Sensing the energetic status of plants and ecosystems

Josep Peñuelas[1,2], Mireia Bartrons[1,2], Joan Llusia[1,2], Iolanda Filella[1,2]

[1]CSIC, Global Ecology Unit CREAF-CSIC-UAB, Cerdanyola del Vallès 08193, Catalonia, Spain

[2]CREAF, Cerdanyola del Vallès 08193, Catalonia, Spain

Corresponding author: Peñuelas, J. (josep.penuelas@uab.cat).

Keywords: monitoring of energetic status, NADPH/NADP, PRI, BVOCs, isoprenoids, plants, ecosystems

Abstract

The emerging consistency of the relationship between biochemical, optical and odorous signals emitted by plants and ecosystems offers promising prospects for continuous local and global monitoring of the energetic status of plants and ecosystems, and therefore of their processing of energy and matter.

NADPH/NADP as biochemical indicator of reducing power

Photosynthesis converts solar energy into chemical energy in the form of reducing power (NADPH) which is essential for the primary metabolism. Plants very often generate more reducing power than is needed for their primary metabolism, for example under light saturation or stressful conditions. The NADPH/NADP ratio thus becomes an excellent biochemical indicator of this over-reduction of the photosynthetic electron-transport chain and thus of the cellular energetic status of plants. Indeed, this ratio has been used as a biochemical indicator of changes in the availability of reducing power linked to stressors such as drought [1], high light [2], salinity [3], nutrient deficiency [4] or pathogens [5].

Reflectance and fluorescence signals

The rate of electron transport is down-regulated by various mechanisms to overcome the over-reduction of the photosynthetic electron-transport chain and to dissipate the excess energy signaled by high NADPH/NADP ratios. The dissipation of energy by non-photochemical quenching through the xanthophyll cycle is one of these mechanisms. It is especially interesting because it can provide an indirect optical signal of excess reducing power, increased NADPH/NADP ratios and reduced light-use efficiency (LUE) through the associated changes in reflectance at the blue side of the green region of the spectrum. Increases in the concentration of zeaxanthin translate into decreases in reflectance at 531 nm, while reflectance at 570 nm is insensitive to short-term changes in zeaxanthin. The Photochemical Reflectance Index (PRI), defined as $[R_{531}-R_{570}]/[R_{531}+R_{570}]$ where R indicates reflectance and the numbers indicate wavelength in nanometers [6, 7], is thus used as a reflectance index for reducing power and LUE. The PRI also measures the relative reflectance on either side of the green reflectance "hump" (550 nm), i.e. the reflectance in the blue side of the green region of the spectrum (chlorophyll and carotenoid absorption) relative to the reflectance in the red side (chlorophyll absorption only). The PRI consequently also behaves as an index of the chlorophyll/carotenoid ratios and therefore of the energetic status and photosynthetic activities associated with changes in chlorophyll/carotenoid ratios throughout foliar development, aging or stress [8]. The PRI estimation of LUE and photosynthetic performance has been studied extensively at the leaf and canopy levels and is now also increasingly used at the ecosystem level [9].

In addition to changes in reflectance such as those monitored with the PRI, the shifts in energetic status translate into changes in fluorescence and temperature that may thus become relevant optical signals of different stresses. Two major fluorophore groups that dominate plant fluorescence emissions can potentially be sensed remotely. The first group of compounds, which includes NADPH itself, emits photons in the blue and green spectral regions under natural or artificial UV excitation, but it is Chlorophyll a (Chl a) the fluorophore that contributes most to plant fluorescence. Chl a emits fluorescence in two broad bands with peaks at 684–695 and 730–740 nm. Various ratios of fluorescence intensity, combining the emissions at blue (F440), green (F520), red (F690) and far-red (F740) wavelengths, have been proposed for probing the status of vegetation vitality and stress responses, but the relationship between fluorescence and photochemistry is complex [10].

Further research is clearly warranted to understand better the temporal and spatial dynamics of these reflectance and fluorescence signals and their relationships with the energetic status, reducing power and LUE of plants and to resolve the problems that may still preclude the generalization of their use at ecosystemic and biospheric scales. In brief, these problems are related to the structural differences of canopies, to varying “background effects” (e.g. soil color, moisture, shadows or the presence of other non-green landscape components), to the effects of seasonality or to the signals derived from variations in illumination and viewing angles [10, 11]. The emerging consistency of the relationships among the PRI, sun-induced fluorescence (SIF), LUE and ecosystemic CO_2 uptake [9, 12], however, suggests a surprising degree of "functional convergence" of biochemical, physiological and structural components affecting ecosystemic carbon fluxes. In other words, ecosystems possess emergent properties that may allow us to effectively explore their seemingly complex photosynthetic-energetic behavior using surprisingly simple optical sampling methods based on energetic status, such as the measurement of the PRI or SIF. The enormous potential benefits are worth exploring.

Odorous signals

Plants and ecosystems emit not only optical signals (reflectance and fluorescence) of their physiological status associated with the imbalance between supply and demand of reducing power; they also emit “scents” of such status. The excess reducing power and higher NADPH/NADP ratios generated when the NADPH sink in carboxylation decreases also increases the synthesis of highly reduced secondary metabolites, including volatile metabolites such as isoprenoids that are then emitted in significant amounts [13, 14]. The synthesis and emission of isoprenoids would be highest when the demand of carbon assimilation for reducing power is lowest [13, 14]. In fact, isoprene and monoterpene emissions increase when LUE decreases [15], which has driven the use of the PRI signal for estimating not only carbon fixation but also isoprenoid emissions themselves [15]. Isoprenoids are emitted at the nanomolar scale, but electron flux involved in the NADPH/NADP ratio is at the micromolar scale, so the emission is not a matter of mass balance of competing processes but of an enhancement under higher flow.

Monitoring of the energetic status

We thus propose that the energetic status of plants (and ecosystems) resulting from the balance between the supply and demand of reducing power can be assessed biochemically by the cellular NADPH/NADP ratio, optically by using reflectance and fluorescence as indicators of the dissipation of excess energy, and odorously by the emission of volatile organic compounds such as isoprenoids, as indicators of an excess of reducing equivalents. These signals can provide information on the energetic status, the associated health status and the functioning of plants and ecosystems. The integration of these three ways of assessing the excess of reducing power in different species and ecosystems with different ecophysiological traits will provide further knowledge of the links among the three signals and the strategies of the different species to deal with excess of energy. These signals and their integration are thus of academic interest, but may also have multiple applications for environmental and agricultural monitoring, e.g. by extending the spatial coverage of carbon-flux observations to most places and times, or/and for improving the process-based modeling of carbon fixation and isoprenoid emissions from terrestrial vegetation at ecosystemic and global scales. Significant benefits can thus be expected if we are able to solve the considerable challenges that remain for a wide-scale and routinary implementation of these biochemical, optical and odorous signals for ecosystemic and/or agronomic monitoring, a key issue in global ecology, agricultural applications, the global carbon cycle and Earth science.

Acknowledgments

The authors would like to thank the European Research Council Synergy grant ERC-SyG-2013-610028, IMBALANCE-P, the Spanish Government grant CGL2013-48074-P and the Catalan Government grant SGR 2014-274.

References

1 Khanna, S.*, et al.* (2014) Glycolytic enzyme activities and gene expression in *Cicer arietinum* exposed to water-deficit stress. *Applied Biochemistry and Biotechnology* 173, 2241-2253

2 Shen, W.*, et al.* (2015) High light acclimation of *Oryza sativa* L. leaves involves specific photosynthetic-sourced changes of NADPH/$NADP^+$ in the midvein. *Protoplasma* 252, 77-87

3 Lokhande, V.*, et al.* (2011) Regulated alterations in redox and energetic status are the key mediators of salinity tolerance in the halophyte *Sesuvium portulacastrum* (L.) L. *Plant Growth Regulation* 65, 287-298

4 Ostaszewska, M.*, et al.* (2014) Long-term sulphur starvation of *Arabidopsis thaliana* modifies mitochondrial ultrastructure and activity and changes tissue energy and redox status. *Journal of Plant Physiology* 171, 549-558

5 Mhamdi, A.*, et al.* (2010) Cytosolic NADP-dependent isocitrate dehydrogenase contributes to redox homeostasis and the regulation of pathogen responses in *Arabidopsis* leaves. *Plant, Cell & Environment* 33, 1112-1123

6 Gamon, J.A.*, et al.* (1992) A narrow-waveband spectral index that tracks diurnal changes in photosynthetic efficiency. *Remote Sensing of Environment* 41, 35-44

7 Peñuelas, J.*, et al.* (1995) Assessment of photosynthetic radiation-use efficiency with spectral reflectance. *New Phytologist* 131, 291-296

8 Filella, I.*, et al.* (2009) PRI assessment of long-term changes in carotenoids/chlorophyll ratio and short-term changes in de-epoxidation state of the xanthophyll cycle. *International Journal of Remote Sensing* 30, 4443-4455

9 Garbulsky, M.F., *et al.* (2011) The photochemical reflectance index (PRI) and the remote sensing of leaf, canopy and ecosystem radiation use efficiencies: A review and meta-analysis. *Remote Sensing of Environment* 115, 281-297

10 Porcar-Castell, A., *et al.* (2014) Linking chlorophyll a fluorescence to photosynthesis for remote sensing applications: mechanisms and challenges. *Journal of Experimental Botany* 65, 4065-4095

11 Hilker, T., *et al.* (2010) Remote sensing of photosynthetic light-use efficiency across two forested biomes: Spatial scaling. *Remote Sensing of Environment* 114, 2863-2874

12 Guanter, L., *et al.* (2014) Global and time-resolved monitoring of crop photosynthesis with chlorophyll fluorescence. *Proceedings of the National Academy of Sciences* 111, E1327-E1333

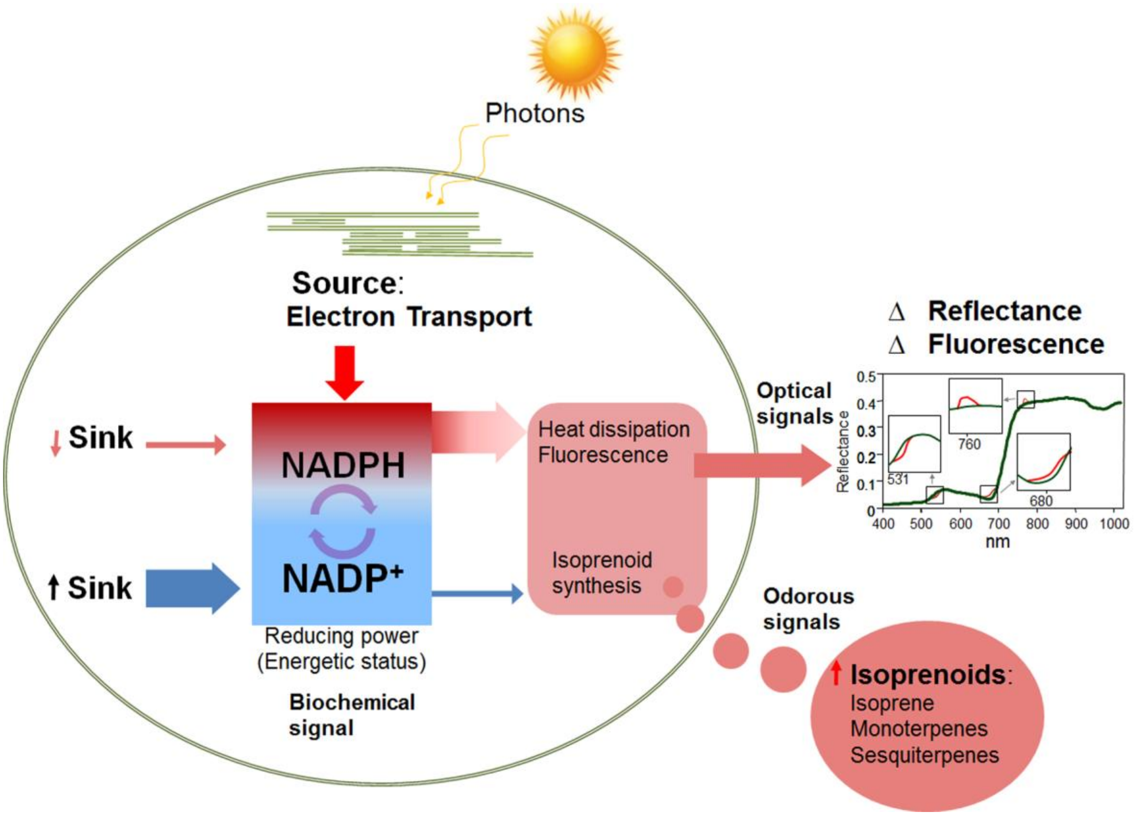
13 Owen, S.M. and Penuelas, J. (2005) Opportunistic emissions of volatile isoprenoids. *Trends in Plant Science* 10, 420-426

14 Morfopoulos, C., *et al.* (2014) A model of plant isoprene emission based on available reducing power captures responses to atmospheric CO_2. *New Phytologist* 203, 125-139

15 Penuelas, J., *et al.* (2013) Photochemical reflectance index as an indirect estimator of foliar isoprenoid emissions at the ecosystem level. *Nature Communications* 4, 2604

Figure caption

Figure 1. Overview of the biochemical, optical and odorous signals in response to changes in the reducing power of plants. The energetic status of plants (and ecosystems) resulting from the balance between the supply and demand of reducing power can be assessed by the resulting biochemical changes in the cellular NADPH/NADP ratio, optical changes in the foliar reflectance and fluorescence, and changes in production and emission of odorous volatile organic compounds such as isoprenoids.



Submitted version of: Peñuelas, J. et al. “Sensing the energetic status of plants and ecosystems” in Trends in plant science, vol. 20, no. 9 (sep. 2015), p. 528-530 (Elsevier). The final version is available at DOi 10.1016/j.tplants.2015.07.002