In S. cerevisiae, there are five genes that encode alcohol dehydrogenases involved in ethanol metabolism, ADH1 to ADH5. Four of these enzymes, Adh1p, Adh3p, Adh4p, and Adh5p, reduce acetaldehyde to ethanol during glucose fermentation, while Adh2p catalyzes the reverse reaction of oxidizing ethanol to acetaldehyde.The five ethanol dehydrogenasesas well as the bifunctional enzyme Sfa1p are also involved in the production of fusel alcohols during fermentation. Fusel alcohols are end products of amino acid catabolismvia the Ehrlich pathway and contribute to the flavor and aroma of yeast-fermented foods and beverages. They may also have physiological roles. For example, exposing cells to isoamyl alcohol, derived from catabolism of leucine, stimulates filamentous growth. Similarly, other fusel alcohols also stimulate filamentous growth in S. cerevisiae and biofilm formation in the pathogens Candida albicans and Candida dubliniensis.Based on sequence, Adh4p is most closely related to a bacterial iron-activated alcohol dehydrogenase, but experimental evidence demonstrates that Adh4p activity is activated by zinc like the other S. cerevisiae ADH proteins. However, unlike Adh1p, Adh2p, and Adh3p, which are thought to function as a tetramers, Adh4p is a dimeric protein. Adh4p requires zinc to function but depleting zinc from the media has been shown to induce ADH4 transcription. ADH4 expression is also upregulated by lithium, a compound that is toxic to yeast cells grown in galactose, and downregulated by DMSO. Spontaneous chromosomal amplifications of ADH4 are able to rescue null mutations in the major isozyme ADH1. While ADH4 is often expressed at only low levels in laboratory strains, it is often highly expressed in brewing strains.