Chapter 2
Introduction to Plant Biomolecules and Cellular Metabolism

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Chapter Highlights

- Lipids, carbohydrates, and proteins represent the major starting materials for the production of various bioproducts in plants.
- These organic compounds contain carbon atoms that share electrons with hydrogen and other elements.
- Lipids comprise fatty acids and their derivatives and tend to be either hydrophobic or amphipathic in nature.
- Carbohydrates include sugars and sugar polymers and are made up of carbon, hydrogen, and oxygen atoms.
- Proteins are made of 20 different amino acids and include enzymes, which act as biological catalysts to speed up the chemical reactions that constitute metabolism.
- Plant metabolites offer an abundance of structural diversity and thus offer enormous potential in terms of bioproduct production.

2.1 Introduction

Some knowledge of elementary chemistry and biochemistry is required to appreciate why certain components of plant biomass are used for producing specific bioproducts with desired functionality. In order to reach a broader audience of readers interested in plant bioproducts, this book only relies on a basic knowledge such as that

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provided by a junior undergraduate course in biology. This chapter begins with a brief and simplified review of how atoms can be united to form biomolecules of increasing complexity. Most of the discussion in this chapter will focus on lipids, carbohydrates, and proteins, which represent the major components of plants used as starting materials for production of various bioproducts. The goal is to develop an appreciation of the complexity and chemical diversity of plants as it relates to providing starting material for bioproducts rather than becoming overly obsessed with developing an in-depth structural understanding of these biomolecules. The chapter is mainly based on information found in introductory chemistry (e.g., Silberberg and Amateis 2015), biology (e.g., Purves et al. 2001), and biochemistry (e.g., Buchanan et al. 2015; Moran et al. 2012; Nelson and Cox 2005) textbooks.
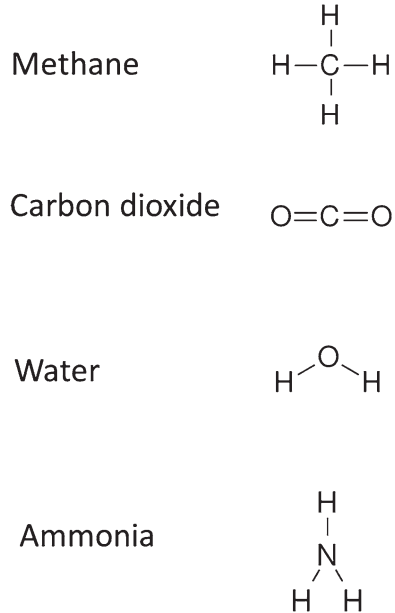
2.2   Atoms and Molecules

Living organisms are composed of a small number of elements which appear as part of the periodic table. The proportions of elements in plants, animals, and bacteria are depicted in Table 2.1. Oxygen (O) is the most abundant element followed by carbon (C), hydrogen (H), and nitrogen (N). Among the remaining elements, phosphorous (P) and sulfur (S) are also found in living organisms. In their simplest form, elements exist as atoms. An atom consists of a nucleus surrounded by electrons. The outer electrons of an atom tend to be unstable because they are unpaired. Stability can be achieved, however, when electrons from different atoms participate in electron sharing to form molecules. When electrons are shared between two atoms, this is often referred to as a **covalent bond**. Four examples of two-dimensional representations of abundant simple molecules are shown in Fig. 2.1. An **organic molecule** (or compound) contains carbon atoms which share electrons (or form covalent bonds) with hydrogen and possibly other elements. Methane, which is an example of a greenhouse gas, is categorized as an organic molecule. The chemical formula for methane is CH_4. In essence, carbon "shakes hands" four times to form methane. Carbon can also share electrons with oxygen to form carbon dioxide (CO_2), and oxygen can share electrons with two hydrogen atoms to form water (H_2O) (Fig. 2.1). Ammonia (NH_3), which is the result of nitrogen sharing electrons with three

Table 2.1 Proportions of elements found in plants, animals, and bacteria

Element	Composition by weight (%)
Oxygen (O)	65
Carbon (C)	18
Hydrogen (H)	10
Nitrogen (N)	3
Other elements	4

Other elements include phosphorous (P) and sulfur (S)

Fig. 2.1 Four examples of two-dimensional representations of simple molecules

Methane

$$H-\overset{\displaystyle H}{\underset{\displaystyle H}{C}}-H$$

Carbon dioxide

$$O=C=O$$

Water

$$H^{\diagup O}{}^{\diagdown}H$$

Ammonia

$$\overset{\displaystyle H}{\underset{H\ \ \ H}{N}}$$

hydrogen atoms, is also shown in Fig. 2.1. Unlike methane, carbon dioxide, water, and ammonia are not organic molecules because none of these represent a situation where carbon shares electrons with hydrogen.

2.3 Lipids

Lipids are described as "fatty acids and their derivatives, and substances related biosynthetically or functionally to these compounds" (http://lipidlibrary.aocs.org/). Many lipids tend to have **hydrophobic** attributes which are "water-fearing." Hydrophobic groups can associate in a watery environment through hydrophobic interactions. Just imagine two droplets of oil coalescing in a glass of water. The increased disorderliness of water as a result of lipid droplets coming together can be thought of as the driving force for hydrophobic interactions. Other lipids have both hydrophobic and polar ("water-loving") components as part of the same molecule and can be thought of as "schizophrenic" molecules. These types of lipids are often referred to as **amphipathic** molecules. Lipids can serve as an energy store, are critical component of membranes, and can have biological activity within cellular signaling pathways. Compared to other organic molecules, lipids are the most highly reduced yielding a maximum amount of energy when burned (Durrett et al. 2008).

Palmitic acid is an example of a fatty acid. Two different ways of depicting palmitic acid are shown in Fig. 2.2. From Fig. 2.2a, it can be seen that all the bonding requirements are fulfilled (i.e., carbon forms four covalent bonds, hydrogen forms
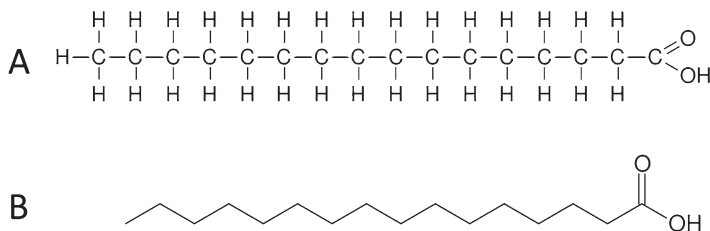
Fig. 2.2 Two representations of palmitic acid (16:0) which is a saturated fatty acid. (**a**) All atoms are shown; (**b**) a more concise representation

one covalent bond, and oxygen forms two covalent bonds). The CH_3- end of palmitic acid is known as the methyl end, whereas the opposite end, containing oxygen, is known as the carboxyl end. The jagged line in Fig. 2.2b implies the tetrahedral nature of the carbon center, and all the H atoms are assumed to be in place. In a watery environment, the carboxyl group can ionize to release a proton (H^+) and become –COO^-. This is an attribute of a weak acid, which explains the term fatty acid. Palmitic acid is known as a **saturated fatty acid** because all of the carbons, other than the carbon in the carboxyl group, are saturated with hydrogens. Palmitic acid can be described in shorthand form as 16:0 where "16" means 16 carbon atoms and ":0" refers to the absence of unsaturation or a double bond in the interior of the fatty acid chain.

In contrast, oleic acid has a double bond at the ninth carbon from the carboxyl group (Fig. 2.3). This bond results in a "kink" in the hydrocarbon chain. This introduced bend in the hydrocarbon chain results a compound that has a much lower melting point than palmitic acid or stearic acid (18:0), which is a commonly occurring saturated fatty acid which is two carbons longer than palmitic acid. Oleic acid is an example of a **monounsaturated fatty acid** because it has one point of unsaturation in the fatty acid chain outside of the carboxyl group. In shorthand form, oleic acid can be described as $18:1\Delta^{9cis}$ where "18" means 18 carbon atoms with ":1" meaning one point of unsaturation in the interior of the fatty acid chain. "Δ^9" indicates that the double bond occurs at position number 9 from the Δ (delta) end of the fatty acid chain, which is the carboxyl end. "*cis* refers to the configuration of the two hydrogens participating in the double bond. In the *cis* configuration, both hydrogens are on the same side of the double bond as shown in Fig. 2.3. In the *trans* configuration, the hydrogens would be located diagonally from each other around the double bond. Another shorthand form, which tends to be used more by nutritionists, uses the ω (omega) end of the fatty acid chain as a reference point. The ω end is the methyl end of the fatty acid chain. Thus, oleic acid can also be described as 18:1ω9 or 18:1*n*-9. This type of nomenclature is useful in understanding metabolic relationships involving different fatty acids.

Linoleic acid is an example of a **polyunsaturated fatty acid** because it has more than one double bond, or point of unsaturation, in the interior of the fatty acid chain (Fig. 2.3). In shorthand form, linoleic acid can be described as
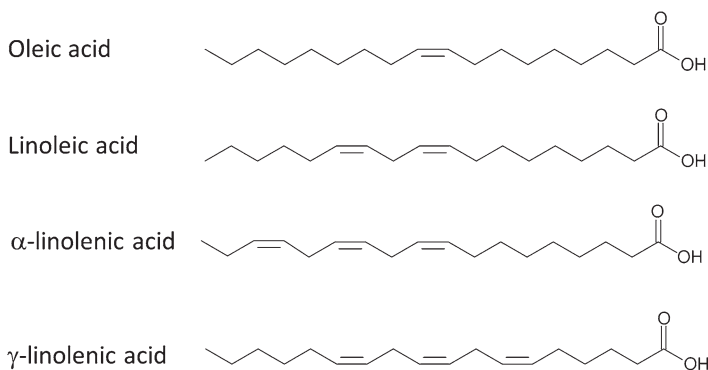
Fig. 2.3   Four examples of unsaturated fatty acids

$18:2\Delta^{9cis,12cis}$ or $18:2n$-6 ($18:2\omega6$). Note that the omega system only tells you about the bond closest to the methyl end of the fatty acid chain. α-Linolenic acid is an example of a polyunsaturated fatty acid with three double bonds in the interior of the fatty acid chain (Fig. 2.3). In shorthand form, α-linolenic acid can be described as $18:3\Delta^{9cis,12cis,15cis}$ or $18:3n$-3 ($18:3\omega3$). γ-Linolenic acid (Fig. 2.3) is another "isomer" of linolenic acid (18:3) which can be described in shorthand form as $18:3\Delta^{6cis,9cis,12cis}$ or $18:3n$-6 ($18:6\omega6$).
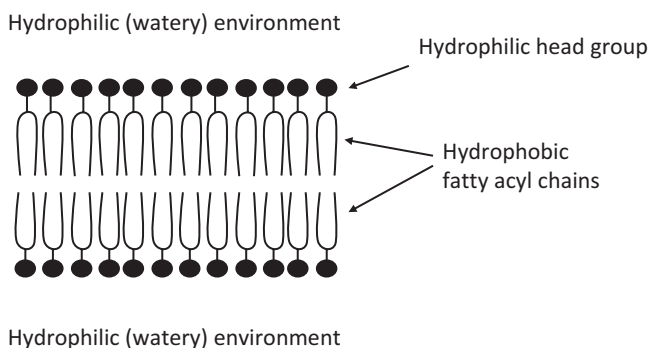
Fatty acids are typically found as components of more complex lipids such as **triacylglycerol** and **phospholipid** (Fig. 2.4). In triacylglycerol, fatty acids are "esterified" to a three-carbon glycerol backbone. The result is a very hydrophobic molecule since esterification greatly diminishes the polar character of the carboxyl groups. Triacylglycerol is the major component found in plant seed oils and is the main lipid feedstock for producing biodiesel and other bioproducts. A **feedstock** is a starting material for the production of industrial products. Triacylglycerol occurs in micro droplets, known as oil bodies, in the cytoplasm of the oil-forming cells of developing seeds.

Phospholipids, such as phosphatidylcholine (Fig. 2.4), are involved in the formation of cellular membranes which usually consist of two layers of phospholipid molecules (Fig. 2.5).

Phosphatidylcholine is an amphipathic molecule with two fatty acid chains comprising the hydrophobic component and phosphocholine comprising a water-loving polar head group. The fatty acyl chains interact through hydrophobic interactions in the interior of the membrane, while the phosphocholine head group faces a watery environment. The polar head group of a phospholipid can participate in **hydrogen bonding** and ion-dipole interactions with water. In a hydrogen bond, a hydrogen atom with a partial positive charge is shared between two atoms which have tendency to attract a bonding pair of electrons (referred to as electronegative). In a water molecule, the electrons tend to spend more time around the hydrogen atoms than the oxygen atom. This results in a distribution of charge, known as **dipole**, such that one end of a water molecule is positive and the other end is negative.

Triacylglycerol

Phosphatidylcholine
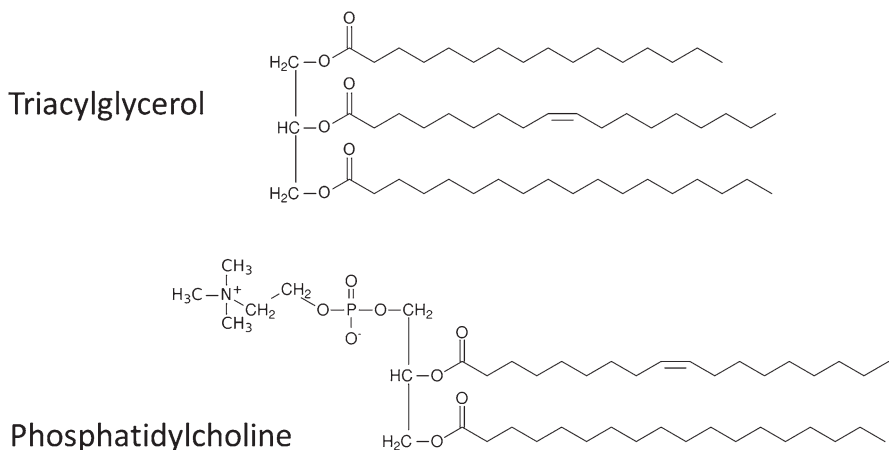
Fig. 2.4 Structures of triacylglycerol and phosphatidylcholine. In the triacylglycerol molecule shown, the glycerol backbone is esterified, from top to bottom, with palmitic acid, oleic acid, and stearic acid, respectively. The phosphatidylcholine molecule is esterified with oleic acid and stearic acid at the middle and bottom position of the glycerol backbone, respectively

Hydrophilic (watery) environment

Hydrophilic head group

Hydrophobic
fatty acyl chains

Hydrophilic (watery) environment

Fig. 2.5 Cross section of a segment of a lipid bilayer. Hydrophobic interactions occur between the fatty acyl chains in the inner region of the bilayer. The polar head groups of phospholipid can participate in hydrogen bonding and ion-dipole interactions with water

Therefore, the positive charge on the choline group can interact with the negative end of a water molecule.

A simplification of a plant cell is shown in Fig. 2.6. Plant cells have a **plasma membrane**, below a **cell wall**, which defines the outer boundary of the cell. In contrast, animal cells do not contain a cell wall. A plant cell contains a nucleus along with various subcellular organelles, which include **mitochondria**, **plastids**, **vacuoles,** and **peroxisomes**. All of these organelles have membranes. In addition, the plant cell contains an extensive network of membrane known as the endoplasmic reticulum. The nucleus houses the genetic material of the cell, which contains the
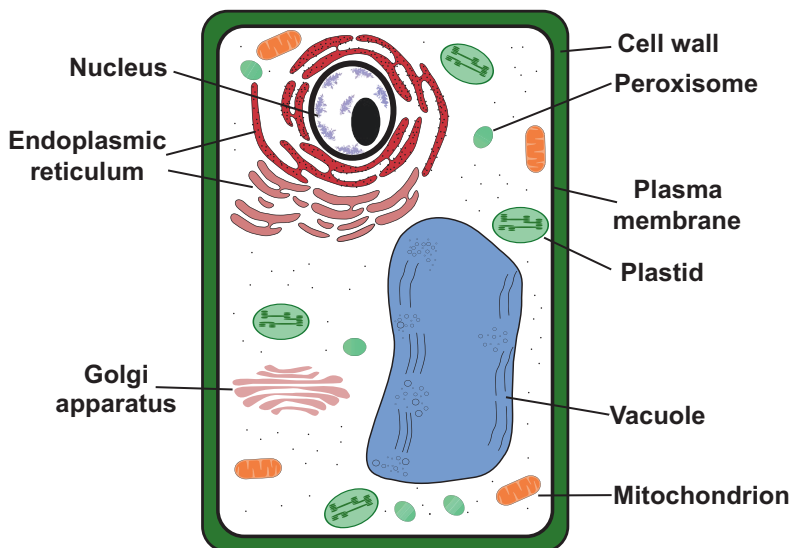
**Fig. 2.6** Schematic representation of a plant cell. (Adapted from Alberts et al. 1994)

"blueprint" for the formation of components of the cell and its operation. Mitochondria are known as the "power houses" of the cell because of respiration and the formation of adenosine triphosphate (ATP), the universal energy currency. Fatty acid formation occurs in plastids. The plastids of leaves are known as **chloroplasts** because they contain chlorophyll and are involved in photosynthesis. Fatty acid degradation occurs in both mitochondria and peroxisomes. Vacuoles are multifunctional organelles. In seeds, vacuoles serve as storage sites for reserve proteins and soluble carbohydrates. These various subcellular structures characterize what are known as **eukaryotic cells**. These subcellular organelles are absent in **prokaryotic cells** such as bacteria. In a eukaryotic cell, the content of the cell, minus the nucleus, is known as the **cytoplasm**, whereas the soluble component of the cytoplasm (without subcellular organelles and internal membranes) is known as the **cytosol**.

Bioproducts produced from lipids are dealt with in Chaps. 4 and 5.
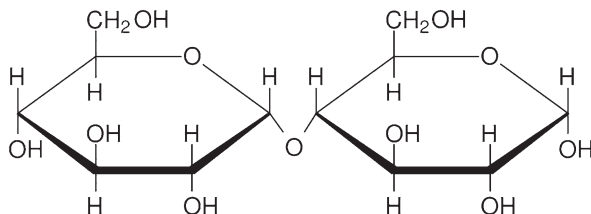
2.4   Carbohydrates

Carbohydrates can be thought of as sugars and sugar polymers. Carbohydrates consist of carbon, oxygen, and hydrogen and have the general formula $(CH_2O)n$. Most carbohydrates have cyclic monomers as fundamental structural components. Complex carbohydrates have roles in energy storage and cellular structure, such as contribution to the rigidity of the cell wall. Carbohydrates also serve as a source of

Fig. 2.7 Haworth structure of α-D-glucose. The carbon numbering system is indicated with C1 representing the anomeric carbon. α-D-Glucose is an example of a monosaccharide
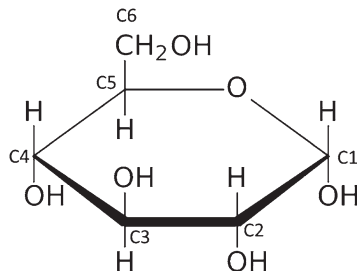
**Fig. 2.8** Structure of maltose which is an example of a disaccharide

carbon for various biosynthetic processes. Carbohydrates yield less than half the energy of lipids when burned.

α-D-Glucose is an example of a **monosaccharide** which exists mainly as the ring form in solution. The Haworth projection is shown in Fig. 2.7. Imagine the ring being embedded into the page with the portion in bold projecting out toward you. Hydrogen atoms, hydroxyl groups (–OH), and the –CH₂OH group are above the plane of the ring with some hydrogens and –OH groups below the plane of the ring. Note that all bonding requirements are fulfilled. The carbon (C1) on the right side of the ring is known as the **anomeric carbon**. If the –OH group is downward, then the glucose molecule is known as α-D-glucose. In contrast, if the –OH group is above the plane of the ring, the resulting molecule is β-D-glucose. In reality, the **Haworth projection** is only an approximation of the structure of glucose, and the ring adopts a somewhat different **conformation**. By definition, this has to do with "the spatial arrangements of a molecule that can be obtained by rotation of the atoms about a single bond" (https://www.merriam-webster.com/dictionary/conformation). Glucose, for example, can take on a "boat" or "chair" conformation.

The loss of a water molecule between two α-D-glucose molecules can result in maltose (Fig. 2.8), which is a **disaccharide**. The glucose rings are linked by an α-1-4 glycosidic linkage. The formation of maltose is an example of a condensation reaction. The reverse of the condensation reaction is known as hydrolysis reaction. The addition of a water molecule to maltose can result in the splitting of maltose into two α-D-glucose molecules.

Starch is an example of **polysaccharide** which can vary in molecular weight. Starch can accumulate as an energy reserve in developing cereal grains. Starch also forms transiently in the chloroplasts, accumulating during the day and disappearing at night. Starch consists of long stretches of α-D-glucose molecules linked by α-1-4 glycosidic linkages. On average, α-1-6 glycosidic linkages occur about every 25
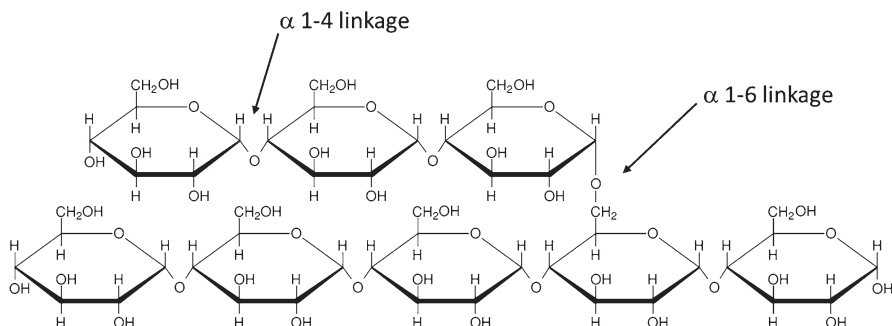
Fig. 2.9 Partial structure of starch
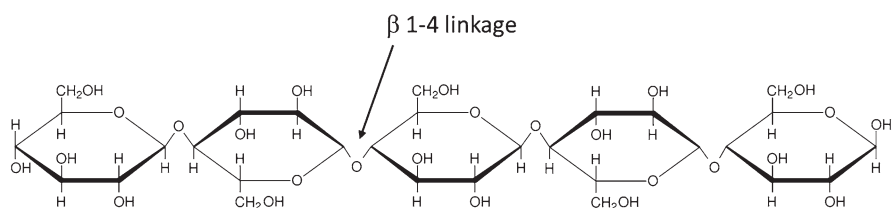

Fig. 2.10 Partial structure of cellulose

glucosyl residues resulting in branching. A partial structure of starch is shown in Fig. 2.9. In contrast, **cellulose** consists of strands of glucose units which are linked by β-1-4 glycosidic linkages (Fig. 2.10). Extensive hydrogen bonding occurs between the glucose chains in cellulose contributing to its strength and insolubility. Cellulose is the most common organic compound on earth. Both starch and cellulose are used as feedstocks in the production of ethanol.

There are numerous other monosaccharides, disaccharides, and polysaccharides. Disaccharides and polysaccharides can consist of mixtures of different monosaccharides, which can also vary in the number of carbon atoms in their rings. Various combinations of linkages can also occur. Additional information on carbohydrates and bioproducts produced from them are discussed in Chaps. 6 and 7.

2.5   Amino Acids and Proteins

A generalized structure of an **amino acid** is shown in Fig. 2.11. The central carbon is known as the α-carbon and to it is bonded a carboxyl group, a hydrogen atom, an amino group, and a variable side group or R group. **Proteins** are made up of 20 different amino acids, which can be generally categorized as nonpolar, polar, and electrically charged (Fig. 2.12). The latter can be further subcategorized as acidic or basic. The pH of the medium can influence the state of ionization of the carboxyl

Fig. 2.11 Generalized structure of an amino acid
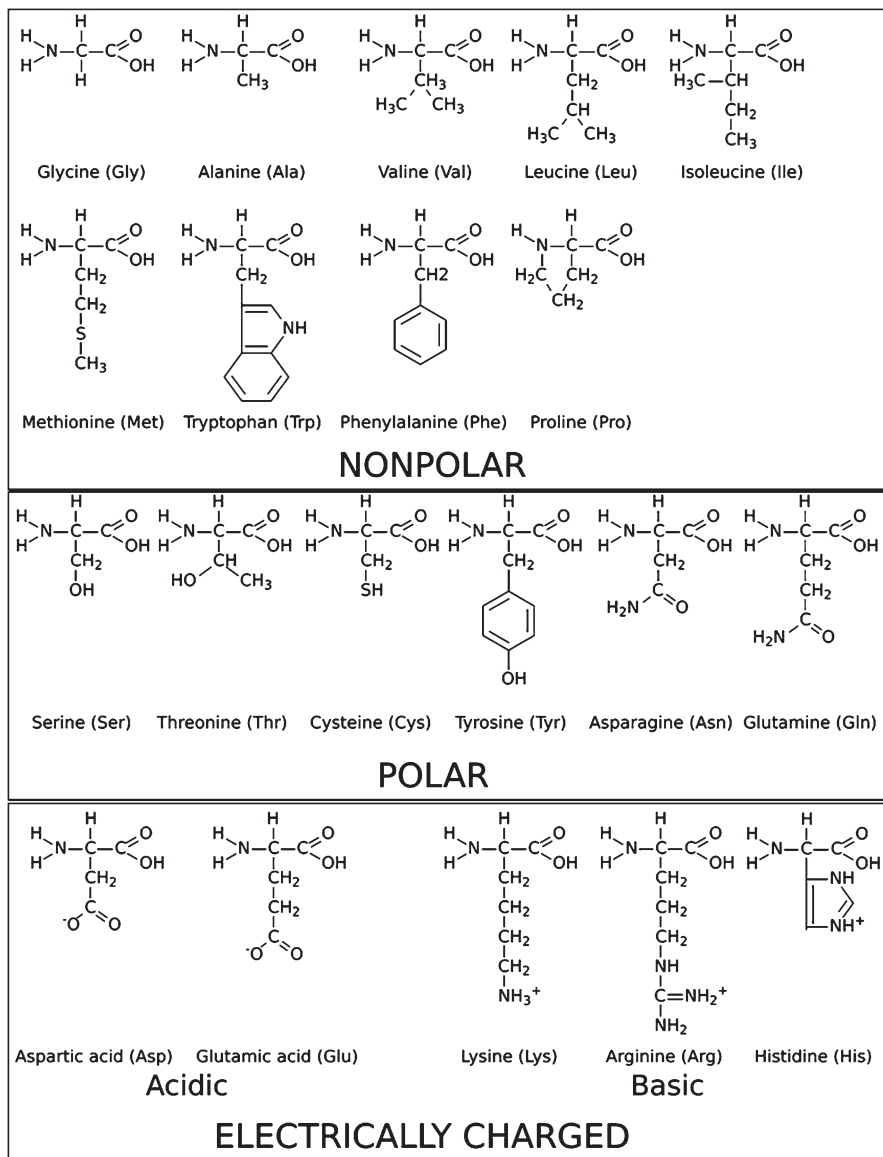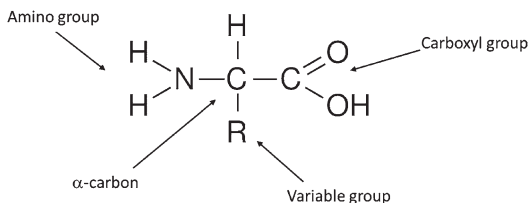

**Fig. 2.12** Twenty different amino acids typically found in proteins

and amino groups and some of the variable side chains. For aspartic acid, at pH 7, the main carboxyl group and carboxyl group of the side chain have both lost their protons, whereas the amino group bears a positive charge because of an additional proton (Fig. 2.13). To form polypeptides, amino acid "residues" are connected by **peptide bonds**. A peptide bond connecting two amino acid residues is shown in Fig. 2.14. This linkage also results from the loss of a water molecule.

Different levels of protein structure are depicted in Fig. 2.15. A **monomeric protein** consists of a single polypeptide chain. The sequence of amino acids in the polypeptide chain is known as the **primary structure**. Shorter segments within a polypeptide chain can also exhibit different types of folding including the α-helix and β-strand. This is known as **secondary structure**. Typically a polypeptide collapses upon itself to form the **tertiary structure**. This level of structure is characterized by the formation of β-sheets involving more than one β-strand. Regions of α-helix, β-sheet, and random coil can all exist in one polypeptide. The polypeptide is stabilized by various interactions between the side chains of the amino acid residues. For example, an ionic interaction or salt bridge can occur between the negatively charged carboxyl group of the side chain of an aspartic acid residue and the positive charge on the side chain of a lysine residue. In some cases, disulfide linkages (-S-S-), which are covalent, can occur between cysteine residues that are far apart in the linear sequence of amino acid residues. Disulfide linkages tend to stabilize the tertiary structure. In **quaternary structure**, identical or different subunits, which have their own tertiary structure, can associate through various interactions. A protein consisting of two identical polypeptides, or subunits, is referred to as a homodimer. If the subunits differ, the protein would be a heterodimer. A protein with four identical subunits would be a homotetramer, whereas a protein with a mixture of different subunits would be a heterotetramer. Proteins can be structural, have a role as a storage reserve, or have biological activity such as an enzyme. More detailed information on proteins and bioproducts derived from proteins is the subject of Chaps. 8 and 9.

Fig. 2.13 Aspartic acid at pH 7
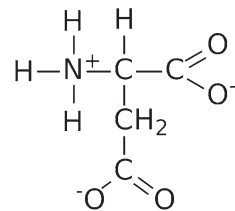
Fig. 2.14 Two amino acid residues connected by a peptide bond
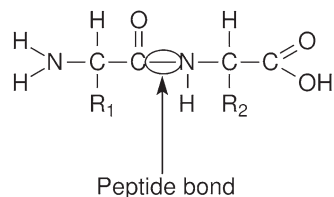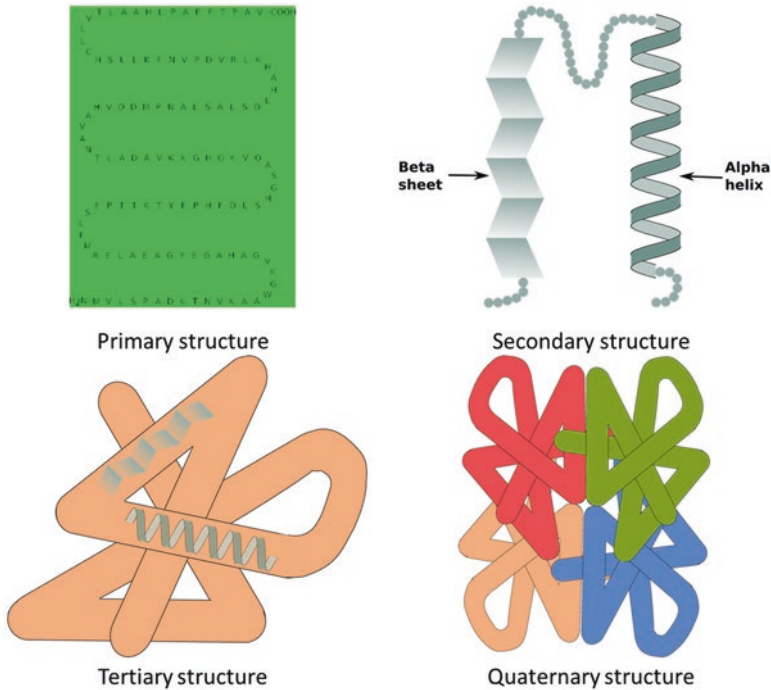
Fig. 2.15 Four different levels of protein structure

2.6 Biochemical Reactions Are Catalyzed by Enzymes

Enzymes are proteins which can act as biological catalysts to speed up chemical reactions such as condensation and hydrolysis. In enzyme-catalyzed reactions, the molecules first interacting with the enzyme are known as **substrates**, and released molecules are **products**. The enzyme has a specialized region or **active site** that can interact with the substrate and can facilitate the reaction much more effectively than without enzyme. The active site has amino acid residues that can temporarily interact with the substrate and other amino acid residues that are involved in the actual process of catalysis. A cartoon showing enzyme action is depicted in Fig. 2.16. Once the product(s) is released from the enzyme, it is ready for another catalytic cycle. Unlike substrates, enzymes are not consumed in the catalytic process. Generally, enzymes are essential for catalyzing biochemical reactions in plants and other organisms under non-extreme temperature conditions. Many of these reactions could be encouraged through a drastic increase in temperature without enzymes, but the consequences on life would be devastating. Later, it will also be shown that enzymes can be useful in the production of bioproducts from plant biomass.
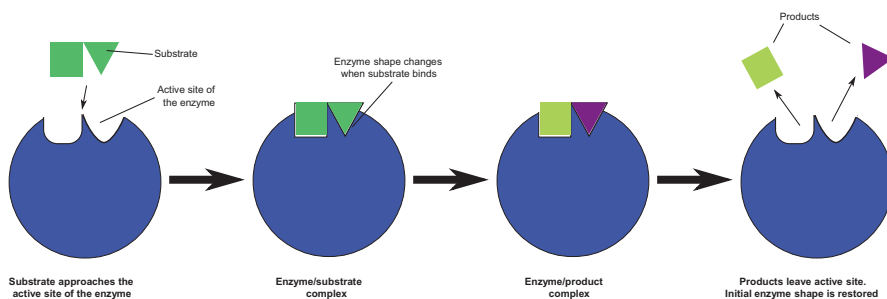
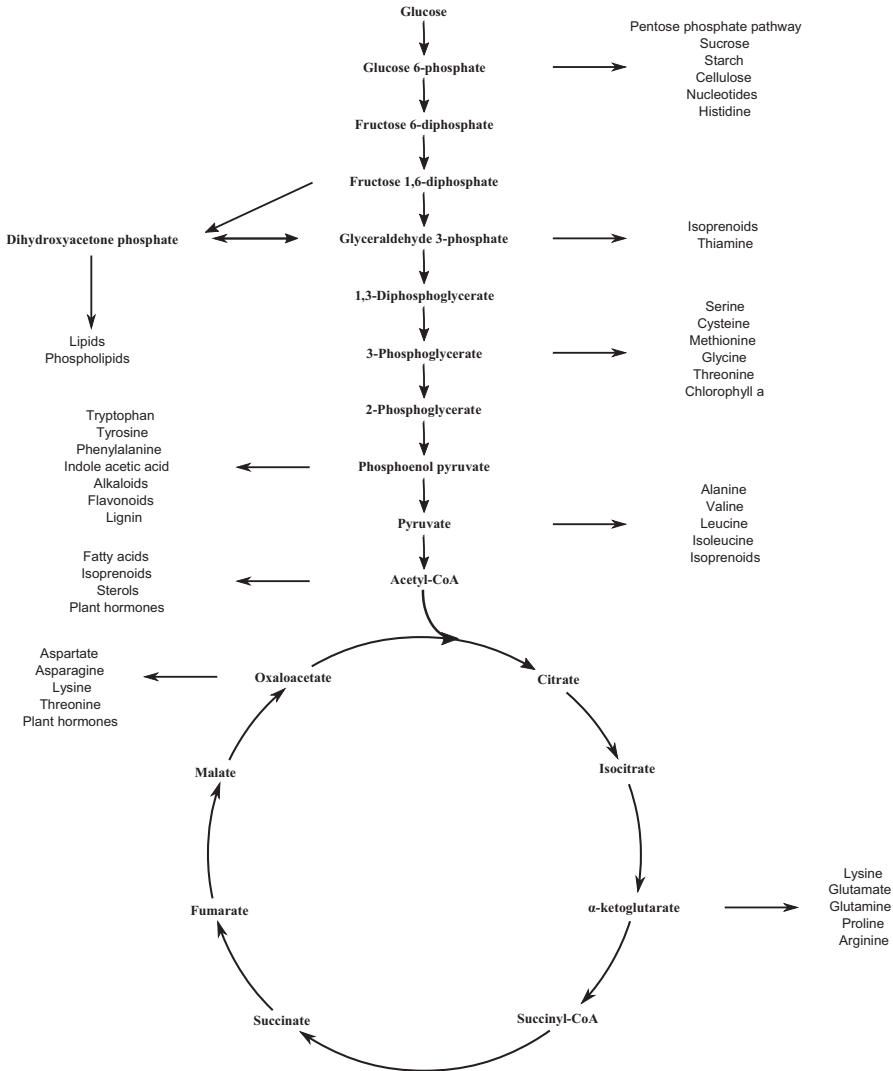**Fig. 2.16**   Schematic representation of enzyme action

2.7   Elementary Plant Metabolism

Cellular biochemical pathways involve a plethora of reactions catalyzed by enzymes. All of these reactions constitute metabolism. Metabolism can be divided into **catabolism** and **anabolism**. Catabolism has to do with metabolic processes that break down biomolecules, while anabolism is a building process. Energy production is often associated with catabolic processes, while anabolic processes may require energy input. **Primary metabolism** represents fundamental biochemical processes that are essential to the survival of a cell. These processes include energy production through photosynthesis and respiration and the formation of larger complex biomolecules including lipids, carbohydrates, and proteins. In plants, the products of **secondary metabolism** can aid in the growth and development of plants but are not absolutely required for survival.

Plants are **autotrophs,** which means that they can convert energy from light into primary metabolites. Photosynthesis uses carbon dioxide, water, and light to produce glucose and oxygen. The overall reaction is shown below:

$$6CO_2 + 12H_2O + light \rightarrow C_6H_{12}O_6 \left(glucose\right) + 6O_2 + 6H_2O$$
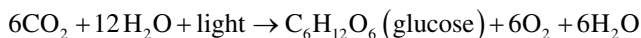
Glucose in turn provides a source of energy and biosynthetic precursors for fatty acid biosynthesis, amino acid biosynthesis, further carbohydrate metabolism, and secondary metabolism. The way in which cellular respiration can yield precursors for various biosynthetic processes is illustrated in Fig. 2.17. This, however, only represents a glimpse of the complexity of the processes. Many of these metabolites and biopolymers can serve as feedstock for the production of bioproducts. In eukaryotes such as plants, various metabolic processes can be compartmentalized. The process of glycolysis wherein glucose is converted to pyruvate occurs in the cytosol, whereas the conversion of pyruvate to **Acetyl-coenzyme (Co)A** and the Krebs cycle occur in the mitochondria. Special transport systems have evolved for moving metabolites across the membranes of organelles.

Glucose

Glucose 6-phosphate → Pentose phosphate pathway
Sucrose
Starch
Cellulose
Nucleotides
Histidine

Fructose 6-diphosphate

Fructose 1,6-diphosphate

Dihydroxyacetone phosphate ⇄ Glyceraldehyde 3-phosphate → Isoprenoids
Thiamine

Lipids
Phospholipids

1,3-Diphosphoglycerate

3-Phosphoglycerate → Serine
Cysteine
Methionine
Glycine
Threonine
Chlorophyll a

2-Phosphoglycerate

Tryptophan
Tyrosine
Phenylalanine
Indole acetic acid ← Phosphoenol pyruvate
Alkaloids
Flavonoids
Lignin

Alanine
Valine
Pyruvate → Leucine
Isoleucine
Isoprenoids

Fatty acids
Isoprenoids ← Acetyl-CoA
Sterols
Plant hormones

Aspartate
Asparagine
Lysine ← Oxaloacetate   Citrate
Threonine
Plant hormones

Isocitrate

Malate

Lysine
Glutamate
Fumarate   α-ketoglutarate → Glutamine
Proline
Arginine

Succinate   Succinyl-CoA

Fig. 2.17 Cellular respiration yields precursors for various biosynthetic processes

Secondary metabolites are usually produced from a product of primary metabolism. Secondary metabolites can have roles as pigments, attractants for pollinators, insect repellents, and antimicrobial or antifungal agents. Examples of some classes of secondary metabolites include alkaloids, terpenoids, polyphenols, and polyketides. Alkaloids contain nitrogen and are often derived from amino acids. Caffeine and nicotine are well-known alkaloids (Fig. 2.18). Terpenoids are derived from the basic five-carbon building block known as isoprene and are often categorized as lipids. The antioxidant lycopene, from the tomato, and the blood thinner, warfarin, are examples of terpenoids (Fig. 2.19). Polyphenols are derived from
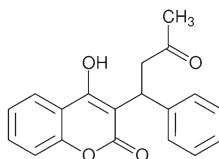
**Fig. 2.18** Caffeine and nicotine are two examples of alkaloids

Caffeine

Nicotine
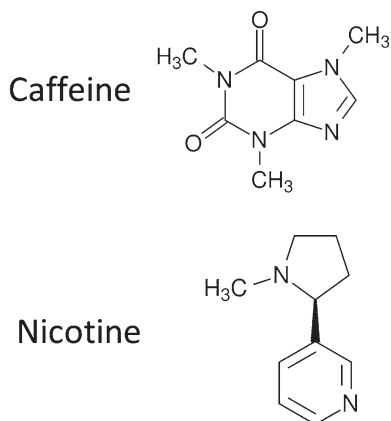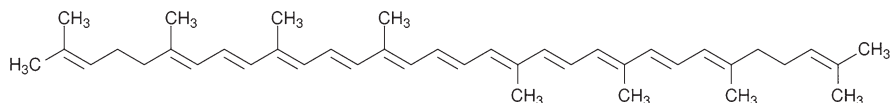
Lycopene

Fig. 2.19 Lycopene and warfarin are two examples of terpenoids

aromatic amino acids and have ring structures substituted with –OH groups. Resveratrol, an antioxidant in red wine, and vanillin, a flavor component of vanilla, are two examples of polyphenols (Fig. 2.20). Polyketides are produced from two- or three-carbon units in a process similar to fatty acid biosynthesis. Two examples include lovastatin, a cholesterol-lowering drug, and tetracycline, which is an antibiotic (Fig. 2.21).

2.8 Structural Diversity as a Major Advantage for Bioproducts

Petrochemicals are all based on a few simple hydrocarbon structures. The short-chain hydrocarbon, octane, is shown in Fig. 2.22. Petrochemicals can be straight chain, branched chain, cyclic, and aromatic with variations in chain length. In general,

Fig. 2.20 Resveratrol and vanillin are two examples of polyphenols

Resveratrol

Vanillin
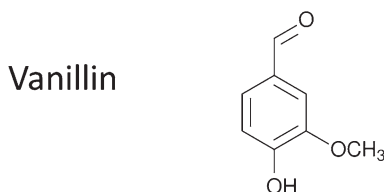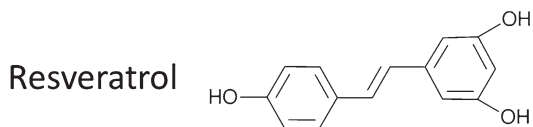
Fig. 2.21 Lovastatin and tetracycline are two examples of polyketides

Lovastatin

Tetracycline
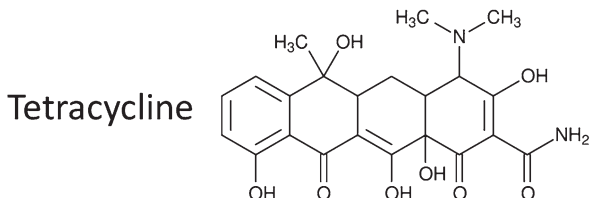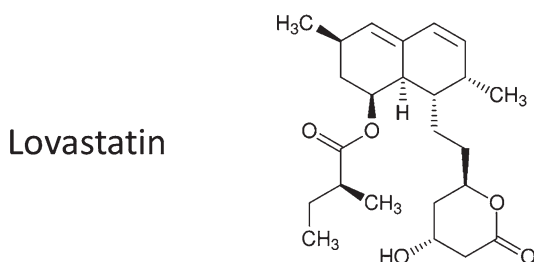
Fig. 2.22 Octane, a straight chain petrochemical

there are a limited number of functional groups. As a result, petrochemicals require extensive processing, which necessitates expensive starting materials and catalysts. The synthesis of complex organic molecules from petrochemicals therefore tends to be time-consuming, expensive, energy intensive, low-yielding, non-stereoselective, and not environmentally friendly.

In contrast, there is an abundance of structural diversity in the plant kingdom. For example, there are over 100,000 different secondary metabolites representing 25 major structural groups. There is thus an enormous potential for bioproduct production, especially with regard to platform or building block biochemicals

(see Chap. 10). Proteins also have enormous structural diversity based on the fact that the 20 different amino acids can be linked in different sequences. With 20 amino acids to choose from, for a two amino acid combination, there are 20^2 or 400 possibilities for different amino acid sequences. With four and six amino acid combinations, the possibilities rise to 160,000 and 64 million, respectively. Thus, enormous diversity is possible with a moderately sized polypeptide consisting of 400 amino acid residues.

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