CROP SCIENCE

Volume 31 July–August 1991 Number 4

REVIEW & INTERPRETATION

Genetic Nomenclature in Clovers and Special-Purpose Legumes: I. Red and White Clover

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ABSTRACT

Clover and special-purpose legumes (not including alfalfa, *Medicago sativa* L.) constitute the primary genetic resource of legumes for grass–legume based pasture and hay systems. The group is diverse and contains species from the genera *Trifolium, Lotus, Lespedeza, Vicia,* and others. Although species in these genera have been the subject of research for at least six decades, no systematic scheme for genetic nomenclature has been adopted and a variety of conventions and gene symbols have been used. Absence of a centralized repository for genetic marker stocks has contributed to the loss of seed stocks of named genes. This paper (i) outlines a set of rules for uniform nomenclature and symbolization for the clovers and special purpose legumes, (ii) defines the membership of a permanent committee on gene symbolism and designates a central repository for named genes, and (iii) tabulates gene symbols published to date for red clover (*Trifolium pratense* L.) and white clover (*T. repens* L.) and attempts to clarify cases of duplicate nomenclature with establishment of a list of recommended gene symbols. The inheritance and gene symbols are tabulated for 61 previously published red clover genes and 28 previously published white clover genes. The genetic behavior of 27 other traits in red clover for which gene symbols were not published is summarized. Gene nomenclature and symbols according to the rules outlined are proposed for 27 genes in red clover and 28 genes in white clover. Two linkage groups are described for white clover.

CLOVERS and special-purpose legumes are of great economic worth to world agriculture as components of grass–legume based pasture and hay systems. These plants are adapted to a wide range of soil and climatic conditions. Unlike alfalfa, which is grown extensively on well-drained fertile soils in many temperate areas of the world, these species have a much wider area of adaptation and ability to adjust to wet and acid soils. The perennial clovers, primarily red clover and white clover, have been the subject of extensive genetic improvement research for more than 60 years (Smith et al., 1985; Gibson and Cope, 1985). Annual clovers, including crimson clover (*T. incarnatum* L.) and subterranean clover (*T. subterraneum* L.), are used mainly for winter grazing in the southern and western USA, as well as in many other areas of the world with Mediterranean-type climates. Considerable genetic improvement research has been conducted in both the USA and Australia on these species (Knight, 1985; Francis et al., 1970). Birdsfoot trefoil (*Lotus corniculatus* L.) has seen increased use on marginal lands both in the north-central areas of the USA and, with the release of a more southern-adapted cultivar (Pedersen et al., 1986), is increasing in use in the upper South of the USA. Several species of *Lespedeza* and *Vicia* have been evaluated for forage potential, and genetic studies have been carried out in both of these genera (Townsend, 1980).

To provide guidance regarding germplasm resources and needs for these species and other tropical and temperate special-purpose legume genera, a Clovers and Special Purpose Legumes Crop Advisory Committee composed of research specialists has been formed. This committee provides advice and counsel to the U.S. National Plant Germplasm Resources Board. At the Ninth *Trifolium* Conference held at Guelph, ON, Canada, in 1986, a workshop was held on standardized gene nomenclature for clovers and special-purpose legumes. Members of this workshop were designated as a committee to develop a set of rules for genetic nomenclature and to propose membership for a permanent gene nomenclature committee, which would act as a clearing body for naming and assigning symbols to new genes as they are identified (Smith and Quesenberry, 1986). The rules and committee structure outlined in this paper were unanimously approved by the members of the Tenth *Trifolium* Conference in Corpus Christi, TX, in 1988. Recent reports of genetic transformation in white clover (White and Greenwood, 1987) emphasize the need for a uniform system of qualitative gene nomenclature and centralized repositories of genetic stocks.

This paper describes the composition and responsibilities of the committee on genetic nomenclature and proposes a uniform nomenclature and symboli-

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Published in Crop Sci. 31:861–867 (1991).

Abbreviations: CSPL CAC, Clovers and Special Purpose Legumes Crop Advisory Committee.

zation for genes in clovers and special-purpose legumes. Adherence to this set of rules is voluntary, but it is hoped that publication of these rules will ensure their permanency and encourage uniform usage among interested researchers.

PROPOSED SYSTEM OF GENETIC NOMENCLATURE

Gene Symbol Review Committee

Membership on the committee shall be as follows: Curator of *Trifolium* spp. [chair]; curator of *Lotus, Lespedeza,* and *Vicia* spp.; perennial clover breeder/geneticist; annual clover breeder/geneticist; and special-purpose legume breeder/geneticist. Membership rotation on the committee will be determined by the CSPL CAC. Documentation on newly proposed gene symbols should be sent to: Trifolium curator, Department of Agronomy, University of Kentucky, Lexington, KY 40546-0091. The committee's responsibilities will include (i) reviewing proposed descriptive terms and symbols and assisting authors in making the appropriate choice, (ii) establishing guidelines on the evidence necessary for assignment of gene symbols, and (iii) publishing periodic lists of symbols in the Progress Report Clovers and Special Purpose Legumes Research as needed. The curator for each species will be the individual so designated by the U.S. National Plant Germplasm System under advisement of the CSPL CAC.

This system of nomenclature and symbolism for gene symbols and chromosomal alterations in clovers and special-purpose legumes is modeled after the rules of the International Committee on Genetic Symbols and Nomenclature (Anonymous, 1957) with some reference to Genetic Nomenclature in Guar (Ray and Stafford, 1985) and Rules for Genetic Symbols in Soybean (Anonymous, 1986). A committee appointed to function under the auspices of the CSPL CAC will implement the system.

Rules for Gene Symbols

1. Gene symbols shall be assigned only to loci for which inheritance data are presented.
2. A gene symbol may consist of one to three letters. Superscripts and subscripts will not normally be used (see Rule 4 for exception).
3. The descriptive name and symbol for a dominant trait shall be written with the initial letter of the name and symbol capitalized. The descriptive name and symbol for a recessive trait shall be written with all letters in lower case.
4. Genes that are allelic shall be symbolized by the same letter(s) so that each gene locus will be recognized by a common symbol base. If more than two alleles exist at a locus, the additional alleles or those symbolized subsequently to the first published dominant/recessive pair shall be designated by adding one or two lower case letters on the same line or as superscripts to the base (e.g., *B, b, bx,* b^a). This shall be the only use of superscripts. The base for additional alleles is capitalized only when the gene is dominant or equivalent to the allele originally designated with a capitalized symbol.
5. Mutants that are phenotypically similar, but at different loci, will be designated with the same symbol as the first described mutant, with an Arabic numeral added to the symbol on the same line (e.g., *ms-1, ms-2*). Mutants will be numbered sequentially in order of valid published descriptors.
6. When a gene symbol is proposed for an isozyme variant, the gene symbol should indicate the name of the enzyme (e.g., *adh* for alcohol dehydrogenase). The published documentation for such a gene symbol should include the appropriate Enzyme Commission name and number (IUB, 1984), the specific enzyme activity, the electrophoretic conditions used to characterize a locus or allele, and a photograph and/or interpretive zymogram.
7. Linkage groups and corresponding chromosomes shall be designated with Arabic numerals. The chromosomes of a species shall be numbered in order from longest to shortest. Trisomics shall be designated with Tri- followed by the Arabic numeral corresponding to the chromosome number (e.g., *Tri-1* for a trisomic of Chromosome 1).
8. Symbols for chromosomal aberrations shall include an italic symbol to denote the type of aberration plus the chromosome number(s) involved. The following symbols shall be used: *Tran* for translocations, *Inv* for inversions, *Dp* for duplications, and *Df* for deficiencies. For example, *Tran 1-2a* would be used to symbolize the first case of reciprocal translocations between chromosomes 1 and 2, *Tran 1-2b* the second, etc. Since it may be several years before chromosomal aberrations are located to specific chromosomes, *Tran 1* shall temporarily be used to represent the first case of a published reciprocal translocation, *Tran 2* the second, etc. The first published inversion shall be symbolized as *Inv 1a,* the second in the same chromosome as *Inv 1b,* etc. Since the chromosome containing the inversion may not be known initially, the first published inversion shall temporarily be designated *Inv 1,* the second *Inv 2,* etc., until the identity of the chromosome is determined. Duplications and deficiencies shall be designated in a similar manner.
9. Cytoplasmic factors shall be designated with one or more letters prefixed by *cyt-* (e.g., *cyt-ms1* for the first reported source of cytoplasmic male sterility).
10. A symbol will be considered valid when published in a recognized scientific journal or the Progress Report Clovers and Special Purpose Legumes Research with conclusions adequately supported by data that establish the existence of the entity being symbolized and when seed stocks of the gene have been provided to the appropriate curator. If different symbols have been assigned to the same factor, the symbol first published shall be the accepted symbol, unless the original interpretation is shown to be incorrect, the symbol is not in accordance with these rules, or additional evidence shows that a

change is necessary. Where the germplasm is no longer available and there appears to be no way to determine if a newly discovered factor is the same as one reported many years before, a newly reported trait will be considered as valid upon compliance with the above procedure.

11. These rules may be amended or revised by a majority vote of the Gene Symbol Review Committee.

INHERITANCE OF CHARACTERS IN RED AND WHITE CLOVER

Extensive genetic research on red clover was conducted in Europe in the 1920s and 1930s (Wexelsen, 1932; Nijdam, 1937, 1938; Williams, 1935, 1937, 1939a,b) with little activity in the 1940s and 1950s. Since the 1960s, however, genetic research on red clover has been conducted in both Europe and the United States (Smith et al., 1985). Seed of many genetic stocks identified in earlier European work are no longer available.

Early research with white clover in the USA was conducted at the U.S. Regional Pasture Research Laboratory, State College, PA, on S alleles, but no specific seed has currently been located that trace to those genetic studies (Atwood, 1942). This is true of later work conducted at Cornell University by Brewbaker and Carnahan (1956) on this and other traits. Work on white clover at Clemson University in cooperation with the USDA verified many of the previous genetic studies and added to the list of known genes (Gibson and Hollowell, 1966), but no seed has been located specifically relating to these studies. The Grasslands Division at Palmerston North, New Zealand (Dr. J. Caradus, 1990, personal communication) has seed of most of the genetic markers published by Corkill (1971).

In our review of previously published gene symbols for red and white clover, we have attempted to clarify discrepancies among previously published symbols and to modify previously assigned symbols to conform to the above rules. The original designation was retained whenever feasible.

The reported inheritance and originally assigned gene symbols for qualitative characters in red clover and white clover are reported in Tables 1 and 2, respectively. With red clover, some redundancy of symbol use has occurred over time. For example, the symbols *R*, *r* have been used for powdery mildew, rust resistance, rudimentary corolla, and seed color. In addition, different symbols have been used to describe

Table 1. Red clover genes, reported gene symbols, and originating scientist, with reference.

Gene name	Reported gene symbol	Originating scientist
Anthocyanin production	*G*	Nijdam, 1937
	C	Wexelsen, 1932
	An	Williams, 1937
Disease resistance		
Bean yellow mosaic virus	*N*	Diachun and Henson, 1965
Powdery mildew	*A* or *b* or *c*	Kolp, 1958
Powdery mildew	*R*	Stavely and Hanson, 1967
Red clover vein mosaic virus	*Rc*	Khan et al., 1978
Rust	*R*	Engelke et al., 1977
Dwarfism	*d*	Nijdam, 1937
	dw_1	Smith, 1974
Floral characters		
Blue	*e*	Nijdam, 1938
Faint pink	*ca*	Williams, 1939b
Pink	*b*	Nijdam, 1937
Pink	*cl*	Williams, 1939b
Pink	*bbB-* or *B-bb*	Nijdam, 1951
Purple-red	*B*	Nijdam, 1937
Purple-red	*B-B-*	Nijdam, 1951
Purple-red	*p*	Picard, 1956
Purple-red	*p*	Parrott and Smith, 1986
Rudimentary corolla	*r*	Taylor and Snead, 1986
Variegated	*Cp*	Williams, 1935
White	*c*	Wexelsen, 1932
White	w_1	Wexelsen, 1932
White	*g*	Nijdam, 1937
White (pink tube)	wp_1 or wp_2	Wexelsen, 1932
White (pink tips)	wp_3	Wexelsen, 1932
White (ivory seed)	*c*	Williams, 1935
White (yellow seed)	*cd*	Williams, 1935
White (yellow seed)	*cy*	Williams, 1939b
Leaf characters		
Leaf mark	*M*	Williams, 1937
Leaf mark (central)	*Mb*	Williams, 1937
Long petiolule	*lp*	Smith et al., 1985
Petiolulate leaflets	*pll*	Jaranowski and Broda, 1978
Short petioles with long petiolules	*a* or *b*	Hanson and Hanson, 1952
Split leaflet	*sl*	Parrott and Smith, 1986
Male sterility		
Male sterile	*P*	Nijdam, 1937
Male sterile	ms_1	Smith, 1971
Male sterile	ms_2	Taylor et al., 1978

(continued)

Table 1. (cont.)

Gene name	Reported gene symbol	Originating scientist
Miscellaneous		
Appressed hairs (petiole)	*hp*	Williams, 1939b
Appressed hairs (stem)	*hc*	Williams, 1939b
Glabrous	*hg*	Williams, 1939b
Glabrous (basal internodes)	*hb*	Williams, 1939b
Hairless stipules	*hs*	Williams, 1939b
Lethal seedling	*la*	Williams, 1939b
Parallel spindle orientation	*ps*	Smith et al., 1985
Polyphylly	*n* or *b*	Simon, 1962
Round pollen	*rp*	Parrott and Smith, 1986
Self fertility	S_f	Williams, 1937
Self incompatibility	$S_1, S_2, \ldots S_n$	Williams, 1937
Synaptic mutant	*sy*	Parrott and Smith, 1986
Nodulation		
Effectiveness restorer	m_1	Nutman, 1954
Ineffective	i_1	Nutman, 1954
Ineffective	*ie*	Nutman, 1957
Ineffective	*n* or *d*	Nutman, 1968
Pigmentation		
Albino	w_1–w_6	Williams, 1939a
Chlorina	*n*	Nijdam, 1937
Chlorophyll production	*Q*	Nijdam, 1937
Variegated	w_7 or w_8	Williams, 1939a
Yellow seedlings	y_1–y_7	Williams, 1939b
Seed color		
Purple-blue	*V*- and *R*-	Nijdam, 1937
Violet	*V*	Nijdam, 1937
Violet intensifier	*X*	Nijdam, 1937
Yellow	*C*	Nijdam, 1937
Other genetic behaviors		
Cornucopia leaf	polygenic	Taylor, 1982
Crimson flower	4+ genes	Taylor, 1982
Crownless	1, 2+ rec.	Strzyzewska, 1974
Himalayan seed pattern	1 rec.	Nijdam, 1937
Hypersensitivity (bean yellow mosaic virus)	1 dom.	Diachun and Henson, 1974a,b
Immunity (bean yellow mosaic virus)	1 dom.	Diachun and Henson, 1974a
Leaf color (dark green)	1 dom.	Wexelsen, 1932
Leaf color (med. green)	1 dom.	Wexelsen, 1932
Leafmark	1 dom.	Rinke and Johnson, 1941
Leafmark (central)	1 gene	Wexelsen, 1932
Leafmark (extended)	1 gene	Wexelsen, 1932
Leafmark (strong/weak)	2 genes	Wexelsen, 1932
Leafmark (yellow)	1 dom.	Wexelsen, 1932
Multifoliolate	quant.	Taylor, 1982
Multiple head	quant.	Taylor, 1982
Purple seed	1 dom.	Taylor, 1982
Resistance (rust)	1 dom.	Diachun and Henson, 1974c
	polygenic	Engelke et al., 1975
Resistance (southern anthracnose)	1 rec.	Athow and Davis, 1958
Resistance (northern anthracnose)	2 dom.	Sakuma et al., 1973
	3 dom.	Smith and Maxwell, 1973
Resistance (stem nematode)	2 dom.	Nordenskiold, 1971
"Sun red" stem	1 dom.	Taylor, 1982
Variegated	1 rec.	Strzyzewska, 1974
White flower (white seed)	1 rec.	Taylor, 1982
White stem	1 rec.	Taylor, 1982
Yellow seedling	1 rec.	Strzyzewska, 1974

the same characteristic, such as both *B* and *p* for purple-red flower color. Several traits have been reported to be controlled by one gene but no symbol was assigned.

The majority of the traits listed for white clover (Table 2) deal with leaf markings, such as variations of a white V, red flecking, solid green leaves, and red areas. The white V trait with its various locations and shapes has been reported as dominant (*V*) to the solid green leaf (*v*). Few tests of allelism of the various V marks have been conducted, and they are currently treated as separate genes. The symbols used to describe other traits in white clover are straightforward, but some do not fit the proposed nomenclature rules.

RECOMMENDED SYMBOLIZATION

Tables 3 and 4 list the recommended nomenclature and gene symbols for qualitative, cytological, and biochemical characters in red clover and white clover, respectively. In red clover, numerous symbols had been used for flower and seed pigmentation, with little comparison between genetic stocks to establish similarities or linkages. However, the symbol *c* has been used most frequently for the absence of flower pigmentation (white) that is recessive to other levels of pigmentation. Until published linkage relationships are reported it seems reasonable to use the symbol *c* for lack of flower pigmentation (white) and the symbol *p* for pigmentation (purple-red). Seed is available for

Table 2. White clover genes, reported gene symbols, and originating scientist with reference.

Gene name	Reported gene symbol	Originating scientist
Chemical characters		
Cyanogenetic glucosides	*Ac*	Atwood and Sullivan, 1943
HCN	*Li, Ac*	Atwood and Sullivan, 1943
Linamarase (enzyme)	*Li*	Atwood and Sullivan, 1943
Floral characters		
Blush-colored corolla	*b*	Brewbaker, 1962
Cyanadin-red corolla (with black seed)	c^1, c^2	Brewbaker, 1962
Nonclasping bracts	*br*	Brewbaker, 1962
Vestigial florets	Vg^1, Vg^2	Gibson and Hollowell, 1966
Leaf characters		
Green leaf	*v*	Brewbaker and Carnahan, 1956
Halo marking	V^h2	Corkill, 1971
Marginal	*Vm*	Lenoble and Papineau, 1970
Mottling (virosis)	M^1, M^2	Atwood and Kreitlow, 1946
Red leaflet	$V^{rl}2$	Corkill, 1971
Diffuse red leaf	R^{ld}	Corkill, 1971
Red leaf	R^l	Carnahan et al., 1955
Red flecking	R^f	Carnahan et al., 1955
Red midrib	R^m	Carnahan et al., 1955
Redspot (close to V)	V^r2	Hovin and Gibson, 1961
Full V-high	V^h	Brewbaker and Carnahan, 1956
Full V-intermediate	V^i	Brewbaker and Carnahan, 1956
Full V-low	V^l	Brewbaker and Carnahan, 1956
Broken V	V^b	Brewbaker and Carnahan, 1956
Broken V-dominant	V^{bd}	Brewbaker and Carnahan, 1956
V-point	V^p	Brewbaker and Carnahan, 1956
Filled V	V^f	Brewbaker and Carnahan, 1956
Basal V	V^{ba}	Brewbaker and Carnahan, 1956
Broken V (with yellow tip)	V^{by}	Brewbaker and Carnahan, 1956
Filled V (with green base)	V^{fg}	Brewbaker and Carnahan, 1956
Miscellaneous		
Self-incompatibility	$S_1, S_2, \ldots S_n$	Atwood, 1942
Linkage groups		
R^m, R^{ld}, and R^l are linked		Corkill, 1971
V, $V^{rl}2$, and V^h2 are linked		Corkill, 1971

both the white (Taylor, 1982) and purple-red (Parrott and Smith, 1986) flower color types.

The major proposed changes in gene symbolism for white clover have been to move superscripts to a regular part of the symbol, as outlined in Rules 2 and 4. No relationship of the two previously described linkage groups to a given chromosome has been developed, so they have been assigned 1 and 2.

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Table 3. Gene names and recommended gene symbols for red clover.

Gene name	Recommended gene symbol	Previously reported gene symbol
Disease resistance		
Bean yellow mosaic virus	*N*	*N*
Powdery mildew	*Pm*	*Pm*
Red clover vein mosaic virus	*Rc*	*Rc*
Rust	*Ru*	*R*
Dwarfism		
Dwarf plant	*dw*	d, dw_1
Floral characters		
Purple-red flower	*p*	*p*
Rudimentary corolla	*r*	*r*
White flower	*c*	c, w_1, g
Leaf characters		
Elongated petiolule	*ep*	*lp*
No leaf mark	*m*	–
(Leaf mark)	–	*M*
Petiolulate leaflet	*pl*	*pll*
Split leaflet	*sp*	*sl*
Male sterility		
Male sterile 1	*ms-1*	ms_1
Male sterile 2	*ms-2*	ms_2
Miscellaneous		
Appressed stem hairs	*hc*	*hc*
Appressed petiole hairs	*hp*	*hp*
Glabrous stems	*hg*	*hg*
Glabrous (basal internodes)	*hgb*	*hg*, *hb*
Hairless stipules	*hs*	*hs*
Parallel spindles	*ps*	*ps*
Round pollen	*rp*	*rp*
Self fertility	*Sf*	S_f
Self incompatibility	*S1*, *S2*, ... *Sn*	S_1, S_2, ... S_n
Synaptic mutant	*sy*	*sy*
Nodulation		
Ineffective nodulation	*i*	*i*
Pigmentation		
Chlorophyll	*Q*	*Q*
Albino	*w*	*w*
Yellow	*y*	*y*
Seed color		
Violet	*v*	*v*

Table 4. Gene names and recommended gene symbols for white clover.

Gene name	Recommended gene symbol	Previously reported gene symbol
Chemical characters		
Cyanogenetic glucosides	*Ac*	*Ac*
Linamarase (enzyme)	*Li*	*Li*
Floral characters		
Blush-colored corolla	*b*	*b*
Cyanadin-red corolla (with black seed)	*c1*, *c2*	c^1, c^2
Nonclasping bracts	*br*	*br*
Vestigial florets 1	*Vg1*	Vg^1, Vg^2
Leaf characters		
Green leaf	*v*	*v*
Halo marking	*Vh2*	V^h2
Marginal marking	*Vm*	*Vm*
Mottling (virosis)	*M1*	M^1, M^2
Red flecking	*Rf*	R^f
Diffuse red leaf	*Rld*	R^{ld}
Red leaf	*Rl*	R^l
Red leaflet	*Vrl*	$V^{rl}2$
Red midrib	*Rm*	R^m
Redspot (close to V)	*Vr2*	V^r2
Full V, high	*Vh*	V^h
Full V, intermediate	*Vi*	V^i
Full V, low	*Vl*	V^l
Broken V	*Vb*	V^b
Broken V, dominant	*Vbd*	V^{bd}
V-point	*Vp*	V^p
Filled V	*Vf*	V^f
Basal V	*Vba*	V^{ba}
Broken V (with yellow tip)	*Vby*	V^{by}
Filled V (with green base)	*Vfg*	V^{fg}
Miscellaneous		
Self-incompatibility	*S1*, *S2*, ... *Sn*	S_1, S_2, ... S_n
Linkage groups		
Rm, *Rld*, *R1*	2	
v, *Vr12*, *Vh2*	1	

and SSSA, Madison, WI.

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