The most important process in fermentation is the conversion of sugars to ethanol and CO₂. However, a great many other reactions occur during brewery fermentations with far reaching impacts on the flavour of beer. It is difficult to separate reactions occurring in fermentation from those occurring during maturation, so it is best to consider it as a continuous process. For purposes of our discussion we can divide fermentation flavour characteristics into two categories:

1) Green beer flavour substances: diacetyl, aldehydes, sulphur compounds. These are produced early in fermentations, giving beer an immature, unripe and unbalanced taste and can be biochemically removed by yeast during maturation.

2) Mature beer flavour substances: Higher alcohols, esters. These are responsible for the complex
aroma of beer and once formed cannot be removed by yeast.

Although many different types of flavour compounds are developed during fermentation, it is only those with a sufficiently low flavor threshold that will affect the character of the beer. The compounds that have the greatest affect on the aroma of a beer are those with high volatility, which will allow them to escape from the beer when served. We will examine the biochemical pathways responsible for the formation of many of the most important beer flavour compounds, including:

- Esters (fruity characters)
- Higher alcohols (winey characters)
- Vicinal Diketones (buttery characters)
- Aldehydes (oxidation characters)
- Sulphur Compounds (rotten egg and vegetal characters)
- Organic acids (staling compounds)

Many of the reactions producing flavour compounds are influenced directly by the rate of fermentation, which is controlled by many other factors, including:

1) Wort properties:
   - hot / cold break removal
   - wort aeration level
   - wort composition
2) Fermentation temperature (increase in temperature leads to faster fermentation)
3) Pitching rate (higher pitch rate leads to faster fermentation)
4) Motion (greater movement equals faster fermentation)
5) Yeast strain (fermentation rates are strain dependent)
6) CO₂ Pressure (CO₂ saturation retards fermentation)

Growth vs. Metabolism

Yeast growth describes both the growth of individual cells and the budding of cells leading to a growth in total population. Yeast metabolism is the breakdown (catabolic) and synthesis (anabolic) of various compounds that may be used growth or maintenance of the yeast.

The flavors generated during fermentation are generally not required products for the yeast. In many cases they are waste products or intermediates of the pathways used by the cell to facilitate metabolism and growth. Often yeast cells that are stressed or metabolizing quickly will make more of these by-products. In general a healthy yeast cell that is allowed to grow gradually will tend to produce less by-products.
The rate of yeast growth and yeast metabolism both affect the generation of flavor compounds during fermentation, but they are not linked directly. Even though a yeast cell that is growing quickly will also be metabolizing at a high rate, the products of these reactions will be quite different than a yeast cell with slow growth and high metabolism. For most microbreweries the most important factor governing yeast growth is the pitching rate.

After pitching the yeast will grow and divide until their population reaches a sufficient level. The amount of growth required depends more on the initial concentration since the final population generally shows little variation. So a low pitch rate will result in greater growth and a high pitch rate will result in lower growth.

There are often situations where the yeast cell will metabolize quickly, but not grow proportionally. An example might be a high gravity wort (with lots of sugars and nutrients) with a high pitch rate (leading to low growth). The products of this fermentation would be considerable different from a fermentation with high growth and high metabolism. This points out why it is important to think of growth and metabolism as related, but not directly linked.

**Nutrient Uptake**

At the start of fermentation the yeast cell is functioning on stored energy in the form of glycogen and begins to absorb oxygen from the wort. It uses this oxygen, not to respire, but to produce unsaturated fats, lipids and sterols that it requires to build membrane material for future yeast cells.

**Sugar Uptake**

Yeast also begin the preferential uptake of simple sugars to provide rapid energy for growth. Although the yeast cell can ferment on several different types of sugars, some are easier to assimilate, and therefore are taken up first. The sequence of uptake is:

1) Glucose
2) Fructose
3) Maltose
4) Maltotriose
Amino Acid Uptake

Yeast also begin the preferential uptake of amino acids from the wort to provide proteins for growth. The amino acids can be divided into four groups based on their rate of uptake.

### Amino Acid Uptake Classifications

<table>
<thead>
<tr>
<th>Group A</th>
<th>Group B</th>
<th>Group C</th>
<th>Group D</th>
</tr>
</thead>
<tbody>
<tr>
<td>glutamate</td>
<td>histidine</td>
<td>glycine</td>
<td>proline</td>
</tr>
<tr>
<td>aspartate</td>
<td>valine</td>
<td>phenylalanine</td>
<td></td>
</tr>
<tr>
<td>asparagine</td>
<td>methionine</td>
<td>tyrosine</td>
<td></td>
</tr>
<tr>
<td>glutamine</td>
<td>leucine</td>
<td>tryptophan</td>
<td></td>
</tr>
<tr>
<td>serine</td>
<td>isoleucine</td>
<td>alanine</td>
<td></td>
</tr>
<tr>
<td>threonine</td>
<td>cysteine</td>
<td></td>
<td></td>
</tr>
<tr>
<td>lysine</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>arginine</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

- **Group A**: Absorbed immediately and consumed in first 20 hours
- **Group B**: Absorbed gradually during the whole fermentation
- **Group C**: Absorbed after 20 hour lag phase
- **Group D**: Not absorbed

Ammonia can be absorbed by the cell for nitrogen use, and it falls into group C in terms of preference. Asparagine and Glutamine both have NH₂ groups on their side chains, giving them twice the nitrogen content of other amino acids. Also note that valine, leucine and isoleucine share an active uptake system.

The preference for certain amino acids is based on ease of uptake. Since the yeast need a full range of amino acids to be present for protein production and growth, it must synthesize amino acids internally. By-products of the synthesis of amino acids are responsible for the majority of flavor compounds found in beer.
**Vicinal Diketones**

Vicinal diketones are highly volatile green beer characteristics, giving a buttery, butterscotch, caramel, toffee, honey or rancid butter character to beer. The naming of this class of compounds gives insight to their structure:

- **Vicinal** = adjacent
- **Di** = two
- **Ketone** = double bond oxygen inside the molecule

The two most common vicinal diketones are shown below:

Diacetyl is responsible for a majority of the buttery characteristic of a beer, and has a much lower flavor threshold than 2,3 pentanedione.

<table>
<thead>
<tr>
<th>Flavour Threshold of Diacetyl</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.04ppm in U.S. lagers</td>
</tr>
<tr>
<td>0.08ppm in lighter ales</td>
</tr>
<tr>
<td>0.1ppm in stronger beers</td>
</tr>
</tbody>
</table>

Formation of Vicinal Diketones

Vicinal diketones are by-products of the synthesis of valine, leucine and isoleucine. Using diacetyl as the example, we can see that during primary fermentation the yeast will produce α-acetolactate from pyruvate excrete α-acetolactate (a precursor to valine or leucine production). As with many intermediates, the yeast cell produces extra α-acetolactate to ensure that there are no delays in the pathway. Once outside of the cell, the α-acetolactate is oxidized and decarboxylated (nonenzymatically) to produce diacetyl. It is important to note that oxygen is not required for the oxidation of α-acetolactate, and the presence of calcium (Ca$^{2+}$) or metals such as zinc (Zn$^{2+}$) or iron (Fe$^{3+}$) will readily catalyze this reaction. This reaction is also favored in lower pH and higher temperature conditions.

Once the diacetyl has been formed it will remain outside of the cell until late in the fermentation. Given the chance, the yeast will absorb the diacetyl and reduce it to acetoin (that has a slight musty character) and then finally to 2,3 butanediol (a higher alcohol with little aromatic character). The yeast cell carries out this reduction to use up the NADH (“reducing power”) produced earlier in the fermentation, but can only do this if it is still healthy and active.
Diketone content is seen by many brewers as the criterion for judging the state of maturation of a beer. Many large commercial breweries measure the diacetyl content of maturing beer regularly and begin finishing processes once the level has dropped sufficiently.
CONTROL OF DIACETYL

Factors leading to a decrease in diacetyl
- Presence of live active yeast during maturation.
- Removal is accelerated at higher temperatures (“diacetyl rest”)
- Krausening. Addition of actively growing yeast encourages rapid removal.

Factors leading to an increase in diacetyl
- Lack of aeration at start of fermentation. Tired or stressed yeast with rigid membranes cannot quickly absorb the diketones.
- Uptake of oxygen late in fermentation. α-acetolactate may still be present late in maturation, and diacetyl can still be formed if oxygen is present. This has implications with bottle conditioned beers.

To facilitate the removal of diacetyl the brewer must first ensure that it is formed rapidly and consistently during the primary fermentation. A rapid fermentation (i.e. higher temperature), low pH and sufficient Ca$^{2+}$ or Zn$^{2+}$ will aid in the formation of diacetyl. Subsequent removal of diacetyl is facilitated by contact with live active yeast during maturation. Removal of yeast before the end of maturation (due to fining, filtration or cooling) will leave residual diacetyl in the finished beer. If the yeast are unhealthy (due to poor aeration at the beginning of fermentation or high alcohol contents in green beer) they may have rigid membranes (resulting in poor uptake of diacetyl) or insufficient reducing power (to reduce diacetyl to 2,3 butanediol). Petite mutant yeasts, also known as respiratory deficient yeast also tend to leave vicinal diketones in the beer because they lack reducing power at the end of the fermentation (even though they tend to stay in solution due to poor flocculation qualities).
**Organic Acids and Higher Alcohols**

Yeast produce many of the amino acids needed for growth from intermediates in the degradation of sugars, others are produced from other more easily absorbed amino acids using transamination reactions.

This leaves the original amino acid without an amino group and now is an oxo acid, (unsaturated fatty acid or an α-keto acid) these can be converted into an aldehyde by the loss of a CO\textsubscript{2} molecule, which is then reduced to a higher alcohol. The formation of higher alcohols reduces the potential toxicity of the
The presence of an amino acid in wort may inhibit the formation of the corresponding higher alcohol. The most common oxo-acids. The presence of an amino acid in wort may inhibit the formation of the corresponding higher alcohol. The most common

The faster yeast grow the more rapid is the production of amino acids and the more oxo-acids and hence higher alcohols are produced. Since the oxo-acid pool contents are also derived from carbohydrate metabolism some higher alcohol production come directly from carbohydrate metabolism.

Several different higher alcohols can also be produced by the reduction of vicinal diketones. Diacetyl can be reduced to isobutanol and isoamyl alcohol, while 2,3 pentanedione can form propanol, bunanol and amyl alcohol.

Around 80% of the higher alcohols are formed during primary fermentation, and unlike vicinal diketones or aldehydes they will not be removed during maturation.
# Flavour Biochemistry

## Alcohols and their Corresponding Aldehydes, Oxo-acids and Amino Acids

<table>
<thead>
<tr>
<th>Alcohols</th>
<th>Aldehydes</th>
<th>Oxo-acids</th>
<th>Amino acids</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ethanol</td>
<td>Acetaldehyde</td>
<td>Pyruvic acid</td>
<td>Alanine</td>
</tr>
<tr>
<td>Glycol</td>
<td>Glyoxal</td>
<td>Hydroxypyruvic acid</td>
<td>Serine</td>
</tr>
<tr>
<td>Propanol</td>
<td>Propionaldehyde</td>
<td>a-Oxobutyric acid</td>
<td>a-Aminobutyric</td>
</tr>
<tr>
<td>Isopropanol</td>
<td>Isobutyraldehyde</td>
<td>a-Oxoisovaleric acid</td>
<td>Valine</td>
</tr>
<tr>
<td>Isobutanol</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sec-butanol</td>
<td>Isovaleraldehyde</td>
<td>a-Oxoisocaproic acid</td>
<td>Leucine</td>
</tr>
<tr>
<td>Tert-butanol</td>
<td>2-Methylbutanal</td>
<td>a-Oxo- b-methyl valeric acid</td>
<td>Isoleucine</td>
</tr>
<tr>
<td>Isoamyl alcohol</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2-Methylbutanol</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hexanol</td>
<td>Hexanal</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Heptanol</td>
<td>Heptanal</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Phenethyl alcohol</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tyrosol</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tryptophol</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Hough, Briggs, Stevens and Young, 1982

## Higher Alcohols and Organic Acids

<table>
<thead>
<tr>
<th>Alcohols</th>
<th>Found in beer</th>
<th>Threshold</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>2-methyl propanol</td>
<td>5-20ppm</td>
<td>10ppm</td>
<td>alcohol</td>
</tr>
<tr>
<td>2-methyl butanol</td>
<td>10-20</td>
<td>10</td>
<td>alcohol, solvent</td>
</tr>
<tr>
<td>Isoamyl alcohol</td>
<td>35-70</td>
<td>10</td>
<td>alcohol, banana</td>
</tr>
<tr>
<td>butyric acid</td>
<td>0.2-0.6</td>
<td>1.2-2.2</td>
<td>cheesy, rancid</td>
</tr>
<tr>
<td>isovaleric acid</td>
<td>0.5-1.2</td>
<td>1.5-1.6</td>
<td>cheesy, old hops</td>
</tr>
<tr>
<td>octanoic acid</td>
<td>3-10</td>
<td>10-13</td>
<td>oily</td>
</tr>
<tr>
<td>decanoic acid</td>
<td>0.8</td>
<td>10</td>
<td>rancid</td>
</tr>
<tr>
<td>dodecanoic acid</td>
<td>0.1-0.5</td>
<td>6</td>
<td>soapy</td>
</tr>
</tbody>
</table>
Factors Increasing Higher Alcohols in Beer

- Increasing the fermentation temperature
- good motion in the fermenter
- intensive, early wort aeration
- repeated wort additions
- higher wort gravities (above 13 % P.)
- reduced wort amino acids

Factors Decreasing Higher Alcohols in Beer

- increasing the pitching rate
- colder fermentation temperature
- avoiding oxygen entry after pitching
- having sufficient amino acids present in the wort
- having top pressure on the early phase of fermentation

Formation of Higher Alcohols

ALDEHYDES

Aldehydes are similar to ketones but they contain a carbon with a hydrogen and a double bonded oxygen in their structure. Complex aldehydes are found in beer from the pathways that lead to higher alcohols, but the most common aldehyde in beer is acetaldehyde and this is a normal intermediate in the fermentation pathway.

Acetaldehyde is excreted by the cell in the first 3 days of fermentation and is a “green” beer flavour. Like vicinal diketones acetaldehyde can be removed by healthy yeast during the maturation phase. Acetaldehyde has a flavour threshold of around 15 ppm in beer.

Acetaldehyde formation is generally favored by conditions of high metabolism coupled with low growth. Zinc appears to be a cofactor in the conversion of acetaldehyde to ethanol, so trace amounts of this metal are required for conversion. Carbon dioxide pressure can lead to toxic levels of the gas in yeast cells, which changes their permeability and affects their ability to convert acetaldehyde to ethanol. Early wort aeration will result in healthy active yeast capable of converting acetaldehyde to ethanol.

STALE FLAVORS

Recent research into the flavor stability of beer has focused on the oxidation of fatty acids to aldehydes which are responsible for stale flavors.

FACTORS AFFECTING ACETALDEHYDE PRODUCTION

Acetaldehyde formation is increased by:
- Rapid fermentation
- Higher fermentation temperatures
- Increased pitching rate
- Insufficient wort aeration
- Pressure early in fermentation
- Sufficient Zn$^{2+}$ ions

Removal of aldehydes is favoured by:
- All measures that promote vigorous maturation including:
  - increased yeast concentration
  - viable yeast
  - good contact of yeast with maturing beer
  - warmer maturation
- Sufficient wort aeration
Lipids (particularly unsaturated fatty acids and sterols) are formed early in fermentation to provide material for membrane production. As the need for lipid production ends the intermediates still being produced may be shunted off to form esters. Esters are a combination of alcohols and fatty acids, the most common of which is ethyl acetate.

Under fermentation conditions the simple combination of alcohols and fatty acids will occur very slowly if at all. The reaction is catalysed CoEnzymeA, which will attach to the fatty acid and "activate" it. CoEnzymeA (sometimes shown as CoASH to denote the open sulfur group) carries small fatty acids active in pathways throughout the cell. When attached to a fatty acid the complex is known as Acyl CoA. During fermentation acetate forms Acetyl CoA which is involved in many reactions. Since Acetyl CoA is the most common acid and ethanol is the most common alcohol, the most common ester produced during fermentation is ethyl acetate.
Lipid Granule and Membrane Production

- Unsaturated Fats and Phospholipids
- Saturated Fats and Phospholipids
- Sterols

Unsaturated Acyl CoA → O₂ → Saturated Acyl CoA → Squalene

Acetyl CoA

- Oxo Acids
- Pyruvate
- Transamination Nitrogen Metabolism
- Ethanol and Higher Alcohols

Acyl CoAs

Esters

Cell Membrane

- Amino Acids
- Fermentable Carbohydrate
Beer contains around 60 different esters but only a few are important to beer flavour and aroma. To understand the factors that affect ester formation we must look at the compounds that are the key precursors in ester formation: Acetyl CoA and higher alcohols. Acetyl CoA is required by the cell for the production of fatty acids, phospholipids and sterols, key components in cell membranes. As we have already seen, high yeast metabolism will lead to more higher alcohols, as by-products from the transamination of amino acids. High yeast metabolism coupled with relatively slow growth (i.e. high gravity worts) will also lead to an excess of Acetyl CoA, as the yeast cell does not have high requirements for fatty acids and phospholipids, leading to a bottleneck in the pathway that results in Acetyl/Acyl CoA combining with higher alcohols to form esters. It is important to note that proper aeration of the wort, especially several hours after the start of fermentation, will result in lower ester production as more Acetyl/Acyl CoA is shunted off for the production of unsaturated fatty acids and sterols.

As long as lipids are being formed, for membrane production, ester production is inhibited, so it is generally later in the primary fermentation esters develop. It is advantageous for yeast to form esters since it provides a method of removing some toxic long chain fatty acids from the cell, and also allows the cell to regenerate CoEnzyme A to catalyse other reactions.

High gravity brewing above 18°P causes an increase in ester production, which causes flavour problems with subsequent dilution. This is probably due to the decreased solubility of oxygen in stronger worts and hence proportionally less yeast growth. This can be helped by introducing more oxygen to the fermenting wort to encourage more yeast growth.

In large cylindroconical fermenter fewer esters are formed due to motion, and at the same time higher pressure due to the height is also producing fewer.

### Factors Affecting Ester Formation

#### Ester production is increased by
- Increasing the gravity above 18% P.
- Increasing the attenuation limit
- Restricting wort aeration
- Restricting yeast growth
- Changing fermentation temperature (see below)
- Decreased motion during fermentation

#### Ester production is decreased by
- Lower gravity
- Increased wort aeration
- Decreased attenuation limit
- Changing fermentation temperature (see below)
- Increased pressure during primary fermentation
- Underpitching
### Ester and Fatty Acid Formation

**Simplified Ester and Fatty Acid Formation**

Nordstrom, K., Svensk Keminsk Tidskrift, 1964, 76, 510

<table>
<thead>
<tr>
<th>Ester</th>
<th>Found in Beer</th>
<th>Threshold</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ethyl acetate</td>
<td>5-30</td>
<td>25-30</td>
<td>fruity, solventlike</td>
</tr>
<tr>
<td>Isobutyl acetate</td>
<td>0.1</td>
<td>0.4</td>
<td>fruity, banana</td>
</tr>
<tr>
<td>Isoamyl acetate</td>
<td>0.5-2.5</td>
<td>1.0</td>
<td>fruity, banana</td>
</tr>
<tr>
<td>ethyl butyrate</td>
<td>0.3</td>
<td>0.4</td>
<td>apple</td>
</tr>
<tr>
<td>ethyl hexanoate</td>
<td>0.1-0.3</td>
<td>0.12</td>
<td>apple, fruity</td>
</tr>
<tr>
<td>ethyl lactate</td>
<td>0.1-0.5</td>
<td>250</td>
<td>strawberry</td>
</tr>
</tbody>
</table>
Influence of Temperature on Ester Formation

The researchers and the literature are divided on the issue of ester formation and the relationship to temperature. It would seem that increasing the fermentation temperature will increase the rate of yeast growth and decrease the availability of acetyl CoA for ester formation, but experiments have frequently shown that esters are actually increased at higher fermentation temperatures. One experiment showed that changing the fermentation temperature from 15°C up to 25°C increased the measured esters by 75%. There is also ample research that shows that yeast will produce more total esters at lower temperatures, leading one to believe that there is a comfortable middle ground for low ester production. There are several theories that attempt to explain this paradox.

One possible explanation is that higher fermentation temperatures causes the level of higher alcohols to increase and some researchers suggest that the rate of formation of esters is more closely linked to alcohol concentrations than acetyl CoA concentration.

Between the 1960’s and the early 1980’s research focused on linking ester formation to acyl CoA flow within the cell. The discovery of an enzyme called alcohol acetyl transferase (AAT) that catalyses the formation of ethyl acetate from acetyl CoA and ethanol, has lead to theories that other esters are produced by other specific enzymes. This means that it is possible that the reaction by which acids and alcohols combine is enzyme dependant and therefore is also temperature dependant. The theory that there are many specific enzyme systems involved, with substrate and feedback inhibitions in operation, may help explain why certain yeast will tend to produce more of one particular ester.

In addition to AAT, an esterase enzyme (that hydrolyses the ester bond) has been detected and isolated and that has no requirement for CoEnzyme A. This is present to varying degrees in different yeast strains and may help explain strain specificity of total ester formation in yeast (a yeast lacking the esterase will leave more esters in the beer). Another esterase isolated from yeast has the ability to produce simple esters from more complex esters which may explain early laboratory tests that paradoxically showed an increase of some measured esters with an increase in the esterase.

Research in the early 1980’s started to focus on the cell membrane in order to explain temperature dependency. One theory is that the fluidity of the membrane increases with higher temperature, as does the membrane’s porosity, allowing a greater release of esters. Another answer may lie in the fact that complex esters of higher alcohols are present in very small amounts but have very low flavour thresholds, compared to the most common (and simple) ester; ethyl acetate. So even though a low temperature would result in high ester (mainly ethyl acetate) concentrations, the complex esters formed at higher temperatures would have a greater flavor impact due to their lower flavor threshold.
Sulphur Compounds

Yeast metabolism results in the formation of sulphur compounds. Yeast require sulphur for amino acid production, protein structure, and CoEnzymeA formation. Sulphate ions are actively taken up by yeast once the supply of sulphur containing amino acids is exhausted. Once the need for those certain amino acids is met then a feedback inhibition causes intermediates to still be produced and excreted from the cell in the form of H$_2$S and bisulfite ions.

If the cell has enough methionine it will convert some of it to S adenosyl methionine which has the ability to block the pathway during the sulphur producing steps. If the cell also has enough isoleucine, then threonine builds up in the cell and causes homoserine production to cease. Homoserine is a co-factor in the methionine pathway, so if the cell still needs methionine, but has enough isoleucine then the methionine pathway will continue to produce sulphur, causing the excretion of H$_2$S and HOSO$_2$ from the cell.
Hydrogen Sulphide is very volatile and is removed with carbon dioxide during fermentation, and is dependant on increasing temperature and pressure. Sulphur dioxide can combine with acetaldehyde to form a compound that survives packaging. If this comes into contact with air in the package it can oxidize back to sulphate and acetaldehyde, which in turn reacts with a higher alcohol to produce trans-2-nonenal which is responsible for the cardboard taste in stale beer.

Mercaptans are thioalcohols where the -OH group is replaced with an -SH group. They have very low flavour thresholds. They are responsible for the skunky aroma in beer but can be oxidised to compounds with higher taste thresholds.

DMS cannot be removed by yeast but more can be formed by the reduction of DMSO. Some is removed with CO$_2$ during primary fermentation.

**PH**

pH falls during fermentation from 5.3 to around 3.9-4.4.

This is due to:

- Formation of organic acids
- Absorption of phosphate ions
- Yeast uptake of ammonia ions
- Yeast uptake of potassium ions which leads to the release of hydrogen ions
SUMMARY

Regardless of the style of beer that you wish to produce, the aroma compounds produced during fermentation should be under your control. In particular you should control the levels of sulphur, vicinal diketones and aldehydes formed in your beers (of course, the acceptable levels of these products are all style dependent).

Of the other main flavor contributions from yeast ester content is influenced primarily by wort qualities (i.e. aeration, gravity, amino acids, fatty acids, etc..) while higher alcohol content is influenced primarily by fermentation conditions (temperature, motion etc..)