1. Carbon Balance of Stressed Plants: A Conceptual Model for Integrating Research Results

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INTRODUCTION

Plant growth is generally proportional to the balance of carbon gains and carbon losses. It is important to identify all the components of this balance, since it is only when all the gains and losses of carbon by a plant are considered that a full account of the carbon balance, and growth, can be made. The daily (24 h), whole-plant carbon balance is the carbon exchange measure that is most closely related to growth and productivity (McCree, 1986b). Furthermore, instantaneous rates of various carbon exchange processes are often not well related to whole-plant growth over the long term.

In this chapter, we describe a conceptual whole-plant carbon balance model that can be used to evaluate responses to stresses using general principles. All of the processes of carbon gain and loss may be influenced by stress. In fact, stress may be defined as any factor (in excess or limiting supply) that detrimentally affects any aspect of a plant’s carbon balance. The conceptual model can be used to integrate various responses to stress into a picture of the overall effect on the whole-plant carbon balance. The model is to be used as a tool (Moorby, 1987) in the development of important questions, for meaningful answers are the result of asking the right questions. The conceptual nature of the model means that emphasis is placed on types of responses rather than on measures of specific responses to one particular set of environmental
conditions. The underlying theme of this chapter is that measuring only a few physiological responses to stress may not reveal much about long-term whole-plant growth. We advocate accounting for all important gains and losses to the plant, and thinking in terms of efficiencies rather than rates of carbon exchange.

Although we shall emphasize the response of field-grown or field-grown-like plants, most experimental work deals with plants growing under conditions far removed from the field. Often only parts of plants are studied, and experiments cover only short periods of time. Although these are not the most desirable ways of studying stress effects on plant growth and productivity, present understanding of biochemical and physiological stress effects relies heavily on such experiments. A problem that is often overlooked is that plants adapt or acclimate to a stressful environment. These adaptations and acclimations are observable only in longer-term experiments. Another major difficulty, encountered when attempting to monitor the carbon balance of plants in situ, is that access to roots is limited, and roots are a strong sink for carbon.

CARBON GAIN

*Photosynthesis* is the primary physiological process responsible for carbon acquisition. Photosynthesis in higher plants can be defined as the process whereby CO₂ diffuses down a concentration gradient from the atmosphere, through the epidermis, and into chloroplasts, where energy derived photochemically is used to assimilate the CO₂ in the formation of organic compounds. A stress that affects any component of this process will affect the rate of carbon gain by the plant.

The most common measure of photosynthetic rate is the rate of apparent photosynthesis by individual leaves (Nelson, 1988). These rates are usually measured only on the most active young leaves under "optimal" conditions. In contrast, whole-plant photosynthesis is strongly linked to the geometry, size, and longevity of photosynthetically active organs as they co-occur on a plant or within a community. There is no unique relationship between the whole-plant photosynthetic rate and the rate of any given leaf on the plant.

*Photorespiration* is an intimate component of the photosynthetic machinery that represents a limitation on the utilization of radiant energy in CO₂ assimilation in a high O₂–low CO₂ environment, especially in C₃ species (Artus et al., 1986). Photorespiration negatively affects the photosynthesis component (carbon gain) of the carbon balance.
CARBON LOSS

Respiration (true or dark respiration) is a process whereby organic compounds are oxidized by a series of enzyme-catalyzed reactions in the cytosol and mitochondria of all living cells. It is an essential component of plant metabolism; life is impossible without respiration. Respiration produces intermediates (carbon skeletons) for growth processes; the energy and reductant used in growth, maintenance and repair, intercellular transport, and mineral nutrient assimilation; and CO₂ (Penning de Vries et al., 1974). The CO₂ diffuses out of the plant or is reassimilated by additional photosynthesis or other carboxylation reactions.

Other losses of carbon occur during abscission, leaching, herbivory, volatilization, exudation, etc. (Mooney, 1972). Tissue senescence results in a decrease in the amount of physiologically active phytomass. An increase in dead or senescing tissue, whether abscised or not, is a loss of functional carbon. Effects of stress on the extent and rate of any of these carbon loss processes will impact the carbon balance of a plant, crop, or ecosystem.

CARBON BALANCE AND PLANT GROWTH

We define growth as the biosynthesis of new structural phytomass. The instantaneous carbon balance is not equivalent to growth rate since whole-plant mass changes include changes in the dynamic nonstructural storage pool; growth and total mass changes are uncoupled since the proportion of plant mass made up of nonstructural carbon is always changing. In some cases (Munns, 1988), changes in the size of the storage pool may be central to stress responses.

The chemical reduction state of the structural components of the plant should be considered. Even if the fraction of carbon in different plants is the same, the degree of reduction and hence the amount of substrate respired during synthesis may vary greatly (Penning de Vries et al., 1974; McDermitt and Loomis, 1981). Because of this, phytomass that is, for example, 40% carbon need not be energetically equivalent to other phytomass that is also 40% carbon.

CARBON BALANCE MODEL

The following equation describes the carbon balance of a plant:

\[ \frac{dW_s}{dt} = Y_G (P - \frac{dW_n}{dt} - mW_s) - L \]  \hspace{1cm} (1)
where $W_S$ is the amount of structural phytomass present at a particular time (in g C); $\frac{dW_S}{dt}$ is the rate of change of this component (in g C d$^{-1}$ when the daily carbon balance is being considered); $Y_G$ is the growth conversion efficiency, and represents the efficiency of converting substrate into new structural phytomass (in g C [new phytomass] g$^{-1}$C [substrate input to growth]); $P$ is the rate of photosynthesis (in g C d$^{-1}$), taken to be gross photosynthesis less any photorespiration that may occur; $\frac{dW_N}{dt}$ is the rate of change in the amount of nonstructural phytomass, i.e., the pool of nonstructural carbohydrates, amino acids, etc. (in g C d$^{-1}$), including any metabolic costs of maintaining this temporary storage; $m$ is the maintenance respiration coefficient, also called specific maintenance respiration rate (in g C g$^{-1}$C $[W_S]$ d$^{-1}$), with maintenance respiration rate equal to $mW_S$; and $L$ is the rate of loss of structural phytomass due to processes such as abscission and herbivory (in g C d$^{-1}$).

The composition and reduction state of growing tissue is implicitly accounted for in the value of $Y_G$. Nonstructural carbon may be lost to processes other than respiration and growth, such as herbivory, leaching, and volatilization, but these are not included in this model. Note that $\frac{dW_S}{dt}$ may be negative. This can be the case even when growth is occurring if the rate of loss of structural phytomass, $L$, is greater than the rate of growth. That is, $\frac{dW_S}{dt}$ is equal to growth rate minus $L$, where growth rate is equal to $Y_G(P - \frac{dW_N}{dt} - mW_S)$. We consider "permanent" storage, such as starch in seeds, to be structural. Methods of experimentally solving this equation (or similar formulations) have been previously reviewed (McCree, 1986a; Amthor, 1989).

Including $\frac{dW_N}{dt}$ and $L$ in the equation allows the value of $Y_G$ to be estimated more accurately than is possible with measures of photosynthesis and respiration alone (Amthor, 1984). Thus, if the amount of nonstructural carbon increases ($\frac{dW_N}{dt}$ is positive) but is not accounted for, the value of $Y_G$ will be artifically inflated, since less structural growth will be occurring than is implied by measures of CO$_2$ exchange only.

When $(P - \frac{dW_N}{dt} - mW_S)$ is negative, a net degradation of structural tissue is implied. This may occur during senescence, for example. The relationship between $Y_G$ and $\frac{dW_S}{dt}$ is complicated under such circumstances, and care must be taken to evaluate new structural mass in growth estimates.

All the factors on the right side of equation 1 affect the rate of accumulation of structural phytomass. Because all the components of the model influence the carbon balance, effects of stress on all the components should be studied. Furthermore, it is important to study the inte-
gration over time of the contributions of all the components. Each of the components of the model changes over time independent of stress (i.e., during ontogeny). These changes have been reviewed for leaves in Sestak (1985) and studied in whole plants by McCree (1983). Responses to stress also change over time, in part due to induction of various adaptation mechanisms. In addition, response to stress is determined by the level of stress, by the other environmental conditions during a period of stress, and by the history of the plant and its environment.

Allocation

Allocation of carbon among and within various organs is not explicit in this carbon balance model, but it is frequently affected by stress. Altered patterns of allocation may affect several components of the model as time progresses. Changes in patterns of allocation among organs due to stress complicate the study of the whole-plant carbon balance, especially when only one part of the plant is investigated.

In many cases, changes in patterns of allocation among organs have been interpreted as adaptation mechanisms. For example, it is commonly observed that water stress and nitrogen deficiency tend to increase the relative allocation of available substrate to roots (Jones et al., 1986). Leaf production is then reduced proportionately. Air pollution may have the opposite effect: new leaf production may be given a somewhat higher “priority” for existing substrate (Darrall, 1989). This response counteracts the commonly observed reduction in the rate of photosynthesis (carbon gain) on a leaf area basis (Darrall, 1989) by producing relatively more leaf area. Whole-plant photosynthesis, however, is still often reduced. In these examples, the organ acquiring the “most limiting” factor for growth (water, nitrogen, and carbon, respectively) is given priority for existing substrate. These and similar responses to stress may be interpreted in terms of a “functional equilibrium” among various organs (Brouwer, 1983).

Carbon allocation among the components of the model (equation 1) is also often affected by stress; that is, the fraction of carbon assimilated in photosynthesis that is allocated to storage and various processes involving carbon loss can be altered. A relative increase in carbon lost to maintenance respiration, for example, could significantly decrease the overall efficiency of converting photoassimilate into new structural mass. This would exacerbate detrimental effects of stress on $P$, and hence limit growth even further. The opposite effect may also occur: altered patterns of carbon allocation among the model parameters may mitigate effects of stress on growth and the carbon balance.
EVALUATING STRESS WITH THE CARBON BALANCE MODEL

In this section, we describe some effects of stress on the components of the conceptual model. Examples are given to illustrate types of responses. We reemphasize that it is the integrated response of all the components that determines the overall effect of a stress on the whole-plant carbon balance.

Several stresses may occur at the same time, and many environmental stresses interact. For example, in the field, heat stress is not likely without a water stress, and water stress itself will usually result in higher plant temperature due to a reduction in latent heat loss. As another example, root zone salinity often accompanies root zone water deficits, and irrigation water in arid regions is often somewhat saline. Heat or salinity stresses should therefore be studied in conjunction with water stress treatments (McCree, 1986b). Conflicting conclusions of studies of a particular stress, especially under field conditions, are doubtless due to ignoring interactions with other stresses (Mooney and Winner, 1988).

Photosynthesis

Effects of stress on leaf photosynthesis (CO₂ assimilation) have been relatively well studied. Stress reduces the rate of CO₂ uptake by individual leaves and whole plants (e.g., Reich and Amundson, 1985; Schulze, 1986). A decrease in photosynthesis elicited by a stress need not be accompanied by a proportional decrease in dWₜ/dt, since other components of the carbon balance may respond differently. Nonetheless, a less favorable whole-plant photosynthetic rate will nearly always diminish the growth rate. This is because the supply of substrate for growth is reduced.

Inhibition of leaf photosynthesis may result from a decrease in the conductance of CO₂ from the atmosphere to the chloroplasts, such as occurs when stomata close; from a detrimental effect on the photosynthetic mechanism (mesophyll activity) itself; or from a combination of the two. In an expanded version of the model, photosynthesis could be written as an explicit function of both CO₂ conductance and mesophyll biochemistry as well as exogenous and other endogenous factors (Charles-Edwards et al., 1986; Farquhar, 1989). Differentiation of stress effects on photorespiration and on photosynthesis is also possible (Perry et al., 1983), but this is more detailed than the present model, where the value of P is the result of the combined response of all facets of photosynthesis and photorespiration. In the context of the whole plant, changes in leaf photosynthesis must be related to whole-plant leaf area, leaf duration, and patterns of leaf display.

Exactly how stresses affect photosynthesis, i.e., via stomatal closure or some more direct effect in the mesophyll, is not always clear. Once
mesophyll activity is decreased, stomata frequently close, and vice versa. The precise links between stomatal function and CO₂ assimilation rate in the mesophyll are at present unknown, but it seems clear that a link exists (Morison, 1987). Which factor is affected first by a stress? Does stomatal closure cause the observed decrease in CO₂ assimilation, or does non-stomatal inhibition of photosynthesis give rise to stomatal closure? Experimental techniques do not necessarily differentiate the two responses in an adequate manner (Dowtown et al., 1988a,b; see also Robinson et al., 1988 and Farquhar, 1989).

Stomatal closure in response to soil water deficit is commonly observed, and obviously limits transpiration and conserves available water (although the energy balance of the canopy is then affected and leaf temperature increases [Tanner, 1963]). Plants respond quite differently to soil water deficits developing naturally and slowly in the field and those imposed artificially and rapidly. Plants growing in the field maintain a greater leaf conductance for a given soil water deficit and leaf water potential (Jordan and Ritchie, 1971). Presumably this is due to adaptation during growth under somewhat stressful conditions (McCree, 1974; Ludlow et al., 1985). Greater leaf conductance leads to greater rates of CO₂ assimilation, and often lower leaf temperatures under field conditions, at a given soil water status.

Not only will a decrease in leaf photosynthesis lead to a decrease in growth due to substrate limitations, but also a decrease in growth itself will limit whole-plant photosynthesis through a reduced rate of leaf initiation and expansion. This reduction in leaf growth in turn leads to a reduction in the amount of photosynthetically active radiation (PAR) absorbed in comparison with a nonstressed plant. Any change in the geometry of photosynthetic organs due to stress may also affect PAR absorption and hence plant photosynthetic rate. Leaf rolling is a common response by grasses to a water stress, and in dicots leaves become vertical due to wilting. This reduces water use, but also inhibits CO₂ assimilation per plant.

As important as carbon gains are, growth need not be carbon substrate limited under stress conditions (e.g., Curtis et al., 1988). In such cases, growth rate is limited by the rate of carbon substrate utilization, not the supply rate. This will be seen as an increase in $P/W_s$, and often as a decrease in $P/W_N$.

Growth Conversion Efficiency and Growth Respiration

There are two components to respiration in the carbon balance model: growth and maintenance. (A component associated with mineral nutrient assimilation is explicitly included in some formulations, but not in
equation 1.) While these two components of respiration are not biochemically distinct, they do have different functions.

Growth respiration is responsible for satisfying the energetic requirements of converting substrate into new structural phytomass and for generating the required carbon skeletons (Penning de Vries et al., 1974). Growth respiration rate is dependent on both the growth rate and the value of $Y_G$, or conversely stated, growth rate is dependent on the growth respiration rate and on the value of $Y_G$. The rate of carbon loss because of growth respiration is equal to $(1 - Y_G)/Y_G$ times the growth rate.

Stress can affect growth respiration in two fundamentally different manners. In the first type of response, the rate of growth respiration is reduced due to reduced availability of substrate, but $Y_G$ is not affected. Generally, any factor that reduces photosynthesis will lead to such a reduction in growth rate and growth respiration rate (Wilson et al., 1980). We feel this is the most common effect of stress on growth respiration. A corollary to this is that a reduction in the rate of growth respiration leads directly to a reduction in the rate of growth. This is counter to the common perception that a reduction in respiration should result in enhanced growth due to a more positive carbon balance.

In the second type of effect of stress on growth respiration, a change in growth respiration rate is accompanied by a change in the value of $Y_G$. The value of $Y_G$ can be changed by a stress if the composition of the substrates used in growth, composition of the products of growth, or pathways of biosynthesis are changed. Singh and Mishra (1988), for example, noted a decrease in leaf energy content ($J \text{ g}^{-1}$) as a result of air pollution stress. This may have been related to changes in $Y_G$. Shone and Gale (1983) reported decreases in $Y_G$ due to salinity. Changes in patterns of allocation among organs due to stress can affect whole-plant values of $Y_G$ because values for root, stem, leaf, and seed often differ (Stahl and McCree, 1988).

We conclude that when changes in whole-plant values of $Y_G$ occur due to stress, they are because of changes in the substrates used in growth, changes in the products of growth (e.g., altered ratios of structural carbohydrates, proteins, and lipids), and/or changes in allocation of growth among various organs. Apparent changes in $Y_G$ can result from stress-induced changes in ratios of $W_N$ to $W_S$ when structural growth is not measured.

**Maintenance Respiration**

Maintenance respiration is the CO$_2$ generated in the production of usable energy for resynthesis of substances undergoing renewal, for maintenance of required gradients of ions and other metabolites, and for
acclimation to changing or stressful environments. A certain level of maintenance respiration is required to maintain physiological integrity. This can be particularly important during stress (Gale, 1982), when maintenance requirements may increase. Penning de Vries (1975) outlined the biochemistry associated with various maintenance processes.

A change in whole-plant $m$ has important consequences for the carbon balance. Although daily maintenance respiration is typically equivalent to only 1-5% of the whole-plant mass (Amthor, 1984), this can be a large fraction of daily growth if $W_S$ is large. Thus maintenance respiration is most significant in large plants for which daily photosynthesis is equivalent to a relatively small fraction of existing phytomass (i.e., when the relative growth rate, RGR, is small). It is important to note, however, that the value of $m$ changes as plant size changes; the value of $m$ is not constant during ontogeny. As plant size increases and RGR decreases, the value of $m$ decreases also (McCree, 1983; Amthor, 1989). The value of $m$ also varies among different growth environments (McCree, 1982). These factors may maintain an equilibrium between whole-plant respiration and photosynthesis.

Two types of stress can be identified when considering effects on $m$ (reviewed by Amthor, 1989). (1) Stress that results primarily in a decrease in carbon gain and utilization, such as water stress, nutrient deficiency, or low temperature. (2) Stress that requires a active response by the plant, such as the detoxification of an air pollutant or osmotic adjustment due to salinity.

The first type of stress results in a reduced level of general metabolic activity that will result in a reduced level of maintenance respiration, manifested by a decrease in the value of $m$. For example, whole-plant $m$ decreases during development of a water stress when that stress develops slowly (Wilson et al., 1980), as is the case in the field (see also McCree, 1986b).

The second type of stress elicits an increase in the rate of respiratory metabolism to perform functions such as repair of damaged cellular constituents or increased production of some compound(s), ATP, or reductant required for detoxification or defense. This often occurs when plants are stressed rapidly and severely in the laboratory (McCree, 1986b). It is a common response to chronic air pollution stress, though at the same time energy and carbon skeleton production for growth may be curtailed, resulting in more complicated effects on total respiration (Amthor, 1988).

Storage

Storage serves many functions in growth and development, not the least of which is a buffer between carbon acquisition and utilization
processes. Because of this buffer, carbon gains and losses (uses) need not be tightly coupled. The plant may respond to a stress in one area of metabolism without having to respond equally in all others. For example, photosynthesis could be reduced while growth rate was maintained, and vice versa.

There are two possible responses of $dW_N/dt$ to stress: an increase or a decrease. Examples of the first type of response are the increases in stored carbon due to water stress, salinity, low temperature, or nutrient deficiencies (Munns, 1988). Increases in concentration of organic solutes due to, for example, drought or salinity are the result of reduced growth rate, not increased carbon assimilation rate. That is, growth is reduced to a greater extent than photosynthesis. In such cases, substrate may be used for osmotic adjustment (storage in the model), but if it is, then it will not be available for growth (Cheeseman, 1988). Diversion of organic solutes from growth to osmotic adjustment and the notion that osmotic adjustment is an important adaptation to dry or saline environments are reviewed by Munns (1988).

An increase in storage in water-stressed plants, in lieu of leaf expansion and initiation, results in soil water conservation by limiting the area of transpiring surfaces. When the water stress is later relieved, by an irrigation or rain event, growth can proceed rapidly (Ludlow and Ng, 1977) using the large storage pool (perhaps more rapidly than would be possible if growth were dependent on current photosynthesis alone). This is accompanied by an increase in growth respiration (McCree et al., 1984).

Decreases in storage without a corresponding increase in growth can also occur as the result of stress; air pollution stress is an example (Miller, 1987). This may be linked to detoxification, repair, and energy-requiring adaptation processes. When current photosynthesis cannot supply carbon substrate rapidly enough for these processes, $W_N$ can be used to supply needed substrate for a time. A decrease in $W_N$ in such circumstances might be linked to an increase in the parameter $m$ in the model.

**Senescence and Abscission**

Many stresses (e.g., water stress, air pollution stress, nutrient deficiency) tend to accelerate the rate of senescence (or aging) of organs, particularly leaves (Nooden and Leopold, 1988). This may affect the whole-plant carbon balance in several ways.

1. Carbon gains due to photosynthesis are generally reduced because physiological aging of leaves results in lowered photosynthetic capacity per unit leaf area (Sestak, 1985).
2. Leaves and reproductive organs abscise more frequently, resulting in direct losses of carbon (increased $L$) and reduction in leaf area available for the interception and utilization of PAR. The loss of existing leaf area, coupled with a general reduction in the rate of leaf initiation and growth under stress, will clearly reduce whole-plant carbon gain.

3. Senescence is often accompanied by an increase in respiration (McCree, 1986b; Warman and Solomos, 1988). This is because senescence is an orderly, programmed, energy-requiring process (Nooden and Leopold, 1988). The respiratory climacteric during ripening of climacteric fruits is a similar phenomenon (Brady, 1987), but is not generally applicable to higher plants. Perhaps a separate respiratory component should be added to the model to account for this "senescence respiration." Respiration associated with senescence, and abscission of dead organs, have been underemphasized in the carbon balance literature.

**SIMULATION MODELING AS A MEANS OF EVALUATING STRESS EFFECTS**

Simulation models can be used to integrate knowledge about physiological processes and their responses to the environment. Once a simulation model has been developed and found both to produce reasonable results and to mimic actual observations (so-called validation), it can be used as a tool to predict and understand stress effects. Progress is now being made in the development and testing of physiologically based models at various levels of complexity (e.g., Reynolds et al., 1980; Acock et al., 1985; Whisler et al., 1986; Sinclair et al., 1987; Farquhar, 1989; McCree and Fernandez, 1989; McCree et al., 1990). Their use will increase in the future. The full utility of many current simulation models is limited by a lack of mechanistic accounting of stress (Gutschick, 1987). If a simulation model is to fully account for effects of stress it should contain each element of the model presented in equation 1.

It is not possible to manipulate and observe more than a few factors at one time by experiment. With a good physiologically based simulation model, i.e., one that combines response mechanisms in a way that allows the simulated plant to behave realistically, many factors can be varied at once. The simulated plant will respond in a complicated and often unexpected manner, just as a plant does in nature. This allows an evaluation of the relative importance of multiple response mechanisms. Simulations may also be used to suggest previously unexplored mechanisms of adaptation, and to do so in a quantitative manner. All this hinges on quantitative descriptions of mechanisms of adaptation to stress.
CONCLUSIONS

The conceptual whole-plant carbon balance model described here can be used by the research scientist and student as a framework with which to evaluate the implications of stress for plant growth and productivity. The model presented here is a tool. It is not meant to be solved for every possible set of conditions, but merely to point out broad relationships among the components. The model can facilitate the integration of existing observations concerning stress, as well as suggest additional experiments that are likely to increase knowledge of effects of whatever particular stress(es) one is interested in evaluating.

Study of an individual component of the model is not sufficient to comprehend the effect of stress on a plant’s carbon balance. A holistic approach is required. Some estimate should be made of the response of every component of the model in a given environment. This will make it possible to predict at least the direction of change due to a stress, and to evaluate the overall impact of stress on the whole-plant carbon balance.

Successful adaptation to stress will enhance the growth and carbon balance of plants in a given environment. In so doing, adaptation will balance the individual components of the model to the benefit of the plant under existing environmental constraints. The conceptual model described here can be used to obtain a better understanding of the many ways in which a plant can obtain such a balance.

Experimental evaluation of the effects of stress on the carbon balance of plants is currently hampered by two factors: (1) Plants growing in the field and plants growing under controlled conditions often respond quite differently to the same level of stress (e.g., Jordan and Ritchie, 1971). Most physiological experiments are conducted under controlled conditions. Experimental work with plants under artificial conditions is a source of understanding of mechanisms of adaptation, but laboratory observations should be used along with information concerning the physical and physiological condition of plants growing in the field (Burke and Hatfield, 1987). (2) Field-grown plants often experience a combination of stresses. Future research must better address these two issues if our understanding of effects of stress on the carbon balance of plants is to be improved.

Simulation modeling can play an important role in understanding the significance of various stresses to overall plant growth. Only a simulation model allows the study of complex interactions among stresses and physiological processes. Present limitations of simulation models, of which there are many, arise in large part from ignorance of rates of fundamental biochemical and physiological processes of intact plants,
especially under field conditions. Lack of knowledge of the mechanisms of acclimation and adaptation to stress are not the least of these limitations.

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