IF THE YEAST AIN’T HAPPY,
AIN’T NOBODY HAPPY

The Microbiology of Beer
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STEEERING COMMITTEE:

Charles Bamforth, Ph.D., D.Sc.
University of California Davis
Department of Food Science and Technology

Morten Kielland Brandt, Ph.D., Dr.H.C.
DTU Systems Biology

Chris White, Ph.D.
White Labs

Ann Reid
Director
American Academy of Microbiology

Michael Ingerson-Mahar, Ph.D.
Colloquia Fellow
American Academy of Microbiology

PARTICIPANTS:

Nicholas Bokulich
University of California Davis
Department of Viticulture and Enology

Chris Boulton, Ph.D.
University of Nottingham
Department of Brewing Science

Kyria Boundy Mills, Ph.D.
University of California Davis
Department of Food Science and Technology

Sue James, Ph.D.
Heineken
Supply Chain

William Maca
MillerCoors LLC.

John Sheppard, Ph.D.
North Carolina State University
Dept. of Food, Bioprocessing and Nutrition Sciences

Bill Simpson, Ph.D.
Cara Technology Limited

Katherine Smart, Ph.D.
SABMiller

Jan Steensels
CMGG lab for Genetics and Genomics, KULeuven
VIB Laboratory for Systems Biology

Graham Stewart, Ph.D., D.Sc.
GGStewart Associates

Erna Storgards, Ph.D.
VTT Technical Research Centre of Finland

Graeme Walker, B.Sc., Ph.D., D.Sc., FIBD
University of Abertay Dundee
Food Division

Barry Ziola, Ph.D.
University of Saskatchewan

Written by Ann Reid and Michael Ingerson-Mahar
1. What does microbiology have to do with beer?

In a word — yeast. Without yeast, there would be no beer. It’s that simple. And yeast is a microbe, that is, a living organism that is too small to see with the human eye. Every time someone brews a batch of beer, in a very real sense he or she is doing a microbiology experiment. If you brew beer at home, you’re a microbiologist! (In fact, you might even want to join the American Society for Microbiology!) So let’s talk about yeast.
YEAST — YOUR SOPHISTICATED BEER-MAKING PARTNER, AND NOT SO DISTANT COUSIN:
You may remember from high school a description of biodiversity that divided the living world into five kingdoms: animals, plants, fungi, monera and protists. This classification, proposed in 1969 and now seriously outdated, is heavily influenced by what humans can see — plants, animals and fungi are all visible and their diversity is obvious. Monera and protists are single-celled microscopic organisms that are invisible to the naked eye and cannot all be reliably distinguished visually, even under the microscope. New molecular techniques that look at an organism’s genes to see how closely they are related have shed new light on life’s diversity. Now instead of five kingdoms, scientists recognize three domains of life: bacteria, archaea, and eukaryotes. Animals, plants, fungi and protists actually all belong to just one large domain, the Eukaryotes. As you can see in the tree of life in Figure 1, the group that used to be called “monera” in reality represents a huge proportion of overall biodiversity.

But back to yeast. Yeasts are members of the fungal kingdom, so they, like humans, are eukaryotes. In addition to approximately 1500 species of yeast, the fungal kingdom also includes mushrooms and molds. Yeasts, while unicellular, are much more closely related to humans than they are to bacteria. Each yeast cell has about 6,000 genes (compared to 30,000 in a human cell) and most of its basic life processes (DNA replication, cell cycle control, gene regulation) are so similar to humans that for decades yeast has been used as the quintessential model organism in labs studying how cells work. In the wild, the yeast family is diverse. Many kinds of yeast seem to have evolved to fill ecological niches based on feeding on simple sugars produced by animals and plants. Yeasts are found in every environment: on grape skins and human skin, in the stomachs of bees and in tree sap, from the bottom of the ocean to the soil under our feet.

Once you realize that the yeast you’re pitching into your beer is a highly sophisticated, complex organism, and a member of a diverse and evolutionarily ancient family, you will begin to appreciate how each step of the brewing process is essentially an elaborate effort to ensure that a very particular, highly specialized yeast strain is given precisely the conditions that will help it to produce the kind of beer you want.
2. What’s so special about brewer’s yeast?

Brewer’s yeast is a domesticated organism. For centuries, humans have been selecting yeast for particular characteristics including the ability to grow quickly on a diet of malted grain, to produce satisfactory levels of alcohol, and of course, to make a final product that keeps well and tastes good!

There are two main yeasts used to brew beer, each with several closely related varieties. Commonly called “brewer’s yeasts,” they are very different from any yeasts found in the wild, just as house cats are very different from lions and corn is very different from its ancestor, teosinte. Brewer’s yeast is different for exactly the same reason — like other domesticated animals and plants, humans have selected and used the strains that best provide the characteristics that make it much better for brewing beer than wild yeast. No one knows exactly when the first beer was brewed or by whom. The discovery might have been accidental, but it probably happened almost as soon as humans began growing grain. The first historical evidence of beer brewing comes from ancient Sumaria. Most grains in the right conditions can be fermented by wild yeast that live in virtually all environments and are easily carried in air currents. Grain has long been allowed to sprout because this makes it easier to digest (this is still a common practice with chicken feed, for example). If a store of sprouted grain was left exposed to the elements, it could have been flooded and seeded with wild yeasts carried with the wind. A few weeks later, the mixture would have fermented, producing the first “beer.” Brewing beer caught on very quickly. It made good use of grain — especially of grain that had begun to sprout; it was safer to drink than water (more on that later), and, of course, it contained alcohol, which many animals, including humans, find appealing. Recognition that brewing beer required expertise came early as well; at least in Europe, communities often had a designated brewer, a tradition that later passed to monks in monasteries.
Our ancestors did not know that an invisible living organism was crucial to their beer-making success, but they learned by experience that material skimmed from the top of the fermenting beer, called barm, would kick-start the next batch. An indication of brewers’ appreciation for barm was that it was also called Godesgood, meaning “God is good.” Home brewers used a designated “beer stick” to stir their brews — unwittingly transferring yeast from one batch to the next. It was not until the early- and mid-1800’s when first Charles Cagniard-Latour and Friedrich T. Kützing and later Louis Pasteur studied yeast, that it became clear that beer making was not just a chemical process but rather that living organisms were responsible for fermentation (please see the sidebar: “Fermentation: a transformative experience (and a lifesaver)”). In the late 1800’s, Emil Christian Hansen, a scientist and brewer at the Carlsberg laboratories made a startling discovery. The yeast that brewers had been using to produce beer was actually a mixture of several different strains of yeast. He was the first brewer to isolate and propagate one specific strain of yeast. Hansen’s accomplishment helped brewers standardize the brewing process, making beer more consistent from batch to batch.

What makes brewer’s yeast so special? The most important answer is that unlike wild yeast, brewer’s yeast grows very effectively on a particular sugar, maltose, which just happens to be the predominant sugar in the mash that brewers make from sprouted barley. Brewer’s yeast also exhibits a variation on the two distinct lifestyles that are typical of all yeast. In the presence of oxygen and nutrients, yeast will use available nutrients to reproduce — that is, make more yeast. When the oxygen becomes scarce, yeast will switch over to another lifestyle based on fermentation in which they consume sugars to produce alcohol and carbon dioxide instead of just making more yeast. Many yeasts do not turn to fermentation until oxygen is entirely absent but brewer’s yeast make this switch when there is still some oxygen around. Brewer’s yeast’s ability to ferment when there is still some oxygen around is essential to brewing beer. Early beers were probably weakly alcoholic because most common wild yeasts stop fermenting at quite a low alcohol concentration, around 3%. Brewer’s yeast will continue to ferment even when the alcohol content rises to 7-9%. In fact, if provided with supplemental nutrients, some strains of brewer’s yeast will continue to ferment to an alcohol concentration of over 16%!

Fermentation: a transformative experience (and a lifesaver)

Very broadly, fermentation is a biological reaction that harvests energy from the chemical bonds in sugars. When yeast carries out fermentation, it breaks down simple sugars, and produces carbon dioxide and alcohol as waste products. It is likely that yeast evolved this life strategy to maintain a competitive advantage over other microbes that also feed on simple sugars. Most of those microbes cannot tolerate alcohol or the high acidity caused by the carbon dioxide and organic acids produced by the yeast. Most beers have a pH in the range of 4.0-4.5 — intermediate between pure water (pH = 7.0) and lemon juice (pH = 2.0) — too acidic for most bacteria. So by switching to fermentation, the yeast ensures that it keeps the sugar source to itself. For humans, this turned out to be a public health bonanza. Before the development of water sanitation systems in the late 1800’s, water sources were frequently contaminated with disease-causing bacteria and viruses. All of these organisms are killed by the brewing process (especially when the grain extract is boiled) and cannot grow in the finished product. The disease-causing bacteria can contaminate water are inhibited by beer’s alcohol content, high acidity, low oxygen content and by antibacterial compounds that come from hops. Thus for much of human history, beer was often safer to drink than the local water supply.

There are other microbes that can carry out fermentation, but they produce different waste products; for example, when Lactobacillus bacteria ferment the sugars in milk to make yogurt, they produce lactic acid, not alcohol. Again, the high acidity inhibits bacterial growth. In both cases, humans have taken advantage of microbial fermentation to convert food into a form that is safer to consume and can be stored longer.

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3. Is all brewer’s yeast the same?

Yes and no. Brewer’s yeasts are all closely related, but there are hundreds of different strains with subtle differences that affect what conditions they prefer and what kind of beer they produce. Just as you wouldn’t select a Great Dane to be a lap dog, you wouldn’t select a lager yeast to produce ale.

The story of how brewer’s yeast came to be is complex and still unfolding. In general, there are two major kinds of brewer’s yeast — ale yeasts and lager yeasts. Ale yeasts are members of the species *Saccharomyces cerevisiae* — the same species used to make wine and bread. However, after millennia of domestication and selection for optimal performance in a particular growth environment, the strains of *S. cerevisiae* now known as baker’s yeast (used for bread) and brewer’s yeast are genetically quite different. Yeast has a lot of ways to generate genetic diversity; it can reproduce both asexually (a single cell buds off a nearly identical copy) and sexually (two yeast strains make new combinations of their genetic material, resulting in offspring with characteristics of both parents). The yeast genome is carried on 16 separate chromosomes, but yeast can tolerate quite a high degree of chromosomal variation, including carrying more than 2 copies of some or all of its chromosomes and multiple copies of large chunks of chromosomes. Yeast can also maintain additional genetic material on pieces of DNA that reproduce separately from the chromosomes. These pieces of DNA, called plasmids, can be shared between different yeast cells. What’s important about all this genetic variety is that genes carry the instructions for various life processes. When a yeast strain picks up or loses genes, it gains and loses various capabilities. Not surprisingly, brewer’s yeast is genetically enriched for many of the genes that are important for fermentation, and especially for the ability to ferment maltose. It also has extra copies of the genes that allow it to tolerate high levels of alcohol.
Ale yeasts prefer a warm temperature (18-25°C, 65-77°F) for fermentation and rise to the top of the fermentation tank when they are finished fermenting. The origin of the cold-fermenting (7-15°C, 45-60°F), or lager yeast, strain is more genetically complex. Lager yeast's scientific name is *Saccharomyces pastorianus* (to honor the great microbiologist Louis Pasteur), or *Saccharomyces carlsbergensis* (to honor Emil Christian Hansen, who first isolated the strain while working for the Carlsberg brewery in the late 1800’s). It has long been known that *S. pastorianus* was a hybrid between traditional ale yeast and another yeast strain, but it was only in 2011 that the other member of the hybrid was isolated from beech forests on the southern tip of South America. Researchers recently showed that the genome of the newly identified *Saccharomyces eubayanus* is virtually identical to the parts of the *S. pastorianus* that differ from ale yeast. Why is this important? *S. eubayanus* is what scientists call “cryotolerant,” that is, it grows well at low temperatures. For brewers in Northern Europe, this quality was important. When and where *S. eubayanus* and *S. cerevisiae* mated to form *S. pastorianus* is unknown, but cold-fermented beer began to be produced in Bavaria in the 15th century. The new style of beer spread quickly as Northern European brewers recognized the value of a strain that could ferment at cooler temperatures. The resultant clear, crisp product that came to be known as lager proved very popular. Today it accounts for the lion’s share of beer production worldwide.

Ale and lager yeasts are responsible for virtually all beer production, but there are a few styles of beer that rely on other kinds of yeast for fermentation. Of these, the lambics of Belgium, are the best-known. To make a lambic beer, the boiled wort (see below) is exposed to the open air for about a day before going into the fermentation tank. Fermentation is carried out not only by wild yeast but also by bacteria that settled on the wort while it was exposed to the air. Clearly, this leaves a great deal to chance, and true lambics can only be made around Brussels, and only during certain times of the year. In the summer, the air contains too many bacteria that make the beer taste bad. Even in its home territory, batches of lambic are usually blended to produce a more consistent final product. Using the lambic technique will make quite a different product from place to place, depending on what yeast and bacteria are found in the local atmosphere. Fortunately for those who love lambics, but don’t live in Brussels, some of the microbes specific to the area of Belgium where lambics originated have been characterized, so brewers wanting to re-create the flavor can purchase pure strains of *Brettanomyces* (the yeast genus found in Belgian lambics) and its two predominate bacterial strains: *Lactobacillus delbrükii* and *Pediococcus damnosus*. 
4. How is beer made?

Barley, hops, water, and yeast. That’s all it takes to make beer. But every step in the process is important, and most of them have a direct impact on how happy and productive the yeast will be. Because if the yeast ain’t happy, ain’t nobody happy.

**STEP 1: MALTING**

The main ingredient in beer is water, followed by grain — usually barley, sometimes wheat, and occasionally rice or corn. But in order for barley to make good beer, it has to be sprouted, which is called malting. Why? The part of the barley plant that is used in beer is the seed — which is like a miniature storage container for the baby barley plant. In addition to the plant embryo, the seed contains starch that the baby plant will feed on when it sprouts. When the seed is moistened (think spring rain), enzymes in the seed are activated that start to break down cell walls and proteins to expose the seed’s stored starch. Brewers take advantage of this process because yeast cannot feed directly on barley seeds. During the malting process, the barley seed is moistened and allowed to begin sprouting. Before the sprout breaks through the seed’s hull, the barley is roasted, or kilned (to stop the sprouting process and develop flavor). The kilning must be conducted in such a way as to maintain the seed’s enzyme activity.

**STEP 2: MASHING**

During the mashing process, the ground malt is mixed with water and heated. This provides an ideal environment for the various enzymes that were produced in the barley seed during sprouting to break down the barley starch into simpler, fermentable sugars. The enzymes are quite specific — each has a particular job to do in breaking down starch and each has a temperature at which it is most efficient. As a result, beer recipes contain detailed instructions for how long to hold the mash at particular temperatures.

**STEP 3: PREPARING THE WORT**

Now that the sugars have been released from the barley, the yellow-brown sweet liquid called the wort can be drained away from the remains of the barley seeds (spent grains). If you taste the wort now, you will find it very sweet. The sugary liquid — designed to be yeast food — also provides a highly attractive environment for the growth of any bacteria or wild yeast that might have survived the mashing process. Therefore the wort is now boiled. At the same time, hops are added. Hops are the dried flowers of the hops plant; they release a number of compounds some of which are toxic to bacteria. The same compounds also add a bitter flavor to the wort that balances out the sweetness of the barley sugars. Hops also provide oils that contribute to the characteristic aroma of many beers. Bitter herbs have been added to beer for centuries because early brewers probably recognized that the beer with added herbs was less likely to spoil. The hops are boiled with the wort for about an hour, and then the wort is filtered and cooled.
STEP 4: FINALLY! ADDING THE YEAST
At this point the yeast finally enters the brewing process, but the preceding steps have produced a nourishing broth that is ideal for yeast growth. One final step is necessary for the wort to be an ideal environment for the yeast. Yeast needs oxygen to grow and reproduce, and boiling drives most of the oxygen out of the wort; so it is important to re-aerate the wort before adding the yeast. This is usually accomplished by bubbling air or oxygen through the wort (as you would with an aquarium), although oxygenation can also be accomplished by vigorously shaking the wort. Yeast is now added (the brewing term is “pitched”) into the oxygenated wort, and the mixture goes into a fermentation tank. What happens next is a two-step process. In the presence of plentiful nutrients and oxygen, yeast reproduces rapidly. In the case of brewer’s yeast, this means making lots of new yeast cells through a process called budding.

When conditions are just right, a yeast cell can bud every 80 minutes. As the oxygen is used up, growth slows and the yeast cells switch to another kind of lifestyle — fermentation. Successful brewing requires both steps — the growth phase to increase the number of yeast cells, and the fermentation phase to convert much of the remaining sugar in the wort to alcohol and carbon dioxide. As the fermentation proceeds, available sugar declines and the alcohol concentration rises. Eventually most of the yeast stop trying to extract any more energy from the wort and enter a hibernation-like stage. Entering this stage triggers physiological changes that cause the yeast to clump together — a process called flocculation. Some strains of yeast drop to the bottom of the fermenting vessel when they flocculate, and others rise to the surface. If they rise, they can be skimmed off the top of the beer. If they drop, the beer can be carefully poured off the layer of yeast cells and other debris (called trub) that settles at the bottom of the tank.

STEP 5: SECONDARY FERMENTATION
Even after the main fermentation has ceased and most of the yeast has flocculated out of suspension, a small amount of yeast remains in the beer and continues to break down sugars and produce other compounds. This stage is called secondary fermentation, although very little actual fermentation is occurring. It is important, however, because it is during this time that the yeast metabolizes (or digests) diacetyl and acetaldehyde that have been produced during primary fermentation. The tastes imparted by these compounds — butterscotch and green apples, respectively — are considered undesirable in most beers. Depending on the type of beer, this secondary fermentation may be prolonged for weeks or even months at quite a cool temperature — about 7°C (45°F). If the secondary fermentation is going to be very lengthy, it is often recommended to decant the beer into a different vessel to get it away from the spent yeast. Yeast cells can remain dormant for a long time, but eventually they will begin to die off and the cells will burst, releasing their not-very-tasty cellular contents into the beer. After secondary fermentation, beer is often held at an even lower temperature which promotes settling of any remaining solid residues or yeast and makes the beer less cloudy.

STEP 6: BOTTLING
One last way in which yeast contributes to the quality of finished beer; it adds natural carbonation. After the beer is bottled, any remaining yeast will continue to ferment any remaining sugar, and add carbon dioxide to the beer in the bottle. Sometimes, a little more sugar and some fresh yeast is added just before bottling to ensure an appropriate amount of carbonation (a process called conditioning). Restraint is called for, though; too much additional carbon dioxide can cause bottles to explode. More commonly these days, brewers add carbon dioxide just before bottling to bring the level of carbonation up to desired levels.
How much yeast does it take to make beer?

The yeast you pitch into your wort is made up of billions of individual yeast cells. Ideally each cell is alive and ready to begin fermenting as soon as you add it to your cooled and oxygenated wort. The individual cells are far too small to see and count without a microscope, but it is important to get the number right. Imagine you were planting a field of corn. You want to plant exactly the right amount of seeds to optimize your yield: if you plant too few, you will end up with less corn and more open space for weeds to occupy. If you plant too many, the plants will crowd each other and may exhaust the nutrients in the soil, reducing the yield. Exactly the same is true for yeast: add too little and fermentation will take a long time to get started, increasing the risk that bacteria will outcompete the yeast. Add too much, and the yeast will turn quickly to fermentation without having made many new yeast cells. Since all those growing yeast cells release complex compounds like esters, the finished beer will have a less complex flavor and aroma.

Brewers use formulas to figure out how many yeast cells to add. They are slightly different depending on the type of beer being brewed, but all have the following factors: number of yeast cells per milliliter of wort per degrees Plato of the wort. Degrees Plato is a measurement of the specific gravity of the wort, which in turn is simply a measurement of how much sugar and other compounds are dissolved in the wort. For comparison’s sake, the specific gravity of water is (by definition) equal to one. The specific gravity of, say, molasses, is around 1.4. Most worts have a specific gravity of about 1.04 to 1.05 — in other words, about 4-5% higher than pure water. Pitch rates are calculated to add enough yeast to reproduce for a few days with that amount of nutrients before turning to fermentation. The fermentation, therefore, will take place with many more yeast cells than were originally added, and those new yeast cells will be young and healthy, leading to a vigorous fermentation.

Companies that sell yeast to home brewers grow it from pure cultures under standardized conditions and provide it in packets that contain the correct number of yeast cells to inoculate 5 gallons of standard wort (that’s about 100 billion yeast cells!). Buying new yeast for each batch of beer ensures that you know exactly how many cells you’re adding, and that the cells are at the right life stage and healthy. However, it is also possible to re-use — or re-pitch — yeast from batch to batch. After all, not only are most of the original yeast cells still alive, but they will have budded off several generations of new yeast cells. The risk, however, is that the yeast that is left at the end of fermentation is not exactly the same as the yeast you started with; along with young, newly budded cells, there will be dead yeast cells, cells that have already budded off so many offspring that they can no longer reproduce, and cells that have undergone various mutations. Furthermore, the yeast that was originally pitched was not genetically identical, but contained billions of individuals that each differed very slightly from each other. The genetic variants that were most successful in the particular conditions of that fermentation will be slightly more frequent in the next generation; that’s evolution at work. Over time, the character of the yeast can change substantially. Judging how much of the leftover yeast to re-pitch, and how often, is something of an art. In general, it is recommended to re-pitch no more than 5 to 10 times.
5. How else does the yeast affect the beer?

Remember, yeast is a sophisticated, living organism. In addition to fermentation, it carries out thousands of additional reactions as part of its general internal housekeeping and its interaction with the environment. During the fermentation process, yeast produces hundreds of chemical compounds that can affect the final product in many ways including flavor, appearance and stability. Even the foam is affected by chemical compounds and enzymes made by the yeast.

**FLAVOR:**

Flavor is a complex characteristic that includes taste, aroma, and mouthfeel, and it is this quality that beer drinkers are most concerned with beer. Of the thousands of other compounds produced by yeast, about twenty five to thirty are critical in giving a distinctive flavor to a given beer style. These flavor compounds include acids, aldehydes, sulfur compounds, ketones, and esters. The exact mix of these components is different in every type of beer and even from batch to batch if conditions are not carefully controlled. Yeast can also change beer’s flavor when they do not consume certain components, for example complex sugars, contributed by the wort or hops.

**Acids:** The acids in beer are not the kind that you have to worry about burning your skin — at least not in the levels present in beer, but they do contribute to the taste of the beer. The most commonly found acids in beer are citric, acetic, malic, pyruvic, and succinic acids. They generally confer sour flavors to the beer. These acids also affect the beer’s pH.

**Aldehydes:** The most common aldehyde in beer is acetaldehyde. Acetaldehyde confers a green apple taste to the beer and, as mentioned above, is considered undesirable at high levels. Levels of acetaldehyde are highest just after the start of fermentation because yeast must convert sugars into acetaldehyde before they can be converted into ethanol. As the fermentation
progresses, yeast will generally complete the process of converting acetaldehyde (and other aldehydes and ketones that might make the beer taste stale) to ethanol. Many essential yeast life processes require zinc, including the conversion of aldehydes, so brewers will add trace amounts of the metal if the wort has a low zinc level in part to ensure that acetaldehyde levels do not become too high. Brewers have another reason to make sure acetaldehyde is at acceptable levels in the beer — acetaldehyde has been implicated as one component of beer that causes hangovers!

**Sulfur compounds:** There are several sulfur compounds that can be introduced into beer by the yeast. Like the acids and aldehydes small amounts of many sulfur compounds are acceptable or even desirable in beer, but at higher levels, can be off-putting. Hydrogen sulfide, for example can improve the taste of pale ale at low levels, but in greater quantities can confer the flavor of rotten eggs. Dimethyl sulfide is a similar story, as low levels are an expected part of the taste of Pilsner-style beers, but higher levels can leave beer tasting like cabbage or corn.

**Ketones:** Ketones can show up in both beer’s aroma and taste. Diacetyl, one common ketone, can confer a butterscotch flavor to beer, however too much diacetyl can result in an off-flavor. Another ketone, with the chemical name 2,3-pentanedione, can also give beer a buttery or stale milk flavor.

**Esters:** Humans are thought to be able to distinguish about 10,000 different chemical compounds by their aroma, so many of the compounds produced by, or not digested by, yeast could contribute to a beer’s aroma. However, one particular family of chemical compounds, the esters, has a disproportionate effect on the overall aroma of beer.

Many fruits produce high levels of distinctive esters. The easily identified smells of oranges, pears, lavender and cinnamon all come from esters. Small amounts of such esters may be desirable in a beer. Some others, like the esters that give glue and nail polish remover their distinctive smells would not be so welcome. Yeast produces as many as 90 different esters, and while they are not identical to those produced by plants or herbs, they can have a powerful effect on the beer’s aroma. For example, yeast can produce the esters isoamyl acetate, which smells like banana, and phenylethyl acetate, which smells like roses.

**MOUTHFEEL:**
Mouthfeel, the sensation of the beer coming in contact with the mouth, is the final component of flavor. Carbon dioxide is a major component of the mouthfeel, giving the tingly feeling associated with beer and other carbonated beverages like soft drinks. Both the size and numbers of carbon dioxide bubbles affect the mouthfeel (imagine the difference in carbonation between a dark stout beer and champagne, for example). Sugars can also affect the mouthfeel of the beer. *S. cerevisiae* is very good at metabolizing maltose, but cannot consume certain other types of larger sugars. These sugars remain in the beer. Different amounts and types of residual sugars can give the beer a fuller or thinner body and are responsible for much of the calorific content of the beer.

**FOAM:**
One final characteristic of beer that is affected by yeast is the foam, or head, that forms on the top of a glass of beer. The head on beer is deemed important by most drinkers and can “make or break” its acceptability. Yeast can have positive and negative effects on beer foam. Clearly the carbon dioxide produced by the yeast is what is inside the bubbles, but the bubbles themselves are stabilized by proteins from the grains and the bitter substances from the hops. Yeast can seriously damage the foam in two ways. If the initial fermentation is too vigorous, too many of these foam-stabilizing proteins may be lost in the head that forms as the carbon dioxide rises. Second, if yeast deteriorates by becoming stressed (for example, because the alcohol level gets too high, or the yeast gets too old) then it can start to secrete enzymes called proteases that chew up the foam proteins.
While yeast is essential to brewing and affects the final product in many ways, many other factors affect the flavor, color and stability of beer. What kind of grain is used, the mashing characteristics, the variety and amount of hops, other flavoring components, the length and temperature of fermentation and many other factors also have important effects. Hopefully, you now see that part of the reason these factors make a difference is because they affect yeast health and activity — but they also have impacts that are not related to their interaction with yeast.

Also, yeast is not the only microbe that affects beer, for good or ill. Some of these other microbial effects are quite interesting. For example, barley can be infected by a fungus called *Fusarium* that produces proteins that survive the entire malting, mashing, and fermentation process. Their presence is revealed only when the beer bottle is opened; the beer will foam over, or “gush”, upon opening when these proteins are present.

As discussed above, beer’s high alcohol and low oxygen content, plus the antibacterial compounds produced by hops, tend to inhibit the growth of most bacteria. Bacteria, however, are extraordinarily adaptable, and given time and opportunity, many of them are able to evolve in ways that allow them to grow under once-hostile conditions. For example, just as many human pathogens have developed resistance to antibiotics, there are bacteria that have developed resistance to antimicrobial compounds from hops. These bacteria are not human pathogens — beer that contains them will not make you sick — but they do produce compounds that make the beer taste bad. Proper sanitation procedures are crucial in commercial breweries and for home brewers; once a ‘beer spoiler’ organism finds its way into a brewery, it can be practically impossible to eliminate.