Chapter 4

Characteristics and Species-Dependent Employment of Flexible Versus Sustained Thermal Dissipation and Photoinhibition

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Summary

Photoprotective energy dissipation is a process in which xanthophylls (particularly zeaxanthin and antheraxanthin; Z + A) facilitate the dissipation of excess absorbed light energy as heat. This process can occur in different versions that meet the demands of different environments. Flexible thermal dissipation (qE type) responds to intra-thylakoid pH, is controlled by the PsbS protein, and relaxes rapidly upon darkening at warm temperatures. This flexible, PsbS/ΔpH-dependent dissipation is the predominant form of energy dissipation under environmental conditions favorable for growth, irrespective of plant species. In comparison with short-lived species, perennial evergreens not only have slower growth and lower photosynthetic capacities but also possess higher capacities for flexible thermal dissipation and show greater increases in PsbS level and Z + A in full sun versus moderate growth light intensity. Furthermore, a sustained form of thermal dissipation (qI type) is observed predominantly in photoinhibited evergreens under environmental conditions unfavorable for growth, irrespective of the environmental factor(s) involved. Sustained thermal dissipation is associated with Z + A retention, but is not ΔpH-dependent and does not relax rapidly in darkness even at warm temperatures. The role of PsbS in sustained dissipation versus other factors is discussed. Moreover, a correlation between sustained thermal dissipation in Z + A-retaining photoinhibited leaves and sustained phosphorylation of the photosystem II (PS II) core's D1 protein is shown. In overwintering Douglas fir, this is associated with an upregulation of an inhibitor (TLP40) of PS II core protein phosphatase.

I. Introduction

When plants absorb more light than they can utilize in photochemistry, they dissipate the excess as thermal energy in order to limit the formation of reactive oxygen species that can ultimately cause cell death (Niyogi, 2000; Demmig-Adams and Adams, 2002). In this chapter, two different forms of photoprotective thermal energy dissipation (assessed from non-photochemical chlorophyll fluorescence quenching or

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NPQ) are compared and contrasted. These two forms differ in their flexibility (e.g. speed of recovery), and are often referred to as flexible, rapidly reversible dissipation (qE type of NPQ or "feedback de-excitation") versus sustained dissipation (qI type of NPQ), respectively. Pronounced differences among plant species in the employment of these two forms of thermal dissipation are documented here. It is concluded that evergreen species employ both forms of thermal dissipation to a greater extent than species with shorter-lived leaves. In addition, sustained thermal dissipation is shown to be closely associated with photoinhibition of photosynthesis that is, furthermore, demonstrated to be considerably more common in evergreen species than in short-lived species.

II. Interspecies Differences in the Capacity for Flexible Thermal Dissipation

Long-term growth in different light environments, but under otherwise optimal conditions, reveals different strategies in an annual crop versus a perennial tropical evergreen (Fig. 1). Only the highly shade-tolerant evergreen species is able to survive and grow in deep shade. The crop species grows best at full sunlight and has a higher photosynthetic capacity in full sun compared to an intermediate light level (Fig. 1A). In contrast, the evergreen does not increase its photosynthetic capacity between moderate and full sunlight, and thus utilizes less of the extra energy of full sunlight for increased growth and photosynthesis than the crop species (Fig. 1B). On the other hand, the crop species does not increase its capacity for thermal energy dissipation between moderate and full sunlight, whereas the evergreen shows a strong increase in this capacity. The allocation of full sunlight to photosynthesis versus thermal dissipation is thus very different in the fast-growing crop versus the slow-growing evergreen species. Consistent with the increase in thermal dissipation capacity at full sunlight in the evergreen, the levels of the PsbS protein as well as the maximal level of zeaxanthin and antheraxanthin (Z + A) are also considerably increased in full versus moderate sunlight in the evergreen (Fig. 1D,F) but not in the crop species (Fig. 1C,E).

The PsbS protein and the de-epoxidized, excess-light-induced forms (Z + A) of the xanthophyll cycle are both required for ΔpH-dependent, rapidly reversible NPQ (Niyogi, 2000; Jung and Niyogi, this volume). The thermal dissipation process employed in either plant species under these favorable conditions is this flexible, reversible form of NPQ (qE type). This is supported by the fact that the majority of NPQ under these conditions can be abolished with uncouplers as well as by the absence of sustained increases in NPQ or decreases in predawn PS II efficiency (from the ratio of variable to maximal Chl fluorescence, F_v/F_m; Fig. 1 I,K). Under high light in the absence of additional environmental stresses, the PsbS/ΔpH-dependent form of thermal dissipation thus predominates irrespective of a species' inherent growth rate. It can also be concluded that the capacity for PsbS/ΔpH-dependent NPQ is higher in evergreens with lower growth and maximal photosynthesis rates than in species with short-lived leaves. Maximal NPQ capacity in sun-grown *Monstera deliciosa* was as high as that of PsbS-overexpressing *Arabidopsis* strains (Li et al., 2002a). The authors of the latter study brought up the question of potential costs of a greater constitutive expression of PsbS that may not be compatible with maximal light harvesting, growth, and/or reproduction. In short-lived species, high growth rates are necessary for rapid completion of their life cycle. Since perennial evergreens do not possess, and would not appear to require, the high growth rates of annuals, their higher level of PsbS in full sun would seem to offer only benefits (in the form of maximal photoprotection).

III. Sustained Thermal Dissipation in Photoinhibited Evergreens

A. Photoinhibition, Xanthophyll Cycle Arrest, and Sustained Dissipation

Excess light can lead to a lasting inactivation of PS II that is termed "photoinhibition" of photosynthesis and of PS II (see e.g. Powles, 1984; Demmig-Adams and Adams, 2003) under certain conditions. These include (a) a sudden transfer of shade-grown leaves to high light levels and (b) sun exposure in the presence of additional environmental stresses such as e.g. cold temperature during seasonal transition to winter in temperate climates. However, not all plant species respond in the same fashion. During summer-winter transition, overwintering annuals and biennials typically continue growing and maintain a high photosynthetic capacity. On the other hand, overwintering evergreens frequently cease growth and downregulate their photosynthetic capacity (Adams et al., 2002, 2004, this volume; Öquist and Huner, 2003; Huner et al., this volume). In such an inactivated state, the continuously light-absorbing leaves of evergreens must be protected by formidable photoprotection to prevent excess excitation energy from leading to a massive production of reactive oxygen species.