(1)The Chemistry of Seeds

Samuel Contreras
Departamento de Ciencias Vegetales
Pontificia Universidad Católica de Chile
scontree@uc.cl

(2)1. Importance

There are several reasons why it is important to know the chemistry of seeds (Copeland and McDonald, 2001):

(3)First, seeds are a basic source of food. Most food consumed by humans comes from seeds or animals that are fed with seeds. Species from the Poaceae family, such as wheat, maize and rice contribute more to human nutrition than any other plant family. These species provide mainly carbohydrates to our diet; however, they are also a source of proteins and other essential nutrients. The Fabaceae family follows in importance. Plants included in this family, such as soybean, peanut, and beans, are important sources of proteins and oils. Other species that are an important source of edible oils are sunflower, canola, palm, and cottonseeds.

(4)Second, seeds are an important source of pharmaceuticals. The seed itself - or chemical compounds extracted from the seed - may be used in the preparation of medicines, either as active ingredients or as components of the formulation. Common chemical compounds extracted from seeds and used as active ingredients in medicines include (Houghton, 2006): (5) i) alkaloids, ii) amino acids, amines and proteins, iii) glycosides, iv) phenolics, volatile oils, and polysaccharides.

Many different oils extracted from seeds have been used in medical formulations to improve the delivery of the active ingredients. For example, when used in preparations such as massage oils, ointments and creams, these oils help the respective drug penetrate through the skin. Some examples of seeds in which oils are used for this purpose are coconut, castor bean, peanut and almond.

(6)Third, seeds may contain undesirable or even toxic compounds such as alkaloids, lectins, proteinase inhibitors, phytin, and raffinose oligosaccharides. Biologically active compounds present in seeds may be harmful to humans and animals. In some cases, depending of the dose, the same compound can both be used as part of the medicine while simultaneously being toxic.

(7)Fourth, seeds are an important source of raw materials that may be used in the manufacture of food and a diversity of other products such as soaps, cosmetics, resins, paints, varnishes, etc. For example, some seeds may be an important source of gums, which are high molecular weight polymeric carbohydrates that are important in the food, cosmetics, paper, and textile industries.

Fibers are another type of material obtained from some seeds and fruits, having diverse uses such as in clothing products, paper, brushes, and stuffing.

(8)Fifth, seed chemical composition includes nutrients and growth substances that affect different aspects of seed quality such as germination, vigor, dormancy, and longevity.

In general, the main components of a seed are found in its food reserves, which provide the energy required during germination and emergence. (9) As shown in this table, carbohydrates, fats (or oils), and proteins are the main forms in which these food reserves are stored. This presentation will focus on these three compounds and the factors that affect their quantity and quality in seeds.

(10) 2. Carbohydrate storage in seeds

(11) Carbohydrates are the major food reserve found in seeds of most cultivated plants. The most common carbohydrate that serves as a nutritional reserve is starch, although hemicelluloses, amyloids, and raffinose oligosaccharides may also be important. Cellulose, pectins, and mucilages are the most common forms of non-storage carbohydrates.

(12)Starch

Starch is an insoluble polysaccharide carbohydrate that is formed by the polymerization of many glucose moieties and may be easily broken down enzymatically to glucose monomers.

In seeds, starch is stored in two forms: *amylose* and *amylopectin*.

(13)Amylose is an unbranched polymer formed by 100 to 1,000 D-glucose units connected by (14) α-1,4 glucosidic bonds. It has a molecular weight from 10,000 to 100,000, stains dark blue when exposed to iodine, and is 100% digestible by α-amylase. Although amylose is not truly soluble in water, it forms hydrated micelles in water and may assume a helical structure.

(15) Amylopectin is a brunched version of amylose. It is a much larger molecule, having a molecular weight from 50,000 to 1,000,000. In amylopectin, glucose units are linked by (16) α-1,4 glucosidic bonds to form a linear chain, and α-1,6 glucosidic bonds to form branches or side chains with 15 to 25 glucose units each. Amylopectin stains purplish-red when exposed to iodine and is only 50% digestible by α-amylase.

(17) In the seed, starch is found in discrete subcellular bodies known as *starch grains*. Most starch grains are composed of 50-75% amylopectin and 20-25% amylose. Species or genotypes which have amylose concentrations higher than average are classified as “starchy”. For instance, in wrinkled peas, approximately 66% of the starch is composed of amylose, compared to 33% in smooth peas and other legumes. There are also examples of mutants that have a lower than average amylose content. For example, in waxy mutants of maize, starch is composed almost completely of amylopectin.
The size of the starch grains varies from 2 to 100 μm even within a seed. The shape of the starch grains is mainly determined by the amylose content, being rounder with higher amylose content. Different plant species may have starch grains of characteristics shapes; for instance, they are predominantly spherical in barley seeds, angular in maize, and elliptical in runner bean.

This picture shows starch grains in rye endosperm; there are large grains up to 40 μm diameter and many small grains at less than 10 μm diameter.

(18) In addition to its important role in human and animal nutrition, starch is also an important industrial material. It is used as an emulsifying and thickening agent in the food industry and also in the production of binding agents, strengthening agents, and coating materials.

(19) Maize is the dominant crop for starch production. Much of the starch produced by maize is hydrolyzed to glucose, which is converted primarily into fructose and ethylene. Fructose is a common sweetening agent for foods and beverages, while ethanol is an increasingly important alternative fuel source.

(20) Hemicelluloses

Hemicelluloses are large heteropolymers of several sugars which are common components of cell walls. In general, hemicelluloses are the second most important form of carbohydrates stored in seeds and, in some species, particularly in endospermic legumes, hemicelluloses are the primary source of carbohydrates. Usually, starch is absent in seeds that are rich in hemicelluloses.

(21) Hemicelluloses are generally composed of five sugars: glucose (6C), galactose (6C), mannose (6C), xylose (5C), and arabinose (5C). These sugars arrange themselves in a long backbone chain of one or two sugars with side chains or branches that vary in number and spacing and are composed of one or two sugars, different to the ones that compose the backbone.

(22) In this table, common cell wall storage hemicelluloses, with the sugars that compose their main chain or backbone and the sugars composing their side chains or branches are presented. Additionally, species having seeds with these hemicelluloses are shown.

The structures of most common storage hemicelluloses are formed by mannose, especially mannans, glucomannans or galactomannans. In species such as coffee, ivory nut, and date, these polymers accumulate in the cell walls of the endosperm and/or perisperm, making these tissues extremely hard. Less frequently, carbohydrates are stored as accumulations of xyloglucans (amyloids) or arabinogalactan in the cell walls of the cotyledons.

(23)This picture shows the chemical structure of galactomannans. It consists of a main chain of the sugar mannose linked by β-1,4 bonds with galactose units as side chains linked by α-1,6 bonds. The type of galactomannan is determined by the number of galactose brunches, being harder when less galactose units are present and more mucilaginous when more galactose units are present.

In addition to their role as storage compounds, the presence of galactomannans in some seeds has been associated with protecting the germinating embryo against temporary drought. This protective function is achieved by the affinity of galactomannans for water which causes the seed to swell, become mucilaginous and maintain humidity around the embryo when the seed is in contact with water. The presence of galactomannans in the relatively thin endosperm surrounding the embryo of tomato and lettuce seeds has been linked to causing seed coat dormancy.

(24) Glucomannans are another form of hemicellulose in which a large portion of the mannose residues (units) is replaced by glucose. Glucomannans are found in the thick

cell walls in the endosperm of monocots such as the Liliaceae (e.g., asparagus) and Iridaceae families.

(25)Raffinose series oligosaccharides

Raffinose series oligosaccharides are composed of sucrose plus a variable number of galactose units. As shown in this figure, sucrose is a disaccharide composed of one fructose and one glucose unit. Raffinose, stachyose, and verbascose contain one sucrose molecule bound to one, two, or three galactose molecules, respectively. In the mature seed, these oligosaccharides are found predominantly in the embryo, in amounts between 2 and 6% of the seed dry weight. (26) This table shows the content raffinose oligosaccharides in seeds from selected species.

During germination, raffinose oligosaccharides are used as an early source of energy so their presence decreases quickly. The enzyme required to break the bonds between sucrose and galactose and between adjacent galactose sugars is α-galactosidase. This enzyme is not produced by humans and monogastric animals, so these oligosaccharides escape digestion and are degraded by bacteria in the colon. This produces hydrogen and carbon dioxide which can cause flatulence and diarrhea.

There is evidence that sucrose, raffinose and stachyose are involved in the acquisition of desiccation tolerance during seed development. The amount of these carbohydrates has been found to simultaneously increase with the acquisition of desiccation tolerance in seeds of several species. It is suspected that this role is achieved through the promotion of water vitrification and protection of cytosolic structures during desiccation. In addition, these sugars may also help maintain the integrity of cell membranes through the stabilization of lipids and proteins that form the membrane.

(27) 3. Lipid storage in seeds

(28) Lipids are a diverse group of organic compounds such as fats, oils, waxes, sterols, glycolipids, phospholipids, fat-soluble vitamins (e.g., vitamins A, D, E and K), etc. These compounds are insoluble in water, but soluble in organic solvents such as alcohol, ether, chloroform, and benzene. Lipids have many biological functions including: 1) energy storage, 2) structural components of cell membranes, and 3) participating in signaling pathways.

Most lipids found in seeds are fats, oils or waxes. (29) The term lipid is sometimes used as a synonym for fat or oil; however, these terms represent different types of lipids. Oils and fats share a common structure, both are triacylglycerols. However, oils differ from fats because they remain in liquid form at room temperature (i.e., around 20°C) while fats remain solid. A triacylglycerol (or triglyceride) is a glycerol molecule esterified with three fatty acids.

(30) This figure shows a glycerol molecule, which is a three carbon sugar alcohol.

(31) Fatty acids are molecules consisting of a long hydrocarbon tail that is initiated with a carboxyl group.

(32) This scheme shows how three fatty acids combine with a glycerol molecule to form a triacylglycerol. Note that in the formation of the ester bounds, water is released. As a result, cleavage of these bonds occurs by hydrolysis.

(33) This figure shows the general structure of a triacylglycerol molecule, with glycerol as the backbone to which three fatty acyl residues are esterified. Unlike carbohydrates, triacylglycerols must be stored in anhydrous form because they are very hydrophobic, which increases the efficiency of energy storage.

(34) Fatty acids are classified as saturated or unsaturated depending on the type of carbon linkages in the hydrocarbon tail. Saturated fatty acids do not have carbon-to-carbon double bonds. In this figure (35), stearate is shown as a saturated fatty acid; that is, there are not double bonds in the molecule. Unsaturated fatty acids have one or more carbon-to-carbon double bonds. When they have only one double bond, they are classified as monounsaturated; when they have two or more double bonds, they are classified as polyunsaturated.

Fatty acids have unique physical properties, such as differing melting points, that primarily vary based on the length of the hydrocarbon tail and its level of unsaturation. Generally, the longer and more saturated fatty acids melt at higher temperatures than shorter and more unsaturated fatty acids. Saturated fatty acids are typically solids whereas unsaturated fatty acids are liquids at room temperature. Fatty acids in a free state are not commonly found in living cells, although they may be found in germinating or deteriorating seeds as a result of triacylglycerol hydrolysis.

(36) As seen in this table, the content of triacylglycerols in seeds varies greatly among species, from 1% to over 60% on a dry weight basis. Seed oil content in common commercial species ranges from 5% (e.g., maize) to 40-50% (e.g., canola, flax, peanut, palm kernel, sesame and sunflower). Soybean and cotton seeds have intermediate levels of oil around 15-20%.

(37) This table shows the concentration of the five principal fatty acids that comprise commercial oils from various plant sources. Palmitic acid is the most common saturated fatty acid in seed oils followed by stearic acid. However, unsaturated fatty acids are the predominant type in seeds with oleic and linoleic acids accounting for more than 60% of the oil in oil seeds.

Seed lipids are widely used in food applications such as baking and frying, salad dressing, and confectionary coating. Nutritional use of seed oils of species such as sunflower and maize has been favored by their high content of linolenic acid. This polyunsaturated fatty acid cannot be synthesized by mammals, which makes it an essential fatty acid that must be included in their nutrition.

Common non-food applications of seed oils include paints, coatings, finishes and inks. These applications are the result of the drying properties of linseed and other oils with high polyunsaturated fatty acid content. These fatty acids have the ability to react with oxygen in the air (free-radical polymerization reactions) resulting in solid, waxy compounds.

Other oil seed fatty acids have unusual functional groups in their hydrocarbon tail, which makes the oil valuable for industrial applications such as stabilizers for PVC. This is the case for hydroxyl-fatty acid ricinoleic acid, which is abundant in castor bean (*Ricinus communis*) oil.

(38) In seeds, lipid reserves are accumulated in discrete sub-cellular organelles known as oil-bodies, lipid bodies, oleosomes, or spherosomes. Oil bodies are bounded by a phospholipid membrane monolayer and their size ranges from 0.2 to 6.0 μm in diameter. Many of the enzymes required for lipid biosynthesis and hydrolysis are present in these bodies. The principal site for lipid storage in cereal seeds is the scutellum, whereas in dycotyledonous seeds, lipids are stored primarily in the cotyledons. In the case of castor bean, lipids are found in the endosperm cells; this picture shows the abundant presence of oil bodies (white spheres) in castor bean endosperm.

(39) 4. Protein storage in seeds

(40) Proteins are polymers of amino acids linked by covalent peptide bonds between the carboxyl- and amino- groups. This picture shows the condensation of two amino acids to form a peptide bond.

Protein composition varies from a single polypeptide chain which is a sequence of amino acids residues to several polypeptides linked to each other by non-covalent hydrogen bonds or covalent disulphite bonds. (41) Four categories are used to describe protein structure:

1) Primary structure is the sequence of amino acids from the amino group to the carboxyl end.
2) Secondary structure represents the interactions between amino acids from some regions in the same polypeptide chain by hydrogen-oxygen bonds, which results in helical-shaped (α-helices) or sheet shaped (β-sheet) configurations.
3) Tertiary structure describes the shape of the fully folded polypeptide chain.
4) Quaternary structure refers to the arrangement of two or more polypeptide chains into a multi-subunit or oligomeric protein.

(42) Protein properties depend on their amino acid composition. Twenty different amino acids combine to form proteins. They share a common structure as shown in this slide with an amino group and a carboxyl group bounded to the same carbon.

Under normal cellular physiological conditions (pH ~7.4), the amino group is protonated and the carboxyl group is ionized. The atomic conformation of the R group is what makes each amino acid unique from the others. Some R groups are nonpolar and thus hydrophobic, whereas others are polar or ionized in which case they are hydrophilic. Additionally, there are two amino acids (methionine and cysteine) that have sulfur-containing R groups. One of these amino acids, cysteine, has a terminal sulfhydril group capable of forming disulfide bonds, which are important in stabilizing three-dimensional structure in some proteins.

A protein, or a region of a protein, therefore would be positively or negatively charged, and hydrophobic or hydrophilic, depending on its amino acid composition.

(43) Proteins are vital for organisms and are involved in all physiological reactions in living cells. For instance, enzymes that catalyze biochemical reactions are proteins. Proteins also have structural or mechanical functions, along with being involved in cell signaling and transport through membranes.

In seeds, the greatest quantity of proteins is found in storage proteins. However, there still remain many diverse proteins that have structural (e.g., components of cell membranes and walls) or metabolic functions (e.g., enzymes and transporters). Some proteins found in seeds also provide protection against pests and pathogens. Many of the enzymes present in seeds are essential for storage reserve utilization by the embryo during the germination process.

(44) In the seed, most proteins are stored in protein bodies 1 to 20 µm in diameter bounded by a lipoprotein unit membrane and are widely distributed in cotyledons and the endosperm of seeds. According to Smith (1984), protein bodies have the following characteristics: 1) some contain crystalline inclusions of phytic acid, 2) they contain most of the cellular protein, but none of the oil, 3) their synthesis commences after most of the cells of the seed have been formed, and 4) they swell, coalesce, and disappear early in germination. In aleurone layer cells, numerous small vacuoles known as *aleurone grains* contain storage proteins, phytin and oils.

(45) Seed proteins have been classified in four groups according to their solubility:

1) Albumins, soluble in water at neutral or slightly acid pH. This fraction is primarily enzymes.
2) Globulins, soluble in saline solution, but insoluble in water
3) Glutelins, soluble in acid or alkali solutions
4) Prolamins, soluble in 70-90% ethanol

In general, cereal seeds are rich in prolamins and glutelins, with low concentrations of globulins, whereas seeds of legumes and other dicots have high concentrations of globulins and small amounts of glutelins and prolamins.

(46) Storage proteins in cereal seeds

This table shows the relative concentration of each protein type in cereal seeds. In general, prolamine and glutelin are the predominant protein types in this group of crop species. However, there are exceptions such as oat seeds which have over 50% globulins.

Prolamin proteins are of relatively low in human and monogastric animal nutrition because they are deficient in lysine and tryptophan, essential amino acids for these organisms. On the other hand, gluteline proteins have a better balance of essential amino acids for monogastric animals.

(47) This table shows a list of essential amino acids for humans. These amino acids are called essential because humans cannot synthesize them at the level needed for normal growth and development, so they must be obtained from food.

(48) In maize seeds, zein (a prolamin) is the most abundant storage protein. Zein is relatively rich in alanine and leucine, with low levels of lysine and almost no tryptophan. Thus, maize protein is of poor quality if used as the only protein source in monogastric animal nutrition. Zein is primarily stored in protein bodies in the maize seed endosperm.

(49) The major storage protein in wheat is gluten, which is composed of the proteins gliadin and glutenin. Gluten, which is also abundant in rye and barley seeds, has elastic properties that make it valuable for baking products such as bread. (50) Globally, gluten is one of the most important nutritional proteins. This table shows the relative

nutritional value of wheat proteins in relation to their essential amino acid content and human requirements.

(51) Storage proteins in dicotyledonous seeds

This table shows the protein concentration and protein composition of some dicotyledonous seeds. Proteins, in this case, are predominately globulins with very little prolamin and glutelin presence which is different from cereal seeds. The quality of these globulin-rich proteins for human and monogastric animal nutrition is relatively high.

In general, the percentage of protein concentration in dicotyledonous seeds is high, with soybean and other legume seeds ranging from 25 to 50% compared to only 10 to 15% in cereal seeds. Dicotyledonous seeds are relatively high in lysine and have significant amounts of tryptophan, which makes them an excellent complement for diets rich in cereals. However, legume seeds are low in methionine.

(52) 5. Other chemical compounds found in seeds

(53) Alkaloids

Alkaloids are chemically heterogeneous organic compounds containing nitrogen. Due to their complex structures that usually include one or more heterocyclic rings, alkaloids may mimic receptors or enzyme-binding sites making them physiologically active and, in many cases, poisonous.

Alkaloids may also serve as protective mechanisms of seeds against pests and pathogens because of their bitter flavor. Alkaloids can be classified according to their molecular structure. Some examples are presented in this table:

- Caffeine is an example from the purine type. It is extensively used as a mild stimulant of the central nervous system. Caffeine is found in Coffee beans (*Coffea arabica* and *C. robusta*) as well as seeds of the cola nut, *Cola nitida* and *C. acuminata*, whose extracts are used for popular soft drink production. Additionally, in Brazil, seeds of the *Paullinia cupana* bush are used for production of guaraná, a pulp containing about 5% caffeine and commonly used in soft drink production.
- Hyoscyamine is an example of the tropane type extracted from seeds of *Datura stramonium*. This alkaloid is used as a pharmaceutical drug to reduce cramping and gastrointestinal tract movements,by relaxing or suppressing central nervous system acitivity as well as decreasing feelings of nausea.

These are just two examples of the numerous alkaloids extracted from seeds with a wide range of uses such as pharmaceuticals, poisons and insecticides.

(54) Tannins

This is a group of complex astringent polyphenolic compounds occurring widely in plants. Tannins are especially common found in tree bark, unripe fruits, and leaves. They also occur in seeds, particularly in the seed coat. Examples of seeds containing tannins are cocoa, many legumes (especially red and black beans), pecans, cashews and walnut.

Tannins have a high molecular weight that ranges from 500 to over 3000, contain hydroxyls, carboxyls or other suitable groups that form strong complexes with proteins and other macromolecules. This property is the basis for their use in the tanning process or hair removal from animal skins. During tanning, tannin molecules tie up enzymatic proteins and inhibit their activity. Other uses for tannins are in medicine to include antidiarrheal, homeostatic, and antihemorrhoidal compounds. When excessive amounts are ingested, tannins inhibit the absorption of minerals such as iron and calcium, which may cause anemia and osteoporosis.

(55) Glycosides

Glycosides are compounds formed from the reaction of a sugar, usually glucose, with one or more nonsugar compounds, which are called aglycones. Aglycones vary from simple molecules such as benzylaldehyde to various types of phenols, steroids and alkaloids. Glycosides can be classified according to their pharmaceutical effects or to the aglycone chemical structure.

Glycosides are present in seeds and cause a bitter taste. Some examples are amygdalin in seeds of almonds, peaches, and plums; esculin in horse nut; and saponin in tung seed. Saponin is highly poisonous to both animals and humans.

(56) Phytin

Phytin is the insoluble mixed potassium (K^{+}), magnesium (Mg^{++}), and calcium (Ca^{++}) salt of *myo*-inositol hexaphosphoric acid (phytic acid). As may be seen in this figure, the chemical structure of phytic acid has 6 phosphate groups, each with two negatively charged sites. Thus, there are a total of 12 sites to which the mineral cations bind. In addition to potassium (K^{+}), magnesium (Mg^{++}), and calcium (Ca^{++}), other ions may also be present, but in much smaller amounts. For example, iron (Fe^{+++}), manganese (Mn^{++}) and zinc (Zn^{++}) can also be bound to phytin. (57) The content of the main inorganic elements of phytin in various seeds is given in this table. The phytin content of seeds and its mineral composition can be affected by genotype and the mother plant environment, especially as influenced by soil fertility. Phytin concentrations usually range between 0.5 and 2.0% of the total seed dry weight.

(58) In the seed, phytin is stored in protein bodies and aleurone grains forming a distinct structure known as a globoid. Phytin is not present in all seed protein bodies. Additionally, phytin mineral composition varies depending on the cell type. For example, calcium is abundant in radicle and hypocotyl cell globoids, but is present in only limited amounts in cotyledon cell globoids.

Phytin is considered nutritionally undesirable because it is not metabolized by animals and can bind essential dietary minerals (e.g. Ca^{++}, Fe^{+++}, Zn^{++}), reducing their ability to be absorbed.

(59)Vitamins

Vitamins are a heterogeneous group of chemical compounds synthesized by plants. They function principally as enzyme cofactors and, although vitamins are characterized as being essential in very low quantities, their absence can cause plant and animal diseases. Vitamins may be classified in two groups: water soluble vitamins and fat soluble vitamins. Plants synthesize and store vitamins in different organs, including seeds.

This table shows the concentration of some water and fat soluble vitamins in seeds of selected crop species. In general, cereal seeds have relatively high amounts of vitamins B and E.

(60) Hormones

Hormones are organic compounds that, in small concentrations, have important regulatory effects on plant and animal metabolism. Plant hormones, also known as phytohormones or plant growth regulators, play important roles in regulating seed development, maturation, desiccation, dormancy and germination. Abscisic acid, gibberellins, ethylene, cytokinins, auxins, and brassinosteroids are phytohormones reported to have regulatory effects of different physiological processes in seeds (see Kucera et al., 2005 for review).

(61) 6. Factors affecting chemical composition of seeds (based on Fenner, 1992)

We have seen that seed chemical composition varies among different species and cultivars. Additionally, chemical composition within seeds from the same genotype can vary significantly depending on the maternal plant environment and/or the position of the seed within the plant or inflorescence. The reason for this variation is that the micro-environment in which each seed develops can affect the availability of resources and the growing period for the developing seed.

(62) Position in the mother plant

The variation in seed chemical composition in seeds from the same plant is caused by competition for nutrients among seeds. In general, seeds that grow closer to the source of nutrients are favored in this competition. For example, first and second seeds in a wheat spikelet have higher nitrogen content than the third and fourth seeds. Another example is *Abutilon theophrasti* from the Malvaceae whose seeds have a higher nitrogen concentration when produced in the first two fruits compared to seeds produced in the last two fruits. In oilseed rape, the proportion of seven fatty acids varies depending on the position of the pod in the inflorescence.

(63) Season effects

Seed chemical composition can also be affected by the season that the seed experiences during maturation. For example, late season soybean seeds have higher protein concentration. In sunflower, seed oil quality tends to improve gradually over the season, with seeds produced in late summer having the best quality. In this case, it is believed that the differences in oil composition are related to differences in temperature or photoperiod throughout the growing season.

(64) Temperature

There are several reports that link higher temperatures during seed growth with production of smaller seeds. Although this temperature effect has been studied by measuring seed mass, it can be concluded that smaller seeds have a lower accumulation of storage reserves, especially carbohydrates. In most cases, the temperature effect on seed size is the consequence of changes in seed growth rate and seed filling period.

The effect of temperature on seed oil and protein composition has also been studied. In the case of oils, temperature influences the quantity of polyunsaturated linolenic acid compared to monounsaturated oleic acid. Oil extracted from seeds that mature at cooler temperatures had higher linolenic:oleic acid ratios, which is considered a better quality oil. These effects have been observed in commercial and wild sunflower genotypes. Similar changes in oil quality by temperature have also been reported in flax and cocoa seeds.

In general, seeds produced under higher temperatures have a higher protein concentration in wheat and soybean. It may be that the higher protein concentration of seeds produced at higher temperatures is a result of lower carbohydrate accumulation during development.

(65) *Nutrients*

Evidence about the effects of nutrient supply on seed size and composition comes from several fertilization experiments. These experiments showed that the mineral nutrient supply to the mother plant is one of the most important external factors affecting seed chemical composition. In general, addition of a particular mineral nutrient to the mother plant causes increases in the concentration of that nutrient to the seed. This effect has been reported in several species for both macro- and micro-nutrients. For example, addition of nitrogen resulted in higher protein content in wheat, rice, maize, and cotton seeds. Addition of phosphate resulted in higher phosphorous concentration in pea, soybean, wheat, and common bean seeds. Additionally, increased presence of trace elements in seeds after fertilization has been observed for manganese and boron in soybean, copper in wheat, zinc in soybean, cobalt in lupin, and cadmium and selenium in lettuce seeds.

With respect to the influence of mineral nutrient supply to the parent plant on protein content, not only is the protein concentration affected, but also the amino acid composition of these proteins. From several experiments, it has been shown that the balance of nitrogen and sulphur availability affects the relative content of some amino acids. For instance, the portion of methionine and cysteine (S-containing amino acids) is lower in proteins from seeds that grow under conditions of low sulphur availability.

In oil- rich seeds, such as soybean, sunflower, and meadowfoam (*Limnanthus alba*), the increase in nitrogen availability resulted in more seed protein and less oil content.

(66) *Water stress*

Water stress causes an increase in seed protein concentration in winter wheat, perennial ryegrass, maize, spring wheat, soybean, and common bean. In maize, plants subjected to water stress during seed filling produced seeds with 33% higher protein concentration and 18% lower oil concentration. In general, the magnitude of water stress effects depend on the timing that it occurs during seed development.

(67) 7. Relationship of chemical composition, hygroscopic equilibrium and seed storability

In addition to the importance that chemical composition has on seed quality and nutritional value as well as being a source of pharmaceutical or industrial materials, seed composition also affects the seed hygroscopic equilibrium and storability.

Hygroscopy is defined as the ability of a compound to attract water molecules from the surrounding environment. (68) In the case of seeds, seed water content in equilibrium at a determined relative humidity is affected by seed composition, especially lipid content. Lipids have a low affinity for water or hygroscopy, thus seeds with high lipid content have lower water content at the same relative humidity as seeds with low lipid content. A good example of this principle is represented in this graph, which shows the moisture isotherm curves for snap bean (1% lipid content) and broccoli (31% lipid content) seeds. Note that at the same relative humidity, snap bean seeds have higher water content than broccoli seeds.

(69) In addition, seeds with high lipid content generally have lower storability. This effect is observed in this table, which identifies the lipid content and half-viability period (P50) for different vegetable seeds. The half-viability period, P50, is defined as the period of time in years for viability to be reduced by half; in this case P50 was calculated after seed storage in ambient conditions. (70) This graph is based on the same data from the table, and the lower storability of seeds with higher lipid contents is more clearly observed. However, there are notable exceptions, (71) such as tomato. These exceptions are also observed in agronomic seeds. These results suggest that the total amount of lipids present in the seed is less important than the total amount of lipids present in the organ responsible for germination, i.e. the embryo. For example, wheat seeds contain only 3% lipids which should suggest good storability. However, wheat exhibits intermediate storability and this may be explained by the high lipid concentration in the wheat embryo, which is close to 30%.

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