accession (Table 1, Fig. 2). However, no association with resistance was identified. None of the banding patterns was in common with the *Ep-A1b* band found in Cappelle Desprez. Only one accession (PI182461) was found with banding pattern 4 (Fig. 2), and it was determined to be hexaploid by chromosome counts.

The technique used here for endopeptidase isozyme electrophoresis is a significant modification of techniques described by Koebner et al. (23), involving isoelec-

tric focusing, and Vahl et al. (35), that requires bulking five individuals for detection. The present system reduces the cost of this assay and allows detection of isozyme bands in individual plants. This technique may be of value for breeders or others making selections on large numbers of single early generation lines.

An estimate of diversity for the collection was calculated using Shannon's diversity index for isozyme data, $H = -(\sum p_i \ln p_i)$ (Table 3; 15). The resultant value of $H = 1.371$ indicates a moderate level of diversity. This result is consistent with the low levels of diversity in *T. monococcum* var. *boeoticum* enzyme populations found by Smith-Huerta et al. (34) using Nei's Identity index (NI) and among random amplified polymorphic DNA (RAPD) markers used by Vierling and Nguyen (36), who used Jaccard's similarity coefficients in collections of *T. urartu* and *T. monococcum*. Smith-Huerta et al. (34) found values of NI for *T. monococcum* ranging from 0.894 to 1.000 for 12 isozyme systems, whereas Vierling and Nguyen (36) calculated a range of 0.67 to 0.81 for Jaccard's coefficient using 60 RAPD markers. Each of the studies presented used a different index for diversity or similarity, as well as the use of only a single marker in the present study; therefore, none of the values can be compared directly. However, each study either indicates very high similarities or moderate to low levels of diversity within *T. monococcum*.

Comparisons between diploid wild wheat relatives and hexaploid wheats for effectiveness of resistance and genetic control should not be made because of the potential epistatic effects with other loci in the genomes of hexaploid wheat. The resistant phenotype observed in hexaploid wheat is potentially affected by other loci in all three ancestral genomes, including two additional homoeoloci. In a diploid wheat such as *T. monococcum*, epistatic effects occur only within the single genome present and there are no other homoeoloci. The effectiveness of *T. monococcum* resistance gene(s) when introgressed into the hexaploid milieu is unknown.

Furthermore, to determine if resistance in *T. monococcum* is allelic to *Pch2*, crosses would have to be made between Cappelle Desprez and *T. monococcum*. Although it is possible to cross *T. monococcum* with hexaploid wheat, the F_1 plants exhibit low fertility, and any progeny from such crosses would have unstable chromosome constitutions. Consequently, genetic studies on resistance using populations derived from hexaploid $\times$ diploid crosses would be of little use, due to the confounding effects of reduced fecundity and chromosome loss. The number of genes present in *T. monococcum* and their allelism can be determined in the diploid species; however, the most useful genetic analyses with *Pch2* would be at the hexaploid level.

Transfer of disease resistance genes against leaf rust, Karnal bunt, and Russian wheat aphid from *T. monococcum* to hexaploid wheat has been successful without the use of embryo rescue or culturing techniques (5,28,33). Additionally, resistance genes that have been transferred from this species to common wheat have retained their effectiveness at the hexaploid level (28,33). This is in contrast to studies by Lange and Jochemsen (24) and Kema et al. (20), for example, that show reduced resistance of synthetic hexaploids derived from the wild species *T. tauschii* (genomes DD).

The fact that resistance conferred by *Pch2* is less effective than that conferred by *Pch1* has led to less emphasis on utilization of the former resistance gene (9,10,30). However, there may be alleles at this locus in *T. monococcum* that are more effective. In the present core collection, we found diploids with apparently greater resistance than that conferred by *Pch2* and also greater than *Pch1*. The relative ease with which amphiploids between *T. monococcum* and tetraploid and hexaploid wheats can be made makes this a valuable new source of resistance to *P. herpovtrichoides*. The addition of a second highly effective resistance gene, and the potential for gene pyramiding in adapted wheats, will be a significant advancement for cultivar improvement.

Table 3. Frequency of endopeptidase banding patterns in *Triticum monococcum* screening population

<i>Ep-A1b</i>	#	Frequency ^z
1	37	0.3394
2	47	0.4312
3	1	0.0092
4	1	0.0092
5	7	0.0642
6	6	0.0550
7	10	0.0917
Total	109	

^z Shannon's diversity index (H) = 1.371.

Fig. 2. *Triticum monococcum* endopeptidase (*Ep-1a*) banding patterns and scoring scheme.

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