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Department of Food Science and Human Nutrition, Washington State University, Pullman, WA, USA

A comparison of the fermentation patterns of six commercial wine yeasts[1])

by

CH. W. NAGEL, J. D. ANDERSON[2]) and KAREN M. WELLER

Vergleichende Untersuchung des Gärungsverhaltens von sechs kommerziellen Weinhefen

Zusammenfassung: Die Gärungseigenschaften von sechs im Handel befindlichen Weinhefestämmen — Prise de Mousse (PM), Pasteur Champagne (PC), Swiss (S), Montrachet (M), Epernay 2 (E) und Chanson (C) — wurden sowohl in Traubenmosten wie in YNB- (Yeast Nitrogen Base-)Medium untersucht. Keinem Stamm gelang es, einen Chardonnaymost von 23 °Brix bis zur völligen Zuckerfreiheit zu vergären. Stamm S erzielte den niedrigsten Restzuckergehalt, dann folgte E. Die Stämme PM, PC und S vergoren Gewürztraminermoste von 19,7 und 22,0 °Brix vollständig. In einem auf 30 °Brix angereicherten Chardonnaymost erzeugte PM den höchsten Alkoholgehalt; PC, S, sowie M, E und C folgten mit abnehmenden Ethanolkonzentrationen. C produzierte stets am wenigsten Alkohol. Bei 20 °Brix waren zwischen den ersten fünf Stämmen, bei 25 °Brix zwischen den ersten vier Stämmen keine signifikanten Unterschiede der Alkoholausbeute festzustellen. PM erzeugte in YNB mit einem Gehalt von 11,1 oder 12,9 % (v/v) Ethanol zur Zeit der Inokulation die höchsten Alkoholkonzentrationen. PC und C produzierten signifikant weniger Alkohol. Die Temperatur hat einen weitreichenden Einfluß auf das Wachstum der Hefestämme und die Zuckervergärung in YNB-Medium. Mit Ausnahme von PM bei 20 °C hatte kein Hefestamm 22 % Glucose in YNB nach Ablauf von 25 d vollständig vergoren. Die hohe Temperatur von 30 °C war dem Hefewachstum und der Gärung besonders abträglich. Im allgemeinen wurde bei 20 °C am meisten Zucker abgebaut. Gegen Caprin- und Caprylsäure war der Stamm am tolerantesten.

Key words: Yeast, systematics, growth, fermentation, sugar, ethanol, temperature.

Introduction

Stuck fermentations have been associated with winemaking since its inception. Stuck fermentations are not well understood although much work surrounding the subject has been done. High concentrations of ethanol, carbohydrate and short-chain fatty acids, as well as extreme fermentation temperatures, have been implicated as causes of stuck fermentations.

As the carbohydrate concentration of a medium increases, the ability of wine yeasts to grow and stay viable decreases (SLATOR 1906; OUGH 1966 a; PANCHAL and STEWART 1980; MOTA *et al.* 1984; NISHINO *et al.* 1985). High concentrations of ethanol have also been found to be inhibitory to yeast growth (HOHL and CRUESS 1936; HOHL 1938; GRAY 1941, 1945; NOVAK *et al.* 1981). The combined effects of ethanol and carbohydrate concentration on yeast growth are currently thought to be a major reason for stuck fermentations (PANCHAL and STEWART 1980; MOTA *et al.* 1984).

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[2]) Present address: Calreco, 8015 Van Nuys Blvd., Van Nuys, CA 91412.

In addition, high fermentation temperatures increase the inhibitory effects of ethanol (FERRIERA 1959; OUGH 1966 b) and influence the nutritional needs of the yeasts (CASEY *et al.* 1984; TROMP 1984). Most recently, the presence of octanoic and decanoic acids have been implicated as a cause of stuck fermentations (NORDSTROM 1964; LAFON-LAFOURCADE *et al.* 1984; RIBÉREAU-GAYON 1985).

Knowing how different wine yeasts perform under various fermentation conditions could assist the winemaker in preventing stuck fermentations. Studies were conducted to evaluate the performance of six commercial wine yeasts using various concentrations of ethanol and carbohydrate and various temperature conditions. In addition, the inhibitory effects of octanoic and decanoic acids on yeast growth were studied for each strain.

Materials and methods

Six commercial wine yeasts were used in the fermentation trials. Chanson *(Saccharomyces cerevisiae)* was obtained from The Wine Lab (St. Helena, CA). Montrachet (*S. cerevisiae*, UCD No.522), Pasteur Champagne (*S. bayanus*, UCD No.595) and Epernay 2 *(S. cerevisiae)* were obtained from Universal Foods Corporation (Red Star Yeasts, Milwaukee, WI). The Prise de Mousse *(S. bayanus)* and the Swiss yeast (*S. cerevisiae*, Wädenswil 27) were obtained from Lallemand Inc. (Lalvin Wine Yeasts, Montreal, Quebec, Canada). The yeasts were isolated and maintained on potato dextrose agar (Difco, Detroit, MI) acidified to pH 3.5 with a 10 % (w/v) tartaric acid solution.

In order to ensure a standard inoculum a standard curve relating Klett units to cell concentration was prepared using the Prise de Mousse strain. Filter sterilized Yeast Nitrogen Base (YNB; Difco, Detroit, MI) containing 10 % (w/v) glucose (100 ml) was placed in a sterile 250 ml Erlenmeyer flask fitted with a cotton plug and a side arm capable of insertion into a Klett-Summerson photoelectric colorimeter (red filter, Klett Mfg. Co., Inc., New York, NY). After inoculation, incubation was on a gyrotary shaker (model S-3 or G-10, New Brunswick Scientific Co., New Brunswick, NJ) at 120 rpm and 30 °C. A turbidity value of 270 Klett units was needed to achieve approximately 10^6 CFU/ml after dilution of 0.2 ml with 6.8 ml of medium.

The Gewürztraminer, Chardonnay and Sauvignon blanc juices were prepared from grapes harvested at the Irrigated Agriculture Research and Extension Center, Prosser, WA by Dr. SARA SPAYD. The clarified juice containing 75 mg/l total sulphur dioxide was stored under anaerobic conditions at 3 °C. The analysis of the grape juices is shown in Table 1. Soluble solids (°Brix), pH and total acidity were determined as outlined by

Table 1

Must analysis: all varieties

Mostanalysendaten der untersuchten Sorten

Variety		°Brix	pH	Total acidity (%)
Gewürztraminer	E [1])	19.7	3.2	9.6
Gewürztraminer	L [2])	22.0	3.4	5.7
Chardonnay	E	20.4	3.2	11.4
Chardonnay	L	23.0	3.3	8.6
Sauvignon blanc		17.5	2.7	12.4

[1]) E = Earlier maturity.
[2]) L = Later maturity.

AMERINE and OUGH (1980). The dryness of the resultant wines was determined using the Dextro-Check kit of Miles Laboratories (Elkhart, IN).

For the experiment on carbohydrate concentration effects on yeast growth, the Chardonnay juice was adjusted to 20, 25 and 30 °Brix by addition of sucrose. The Chardonnay juices were diluted prior to addition of sucrose such that the nutrient content was the same in all samples. The juices were pasteurized by heating at 70 °C for 5 min. The juice samples (100 ml) were placed in sterile 250 ml Erlenmeyer sidearm flasks, flushed with nitrogen and fitted with sterile wine airlocks containing distilled water. All samples were prepared in duplicate and incubated at 20 °C. The yeast inocula were grown in the same medium.

Ethanol, glucose, and fructose contents were determined in duplicate by high performance liquid chromatography (HPLC, PFEIFFER and RADLER 1985). The HPLC system consisted of: a single chromatography pump (model M-6000a, Waters Associates, Milford, MA), an auto sampler (WISP 710 B, Waters Associates, Milford, MA), a heated column jacket (Rainin Instrument Co., Inc., Woburn, MA), a differential refractometer (model 401, Waters Associates, Milford, MA), an integrator (Spectra-Physics Auto-Lab Minigrator, Santa Clara, CA) and a chart recorder (Houston Instruments, Austin, TX). An organic acid analysis column (Aminex Ion Exclusion HPX-87, 300 × 7.8 mm, Bio-Rad Laboratories, Richmond, CA), held at 65 °C, was used with degassed 0.013 N H_2SO_4 as the carrier solvent at a flow rate of 0.5 ml/min.

YNB containing 10.0 % (w/v) glucose with 11.1, 12.9 and 14.7 % (v/v) ethanol after addition of starter culture was used for the alcohol tolerance studies. All media were adjusted to pH 3.2 with 1.0 N HCl and filter sterilized. Sterile 13 × 100 mm screwcap test tubes were aseptically filled with 6.8 ml of fermentation medium and 0.2 ml of the appropriate yeast starter culture. All fermentations were conducted in duplicate at 20 °C. The yeast inocula were grown in the same medium without alcohol. Gas pressure was released daily by loosening the cap of the test tube just enough to let the gas escape.

For the inhibition studies with octanoic and decanoic acids, ethanolic solutions (0.7 ml) of the proper dilutions were added to YNB (1.15 × 6.1 ml) containing 5.75 % (w/v) glucose and adjusted to pH 5.4 or 3.2 with 1 N HCl in sterile 13 × 100 mm screwcap test tubes. Control samples contained 0.7 ml of 95 % ethanol. Fermentations were conducted in duplicate at 20 °C. The yeast inoculum (0.2 ml) was grown up in the same YNB medium. The relative effectiveness (RE), 1/RE and infinite inhibitory concentration (IIC) were calculated as described by MARWAN and NAGEL (1986).

For the temperature studies, 6.8 ml YNB containing 22 % (w/v) glucose adjusted to pH 3.2 with 1 N HCl and sterile filtered was added to sterile 13 × 100 mm screwcap test tubes. Fermentations were conducted in duplicate at 15, 20 and 30 °C with turbidity measurements being taken daily. The inoculum was prepared in the same medium.

Data for the ethanol tolerance and carbohydrate concentration studies were analyzed using the general linear model (GLM) procedure (S.A.S., S.A.S Institute, Inc., Cary, NC). Duncan's Multiple Range Test (STEELE and TORRIE 1980) was used to analyze the effect of temperature on ethanol production in YNB.

Results and discussion

The results of fermentation by the yeast strains in the Gewürztraminer and Chardonnay juices are shown in Table 2. The Prise de Mousse, Pasteur Champagne and Swiss yeasts fermented all the juices to dryness except the late maturity Chardonnay. In this case, the Swiss strain appeared to be more effective in reducing the sugar con-

Table 2

Fermentation analysis · Gewürztraminer and Chardonnay juices fermented at 20 °C

Analyse der Gärung · Bei 20 °C vergorene Moste von Gewürztraminer und Chardonnay

Yeast strain	Gewürztraminer				Chardonnay			
	Fermentation time (d)		Residual sugar (%)		Fermentation time (d)		Residual sugar (%)	
	Early [1]	Late [2]	Early	Late	Early	Late	Early	Late
Prise de Mousse	23	28	0.2	0.2	20	42	0.1	0.6
Pasteur Champagne	30	28	0.2	0.1	20	42	0.1	0.6
Swiss	30	21	0.2	0.1	20	31	0.1	0.3
Montrachet	41	28	0.4	1.0	28	42	0.5	0.6
Epernay 2	30	49	0.4	0.8	49	73	0.6	0.4
Chanson	41	59	0.2	0.8	49	73	0.1	0.6

[1]) Earlier maturity. [2]) Later maturity.

tent than the other two. However, variable results were obtained depending upon the juices fermented. In a 26 °Brix Muscat Canelli juice the Swiss strain even had difficulty initiating growth. The slower growing Chanson strain fermented the earlier maturity juices to dryness but was not capable of doing the same with the later maturity higher Brix samples (22 and 23 °Brix). The Montrachet and Epernay 2 strains did not ferment any of the juices to dryness (< 0.2 % residual sugar). All of the strains seemed to exhibit difficulty in fermenting the late maturity Chardonnay juice to dryness. Chardonnay juice has been noted for producing more stuck or sluggish fermentations than other juices, particularly due to a lack of nitrogen and/or amino acids which are necessary for yeast growth (OUGH 1964; INGLEDEW and KUNKEE 1985). As noted by other researchers, the higher sugar content juices were more difficult to ferment to dryness. This would indicate that either the sugar or the resultant alcohol is affecting the fermentation. OUGH (1966 a), using the Montrachet yeast strain, found that the optimum fermentation rate, as well as the optimum growth rate, occured between 15 and 22 °Brix in grape juice. Higher concentrations resulted in slower rates.

Temperature had very little effect on the total ethanol produced by the strains in the earlier maturity Chardonnay juice except Chanson at 20 °C (Table 3). In Sauvignon blanc juice no differences were observed at 30 °C but Chanson definitely produced less ethanol at 15 and 20 °C than the other strains (Table 3).

The final ethanol concentrations produced in Chardonnay juices of 20, 25 and 30 °Brix after 25 d are shown in Table 4. The Chanson strain produced a significantly lower concentration of ethanol than the other yeasts. At 30 °Brix, there were significant differences in the final amount of ethanol produced. The Prise de Mousse strain produced the greatest amount followed by the Pasteur Champagne and the Swiss and Montrachet strains. Thus one could conclude that the Prise de Mousse strain is capable of producing the greatest amount of ethanol in high-sugar juices. Of interest is the fact that in the 25 °Brix juice the first four strains had produced 94, 99, 99 and 97 % of their total ethanol, respectively, after just 14 d while the Epernay 2 and Chanson strains had produced significantly less of the total, 84 and 74 %, respectively. Part of this can be explained by the fact that, at least in the case of the Chanson strain, the cells grow much slower and produce a smaller population.

Table 3

Ethanol concentrations (% v/v) after 30 d fermentation in earlier maturity Chardonnay and Sauvignon blanc juices at 15, 20 or 30 °C

Ethanolkonzentration (% v/v) nach 30tägiger Gärung · Moste von Chardonnay (früh gelesen) und Sauvignon blanc bei Gärtemperaturen von 15, 20, und 30 °C

Yeast strain	Chardonnay			Sauvignon blanc		
	15 °C	20 °C	30 °C	15 °C	20 °C	30 °C
Prise de Mousse	11.9 a	12.0 a	11.8 a	9.8 a	9.8 ab	9.6 a
Pasteur Champagne	11.8 a	11.9 a	11.6 a	9.5 b	10.2 a	9.5 a
Swiss	12.0 a	11.6 ab	11.6 a	9.7 b	9.5 bc	9.6 a
Montrachet	11.9 a	11.9 a	12.0 a	9.8 ab	9.7 ab	9.2 a
Epernay 2	11.8 a	12.1 a	11.9 a	10.0 a	10.1 a	9.7 a
Chanson	11.7 a	10.6 b	11.8 a	8.9 c	9.0 c	9.1 a

Means in columns with different letters are significantly different ($P < 0.05$).

Table 5 shows the maximum turbidity obtained by the different yeast strains in 0, 11.1 and 12.9 % (v/v) ethanol in YNB. In all cases, the Prise de Mousse strain produced a greater turbidity and, therefore, presumably greater cell population than the other strains. The Chanson strain was compared against the Prise de Mousse strain in a separate experiment and produced significantly less turbidity. The ethanol concentrations obtained in the 11.1 and 12.9 % (v/v) ethanol media are shown in Table 6. Again the Prise de Mousse strain produced the greatest amount of alcohol, although it was only significantly different from the Pasteur Champagne strain and in the case of the 12.9 % alcohol medium the Swiss strain. Again in a separate experiment, the Prise de Mousse strain produced significantly more alcohol than the Chanson strain in all of the media. None of the strains were able to grow in YNB medium containing 14.7 % ethanol.

The ability of the Prise de Mousse strain to produce turbidity readings greater than the other strains, which in turn could mean a greater number of viable cells, may be one reason for its ability to produce and tolerate more ethanol than the other

Table 4

Ethanol content (% v/v) of 20, 25 and 30 ° Brix Chardonnay juices after fermentation for 25 d at 20 °C

Ethanolgehalt (% v/v) von Chardonnaymosten mit 20, 25 und 30 ° Brix nach 25tägiger Gärung bei 20 °C

Yeast strain	20 °C	25 °C	30 °C
Prise de Mousse	12.1 ab	15.8 ab	19.4 a
Pasteur Champagne	11.9 ab	15.8 ab	18.9 b
Swiss	12.2 a	15.9 a	18.1 c
Montrachet	12.2 a	15.8 a	17.7 c
Epernay 2	12.2 a	15.4 b	15.9 d
Chanson	11.8 b	13.6 c	13.2 e

Means in columns with different letters are significantly different ($P < 0.05$).

Table 5

Maximum turbidity (Klett units) in Yeast Nitrogen Base containing 0, 11.1 or 12.9 % (v/v) ethanol and 10 % (w/v) glucose at 20 °C

Maximale Trübung (Klett-Einheiten) in YNB mit einem Gehalt von 0, 11,1 und 12,9 % (v/v) Ethanol und 10 % (w/v) Glucose bei einer Gärtemperatur von 20 °C

Yeast strain	Ethanol % (v/v)		
	0	11.1	12.9
Prise de Mousse	208	119	84
Pasteur Champagne	172	91	58
Swiss	193	101	57
Montrachet	189	90	53
Epernay 2	148	97	60

strains. LAFON-LAFOURCADE *et al.* (1979) and LARUE *et al.* (1980) state that not only does the total number of viable yeast cells need to be high (greater than 10^7/ml) for fermentations to go to completion but the cells must stay viable. STREHAIANO and GOMA (1983) support the fact that strains of *Saccharomyces bayanus* produce a greater amount of biomass and tolerate ethanol better than strains of *Saccharomyces cerevisiae*.

Table 6

Ethanol tolerance study in Yeast Nitrogen Base containing 11.1 or 12.9 % (v/v) ethanol and 10 % (w/v) glucose at 20 °C

Untersuchung der Ethanoltoleranz in YNB mit einem Gehalt von 11,1 und 12,9 % (v/v) Ethanol und 10 % (w/v) Glucose bei einer Gärtemperatur von 20 °C

Yeast strain	Final concentrations	
	Ethanol % (v/v)	Glucose % (w/v)
Initial ethanol 11.1 % (v/v)		
Prise de Mousse	15.6 a	2.6
Pasteur Champagne	13.7 b	6.6
Swiss	15.0 ab	4.1
Montrachet	14.9 ab	4.2
Epernay 2	14.2 ab	4.3
Initial ethanol 12.9 % (v/v)		
Prise de Mousse	16.5 a	5.0
Pasteur Champagne	14.2 c	7.6
Swiss	15.1 bc	7.2
Montrachet	15.5 ab	7.2
Epernay 2	15.5 ab	7.0

Means with different letters are significantly different within one initial ethanol concentration ($P < 0.05$).

The final concentrations of ethanol for the 11.1 % medium were lower than those of the 12.9 % medium. With the Swiss strain there is not much difference in the final ethanol concentration of either medium. This may indicate that the ethanol concentrations of the medium is a primary reason for the inhibition of growth for this strain.

The effect of temperature on ethanol production and glucose utilization in YNB is shown in Table 7. Only in the case of the Prise de Mousse strain grown at 20 °C, all of the glucose was fermented to ethanol. This strain produced significantly more ethanol than the other strains at all temperatures. It is apparent that maximum conversion of glucose under the limited nutritional conditions of the YNB occurred at 20 °C. Based upon turbidity readings, growth was more rapid at 30 °C and maximum populations were obtained sooner than at 20 °C. At 30 °C the maximum population was often reached within 5—10 d, whereas at 20 °C most of the strains were showing an increase in numbers even at the end of 26 d. These results would indicate that the viability of the yeasts at 30 °C must have dropped off markedly, shortly after maximum populations were obtained. At 15 °C cell growth apparently was still occurring, although the Pasteur Champagne and Epernay 2 strains did appear to reach a maximum population by the end of 20 d.

Table 7

Effect of temperature on ethanol content (% v/v) produced by the yeasts in Yeast Nitrogen Base containing 22 % (w/v) glucose after fermentation for 25 d

Einfluß der Temperatur auf den Gehalt des durch die Hefen erzeugten Ethanols (% v/v) · YNB mit einem Gehalt von 22 % (w/v) Glucose nach 25tägiger Gärung

Yeast strain	15 °C	20 °C	30 °C	Ave.
Prise de Mousse	10.2	12.2	6.5	9.6 a
Pasteur Champagne	8.0	8.3	4.0	6.8 b
Swiss	7.0	7.2	4.6	6.3 b
Montrachet	8.0	7.9	5.3	7.1 b
Epernay 2	7.0	8.6	4.7	6.8 b
Chanson	6.7	8.4	4.8	6.6 b
Ave.	7.8 a	8.8 b	5.0 c	

Average of two experiments run in duplicate. Means with different letters are significantly different ($P < 0.05$).

These results show that temperature does have a marked influence on the nutritional requirements of the various yeasts. Determining how temperature influences the nutritional requirements of these wine yeasts may be very beneficial in helping to predict if a juice will be a problem to ferment at the temperature desired. The effect of nutrient addition on yeast growth by a single yeast strain at various temperatures has been investigated (TROMP 1984; INGLEDEW and KUNKEE 1985). However, literature relating fermentation temperature to the nutritional requirements of yeasts used in fermentations could not be found.

The inhibitory effects of octanoic and decanoic acids in Yeast Nitrogen Base at 20 °C are shown in Table 8. In both cases, the Prise de Mousse strain is much more resistant to the inhibitory effects of these organic acids. The Pasteur Champagne strain seems to be the next most resistant at pH 5.4. Differences between the other strains are minor. GENEIX *et al.* (1983), LAFON-LAFOURCADE *et al.* (1984) and RIBÉREAU-GAYON (1985)

Table 8

Infinite inhibitory concentrations (IIC, mg/l) of octanoic and decanoic acids in Yeast Nitrogen Base at 20 °C

Hemmwirkung (IIC, mg/l) von Caprylsäure und Caprinsäure in YNB bei einer Gärtemperatur von 20 °C

Yeast strain	Octanoic acid		Decanoic acid	
	pH 5.4	pH 3.2	pH 5.4	pH 3.2
Prise de Mousse [1])	50.7	49.9	35.1	31.1
Pasteur Champagne [1])	41.7	31.4	28.2	18.0
Swiss [1])	36.0	31.8	18.0	14.7
Montrachet [1])	31.8	27.1	18.9	15.1
Epernay 2 [1])	32.7	27.7	21.1	14.8
Chanson [2])	36.1	29.3	27.1	15.4

[1]) Using 70 Klett units for RE.
[2]) Using 40 Klett units for RE.

have all reported that octanoic and decanoic acids have an inhibitory effect on yeast viability and that as little as 3 mg/l decanoic and 10 mg/l octanoic acid can show this effect. They also state that concentrations of octanoic and decanoic acids encountered in wine are very similar to these concentrations. Given these values and the IIC values for octanoic and decanoic acids in Table 8, it would appear that stuck fermentation do not occur solely due to the presence of 3—5 mg/l decanoic acid and 10—15 mg/l octanoic acid. Perhaps the synergistic effects of octanoic and decanoic acids along with ethanol, osmotic pressure and/or a lack of essential nutrients would be a more plausible reason. Presently, there is not any literature which discusses the effects of octanoic and decanoic acids combined with the effects of ethanol on yeast viability. Work of this nature could be very valuable in relation to the study of stuck fermentations.

Conclusions

No yeast strain tested was capable of fermenting all juice samples to dryness. The slower growing Chanson strain tended to produce lower alcohol concentrations after 30 d fermentation of juices at 15 and 20 °C. There were no significant differences between the yeast strains at 30 °C. In 30 °Brix Chardonnay juice, the Prise de Mousse strain produced the greatest amount of alcohol followed in order by the Pasteur Champagne, Swiss and Montrachet, Epernay 2 and Chanson strains. There was no significant difference between the first four strains at 20 and 25 °Brix. The Prise de Mousse strain was most tolerant to ethanol in YNB, produced the greatest amount of ethanol regardless of temperature, and was most tolerant to octanoic and decanoic acids.

Summary

The fermentation properties of six commercial yeast strains, Prise de Mousse (PM), Pasteur Champagne (PC), Swiss (S), Montrachet (M), Epernay 2 (E) and Chanson (C) were compared in grape juices and Yeast Nitrogen Base (YNB). None of the strains fermented a 23 °Brix Chardonnay juice to complete dryness. S resulted in the smallest

amount of residual sugar followed by E. PM, PC and S all fermented 19.7 and 22.0 °Brix Gewürztraminer juices to dryness. PM produced the greatest amounts of alcohol in Chardonnay juice fortified to 30 °Brix followed in order by PC, S, and M, E and C. C consistently produced the least amount of alcohol. There was no significant difference in alcohol production by the first five strains at 20 °Brix and no significant difference among the first four strains at 25 °Brix. PM produced the highest concentrations of ethanol in YNB containing 11.1 or 12.9 % (v/v) ethanol at the time of inoculation. PC and C produced significantly less alcohol. Temperature has a profound effect on the ability of the yeast strains to grow and ferment sugar in YNB. With the exception of PM at 20 °C, none of the strains fermented the 22 % glucose completely in YNB by the end of 25 d. The higher temperature 30 °C was particularly detrimental to yeast growth and fermentation. Generally, the most complete fermentations occurred at 20 °C. PM was most tolerant of decanoic and octanoic acids.

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Dr. CH. W. NAGEL
Professor
Department of Food Science and Human Nutrition
Washington State University
Pullman, WA 99164—6330
USA