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Metabolic Characteristics of Wine Strains During Spontaneous and Inoculated Fermentation

Patrizia Romano

Dipartimento di Biologia, Difesa, Biotecnologie Agro-Forestali, Università della Basilicata, Via Anzio 10, 85100 Potenza (Italy)

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Summary

The spontaneous alcoholic fermentation is characterized by the contribution of different Saccharomyces cerevisiae strains, which grow in succession or in combination throughout the fermentation process and exhibit different metabolic patterns. The formation of secondary compounds is a strain-specific characteristic and the strains are distinguishable in phenotypes through the production of different amounts of by-products. Natural fermentation is a source of indigenous Sacch. cerevisiae strains, which seem more suitable to be used as starter cultures for that particular wine because they were isolated from the original region and, consequently, better adapted to the particular vinification conditions of that enological area. Among the indigenous strains, the cultures for must fermentation should be chosen on the basis of aroma and flavour determinants typical of the wine under study. Successively, the selected cultures should be tested for the genetic segregation of traits under consideration in order to identify strains completely homozygous for the metabolic characteristics. Only a small proportion of natural wine strains is completely homozygous, the majority being heterozygous for one or more traits. In addition, a significant proportion of natural wine strains can sporulate on rich media, such as grape must, and, as a consequence, the progeny of such strains can exhibit differences in the levels of by-products, thereby affecting the organoleptic properties of the final product. Determination of the degree of strain stability overcomes this problem and allows the choice of the most suitable selected culture to be used in inoculated fermentation. The feature, »stability of metabolic phenotype in industrial strains«, represents a selective index, which ensures that the final product is always consistent with the own properties of each wine.

Keywords: selected wine strains, metabolic characteristics, *Saccharomyces cerevisiae*

Introduction

A great variety of yeasts are present on grapes, but only a small part of them can participate in alcoholic fermentation through a common pattern of yeast species succession *(1,2)*. Wine fermentation is always dependent on the activity and growth of these yeasts. The different yeast genera and the different strains involved in the fermentation can be distinguished on the basis of several characteristics, such as the production of secondary compounds *(3,4)*. By-products are produced as a consequence of yeast metabolism, the amount formed varies among yeast species. The yeast strain used to ferment grape juice is one of the factors which can influence wine quality *(5)*, with the sensory characteristics imposed on wine by different yeasts being extremely varied. Consequently, the use of pure yeast cultures leads to more predictable control of wine fermentation and quality. The beneficial contribution of yeast becomes more significant when starter cultures for wine-making are able to complement grape quality and maintain the individual characteristics of wine.

The formation of by-products by different wine yeasts

Spontaneous fermentation is characterized by the growth in succession or combination of different yeasts, which determine the aromatic quality of the final product. The differences in the composition of wines made from different yeasts appear to be largely quantitative rather than qualitative *(4,6)*. The products of fermentation are usually identical, but the relative amounts of the various compounds differ. The yeast species represents a prominent factor in determining the content of some by-products in wine *(7–9)*.

P. Romano: fax. +39 971 46 400, e-mail: pot2930@iperbole.bologna.it

The products formed can be distinguished in two classes:

- by-products formed with a minimum-level variation in each species can be considered as differentiating characteristics; for example, acetoin and 2,3-butanediol are always produced by wine yeasts with an inverse pattern: yeasts that are high producers of acetoin are always low producers of 2,3-butanediol and *vice versa (10)*;
- by-products formed with a wider variability within the species can be considered as individual strain characteristics, for example acetaldehyde (11,12).

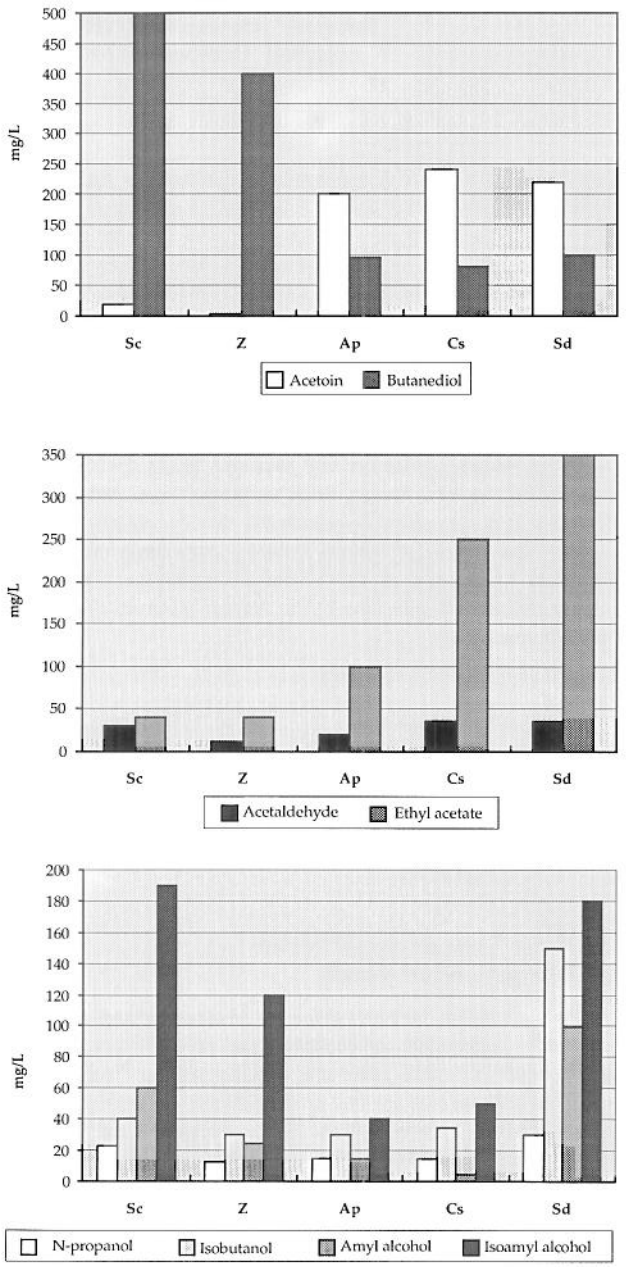

Fig. 1. Metabolic characterization of different wine yeast species: Sc = *Saccharomyces cerevisiae*; Z = *Zygosaccharomyces* wine spp.; Ap = apiculate yeasts; Cs = *Candida stellata*; Sd = *Saccharomycodes ludwigii*.

The characterization of a large number of strains for by-product formation can be used to differentiate yeast strains at the species level. Using the behaviours of the different yeast species as a guide, it is possible to construct a presumed metabolic profile, which represents the most common pattern for each species (Fig. 1).

Thus, apiculate strains, the predominant yeasts of the early fermentation phases, are characterized by a general low production of higher alcohols *(9,13)* and a very high production of acetoin *(14)*, whereas *Saccharomyces cerevisiae*, the principal yeast of alcoholic fermentation, is characterized by a high production of isoamyl alcohol *(15)* and low production of acetoin *(16)*. Other yeasts, such as *Saccharomycodes ludwigii*, a well-known wine spoilage yeast, can be considered a high producer of numerous compounds, such as acetoin, ethyl acetate, amyl alcohols and isobutanol *(17)*.

The formation of by-products by *Sacch. cerevisiae* during spontaneous fermentation

Collections of strains of *Sacch. cerevisiae* and non-*Saccharomyces* yeasts from natural fermentations have demonstrated the existence of a strong polymorphism within each species, particularly in *Saccharomyces* wine strains *(12,15,16,18–20)*.

There is a strain diversity in wine yeasts isolated from given fermentations: some fermentations often have different strains of *Sacch. cerevisiae* and also of other species *(6,21–23)*, all of which participate actively in the fermentation process. Each fermentation seems to have its own population of yeasts and the different yeast/strain specific pattern can be presumed as being typical for each fermentation. The characteristics of the yeasts involved in fermentation play an important part in wine quality, and the concentration levels of the compounds analyzed in wines depend on the predominance of the different strains of *Sacch. cerevisiae* and non-*Saccharomyces* during alcoholic fermentation *(24)*.

Noting the differences in by-product formation, different metabolic phenotypes can be identified for each of the species involved. An example of *Sacch. cerevisiae* strains isolated during spontaneous fermentation of a Cabernet must is reported in Fig. 2.

In this case ten strains of *Sacch. cerevisiae* were isolated at different fermentation stages and characterized for the production of some secondary compounds. A consistent strain diversity was monitored in acetaldehyde and acetic acid production, whereas equal amounts were noted in the other compounds tested. It appears that on the basis of the levels of acetaldehyde and acetic acid production, the strains were distinguishable in three different phenotypes: A = low acetaldehyde and high acetic acid production; B = high acetaldehyde and high acetic acid production; C = low acetaldehyde and low acetic acid production.

At different stages of fermentation different phenotypes were represented: at the early fermentation stage (1st isolation) only the phenotype A was represented, at the tumultuous stage (2nd isolation), the phenotype A was accompanied by the phenotype B, and at the end of fermentation (3rd isolation) another phenotype (C) ap-

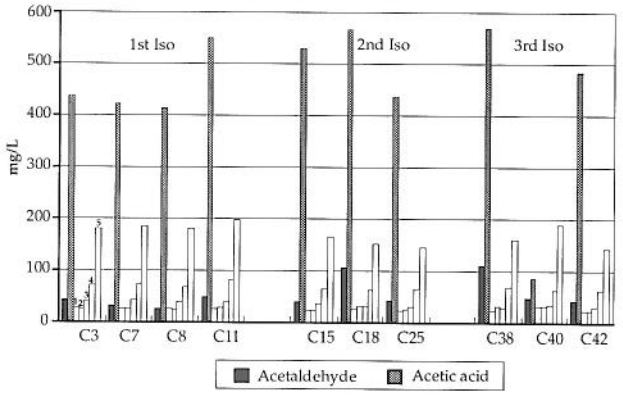

Fig. 2. Metabolic characterization of ten *Saccharomyces cerevisiae* strains isolated at different fermentation stages of a Cabernet must: 1st Iso = start of fermentation; 2nd Iso = middle of fermentation; 3rd Iso = end of fermentation.
By-products, non-differentiating the strains: 1 = ethyl acetate; 2 = n-propanol; 3 = isobutanol; 4 = active amyl alcohol; 5 = isoamyl alcohol.

peared, the phenotypes A and B being also present. These data confirm the uniqueness of each fermentation and the main role played by the natural microbiota and its subsequent effect on the sensory quality of wine.

The formation of by-products in selected cultures of *Sacch. cerevisiae*

The present trend in wine-making is to carry out inoculated fermentation with starter cultures of *Sacch. cerevisiae*. In fact, the use of pure yeasts yields a rapid onset of fermentation and complete fermentation leaving no residual sugar. It also avoids the possible occurrence of »bad« wines due to unknown yeast participation in fermentation and it eliminates undesirable products *(25,26)*. The aim of this technique is to induce reliable and rapid fermentation, resulting in a wine of consistent quality. Thus, the strains employed should possess desirable characteristics *(27)*, such as the production of a desirable fermentation bouquet *(28–31)*. Different *Sacch. cerevisiae* strains, producing differing amounts of secondary compounds, can impart desirable or undesirable flavour determinants to the wine, thereby affecting the ultimate product quality *(32–36)*.

Thus, in Fig. 3, by-product formation in about 120 natural wine strains of *Sacch. cerevisiae* is represented as varying classes of production. It appears that the majority of the compounds were produced with a minimum-level variation, confirming the general metabolic behaviour of this species. Conversely, other compounds were formed with a wide production variability. As is the case, in the example of Fig. 3, of active amyl alcohol, produced from less than 30 up to 120 mg/L. This wide variability underlines the importance of characterizing wine selected cultures, also in the production of secondary compounds. Therefore, the feature, »production of secondary compounds«, should be included in the selection program of starter cultures for wine-making with the aim of finding the particular yeast strain suitable for each specific fermentation.

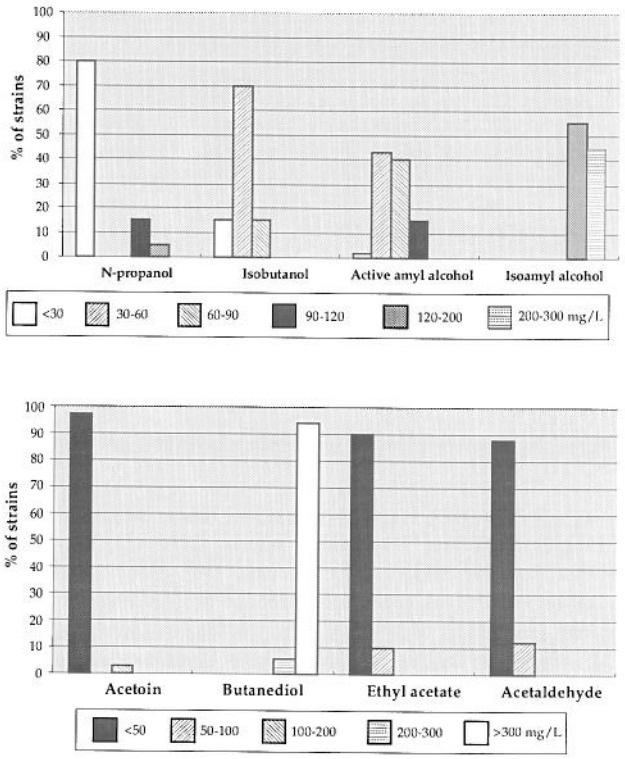

Fig. 3. Variability of secondary compounds production in *Saccharomyces cerevisiae*

Metabolic profile of selected strains as a determinant in the characteristics of individual wine

The selected yeasts utilized for inoculated fermentation are often anonymous strains. They are selected strains belonging to the species *Sacch. cerevisiae*, which may have been isolated by a particular winery, characterized for the principal technological traits and widely distributed and employed in wine-making. As wine is the result of action of the particular strains present, the activity and growth of which is reflected in the organoleptic wine quality, it is necessary to investigate the relationship between strain metabolic profile and wine sensory profile. It has been reported that grape variety and the yeast species/strain involved in the fermentation process contribute mostly to the characteristics of the resulting wine. Credible proof now exists that the vineyard is a primary source for wine yeasts and that strains found on grapes can be followed through the fermentation process *(37)*. This has recalled the attention of wine-researchers and wine-makers to the autochtonous strains with the aim of selecting starter cultures on the basis of aroma and flavour determinants typical of each wine, their characteristic sensory profiles being determined by those particular yeasts/strains, which have undergone alcoholic fermentation *(6)*.

Indigenous strains of *Sacch. cerevisiae* are probably better adapted *(38)* to grow in the grape must than any other inoculated strain. Moreover, inoculation can influence the natural microbiota of must. As reported by some authors *(39,40)*, higher alcohols, isoamyl acetate

Table 1. Genetic analysis for the feature, »production of secondary compounds«, in 10 strains of *Saccharomyces cerevisiae* isolated at different stages of a spontaneous fermentation

Strain		Range in by-product formation (mg/L) in single spore cultures							Het
		N-prop.	Isobut.	D-amyl.	Isoamyl.	Acetald.	Ethyl acet.	Acetic ac.	
1st Iso	C3	20/75	17/88	55/68	186/205	22/91	20/24	490/560	3
	C7	17/113	9/98	52/72	105/220	22/61	19/25	198/1320	5
	C8	10/102	19/27	48/56	175/189	24/35	25/33	74/759	2
	C11	30/43	28/39	55/64	146/176	63/217	18/21	613/853	1
2nd Iso	C15	36/45	12/55	38/43	138/145	36/220	23/27	596/714	2
	C18	27/39	28/40	40/53	139/158	68/202	22/24	611/830	1
	C25	27/35	27/35	41/50	140/159	39/168	20/23	565/716	1
3rd Iso	C42	26/32	30/43	62/73	144/160	43/63	23/27	413/550	0
	C38	28/33	26/37	42/50	139/145	170/188	20/24	456/692	0
	C40	25/32	25/32	64/71	180/197	48/110	20/28	88/540	2

Het = the number of metabolic traits scored that were heterozygous

and ethyl acetate were produced in lower amounts than in spontaneously fermented wines. Other authors *(41)* have reported the occurrence over the years of specific native strains as representative of an enological area. From the point of view of the particular characteristics of each wine region, the inoculation of musts with *Sacch. cerevisiae* strains selected from indigenous yeasts can contribute not only to better control of alcoholic fermentation, but above all to the production of more uniform and balanced wines *(38,42,43)*.

The idea of individual wine characterictics involves the use of indigenous yeasts, as each wine produced comes from the special wine yeast located on the grapes of the chosen vineyard. In this context, a methodological approach for choosing selected strains, which are appropriate to the standard individual characteristics of that wine quality has been pointed out *(44)*.

Technological and metabolic traits of selected strains of *Sacch. cerevisiae* are transformed into individual functions of desirability (d_i), i.e. adimensional values between 0 and 1, which are assigned on the basis of the known levels of the desired optimal response for each trait under consideration. These values are then combined to obtain a response of total desirability (D_{tot}) for each strain, allowing the classification and selection of the most suitable one. This approach allows us to define the appropriate value for each parameter, correlating strain characteristics to quality and individual determinants of the wine. The strain selection program is completed by comparing the technological and sensorial characteristics of the commercial wine under consideration with experimental wines obtained by selected cultures.

Strain homozigosity in by-product formation

The considerable variability in the phenotypic expression of some characteristics in wine yeast strains has stimulated genetic analyses of natural strains of *Sacch. cerevisiae*, showing that all are diploid and nearly all are homozygous for the homothallism gene *(45)*. In spite of that, they are genetically heterogenous for technological characteristics, such as killer capability, copper resistance and hydrogen sulphide production *(31)*. A genetic analysis carried out on 43 strains of *Sacch. cerevisiae*, isolated from fermenting grape musts, revealed that most of these strains were unique and many had heterozygosities at one to seven loci *(46)*. *Sacch. cerevisiae* wine strains can sporulate at relatively high frequencies during part of their life cycle, also on rich media, and consequently, if they are heterozygous for some characteristics, they can, by sporulating, yield homozygous diploid spore clones, expressing thus the different phenotypes. It means that natural wine yeast strains can change from a multiple heterozygote into completely homozygous diploids by a process called »genome renewal« *(46,47)*. An example of this phenomenon is the appearance of high acetoin production in *Sacch. cerevisiae* wine strains *(48)*. From the technological point of view, this fact has practical implications and suggests testing starter cultures for the stability of the selected traits. The homozigosity degree for the traits under consideration becomes a technical parameter useful in ascertaining the strain stability. Thus from the example in Fig. 3, by using classical genetic analysis, monosporic clones of ten strains were obtained and tested for the production of secondary compounds. For each strain six tetrads were dissected yielding 24 monosporic clones. The results, reported in Table 1 as ranges of production for each compound, underline a high potentiality of metabolic variability in single spore cultures of natural wine strains. It can be noted that the single spore cultures of all the strains showed a general correspondence in the production of ethyl acetate and amyl alcohols, whereas a wide and consistent variability was found for acetaldehyde production. In the same table the production ranges which express a significant variability are rectangled, the parental strain being considered as heterozygous for the production of that compound. In this context, the majority of the strains were heterozygous at one to five compounds. In addition, it is interesting to note that the first fermentation phase is characterized by strains with the highest number of heterozygosities, which diminish as the fermentation progresses. At the end of the process, the strains show a tendency to be homozygous.

The genetic control of levels of secondary compounds formed by fermenting wine yeasts allows the attainment of wines with distinctive and constant flavour and aroma characteristics *(49)*.

Strain stability in by-products formed during inoculated fermentation

When grown under glucose-repressed or nitrogen limited conditions *(50,51)* or in continuous cultures *(52)*, diploid or polyploid strains of *Sacch. cerevisiae* always show morphological changes, such as the development of well-defined pseudohyphae or elongated cells. Taking into account that different strains can produce significantly differing amounts of secondary compounds, this discovery might have significance also in the potential change of other genetically modifiable properties, such as metabolic characteristics. In a preliminary study, by means of genetic analysis, the stability of by-product formation by a homozygous strain of *Sacch. cerevisiae* was evaluated during the inoculated fermentation *(53,54)*. In some cases, at the end of the fermentation new phenotypes were found, which could substitute the original metabolic pattern of the parental strain. In particular, a significantly higher production of acetoin and amyl alcohols was exhibited by the monosporic cultures. This variability in the levels of some by-products can also affect the organoleptic properties of the final product. This suggests the introduction of an index which measures the potential stability of the selected strains for the genetically modifiable traits of interest.

Conclusions

Numerous selected strains are nowadays used for commercial wine fermentation, and the choice of a suitable strain for each grape variety can ensure not only the production of quality wine, but also the maintaining of the wine individual characteristics. In the future, mixed cultures of both different yeast species and strains would have the advantage of simulating natural fermentation. The result would be a final product characterized by the desired aromatic profile, consistent with flavour determinants which are typical of each wine. Finally, the determination of the degree of strain stability for the metabolic traits allows the choice of the most suitable cultures to use in inoculated fermentation.

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Metaboličke značajke vinskih sojeva za vrijeme spontane i inokulirane fermentacije

Sažetak

Spontana alkoholna fermentacija provodi se sudjelovanjem raznih sojeva Saccharomyces cerevisiae, koji rastu uzastopce ili u kombinaciji tijekom fermentacije, a pokazuju različite metaboličke putove. Tvorba sekundarnih spojeva značajka je određenoga soja, a prema različitoj količini nusproizvoda sojevi se po fenotipu međusobno razlikuju. Prirodnu fermentaciju provode urođeni sojevi Sacch. cerevisiae jer su pogodniji kao starter kulture za određeno vino, a izolirani su iz izvornog područja i bolje su prilagođeni uvjetima vinifikacije. Između urođenih sojeva za fermentaciju mošta treba odabrati kulturu prema aromi i ukusu tipičnim za vino koje se želi proizvesti. Odabrane kulture treba sukcesivno ispitati prema genetski odvojenim poželjnim značajkama kako bi se mogli izdvojiti potpuno homozigotni sojevi s određenim metaboličkim osobinama. Samo je mali dio prirodnih vinskih sojeva potpuno homozigotan, većina je heterozigotna za jednu ili više osobina. Nadalje, znatan dio prirodnih vinskih sojeva sporulira u bogatoj podlozi kao što je mošt, pa stoga potomstvo takvih sojeva može uzrokovati razlike u količini nusproizvoda utječući time na organoleptička svojstva konačnog proizvoda. Određivanjem stupnja stabilnosti određenog soja izbjegnuta je ta poteškoća te omogućuje izbor najpodobnijeg soja za inokuliranu fermentaciju. Oznaka »stabilnost metaboličkog fenotipa u industrijskim sojevima« predstavlja indeks selektivnosti koji osigurava da je konačni proizvod uvijek usklađen sa svojstvima određene vrste vina.