Prospects for using environmental levers in greenhouses to stimulate plant defences and the quality of fruits and vegetables.

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Prospects for Using Environmental Levers in Greenhouses to Stimulate Plant Defences and the Quality of Fruits and Vegetables

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Abstract

The environment of greenhouses is commonly modified to reduce the pressure of pests and diseases, but it can also be exploited to stimulate natural defences of plants. In addition to genetic influences, several agronomic factors can be used as levers to increase the concentrations of secondary metabolites involved in the defence of fruit and vegetable crops. Many secondary metabolites involved in plant defences are also phytonutrients, i.e., compounds that have beneficial effects on human health, including protection against cardiovascular diseases, cancers, and metabolic or neurodegenerative diseases. Nitrogen deprivation, photooxidative stress and exposure to specific wavelengths such as those supplied by UV radiations are well known for stimulating the production of secondary metabolites in a large range of plants. We propose here a review of factors meeting the specifications of organic farming, which are both effective and applicable in greenhouse conditions. Among all these factors, mild stress and innovative covering materials emerge as especially promising.

INTRODUCTION

Plants produce a diverse set of organic molecules, some of which are traditionally considered not to participate directly in the major processes involved in growth and development. These substances, secondary metabolites, encompass terpenes (e.g., carotenoids, vitamin E), phenolic compounds (e.g., stilbenes, flavonoids, anthocyanins), nitrogen-containing compounds (e.g., alkaloids, glucosinolates), and sulfur-containing compounds such as diallyl disulfide (Goldberg, 2003). They play many roles in plants. Some of the secondary metabolites are involved in defence functions or are antioxidants, which indicates that they have strong biological effects. Some have positive dietary effects, and some even have medicinal properties. It is well established that fruits and vegetables (FAVs) represent a major source of useful secondary metabolites, the so-called phytochemicals (Kaur and Kapoor, 2001). The high concentrations of phytochemicals in FAVs are considered to exert protective effects against cardio-vascular diseases, metabolic diseases (e.g., obesity, diabetes), neuro-degenerative diseases (e.g., Parkinson's, Alzheimer's) (UNESCO, 2008), and certain forms of cancer (Jansen et al., 2013; Park et al., 2013). Although the nutritional benefits of fresh FAVs are well established, their consumption remains insufficient. In developed countries, it may be tempting for the fruit and vegetable industry to offer consumers FAVs with increased or guaranteed amounts of micronutrients (Dorais and Ehret, 2008; Poiroux-Gonord et al., 2010). This could help the cause of public health while contributing to the competitiveness of the industry in a more and more challenging global market. There are basically two ways to reach the objective of increased or guaranteed amounts of micronutrients in FAVs: the genetic approach and the environmental approach. A recent survey of the existing literature provided evidence that agronomic methods may stimulate an increase in the concentrations of secondary metabolites of FAVs, likely without attaining undesirable levels (Poiroux-Gonord et al., 2010). The good news for greenhouse growers is that they have a much wider range of environmental levers at their disposal than growers in open field conditions.

This review will cover the most common environmental levers exploitable in organic greenhouse conditions to increase the concentrations of phytochemicals in FAVs. Then we shall discuss the consequences regarding plant natural defences.

THE STRESS THEORY

The stress theory is based on the idea that all stresses stimulate the production of secondary metabolites by generating an oxidative stress, i.e., the production of Reactive Oxygen Species (ROS), namely O_2^-, $^1O_2$, and H_2O_2. There is a large body of evidence that all biotic and abiotic stresses are conducive to oxidative stress, and more specifically to photooxidative stress, i.e., the production of ROS associated with the functioning of the photosynthetic machinery (Grassmann et al., 2002) as shown in Figure 1. The photosynthetic machinery is considered to be the major contributor to the production of ROS in green plant parts, and even in plant parts that have lost their photosynthetic machinery. The synthesis of carotenoids can be stimulated in the pulp of non-stressed fruits that lost their chlorophyll by submitting nearby leaves to photooxidative stress (Poiroux-Gonord et al., 2013b). Other physiological processes can be involved in ROS production as a consequence of stress, such as mitochondrial respiration and activity of the membrane-located NADPH oxidase. Generally, plants are well equipped to deal with ROS. However, even small and transient accumulations of ROS or the associated imbalances in redox status are involved in the stimulation and regulation of processes that eventually lead to the production of secondary metabolites (Fanciullino et al., 2013). There is ample evidence that ROS either directly or indirectly influence the expression of genes of the biosynthetic pathways, arguably via the redox-sensitive thiols-disulfite systems. Moreover NADPH, whose availability dependsin part on the scavenging activity of the ascorbate-glutathione cycle, and thus the abundance of ROS, is required by several steps of the biosynthetic pathways of terpenes and glucosinolates. The idea that oxidative stress stimulates the secondary metabolism makes sense from a deterministic point of view since many secondary metabolites are involved either directly or indirectly in the defence against oxidative stress.

The scientific literature abounds in references about the positive effects of mildly stressing conditions (e.g., drought, high salinity or electrical conductivity, NaCl, high light, low temperature) on the concentrations of carotenoids and phenolic compounds in FAVs (Maggio et al., 2011; Poiroux-Gonord et al., 2010). Some growing systems could be more favourable to the accumulation of phytonutrients in FAVs than others. It has been hypothesised that organic FAVs could be richer in secondary compounds because organic plants are less intensively managed (e.g., plants in conventional growing systems are better protected against pests and diseases by pesticides, in contrast to plants in organic systems) (Urban, 2009). The idea that organic tomatoes are better because they are picked from plants that have undergone oxidative stress has received some support by a recent study (Oliveira et al., 2013).

THE CARBON THEORY

The carbon theory stipulates that carbohydrate concentration determines the synthesis of both primary and secondary metabolites. While ecologists still debate the relationships between the primary and secondary metabolisms in terms of competition or optimal allocation (Herms and Mattson, 1992; Loomis, 1932; Wilkens et al., 1996), there is mounting evidence from physiological studies that availability of resources does not necessarily directly determine the synthesis of all types of secondary metabolites in all plant organs (Fanciullino et al., 2013). This idea certainly has merits as far as defence compounds are concerned, but there are contradictory observations. In leaves, accumulation of carbohydrates generally represses the synthesis of carotenoids; whereas in fruits, low availability of carbohydrates may reduce carotenoid concentrations of (Poiroux-Gonord et al., 2013a). It is interesting to note that there are links between the stress and carbon theories. On the one hand, sugars play a generally positive role in the protection of cells against ROS. Soluble sugars can feed NADPH-producing metabolic processes such as the oxidative pentose-phosphate pathway. On the other hand, sugars are potentially exacerbating factors of photoinhibition and the associated production of ROS in photosynthetic tissues (Urban and Alphonsout, 2007). To summarise, manipulation of the carbon lever does not reliably generate predictable results in terms of concentrations of useful secondary metabolites. Moreover, manipulating a plant's primary metabolism may reduce yield and quality criteria such as harvested organ size, dry matter content and concentrations in sugars and organic acids.

THE EFFECT OF NITROGEN DEPRIVATION

One may be tempted to provoke a nitrogen deficit in plants. It is well established that nitrogen deprivation stimulates the Phenyl Ammonia Lyase (PAL) which is the first enzyme of the biosynthetic pathway of phenolic compounds. The PAL is also a rate-determining enzyme, which means that stimulating the PAL will actually result in the accumulation of end-of-the-chain phenolic compounds. Recent observations suggest that phenolic compounds do not accumulate in tomato fruit as a consequence of nitrogen deprivation (Bénard et al., 2009); however, defence compounds such as tomatine, a glycoalkaloid, do accumulate in other plant parts (Royer, 2013). This said, it could be risky to recommend a substantial reduction in nitrogen supply because nitrogen is the major ingredient of the photosynthetic machinery. In other words, nitrogen deficit would automatically result in a decrease in photosynthetic capacity, net photosynthetic rate, and eventually, commercial yield.

THE EFFECT OF SPECIFIC WAVELENGTHS

Evidence exists that the light spectrum provides opportunities for stimulating the synthesis of secondary metabolites in plants, especially in FAVs. For instance, red light increased concentrations of anthocyanins in tomato fruit (Mancinelli, 1985), whereas blue light increased concentrations of carotenoids (Gautier et al., 2005). Even green light, long believed to play no role in plants, has recently been reported to increase the concentration in anthocyanins in lettuce (Samuolienė et al., 2013). Ultraviolet (UV) radiations also have been observed to stimulate the synthesis of secondary metabolites (Jansen et al., 2008) and can be exploited to stimulate natural defences against diseases such as grey mould (Charles et al., 2008, 2009). An interesting perspective with the effect of light is that the spectrum can be easily modified in greenhouses, either by using innovative plastic materials or by using LED lamps. Depending on organic regulations, artificial lighting with specific wavelengths may not be acceptable for some organic growers. There is still a lot of work ahead to find the right combinations of wavelengths that will prove beneficial to both yield and quality or defences, but there is little doubt that innovation in plastic materials and LEDs will foster the development of greenhouse systems that will perform substantially better in terms of yield and quality than the existing systems.

THE CROSS-TALK THEORY

Complex signalling pathways involving ROS and the production of defence compounds, including secondary metabolites (e.g., terpenoids, phenolic compounds, glucosinolates) originate from biotic stresses (Fig. 2). The idea that responses to biotic and abiotic stresses share, to a certain extent, the same signalling and metabolic pathways has been extensively discussed and theorised, giving birth to the so-called cross-talk theory (Fujita et al., 2006; Orsini et al., 2010). This scientific concept holds many interesting perspectives for growers. For instance, abiotic stress could be exploited to increase plants' resistance to pests. The possibility of using stimulators of natural plant defences to increase the concentrations of phytonutrients has not formally been tested to our knowledge, but there is good hope that it will work. Similarly, it would be interesting to test the idea that tolerant or resistant cultivars may also be better in terms of micronutritional value. There are known limits to the cross-talk theory and to what can be achieved, but at least this theory clearly shows that the issue of nutritional quality and the issue of plant defences should be addressed jointly.

CONCLUSION

Environmental factors represent powerful natural levers to increase concentrations of secondary metabolites in plants, which should benefit both plant defences and produce quality. While modifying the carbon status and creating conditions of nitrogen deficit are certainly effective methods regarding this objective, they must be used with caution because of the negative effects they may produce in terms of yield and quality. Specific light wavelengths could be exploited in greenhouses by using innovative plastic covering materials or LED lamps. In addition, oxidative stress could be applied by reducing irrigation, ideally at the end of the cropping cycle, at a time when the benefits of a mild stress will have only a very low, if any, negative side-effect on yield. All the exciting and promising observations made and ideas expressed should represent a strong incentive to develop techniques that will stimulate plant defences and improve the micronutritional quality of produce. It seems only too natural that organic growers take the lead in that field.

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Figures

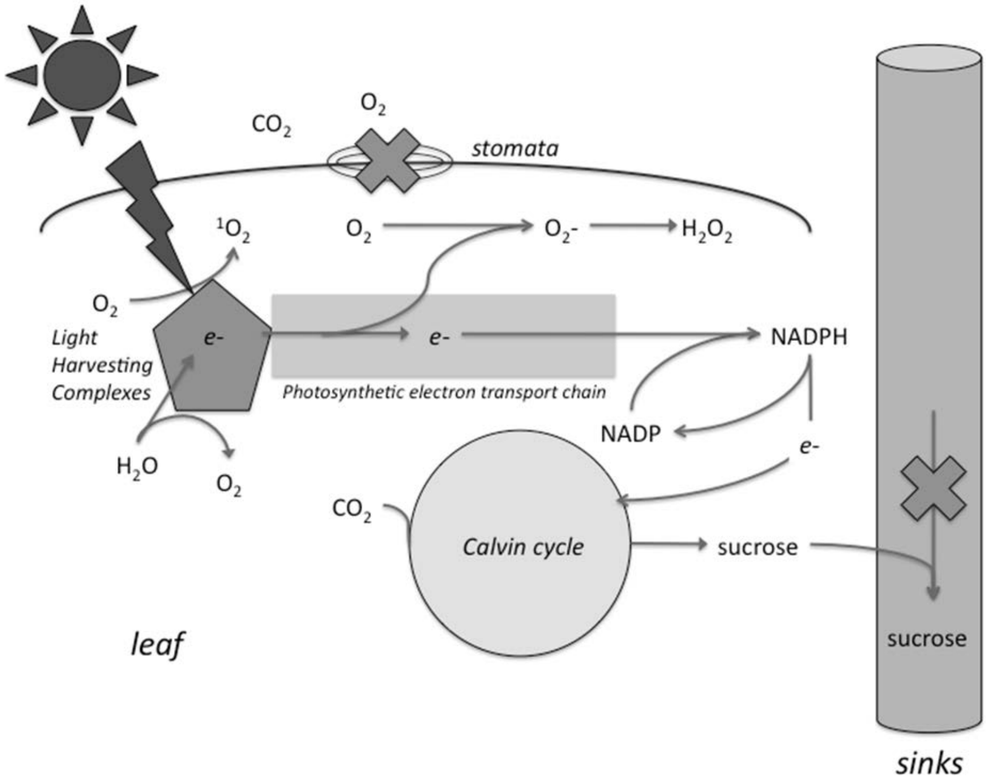

Fig. 1. Photooxidative stress. Crosses indicate common limitations to photosynthesis that create conditions favorable to the production of Reactive Oxygen Species.

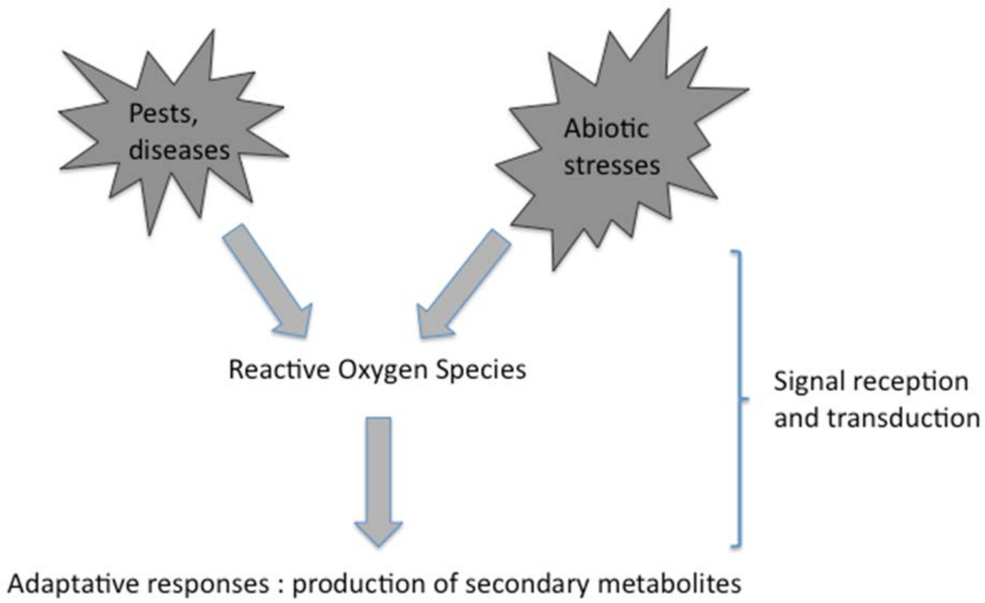

Fig. 2. Illustration of the cross-talk theory and its implications for the production of secondary metabolites.