The Stress Concept in Plants: An Introduction

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INTRODUCTION

The stress concept, originally developed by Hans Selye in 1936,[1] has also been applied in describing unfavorable and environmental constraints in plants. The definition of plant stress is, however, quite different from the definition of stress in animals and human beings. In the past 10 years an enormous increase has occurred in the number of scientific publications found in journals of botany, plant physiology, ecophysiology, and plant biochemistry dealing with plant stress and plant stress detection. This process is yet continuing and may proceed in the future at an even more enhanced rate. Various recent books, for example *Stress and Stress Coping in Cultivated Plants* by McKersie and Leshem,[2] *Plant Adaptation to Environmental Stress* by Fowden *et al.*,[3] and proceedings of symposia[4] or plant stress reviews by Larcher[5] and Lichtenthaler[6,7] have appeared as well as the new book *Vegetation Stress* edited by Lichtenthaler,[8] with more than 90 original contributions on stress detection and stress effects in plants showing the state of the art of present stress research. In addition, an appealing new textbook written in German, *Stress bei Pflanzen,"*[9] has been edited.

Most authors use the term "plant stress" in a very broad sense, and this requires the establishment of a unifying concept of plant stress. In fact, a multitude of stressors with different modes of action often induce, besides very specific effects, the same or at least very similar overall responses of and in the plant. Plants are bound to their habitat, they cannot run away from the many threatening environmental or anthropogenic stressors, and therefore need special mechanisms of stress avoidance and stress adaptation. Plants do not have many response options to stress, but they respond in general, besides specific acclimations, with either a high-light type or a low-light type of growth or adaptation response (Lichtenthaler, 1984[10]), which is favorable for the particular high or low light regime under which they grow.

One should, however, not regard every little modification and change of a metabolic pathway, growth response, or development pattern of plants as a stress response, a stress effect, or a stress coping mechanism. In other words, the term "stress" should not be applied to fast readjustments of metabolic fluxes, photosynthetic rates, or transpiration rates as induced by changes in the photon flux density (sunlight ⇔ clouds), a slight change in temperature, or an increase or decrease in air humidity. Plants are acclimated and usually respond flexibly to such steadily re-occurring changes of cell metabolism and physiological activities as a response to changing environmental conditions. This also applies to the diurnal

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changes in metabolic activities, in the growth pattern, and in cell division and differentiation processes, which regularly show up at the day/night and night/day changes. Such modifications can only be regarded as a reorientation of metabolic and growth responses according to the preferential day or night activity of certain metabolic processes.

Besides fast acclimations, plants can also respond to environmental changes by special long-term adaptations to high-light or low-light growth conditions by modifying various parameters such as size and thickness of leaves, number and density of stomata, ultrastructure and function of the chloroplasts by increasing the levels of photoprotecting enzymes and of stress metabolites. Such adaptations may take place within 1 or 2 days or in one week at the latest. With such light adaptation responses,[11–13] plants not only avoid stress constraints, but adapt their metabolism and growth in an optimal way to the always changing outdoor growth conditions. The high-light and low-light adaptation responses often show up not only at a changing irradiance, but also as a response to several other stress constraints.

Despite their capacity for fast acclimation of metabolic fluxes and specific adaptations as well as the development of certain stress tolerance mechanisms, plants are often exposed to sudden short-term or long-term stress events that eventually reduce cell activity and plant growth to a minimum. This can lead to severe damage ultimately causing cell death if the stress coping mechanisms or repair mechanisms of plants are overworked. Various natural or anthropogenic stress factors exist that, depending on their intensity and duration, can reduce the plants' vitality and cause damage to plants. All these stress factors can be classified as abiotic or biotic stresses as well (TABLE 1).

In order to better differentiate between regular acclimation and adaptation responses of plants on the one hand, and stress effects, stressors, and stress constraints on the other hand, a general stress concept of plants has successively been developed for plants by various authors.[5,6,7,14,15] This unifying stress concept[7] seems to be little known to the botanical community, although the term stress is presently being used in many publications.

DEFINITION OF PLANT STRESS

The original general stress concept for living organisms was developed by Hans Selye[1] and can be summarized in the following two sentences: "All agents can act as stressors, producing both stress and specific action," and "There exist stressor-specific responses and non-specific general responses." J. Levitt[15] defined stress as: "Any environmental factor potentially unfavorable to living organisms."

On the basis of various observations in plants, and also under inclusion of the original concept on drought resistance,[15,16] Larcher[5] described plant stress as a "state in which increasing demands made upon a plant lead to an initial destabilization of functions, followed by normalization and improved resistance," and also, "If the limits of tolerance are exceeded and the adaptive capacity is overworked, the result may be permanent damage or even death."

Lichtenthaler[6,7] extended the stress concept of plants by including the regeneration phase of plants, when the stressors are removed, and also by differentiating between eu-stress and dis-stress. Eu-stress is an activating, stimulating stress and a positive element for plant development, whereas dis-stress (as seen in the English word distress) is a severe stress that negatively affects the plant and causes damage. "A mild stress may activate cell metabolism, increase the physio-

TABLE 1. List of Natural and Anthropogenic Stress Factors Acting on Terrestrial Vegetation

I. Natural stress factors:
- high irradiance (photoinhibition, photooxidation)
- heat (increased temperature)
- low temperature (chilling)
- sudden and late frost
- water shortage (desiccation problems)
- natural mineral deficiency (e.g. nitrogen shortage)
- long rainy periods
- insects
- viral, fungal, and bacterial pathogens

II. Anthropogenic stress factors:
- herbicides, pesticides, fungicides
- air pollutants (e.g., SO_2, NO, NO_2, NOx)
- ozone (O_3) and photochemical smog
- formation of highly reactive oxygen species
- ($^1O_2$, radicals $O_2^{\bullet -}$ and $OH^{\bullet}$, H_2O_2)
- photooxidants (e.g. peroxyacylnitrates)
- acid rain, acid fog, acid morning dew
- acid pH of soil and water
- mineral deficiency of the soil, often induced by acid rain
- oversupply of nitrogen (dry and wet NO_3^- deposits)
- heavy metal load (lead, cadmium, etc.)
- overproduction of NH_4^+ in breeding stations
  (uncoupling of electron transport)
- increased UV radiation (UV-B and UV-A)
- increased CO_2, global climate change

logical activity of a plant, and does not cause any damaging effects even at a long duration. Such mild stimulating stress is favorable for the plant."[6]

In any case one has to consider that "stress is a dose-dependent matter."[6] At fairly low concentrations a stressor, for example, an herbicide, can stimulate plant metabolism and plant growth. Thus, low doses of a xenobiotic can, in fact, have the opposite effect of higher doses. However, at a concentration 100 or 1000 times higher, the same xenobiotics will cause damage to the plant and induce early senescence finally leading to death if the stressor is not removed. Such damaging stressor concentrations and all high doses of stress constraints are negative for the physiology and development of plants, and thus represent a true stress in the sense of a dis-stress. Within this concept, true stress shows up when a certain threshold of a stressor, which can no longer be compensated for by the plant, is exceeded. The applicability of the "stressor dose–stress effect relationship" seems to be obvious, but has not been proved so far in all cases, and thus more research is required in this field.

The relative position of the stress tolerance threshold depends not only on the plant species, but also on the type of stressors applied and on the predisposition of the plant, that is, the growth condition and vitality before the stressor starts to act. Plants also differ in their stress-coping capacity. This can be illustrated with the example of the application of herbicides on agricultural crops in order to kill weeds. Many crop plants possess the capacity to detoxify herbicides by introduction of a hydroxyl group into the aromatic ring of the herbicide, which is then glycosylated to an inactive compound that can no longer bind to its target protein.[17,18] However, this detoxifying capacity is often not present in the weeds to be controlled and the latter will eventually die off.

STRESS CONCEPT IN PHYSICS AND BOTANY

The stress concept has also been developed in physics for materials, and there the terms stress, strain and damage are well defined. This stress concept can also be transferred to plants.[6,7] The following are definitions of stress terms used in physics as they are applied to the case of plants: (1) **stress** is the state of a plant under the condition of a force applied; (2) **strain** is the response to the stress and to the force applied to the plant (i.e., the expression of stress before damage occurs); (3) **damage** is the result of too high a stress that can no longer be compensated for.

In botany the term "strain" is seldom used and often not known. Strain is usually replaced by stress responses. Based on this stress concept, it is clear that a plant can grow under strain and long-term strain without acute damage. In fact, with specific strain (and limited vitality), the plant can also survive under continuous stress constraints. This is documented, however, by much reduced metabolic activity and growth rate. The following example illustrates this. In the Northern Black Forest at Herrenalb, a 170-year-old pine (*Pinus silvestris* L.) grows on the portal and thick sandstone walls of a former Romanesque monastery church, ca. 4 m above ground, and its roots are only found above ground in the stones of this wall without access to soil and water. Under continuous stress exposure (primarily water and mineral stress) and a steady strain response, this pine managed to survive in this unfavorable location and to grow within 170 years to a ca. 9-m high tree, which visually appears fully intact and healthy. The growth limitations set by this location are, however, documented by many fewer needles per needle year, as well as much shorter and thinner twigs compared to pines growing in locations with closer to optimal growth conditions. Reducing the leaf or needle area, that is, the area for transpiration, is one of the major water stress-coping mechanisms found in broad-leaf and conifer trees.

The Different Phases Induced by Stress

Based on the original stress concept of Selye[1] and taking into account the proposal of Larcher[5] and Lichtenthaler,[6,7] one has to differentiate among the plant's stress responses in four phases. Before stress exposure, the plants are in a certain standard situation of physiology that is an optimum within the limits set by the growth, light, water, and mineral supply conditions of the location. Stressors or complex stress events will then lead to the first three stress-response phases and later to the regeneration phase (phase 4) after removal of the stressors if the damage had not been too severe. These four phases are the following and have also been summarized in FIGURE 1.

1. **Response phase:** alarm reaction (beginning of stress)
    - deviation of the functional norm
    - decline of vitality
    - catabolic processes exceed anabolism

2. **Restitution phase:** stage of resistance (continuing stress)
    - adaptation processes
    - repair processes
    - hardening (reactivation)

3. **End phase:** stage of exhaustion (long-term stress)
   - stress intensity too high
   - overcharge of the adaptation capacity
   - chronic disease or death
4. **Regeneration phase:** partial or full regeneration of the physiological function, when the stressor is removed and the damage was not too high.

At the beginning of stress, the plants respond with a decline of one or several physiological functions, such as the performance of photosynthesis, transport of metabolites, and/or uptake and translocation of ions. Due to this decrease in metabolic activities, the plants deviate from their normal physiological standard; as a consequence their vitality declines. Acute damage and senescence will occur rapidly in those plants that possess only low or no stress tolerance mechanisms, and thus have a low resistance minimum. In this alarm phase most plants will, however, activate their stress coping mechanisms such as acclimation of metabolic fluxes, activation of repair processes, and long-term metabolic and morphological adaptations. This general alarm syndrome GAS[2] will cause a hardening of the plants by establishing a new physiological standard, which is an optimum stage

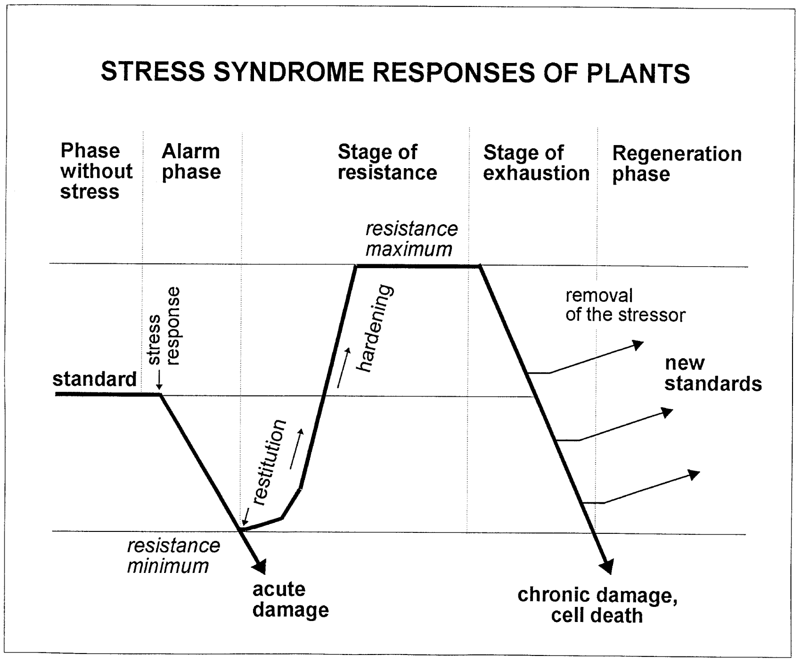

FIGURE 1. General concept of the phase sequences and responses induced in plants by stress exposure (unifying stress concept). Plants growing under stress begin at a physiological standard condition to respond to and cope with stress. Various responses and defense mechanisms will be activated. After removal of the stressor(s), new standards of physiology can, however, be reached in the plant depending on the time of the stressor removal as well as on the duration and intensity of the stress.

of physiology under the impact of the stressor and corresponds to the plants' *resistance maximum* (FIG. 1). At long-term stress and a stress-dose overloading the plants' stress coping mechanism, the stage of exhaustion (end phase) shows up in which physiology and vitality become progressively lost. This will cause severe damage and finally cell death. However, when the stressors are removed at the right time before the senescence processes become dominant, the plants regenerate and move to new physiological standards (regeneration phase). The time and stage of exhaustion, at which the stressors are removed from the plant, determines to which new physiological standard, within the range of resistance minimum and maximum, the plants will move (FIG. 1).

How long the plant will stay at the new physiological standard depends on external and internal factors. In field plants this is certainly not too long. Endogenous changes in the development program of plants have always been associated with changes in their physiology program and activity and have resulted again in a new physiological standard. Furthermore, the next stress events will show up soon, and these again require a reorientation of the plant's physiology standard to a new "optimum" within the limited possibilities set by the stress constraints. One should keep in mind that stress exposure of plants is not a rare event, but can occur daily, since there exist many different stressors. Therefore, stress and strain are routine events in a plant's life. Continuous stress and strain do, however, not mean that damage must necessarily occur in a plant. If the intensity and duration of stress are not too high and long, the plants will orient themselves within the range set by the resistance minimum and maximum, and in such cases damage symptoms are not detectable.

STRESSORS AND STRESS-COPING MECHANISMS

Usually, several stress factors act simultaneously on the plant, such as the frequently combined heat, water and high-light stress during dry, sunny, and warm summer periods. In addition, primary stressors or stress events often act on herbaceous plants and trees, considerably reducing the plants' vitality, such as air pollution followed by secondary stressors (e.g., bark beetles or particular fungi), which further decrease the tree's vitality and finally lead to the dying off of the tree. Much discussed are air pollution and forest decline,[19–21] the effects of sulfur dioxide,[22] salt stress responses,[23] highly reactive oxygen species and ozone,[24–27] or UV-A and UV-B effects including formation of UV-absorbing pigments in the leaves' epidermis,[28,29] to name just a few major topics of investigation.

Many stress-coping mechanisms can also show up depending on the type and strength of stress, such as proline accumulation during drought and salinity, polyol accumulation (e.g., mannitol, sorbitol) at water stress conditions, formation of heat shock proteins, formation of radical scavenging compounds (ascorbate, glutathion, α-tocophenol), increase of the level of superoxide dismutase, formation of the UV-A- and UV-B-absorbing phenols and flavonoids in the epidermis layer to protect the photosynthetic apparatus in the leaf mesophyll against damaging UV radiation or within the photosynthetic biomembranes, thylakoids, the fast photoreduction of the carotenoid violaxanthin to its reduced form zeaxanthin functioning at high-light conditions in the photoprotection of the photosynthetic apparatus.[30–32] Those plants, which are particularly tolerant to photoinhibition, such as the tobacco aurea mutant Su/su, even double their zeaxanthin amounts within a 5-hour high-light exposure by *de novo* biosynthesis.[30] The exact mechanism of the photoprotective action of zeaxanthin is not yet known; it can, however, indirectly increase the quenching of chlorophyll fluorescence. A nonenzymatic oxidation of zeaxanthin to violaxanthin by the highly reactive oxygen species formed at excess high light and other stress conditions (FIG. 2) and by detoxifying stress-induced epoxy groups from thylakoid lipids has also been discussed.[30,32]

One essential mechanism allowing still reasonable, though reduced, photosynthetic rates at an excess of highlight is the partial inactivation of photosystem II centers by the process of photoinhibition (destruction of the D1-protein),[33,34] which protects the remaining photosystem II centers from photodestruction. In this

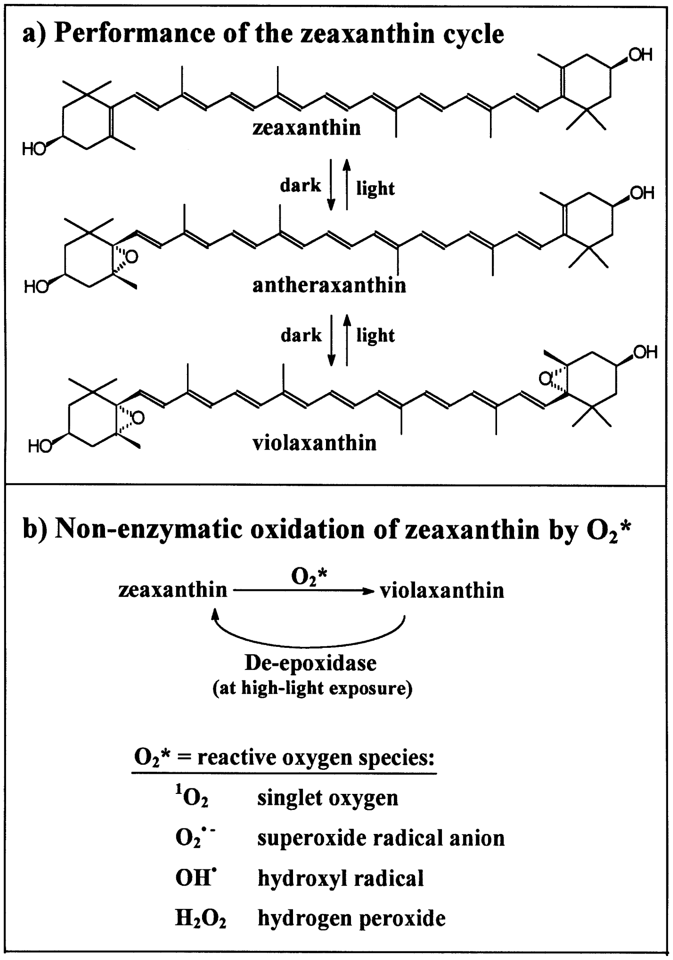

FIGURE 2. Scheme of the light-driven photoprotective zeaxanthin cycle (xanthophyll cycle) in higher plants. (a) At high light conditions, the carotenoid violaxanthin is de-epoxidized via antheraxanthin to its reduced form zeaxanthin, which functions as photoprotective agent of the photosynthetic pigment apparatus. **(b)** The possible function of zeaxanthin in detoxificating highly reactive oxygen species, which show up at high-light conditions, is indicated. The role of the light-driven zeaxanthin would be to re-reduce violaxanthin and to steadily maintain a sufficient level of zeaxanthin.

response, a partial photoinhibition of some chloroplasts guarantees the maintenance of sufficient photosynthetic net CO_2 assimilation rates in other leaf chloroplasts in order to allow plant growth and development even at excess high-light conditions.[32]

The changes in environmental conditions, the stress constraints, and stressors need to be sensed and registered by plants so that they can respond by strain and special stress responses. All biotic and abiotic stressors, natural and anthropogenic, represent external signals. There are multiple means and forms of signal perception and signal transduction in the plant and its organs (leaves, root, stem, flowers), which will lead to direct metabolic responses (e.g., readjustment of metabolic fluxes) on the one hand and to the activation of gene expression, enzyme formation, synthesis of stress proteins, stress metabolites, and stress hormones, and so forth on the other hand (FIG. 3). The latter then further modify the plants' metabolic responses under stress and control the stress resistance minimum and maximum. There are fluent transients and feedback controls between gene expression on the one hand and metabolic responses on the other hand. These processes as well as the whole chain and nature of the signal perception and transduction processes under stress constraints are presently matter of active research in many plant biology laboratories.

PHOTON ENERGY FLOW IN PLANT LEAVES

Plant stress and strain considerably change the chemical and pigment composition of plant leaves, and thus modify in multiple ways the energy flow of photons (sunlight) through the leaf with the result that the absorption, reflectance, and transmittance properties of leaves are changed in various ways. Stress also changes the relative proportions of absorbed light energy, which are used for photosynthetic quantum conversion, chlorophyll fluorescence, blue-green fluorescence, or heat emission as is shown in FIGURE 4. This is why the kinetics and behavior of red and far-red chlorophyll fluorescence, the yield of the blue-green fluorescence of the cell wall phenolics, as well as reflectance spectra can successfully be applied in the stress detection of plants. These active (laser-induced) fluorescence measurements or passive (sunlight-induced) optical reflectance measurements are noninvasive, and can also be applied for remote sensing of plants. In form of the newly developed laser-induced fluorescence imaging system LIFIS,[35–37] which simultaneously screens the whole leaf area (and not only single leaf points), the fluorescence signals provide superior means of stress detection in plants.[38]

SUMMARY

The current concept of stress in plants has been well developed over the past 60 years. Any unfavorable condition or substance that affects or blocks a plant's metabolism, growth, or development is regarded as stress. Vegetation stress can be induced by various natural and anthropogenic stress factors. One has to differentiate between short-term and long-term stress effects as well as between low-stress events that can be partially compensated for by acclimation, adaptation, and repair mechanisms, on the one hand, and strong stress or chronic stress events

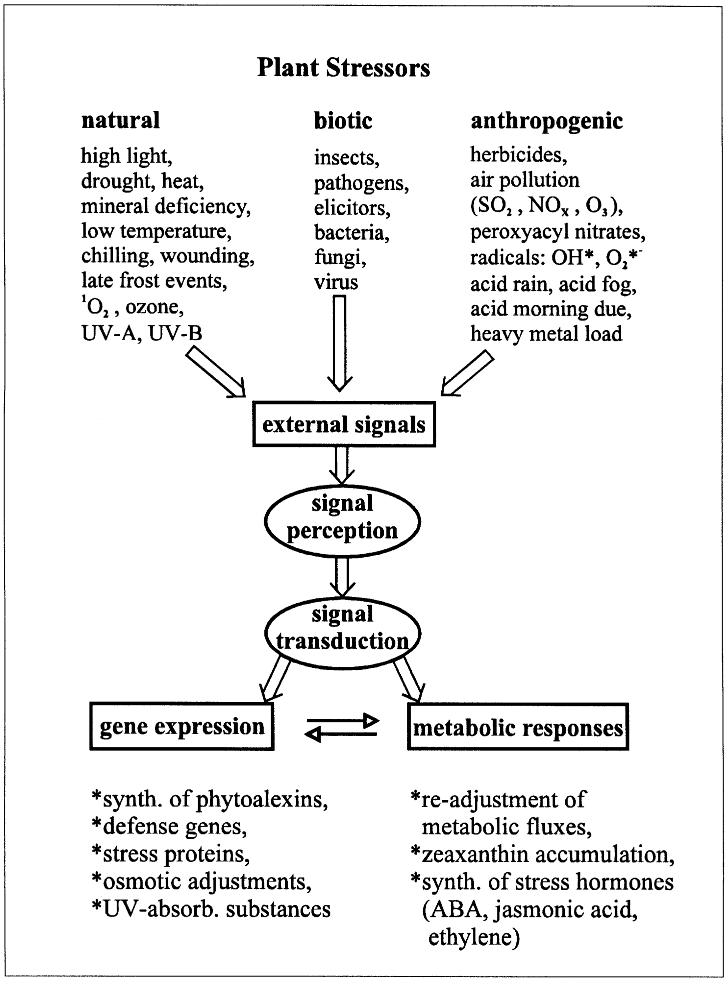

FIGURE 3. Scheme of the stress signal perception and transduction leading to metabolic responses and gene expression as well as stress-induced plant responses.

causing considerable damage that may eventually lead to cell and plant death, on the other hand. Some essential stress syndrome responses of plants are summarized in a unifying stress concept. The major abiotic, biotic, and anthropogenic stressors are listed. Some stress tolerance mechanisms are mentioned.

Stress conditions and stress-induced damage in plants have so far been detected using the classical ecophysiological field methods as well as point data measurements of particular chlorophyll fluorescence parameters and of reflectance spectra. The novel laser-induced high-resolution fluorescence imaging technique, which integrates chlorophyll and blue-green fluorescence, marks a new standard in the detection of stress in plants.

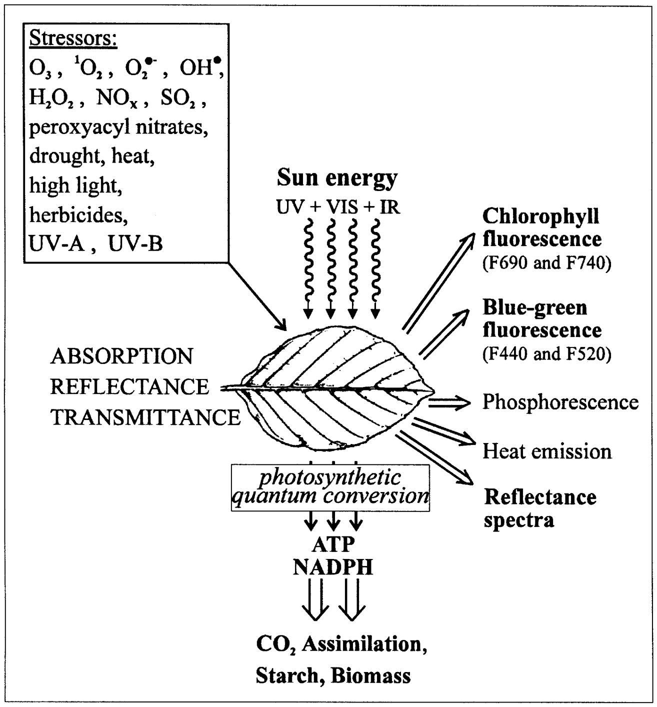

FIGURE 4. Scheme of photon energy flow and dissipation in plant leaves that is modified (either blocked or enhanced) by a multitude of natural and anthropogenic stressors, such as highly reactive oxygen species, herbicides, UV-A and UV-B radiation, or high-light stress or drought. A stress-induced decline in leaf physiology and photosynthetic quantum conversion can be monitored by noninvasive measurements of the red and far-red chlorophyll fluorescence and the blue-green fluorescence as well as by reflectance measurements.

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