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Epicuticular Waxes of Glaucous and Nonglaucous Durum Wheat Lines

Giorgio Bianchi* and Maria L. Figini

Surface chemical constituents of glaucous and nonglaucous wheat lines were obtained by dipping the aerial plant organs into chloroform. Surface chemicals comprised alkanes, aldehydes, alcohols, acids, esters, β-diketones, and hydroxy β-diketones. These classes of compounds were quantitatively separated by column chromatography and the homologues analyzed by glass capillary gas chromatography. The relationships between glaucous and nonglaucous appearance and the presence or absence of β-dicarbonyl components in two Durum wheat cultivars and six derived lines are presented and discussed.

The epicuticular wax layer is the area of contact of plant aerial organs with the surrounding atmosphere. As such it is important in studies on water and gas exchange, retention, and penetration of air-borne substances such as herbicides and plant growth regulators. Epicuticular wax can also be of further agricultural relevance, representing the habitat for parasitic and saprophytic organisms, the barrier to fungal pathogens (Hamilton and Hamilton, 1972).

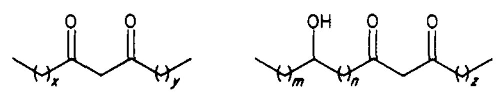
Surface wax is responsible for the appearance and development of the aerial organs of plants that can appear "green" (i.e., nonglaucous) or blue, gray, or even white according to the nature of the epicuticular lipid layer. Glaucousness, due to a superficial deposit of light-scattering crystallites of wax, is generally thought to be due to the amount and chemical composition of the epicuticular material on the aerial organs of plants (Baker, 1982).

Bloom and bloomless sorghum lines have been defined also on the basis of different wax composition (Wilkinson and Cummings, 1981). Furthermore, it has been shown that mutants of *Brassica oleracea* (Holloway et al., 1977), *Pisum sativum* (Holloway et al., 1977), and *Zea mays* (Bianchi et al., 1985), when nonglaucous, have wax of a different chemical composition to that of the normal glaucous plants.

The ubiquitous wax components of the cereals most studied so far, namely wheat, barley, maize, sorghum, oat, rye, triticale, and rice, are alkanes, aldehydes, alcohols, acids, and esters (Tulloch et al., 1980; von Wettstein-Knowles, 1982; Bianchi et al., 1982; Dalton and Mitchell, 1959; Neucere and Sumrell, 1980; Avato et al., 1984; Tulloch and Hoffman, 1973; Streibl et al., 1974; Bianchi et al., 1979).

Department of Organic Chemistry, University of Pavia, 27100 Pavia, Italy.

In addition to these classes of compounds, the waxes of barley, wheat, oat, rye, and triticale comprise relevant amounts of β-diketones and hydroxy β-diketones (henceforth called β-diketones or β-dicarbonyl compounds) of the types 1 and 2.



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The glaucous or less glaucous appearance of the plant organs of the latter cereals has been usually correlated with the presence and percent contents of β-diketones in the surface waxes (von Wettstein-Knowles, 1972; Barber and Netting, 1968; Tulloch and Hoffman, 1974; Streibel et al., 1974; Bengston et al., 1978; Bianchi et al. 1980, 1982).

In particular, a number of studies on tetraploid and hexaploid *Triticum* species and cultivars have been carried out by several investigators during the last two decades to examine the appearance of the plant organ surfaces visually or as seen in the electron microscope and, more importantly because of the compositional data obtainable, the relation betwen visual appearance and wax chemistry. An extensive review on the waxes of numerous genera of the tribe *Triticeae* has been made by Tulloch et al. (1980).

Examination of the data on this subject available in the literature as well as our own results gained from a chemical genetics study on wheat varieties and mutants has evidenced some major points regarding wheat epicuticular wax: (i) The so-called glaucous wheats are characterized with wax structures in which are present long, thin tubes (also called rods and spicules). (ii) Nonglaucous (green, glossy "waxless") lines are associated with plate-type wax structures. (iii) Wax chemical composition studies have disclosed that both glaucous and nonglaucous wheats have waxes comprising the same compounds, that is the ubiquitous classes and β-diketones. In a recent report (Plant

Breeding Institute, Annual Report 1982, p 117) it is stated that several nonglaucous, "waxless" Avalon winter wheats have surface waxes containing β-diketones, although in percentages less that 22% of the normal plant.

Thus, the conclusion is that in wheat β-dicarbonyl compounds when present in large amount are responsible for glaucousness, but a nonglaucous appearance of the plant does not mean absence of β-diketones.

It was found also that β-diketone content in the epicuticular wax is dependent on the plant age and plant organs (Bianchi and Corbellini, 1977). Usually, the mature plant as a whole has the highest content of β-dicarbonyl compounds. Whether the presence or absence in wax of these β-diketones is beneficial is not known. There is a possibility, based on the observation of the UV absorption of β-diketones, that β-dicarbonyl compounds play a role in reception and redistribution of incident radiation.

Furthermore, functional groups present and their chemical structures may interact chemically with applied chemicals so that the release and penetration of such substances across the leaf cuticle may be affected, to some extent.

As it is now well-known, cereal epicuticular wax production and composition is under genetic control (von Wettstein-Knowles, 1979; Bianchi et al., 1985).

In the case of wheat the genetic potential in order to understand wax formation in wheat from a chemical point of view was realized in the later 1960s (Newton-Barber and Netting, 1968), and considerable further research was carried out on this subject by other research groups in following years (Tulloch and Hoffman, 1974; Bianchi et al., 1980).

When this investigation was set up, wax composition had been reported for some 20 tetraploid (Newton-Barber and Netting, 1968; Tulloch and Hoffman, 1971; Bianchi et al., 1982; Bianchi, 1985) and hexaploid wheats and mutants (Tulloch and Weenink, 1969; Tulloch and Hoffman, 1973; Bianchi and Corbellini, 1977; Bianchi et al., 1980, 1982; Bianchi, 1985).

As a part of our interest in the study of chemical genetics of cereal epicuticular waxes, we have previously examined several wheat lines and 29 ditelosomic mutants of the wild Chinese spring type (Bianchi et al., 1984). All the lines studied presented invariably epicuticular waxes comprising β-diketones in mixture with the other ubiquitous classes, although in greatly varying proportions.

The present paper is concerned with chemical analyses and class of compound profiles of the epicuticular waxes of a glaucous and a nonglaucous tetraploid varieties of Durum wheat and six derived lines. Valitalico selection is a Durum wheat with the typical very glaucous appearance and whose wax is made of, in addition to the ubiquitous wax classes of alkanes, aldehydes, alcohols, acids, esters, large proportions of β-diketones and hydroxy β-diketones. On the contrary, Trinakria accession is quite unusual and unique in respect to epicuticular wax which, in fact, is completely deprived of β-diketones.

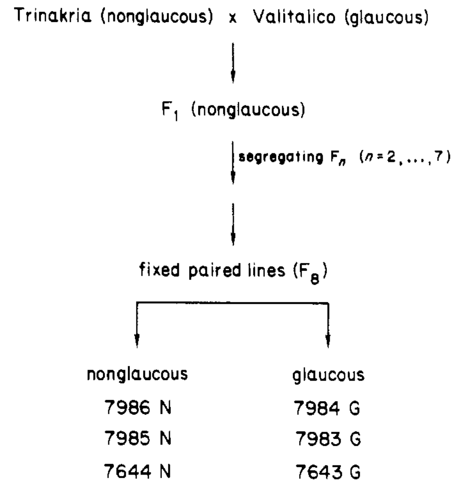
From a genetical point of view, the lack of β-dicarbonyl compounds in this variety may be the result of the presence in this line of a dominant inhibitor of the synthesis of those chemical classes of substances.

EXPERIMENTAL SECTION

Chemicals. Alkanes, aldehydes, alcohols, and acid standard mixtures for comparison purposes in thin-layer chromatography (TLC) and gas–liquid chromatography (GLC) analyses were either Fluka or Supelchem chemicals.

Plant Material. The tetraploid (AABB) varieties Trinakria, Valitalico, and the derived lines were grown in

Scheme I



open-field conditions in a farm near Rome. The parent cultivars are characterized as follows: Valitalico is a dwarf wheat about 85 cm high, very glaucous; Trinakria plants are 120 cm high, nonglaucous. Crosses between Trinakria and Valitalico produced F_1 plants in which the nonglaucous character was dominant.

In the years following the initial cross, three paired selection lines, one glaucous type and the second nonglaucous for each line, were isolated (segregating ratio was monomendelian, about 1:3 glaucous to nonglaucous). The plants of these paired lines were almost identical with one another, except for waxiness character, and were, for example, in fact all 80 cm high.

For the purpose of this study, the glaucous and nonglaucous lines are given the number used in the selection process. For the sake of clarity and easy identification, the number will be followed by a capital letter: G for glaucous and N for nonglaucous appearance.

The sequence of hybridization and segregation that produced the numbered selections is shown in Scheme I.

Extraction of Wax. The mature plants were harvested and kept aside for a 2-week period. For comparison purposes, it was decided to extract the wax of heads separately from that of the other plant organs. Wax extraction was effected by dipping the shoots and the heads into cold chloroform for approximately 60 s. Evaporation of the solvent on the rotary evaporator at reduced pressure gave the wax samples. (It is advisable to carry out all the wax extraction operations in a fume cupboard because chloroform might present a carcinogenic risk to humans.)

Wax Class Detection and Separation. The thin-layer chromatography (TLC) analyses were carried out using precoated plates with a 0.25-mm layer of silica gel, type 60 F_{254} (Merck). A suitable amount of solution of the crude wax in $CHCl_3$ and of comparison standards was applied to the origin of the chromatogram developed in various eluting solvents, namely carbon tetrachloride, chloroform, chloroform plus 1% ethanol, and chloroform plus 1% ethanol plus 1% acetic acid. Spots were detected by spraying with 3% CrO_3 in H_2SO_4 (1:1) followed by charring at 120 °C. β-Diketones were detected also under UV (254-nm) light or by spraying with 1% water solution of Fast Blue B salt (Fluka). Aldehydes were easily detected by spraying with 1% water solution of Purpald (EGA-Chemie). Column separations of wax classes were made by gradient elution on silica gel G (Merck). The ratio of crude wax to silica gel was 1:100. The following solvents were used in succession: carbon tetrachloride to elute alkanes, aldehydes, esters, and β-diketones; chloroform plus 1% ethanol to elute hydroxy β-diketones and alcohols;

Table I. Composition (%)[a] and Yields of Plant (P) and Head (H) Waxes from Valitalico, Trinakria, and Six Lines Derived from Their Crosses

	Valitalico		Trinakria		7983 G[b]		7985 N[c]		7984 G		7986 N		7643 G		7644 N	
components	P	H	P	H	P	H	P	H	P	H	P	H	P	H	P	H
alkanes	27	27	22	20	5	5	15	15	10	10	15	20	5	5	15	20
alcohols	33	18	43	52	30	10	45	35	20	15	35	30	35	15	45	35
aldehydes	2	7	13	4	tr	tr	5	5	5	5	10	10	tr	tr	5	tr
acids	1	4	6	5	1	1	5	5	1	1	1	1	5	1	5	5
esters	5	21	16	19	20	20	30	40	15	15	40	40	15	25	30	40
β-diketones[d]	30	21	–	–	39	54	–	–	15	20	–	–	35	49	–	–
hydroxy[e] β-diketones	2	2	–	–	5	10	–	–	35	35	–	–	5	5	–	–
yield per plant and head, mg	11.5	3.7	4.6	0.9	6.6	2.3	7.8	1.0	7.2	4.2	5.9	1.0	11.6	4.2	5.2	0.9

[a] Percentages rounded off to the nearest 1: tr, ≤0.5; –, absent. [b] G = glaucous. [c] N = nonglaucous. [d] Hentriacontane-14,16-dione. [e] 25-Hydroxyhentriacontane-14,16-dione.

chloroform plus 1% acetic acid to obtain free fatty acids.

Homologue Composition of Wax Classes by Gas–Liquid Chromatography (GLC). GLC analyses were performed by using an OV-1 capillary column of 15-m length and 0.1 + 0.15 nm film thickness on HRGC Carlo Erba gas chromatograph with flame ionization detector, Series 4160, coupled with a Spectra Physics SP 4100 integrator. Programmed chromatograms were used, using appropriate column temperature. Hydrogen flow was adjusted at 0.3 kg cm^{-2}. Alkanes and aldehydes were analyzed as such; alcohols, acids, β-diketones, and hydroxy β-diketones were transformed into the corresponding trimethylsilyl derivatives by treatment with excess *N,O*-bis(trimethylsilyl)acetamide at room temperature for 2 h. Typical conditions for the foregoing classes of compounds but the esters were as follows: start temperature 180 °C held for 3 min; 5 °C/min to 290 °C and then held 15 min at 290 °C. Esters were analyzed as such under the following condition: start temperature 150 °C; 40 °C/min to 270 °C and then held 270 °C for 1 min; 7 °C/min to 355 °C and then held at 355 °C for 15 min.

RESULTS AND DISCUSSION

Wax Production and Wax Class Composition. Wax yields per plant and per head of the two wheat cultivars and the six lines obtained from their crossing are shown in Table I. The glaucous Valitalico plants appear to produce nearly 1.5 the amount of the wax of the nonglaucous Trinakria. Furthermore, this value needs to be corrected considering the size of the plant, the latter being taller than the former. In fact when we evaluate the amount of wax from heads, which are roughly of the same size in both cultivars, we conclude safely that Valitalico is much more rich in surface wax than Trinakria. However, a most objective comparison between glaucous and nonglaucous wheat can be gained from the data regarding hybrid lines wax productions, considering that the plants of all the accessions are identical apart the waxy appearance. Thus, it is seen how glaucous lines 7643 G and 7984 G have about twice the wax of the corresponding nonglaucous lines. Strangely enough, in the case of the plants of the couple 7983 G and 7985 N, the rough production of wax is almost the same.

In Table I are reported the percentages of wax class compositions. The most striking feature of the whole picture is represented by complete lack of β-dicarbonyl compounds in Trinakria. To our knowledge this is the first time that it is reported of a wax of a polyploid (tetraploid in this case) mature wheat plant completely deprived of β-diketones. Furthermore, such a total inhibition of β-diketones production is passed on and maintained in the three nonglaucous lines 7985 N, 7986 N, and 7644 N through hybridization and segregation (see the Experimental Section). On the other hand the glaucous character, that is presence of β-diketones in the wax, of Valitalico is found wholly maintained in the progenies 7983 G, 7984 G, and 7643 G.

Concurrently with the lack of β-diketones in the wax of the nonglaucous lines, there is an overall increase of the proportions of all the classes of compounds. The variations observed, however, do not appear univocal; nevertheless, no general conclusion can be drawn from these results apart from what concerns the esters and the aldehydes whose amounts are more consistent in nonglaucous than in glaucous wheats.

Also, no new components not found in either of the parents were detected in the new progenies.

Alkanes. In general the alkane fractions show as dominant chains the C_{29} and C_{31} homologues, alone making up nearly 90% of the whole class of compounds (Table II). Homologue C_{29} is the major chain in alkanes from heads (86%) and plants (68%) of Trinakria. A different situation is found for Valitalico. In fact, while C_{29} is still the dominant chain in alkanes from plants, C_{31} becomes the major homologue in the fraction from heads. Such an unusual strict difference in compositional pattern for these two wheat alkanes fractions (a literature survey discloses that C_{29} is generally the major alkanes in wheat waxes) is also found in all the other hydrocarbon fractions from the derived line waxes examined in this study. In contrast, the C_{31} homologue is the major component in both fractions of the wax of hybrid 7643 G, in this respect resembling the situation found in Trinakria but with a chain longer by C_2 unit.

Alcohols. In the plant waxes C_{28} is the major component (63–86%). In line 7644 N the percent value of this chain drops to 45%, though still being the dominant homologue (Table II).

Alcohol homologue composition patterns of waxes from heads show a much lesser chain length specificity with varying proportions of shorter C_{22} and C_{26} and longer C_{30} and C_{32} chains accompanying the C_{28} homologue. Of interest and liable to various biochemical speculations, although yet unexplainable, is the presence in so relevant amount of the short C_{22} chain that results in most cases detached from the homologue continuous-chain series C_{26}–C_{32}.

Aldehydes. Beside the absence of aldehydes in two line waxes, relevant features appear from the observation of the data in Table II. The homologue composition patterns resemble the alcohols only loosely. In fact, C_{28} is still the major homologue in the plant aldehyde fraction, but this chain is accompanied by relevant amounts of the closest chain C_{26} and C_{30}. Furthermore, in the aldehydes from the heads, there is a noticeable increase of the C_{30} and C_{32} chains. Presumably this means that in this plant organ some C_{28} acyl chains are diverted to further elongation steps by the inhibition of the preceding reduction pro-

Table II. Major Homologue Distribution (%)[a] of Alkanes, Alcohols, Acids, and Esters in the Waxes of Plants (P) and Heads (H) of Valitalico and Trinakria Wheat Cultivars and Six Derivatives from Their Crossing[b]

no. of carbon	Valitalico		Trinakria		7983 G		7985 N		7984 G		7986 N		7643 G		7644 N	
atoms	P	H	P	H	P	H	P	H	P	H	P	H	P	H	P	H
alkanes																
29	61	28	68	86	60	21	62	32	57	26	66	20	33	25	56	19
31	24	57	16	3	28	60	23	58	22	67	27	55	42	59	32	47
alcohols																
22	tr	15	tr	19	1	8	1	30	tr	2	tr	30	1	3	10	16
24	7	7	12	35	6	5	21	4	4	4	28	2	8	3	19	7
26	7	9	8	5	6	2	8	5	6	70	1	3	7	47	6	47
28	82	9	78	8	7	27	63	23	86	24	69	15	83	23	45	20
30	3	13	2	27	1	7	4	13	3	tr	1	19	1	5	2	9
32	1	43	tr	1	tr	11	1	20	1	tr	1	30	tr	19	1	tr
aldehydes																
24	13	7	4	4	–	–	7	4	5	3	16	tr	–	–	12	–
26	12	19	19	5	–	–	9	6	21	15	16	5	–	–	16	–
28	45	12	56	10	–	–	30	17	53	17	44	5	–	–	41	–
30	17	3	21	78	–	–	42	29	13	21	22	31	–	–	25	–
32	2	53	tr	3	–	–	2	44	tr	44	1	58	–	–	2	–
acids																
14	29	18	6	10	11	14	–	9	3	1	11	4	1	1	2	2
16	26	28	18	37	24	15	–	12	1	1	30	2	tr	tr	2	1
18:1	2	2	–	–	5	18	–	11	1	7	21	7	1	6	5	5
18	4	5	5	8	3	4	17	13	4	5	2	13	1	4	5	12
24:1	tr	1	–	–	1	1	–	–	2	1	9	–	tr	1	4	2
24	2	4	11	7	7	4	22	15	9	5	3	6	2	5	20	7
26	5	4	16	14	9	5	9	10	11	5	2	25	4	11	10	2
28	17	5	28	13	20	14	13	9	30	24	6	9	6	15	17	13
30	10	10	11	11	13	19	1	4	26	19	8	11	8	19	tr	16
32	–	15	tr	tr	1	2	tr	–	4	8	tr	tr	73	39	–	20
esters																
40	6	tr	1	10	3	5	7	8	3	5	5	3	4	4	5	6
42	11	8	4	24	15	9	16	17	7	20	11	11	8	18	9	20
44	29	46	26	38	24	27	37	42	22	29	32	25	32	21	29	29
46	14	32	17	17	19	17	16	16	15	19	18	16	17	19	17	14
48	13	12	18	6	17	15	11	11	16	13	16	13	22	16	16	10
50	14	2	24	1	8	15	8	4	17	5	11	13	10	8	14	6
52	5	tr	8	–	7	7	2	tr	9	3	3	10	6	7	5	5

[a] Based on GC analysis of the purified fractions as described in the Experimental Section. Percentages rounded off to the nearest 1: tr, ≤0.5; –, absent or below detection limits. [b] Other constituents, not shown in the table, making up the differences to 100%: alkanes C_{19}–C_{28}, C_{30}, C_{32}, and C_{33}; alcohols C_{16}, C_{18}, C_{20}, C_{21}, C_{23}, C_{25}, C_{27}, C_{29}, and C_{34}; aldehydes C_{20}, C_{22}, and C_{34}; acids $C_{20:1}$, C_{20}, $C_{22:1}$, C_{22}, and $C_{26:1}$; esters C_{36}, C_{38}, C_{54}, C_{56}, and C_{58} and alkan-2-ol esters.

cesses, yielding aldehydes and alcohols, in that order.

Acids. Small amounts of free fatty acids occur in the waxes of all the lines examined in agreement with the data already reported in the literature (Table I). Two major groups of homologues are observable in the compositional profiles: the shorter chains C_{14} and C_{16} and the longer chain group C_{26}, C_{28}, C_{30}, and C_{32} (Table II). Small amounts of monounsaturated $C_{18:1}$, $C_{20:1}$, $C_{22:1}$, $C_{24:1}$, and $C_{26:1}$ along with the same saturated chains were also found in this fraction. If the hypothesis that free fatty acids arise from a release hydrolitic process on acyl chains is correct, the short homologues should stem from an acyl pool in which precursors of all wax classes of compounds are synthesized, whereas the long homologues are derived from acyl group precursors of long-chain aldehydes and alcohols.

Esters. This class of compounds is characterized by the longest chain molecules of the whole wax. The range of saturated ester chain lengths found was between C_{36} and C_{58}. In some lines also odd-carbon alkan-2-ol esters were found. The dominant homologue is always C_{44} in compositional profiles comprising generally the shorter C_{42} and longer C_{46} and C_{50} chains in relevant proportions (Table II).

β-Diketones and Hydroxy β-Diketones. The β-diketones present in the waxes of Valitalico and glaucous lines is the same, hentriacontane-14,16-dione (1: $x = 12$, $y = 14$) as previously found in most of the waxes of cereals. Similarly for the hydroxy β-diketones, which is the same single 25-hydroxyhentriacontane-14,16-dione (2: $m = 5$, $n = 8$, $z = 12$) as found in the majority of Durum wheat waxes.

CONCLUSIVE REMARKS

The composition of classes of compounds shown in Table I, in our opinion, could be conveniently compared with other data reported into the literature related to barley waxes. Barley, in fact, is the only other major cereal for which glaucous and nonglaucous appearance of some parts of its plant has been definitely explained as depending on the presence or absence of the β-diketone classes of compounds (von Wettstein-Knowles, 1972). It has been observed and reported that, in almost all the species of barley in which β-diketones are absent or in very low percentages, alcohols are the major components (≥50%), while when β-diketones are present (15–35%), alcohol content is correspondingly lower (≤38%) (Tulloch et al., 1980). These findings are generally considered as a proof although not based on experimental evidence of a direct relationship between the formation of alcohols and β-dicarbonyl compounds.

Now, while Valitalico and Trinakria wax compositions appear to fit well into that picture, the data shown in Table I regarding the paired lines present a definitely different pattern. In fact, the major discrepancy between the compositions of the wax samples from glaucous and nonglaucous lines is the noticeable increase in the proportion of esters in the latter ones. In fact the wax from nonglaucous lines contains about twice as much ester as the wax from glaucous lines, and this clearly does not respect the proportions of the two parental varieties. The other class of compounds that results concurrently is that of alkanes whose percentages are considerably decreased in all the paired lines.

The homologue composition analyses within each class of compounds in the six paired lines showed that the dominant chain patterns in alkanes, aldehydes, alcohols, acids, and esters were very similar in all the new lines as they were in the two parent genotypes, with possible minor exceptions. The present observations allow one to infer that substantial interactions in the relative amounts of the non β-diketones wax classes is caused by crossing glaucous and nonglaucous wheat varieties, meanwhile the homologue class compositions results are practically unaffected.

All the β-dicarbonyl compound synthesizing lines examined produced the same hentriacontane-14,16-dione and the 25-hydroxy derivative. It was previously considered of interest to compare waxes from wheat (tetraploid, hexaploid) and rye (diploid) with those of the related hexaploid and octaploid Triticales obtained by crossing wheat with rye varieties (Tulloch and Hoffman, 1974; Bianchi et al., 1982). The results of those studies disclosed that wax composition of Triticale was mostly controlled by wheat genes although there was some contribution of rye genes at the level of alkane composition. Furthermore, the hydroxy β-diketone structural isomerism that resulted was affected by the genes of both parent plants. Also in the present work β-diketones represent a major argument. In the F_1 crosses Valitalico × Trinakria the β-diketone phenotype was completely absent, but in the F_2 and following progenies plants producing β-diketones in varying ratios appeared along with plants with no β-dicarbonyl compounds. This clearly means that inhibiting β-diketone genes of Trinakria are dominant on the allelic of Valitalico, but segregation will create β-diketone producing plants in the following progenies.

Thus, these two varieties and the derived lines can now be used to test the idea of the presence in wheat of biosynthetic and inhibitor biosynthetic genes for the production of β-diketones and hydroxy β-diketones.

It seems not unreasonable to speculate that the ability to produce wheat lines with or without β-dicarbonyl compounds is a desirable feature of some agricultural importance.

It has been in fact found that β-dicarbonyl compound content in epicuticular wax may be associated with the protein content in lines derived from crosses with Trinakria (Zitelli et al., 1983).

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