Glycosides

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Glycosides have been identified in almost every type of plant tissue including leaves, roots, stems, and reproductive organs (i.e., flowering and fruiting bodies). The direct role of glycosides in plants is still uncertain, but it is hypothesized that glycosides were a part of the "chemodiversity" necessary for plants to survive. The addition of sugar moieties onto hydrophobic aglycones changes the overall polarity and water solubility of the aglycone. The increased polarity of the glycoside allows for detoxification, storage, and transport within the plant.

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1. Introduction

Through their association with aroma molecule aglycones, glycosides contribute to the aroma profile of fermented beverages such as wine and beer. Several cultivars of *Vitis vinifera* and *Humulus lupulus* have extensive glycosylation patterns that allow for the accumulation of glycosides in the plant tissues that can be released in their respective beverage products [1][2]. *V. vinifera* berries and *H. lupulus* hop cones contain their own unique glycotransferases within the VvGT and HlUGT protein families [3][4][5][6]. Glycosylation patterns and the role of glycosylated compounds on the sensory properties of beverages made with *V. vinifera* berries have been investigated over the last few decades, while research into *H. lupulus* glycosides and their effects on beer aroma and flavor is an emerging field [7][2][8]. The extent that glycosides affect wine aroma is still being investigated, but there is evidence that glycosides act as a reservoir for aroma compounds as they are hydrolyzed by enzymes or by acid-catalysis mechanisms during the fermentation and ageing process [9][10][11][12].

Grapes and hops have been found to contain several classes of volatile molecule aglycones that include: monoterpene alcohols, monoterpene polyols, norisoprenoids, sesquiterpenoids (not reported in hops), aliphatic alcohols, and volatile phenols [13][14][15][16]. A large breadth of research on aroma glycosides in plant materials has largely focused on grapes. There have been numerous studies on the impacts of external factors (i.e., growing and harvest year, ripening events, and vineyard practices) on grape glycosides [6][17][18][19][20]. For example, vineyard practices such as leaf removal as a part of canopy management have shown to increase the abundances of aroma glycosides in Riesling and Chardonnay varieties [19][20]. In addition to endogenous grape metabolites, it is also known that grapes can take in exogenous volatiles, such as volatile phenols produced during wildfires, and convert them to glycosides within the berry [21][22][23].

The extent of investigations into the glycoside composition of hop cones has focused largely on monoterpene alcohols, compounds often seen as driving factors for the aroma of several hop varieties, and norisoprenoids, such as β-damascenone [2][24][25][26]. However, less information into the development of these glycosides in hops is known, when compared to grapes, although it does appear that external factors such as soil, climate, and agricultural practices can influence glycoside abundances in hop plant materials [16]. It is possible that hops may undergo similar exogenous volatile uptake and glycosylation as grapes and other plants do, but future studies will be needed to investigate these ideas.

While there are several different aglycone classes found in grape and hops glycosides, the glycosylation pattern of glycosides follows specific patterns. In general, the first sugar bound to an aglycone by a UGT enzyme is a glucopyranose [7][4][27][28]. It was generally believed that a glucopyranose sugar was always the primary sugar bound to the aglycone; however, recent tentative identification of sesquiterpene glycosides in Muscat of Alexandria grapes and smoke taint glycosides in Cabernet Sauvignon grapes has shown that it is possible for non-glucosyl sugars to be bound directly to the aglycone [14][29]. Within the glycosylation process, up to three sugars in the glycone have been reported for grapes [18]. Although, there has not been full characterization of the glycone content of hop glycosides, evidence from hydrolysis studies suggests that hop glycosides may have one or two sugars in the glycone [2]. The potential sugars that may be found in the glycone are reported as glucopyranose, apiofuranose, xylopyranose, arabinofuranose, and rhamnopyranose sugars, in addition to malonylated glucosides [7][5][18][30][31]. The release of bound aglycones through enzyme hydrolysis is largely dependent on the sugars present in the glycoside, since specific enzymes are needed to cleave off each terminal sugar before the aglycone is released [7][30][31][32]. Some of these enzymes may not be present during winemaking or brewing, leaving glycosides with specific sugars intact [33][34]. Further discussion of these hydrolysis reactions in winemaking and brewing is included below.

2. Glycosides during Winemaking and Brewing

Both winemaking and brewing processes have several production steps that may influence the glycosidic profile in the finished beverage. Within this section, winemaking and brewing processes are discussed in separate sections with emphasis on the process itself in regard to glycosides. Microbial considerations for the winemaking and brewing sections are limited to *Saccharomyces* yeast as they are used for the majority of wine and beer fermentations. The production of wine and beer products with non-*Saccharomyces* microbes has been organized into its own section due to the large scope of yeast and bacteria that can be introduced into grape juice or wort systems. Outlines of winemaking and brewing processes with respect to glycoside hydrolysis may be found in Table 1.

Table 1. Hydrolytic outline of the winemaking process and the brewing process.

Winemaking Stage	Primary Hydrolysis	References
Destemming and crushing	Endogenous grape enzymes	[31][35][36][37][38][39]

Winemaking Stage	Primary Hydrolysis	References
Fermentation—*Saccharomyces*	Exogenous yeast enzymes	[29][30][31][32][40][41][42][43][44][45][46][47][48][49][50]
Fermentation—non-*Saccharomyces* yeast and/or mixed fermentations	Exogenous yeast enzymes	[51][52][53][54][55]
Malolactic fermentation	Exogenous bacterial enzymes	[52][53][56][57][58][59][60][61][62][63][64][65][66]
Racking, bottling, and storage	Spontaneous Acid Hydrolysis	[34][67][68]
Brewing Stage	**Primary Hydrolysis**	**References**
Mashing	N/A	N/A
Lautering and sparging	N/A	N/A
Boiling and whirlpool	Acid	[2][26]
Fermentation—*Saccharomyces*	Exogenous yeast enzymes	[51][69][70]
Fermentation—non-*Saccharomyces* yeast and/or mixed fermentations	Exogenous yeast or bacterial enzymes	[51][54]
Dry hopping and hop creep	Exogenous hops enzymes	[71][72]
Storage	Spontaneous Acid Hydrolysis	[25]

3. Conclusions

Glycosylated aroma molecules are common metabolites found in the plant families *Vitis vinifera* and *Humulus lupulus*. The glycosylated molecules are of increasing interest due to their connection with free volatile molecules in wine and beer. Comparatively, there is a rich history of knowledge concerning the presence of glycosides and their respective aromas in grapes and wine, while the field of research is starting to develop for hops and beer. A large focus of winemaking has shown that microbial activity during the fermentation process is a key event in the hydrolysis of glycosides. Although much work has shown that microbial activity can trigger the hydrolytic release of glycosides from wine, there is still more work needed to understand how to control the process. Brewing is a complex process that offers several opportunities for hydrolysis such as the boiling and fermentation stages; however, the impact of glycosides from hops is frequently brought into question due to their low abundances. The development of liquid chromatography mass spectrometry methods has allowed for more in-depth and faster analysis of intact glycosides in both plant materials and fermented beverages when compared to traditional hydrolysis methods. More development is still needed for these methods as it can be difficult to distinguish isomeric aroma glycosides from one another through mass spectrometric methods alone.

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