

seedlings ranged from almost entirely green to entirely white. Classification at the cotyledon to first true leaf stage was inaccurate; 10 days later many seedlings classified earlier as normal showed leaf variegation. Data collected from seedlings showing 2-4 true leaves were subsequently analyzed and the results are presented here. The symbol *var* is proposed for the mutant causing green and white leaf variegation.

Inheritance of leaf variegation in *Vitis* species

B. I. Relsch and J. P. Watson

ABSTRACT: Chlorophyll variegation in *Vitis* species was examined in F₁ and S₁ populations. A single recessive gene is proposed to account for the occurrence of 25 percent variegated seedlings in both F₁ and S₁ populations. Variegation was not lethal and might be useful in wine grape breeding (if associated with inactive polyphenol oxidase) and for its ornamental value. This trait is one of very few seedling traits under monogenic control that might be useful in genetic studies of grapes.

LEAF VARIATION in *Vitis* has been described among the progeny of Aramon, an ancient European grape (*V. vinifera*) cultivar⁵. A single recessive gene was reported to cause green and white variegation among selfed progeny of Aramon. However, such variegation was expressed only among plants grown at 20°C, not at 35°C⁵. Variegation also was described in a sport of cv. Sultana, but inheritance was not studied¹. We have observed that, following severe cold damage to dormant buds, small variegated shoots are a common vineyard occurrence.

Well-defined mutants identifiable at an early stage of growth are of importance in genetic studies of plants. De Lattin³ listed 53 genes identified in *Vitis* prior to 1957. Of these, four concerned traits identifiable among seedlings. No further seedling traits have since been reported⁴.

Variegated leaves appeared in seedling grapevine populations planted in 1982 and were studied to identify the genetic basis for their occurrence.

Materials and Methods

Crosses and selfs among hybrid stocks (see Figure 1) and *V. vinifera* grape cultivars (Riesling and Chardonnay) were made in 1981 and 1982 using standard techniques⁴. Seed were stratified for 3 months at 1-2°C and planted in Cornell-Mix² medium in a greenhouse in mid-March of 1982 and 1983. Approximately 4 weeks after planting, seedlings showing true leaves were classified as either variegated (green and white) or normal (entirely green). The available data were subjected to chi-square analysis to determine goodness-of-fit to the Mendelian monohybrid ratio. In June 1982 and 1983, seedlings were transplanted to a field nursery and observed for survival and expression of variegation.

The authors are affiliated with the Department of Horticultural Sciences, New York State Agricultural Experiment Station, Cornell University, Geneva, New York 14456. They wish to thank Dr. R. Pool for valuable discussions.

Most of the variegated seedlings showed a green and white pattern of variegation. A few variegated seedlings had patches of pinkish-purple and patches of green tissue in true leaves and occasionally in the cotyledons. The pinkish-purple color eventually bleached out, leaving white tissue in its place. Leaves on variegated

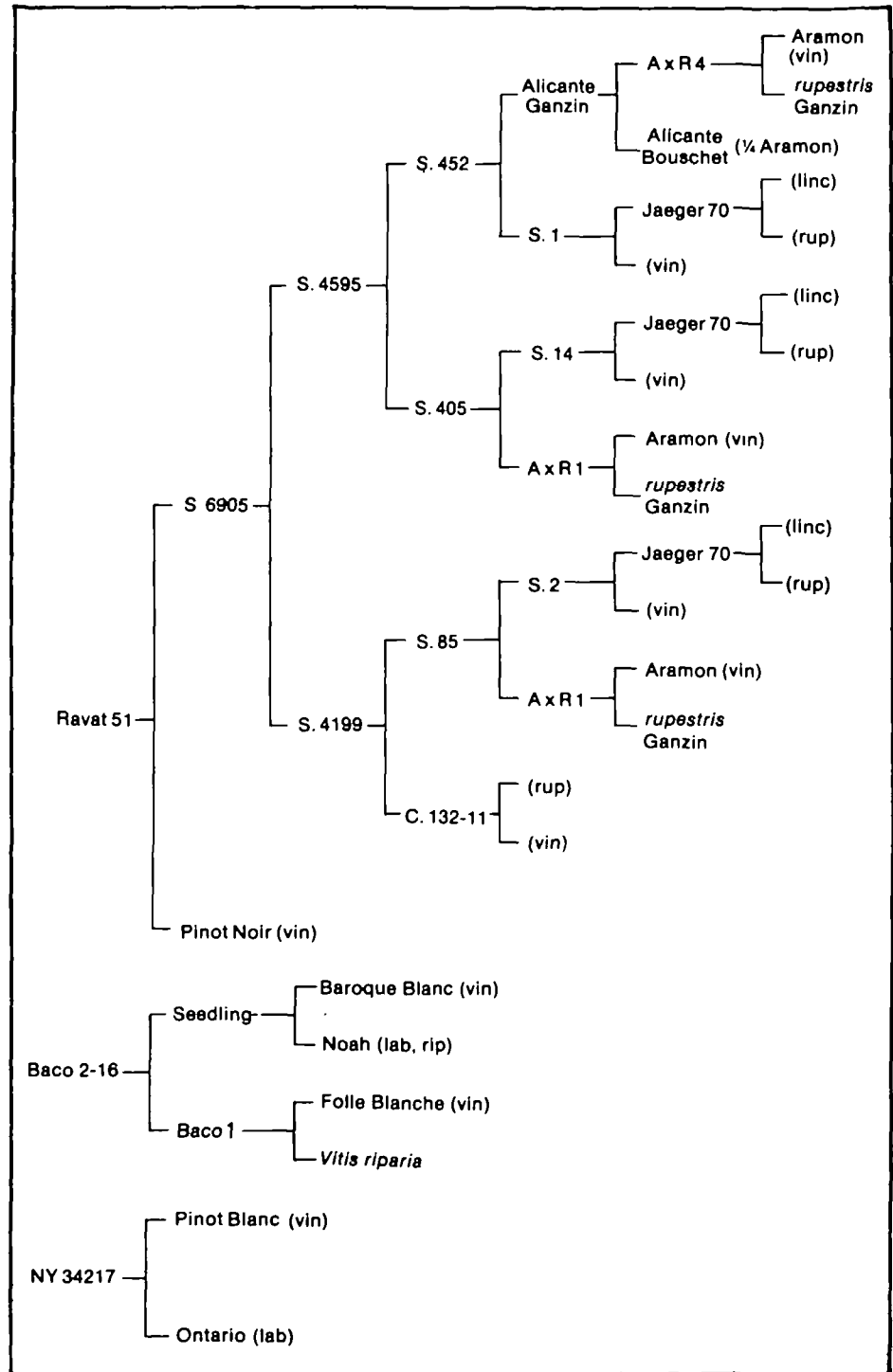


FIGURE 1 Pedigree of hybrid stocks used in the study of variegation in *Vitis*. Abbreviations for species: vin—*vinifera*; lab—*labrusca*; rip—*riparia*; linc—*linceumii*; rup—*rupestris*.

Variegated plants from crosses made in 1981 continued to express the trait in tissues produced in 1982, 1983, and 1984 (Figure 2). Expression within each plant was irregular; some shoots were entirely green, others were intensely variegated. Only a few seedlings classed as normal exhibited variegation in the field. These individuals had apparently been misclassified at the seedling stage. Following two seasons in the field, 78 of 149 green plants in two F₁ populations survived, as did 15 of 48 variegated plants. Apparently, variegation was not a lethal trait, although it appears to decrease plant survival. Surviving variegated plants appeared to be as vigorous as their normal sibling counterparts.

It is proposed that NY 34217, Riesling, Chardonnay, Ravat 51, and Baco 2-16 are heterozygous (+ var) for the variegated trait. Hence, hybrid and selfed progeny within this group should have 25 percent variegated seedlings. Only one of 10 populations (Table I) analyzed using the chi-square test did not fit this hypothesis. In that atypical case, a self-pollinated population from Riesling included only 16 percent variegated seedlings. Misclassification at an early growth stage and possible temperature effects on variegation⁵ would help to explain a deficiency of seedlings classed as variegated.

Albinos occur at very low frequencies (<0.5 percent) in many grape seedling populations. They occurred at a frequency of 16 percent among self-pollinated seedlings of Ravat 51 (Table I) and were considered in the statistical analysis to be an extreme form of expression for the variegated trait. Albinism has been considered to be an extension of leaf variegation traits in other studies as well⁷.

In 14 progeny having one parent in common with those segregating for leaf variegation, all observed seedlings were green (Table II). The cross involved would represent ++ × +var, with the expectation of producing all green seedlings. Self-pollinated progeny of three putative ++ genotypes also produced only green seedlings (Table II).

Studies on the grape cultivar Aramon suggested monogenic inheritance of a variegated trait⁵. Since Ravat 51 derives approximately 9.0 percent of its genetic makeup from Aramon

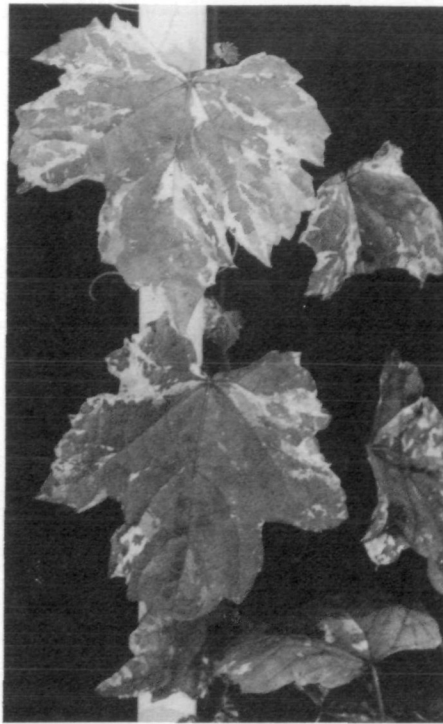


FIGURE 2 Leaf variegation in a 31-year-old *Vitis* seedling.

through four independent sources (Figure 1) it is possible that the gene investigated is identical to that found in Aramon and now identified in the four other grape stocks reported here.

Grapevines grown in pot culture from cuttings are being developed as an attractive florist crop^{6,9}. A variegated stock might have additional ornamental value.

The mutant trait presently under study also may be of some importance in the production of new grape cultivars that resist oxidation in their wine. Grapevine variegation has been found in association with Bruce's sport, a variant of the Sultana grape, which was characterized by a decreased tendency of the fruit to brown while

drying¹. A form of polyphenol oxidase characterized by greatly reduced activity was responsible for resistance to oxidation of grape phenolic compounds sensitive to browning⁸. This altered form of polyphenol oxidase may be a valuable trait in retarding oxidation in commercial wines. The genetic relationship between variegation and altered forms of polyphenol oxidase has not yet been elucidated. However, if the variegated trait presently under study is identical to that found in Bruce's sport and is associated with an inactive form of polyphenol oxidase, it may be a useful trait to manipulate for the benefit of a wine grape breeding program.

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Table II. Other crosses and selfs related to segregating populations in which no variegated seedlings were observed

Cross*	No. seedlings observed
NY 65.444.4 × Riesling	93
NY 65.533.13 × Riesling	37
GW 5 × Riesling	51
Horizon × Riesling	5
Cayuga White × Riesling	186
S. 13047 × Riesling	75
J.S. 23-416 × Riesling	105
J.S. 26-627 × Riesling	141
NY 65.444.4 × Chardonnay	49
S. 10173 × Chardonnay	92
Ill. 172-7 × Chardonnay	47
Horizon × Baco 2-16	32
NY 65.533.13 × Ravat 51	22
Cayuga White × Ravat 51	39
J.S. 23-416 selfed	54
NY 65.444.4 selfed	200
Horizon selfed	54

* Abbreviations used: NY = New York; GW = Geneva White; S. = Seibel; J.S. = Joannes-Seyve; Ill. = Illinois

Table I. Segregation data and chi-square tests for green and variegated (var) leaf traits among *Vitis* seedlings

Cross	No. seedlings			$\chi^2(3:1)$	P
	total	green	variegated		
F ₁ populations					
NY 34217 × Riesling	126	86	40	3.06	0.05-0.20
NY 34217 × Baco 2-16	220	164	56	0.02	0.80-0.95
NY 34217 × Ravat 51	62	52	10	2.60	0.05-0.20
Ravat 51 × Riesling	119	96	23	2.07	0.05-0.20
Ravat 51 × Chardonnay	325	246	79	0.09	0.50-0.80
S ₁ populations					
NY 34217 selfed	14	9	5	0.86	0.20-0.50
Ravat 51 selfed	216	163	19†	0.02	0.80-0.95
Riesling selfed	199	168	31	9.47	<0.01*
Chardonnay selfed	42	33	9	0.29	0.50-0.80
Baco 2-16 selfed	270	205	65	0.12	0.50-0.80

* Does not fit expected ratio

† + 34 albino