Carbohydrates:

Plant Currency That You Should Understand

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Carbohydrates — organic molecules made up of carbon (C), hydrogen (H) and oxygen (O) typically in a 1:2:1 ratio — are the energy currency with which everything in plants operates, and understanding their metabolism is critical to understanding plant growth and development.

In plants, carbohydrates are produced via photosynthesis. Using the sun's energy, plant carbohydrate factories (aka, leaves, specifically the chloroplasts within leaves) take carbon dioxide (CO_2) from the atmosphere and combine it with water (H_2O) taken up by roots and turn them into carbohydrates and oxygen **(Figure 1)**. The simplest carbohydrate is glucose, $C_6H_{12}O_6$, and is the product of photosynthesis.

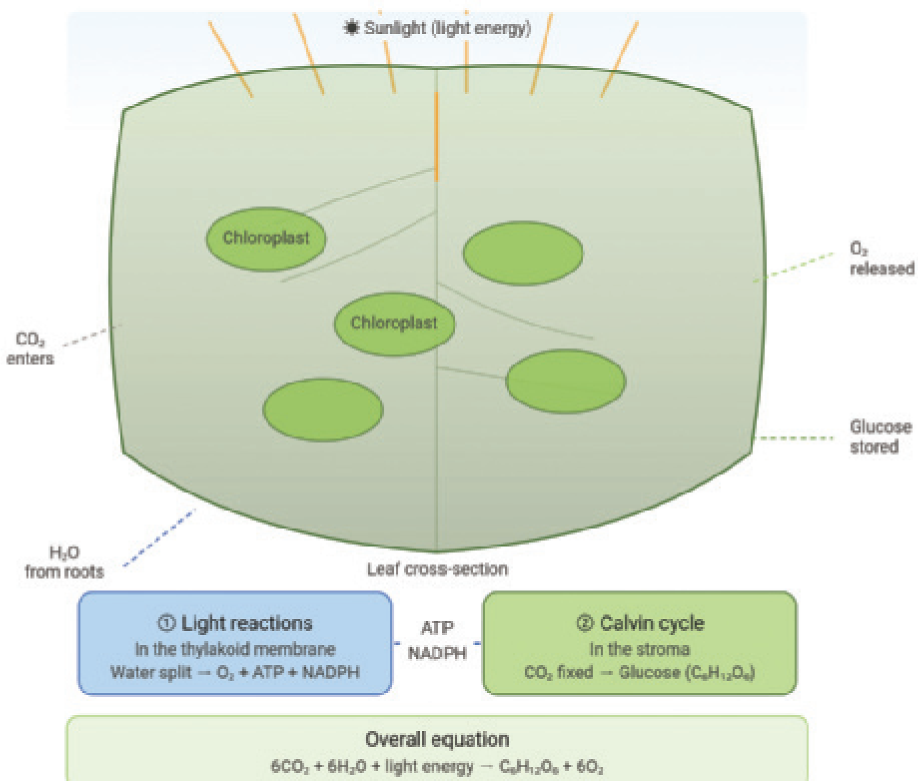

Figure 1. A diagram of a leaf cross-section showing the chloroplasts where photosynthesis reactions take place. First, water (H_2O) from the roots is split into hydrogen (H_2) and oxygen (O_2) in what are called light reactions. Second, carbon dioxide (CO_2) taken from the atmosphere is combined with the hydrogen from the light reactions to produce glucose. It takes six molecules of carbon dioxide and water to produce one molecule of glucose. The biproduct of photosynthesis is oxygen, which is released back to the atmosphere.

Glucose is converted to sucrose ($C_{12}H_{22}O_{11}$; essentially two glucose molecules combined) and transported by plants in phloem tissue to wherever energy is needed — sinks, such as growing shoots, fruit, and roots, generally in a downward direction **(Figure 2)**. The counterpart of the phloem is xylem, which transport water up from the roots and out to the atmosphere through leaves via transpiration.

If there is an excess of energy available, plants can link thousands of glucose molecules together into starch (a complex carbohydrate) for storage until it is needed. Starch can be stored at the source of carbohydrate production, leaves, or formed in other tissues after sucrose is transported to them. Typically, starch can be found at some level in all plant parts, but certain plant tissues are known for accumulating very large quantities of starch, such as potato tubers.

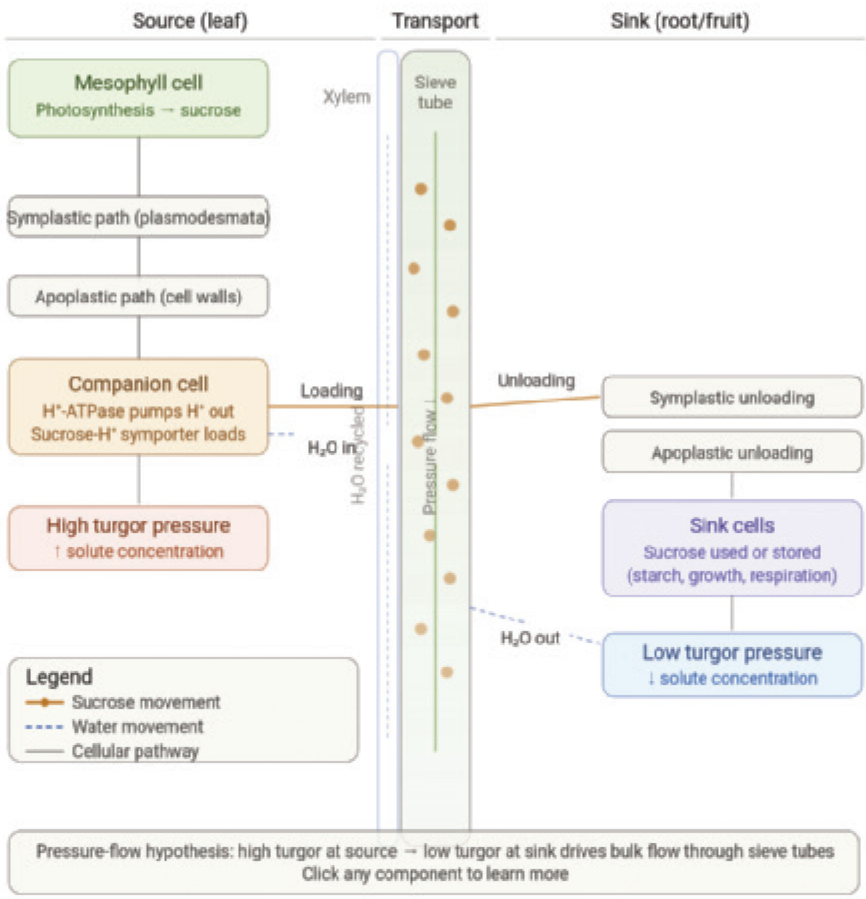

Figure 2. A diagram showing how glucose produced in leaves (source) is converted to sucrose for transport in the phloem to where energy is needed (sinks). The flow into, through and out of the phloem is by osmosis and concentration gradients. There is a high concentration of sucrose near the source (leaves) where sucrose is being loaded into the phloem and a low concentration at the sinks where sucrose is being removed from the phloem.

In a tree, such as avocado, the xylem tissue is wood, with the layers closest to the outside of the tree being active. The phloem is the "bark". Separating the xylem and phloem is the cambium, a tissue that is only a few cells thick, whose sole purpose is to create new xylem cells to the inside and new phloem cells to the outside **(Figure 3)**. Because the cells of the cambium are (nearly) constantly dividing and producing new cells they are not held together tightly, which is why the bark can be easily peeled off a tree when it is actively growing. This can be useful horticulturally such as when we are trying to graft plants.

Anything that disrupts the flow of carbohydrates down through the phloem will result in an accumulation of starch above the disruption as the concentration of glucose builds up. This is the basis for girdling, the process of removing a thin strip of bark around the circumference of a branch, to temporarily disrupt the phloem for horticultural reasons. In addition to the accumulation of starch, girdling also results in hormonal changes that can result in desirable changes above the girdle.

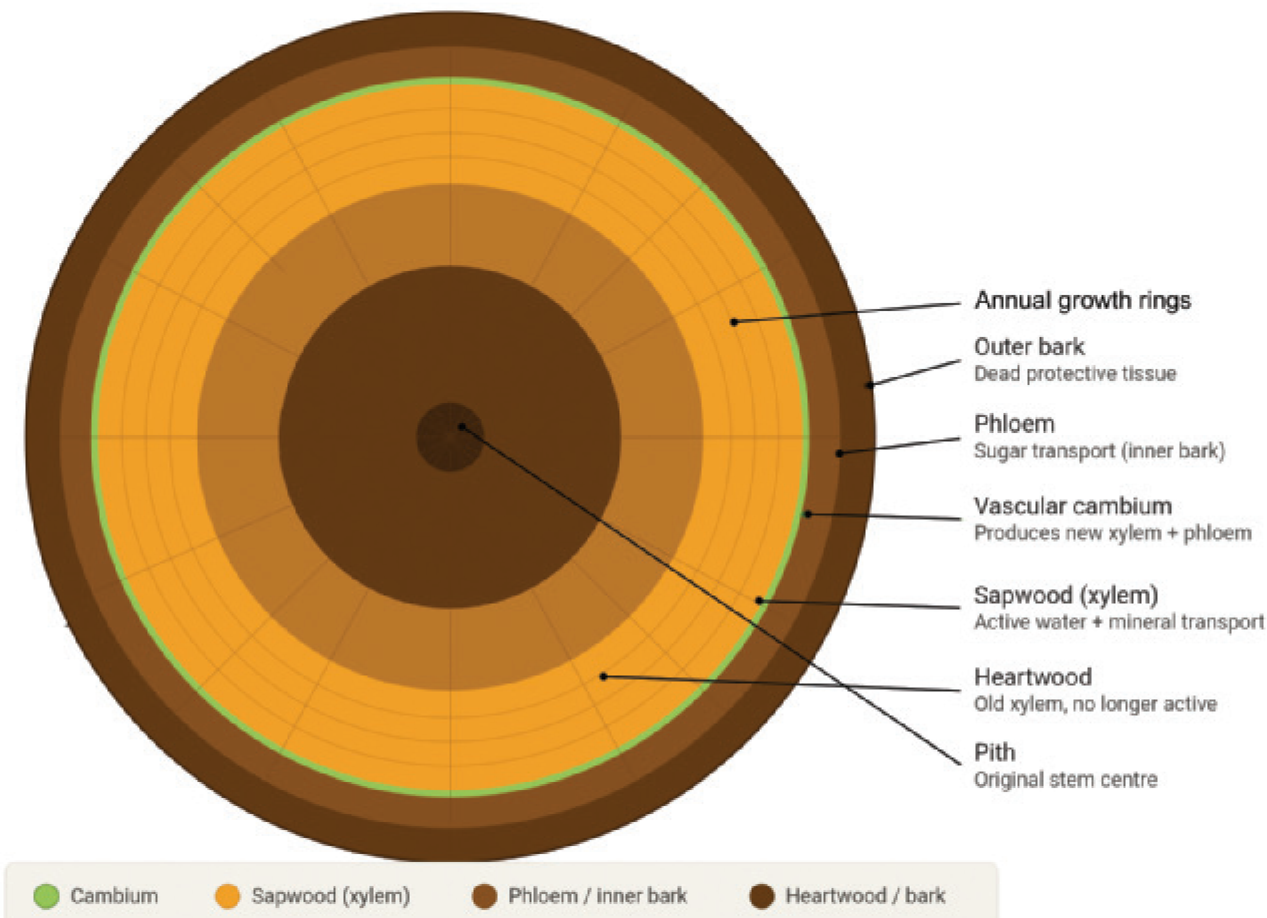

Figure 3. A diagram of a cross-section of a tree trunk. The green layer is the cambium, a thin layer of actively dividing cells that produce xylem to the inside and phloem to the outside. The youngest, active xylem tissue is what is commonly referred to as sapwood and older, inactive xylem is heartwood. The phloem closest to the cambium is active and as new phloem cells are produced the older cells die and are pushed to the outside to become bark.

What Do Carbohydrates Have to Do with Avocados?

The avocado is notorious for producing an abundance of flowers — reportedly as many as 1 million flowers per tree — but very few fruit — several hundred fruit per tree is considered a very good yield. Dr. Iñaki Hormaza, Professor at the Spanish National Research Council, has reported that the success of natural pollination, that is the percent of flowers produced on an avocado tree that eventually become fruit, is about 0.15% at 18-weeks after flowering. The natural tendency is to assume that this is due to poor pollination. However, when flowers are hand pollinated, they were only able to increase fruit-set to 2.8%. This suggests that something else is happening.

Dr. Hormaza and his team asked the simple question, "Are all avocado flowers equal?" The scientific literature suggests that flower quality, as defined by starch content of the flowers, plays a role in determining whether a flower can produce a fruit. This has been documented in olive and sweet pepper. Starch content can be easily quantified because it reacts with iodine, producing a dark blue-black color. Plant tissues can be briefly dipped in iodine and the level of staining quantified. Dr. Hormaza and his team performed this starch test on avocado flowers and found a ten-fold variation in flower starch content **(Figure 4)**.

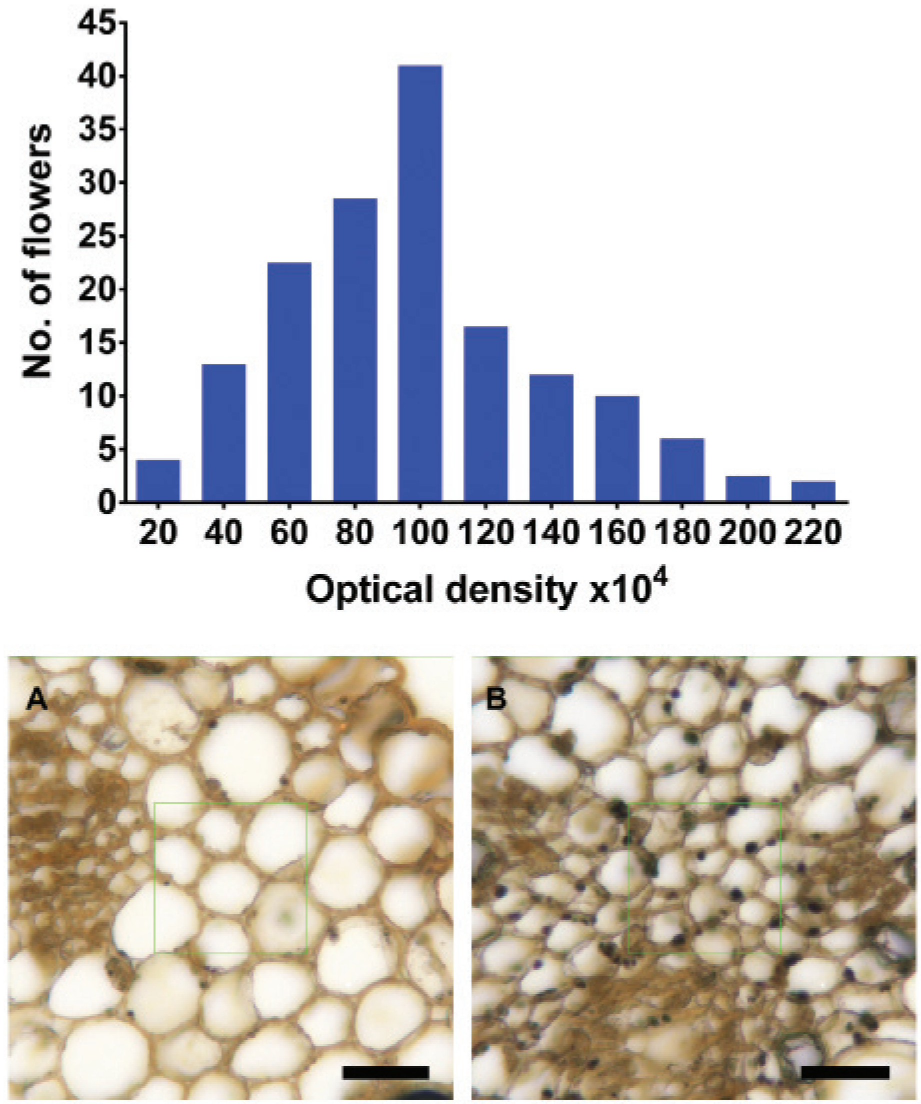

Figure 4. The starch content of individual avocado flowers measured as optical density of starch staining (top; redrawn from Hormaza, 2014, Factors Influencing Avocado Fruit Set and Yield). Iodine-stained sections of Hass avocado flowers with low (A) and high (B) starch content in the style (Image from: Alcazar et al., 2013).

The team then needed to figure out how to measure flower starch content, a destructive measurement, and determine if the flower they destroyed would produce a fruit. The female part of a flower, called the pistil, is composed of three main parts: the stigma, style and ovary **(Figure 5)**. The stigma is a surface at the tip of the pistil where pollen grains (male) land and germinate. When the pollen grain germinates it produces a pollen tube that grows down inside the style where it eventually reaches the ovary. Through the pollen tube passes the sperm cells that fertilize the ovule within the ovary to form the embryo inside the future seed. The fleshy part of the ovary eventually forms the flesh of the fruit. The pollen tube grows quickly and takes less than 24 hours to reach the ovary.

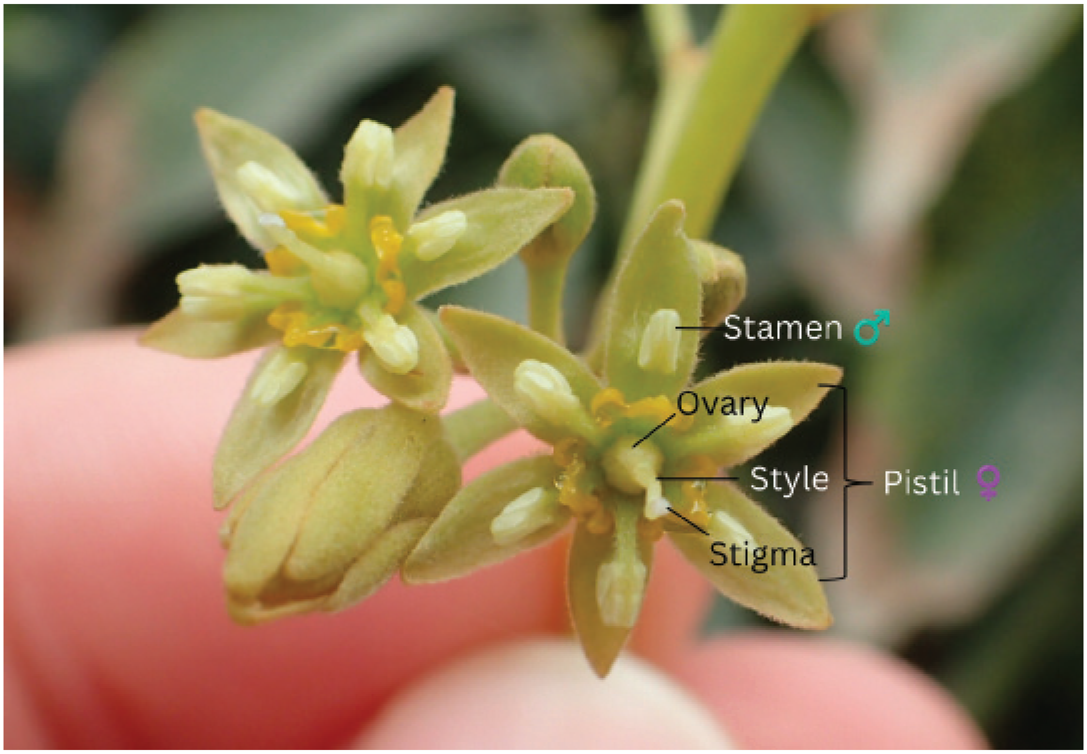

Figure 5. An avocado flower open in the female phase showing the pistil (female part of the flower) composed of the stigma, style and ovary, and the stamens (male parts of the flower) laid out flat around the flower and not shedding pollen.

The team found that they could remove the style 24 hours after pollination without affecting the fate of the flower. This allowed them to test the style for starch content, indicating the quality of the flower, while still tracking the fate of the flower (whether it produced a fruit) **(Figure 6)**.

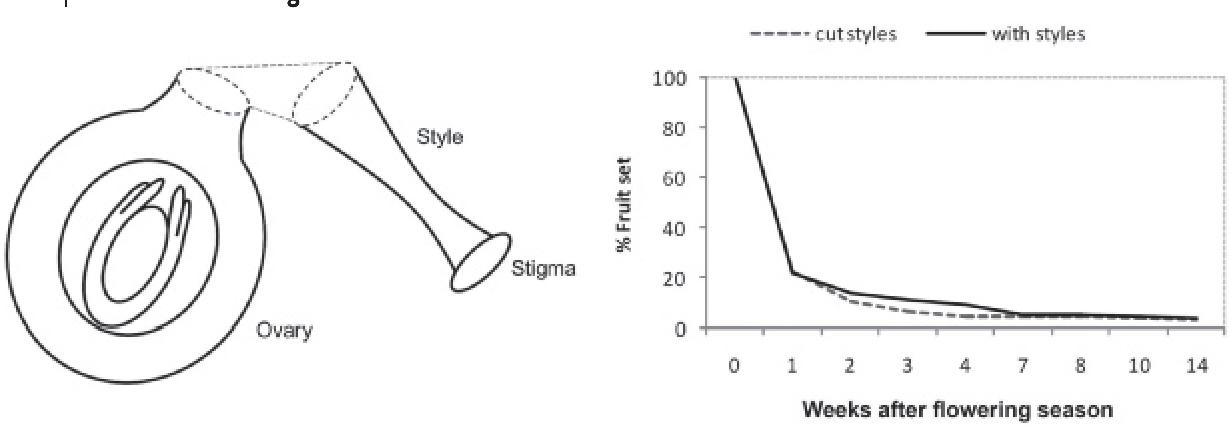

Figure 6. A diagram representing the pistil of an avocado flower showing how the style and stigma are removed (left; from Boldingh et al., 2016). Data showing that flowers with intact styles and flowers with cut styles perform the same 14 weeks after pollination and style removal (right, from Hormaza, 2014).

Dr. Hormaza's team initially conducted this work in Spain where they hand pollinated 597 individual Hass flowers on three different trees with Fuerte pollen. One day after pollination they removed the style from each flower to quantify the starch content and continued to track the fate of the flowers. Their data clearly indicated a strong correlation between starch content and fruit-set, with the flowers with the highest starch content having the highest chance of setting a fruit **(Figure 7)**.

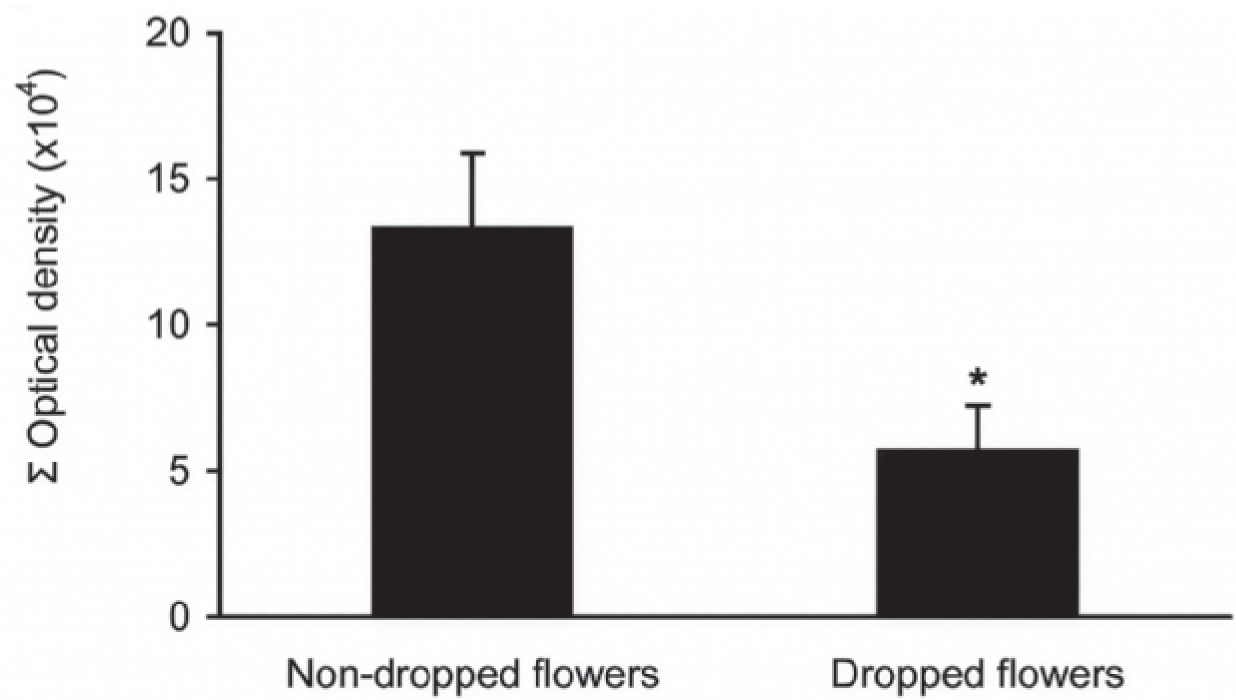

Figure 7. Starch content, reported as optical density, in the styles of flowers that produced a fruit (non-dropped flowers) and those that did not produce a fruit (dropped flowers).

A similar study was later conducted in New Zealand as well as Spain and looked at not only starch content of the styles, but also the content of different types of sugars and boron content. This study found similar results to the previous work conducted only in Spain with some variation between Spain and New Zealand **(Figure 8)**. The amount of total sugars and starch in the flowers was highly indicative of the fate of the flower. However, the relationship of individual types of sugars varied between the two countries. Interestingly, boron levels were strongly indicative of flower fate in New Zealand but not in Spain. The researchers attributed this to the low levels of boron found in New Zealand soils and the need for boron fertilization, whereas in Spain boron levels were higher.

Can You Affect Flower Quality?

A definitive study showing a relationship between cultural practices and flower quality has not been completed. However, we know that maintaining healthy leaves will naturally result in more photosynthesis and more carbohydrate production so it is logical that anything we can do to maintain or improve leaf health will ultimately affect flower quality.

If your water source is high in salinity, proper leaching is critical to leaf health. If leaves show signs of tip burn, they are not photosynthesizing at optimal levels, which may be affecting flower quality.

Pest infestations also can reduce leaf health and photosynthesis. The two most important pests to be mindful of are persea mite and avocado lace bug, which can significantly decrease leaf health if not properly controlled.

Proper fertilization also is very important. If your trees become yellow and partially defoliate during bloom, they are hungry. The yellowing is the result of nutrients, primarily nitrogen, being pulled from the leaves to support the bloom. You may consider several light nitrogen applications during the winter to boost your trees' nitrogen status prior to bloom. And as the New Zealand study showed, boron is very important. Make sure you are taking annual leaf samples in September or early October to assess your trees' nutrient status and work with your analytical lab, field rep or an agronomist to be sure your fertilizer program is optimized.

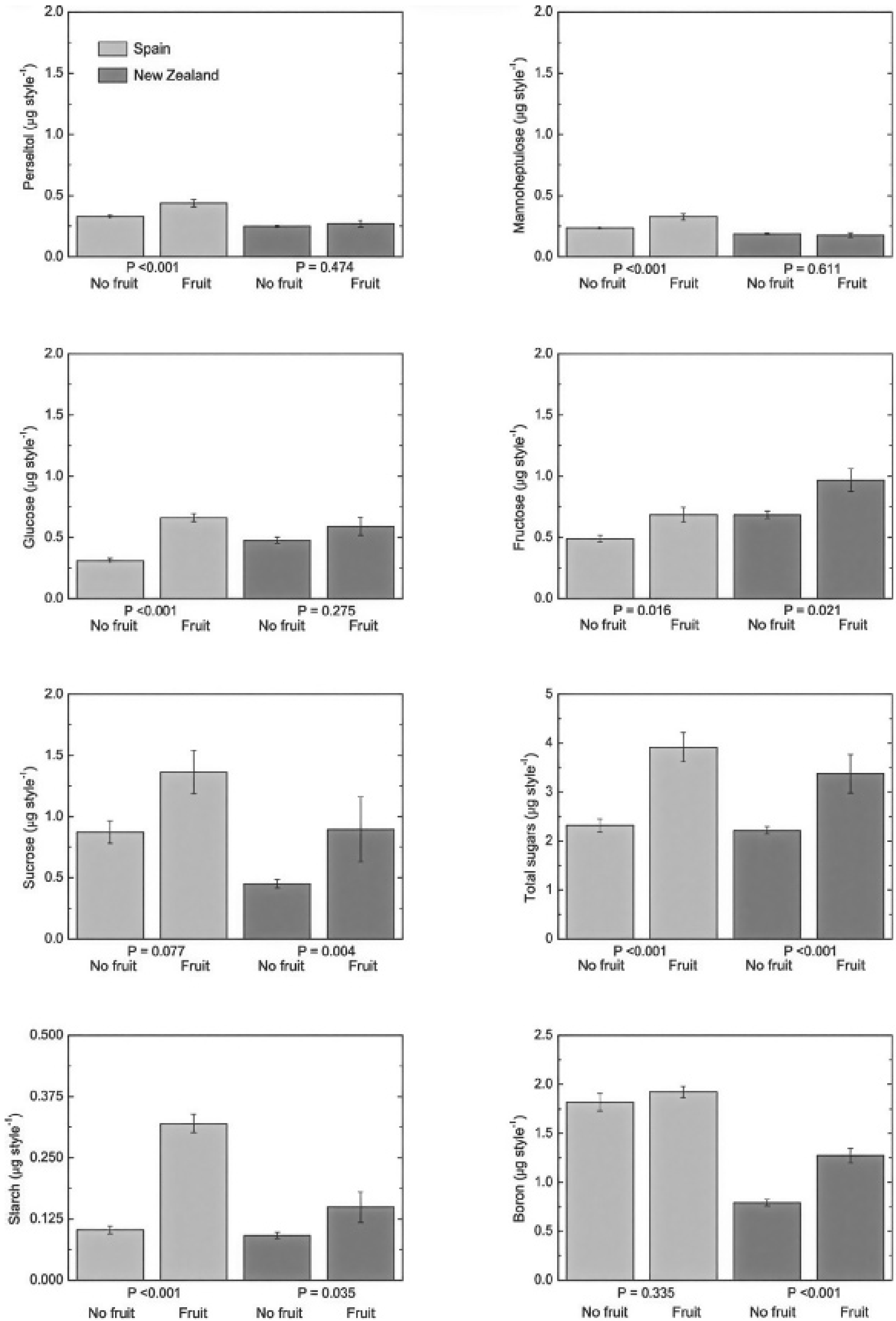

Figure 8. Carbohydrate (sugars and starch) and boron content of the styles of Hass avocado flowers at bloom in Spain and New Zealand. Styles were grouped based on whether the flowers from which they were harvested were successful (fruit) or unsuccessful (no fruit). Image from: Boldingh et al., 2016.