The Colors in Phosphorus Deficient Plants

By Tom Bruulsema

Purple or red coloring sometimes indicates P deficiency for some plant species; however, colored leaf margins seem to serve a wide variety of functions in plant acclimation to environmental stress.

Examining the physiology and biochemistry of pigment production explains some of the variable color responses. It also highlights the role of P in photosynthetic energy transfer, a role crucial to high-yield crop production systems.

"Not all purple plants are phosphorus deficient, and not all phosphorus deficient plants turn purple."

In some species, reddening or purpling of the leaf margin indicates that the plant is under some kind of stress, for example, P deficiency or freezing stress. But other species display these colors all the time, while some not at all. In most cases the pigment causing these colors is—or is presumed to be—anthocyanin. A recent review of potential ecological and physiological functions (Hughes and Lev-Yadun, 2015) brings out a lot of interesting points about these pigments and their relation to P deficiency.

Anthocyanins come in a wide range of colors. They are the same compounds that color flowers. The anthocyanins associated with P deficiency are usually red to purple. In some species, including corn, apples, pears, and strawberries, symptoms are most prominent on leaf margins (**Table 1**). Experiments with apples have shown that when a P deficiency is relieved, the red/purple color of the leaf margins subsides. In other species, for example tomatoes, the undersides between the veins turn purple. Other species—like sugar beet, rice, potato, and onions—don't change color at all, other than perhaps a deepening of greenness as the plant's growth is stunted. Chlorophyll contains no P, so in a deficient plant, chlorophyll may have higher abundance relative to P-containing compounds (Marschner, 1995).

Table 1. Crop species classed by P deficiency symptoms.

Red/purple on leaf margins	Red/purple in other places	None, or dark blue-green leaf
Apple	Cabbage	Onion
Canola	Eucalyptus	Potato
Corn	Sugar maple	Soybean
Lentil	Tomato	Sugar beet
Grape		Rice
Guava		
Pear		
Strawberry		
Sweet potato		

A question that intrigues plant scientists is why plants produce purple and red colors. Possibilities include undermining the camouflage of insect pests to make them more visible to their predators. Or "aposematism"—a warning signal to make the plant part look inedible or dangerous to pests that might be tempted to feed on the leaf. Insects see color, and red or

Abbreviations and notes: N = nitrogen; P = phosphorus.

A P-deficient corn leaf is not photosynthesizing at its maximum rate.

purple could look to them as if the leaf is either well-defended or not very nutritious to eat. Red leaves are generally lower in N and P—and thus less nutritious. They are also higher in phenolics, and anthocyanins themselves may be antinutritional for insects and other herbivores. In one New Zealand shrub species, the width of the red portion of the leaf margin correlated to higher levels of the plant defense compound polygodial and was associated with less damage from herbivory.

Birds are the most common predators of plant-eating insects, and they too see color. Thus a non-green color on the leaf margin can help them find and consume the herbivore insects that have green camouflage. Birds are also smart enough to learn that a leaf margin with breaks from insect feeding is a sign of greater likelihood of finding a caterpillar. A plant that colors its margins will show these breaks more conspicuously.

Pigments can play a role in helping plants deal with excess uptake of certain trace elements. The trace elements can include excess amounts of nutrients like boron (B), cobalt (Co), iron (Fe), manganese (Mn), molybdenum (Mo), nickel (Ni) and zinc (Zn), and other metals like aluminum (Al), cadmium

An extreme example of purpling on the underside of a tomato leaf.

The P-deficient soybeans (right) show no sign of red or purple color.

Even a severe P deficiency in a potato leaf shows no sign of red or purple margins – but the whole leaf may turn a deep bluish green.

(Cd), lead (Pb), and silver (Ag). Several kinds of anthocyanins can chelate metal ions with two or three positive charges. Trace elements are often found to accumulate more at the leaf margins than elsewhere.

Anthocyanin pigments can help plants defend themselves from environmental stresses. They do this by blocking visible and ultraviolet wavelengths of light. They also play an antioxidant role. Both roles are called "photoprotection" and are important in situations where a leaf is exposed to more light than it can use, or more light than it can process in photosynthesis.

Within plant cells, chloroplasts use what is called the Calvin-Benson cycle to harvest the energy of sunlight to make three-carbon sugar phosphates from atmospheric carbon dioxide. Part of the energy is stored in the bond of the phosphate to the sugar. But to move these sugar phosphates out of the chloroplast, the phosphate supply needs to be replenished. If the supply of phosphate in the chloroplasts is depleted, photosynthesis slows down for several reasons. One, not enough phosphate remains available to continue making new sugar phosphates. Two, the chloroplasts accumulate starch, and starch accumulation feeds back to inhibit photosynthesis. The amount of light energy entering the chloroplasts is still the same. That light energy, interacting with chlorophyll and other light-harvesting

Phosphorus deficiency in canola.

Phosphorus deficiency observed in guava.

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Phosphorus deficient lentil plants showing purple lower leaves.

molecules, can produce oxygen free radicals and other damaging oxidative chemicals. When plants respond by producing anthocyanins to protect the chloroplasts from oxidative damage, these non-green pigments also curb maximum photosynthetic capacity.

Environmental stress situations occur with low temperatures, water deficit, low leaf N and P, and light-sensitive stages of leaf development. Leaf margins can be particularly vulnerable to all of these stresses, and thus colors can show there first, rather than across the whole leaf (except N deficiency, which shows symptoms first in the center of most leaves). Leaf margins dry out and experience cold more quickly than the rest of the leaf. They are also further removed from nutrient transport in xylem and phloem tissue, making them last to receive nutrients. In at least some species, leaf tissue is more tightly packed, and the surface has fewer stomatal pores near the margins, and thus internal carbon dioxide levels may be lower owing to restricted diffusion. Lower carbon dioxide means more potential for oxidative damage.

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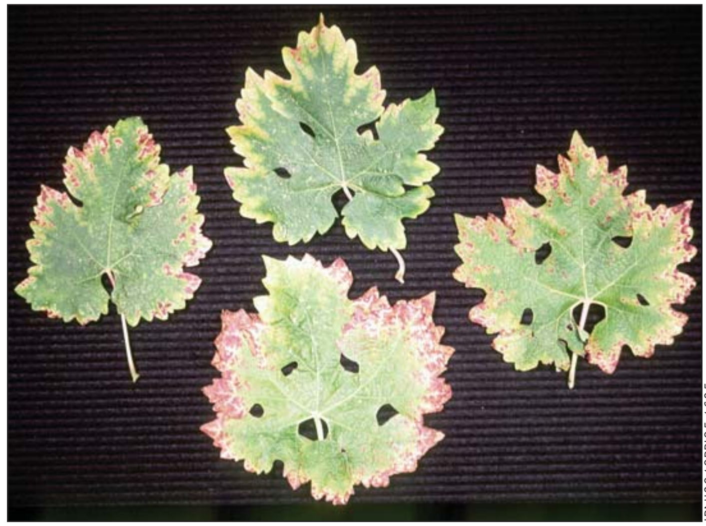
Phosphorus deficiency in sweet potato.



IPNI2010PPI05-1685

Cabernet Sauvignon grape leaves showing purple margins.

Source/sink imbalance is also often associated with red/purple coloring. Within the cells of green plant tissue, P plays key roles in the source/sink balance, because of its involvement in the steps of conversion of carbon dioxide to the various forms of sugars and starches, and transport of sugars.

So what does it all mean for managing P? First, visual symptoms don't stand alone but need backup from soil testing, plant analysis, and growth comparisons. Second, it's clear from the biochemistry that P is involved in the photosynthetic core of any high-yield crop production system, the crucial point at which energy is transformed from light into sugar and then into the myriad of unique compounds that plants provide for us. So as we develop plant production systems for ever higher levels of productivity and sustainability, we need to continue refining assessment methods for assuring the right P nutrition for all crops in the system for every day of their growth cycle. BC

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Whole lower leaves in P-deficient cabbage showing red/purple.

Dr. Bruulsema is Director, IPNI Phosphorus Program, Guelph, ON, Canada. E-mail: tombruulsema@ipni.net

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