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Drought Stress and the Need for Drought Stress Sensing in a World of Global Climate Change

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1. Introduction

Water scarcity imposes huge reductions in crop yield and is one of the greatest limitations to crop expansion outside present-day agricultural areas. Because the scenarios for global environmental change suggest a future increase in aridity and in the frequency of extreme events in many areas of the earth (Schär, 2006), maintaining crop yields under adverse environmental conditions is probably the major challenge facing modern agriculture. Nowadays, approximately 70% of the global available water is used in agriculture and 40% of the world food is produced in irrigated soils (Somerville & Briscoe, 2001). During the next 25 years, world population is expected to increase by about 2.5 billion people expecting food requirements in the developing world to double by 2025. An efficient use of water is therefore needed for the conservation of this limited resource (Somerville & Briscoe, 2001).

2. Effects of drought stress on plant physiology

Drought is a meteorological term which is commonly defined as a period without significant rainfall. Drought stress in plants generally occurs when the water available in the soil is reduced and atmospheric conditions further cause a continuous loss by transpiration and evaporation (Jaleel, 2009). Responses of plants to drought stress however are complex, involving adaptive changes and/or deleterious effects. Strategies to cope with drought stress normally involve a mixture of stress avoidance and tolerance mechanisms that vary with plant genotype (Chaves, 2002). Plant growth is accomplished through cell division, cell enlargement and differentiation, and involves genetic, physiological, ecological and morphological events and their complex interactions. Many yield-determining physiological processes in plants respond to water stress. Yield integrates several of these processes in a complex way. Thus, it is difficult to interpret how plants accumulate, combine and display the ever-changing and indefinite physiological processes over the entire life cycle. For water stress, severity, duration and timing of stress, as well as responses of plants after stress removal, and interaction between stress and other factors are extremely important (Plaut, 2003).

The continuity of water columns from soil pores through the plant to leaf cells, linked to the evaporative flux, is known as the soil-plant-atmosphere continuum (SPAC). Maintenance of this hydraulic system is needed to ensure a continuous water supply to leaves. The higher

the capacity to provide such supply, the faster the leaf expansion (Nardini & Salleo, 2002) and the higher the potential for carbon gain (Sperry, 2000; Tyree, 2003), as has been observed for different life forms (Brodribb *et al.*, 2005), species (Brodribb & Field, 2000; Sack *et al.*, 2003), and genotypes (Sangsing *et al.*, 2004; Maseda, 2006). Under conditions of drought stress, however, genetic variations in leaf area growth, leaf area duration and/or leaf photosynthesis might become very important (Richards, 2000).

Abiotic stress occurring during canopy development will modify many of the canopy characteristics compared with a well watered crop. Leaves are often smaller creating a more erectophile canopy than when unstressed (Araus, 1986). In addition, there may be fewer tillers in grain crops, and this, together with the lower leaf area reduces the leaf area index (LAI), which is defined as the one sided green leaf area per unit ground area. Finally, due to accelerated senescence, shorter green area duration may reduce the potential for assimilation (Araus, 2002) and therewith crop yield, which is dependent on seed filling duration (Egli & Crafts-Brandner, 1996) as well as on leaf area duration (Geisler, 1983; De Costa, 1997). Nonetheless, there is a wide consensus that the reproductive growth stage is the most sensitive to water deficit. It is also recognized that drought stress at the reproductive stage is the most prevalent problem in rainfed drought prone agriculture, at least simply because in most rainfed ecosystems the crop season's rains diminish towards flowering and harvest time (Blum, 2009). In summary, prevailing drought reduces plant growth and development, leading to hampered flower production and grain filling and thus smaller and fewer grains. The reduction in grain filling occurs mainly due to a reduction in the assimilate partitioning and activities of sucrose and starch synthesis enzymes (Farooq, 2009).

On plant level, depletion of soil water reserve causes a variety of symptoms, with timescales ranging from a few minutes (wilting, stomatal closure), to weeks (change in leaf growth, senescence) or months (decrease in total biomass or yield; Tardieu, 1996). Increased senescence rates are regularly observed in plants subjected to water deficit in the field. They already occur at relatively moderate leaf water potentials, and begin in older leaves located in the lowest layer of the canopy (Tardieu, 1996). The shedding of older leaves also contributes to water saving and can be viewed as a recycling program within the plant, allowing the reallocation of nutrients stored in older leaves to the stem or younger leaves (Chaves, 2003).

While the hydration states of different tissues are very sensitive to the magnitude of the hydraulic conductance, the direct physical control of transpiration itself resides almost entirely in environmental conditions of temperature and humidity and the stomatal regulation of gas-phase diffusion between leaf-air spaces and the atmosphere (van den Honert, 1948 in Comstock, 2002). Stomata must regulate transpiration in a way that sufficient carbon is gained while leaf water potential (ψ_w) is prevented from becoming too negative and the break-down of the plants hydraulic system is avoided (Tyree & Sperry, 1988; Jones & Sutherland, 1991; Schultz & Matthews, 1997). A decrease in stomatal conductance can correlate with a declining ψ_w during soil drying, but can also occur before any measurable change in ψ_w is recorded (Gollan, Turner & Schulze, 1985; Trejo & Davies 1991; in Schultz, 2003). However, the relationship between stomatal closure and the lowering of plant water potential varies between different life forms and species as well as between plants of the different photosynthetic types (i.e. C_3 and C_4 and CAM plants).

Depending on how narrowly plants control their ψ_w , homeohydric plants are further classified as either isohydric or anisohydric (Maseda & Fernandez, 2006). A perfectly isohydric plant would close stomata, reducing transpiration as needed to maintain pre-drought leaf water status, whereas a perfectly anisohydric plant would keep stomata comparatively more open, reducing ψ_w just enough to maintain pre-drought leaf transpiration (Maseda & Fernandez, 2006). Maize for example, is an isohydric plant and therefore shows a less negative ψ_w during drought periods compared to wheat which is anisohydric (Henson *et al.*, 1989; Tardieu, 1998). The distinction between isohydric and anisohydric plants, however, is often a matter of degree, and most plants operate under a relatively well-buffered range of ψ_w (Maseda & Fernandez, 2006).

Owing to reduced leaf water potential under conditions of low soil water content, leaf osmotic potential is reduced due to the simple effect of solute accumulation. However, if during the course of cellular water loss, solutes are actively accumulated, osmotic potential would be reduced beyond the rate dictated by the mere effect of concentration. Such accumulation of solutes during the development of water deficit is termed osmotic adjustment or osmoregulation (Zhang, 1999 and references therein). In general, osmotic adjustment (OA) is achieved by absorbing ions (e.g., K^+ , Na^+ , Ca^{2+} , Mg^{2+} , Cl^- , NO_3^- , SO_4^{2-} , and HPO_4^-) or by accumulating organic solutes (e.g. free amino acids, sugar alcohols, quaternary ammonium compounds and sugars). As a consequence, the osmotic potential of the cell is lowered, which in turn, attracts water into the cell and, thereby, tends to maintain its turgor (Morgan, 1984; Serraj & Sinclair, 2002). The accumulation of such compounds can protect cell membranes, proteins and metabolic machinery, which helps to preserve subcellular structure from damage as a result of cell dehydration (Serraj & Sinclair, 2002 and references therein).

Accumulation of solutes in roots leads to a lowering of the osmotic potential of the root, which maintains the driving force for extracting soil water under water deficit conditions (Wright *et al.*, 1983). An increasing number of reports provide evidence on the association between high rate of osmotic adjustment and sustained yield or biomass under water-limited conditions across different cultivars of crop plants. Since osmotic adjustment helps to maintain higher leaf relative water content (RWC) at low leaf water potential, it is evident that OA helps to sustain growth while the plant is meeting transpirational demand by reducing its leaf water potential (Blum, 2005).

At the leaf level, drought stress is generally characterized by a reduction of water content, diminished leaf water potential and turgor loss, closure of stomata and a decrease in cell enlargement and growth, whereby cell enlargement is more strongly inhibited than cell division. Further, various physiological and biochemical processes, such as photosynthesis, respiration, translocation, ion uptake, carbohydrates, nutrient metabolism and growth promoters (Jaleel *et al.*, 2009; for review see Farooq *et al.*, 2009) are affected. Severe water stress may finally result in the arrest of photosynthesis, disturbance of metabolism and at last the death of the plant (Jaleel *et al.*, 2009).

In higher plants, water loss and CO_2 uptake are tightly regulated by stomata. Under continuously changing environmental conditions stomata optimise gas exchange between the interior of the leaf and the surrounding atmosphere. Stomata close in response either to a decline in leaf turgor and/or water potential, or to a low-humidity atmosphere (Maroco *et*

al., 1997). As a rule, stomatal responses are more closely linked to soil moisture content than to leaf water status suggesting that stomata are responding to chemical signals (e.g. abscisic acid, ABA) produced by dehydrating roots whilst leaf water status is kept constant (Gowing *et al.*, 1990; Davies & Zang, 1991; Chaves, 2002; Yordanov, 2003). Under mild to moderate stress the reduction of leaf conductance (g_L) helps to avoid excessive water loss and provides higher water use efficiency to the plant (e.g. Lawlor, 1995; Cornic & Massacci, 1996; Lawlor, 2002; Flexas & Medrano, 2002). However, stomatal conductance not only regulates the efflux of water vapour by the leaf but also controls the influx of CO_2 into the leaf. As reviewed by Cornic (1994), stomatal closure is mainly responsible for the decline of net photosynthetic rates in C_3 plants subjected to moderate drought stress. Nevertheless, under more severe conditions of stress internal CO_2 concentration (C_i) frequently increases indicating the predominance of non-stomatal limitations to photosynthesis (Lawlor, 1995; Brodribb, 1996; Flexas & Medrano, 2002). To the non-stomatal mechanisms, under prolonged or severe soil drought, belong changes in chlorophyll synthesis, functional and structural changes in chloroplasts and also disturbances in accumulation and distribution of assimilation products (Medrano *et al.*, 2002). With this respect, processes like photophosphorylation (Haveaux *et al.*, 1987; Meyer & de Kouchkovsky, 1992), ribulose-1,5-bisphosphate (RuBP) regeneration (Gimenez *et al.*, 1992) and RubisCO activity (Castrillo & Calcagno, 1989; Medrano *et al.*, 1997; Medrano, 2002) are impaired under drought.

3. Effects of drought stress on plant physiology under conditions of elevated CO_2 concentration and temperature

Rising concentrations of atmospheric carbon dioxide (CO_2) contribute to global warming and thus to changes in both precipitation and evapotranspiration (Kruijt, 2008). Climatic shifts in both mean and variability could threaten ecosystem functions and human welfare (Tubiello, 2002). Current research confirms that, while crops would respond positively to elevated CO_2 concentrations ($[CO_2]$) in the absence of climate change, the associated impacts of higher temperatures, altered patterns of precipitation, and possibly increased frequency of extreme events, such as drought and floods, will likely combine to depress yields and increase production risks in many regions of the world. These will widen the gap between rich and poor countries further. A consensus has emerged that developing countries are more vulnerable to climate change than developed countries, because of the predominance of agriculture in their economies, the scarcity of capital for adaptation measures, their warmer baseline climates, and their heightened exposure to extreme events. Thus, climate change may have particularly serious consequences in the developing world, where about 800 million people are currently undernourished (Tubiello & Fischer, 2007; and references therein).

Except for regions where irrigation is employed or dewfall is significant, precipitation is the source of almost all soil moisture. Plants extract almost all their moisture from the soil (a small amount may be absorbed through the surface of wet plant leaves). Any change in timing and/or quantity of precipitation will affect soil moisture supply and crop yield. At times of low precipitation, soil moisture may be insufficient to meet the evaporative demand imposed by the atmosphere. Plant leaves will lose turgor and stomata close to prevent further dehydration of the plant (see section 2). The entry of CO_2 in the leaf is inhibited and photosynthesis, crop growth and yield are reduced (Brown, 1997).

Despite numerous works, up to date quantitative information on the impact of changes in precipitation, temperature and atmospheric CO₂ concentration on the soil and water resources is still required. Such information is needed principally at the watershed level where most of the processes underlying landscape functioning act and which is the scale at which decision making is taken (Chaplot, 2007).

The consequences of global change on plant biomass production and water use are manifold. Such multi-factor interactions are difficult to predict since the different effects might intensify each other, nullify each other or even change the sign of the overall change.

It is well documented that atmospheric CO₂ enrichment typically enhances photosynthesis (Long, 1991; Loreto & Centritto, 2004) mainly due the repression of photorespiration and because of an increased substrate supply (Poorter & Navas, 2002). The increases will be, based on the Farquhar *et al.* (1980) model of leaf photosynthesis, larger at higher temperatures whereas the benefit from CO₂ enrichment will be little when temperature is low (<15°C; Wolfe *et al.*, 1998). Further, growth rates will increase followed by enhanced biomass accumulation (Saralabai, 1997; Fuhrer, 2003) in a wide range of plants. One of the major consequences of this phenomenon is an increased production of edible biomass (Cure & Acock, 1986; Kimball, 1993) as well as an increased allocation of assimilated carbon to the roots (Arp, 1991; Fuhrer, 2003). The relative increase in biomass and yield under elevated [CO₂], however, is expected to be largest if all the other growth parameters remain constant (Amthor, 2001) which is not likely since general circulation models of the atmosphere predict increases in global temperature in the range of 1.5-3°C (and perhaps as much as 5°C) by the end of the 21st century (Lawlor & Mitchell, 1991; IPCC, 2007).

In determinate annual species warmer temperature accelerates ontogenetic development resulting in a (substantial) shortening of the growth period. This in turn leads to less time for carbon fixation and biomass accumulation (Morison & Lawlor, 1999). However, since seed yield is directly related to the seed filling duration (Egli & Crafts-Brandner, 1996) as well as to the leaf area duration (Geisler, 1983; De Costa, 1997), a combined increase of CO₂ concentration and temperature does not necessarily translate into improved yield, especially when other factors like water and nutrient supply are limiting (Amthor, 2001).

Different lines of evidence further indicate that growth in elevated [CO₂] leads to a change in the sink-source balance of the plant. In this context, carbohydrate accumulation in the source leaves is expected if the rate of photosynthesis exceeds the capacity of the sinks to utilize the photosynthates for growth. Therefore, the repeatedly observed variability in the response to CO₂ in different species, developmental stages or environmental conditions can be explained in terms of differing sink strength of the plants. Further, some of the morphological changes seen under elevated [CO₂] can be explained by an increased supply of photosynthates which 'forces' the development of new sinks (Stitt, 1991; Bowes, 1993). For this reason, it has been supposed that plants with a smaller sink size or capacity to develop new or alternative sinks will acclimate to higher levels of [CO₂] by decreasing their photosynthetic capacity to adjust the assimilate production to the demand.

Referring to this, plant species developing N₂ fixing nodules might present a special case. The increased availability of carbohydrates might enhance the development of nodules since they represent a considerable sink for carbohydrates. Higher atmospheric [CO₂] could therefore have complex indirect effects on growth and photosynthetic rates in plants which

develop nodules, because increased nodule development will increase the supply of organic nitrogen to the plant. This might be one explanation for the positive response of soybeans to elevated $[\text{CO}_2]$, and could be of considerable significance under natural conditions (Stitt, 1991). In other plant species, however, one of the most prominent, but not always observed, consequences of atmospheric CO_2 enrichment that has been found is decreased foliar N concentration. In a review of 378 observations obtained from 75 published studies Cotrufo (1998) found that 82% of the experiments related to this subject reported a reduction in plant N concentration under conditions of atmospheric CO_2 enrichment, with a mean concentration reduction for all studies of 14% on a plant dry weight basis whereby C_3 plants showed a mean decrease of 16% and C_4 and N-fixing plants of 7%. These decreases in foliar leaf N concentration are, amongst other factors, due to dilution effects. Higher growth rates in elevated $[\text{CO}_2]$ will lead to an increased demand for mineral nutrients. The acceleration of growth and the increased biomass production in elevated $[\text{CO}_2]$ may further change the nutrient status in the plant (Stitt, 1991). In agricultural situations where man has the capacity to alter the growing environment in a number of different ways, it has been demonstrated by Rogers (1996) and Kimball (1993) that the provision of high levels of nitrogen fertilizer to the soil has the capacity to offset the reduced foliage nitrogen concentration caused by higher levels of CO_2 . As Rogers *et al.* (1996) have described it, "the widely reported reduction in leaf or shoot N concentration in response to elevated CO_2 is highly dependent on nitrogen supply and virtually disappears when N is freely available to the roots".

Alongside with an increase of photosynthetic rates, the reduction of stomatal conductance and consecutively transpiration rates are commonly observed under conditions of elevated atmospheric CO_2 concentrations. However, the response to water stress is variable, in part because, although high $[\text{CO}_2]$ reduces transpiration per unit leaf area, it often increases the total leaf area per plant (Cure & Acock, 1986; Allen, 1990). Whether elevated CO_2 reduces evapotranspiration therefore depends on the effects of elevated $[\text{CO}_2]$ on leaf area index (LAI) as well as on stomatal conductance. No savings in water can be expected in canopies where elevated CO_2 stimulates the increase in LAI relatively more than it decreases stomatal conductance (Drake, 1997). Particularly, in C_3 species such as wheat or cotton (Kang *et al.*, 2002) which are more responsive to increasing $[\text{CO}_2]$ compared to C_4 plants this might become effective (Fuhrer, 2003). Further, in canopies with high LAI, leaf boundary layer and aerodynamic conductance may exert a stronger control on water vapour exchange than stomatal conductance, so that any change in stomatal conductance induced by elevated $[\text{CO}_2]$ may only marginally affect transpiration and hence, plant and stand water use (Wullschleger, 2002).

It is, however, worth to be noted that the reduced evapotranspiration could be cancelled out also by other changes caused by the increase in $[\text{CO}_2]$. At the leaf level, stomatal closure would reduce transpirational cooling and thereby increase leaf temperature (Yoshimoto, 2005). Indeed, increases of leaf temperature in the order of 1-2°C have been measured in various crops with a doubling of CO_2 concentration (Idso *et al.*, 1987). Higher leaf temperature will reduce the longevity and photosynthetic capacity of individual leaves (Kimball, 1995) but also result in larger vapour pressure deficits between the leaf and the air, thereby negating some of the positive effects of elevated $[\text{CO}_2]$ like decreased stomatal conductance (Yoshimoto, 2005). At the canopy level, the accelerated aging of leaves can shorten the growing season (Kimball, 1995) and therewith lead to a reduction in crop yield.

Finally, the decreased stomatal conductance and latent heat transfer might cause a warming of the order of 1-2°C over the continents in addition to warming from the CO₂ greenhouse effect (Sellers *et al.*, 1996).

In summary, while elevated [CO₂] alone tends to increase growth and yield of most agricultural plants (Kimball, 1983; Cure & Acock, 1986; Kimball *et al.*, 2002) as well as increases water use efficiency, warmer temperatures and changed precipitation regimes may either benefit or damage agricultural systems. Water and fertilizer application regimes will further modify crop responses to elevated CO₂ (Tubiello, 2002 and references therein). Consequently, the picture emerging from experiments at the whole plant level is rather diffuse, and this holds even more if we try to scale up CO₂ -induced growth responses from the individual to the stand level (Poorter & Navas, 2002). However, due to the increased need for food supply worldwide and the prediction of the emergence of drier regions in the world, the development of cost effective methods for early stress detection and therewith a possibility to reduce yield losses is inevitable.

4. Sensing drought stress

Irrigation is important in raising crops and achieving considerable yields in many areas of the world. It is essential especially in arid environments but is also becoming increasingly important in semi arid to humid regions due to the increased demand for food. Owing to this growing demand the supply of water available is decreasing and costs are going up (Gonzales-Dugo, 2006). During the last decades, therefore, the effects of drought stress on plant physiological traits have been intensively studied (see section 2 and 3) to develop new methods for early detection and monitoring of drought stress. This should allow developing both short and long term agro-technical measures (e.g. irrigation scheduling) and thus help avoiding substantial yield losses and at the same time reduce water consumption. With this respect, special focus was put on sensing leaf/canopy reflectance, thermal radiation as well as fluorescence emission.

4.1 Leaf spectral reflectance as a measure of plant drought stress

Remote sensing techniques have evolved rapidly during the past decades. Ecological remote sensing now encompasses a wide range of applications including vegetation mapping, land-cover change detection, disturbance monitoring and the estimation of biophysical and biochemical attributes of ecosystems (Asner *et al.*, 1998a). A lot of effort has also been made towards the use of spectral reflectance of leaves and canopies for stress detection in agricultural environments since these techniques could offer a powerful tool not only for crop stress detection but also for quantifying crop development and yield (Asner, 1998b).

Leaf reflectance is driven mainly by the chemical composition of the leaves but can vary independently of pigment concentrations due to differences in internal structure, surface characteristics (e.g. hairs, waxes) and moisture content (Blackburn, 2007). The reflectance pattern of a canopy is even more complex since it is influenced not only by the reflectance of single leaves but also by its geometry - the leaf area index, inclination and clumping of the leaves - as well as the percentage of canopy ground coverage and presence of non-leaf elements (Gao, 2000; Blackburn, 2007).

Agricultural monitoring is a process by which crop development is tracked and treatments are applied with the aim of increasing income while minimizing expenditure (Beeri, 2006). To accomplish this numerous spectral reflectance indices were developed, most of them based on simple mathematical formulas, such as ratios or differences between the reflectance at given wavelengths (Araus *et al.*, 2001; Babar, 2006). Most of the indices based on the reflectance of single leaves aim to trace plant physiological status, i.e. plant water status or nutritional status. However, indices developed for canopy spectra can not only be used for the assessment of plant water and nitrogen status but also for the estimation of plant productivity (measurement and interpretation of absorbed photosynthetically active radiation; Ferri, 2004).

Largely as a result of interests in remote sensing, leaf reflectance has been studied intensively. Pioneering efforts in this field have been reviewed elsewhere (Myers *et al.*, 1983; Jackson, 1986; Carter, 2001). The shape of leaf reflectance spectra is determined by the absorption of leaf pigments, mainly chlorophyll. Reflectance spectra of green leaves are characterized by a low signal in the blue region between 400 and 500nm and a high signal in the near-infrared between 750 and 800nm (Figure 1). With increasing leaf chlorophyll content the reflectance signal around 680nm decreases (Buschmann, 1993). Typical leaf reflectance spectra (500 - 2500nm) can be separated in three parts:

1. Wavelength spectrum between 500-750nm, the visible light absorbance region which is dominated by pigments (chlorophyll a and b, carotene, and xanthophyll pigments);
2. Wavelength spectrum between 750-1350nm, the near-infrared region which is affected by internal leaf structure; and
3. Wavelength spectrum between 1350-2500nm, a region influenced to some amount by leaf structure, however significantly affected by water concentration in the tissue. Strong water absorption bands occurring between 1450 and 1950nm (Myers, 1983; in Tanriverdi, 2006).

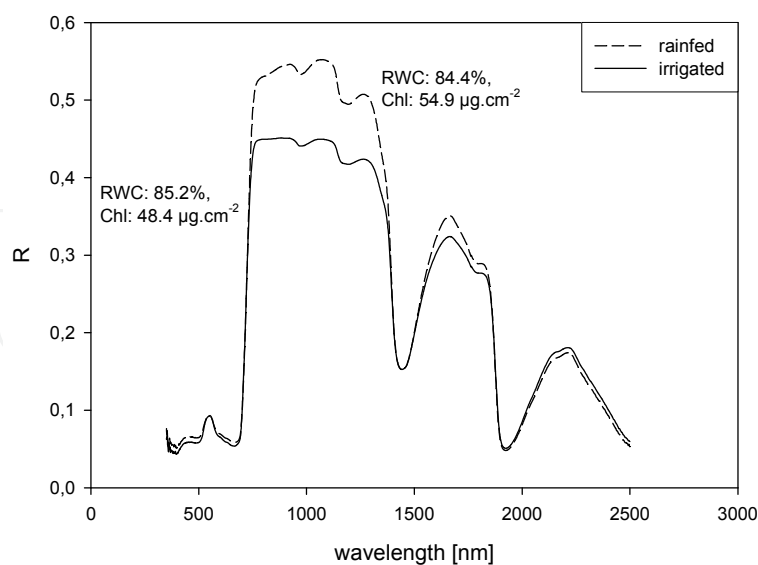


Fig. 1. Reflectance spectra of leaves from irrigated and rainfed grown *Triticum aestivum* L. Abbreviations: Chl: chlorophyll content, RWC: relative water content.

Concerning the occurrence of stress (e.g drought stress, nutrient deficiency, diseases), leaf reflectance is altered more consistently at visible wavelengths (400–720nm) than in the

remainder of the incident solar spectrum (730–2500nm). These changes were found to be spectrally similar among many common stressors and vascular plant species. Increased reflectance in the far-red 690–720nm spectrum is a particularly generic response, providing an earlier or more consistent indication of stress than reflectance in other regions of the incident solar spectrum (Carter, 2001 and references therein).

Under conditions of drought stress, absorption of radiation by the leaf tends to decrease due to lower leaf water content. Although water absorbs most strongly in the wavelengths of the infrared region of the spectrum from approximately 1300 to 2500nm (Curcio & Petty, 1951), some absorption also occurs at lower wavelengths. As water is lost from a leaf reflectance increases and absorption decreases, primarily as a result of water's radiative properties (Bowman, 1981; Hunt & Rock, 1989). Even after accounting for the radiative characteristics of water, secondary effects occur. These include the influence of water content on absorption by other substances in the leaves, such as pigments. Also included as secondary are the effects of water content on wavelength-independent processes, particularly multiple reflections inside the leaf (Carter, 1991).

Moreover, drought stress not only causes leaf water content to decline but also affects physiological processes such as, for example, leaf conductance and photosynthetic rates (see section 2). Changes in pigment and nitrogen concentration of plant tissue will follow. For example, chlorophyll and RubisCO contents decline as the leaf remobilizes resources under stress conditions (Parry, *et al.*, 2002). Chlorophyll and accessory pigments absorb strongly in the visible range (Knipling, 1970). Carter & Knapp (2001) described a consistent stress induced alteration of leaf reflectance at visible wavelengths (~400–720nm) since chlorophyll is the major absorber in the leaf and the metabolic disturbance brought about by stress alters leaf chlorophyll concentrations (Knipling, 1970). Plant responses to water deficit therefore include both biochemical and morphological changes that primarily lead to acclimation and later to functional damage and the loss of plant parts (Chaves, *et al.*, 2002). However, it is worth pointing out that leaf reflectance in the visible range of plants experiencing nutrient deficiency was also found to increase since nitrogen (and magnesium) is essential in the formation of chlorophyll. As leaves become more chlorotic, reflectance increases and the reflectance peak, normally centred at about 550nm, broadens towards the red as absorption of incident light by chlorophyll decreases (Ayala-Silva, 2005). Therefore, identifying the release of a stress situation by leaf reflectance spectra alone might be difficult to a certain extent.

Concerning the detection of plant water status and nutrient deficiency numerous spectral indices have been developed. Table 1 summarizes some of the most often used indices without attempting to give an exhaustive overview of all indices appearing in literature. Further, several indices were later on modified to better fit different plant species and/or conditions in different geographical regions.

Some of the most common indices are, for example, the photochemical reflectance index (PRI), indices to determine leaf chlorophyll content, nitrogen content or indices for the estimation of leaf water content. The PRI is widely used for the estimation of photosynthetic radiation use efficiency. It was proposed based on the finding that the interconversion of xanthophyll cycle pigments in intact leaves can be detected as subtle changes in absorbance at 505–510nm (Bilger *et al.*, 1989) or the reflectance at 531nm (Gamon *et al.*, 1990). The

Index	Related to	Reference
NPQI $(R_{415}-R_{435})/(R_{415}+R_{435})$	chl, stress	Barnes <i>et al.</i> , 1992
SR R_{800}/R_{680}	chl	Birth & McVey, 1968
REIP	chl, stress	Collins, 1978
PRI $(R_{531}-R_{570}) \times (R_{570}+R_{531})$	chl	Filella, 2004
SIPI $(R_{800}-R_{445})/(R_{800}-R_{680})$	chl	Penuelas <i>et al.</i> , 1995
PSSRa R_{800}/R_{680}	chl a	Blackburn, 1998
PSSRb R_{800}/R_{635}	chl b	Blackburn, 1998
PSSRc R_{800}/R_{500}	chl	Blackburn, 1998
PSNDa $(R_{800}-R_{680})/(R_{800}+R_{680})$	chl a	Blackburn, 1998
PSNDb $(R_{800}-R_{650})/(R_{800}+R_{650})$	chl b	Blackburn, 1998
PSNDc $(R_{800}-R_{500})/(R_{800}+R_{500})$	chl	Blackburn, 1998
(R_{675}/R_{700})	chl a	Chapelle, 1992
$R_{675}/(R_{700} \times R_{650})$	chl b	Chapelle, 1992
$(R_{800}-R_{700})/(R_{800}+R_{700})$	chl	Gitelson & Merzlyak, 1994
$(R_{750}-R_{800})/(R_{695}-R_{740}) - 1$	chl	Gitelson, 2003
$R_{860}/(R_{708} \times R_{550})$	chl a, chl tot	Datt, 1998
R_{675}/R_{700}	chl	Datt, 1998
$R_{675}/(R_{650} \times R_{700})$	chl	Datt, 1998
R_{760}/R_{500}	chl	Datt, 1998
R_{750}/R_{700}	chl	Datt, 1998
R_{750}/R_{550}	chl	Datt, 1998
$R_{672}/(R_{550} \times R_{708})$	chl a, chl tot	Datt, 1998
R_{672}/R_{708}	chl	Datt, 1998
$R_{800}-R_{550}$	chl	Buschmann & Nagel, 1993
R_{800}/R_{550}	chl	Buschmann & Nagel, 1993
PSR R_{430}/R_{680}	total pigments, chl, stress	Penuelas <i>et al.</i> , 1994
NPCI $(R_{680}-R_{430})/(R_{680}+R_{430})$	total pigments, chl, stress	Penuelas <i>et al.</i> , 1994
$(Chl)RI_{green} [(R_{750-800}-R_{430-470})/(R_{520-580}-R_{440-480})]^{-1}$	chl	Gitelson, 2004
$(Chl)RI_{red\ edge} [(R_{750-800}-R_{430-470})/(R_{695-740}-R_{440-480})]^{-1}$	chl	Gitelson, 2004
$CRI_{green} [(R_{510})^{-1} - (R_{550}-R_{570})^{-1}] \times (R_{750}-R_{800})$	carotenoids	Gitelson, 2004
$CRI_{red\ edge} [(R_{510})^{-1} - (R_{700}-R_{710})^{-1}] \times (R_{750}-R_{800})$	carotenoids	Gitelson, 2004
ARI $(R_{550})^{-1} - (R_{700})^{-1}$ or ARI $[(R_{550-570})^{-1} - (R_{700-710})^{-1}] \times R_{750-800}$	car, anthocyanin	Gitelson, 2001 Gitelson, 2004
R_{1483}/R_{1650}	LWC	Yu <i>et al.</i> , 2000
R_{1100}/R_{1430}	LWC	Yu <i>et al.</i> , 2000
R_{1121}/R_{1430}	LWC	Yu <i>et al.</i> , 2000
R_{1430}/R_{1650}	RWC	Yu <i>et al.</i> , 2000
R_{1430}/R_{1850}	RWC	Yu <i>et al.</i> , 2000
R_{1483}/R_{1650}	RWC	Yu <i>et al.</i> , 2000
R_{2200}/R_{1430}	RMP	Yu <i>et al.</i> , 2000
R_{1430}/R_{1650}	RMP	Yu <i>et al.</i> , 2000
R_{1483}/R_{1430}	RMP	Yu <i>et al.</i> , 2000
R_{695}/R_{420}	stress	Carter, 1994
R_{695}/R_{760}	stress	Carter, 1994
R_{605}/R_{760}	stress	Carter, 1994
R_{710}/R_{760}	stress	Carter, 1994
R_{695}/R_{670}	stress	Carter, 1994

Table 1. Compilation of frequently used spectral indices to detect stress situations (e.g. drought stress, nutrient deficiency, etc.) in plants at the leaf level. *Abbreviations:* chl: chlorophyll, car: carotenoids, ARI: Anthocyan Reflectance Index, CRI: Carotenoids Reflectance Index, LWC: Leaf Water Content; NPCI: Normalized Difference Pigment Index, PSR: Pigment Simple Ratio, REIP: Red Edge Inflection Point, RMP: Relative Leaf Moisture Percentage on Fresh Weight Basis, SIPI: Structure Independent Pigment Index, SR: Simple Ratio.

photochemical reflectance index (PRI), incorporating reflectance at 531nm (xanthophyll cycle signal), was then defined as $[(R_{570}-R_{531})/(R_{570}+R_{531})]$ to establish a reflectance-based photosynthetic index (Gamon *et al.*, 1997). Concerning the attempt to trace the relative and actual leaf water content (RWC and AWC) with spectral indices, a lot of effort has been made and a number of different indices have been developed for numerous crop species, amongst many others the water index (WI; R_{900}/R_{970} ; Penuelas & Filella, 1998), the water band index (WBI; R_{905}/R_{980} ; Davenport *et al.*, 2000), RWC (R_{1483}/R_{1650}) or AWC (R_{1121}/R_{1430}).

Although much hyperspectral reflectance work to date has been done at the leaf scale, in situ measurements made above the canopy are becoming more widely used, driven by the need to simulate the scales involved in airborne or satellite measurements (i.e. remotely sensed imagery at the canopy scale; Strachan, 2002). Table 2 summarizes some of the indices frequently used in remote sensing.

The most known and often used index in remote sensing of green phytomass is the NDVI (normalized difference vegetation index). The NDVI is a broad-band vegetation index which has largely been employed to determine quantitative parameters of green phytomass, using wide spectral bands in the red and near infrared, generally acquired by multispectral sensors in satellites (Ferri, 2004). It was proposed by Rouse *et al.* (1973) and is based on the contrast between the maximum absorption in the red due to chlorophyll and the maximum reflection in the infrared caused by leaf cellular structure (Haboudane, 2004). However, despite its intensive use in remote sensing applications the NDVI has the disadvantage to saturate in cases of dense and multi-layered canopies and further shows a non linear relationship to biophysical parameters such as the leaf area index (LAI; Haboudane, 2004). Several studies reveal a saturation level of NDVI at LAI values between 2 and 3 implying that a further increase in standing biomass does not yield a further increase in NDVI (e.g. Gilabert *et al.* 1996; Haboudane, 2004).

However, as much as the saturation of vegetation indices at high LAI values is a problem, the influence of soil background is one at very low LAI values. To account for changes in soil optical properties, soil adjusted indices minimizing the effect of soil background were developed (Haboudane, 2004). The leading index with this respect is the Soil-Adjusted Vegetation Index (SAVI) which is less sensitive to soil reflectance at low LAI than NDVI (Huete, 1988). It is based on the linear relationship between near-infrared and visible reflectance for bare soil and therefore reduces the influence of the soil on canopy reflectance. The SAVI index was modified further several times to optimize the removal of soil background influences (Dorigo, 2007 and references therein). For a good overview of all the modified SAVI indices see e.g. Broge & Leblanc (2000).

Tracing changes in plant water status can, for example, be done by the setup of simple ratios between two wavelengths, one of which characterized by strong water absorption and a second one outside the absorption band. One of these indices is the NDWI which is given by $(R_{860} - R_{1240})/(R_{860} + R_{1240})$ and is sensitive to changes in liquid water content of vegetation canopies (Gao, 2000; Serrano, 2000). Another index commonly used to trace plant water deficits is the water index (WI), which was developed by Penuelas *et al.* (1997) and is calculated as the ratio between reflectance at 900nm and 970nm (R_{900}/R_{970}). Further indices used for the estimation of plant water status from remotely sensed data would be for

example the moisture stress index (MSI) which is given by the ratio of R_{1600}/R_{817} (Hunt & Rock, 1989) or the maximum difference water index (MDWI, Eitel *et al.*, 2006).

To assess leaf chlorophyll (and leaf N) status from remotely sensed observations, spectral indices are needed that are sensitive to leaf chlorophyll concentration and minimize variations in canopy reflectance associated with background reflectance and LAI (Daughtry, 2000). Most hyperspectral ratios used for estimating leaf chlorophyll content make use of the three discrete bands describing the typical reflectance pattern of green vegetation: the reflectance peak in the green and NIR and the region of maximum absorption in the red (Dorigo, 2007). Amongst many other indices, some of the most widely used ones to measure chlorophyll (and leaf N) are the CARI (Chlorophyll Absorption Ratio Index), the MCARI (Modified Chlorophyll Absorption Ratio Index), the TVI (Triangular Vegetation Index) and the REIP (red edge inflexion point).

The Chlorophyll Absorption Ratio Index (CARI), which measures the depth of chlorophyll absorption at 670nm relative to the green reflectance peak at 550nm and the reflectance at 700nm, was developed by Kim *et al.* (1994) for minimizing the effects of non-photosynthetic materials on spectral estimates of absorbed photosynthetically active radiation (PAR; Daughtry; 2000, Haboudane, 2004). Subsequently, different alterations of this index were proposed (see e.g.: Daughtry *et al.*, 2000; Haboudane *et al.*, 2002) to make it more sensitive to chlorophyll. The MCARI was simplified from the CARI by Daughtry *et al.* (2000) and is given by $[(R_{700}-R_{670})-0.2(R_{700}-R_{550})]*(R_{700}-R_{670})$ (Haboudane, 2004). The TVI (Triangular Vegetation Index), however, follows a different concept. It was introduced by Broge *et al.* (2000) and is based on the fact that the total area of the triangle (green, red, infrared) will increase as a result of chlorophyll absorption (decrease of red reflectance) and leaf tissue abundance (increase of near-infrared reflectance; Broge & Leblanc, 2000; Haboudane, 2004).

The red-edge, finally, describes the abrupt increase in leaf reflectance at wavelengths between 680nm and 740nm which is caused by the combined effects of strong chlorophyll absorption and leaf internal scattering (Dawson, 1998). Increases in the amount of chlorophyll visible to the sensor, either through an increase in leaf chlorophyll content or Leaf Area Index, result in a broadening of a major chlorophyll absorption feature centred around 680nm. The effect is to cause a movement of the point of maximum slope, termed the red edge position (REP; Dawson, 1998). Several studies have subsequently illustrated the use of the red edge in the estimation of foliar chlorophyll content (e.g. Lamb, 2002 and references therein). To date various techniques have been developed for parameterizing the shape of the red-edge and determining the position of the red edge inflection point (REIP), including inverted Gaussian models (Miller *et al.*, 1990), fitted high-order polynomials, linear interpolation (Guyot *et al.*, 1988; Clevers *et al.*, 2002) and Langrangian interpolation (Dawson & Curran, 1998b; in Dorigo, 2007). The structure of the chlorophyll red-edge might be best observed by plotting $dR/d\lambda$, the first derivative, with respect to wavelengths. A common approach for locating the red-edge wavelength is to manually or computationally locate the highest peak in the derivative spectra (Lamb, 2002 and references therein). The use of derivative spectrometry is commonly employed to resolve or enhance absorption features that might be masked by interfering background absorption (Curran *et al.*, 1990; Filella & Penuelas, 1994). Spectral derivatives also aid in suppressing the continuum caused by other leaf biochemicals (such as lignin and secondary pigments) and canopy background effects (Elvidge 1990; Curran *et al.* 1991).

Index	Related to	Reference
SR R_{800}/R_{680}	chl	Birth & McVey, 1968
CARI	chl	Kim <i>et al.</i> , 1994
MCARI $[(R_{700} - R_{670}) - 0.2(R_{700} - R_{550})](R_{700} - R_{670})$	chl, LAI	Daughtry <i>et al.</i> , 2000
TCARI $3[(R_{700} - R_{670}) - 0.2(R_{700} - R_{550})](R_{700}/R_{670})$		
NDVI $(R_{800} - R_{680}) / (R_{800} + R_{680})$	chl, LAI, Yield	Rouse <i>et al.</i> , 1973
Green NDVI $(R_{780} - R_{550}) / (R_{780} + R_{550})$	chl	Gitelson <i>et al.</i> , 1996
DVI $R_{800} - R_{680}$	chl	Jordan, 1969
RDVI $(R_{800} - R_{670}) / \sqrt{R_{800} + R_{670}}$	chl, LAI	Roujean, 1995
MSR $(R_{880}/R_{670} - 1) / \sqrt{R_{880}/R_{670} + 1}$	chl, LAI	Jordan, 1969
SAVI $(1+L)(R_{801} - R_{670}) / (R_{801} + R_{670} + L)$	chl, LAI	Huete, 1988
OSAVI $(1+0.16)(R_{801} - R_{670}) / (R_{801} + R_{670} + 0.16)$	chl, LAI	Rondeaux, 1996
TVI $0.5[120(R_{750} - R_{550}) - 200(R_{670} - R_{550})]$	chl	Broge & Lelanc, 2000
REIP	chl, LAI, stress	Collins, 1978
PRI $(R_{531} - R_{570}) / (R_{570} + R_{531})$	chl	Filella, 2004
CCCI	chl, N	Fitzgerald, 2010
CNI	chl, N	Fitzgerald, 2010
NDRE	N	Fitzgerald, 2010
WI R_{900}/R_{970}	water	Penuelas <i>et al.</i> , 1997
NDWI $(R_{860} - R_{1240}) / (R_{860} + R_{1240})$	water	Gao, 1996
MDWI $(R_{\max 1500-1750} - R_{\min 1500-1750}) / (R_{\max 1500-1750} + R_{\min 1500-1750})$	water	Eitel <i>et al.</i> , 2006

Table 2. Compilation of frequently used spectral indices to detect stress situations (e.g. drought stress, nutrient deficiency, etc.) in plants at the canopy level. *Abbreviations:* CARI: Chlorophyll Absorption Ratio Index, CCCI: Canopy Chlorophyll Content Index, CNI: Canopy Nitrogen Index, MCARI: Modified Chlorophyll Absorption in Reflectance Index; MDWI: Maximum Difference Water Index; NDRE: Normalized Difference Red Edge, NDWI: Normal Difference Water Index, NDVI: Normalized Difference Vegetation Index; PRI: Photochemical Reflectance Index, REIP: Red Edge Inflection Point; SAVI: Soil Adjusted Vegetation Index, SR: Simple Ratio, TCARI: Transferred Chlorophyll Absorption in Reflectance Index, TVI: Triangular Vegetation Index, WI: Water Index.

As can be seen from the many indices which were developed, intensive research has been made towards sensing the response of leaf optical characteristics to different stressors, such as for example, drought stress and nutrient deficiency, exposure to heavy metals, exposure to gaseous pollutants, UV-B radiation, ozone or increased temperature and CO₂ (Baltzer & Thomas, 2005 and references therein). However, it should be stated that most of the vegetation indices have temporal effects, which are not necessarily correlated to the temporal effects of the spectral indices. Care has to be taken to apply the right indices at the right time in the growing season. Also, it should be mentioned that these vegetation indices are inter-related (e.g. most of them influence the total yield; Zwiggelaar, 1998).

4.1.1 Case study 1 – An attempt to sense reoccurring drought stress events remotely

This study aimed to evaluate the impact of drought stress on plant physiological traits and leaf reflectance of wheat (*Triticum aestivum* L.) occurring at different phenological stages

(flowering and/or grain filling). Further, the consequences of two consecutive drought events and recovery of plants after drought were investigated. The analysis of the effect of consecutive stress periods and recovery on changes in leaf reflectance has rarely been performed until now but might gain in importance considering the predicted increased frequency of drought events whereby plants could be exposed to drought repeatedly (Schär *et al.*, 2004; Seneviratne *et al.*, 2006; Vidale *et al.*, 2007; IPCC, 2007).

4.1.1.1 Material and methods

Plants (*Triticum aestivum* L. cv. Xenos) were grown in 8 litre plastic pots. Simulation of seasons in the growth chamber was based upon long-time observation of temperature and relative air humidity (meteorological station: 16°29' eastern longitude and 48°15' northern latitude). For a detailed description of growing conditions and measurement techniques see Linke *et al.* (2008).

Four different treatments were set up - one control treatment and three treatments exposed to drought at different times during phenology: AC: control plants; AF: plants exposed to drought stress at flowering, recovery after anthesis; AG: plants exposed to drought stress at grain filling and AFG: plants exposed to drought stress at flowering and grain filling.

Soil moisture content of control plants was consistently held at 20-23 vol% (AC; TDR Trime, Imko Micromodultechnik GmbH, Germany). Drought stress at flowering was imposed by halving water supply 10 days before the beginning of pollen shedding resulting in a soil moisture content of ~10 vol% at flowering (AF). After flowering, plants receiving a second stress at grain filling were allowed to recover for 8 days (water supply similar to control plants) before the second stress was imposed by halving water supply again (soil moisture content during measuring period ~10 vol%; AFG). Plants receiving drought stress only at grain filling (AG) were treated similar to control plants until after flowering. Drought stress was imposed at the same time as in plants of the treatment stressed twice.

All physiological and spectral measurements were made in the mid region of the youngest fully expanded leaves at three developmental stages: vegetative growth, flowering and grain filling. Light saturated photosynthetic rates (A_{sat}) refer to measurements at growth conditions under saturating light intensities (CO_2 : 350-370 $\mu\text{mol}\cdot\text{mol}^{-1}$; light: 1000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; CIRAS-I, PP-Systems, U.K), actual leaf conductance (g_L) was measured with a steady state porometer (PMR-4, PP-Systems; U.K.) and total chlorophyll content (Chl_{tot}) of leaves was determined with a SPAD-502 hand held chlorophyll meter (Minolta, Japan). Relative water content was calculated as $\text{RWC} = ((\text{fresh weight} - \text{dry weight}) / (\text{saturated weight} - \text{dry weight})) * 100 [\%]$ and actual leaf water content was calculated as $\text{AWC} = ((\text{fresh weight} - \text{dry weight}) / (\text{fresh weight})) * 100 [\%]$.

Leaf spectral reflectance was measured with a FieldSpec Pro FR in connection with a plant reflectance probe from Analytical Spectral Devices Inc., Boulder, CO. Relative difference of reflectance spectra between stress and control treatments ($\Delta R/R$) was calculated as $((R_{\text{stress}} - R_{\text{control}}) / R_{\text{control}}) * 100 [\%]$.

4.1.1.2 Results and discussion

Drought stress significantly influenced plant physiological traits independently of the time of its application in phenology (Table 3). A lowering of the actual leaf conductance (g_L), as

observed during all stress periods, is one of the first processes occurring under decreased soil water availability providing a higher water use efficiency to the plant (Cornic & Massacci, 1996; Lawlor & Cornic, 2002; Flexas & Medrano, 2002). Moreover, as reviewed by Cornic (1994), stomatal closure is mainly responsible for the decline in net photosynthetic rate of C_3 leaves subjected to moderate drought stress. However, at a certain stage of stress, internal CO_2 concentration (C_i) frequently increases, indicating the predominance of non-stomatal limitations to photosynthesis (Lawlor, 1995; Brodribb, 1996; Medrano *et al.*, 2002). Reductions of light saturated photosynthetic rates (A_{sat}) in the present experiment were mainly due to stomata limitation since a significantly lower C_i was found (data not shown). Leaf reflectance (R) increased over the entire spectrum due to drought stress, a response also found elsewhere (e.g. Wooley, 1971; Penuelas & Inoue, 1999; Yu *et al.*, 2000). However, five regions with relatively high differences were observed: 520–530nm, 570–590nm, 690–710nm, 1410–1470nm and 1880–1940nm.

Rewatering plants after the stress period at flowering allowed them to restore their physiological traits until grain filling (15 days rewatered). Relative water content (RWC) of recovered plants even exceeded that of control (+7%). Therewith, A_{sat} also recovered. Only g_L remained somewhat lower than that of control plants (Table 3). However, the results from leaf reflectance (R) did not follow this trend. The relative difference $\Delta R/R$ within the range of 1410–1470nm and 1880–1940nm remained nearly as high as during the stress period at flowering despite the 7% higher RWC of recovered plants. Within the visible range of leaf spectra $\Delta R/R$ even increased during recovery compared to the actual stress period. These results indicate that quantifying the extent of change for either leaf water content or Chl_{tot} and leaf [N] from changes in leaf R might be problematic. Especially recovery from drought could not be traced using leaf R since the differences between formerly stressed plants and control plants remained rather high despite the complete recovery of physiological traits.

The reason for the enduring differences in leaf R between fully recovered plants and control plants remains rather unclear and information on leaf R during recovery of plants after a stress period is rare in literature. However, it is assumed that secondary effects following drought stress might be involved. Drought can affect the cell structure and biochemistry (e.g.: Yordanov *et al.*, 2000; Larcher, 2003; Read & Stokes, 2006) and is further known to influence the morphology of the leaf surface by means of changes in the content and/or composition of epicuticular waxes (Jordan *et al.*, 1983; Johnson *et al.*, 1983; Deng, 2005; Sehperd, 2006) or the occurrence of hairs (Foyer, 1994). Moreover, drought has the potential to accelerate ontogenetic development (Foyer, 1994; Kimball, 1995). Such alterations of leaf morphology and/or biochemical composition could not only have influenced leaf R after recovery but also have attributed to (or might be the reason for) the unexpectedly great differences in leaf R observed in plants subjected to a second stress period at grain filling. The less pronounced reaction of physiological traits to a second drought period is attributed to the preconditioning of plants already exposed to drought at flowering and/or the higher amount of green biomass (transpiring surface) of plants from the treatment stressed solely at grain filling. Plants of the treatment stressed twice were watered optimally for eight days after the drought stress event at flowering before water supply was halved again. Leaf osmotic potential remained below (more negative) that of control plants during these days providing a better initial situation concerning osmotic adjustment (data not shown) for plants already experiencing a first drought period at flowering.

		<i>Triticum aestivum</i> L.			
		AC	AF	AG	AFG
A_{sat}	Vegetative	21.2			
	Flowering	16.9	10.7***		
	grain filling	13.8	12.2 n.s.	4.4***	6.9***
g_L LS	Vegetative	84.0			
	Flowering	164.1	18.4***		
	grain filling	171.8	116.3 **	15.3***	20.3***
RWC	Vegetative	86.7			
	Flowering	83.8	74.0**		
	grain filling	76.3	81.9 *	57.1***	64.0***
AWC	Vegetative	81.2			
	Flowering	72.2	68.8**		
	grain filling	74.1	74.8 n.s.	68.3 n.s.	71.1**
Chl_{tot}	Vegetative	46.8			
	Flowering	55.0	59.2***		
	grain filling	48.3	50.3 **	61.7***	55.6***
Leaf [N]	Vegetative	4.3			
	Flowering	4.4	4.2**		
	grain filling	2.4	2.3 n.s.	1.9**	2.0**

Table 3. Summary of physiological traits of *T. aestivum*. Significance levels refer to the differences between control and stress treatments. n=5-30; n.s.: not significant, *: $p \leq 0,05$; **: $p \leq 0,01$; ***: $p \leq 0,001$. Abbreviations: AC: control; AF: drought stress at flowering, plants were recovered at grain filling; AG: drought stress at grain filling; AFG: drought stress at flowering and grain filling. A_{sat} [$\mu\text{mol.m}^{-2}.\text{s}^{-1}$], g_L : [$\text{mmol.m}^{-2}.\text{s}^{-1}$], RWC: [%], AWC: [%], Chl_{tot} : [$\mu\text{g.cm}^{-2}$]; Leaf [N]: leaf nitrogen content in % dry matter; LS: lower leaf surface. Bold values highlight performance of recovered plants (measured at grain filling).

The differences observed in $\Delta R/R$ during recovery show that no general prediction can be made concerning the potential to trace recovery from a stress situation with leaf reflectance. Apparently, different species and even cultivars respond inconsistently to drought stress with respect to their spectral signature (compare Linke *et al.*, 2008).

In contrast to changes in leaf R within the range of 1410-1470nm and 1880-1940nm, which can be attributed mainly to differences in leaf water content, the changes within the visible range are not well defined with respect to a certain stressor. As already described by Carter (1994) an increased reflectance at visible wavelengths (400-700nm) is the most consistent response to stress within the 400-2500nm range. The often made assumption that the chlorophyll content of leaves was proportional to moisture content (e.g. Tucker, 1977) may be correct for some species but cannot be generalized to different plant species and ecotypes. Variations in chlorophyll content can be caused by water stress but also by phenological status of the plant, atmospheric pollution, nutrient deficiency, toxicity, plant disease and radiation stress (Ceccato, 2001; Larcher, 2003). These findings are supported by the results

from the present study where different trends for RWC, Chl_{tot} and leaf [N] were found. Due to these adverse effects of leaf [N] (decrease) and Chl_{tot} (increase) an interpretation of the increased leaf R is difficult. At least the specific cause of these differences remains uncertain. However, the increased Chl_{tot} content found might result from leaf shrinkage leading to seemingly higher chlorophyll content per unit leaf area ($\mu\text{g}\cdot\text{cm}^{-2}$).

Finally, three spectral indices (RWC_i , AWC_i and PRI) were tested towards their ability in estimating biophysical parameters (RWC, AWC and A_{sat}). Concerning the estimation of leaf water content a better correlation was found for AWC. Unfortunately, the AWC is the less meaningful parameter since it only gives the water content as percentage of fresh weight which might vary greatly between species, phenology and environmental conditions (Larcher, 2003). The RWC, however, represents the actual leaf water content with respect to a standard measure (leaves under conditions of water saturation; Larcher, 2003) and is therefore the more appropriate indicator of plant water status. Moreover, following changes in biophysical parameters using these indices was not possible due to the different extent of changes in leaf R compared to physiological traits under drought stress at different phenological stages. From these results it is concluded that a good relationship between spectral indices and biophysical parameters does not necessarily lead to an appropriate estimation of biophysical parameters at a given phenological state and/or physiological status.

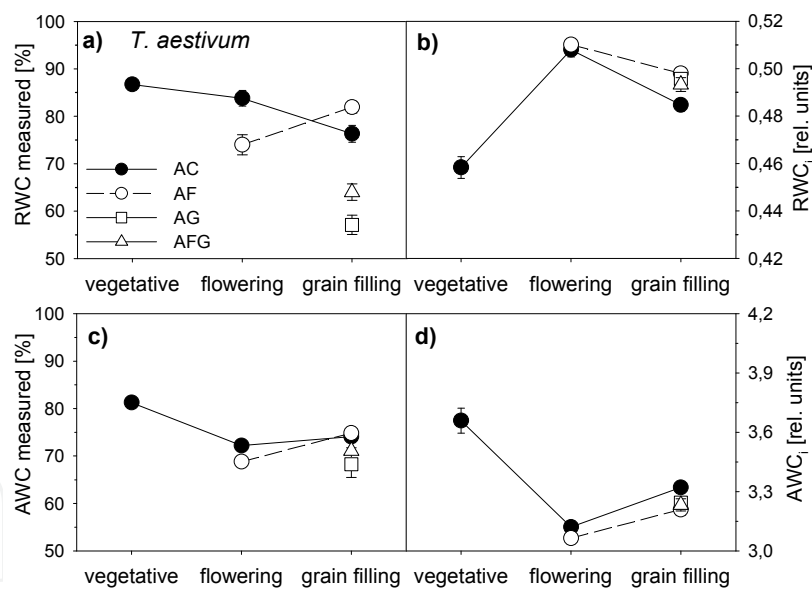


Fig. 2. Comparison of the phenological course of measured and estimated RWC and AWC of *T. aestivum*. **a)-b)** Measured and calculated relative water content; **c)-d)** Measured and calculated actual leaf water content. Legend: AC: control, AF: drought at flowering, recovered at grain filling, AG: drought at grain filling, AFG: drought at flowering and grain filling. $n=6$ for measured RWC and AWC, $n=20-30$ for estimated RWC (RWC_i) and AWC (AWC_i). Errors represent standard error.

In the here presented study, estimating leaf water content (RWC and AWC) as well as Chl_{tot} and leaf [N] from reflectance measurements gave good correlations. For tracing changes in physiological parameters during phenology and stress periods, however, the use of these

indices was not promising due to false estimation of stress situations and recovery (Figure 2 and 3). An appropriate estimation appeared possible only in unstressed control plants. A good correlation between spectral indices and physiological parameters alone is therefore not necessarily sufficient for estimating physiological parameters from leaf spectra appropriately.

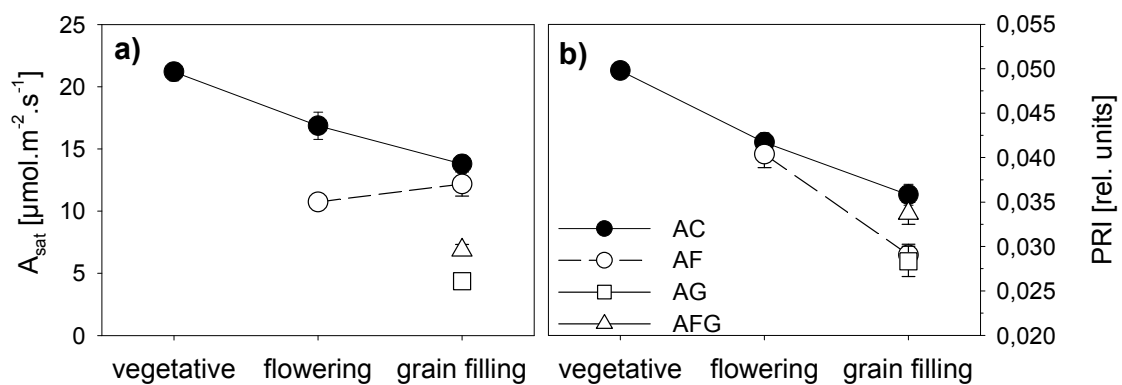


Fig. 3. Comparison of the phenological course of a) light saturated photosynthetic rates (A_{sat}) and b) photochemical reflectance index (PRI). AC: control, AF: drought at flowering, recovered at grain filling, AG: drought at grain filling, AFG: drought at flowering and grain filling. $n=12$ for A_{sat} and $n=20-30$ for PRI. Errors represent standard error.

To summarize, drought stress occurring at different phenological stages increased leaf R throughout the whole spectrum. Unfortunately, the degree to which plant physiological traits and water relations changed could not be quantified by the extent of change in leaf R, at least when drought occurred at different phenological stages. The main concern of this study, however, was to test the ability of leaf reflectance to follow recovery of physiological traits after a stress period which may be of essential importance when considering the occurrence of repeated drought events. Distinguishing between a currently occurring stress situation and an already passed one could become crucial in context with the application of spectral measurements in the field to trace stress situations and to make recommendations on fertilization or irrigation. Unfortunately, recovery from drought stress could not be traced by leaf R since the differences between formerly stressed plants and control plants remained high despite the complete recovery of physiological traits. Further investigations using different species with different leaf morphology and anatomy would be needed.

4.2 Drought stress detection by thermal infrared

Quantifying drought stress by measuring leaf/canopy temperature has become subject of intensive research within the last decades (Tanner, 1963; Wiegand, 1966). In the 1960ies researchers first used crude infrared thermometers to remotely monitor leaf temperature (Fuchs & Tanner, 1966). With the commercial availability of handheld instruments the focus moved from single leaf measurements toward the assessment of canopy temperatures.

The scientific basis for this method relies on the fact that evaporating surfaces are cooled as soon as liquid water is converted to water vapour. Therefore, the less water is available to the plant stomata will close reducing transpiration rates, lowering evaporation and therewith evaporative cooling. The result is an increase in leaf temperature. As the stress

situation becomes more severe, leaf temperature (T_c) will reach the temperature of the surrounding air (T_a) and finally exceed it. Based on this, several indices have been proposed to measure the onset of plant water stress, such as the Critical Temperature Variability (CTV) (Blad *et al.*, 1981; Clawson & Blad 1982), Temperature Stress Day (TSD) (Gardner *et al.*, 1981), Stress Degree Day (SDD) (Idso *et al.*, 1977; Jackson *et al.*, 1977), or Crop Water Stress Index (CWSI) (Jackson *et al.*, 1981; Jackson 1982).

The concept of stress degree days (SDD) relies on a daily value of the difference between T_c and T_a at the time of maximum surface temperature (approximately 1-2 hours after solar noon; Idso, 1977; Idso 1981). However, from basic considerations concerning energy balance it becomes evident that the stress degree day parameter is additionally influenced by other environmental factors like the vapour pressure deficit of the air, net radiation or wind speed (Idso, 1981). Ben-Asher (1992) further cautioned that the sensitivity of IR sensors would be insufficient to sense very small differences in temperature and it would be unable to assess short term fluctuations of transpiration. Moreover, errors might result from stomatal closure during periods of peak solar radiation (midday depression), high ambient CO_2 concentrations, or because of disease (Ehret, 2001).

All together, these findings led to the development of the crop water stress index (CWSI) an index that essentially normalizes the stress degree parameter for environmental variability (Idso, 1981). The crop water stress index (CWSI), which is derived from canopy-air temperature differences ($T_c - T_a$) versus the vapour pressure deficit of the air (VPD), was found to be a promising tool for quantifying crop water stress (Jackson *et al.*, 1981; Idso & Reginato, 1982; Jackson, 1982). The calculation of CWSI relies on the establishment of two baselines: the non water stressed baseline (lower limit), which represents a fully watered crop, and the maximum stressed baseline (upper limit), which corresponds to a non-transpiring crop (stomata fully closed; Yuan *et al.*, 2004; Erdem, 2005). The resultant values of the CWSI normally cover a range from 0 (no stress) to 1 (severe stress). The critical value signifying a reduction in transpiration of plants can be found between 0.25–0.35 (Roth *et al.*, 2004) but the boundary threshold of CWSI indicating irrigation requirements is crop specific, depending, amongst others, on yield response to water stress.

During the last decades many researchers have used the CWSI method for irrigation management (e.g. Pinter & Reginato, 1982; Wanjura *et al.*, 1990; Irmak *et al.*, 2000). Due to the dependency on species, location and climate zones, quite different slope and intercept values have been established in the different studies. Beside these factors the heterogeneity of different plant canopies has to be considered to assure that the fraction of soil background sensed plays only a minor role. This might become a challenging factor especially during early growth stages until complete canopy closure or in crop species where complete soil cover is generally not reached, since spots of soil between the plants induce higher heterogeneity and thus lead to erroneous plant temperature measures.

Another factor strongly influencing the applicability of CWSI for irrigation scheduling is the local climatic situation. The majority of studies which have successfully applied the CWSI concept were carried out in arid or semi arid regions where cloud cover plays a minor role. In contrast, under more humid conditions the validity of CWSI should be seen critical due to low vapour pressure deficit (VPD) values (with a small range) and the frequent occurrence of clouds (Roth *et al.*, 2004). Faraj *et al.* (2001) emphasized that because of the strong impact of changing environmental conditions (such as VPD, net radiation and wind speed) on the

performance of the lower baseline and variable canopy resistance the usefulness of CWSI for irrigation scheduling is rather limited. Moreover, Yuan *et al.* (2004) compared different CWSI approaches and concluded that, due to its large fluctuations and variations, the empirical CWSI is of little practical value for detecting crop water stress in winter wheat in China. When using the empirical approach, CWSI may even range outside of 0 – 1, leading for example to negative values as it was observed by Faraj *et al.* (2001).

Wanjura *et al.* (1995; Wanjura & Upchurch, 1996) introduced an alternative method to determine the non-water stressed baseline. They based their method on the Penman-Montheith equation and considered the surface temperature as a wet bulb temperature which can be determined when further parameters like net radiation (R_n) and the aerodynamic resistance (r_a) to heat flow between the surface and a reference level are known. The baseline, when established by the method of Idso *et al.* (1981), has to be determined experimentally which bears considerable constraints: it precludes its transfer to other regions since baselines will be site specific. They might also not be transferred to different years (or other times of the day) and they will be valid only for the same clear sky conditions (Alves, 2000). Alves & Pereira (2000), however, concluded from their studies that the infrared surface temperature of fully transpiring crops can indeed be regarded as a wet bulb temperature that can be used to calculate the surface temperature (T_s) for non-water-stressed conditions when net radiation (R_n), aerodynamic resistance (r_a) and air temperature are known. This method has the advantage over the experimentally determined non-water stressed baseline that measurements can be made at any time of the day from sunrise to sunset, that they can be made independently of climatic conditions including cloudy conditions and finally, previous observations, to derive or to validate a baseline, are not necessary (Alves & Pereira, 2000). For a detailed derivation of the equation see Alves & Pereira (2000).

To summarize, several studies have successfully applied the CWSI concept to their regions but all these studies have in common that they were carried out in arid or semi arid regions of the world where cloud cover plays a minor role. In these climatic regions the concept provides a solid and cost effective method to schedule irrigation and reduce water consumption. It has, however, to be kept in mind that the CWSI is only an indicator of the onset of a drought event but does not give any further information about the amount of water needed to retain maximum possible yields. But this should not be a detriment to use this technique for irrigation scheduling since in many cases the irrigation amounts are limited by other factors like the irrigation system application rate, soil water intake rate or the amount of water available for irrigating crops. In such situations the knowledge about the theoretically needed amount of water is of little use due to the other restrictions (Nielson & Gardener, 1987).

4.2.1 Case study 2 – Use of CIR sensors for drought stress detection in Pannonian climate

4.2.1.1 Materials and methods

This study was carried out at Versuchsgarten Augarten, Vienna (48°13'35" N, 16°22'30" E, 164 m a.s.l.), and aimed at the short term drought stress detection by the use of thermal infrared measurements. Two areas in the size of 5 x 6 m were available for crop growing: a reference plot, where plants were irrigated ("irrigated") and a second plot where plants were only irrigated until the first leaves were fully developed and then exposed to precipitation only ("rainfed").

Triticum aestivum L. cv. Xenos was sown on 5 April 2006 at a rate of 600 seeds m⁻². The soil, a chernozem, was fertilized with a total amount of 120 kg N/ha (70 kg N from Nitramoncal and 50kg from KNO₃) with the application split in three bits according to local agricultural practice: before sowing, at tillering and at heading. Application of KNO₃ further supplied plants with a total of amount 60 kg K/ha.

For the measurement of plant canopy temperature cloud infrared (CIR) sensors were used. CIR-Sensors are ground-based instruments which were originally designed to infer day and night cloud cover. They operate in a 9 to 14 μm spectral range with a 12-degree FOV. In the here presented study two such sensors of which each generated two distinct output signals, the temperature of the sensor's shell and the infrared temperature of the measured body, were used. From these data and under implementation of meteorological parameters such as air temperature (T_a), vapor pressure deficit (VPD), net radiation (R_n) and aerodynamic resistance (r_a) the canopy temperature of the plant stand was calculated.

In addition, basic plant physiological parameters were determined: instantaneous leaf conductance (g_L) was measured with a steady state porometer (PMR-4, PP-Systems; U.K.), leaf water potential (Ψ_w) was determined predawn (02:30-04:00) and at noon (12:30-14:00) using a pressure Bomb (Scholander *et al.*, 1965) and leaf temperature of single leaves within the plots was measured with a handheld infrared thermometer (Raytek). Relative water content was calculated as $RWC = ((\text{fresh weight} - \text{dry weight}) / (\text{saturated weight} - \text{dry weight})) * 100$ [%]. All measurements were performed on the youngest fully expanded leaf at three developmental stages (vegetative growth, flowering and grain filling). The determination of plant physiological parameters served as a reference to indicate the occurrence of drought stress in rainfed plants.

4.2.1.2 Results and discussion

Regarding the climate, the study region belongs to the northeastern part of Austria, a semi-arid area characterized by deep groundwater level and low precipitation levels. The mean annual precipitation is 577mm and the mean annual temperature is 9.9°C (Eitzinger *et al.*, 2003). The climate is therefore more humid than in other regions where CWSI is applied for irrigation management. It is further known from other studies that the calculation of CWSI is ideally performed during cloudless skies (e.g. Idso *et al.*, 1981). Since such conditions are not frequently available in the study area, the present study aimed at testing the uncertainties of the CIR-Sensor measurements and to calculate CWSI for non-ideal conditions such as cloudy sky, fetch effects and suboptimal orientation of the sensors.

An early response of plants to a lowering of soil water availability is the reduction of leaf conductance (g_L) thus avoiding excess water loss and providing higher water use efficiency to the plant (Cornic & Massacci, 1996; Lawlor, 2002; Flexas & Medrano, 2002; compare also section 2). At all observation dates, g_L of rainfed plants was lower than that of irrigated ones (Table 4) indicating poorer water supply. This further resulted in lower transpiration rates and reduced transpirational cooling. Therewith, slightly increased leaf temperatures were observed in plants of the rainfed plot throughout the whole growing season (Table 4). The differences between leaf temperature of plants from the rainfed and the irrigated plot were highest around noon, where the surface received maximum net radiation. The smallest mean differences were observed between 0:00 and 3:00 MEZ. Therefore, values of the 12:00 to 15:00 MEZ time period were used for the calculation of crop water stress index (CWSI).

time	growth stage	Ψ_w		RWC		g_L US		g_L LS		T_{leaf}	
		ir	rf	ir	rf	ir	rf	ir	rf	ir	rf
pre-d.	veget.	-1.8	-1.9	93.2	94.8						
	flow.	-2.4	-4.6***	94.4	89.4						
	grain f.	-6.8	-11.3***	82.8	83.8						
noon	veget.	-6.8	-7.8	94.4	92.2	541.4	364.2**	601.1	177.0***	18.7	22.4
	flow.	-17.2	-20.1*	77.5	82.1	632.7	523.2**	568.7	361.1**	27.7	28.6*
	grain f.	-18.3	-19.9	79.3	81.5	721.0	537.4**	609.1	328.5***	25.0	30.2***

Table 4. Summary of the results from physiological measurements. *Abbreviations:* pre-d.: pre dawn measurement; noon: noon measurement; veget.: vegetative growth, flow.: flowering; grain f.: grain filling; ir: irrigated; rf: rainfed; Ψ_w : leaf water potential [bar]; RWC: relative water content [%]; g_L : leaf conductance [$\text{mmol.m}^{-2}.\text{s}^{-1}$]; US: upper leaf surface; LS: lower leaf surface, T_{leaf} : leaf temperature. Significance levels refer to the differences between rainfed and irrigated plants. ***: $p \leq 0.001$; **: $p \leq 0.01$; *: $p \leq 0.05$; $n=5-30$.

In addition to the measurement of stomatal conductance and leaf temperature, leaf water potential was determined. A decrease of soil water content resulted in a lowering of leaf water potential (Ψ_w , more negative values; Chaves, 1991; Cornic, 1994; Lawlor, 1995). Predawn leaf water potential ($\Psi_{w,pd}$), which gives a pretty good estimation of soil water content (Richter, 1997; Taiz & Zeiger, 2000; L6sch, 2003), did not differ greatly at vegetative growth (+8%, Table 4) between plants of the two plots. At flowering and grain filling, rainfed plants exhibited significantly lower $\Psi_{w,pd}$ (more negative; +94% and +65%, respectively) compared to irrigated plants.

For wheat, the most critical period concerning the occurrence of drought stress is the period which brackets anthesis. Irrigation recommendations are therefore given for drier periods during vegetative growth until shortly after flowering (Geisler, 1983). Thus, for testing the energy balance method to determine a non-water stressed baseline, data from June (flowering period) were used. Concerning the results obtained from infrared thermometry it could be shown that the effect of wind was rather small and, both the orientation of the CIR sensors as well as fetch effects were not very prominent in this environment during noon time (results not shown). The simulated leaf temperature for the irrigated plot was calculated by applying both the classical method after Idso (Idso *et al.*, 1981) and the energy balance based method (Alves & Pereira, 2000) for all sky conditions. The resultant coefficient of determination (r^2) between simulated and measured leaf temperature was higher for the latter method ($r^2=0.8$), for which reason the set up of a non water stressed baseline by the method based on the energy balance is to be advantaged under such climatic conditions. Figure 4 indicates a satisfying relationship between measured and calculated leaf temperature both for a single week (11.6-17.06.2006) and for almost one month (8.6.-4.7.2006) during the experiment (Table 5 gives a summary of leaf temperatures measured with a handheld IR thermometer). However, when comparing the simulated (energy balance method) and measured CWSI calculated from data recorded at noon time (12.00-15.00) throughout the whole experimental period, the result is not at all satisfying ($r^2=0.3366$).

From this study it can be concluded that one of the most detrimental factors for establishing a non water stressed baseline seems to be cloudiness, a result which was also obtained by Da Silva & Rao (2005). However, the results further suggest that influences other than

cloudiness might be responsible for the poor relationship between measured and simulated CWSI. Idso (1982), for example, defined non-water-stressed baselines for 26 different species for clear sky conditions and found that these baselines were different for various phenological stages in certain crops. He further suggested that, for example, for winter wheat different baselines should be developed for pre and post head stages. Gardner *et al.* (1992) also urged that care has to be taken concerning the use of an inappropriate base line since small errors in its determination can lead to large errors in the calculation of CWSI.

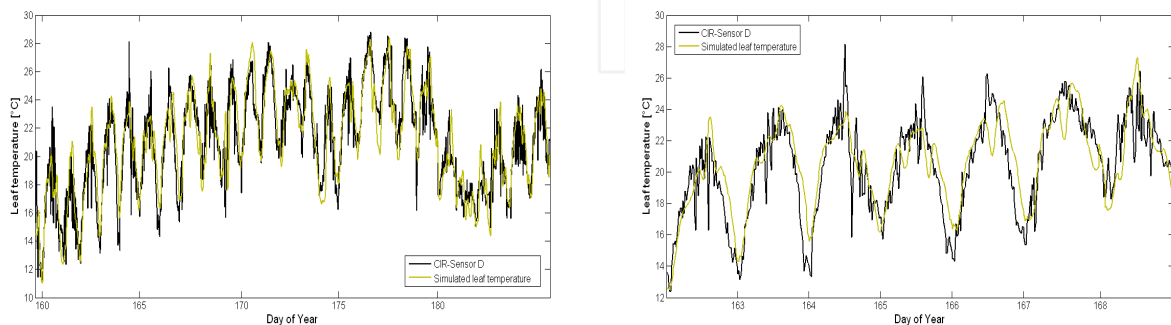


Fig. 4. Simulated (energy balance method) and measured leaf temperature for plants of the irrigated plot during a) one month (8.6.-4.7.2006) and b) one week (11.6-17.06.2006, beginning of flowering) of the experimental period.

date	treatment	time of the day	g_L (Std error)	T_{leaf} (Std error)	T_{air}
19/06/2006	rainfed	morning	531.8 (31.2)	26.8 (1.5)	26.2
		noon	582.6 (57.1)	31.0 (0.9)	29.1
		afternoon	325.4 (39.2)	26.6 (0.4)	29.2
	irrigated	morning	746.7 (88.9)	29.0 (1.1)	26.8
		noon	558.1 (41.7)	28.5 (0.5)	29.7
		afternoon	520.5 (54.3)	26.3 (0.4)	28.5
21/06/2006	rainfed	morning	606.8 (33.3)	27.1 (0.7)	28.0
		noon	538.6 (65.4)	26.1 (0.2)	28.0
		afternoon	513.8 (74.5)	28.5 (0.3)	29.7
	irrigated	morning	651.2 (22.1)	24.0 (0.3)	27.2
		noon	696.6 (72.7)	27.0 (0.4)	28.3
		afternoon	628.6 (61.1)	25.4 (0.4)	29.9

Table 5. Daytime course of leaf temperatures measured with a handheld IR thermometer (T_{leaf}), air temperature (T_{air}) and stomatal conductance (g_L) in *T. aestivum* for the 19.06.2006 and the 21.06.2006 (flowering period).

5. Conclusions

Water scarcity is an increasingly important issue in many parts of the world. Within the next centuries global climate change is expected to result in a long-term trend towards higher

temperatures, greater evapotranspiration, and an increased incidence of drought in specific regions. Concurrently, the increased need for food supply worldwide and the prediction of the emergence of drier regions, demand the development of cost effective methods for early stress detection to reduce yield losses.

The first study presented herein aimed at the evaluation of drought stress, applied at different phenological stages (flowering and/or grain filling), on plant physiological traits and leaf reflectance and their subsequent recovery. An increase of leaf reflectance (R) as observed in the range from 500-600nm is mainly attributed to a lower chlorophyll or nitrogen content. However, in this study, a lower relative water content (RWC) also increased R in this range of the spectrum. A higher R would normally be attributed to a decreased chlorophyll content or nitrogen deficiency but would not be primarily addressed to a lower RWC. Results further showed that rehydrating plants recovers physiological traits but the recovery could not be traced by reflectance measurements since R remained above that of control plants. A distinction between a current stress situation and an already passed one was not possible. Fertilization commendations based on such results would be ineffective since the uptake of nitrogen by plants is strongly restricted under drought.

From the second study presented herein it can be concluded that sensing drought stress by thermal IR works well under clear sky conditions at larger scales without fetch effects and when sensor orientation is optimal. Non-ideal conditions such as small study sites and frequently changing environmental conditions (e.g. cloudiness), however, may introduce uncertainties which might be larger than the drought stress signal itself. As a result, the calculation of CWSI for this study site, characterized by changing environmental factors (e.g. cloudiness), seems not accurate enough to be used for irrigation scheduling.

6. References

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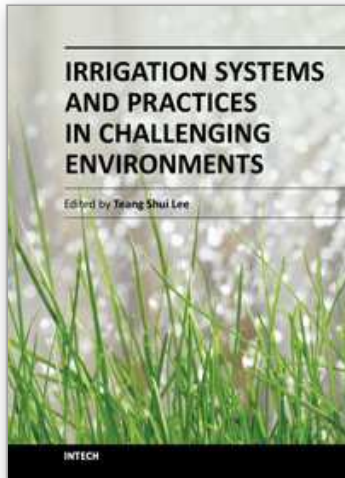
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Irrigation Systems and Practices in Challenging Environments

Edited by Dr. Teang Shui Lee

ISBN 978-953-51-0420-9

Hard cover, 370 pages

Publisher InTech

Published online 28, March, 2012

Published in print edition March, 2012

The book *Irrigation Systems and Practices in Challenging Environments* is divided into two interesting sections, with the first section titled *Agricultural Water Productivity in Stressed Environments*, which consists of nine chapters technically crafted by experts in their own right in their fields of expertise. Topics range from effects of irrigation on the physiology of plants, deficit irrigation practices and the genetic manipulation, to creating drought tolerant variety and a host of interesting topics to cater for the those interested in the plant water soil atmosphere relationships and agronomic practices relevant in many challenging environments, more so with the onslaught of global warming, climate change and the accompanying agro-meteorological impacts. The second section, with eight chapters, deals with systems of irrigation practices around the world, covering different climate zones apart from showing casing practices for sustainable irrigation practices and more efficient ways of conveying irrigation waters - the life blood of agriculture, undoubtedly the most important sector in the world.

How to reference

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Rita Linke (2012). Drought Stress and the Need for Drought Stress Sensing in a World of Global Climate Change, *Irrigation Systems and Practices in Challenging Environments*, Dr. Teang Shui Lee (Ed.), ISBN: 978-953-51-0420-9, InTech, Available from: <http://www.intechopen.com/books/irrigation-systems-and-practices-in-challenging-environments/drought-stress-and-the-need-for-drought-stress-sensing-in-a-world-of-global-climate-change>

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