Chapter 6

The Effects of Water Stress on Plant Respiration

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Summary

Plant growth can be limited by several factors, among which a lack of water is considered of major importance. Despite the vast knowledge of the effect of water stress on photosynthesis, there is much less known about its effect on respiration. Respiration, unlike photosynthesis, never halts, and it reflects the overall metabolism. However, the data available on the effect of water stress on respiration show large variation, from inhibition to stimulation under different water-stress conditions. This chapter combines a review of the latest studies of the effect of water stress on plant respiration with the compilation of data from different authors and recent results to develop a working hypothesis to explain how respiration is regulated under water stress. Leaf respiration shows a biphasic response to Relative Water Content (RWC), decreasing in the initial stages of water stress (RWC > 60%), and increasing as RWC decreases below 50%. Under this hypothesis, the initial decrease in respiration would be related to the immediate inhibition of leaf growth and, consequently, the growth respiration component. The increase of respiration at lower RWC would relate to an increasing metabolism as the plant triggers acclimation mechanisms to resist water stress. These mechanisms would increase the maintenance component of respiration, and, as such, the overall respiration rate. This hypothesis aims to give a metabolic explanation for the observed results, and to raise questions that can direct future plant respiration experiments.

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I. Introduction

Water stress is considered to be a major environmental factor limiting plant productivity world-wide (Boyer, 1982; 1996). Equally, it is well recognized that plant productivity largely depends on the balance between photosynthesis and respiration (Lambers et al., 1998). The effects of water stress on photosynthesis have been studied and debated elaborately (Hsiao, 1973; Boyer, 1976; Chaves, 1991; Lawlor, 1995; Cornic and Massacci, 1996; Flexas and Medrano, 2002; Lawlor and Cornic, 2002). However, since photosynthesis is limited to favorable environmental conditions (including light) and to green biomass, whereas respiration occurs continuously in every cell of every plant organ, the latter may be the more important factor controlling productivity, particularly when photosynthesis is largely suppressed, such as under water-stress conditions. A recent large-scale eddy-correlation study further illustrates the importance of ecosystem respiration in determining productivity (Valentini et al,. 1999). In a transect across Europe, large differences in annual net primary production were independent of gross primary assimilation, which was relatively similar among different ecosystems, but strongly dependent on ecosystem respiration (Valentini et al., 1999). It is now also well documented that ecosystem respiration is strongly affected by water availability (Bowling et al., 2002).

However, in spite of its highly recognized importance, the effects of water stress on respiration at the physiological level are largely unknown, partly because only a limited number of studies are available, and partly because of the apparent contradictions among these studies. Certainly, the available experimental evidence does not support a clear pattern of respiration response to water stress, different studies showing either increased, unaffected or decreased rates of respiration (Hsiao, 1973; Amthor, 1989).

This chapter does not seek to exhaustively review all the literature concerning the response of plant respiration to water stress. This would result merely in a list of contrasting examples. Rather, the aims of the present chapter will be: (i) to summarize the information on effects of water stress on plant respiration, focusing mainly on the literature published after the most recent reviews (Amthor, 1989; Amthor and McCree, 1990); (ii) to search for a theoretical background to reconcile the apparent contradictions about respiration response to water stress; and (iii) to highlight the research priorities in this field for the near future.

II. The Effects of Water Stress on Respiration Rates of Different Plant Organs

Previous reviews concerning plant respiration responses to water stress highlight the apparent discrepancies among studies (Hsiao, 1973; Hanson and Hitz, 1982; Amthor, 1989; Amthor and McCree, 1990). Among the earlier studies, several described a water-stress-induced decreased respiration rate in leaves (Brix, 1962; Brown and Thomas, 1980), shoots (Boyer, 1970), roots (Rice and Eastin, 1986), flower apices (Pheloung and Barlow, 1981) or whole plants (Penning de Vries et al., 1979; Wilson et al., 1980; McCree et al., 1984; McCree, 1986). Others showed almost unaffected (Lawlor, 1976) or even increased respiration rates in water-stressed plants (Upchurch et al., 1955; Shearman et al., 1972). More recent studies, using a diversity of techniques to determine respiration rates, have not resolved these apparent contradictions. While several studies have again shown decreased respiration rates under water stress in different plant organs (Palta and Nobel, 1989; González-Meler et al., 1997; Escalona et al., 1999; Ghashghaie et al., 2001; Haupt-Herting et al., 2001), others have again shown unaffected rates (Loboda, 1993), or an increased respiration rate under water stress (Zagdanska, 1995). Ghashghaie et al. (2001) showed in sunflower (*Helianthus annuus*) that leaf respiration decreased at early stages of water stress, and then increased even above control values at later stages.

Moreover, recent studies have shown the influence of respiratory acclimation in the response to water stress. Collier and Cummins (1996), for instance, in a study with *Saxifraga cernua*, showed a progressive decline in total leaf respiration as water stress developed slowly in plants grown on an organic substrate. In contrast, in plants grown in vermiculite where water stress developed more rapidly, total leaf respiration initially increased, and then declined steeply. Zagdanska (1995) showed that pre-acclimation to water stress resulted in higher total respiration in wheat (*Triticum aestivum*) leaves. However, similar responses of respiration to subsequent water stress

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Abbreviations: CAM – Crassulacean acid metabolism; PEPCK – phosphoenol pyruvate carboxylase kinase; RWC – relative water content.

were observed in both pre-acclimated and non-acclimated plants. Also, Palta and Nobel (1989) showed in *Agave deserti* that root respiration declined as soil water potential decreased, but the precise response was age-dependent and different in established and rain roots. Moreover, the respiration rates of established roots never reached zero, and recovered rapidly and completely upon rewatering. In contrast, the respiration rates of rain roots rapidly reached zero, and did not recover upon rewatering. Bryla et al. (1997) have shown in citrus (*Citrus volkameriana*) seedlings that water stress induced a progressive decline in root respiration.

All these studies have been performed using a single or a few plant species or genotypes, under particular environmental conditions, and using different techniques to assess respiration, thereby making direct comparison difficult. Therefore, the confusion might arise from the difficulties of directly comparing different experiments. In this sense, at least three possible causes for the above-mentioned contradictions are apparent: (i) that the discrepancies in the response of respiration rates to water stress among several studies are simply due to the different species, organs and techniques used; (ii) that different responses to water stress arise from complex interactions with other environmental factors, e.g., ambient temperature; and (iii) that a change in the response of respiration to water stress occurs at a certain threshold of water stress intensity.

In order to discard the first two possible causes, Gulías et al. (2002) compared six species developing water stress under the same conditions in the field. Total leaf respiration rate was determined from light-response curves of CO_2 assimilation. One species (*Rhamnus ludovici-salvatoris*) showed a progressive decrease of leaf respiration during water stress. Another (*Quercus humilis*) showed an initial increase at mild water stress, followed by a large decrease at severe water stress. Leaf respiration was unaffected by water stress in the other four species. To further confirm that interspecific differences do occur, irrespective of the environmental conditions and the technique used to assess respiration rates, J. Galmés et al. (unpublished) have recently analyzed six additional species, growing in a cabinet under identical conditions (800 μmol photons m^{-2} s^{-1}; 50% RH; 25 ºC), all with a similar total leaf area and subjected to identical water stress treatments (withholding water for 15 consecutive days). In this study, respiration during a water-stress cycle, was monitored polarographically with a liquid-phase oxygen electrode, after dark-adapting the leaves for 30 minutes. The response of respiration to water stress turned out to be very variable (Fig. 1). While *Mentha aquatica* and *Pistacia lentiscus* exhibited almost constant values throughout the water-stress cycle, respiration in *Phlomis italica* showed an initial decline until day 8, and a sustained slow respiration rate thereafter. *Lysimachia minoricensis* showed an initial decline, but respiration increased above initial values by day 15. Finally, *Cistus albidus* and *Hypericum balearicum* showed a very irregular response of respiration to water stress. These results clearly demonstrate inter-specific differences, and show that environmental and methodological differences do not fully account for the observed discrepancies.

III. The Relationship between Leaf Respiration and Relative Water Content

The fact that respiration rates decrease under water stress in some studies, while they increase in others may be due to differences in the species tolerance to water stress, as well as to different water stress intensities. Clearly, different species develop different degrees of water stress under similar water shortage. Following the idea of Lawlor and Cornic (2002) that differences in tissue relative water content (RWC) may account for most of the observed metabolic responses to water stress, we have attempted to make a comparison of different studies using RWC as a reference parameter for the intensity of water stress (Fig. 2). We have pooled data from several studies (Zagdańska, 1995; Ghashghaie et al., 2001; Gulías et al., 2002; J. Galmés et al., unpublished), covering a total of 14 species, including herbs, shrubs and trees, and both crop and wild species. The relationship between dark respiration and RWC showed a biphasic response. Initially, as RWC decreased to ca. 70%, there was a decreasing trend of respiration. For RWC values between 70% and 55%, there was a remarkably consistent slow respiration. At RWC below 55% the respiration rate eventually increased, sometimes even above control values (Zagdańska, 1995; Ghashghaie et al., 2001).

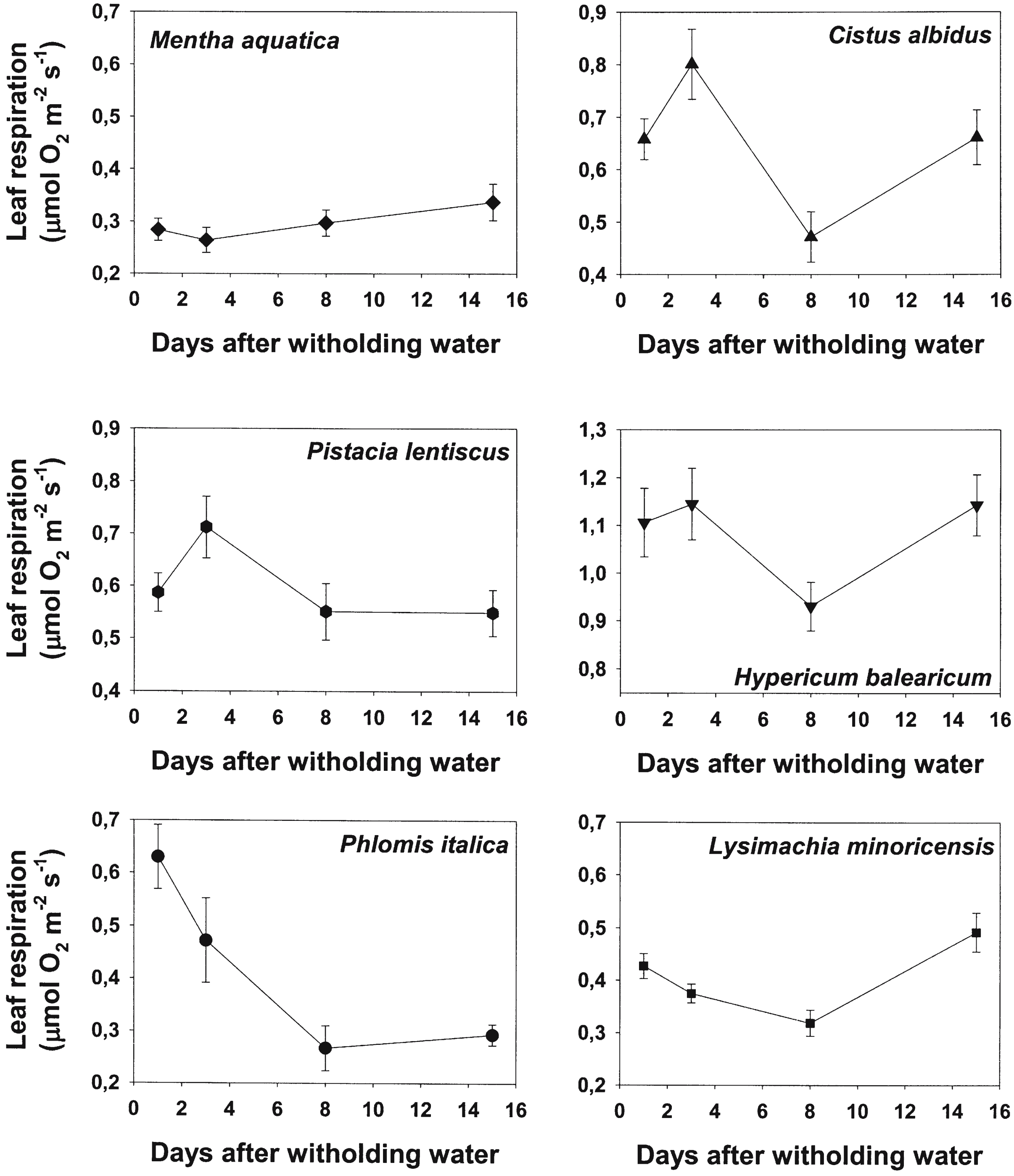

Fig. 1. Different responses of total leaf respiration to water stress in six Mediterranean species. The six species were grown in a cabinet under identical conditions (800 µmol photons m^{-2} s^{-1}; 50% RH; 25ºC), and had a similar total leaf area at the onset of the experiment, they were then subjected to identical water-stress treatments (withholding water for 15 consecutive days). In this study, respiration was measured polarographically with a liquid-phase oxygen electrode, after dark-adjusting the leaves for 30 minutes (from J. Galmés et al., unpublished).

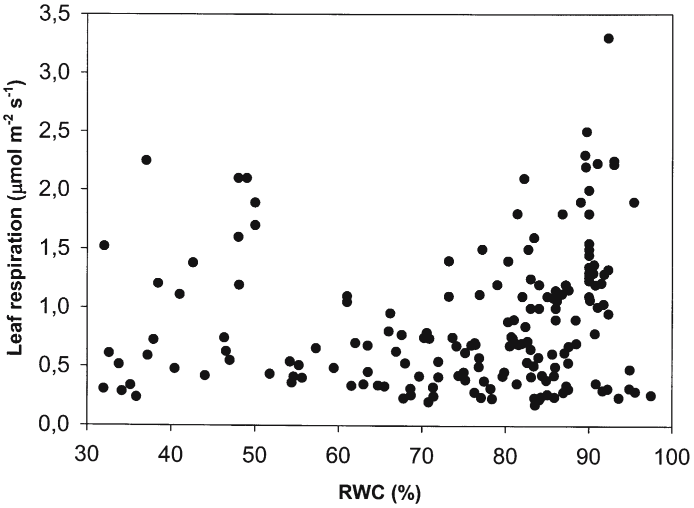

Fig. 2. The relationship between total leaf respiration (μmol O_2 m^{-2} s^{-1} or μmol CO_2 m^{-2} s^{-1}, assuming a 1:1 O_2:CO_2 relationship during respiration) and relative water content (RWC). The set includes data from Zagdańska (1995), Ghashghaie et al. (2001), Gulías et al. (2002) and J. Galmés et al. (unpublished). The species included are: *Triticum aestivum*, *Helianhus annuus*, *Nicotiana sylvestris*, *Rhamnus alaternus*, *Rhamnus ludovici-salvatoris*, *Pistacia lentiscus*, *Pistacia therebinthus*, *Quercus humilis*, *Quercus ilex*, *Hypericum balearicum*, *Lysimachia minoricensis*, *Mentha aquatica*, *Cistus albidus* and *Phlomis italica*.

IV. Possible Causes for the Biphasic Response of Respiration to Relative Water Content

The biphasic response of respiration to RWC may be explained by the differences in sensitivity of different physiological processes to water stress (Hsiao, 1973, Fig. 3). The first physiological consequences of a mild water stress consist of a decrease in cell expansion, cell-wall synthesis, protein synthesis, stomatal closure and photosynthesis. These decreases will result in reduced plant growth, and, therefore, the growth component of respiration would be decreased (R_G; see Chapter 10, Bouma). One, or both of these two factors, may induce a progressive down-regulation of respiration as water stress becomes more intense. However, although respiration in well watered plants depends on photosynthetic rates (Azcón-Bieto and Osmond, 1983; Noguchi, 2004) this may not necessarily be true under water stress. Early studies have shown that both photosynthesis and respiration are affected by water stress; however, photosynthesis is much more affected than respiration (Upchurch et al., 1955; Brix, 1962; Boyer, 1970). While some authors have observed a good correspondence between photosynthetic rates and respiration during a water-stress cycle (Lee Chung et al., 1994), others have not. An example of the latter situation is shown in Fig. 4 (J. Galmés et al., unpublished). Leaf respiration rates during a water-stress cycle were independent of photosynthesis in *Pistacia lentiscus* and *Hypericum balearicum*. While photosynthesis was strongly suppressed in both species, respiration was almost constant during the cycle. Moreover, respiration was always faster in *Hypericum* than in *Pistacia*. Other evidence suggests that the direct relationship between photosynthesis and respiration is impaired by water stress. For instance, Collier and Cummins (1996) showed a good correspondence between leaf respiration rates and soluble sugar content, but the precise relationship differed strongly between plants that were stressed rapidly or slowly. Moreover, ^{13}C-fractionation studies suggest that the patterns of use of recent photoassimilates and reserve substances to drive respiration may well change under water-stress conditions (Duranceau et al., 1999; Ghashaghaie et al., 2001). Taken together, the evidence suggests that decreased rates of photosynthesis, and, consequently, decreased availability of photosynthates, is not the main cause for decreased respiration rates at early stages of water stress.

Recent studies have not differentiated between the responses of the growth and maintenance components of total respiration to water stress. An early study by Wilson et al. (1980) in sorghum (*Sorghum bicolor)* plants subjected to slowly developing water

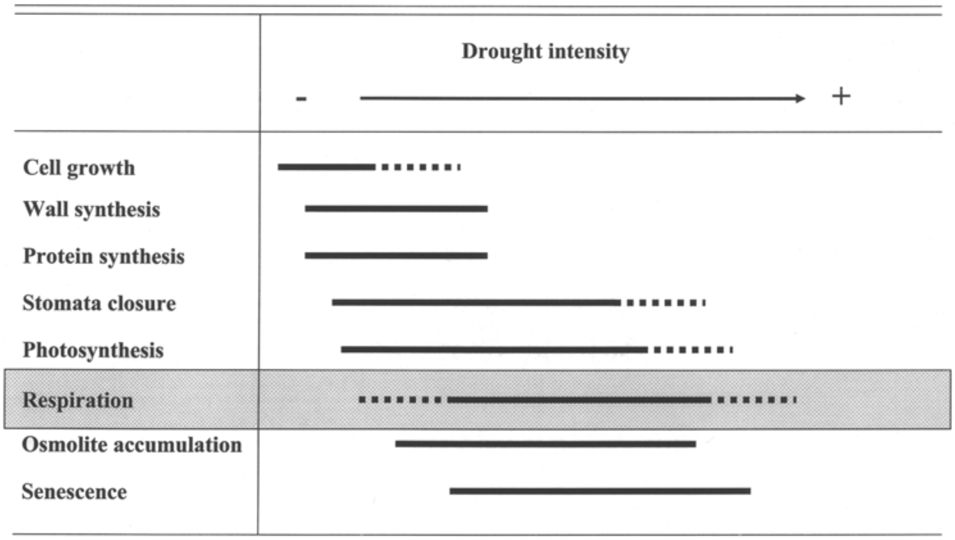

Fig. 3. Theoretical sequence of metabolic processes, including respiration, as affected at different levels of water stress. Modified from Hsiao (1973).

stress showed that whole plant respiration decreased linearly with leaf water potential. However, although both growth and maintenance components of respiration decreased, the slope of the response of growth respiration was three times steeper than that of the maintenance component. This result supports the hypothesis that decreased plant growth is the main reason for the initial decrease in respiration in plants subjected to water stress. Slow-growing species show slower respiration rates, even at high RWC (Lambers et al., 1998). If decreased growth is indeed the main cause for decreased respiration under water stress, then the respiration rates of these species are expected to be less affected by water stress. Certainly, this was the case in slow-growing species such as *Pistacia lentiscus*, *Rhamnus alaternus*, *Quercus ilex* and *Mentha aquatica* (Gulías et al., 2002; J. Galmés et al., unpublished; Fig. 1).

Another possibility to explain the initial decrease of respiration rates would be that water stress might impair some enzymes involved in respiration. However, these seem to be quite insensitive to water stress. The effect of water stress on mitochondrial activity of several key respiratory enzymes and oxidative capacities has been studied in two CAM species, *Prenia sladeniana* (ME-type) and *Crassula lycopodioides* (PEPCK-type) (Herppich and Peckmann, 2000), with the results showing that cytochrome *c* oxidase, NADH-malic enzyme, malate dehydrogenase, fumarase and citrate synthase were unaffected by mild to moderate water stress.

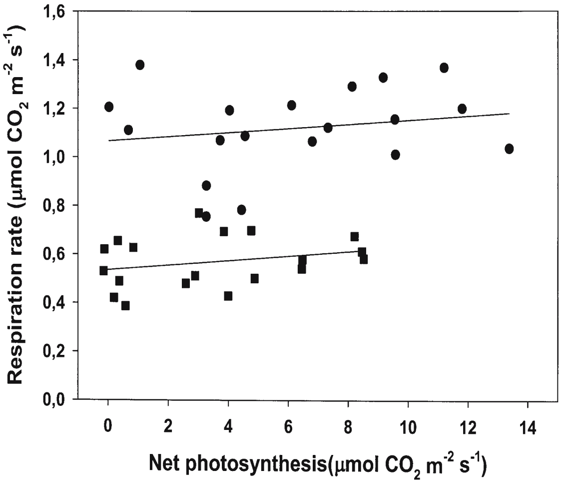

Fig. 4. The relationship between leaf respiration and photosynthesis during a water-stress cycle (see Fig. 1) in *Pistacia lentiscus* (squares) and *Hypericum balearicum* (circles). Data from J. Galmés et al. unpublished.

At more severe levels of water stress, by contrast, the situation can be reversed, i.e. respiration rates may eventually increase (Fig. 2). After hormonal changes take place, there is an accumulation of proline and other compatible solutes, and a general change in metabolism (Fig. 3). All these changes might induce an increase in the maintenance component of respiration under moderate to severe water stress. This was indeed shown by Moldau et al. (1980), Hitz et al. (1982) and Moldau and Rahi (1983). Moreover, since ATP production in the chloroplasts is decreased under water stress, it can be expected that the excess reducing equivalents would be used in mitochondria to overcome an excessive reduction state (and, consequently, susceptibility to oxidative stress) of the system (Lawlor, 1995; Wagner and Krab, 1995). Water-stress-induced senescence and its associated metabolism could also imply higher needs for respiration. Therefore, a biphasic response of respiration to water stress could be expected, consisting of progressive depression of respiration rates at initial stages of water stress, followed by subsequent increases below the threshold water-stress intensity.

An important point to consider is how electron partitioning between the cytochrome pathway and the cyanide-resistant alternative pathway changes under water stress. The role of the alternative pathway is still under debate (Chapter 1, Lambers et al.), but it has been proposed that the activity of this pathway is somehow related to stress and to oxidative stress alleviation (Wagner and Krab, 1995; Lambers et al., 1998; Ribas-Carbo et al., 2000). In this case, it might be hypothesized that the activity of the cytochrome pathway would progressively decrease during water stress, because of the reduced demand for ATP, while the activity of the alternative pathway may eventually increase during the second phase of water stress, to alleviate over-reduction of the electron transport chain. However, there is a general lack of knowledge on the effect of water stress on the electron partitioning between the cytochrome and alternative pathway, and on the role the alternative pathway might play under water stress. A few studies have addressed this subject (Zagdańska, 1995; Collier and Cummins, 1996; González-Meler et al., 1997), but these have used specific inhibitors for the cytochrome (KCN) and alternative (SHAM) respiratory pathways and used the assumption of the 'overflow theory' (Moller et al., 1988) which we now know to be invalid (Day et al., 1996; Chapter 1, Lambers et al.).

Zagdańska (1995) showed in wheat leaves that, while the SHAM-resistant respiration increased in both acclimated and non-acclimated plants, cyanide-resistant respiration was strongly stimulated in acclimated plants and slightly inhibited in non-acclimated plants. Collier and Cummins (1996) studying *Saxifraga cernua* leaves observed that cyanide-resistant respiration decreased as water deficit increased, while SHAM-resistant respiration was differentially sensitive to the rate of development of leaf water deficit. When water stress was applied slowly, SHAM-resistant respiration was initially unchanged, while during a fast-developing water stress its activity initially increased up to 40% with a sharp decrease as the leaves lost turgor. González-Meler et al. (1997) showed that water stress decreased SHAM-resistant respiration in both *Phaseolus vulgaris* and *Capsicum annuum* leaves, but SHAM-sensitive respiration was very slow without any variation in cyanide-resistant respiration. The combination of these analyses suggests that there is variation among species, tissues and conditions.

Recently we addressed the lack of published experiments by studying the effect of water stress on electron partitioning using the oxygen-isotope discrimination technique, which is now known to be the most reliable (Day et al., 1996; Chapters 1, Lambers et al.; and 3, Ribas-Carbo et al.). When soybean (*Glycine max*) plants were subjected to progressive dehydration, the cytochrome pathway decreased progressively, while the activity of the alternative oxidase pathway increased (Fig. 5; M. Ribas-Carbo et al., unpublished results). These results agree with our hypothesis, but further studies would be needed using other species to confirm this trend.

VI. Concluding Remarks

The general knowledge on respiration responses to water stress has increased little since the 1980s. Different studies have reached opposite conclusions regarding the response to water stress of total respiration rates of different plant organs, of various respiratory enzymes or of the partitioning of electron transport between the cytochrome and the alternative pathways. Given the diversity of the results obtained, it seems that the regulation of respiration under water stress reflects a complex metabolic regulation, rather than simply being a consequence of decreased photosynthesis and/or inhibition of one or a few enzymes. Moreover, the recent use of stable-isotope techniques suggests that the pattern of respiratory use of recent photoassimilates versus accumulated reserves may well change under water stress, in a species-dependent manner.

The present evidence indicates a biphasic response of respiration to decreasing relative water content. The initial tendency is for the rate of respiration to

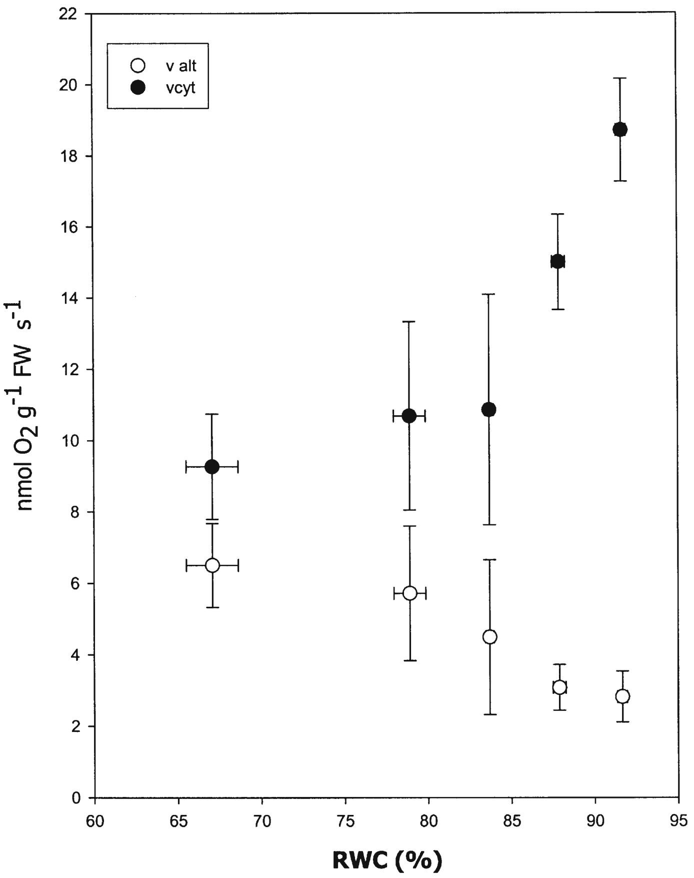

Fig. 5. Activities of the cytochrome and alternative pathway in soybean leaves at different relative water contents (RWC). Values were obtained by oxygen-isotope fractionation measurements (Chapter 3, Ribas-Carbo et al.). Water stress was induced by monitoring and reducing water soil availability. Values are the mean±SEM of five to seven measurements.

decrease, probably as a consequence of decreased energy demand for growth. A second trend that appears at severe water stress is the increase of respiration rates, possibly as a consequence of enhanced metabolism (osmoregulation, water-stress-induced senescence processes). However, the pattern is not yet completely clear. It seems, for instance, that fast-growing species show a more pronounced biphasic response than slow-growing species.

Some research priorities for the near future would be:

(i) To test the possible occurrence of a biphasic response of respiration to water stress in a larger number of species, all grown under similar environmental conditions.

(ii) To analyze the possible metabolic factors underlying the respiratory response to different degrees of water stress. For this, it would be desirable to undertake studies in which a large number of parameters could be analyzed, including any possible water-stress factor that might trigger the response of respiration (soil and plant water potential, relative water content, stomatal conductance, abscisic acid content), and also as many potential targets as possible (activity of respiratory enzymes, mitochondrial structure, content and patterns of use of different respiratory substrates, photosynthesis).

(iii) To prioritize carbon balance studies at the whole plant level. It would be important to determine both the pattern of response of respiration rates of different plant organs to developing water stress, and to discern the response of the growth versus the maintenance components of respiration.

(iv) To further analyze, using appropriate isotope techniques, the effects of water stress on electron partitioning between the cytochrome and the alternative pathways in different species.

All this knowledge would be necessary to fully understand the importance of respiration to plant carbon balance during water stress which is the first step to enable prediction and management of crop growth and yields in water-stress-prone areas.

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