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Modelling for crop response to water: physiological aspects

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SUMMARY - The issue of crop response to water is presented in a theoretical framework which highlights some of the main approaches developed over time. After a brief introduction dealing with the advantages of using modelling as a quantitative tool in serving agricultural science, various physiological processes (i.e., leaf expansion, CO_2 assimilation, partitioning of assimilates, osmotic adjustment and respiration) are synthetically reviewed in terms of their response to water stress. This introduces the basis for conceptual modelling of crop growth with notable focus on response to water. The standing crops are thus considered as dependent on their capture and use of environmental resources such as solar radiation, carbon dioxide, water and nutrients, and their growth and productivity are formulated both in terms of empirical and mechanistic relations. The approaches of solar-radiation and transpiration as related to productivity are discussed. However, all crop models generally allow the construction of a 'production function' of crop yield versus water use, which is necessary for the economic evaluation of water management at farm and regional scale. The specific case of the crop-growth submodel of EPIC (Erosion Productivity Impact Calculator) is reported as a relatively simple example of implementation of process integration to mechanistically simulate growth and productivity. While discussing distinctive features of crop models relative to crop-water relations, limits in their use in the Mediterranean Basin are highlighted. Specifically, modelling aspects on tree crops and salinity are recalled. Relatively extensive literature is reported to allow further insight on the various subjects treated. Finally, words of caution, perspectives, and research needs concerning crop models are remarked in the conclusions.

Key words: Crop-modelling, crop-water relations, yield-response functions.

RESUME *- Ce travail porte sur le problème de la réponse de la culture à l'eau suivant un cadre théorique illustrant les principales approches développées jusqu'à présent. Après une brève introduction sur les avantages de la modélisation en tant qu'outil quantitatif au service de la science agricole, on passe brièvement en revue les différents processus physiologiques (i.e. l'expansion foliaire, l'assimilation de CO_2 , la répartition des assimilats, l'ajustement osmotique et la respiration) et leur réponse à la contrainte hydrique. Cette introduction crée les bases pour la modélisation conceptuelle de la croissance culturale se référant notamment à la réponse à l'eau. Le couvert végétal est considéré en termes de sa capacité d'intercepter et utiliser les ressources environnementales telles que le rayonnement solaire, le gaz carbonique, l'eau et les éléments nutritifs, et sa croissance et sa productivité sont formulées par des relations empiriques et mécanistes. On discute aussi des approches du rayonnement solaire et de la transpiration vis-à-vis de la productivité. Tous les modèles culturaux permettent de construire une "fonction de production" mettant en relation le rendement cultural et l'utilisation de l'eau, ce qui est nécessaire pour évaluer les aspects économiques de la gestion de l'eau au niveau de l'exploitation agricole et au niveau régional. On rapporte le cas spécifique du sous-modèle de la croissance culturale d'EPIC (Erosion Productivity Impact Calculator) en tant qu'exemple relativement simple pour réaliser l'intégration des processus permettant de simuler la croissance et la productivité d'une manière mécaniste. On discute des aspects distinctifs des modèles culturaux par rapport aux relations eau-culture, en soulignant leurs limites d'emploi dans le pourtour méditerranéen. Notamment, des rappels sont faits sur la modélisation des cultures arboricoles et de la salinité. Des références bibliographiques assez étendues permettront d'approfondir les différents aspects. Enfin, dans les conclusions on donne quelques avertissements, les perspectives et les besoins de la recherche sur les modèles culturaux.*

Mots-clés: *Modélisation culturale, relations eau-plante, fonctions de réponse au rendement.*

INTRODUCTION

Crop growth and production are the results of complex processes relating plants to their physical environment where energy, water, CO_2, and nutrients play a fundamental role. These processes can be viewed on different time and space scales (Fig. 1), each one indicating a so-called 'hierarchical level' which allows to reduce a complex system to sub-systems and components (Fig. 2).

Classical agronomic approaches to crop responses to water were largely based on empirical (or same-level) experiments where yield is related to water (or water and other related inputs) applied as an independent variable. When the total quantity per season is considered, typical 'macro' production functions are generated (Yaron and Bresler, 1983) through simple second or third order polynomial regression. When optimal timing and depth of irrigation is considered, 'micro' or 'dated' water production functions are obtained. In this way, response patterns are identified, simplicity is maintained, but explanation for such a response may remain unclear. Moreover, a major shortcoming of same-level experiments is that the results are situation specific. By changing location, cultivar, weather, and/or soil, the experiment should be repeated to generate a new empirical response. By moving to a lower hierarchical level (Fig. 2), some physiological research works may help finding explanations to some responses which, however, are only partial since the approach is 'reductionist' (e.g., we may say how root distribution, leaf conductance, leaf area index, *etc.*, were affected by the irrigation regime, but still we cannot say to what extent that variation in leaf area, root distribution and leaf conductance affected yield).

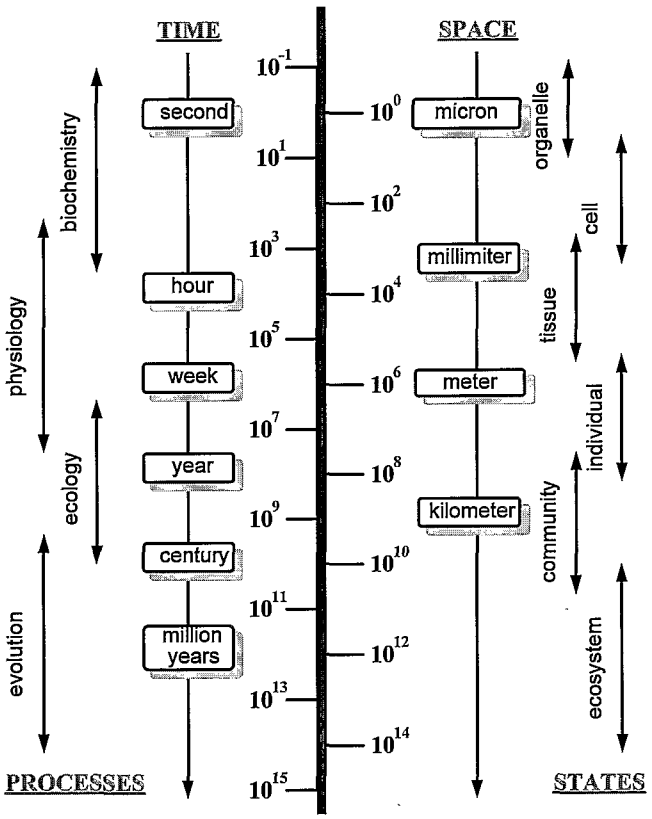

***Fig. 1** - Schematic representation of the space-time scale of biological systems. Transitions between states (a space description) elicit biological processes (description of state-changes over time). Redrawn and modified from Osmond et al. (1980).*

In other terms, a major shortcoming of reductionist research is in the difficulty of integrating the various processes into a quantitative crop yield response. Clearly, crop modelling is the approach aimed at the quantitative integration of the physiological processes for understanding and predicting crop response to environmental resources. Since in the Mediterranean Basin, water (in terms of both quantity and quality) is the most limiting factor to agriculture, an optimization approach is required in order to make the best use of it according to a final objective. In general terms, a 'crop response function', or preferably an 'engineering' production function (Deybe and Flichman, 1991), is wanted to proceed toward the solution of the optimization study. Literature on information technology in agriculture, in fact, (e.g., Heatwole, 1993; Watson *et al.*, 1994) is largely reporting modelling as an essential tool of planning, management, and environmental impact assessment, scaling up and down between the farm (e.g., irrigation scheduling, farm management, pest management, productivity and economic evaluation) and the region (e.g., landscape ecology, soil erosion, grazing land, policy decision making, resource management, ground water contamination assessment).

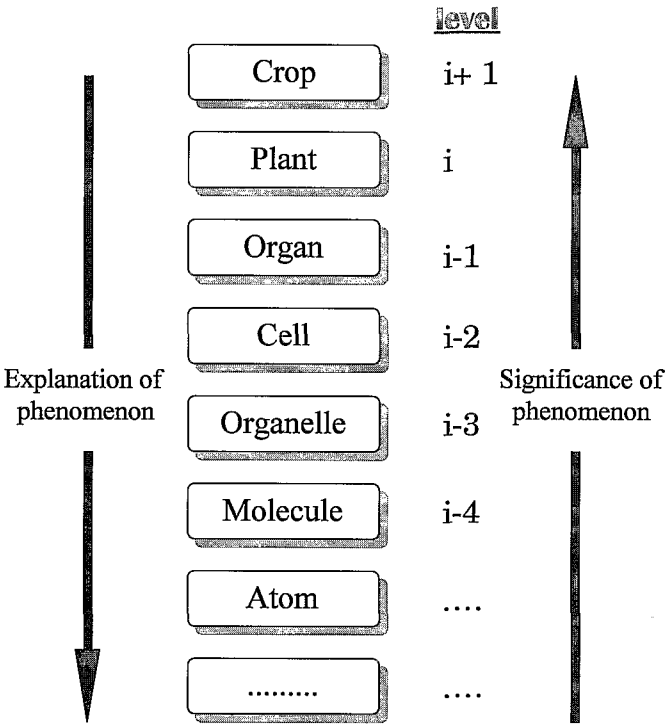

***Fig. 2** - Schematic subdivision of a biological system into hierarchical levels of organization. Phenomena observed at higher levels of organization can be explained by observations made at lower levels of organization. The significance of the phenomena observed at lower levels of organization can be evaluated by examining their quantitative effects on the phenomena at higher levels of organization. Redrawn and modified from Amthor (1989).*

In this sense, a feasible and reliable model can be thought of as a complex production function, and an activities generator (Deybe and Flichman, 1991), relating productivity to various inputs and factors, provided it is tested, calibrated, and sufficiently validated.

Always bearing in mind that all processes of growth and productivity in plants interact with each other in a complex manner, in the present article modelling concerns are mainly focused on the relationships between water and crops, and major physiological aspects of crop-water relationships are highlighted to identify the major strengths and weaknesses of actual crop models and research. To allow the reader to gain further insight into the different subject matters, a relatively large number of references is reported.

PHYSIOLOGICAL ASPECTS OF CROP-WATER RELATIONS

When dealing with crop performance in relation to water, one has always to bear in mind the time-dependence of the occurring events. In other terms, the dynamic nature of plant water status, the dependence of the water stress effects on its severity, duration, and timing of occurrence during the crop cycle, and the developmental rate of events are among the major difficulties encountered in modelling crop-water relations. This time-dependence feature is at times overlooked especially by some genetists who consider the 'resistance' to water stress as an oligo-genic character and attributing the water-stress resistance features observed at a certain stage to any other period of the cultivar life cycle.

These physiological processes in relation to the water status have been treated over time and in different perspectives (e.g., Vaadia, 1961; Slatyer, 1967; Hsiao, 1973; Hsiao *et al.*, 1976; Begg and Turner, 1976; Fisher and Turner, 1978; Turner and Begg, 1981; Hsiao, 1982; Bradford and Hsiao, 1982; Jordan, 1983; Hsiao, 1993a; Smith and Griffiths, 1993). While the reader is referred to such bibliography for further insight, here a synthetic review is reported of the main physiological processes of major concern for crop modelling.

Leaf area development

Cell expansion of many crops has been shown to be the most sensitive process to water stress (Boyer, 1970; Hsiao, 1973; Bradford and Hsiao, 1982; Passioura *et al.*, 1993). The implication of this sensitivity is that, during crop development, leaf area may be reduced with consequent reduction in light interception, and thus in the whole 'source size' for assimilates. This leaf area reduction may be quite strong even at mild water stress, and with no effect at all on stomatal closure.

Following the conceptual framework of Hsiao (1982), for typical annual field crops, the seasonal pattern of biomass accumulation over the cycle can be subdivided into three parts: (i) the 'early phase', when the canopy is incomplete (ground cover limiting phase), the growth is approximately exponential with time, and the source size for assimilates is limiting; (ii) the 'middle phase', when the canopy is fully covering the ground (radiation limiting phase), the growth is about linear with time, and the incident *photosynthetically active radiation* (PAR) is limiting; and (iii) the 'senescence phase', where the rates of assimilation and leaf area decline.

It is during the first phase, when growth is exponential, that mild water stress, slowing even slightly expansive growth of leaves, would have a marked effect on biomass and canopy size (the compound effect over time).

Once the canopy closes (or reaches full development), the crop is limited by the amount of incident radiation. During this stage, the crop is less sensitive to water stress as further leaf area growth would not significantly increase the amount of incident PAR. Though, if water stress is severe enough to induce stomatal closure, the source intensity for assimilates (the photosynthetic rate) would also be reduced, and consequently the resulting biomass as well.

In the last phase, the biomass accumulation is much depending on maturation and senescence. Due to the reduction in green leaf area (reduction in source size), associated to a loss of assimilation capacity (reduction in source intensity), the biomass accumulation slows down continuously up to the end of the cycle. Generally, senescence and maturity are accelerated by moderate water stress.

Carbon dioxide assimilation and stomatal resistance

More than 90-95% of plant dry matter, and almost any process involved in crop growth and productivity, are depending on the assimilates derived from photosynthesis. While leaf area represents the 'source-size' for assimilates, the leaf photosynthetic rate represents the 'source-intensity' for assimilates.

The effect of water stress, then, may lead to stomatal and/or non-stomatal limitations to photosynthesis (Farquhar and Sharkey, 1982; Jones, 1985; Lawlor and Uprety, 1993).

Representing CO_2 assimilation of a leaf (A_l) in terms of flux-gradient diffusion theory, we can write

$$A_l = \frac{c_a - c_\Gamma}{r_b' + r_l' + r_m'} \qquad (1)$$

where: c_a is the atmospheric CO_2 concentration; c_Γ is the CO_2 concentration at the sites of the carboxylation reaction; r_b', r_l', and r_m' are the boundary layer, leaf epidermal (mainly stomatal) and metabolic resistance to CO_2, respectively. In the field, in a progressing depletion of water availability in the soil, the reduction in A_l is first confined to the time of the day with the highest evaporative demand of the atmosphere (at about midday). Then, as soil water depletes and the intensity of stress increases over time, A_l reduction starts earlier and earlier in the day with subsequent more restricted recovery, later in the afternoon (Hsiao, 1993a). Thus, while stress continues to develop, photosynthesis is confined more and more to the morning period (Jones *et al.*, 1986), and the resulting accumulation of biomass becomes slower and slower.

Under such field conditions, root to shoot 'signals' (i.e., hormones), leaf water potential (Ψ), and vapour pressure deficit of the atmosphere (VPD), interactively with the other environmental variables, play a dominant role in affecting stomatal resistance (r_l'). In addition to stomatal closure, the metabolic resistance (the non-stomatal component of the photosynthetic process) is also affected by water stress, though, in a sort of concerted action with stomatal resistance. In fact, much experimental evidence shows that the intercellular CO_2 concentration (c_i) tends to remain constant for variable r_l' and constant c_a and r_b', so that necessarily there is a correlation between stomatal resistance and metabolic resistance (Wong *et al.*, 1979). However, clear-cut answers to the underlying mechanisms governing such concerted action, and the reasons for this specific behaviour, are not fully understood yet.

Although for non extreme conditions, there seems to be a consistent correlative behaviour between r_l' and r_m' also under salinity conditions (Steduto, 1987). It is worth recalling that during senescence, though, c_i tends to rise as a consequence of a reduced metabolic capacity of the photosynthetic machinery with aging.

Reproduction and partitioning of assimilates

When water stress occurs during the reproductive stage, the number of grains or fruits per plant (the 'sink-strength') and/or the biomass per plant grain or fruit (the 'sink-size') can be reduced in a more complex manner than expansive growth. From reproduction time on, the contribution to final yield may derive from any, if not all, of the following phases: flowering, pollination and fertilization, fruit setting, fruit development and maturity.

The number of flowers in general is linked to the plant size. For instance, in cotton the number of flowers is correlated to plant height and in many indeterminate species the number of flowers is associated with the number of branch axes for flower formation. This, in turn, allows a sort of functional balance between source for assimilates and sinks to be supplied with the available assimilates. Thus, the water stress is reflected on the formation of flower number mainly through its effect on plant size. Subsequent abscission of flowers may be caused by hormonal imbalance induced by water stress.

Shortly after flowering, however, the pollination and fertilization phases take place. According to Hsiao (1993a), the literature gives the general impression that pollination is a very sensitive phase to water stress, attributing the reduced final number of fruits per plant to the failure of pollination. Unfortunately, because of the fast sequence of pollination, fertilization, and fruit setting development, it is generally hard to make a clear-cut distinction between the impairment of each phase in terms of water stress. However, more careful analysis brought various authors (e.g., Brocklehurst, 1977; Fisher, 1979; Hsiao, 1982) to indicate that the reduced number of fruits, in the majority of the cases analysed, is due to abortion of the young fruits induced by a reduced rate of assimilate supply. Again, a sort of functional balance in terms of source/sink relationships is established during reproduction. Only when water stress is severe enough at the time of pollination, then fertilization is likely to be inhibited (Hsiao, 1982)

The harvest index (HI), thus, is set by the amount of biomass partitioned into the reproductive organs, or harvestable parts of the crops, of economic interest. When water deficits develop early, or are mild and evenly distributed over the crop cycle, HI is generally unaffected, while, for the reason just exposed, when concentrated around flowering and fruit filling stages, HI can be reduced substantially. Increase in HI is still the major route to increase the yield of various crops. Gifford *et al.* (1984) showed that the increased productivity of wheat cultivars introduced in England over time was only the results of an increased HI.

The assimilate partitioning among plant parts is of basic importance in determining the crop productivity not only because of its impact on HI but also because of the consequent relationships between root and shoot that may derive, and that may be of relevance in arid and semi-arid environment. Though resources partitioning in plant is still poorly understood and, even worse, there is a lack of knowledge in inheritability, some indications of the water status impact on assimilate partitioning are found in the literature (e.g., Wardlaw, 1967, 1980; Morby et al., 1975).

A relatively well acquainted observation is that the root-shoot ratio (R/S) of many crops increases with water stress (Begg and Turner, 1976; Sharp and Davies, 1979; Turner and Begg, 1981), although the extent to which the ratio may vary will decrease from early growth to reproduction. The fact that root growth can be favoured over shoot growth

under water stress also significantly depends on the higher ability of the roots to undergo osmotic adjustment (Sharp *et al.*, 1990). The partitioning of assimilates between root and shoot can be viewed as an optimization in resource use (e.g., Orians and Solbrig, 1977) where carbon is 'invested' in roots to the 'expense' of the shoot to 'gain' more water to sustain the assimilation of more carbon. This behaviour, definitely valid for individuals, may not necessarily be advantageous in plant communities like crops.

In spite of the determinant role played by assimilate partitioning among plant organs, many questions on water stress effect on translocation of assimilates remain unanswered, and the corresponding quantitative relationships are still undefined (Farrar, 1993). For sure, however, the experimental evidence shows that any reduced translocation observed under water stress is the result of a reduced photosynthesis of the source, or growth of the sink, rather than of any direct effect on the conducting system. The distribution pattern of assimilates under water stress, instead, remains mainly descriptive.

Osmotic adjustment

Osmoregulation, or osmotic adjustment, is a relevant physiological mechanism adopted by plants to tolerate water stress (Begg and Turner, 1976; Turner and Begg, 1981; Feng *et al.*, 1994; Peltier *et al.*, 1994). Since total water potential in plant cells (Ψ), at the same reference level, is the sum of osmotic or solute potential (ψ_s) and turgor or pressure potential (ψ_p) with $\psi_s < 0$ and $\psi_p \geq 0$, any increase in osmotic potential, compatible with the cell biochemistry, allows a corresponding increase in turgor. This enables plants to maintain root and leaf expansion and photosynthesis activity at levels of stress which are not possible in its absence.

During a water deficit event, any loss of water from cells generally induces an increase in ψ_s as a consequence of increased concentration. This is considered simply a passive adjustment in ψ_s. In addition to the effect of solute concentration, plants have the ability to actively trigger osmotic adjustment to counteract water stress. The solutes that accumulate during adjustment may be of various nature depending on species and timing of the cycle, but all can be reconducted to typical cell compounds such as soluble carbohydrates, organic acids, proline, exchangeable ions (e.g., K), *etc.* Since also the solutes of the rooting medium affect the water potential in plants, salinity conditions in soils and water may represent an additional source of osmoticum (Lerner *et al.*, 1994).

Osmotic adaptation of roots is also an important mechanism to allow preferential growth of roots under stress. Osmotic adjustment enables plants to deplete the soil water to a lower soil water potential and to explore a larger volume of soil by roots. While the additional water made available by decreasing the soil water potential is likely to be small, the additional water made available by the exploration of a larger soil volume could be significant.

Of course, the degree of osmotic adjustment varies with species, genotype, as well as with rate and degree of stress (Turner and Jones, 1980; Tangpremsri *et al.*, 1995). In general, a rapid rate and a small degree of water stress induce smaller osmotic adjustment than a slow rate and a greater degree of water stress.

Beyond the effects on cell growth, the maintenance of turgor by osmotic adjustment of leaves may also have a significant effect more directly on final yield. There is evidence, in fact, suggesting that maintenance of turgor in leaves reduces the abscissic acid (ABA) produced, which in turn reduces the viability of the pollen (e.g., Morgan, 1980).

However, there are costs for osmotic adjustment which can be identified as energy costs and enzyme inhibition.

Although the osmoregulation mechanism is well known, a few quantitative research results have been obtained in terms of optimizing its use in adaptation to water stress, as well in breeding due to the lack of inheritability characterization.

Respiration

Despite the fundamental role of the photosynthetic process in determining the potential productivity of a plant, it must be recognized that two plants with equal photosynthetic rates might greatly differ in both total biomass and yield, because of the other processes involved in growth and productivity, such as the ones just examined. In addition to these ones, an extremely determinant process is respiration.

Specifically, respiration (dark or mitochondrial) represents a determinant component of the carbon balance, or carbon budget, of crops as it is responsible for the use of assimilated carbon for all the catabolic and anabolic reactions of the metabolism involved during the life cycle of a plant.

The energy cost of respiration (R) can be satisfactorily subdivided into two components: maintenance (R_m) and growth (R_g) respiration, thereby $R=(R_m)+(R_g)$. Though this subdivision was introduced early in time (McCree, 1970), it still holds quite robustly (Amthor, 1989). Essentially, maintenance respiration (R_m) supplies energy for turnover of proteins and lipids and maintenance of electrochemical gradients across membranes (Penning de Vries, 1975). Growth respiration (R_g), instead, supplies energy for the synthesis of compounds and structures for additional biomass (growth), accumulation of compounds in temporary pools for subsequent use, differentiation in secondary products, and translocation of compounds.

In terms of respiration dependence on environmental factors, temperature represents the main influencing variable, essentially through R_m. This is of particular relevance in arid and semi-arid regions, as water deficit periods are coincidental with high temperature regimes. Concerning more specifically water, though, experimental evidence indicates that respiration is generally depressed when water deficit is sufficiently great to close stomata (Begg and Turner, 1976), although the extent of reduction in respiration is comparatively less than in photosynthesis. This is also in agreement with the general observation that any factor that reduces photosynthesis, and therefore growth, should reduce the rate of respiration (Amthor, 1989). This is particularly valid for water stress due to the strict relationship between biomass and water transpired although, on a short-term basis, water-stressed plants may accumulate large amounts of organic solutes requiring a higher maintenance respiration. In fact, there is some increase in respiration during early stress with subsequent decrease with stress development.

With diminishing soil water content, a correlated decrease in respiration rate has been shown (Da Costa *et al.*, 1986). However, when looking at the proportion of carbon used in R_g and R_m no effect of moisture stress appears on the ratio (Loomis and Lafitte, 1987). Furthermore, under actual field conditions, with water stress developing gradually, growth respiration should reduce in proportion to reduced photosynthesis, and maintenance respiration will be reduced in parallel with the general decrease in the metabolic activity of the crop (McCree, 1986).

Commonly, water stress develops concomitantly with salinity stress and the combination of salt and water stress generally results in a decrease of the respiration rate although delayed when compared to water stress alone (e.g., Richardson and McCree, 1985). Under salinity conditions, in addition to the energy costs for the osmotic adjustment as previously mentioned, maintenance costs are expected to be higher also because of the cost associated with possible mechanisms of exclusion and/or extrusion of salts.

In terms of research, simultaneous measurements of photosynthesis, respiration, and growth are needed under various soil moisture levels before a better understanding of the effects of water stress on the carbon balance of field-grown crops will be possible (Amthor, 1989). This is even more so under salinity conditions.

Concluding remarks

In addition to the physiological processes mentioned above, many others, not reported here, also deserve attention. One of these is the communication between root and shoot during soil drying, which adds to the complexity of plant-water relationships. In fact, relatively recently there has been interest in exploring the physiological and adaptive significance of root 'signals' to shoot (e.g., Blackman and Davies, 1985; Tardieu and Davies, 1993; Davies et al., 1994). Such signals are essentially phyto-hormones (e.g., ABA, cytokinin, *etc.*) which can promote an additional control on the stomatal resistance response to environmental stimuli.

Another one is the photoinhibition of photosynthesis which significantly affects the carbon balance of crops grown under conditions of high light intensity in conjunction with temperature and water stresses. Although photoinhibition has been known for many decades as a light-induced process depressing photosynthesis, only recently it began to be elucidated, especially in terms of its significance to plant productivity (e.g., Kyle *et al.*, 1987; Baker and Bowyer, 1994).

Apart from considering the many processes that are involved during a water deficit event in general,

one important aspect of the plant-water relationships is the sensitivity of each of them to increasing stress.

Although incomplete in the list of processes involved in the response to water status, this section can be summarized by indicating the relative time-induction of a process-response to water stress (Fig. 3), as reported by Bradford and Hsiao (1982).

It is important to notice that the restriction of canopy development (or leaf expansion) is the *first line of defence* of a crop when water deficit develops during growth (see also Passioura *et al.*, 1993). Shortly after, the root/shoot ratio is affected, and later an osmotic adjustment may take place. Only when water stress is advanced and intense enough to have reached a threshold in leaf water potential (Ψ), stomata start to close followed by consequent leaf wilting or rolling. All the conditions are then favorable for an acceleration of senescence, and ultimately reaching the plant dessication. Again, intensity, duration, and timing of water stress occurrence will determine the relevance of one response over another.

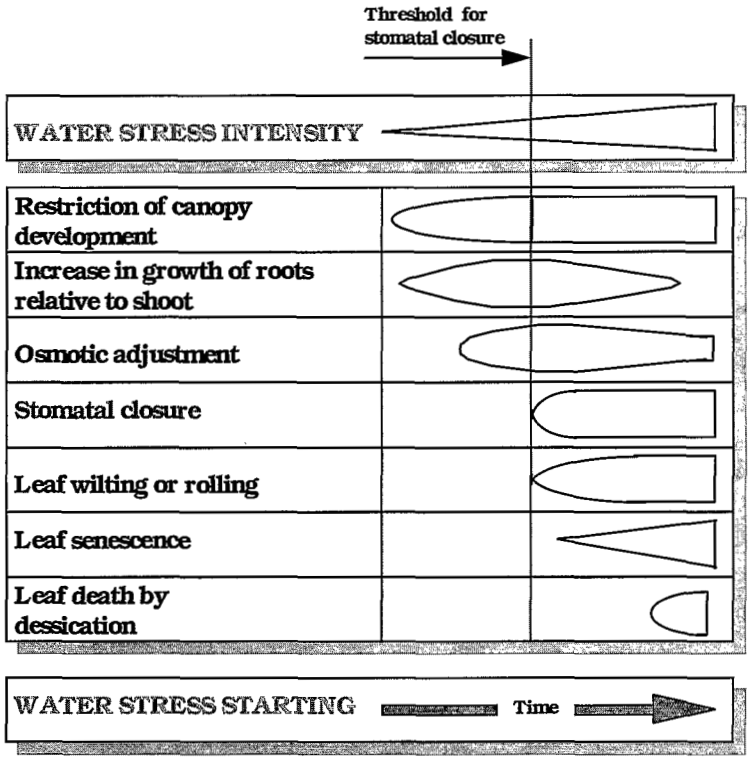

***Fig. 3** - Generalized time course of gross and adaptive changes in crop plants in response to the gradual development of water stress in the field. The width of a band represents the relative magnitude of the response. The shape of a band reflects the variation of responses with increasing stress intensity and duration. The starting position of a band on the time scale indicates the water stress threshold for eliciting the response. Redrawn and modified from Bradford and Hsiao (1982).*

CONCEPTUAL MODELLING OF CROP GROWTH AND RESPONSE TO WATER

In a way, life of crops depends on their 'capture' and use of environmental resources (Azam-Ali *et al.*, 1994), as the already mentioned solar radiation, carbon dioxide, water, and nutrients. Solar radiation, however, is largely recognized as the primary driving force for the photosynthetic process, allowing the carbon assimilation by absorbing radiant energy in the wave band of 400-700 nm. This specific wave band (about 48-50% of global radia-

tion from the sun) is in fact called *photosynthetically active radiation* (PAR). For this reason, "...at the heart of any crop model there is a *growth engine* which provides some means of calculating the amount of assimilates that plants will produce..." (Azam-Ali *et al.*, 1994).

The flux of carbon from the open atmosphere to the intercellular air space of leaves, though, depends in part on the degree of stomatal opening. Since the flux of water from the intercellular air space of leaves to the open atmosphere depends on the same degree of stomatal opening for carbon flux, a link between CO_2 assimilation and transpiration is in principle established. Water, thus, represents the main factor related to the primary driving force, i.e. the solar radiation. Depending on the dominant limiting resource of the environments under study, there might be comparative advantages in using a solar-energy driven or water driven 'growth engine' (Azam-Ali *et al.*, 1994).

Hereafter, the two approaches based on the relationships between growth and solar radiation and between growth and transpiration are discussed.

The biomass-solar radiation relationship

The 'growth engine' of many crop models relies on the Monteith-type approach (Monteith, 1972, 1977), which remains one of proper scale and definition for agricultural productivity purposes.

Typically, these models follow the schematic routes indicated in Fig. 4.

The essential feature of this type of models is the way the photosynthetic process is modelled. Instead of using light response curves of individual leaves to integrate over the whole canopy height, a net conversion coefficient or efficiency (ε), otherwise indicated as 'energy biomass conversion ratio' is adopted. The term ε is, though, a complex factor which includes many other conversion coefficients or efficiencies of the various parts constituting the whole system (Monteith, 1972). For instance, if incident solar radiation captured by the top of a canopy is measured, the resulting energy-biomass conversion factor includes: an efficiency due to the spectral composition of solar radiation and to the optical properties of foliage (εs); an efficiency due to the PAR interception by foliage (ε_i); an efficiency due to the conversion of radiation into carbohydrates (ε_c); an efficiency due to the conversion from carbohydrate into other compounds of different energy value, e.g. proteins and lipids, (ε_q); and an efficiency due to respiration (εr). The overall efficiency, thus, is obtained by the product of the various sub-efficiencies, i.e.

$$\varepsilon = \varepsilon_s \cdot \varepsilon_i \cdot \varepsilon_c \cdot \varepsilon_q \cdot \varepsilon_r \qquad (2)$$

Any portion of the energy-biomass conversion system can be separately analysed. The harvest index (HI) or (ε_h) is an additional efficiency to be added to Eq. (2), and to the schematic diagram of Fig. 4.

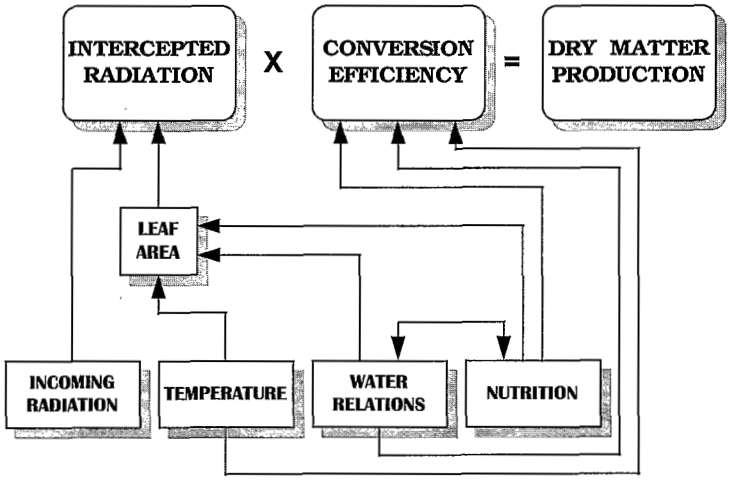

***Fig. 4** - Schematic diagram of the relationships between the variables influencing crop growth, as proposed by Monteith (1977).*

In one equation, the commercial yield of a field crop (Y) can then be expressed as

$$Y = HI \cdot \varepsilon_N \cdot \int_e^h S_i \, dt \qquad (3)$$

where: ε_N is the value of ε normalized for the saturation deficit of the atmosphere; S_i is the incident solar radiation flux; e and h are the emergence and harvest time; and t is time (days).

Under non-limiting field conditions, ε shows to be substantially constant during the majority of the growing season, for given environments and crop species (Fig. 5). Modelling difficulties arise when environmental constraints affect ε, since the occurring interactions are of complex nature. In fact, most of the nowadays available crop models perform satisfactorily under non-limiting field conditions, after relatively little work in testing, calibration, and validation. A much harder work is required in testing, calibration, and validation of models under water and nutritional constraints.

In modelling crop and water relations, stresses are generally handled through indices, or ratios, expressing the relative status of actual to potential expression of the process under consideration. Water and nitrogen stresses, for instance, might be expressed on the basis of the principle of 'supply' and 'demand' in a range going from 0 (total absence of supply) to 1 (full satisfaction of demand).

Timing of stresses and sensitivity of crop stages are accounted through algorithms which may be of higher or lower coherence with the major physiological response of the crop to the environmental stresses. Two main types of difficulties are encountered in modelling the impact of stresses on crop growth and productivity: (a) the proper algorithm representing the response, and (b) the space/time variability of the system to be represented.

One illustrative example for the former case is the partitioning of assimilates among plant organs. Of this expression still little is known in terms of environmental physiology, and the corresponding algorithms in models are very simplistic.

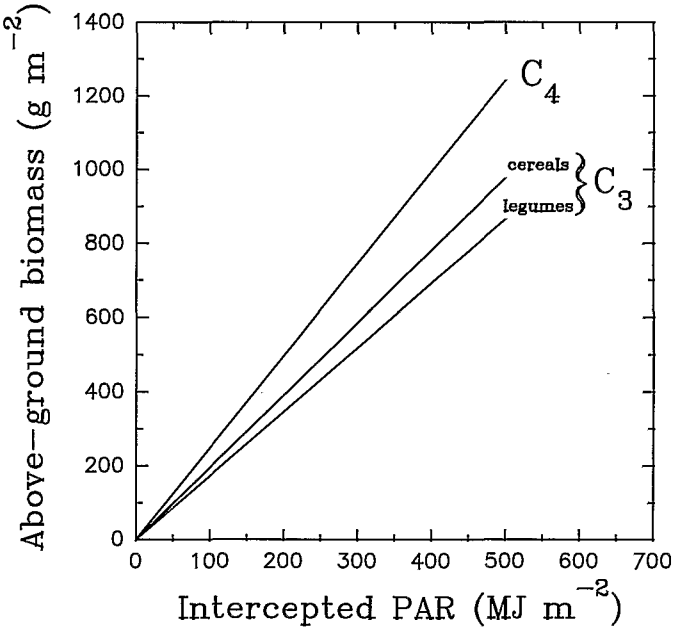

***Fig. 5** - Relationships of cumulative biomass to cumulative intercepted PAR for crops of different photosynthetic metabolism. Synthesis of data from different sources. Redrawn and modified from Gosse et al. (1986).*

This improper representation may lead to a lack of suitable validation with the model being unfeasible in many circumstances, or having a large degree of uncertainty to become useless. Through sensitivity analysis and field tests and calibrations under variable conditions, however, uncertainties might be quantified.

The problem with the latter case implies that, in practice, the deviations between the model results and the experimental results may be caused by uncertainties in the input data (e.g., soil characteristics, weather information, *etc.*) and uncertainties in the model parameters (e.g., max leaf area index, minimum temperature for growth, *etc.*) which add to systematic uncertainties due to simplifying assumptions and approximations inherent in the model, such as uniform crop stand, uniform irradiance during the day, *etc.* (Azam-Ali *et al.*, 1994). The impact of these latter sources of uncertainty on the simulations may be examined through a stochastic treatment of the models. A stochastic model associates a probability distribution to the uncertainty of the input variables (e.g., rainfall) so that it can predict an expected value of output variables (e.g., yield) with an associated variance on which confidence limits are established.

In principle, the greater the uncertainty in the behaviour of a system, the more important is the stochastic approach to modelling (France and Thornley, 1983). However, although stochastic modelling for planning purposes appears to be of higher benefit than deterministic models, in practice they are complex and very difficult to implement and to handle. At the moment, the majority of the agricultural models, of some mechanistic level, are framed into deterministic treatments only.

The biomass-transpiration relationship

One blame to the solar-driven growth-engine is mainly related to the difficulties in making the efficiency term(s) ε a function of environmental constraints such as water. If water is the limiting resource, it might be more appropriate to consider the relationship between crop productivity and transpiration.

Although quantitative studies relating plant growth to transpiration have often been performed at different time in the agricultural history (e.g., Woodward, 1699; Lawes, 1850), systematic research works on the relationships between crop yield and water use have been conducted since the beginning of this century (e.g., Briggs and Shantz, 1913, 1917; Dillman, 1931). The experiments were generally conducted by growing plants in containers, and the amount of water transpired was determined periodically by weight. At harvest, the dry weight of plants was measured and the ratio between total amount of water transpired and total plant dry weight was calculated, defining the so called 'transpiration ratio'. de Wit (1958) made a milestone study on the transpiration ratio investigated worldwide, including field studies, concluding that the relationship between dry matter (DM) and transpiration (T) for arid and semi-arid regions was linear according to the expression

$$DM = m\left(\frac{T}{E_o}\right) \qquad (4)$$

where m is a coefficient (the slope) accounting for crop difference, and E_o represents the evaporative demand of a given environment, introduced to normalize for the different locations. Though most of the data used by de Wit (1958) were not from field studies, the results of subsequent field experiments clearly indicated that the relationship between DM and T (Fig. 6) is of generalizable value (e.g., Hanks *et al.*, 1969; Stewart *et al.*, 1977; Tanner and Sinclair, 1983; Hanks, 1983; Squire, 1990).

Strictly speaking, the slope m, as reported in Eq. (4) with E_o replaced by the atmospheric saturation vapour pressure deficit (D), can be defined as the 'Normalized Biomass Water Ratio' (Monteith, 1993), abbreviated as NBWR, otherwise indicated as 'transpiration equivalent' (Azam-Ali *et al.*, 1994). By analogy with Eq. (3), then, the commercial yield of a field crop (Y) can be expressed as

$$Y = HI \cdot m_N \cdot \int_e^h T\,dt \qquad (5)$$

where: m_N is the value of m normalized for the saturation deficit of the atmosphere; T is the crop transpiration flux; and e, h, and t defined as in Eq. (3).

Since DM generally refers to above-ground biomass, variation in m can be partially affected by the variation in the root/shoot ratio during the crop cy-

cle and when crops are growing under limited soil moisture. Since it is hard to account for root biomass in m, DM of field experiment keeps referring to above-ground biomass only.

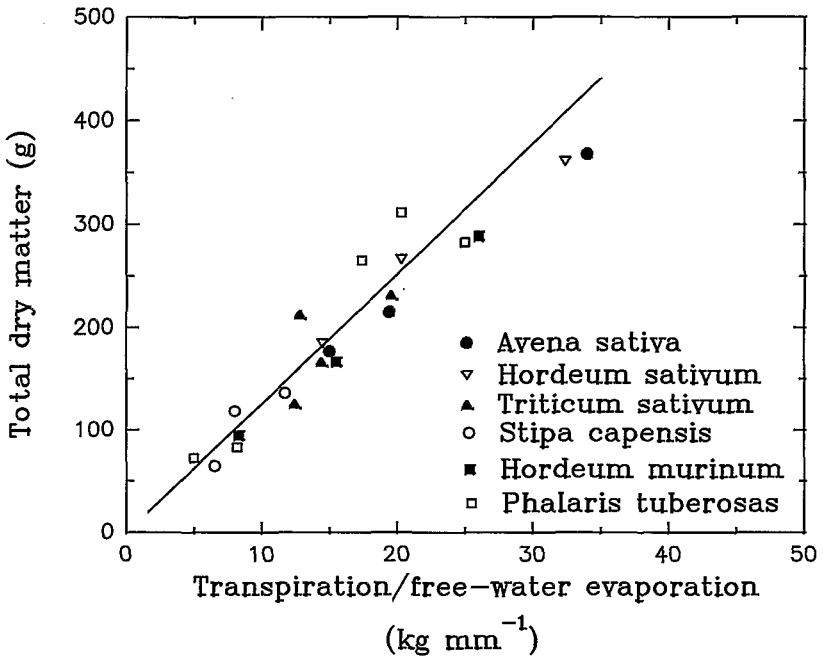

***Fig. 6** - Relationship of cumulative biomass to cumulative transpiration of various field crops grown in containers, normalized for climatic evaporative demand. Redrawn and modified from de Wit (1958).*

This feature, though, must be considered when observing variability among m values resulting from different experiments.

Similarly to the difficulty of considering root biomass in DM, in field experiments there is difficulty in considering soil evaporation (E) separately from transpiration (T), so that the total evapotranspiration (ET) is largely used in place of T. This feature may introduce additional variability in m results depending on the degree of ground cover by crops. Accounting for root biomass and for soil evaporation, the stability of m improves which anyway can be considered as a constant throughout the growing stage of a crop, in different locations, and in different years when normalized for the atmospheric vapour pressure deficit. A word of caution in the constancy of m in different locations and years must be said because of another feature that may induce variability: the dark respiration. In fact, R may vary as a function of temperature and thus be different from location to location with the VPD not necessarily changing accordingly.

The principal blame to the water-driven growth-engine is mainly related to the difficulties in separating soil evaporation from transpiration, and in estimating the root contribution to total productivity. Both approaches, though, (solar-driven and water-driven models) suffer from the limitations due to those factors such as respiration and partitioning of assimilates into harvestable yield.

While more experimental data are necessary to establish the stability of m in various crops, its conservative behaviour can be definitely explained on theoretical ground, provided proper assumptions are considered.

As reported by Hsiao (1993b), two major features can be invoked to explain such conservative behaviour: (a) the role of intercepted radiation in both photosynthetic assimilation and transpiration, and (b) the sharing of the transport pathway by carbon dioxide and water vapour between the atmosphere and the intercellular air space of leaves. However, the role of intercepted radiation shows to be domi-

nant over the sharing of the pathway for most of the agricultural conditions (Hsiao and Bradford, 1983).

Since the extent of solar radiation captured by the crop essentially depends on the leaf area displayed per unit of ground area and the architectural distribution of leaves within the canopy, the difference between assimilation and transpiration of the crop is in the active wave band for the two processes: the photosynthetically active radiation (PAR) for assimilation, and all the waveband radiation captured for transpiration. PAR, however, is a quite constant proportion of the incident solar radiation (Meek *et al.*, 1984) so that also the ratio of PAR to non-PAR wave bands captured by the crop remains fairly constant. The role played by radiation intercepted by crops, then, is in favour of a robust relationship between assimilation and transpiration.

Considering the crop as a 'big-leaf' (Monteith, 1973), an analogy with single leaf can be constructed. Photosynthetic assimilation (A) and transpiration (T) can be expressed, under steady state, as

$$A = \frac{c_a - c_i}{r_b' + r_l'} \qquad (6)$$

$$T = \frac{w_i - w_a}{r_b + r_l} \qquad (7)$$

where: w_i and w_a are the within-leaf intercellular air-space and bulk atmosphere water vapour concentration, respectively; r_b and r_l are the boundary layer and leaf epidermal resistance (mainly stomatal) to water vapour; c_i is the CO_2 concentration in the intercellular air space of the leaf; and c_a, r_b', and r_l' have been already defined (see Eq. 1). Between bulk atmosphere and intercellular air spaces, thus, the gaseous phase of water vapour and carbon dioxide share the same transport pathways. Only CO_2 has an additional path to cross, in the liquid phase, to reach the sites of carboxylation. This path represents an additional resistance (r_m'), as already indicated in Eq. (1). The determination of the complex metabolic changes in r_m' as a function of environmental conditions, however, can be avoided as they are reflected in the c_i value relatively to c_a (Hsiao, 1993b). Since the differences between r_l and r_l' and between r_b and r_b' are only due to binary diffusivity of water vapour and CO_2 in air ($r_l' \cong 1.6\ r_l$, and $r_b' \cong 1.37\ r_b$), the variation in their values will have a similar impact on assimilation and transpiration, so that the ratio of assimilation to transpiration will be proportional to the ratio of the CO_2 to water vapour concentration differences between inside and bulk atmosphere, i.e.:

$$\frac{A}{T} = \alpha \frac{c_a - c_i}{w_i - w_a} \qquad (8)$$

If c_i remains constant, relatively to c_a, and c_a does not change considerably over time, then A/T is inversely proportional to (w_i - w_a). As biomass is the result of net assimilation, normalizing the relationship DM *vs.* T for the atmospheric saturation deficit (*D*) would confer to m its conservative behaviour. Although not for very extreme conditions, in many species c_i has shown to be about constant under the same c_a (e.g., Wong *et al.*, 1979; Morison, 1987, Bolaños and Hsiao, 1991). Evidence is accumulating of this conservative behaviour also under water stress (e.g., Squire, 1990; Steduto, 1995) and theoretical frameworks for using transpiration as basis for estimating crop productivity are available (e.g., Tanner and Sinclair, 1983; Hsiao, 1993a,b; Monteith, 1990, 1993).

All the above has major validity during the vegetative growth of field crops. It already fits properly to crops for biomass production, but requires additional elaboration to account for the reproductive (commercial) yield. Harvest index is generally taken as the factor for converting above ground into commercial yield. Although the reproductive weight shows to be relatively proportional to total biomass, HI is not a conservative factor, depending largely on intensity and duration of possible stresses, on the crop stage at which the stress occurs, on the partition of assimilates, and on the relative interaction between sources and sinks of assimilates (Hsiao, 1982).

Then, based on previous considerations, one way of modelling yield response to water can be set by following the Stewart's approach (1977) reported in guideline format for practical application by

Doorenbos and Kassam (1979) and mathematically expressed as

$$\left(1-\frac{Y_a}{Y_m}\right)=k_y\left(1-\frac{ET_a}{ET_m}\right) \qquad (9)$$

where: Y_a is the actual (commercial) yield; Y_m is the maximum yield; ET_a is the actual evapotranspiration; ET_m is the maximum evapotranspiration; and k_y is an empirically-derived yield response factor. Although Eq. (9) showed to be useful and of practical application (e.g., Cavazza, 1988), adapting k_y also to different sensitivities of individual growth periods of the crop, it assumes that other input resources are not limiting, and suffers from the lack of interaction and integration with other processes involved in crop growth.

The case of the crop-growth submodel of EPIC

Once the simple approach of Eq. (9) is overcome, and more mechanistic modellings to crop growth are developed, three main categories of crop models can be distinguished: (a) single-crop models; (b) multi-crop models; and (c) tree-crop models. Trying to classify all the possible existing agricultural models would be a never-ending job as they multiplicate continuously. Though, among the many single-crop models available, the ones of greater interest and usefulness are those generated for cotton (GOSSYM), maize and wheat (CERES), sorghum (SORGF), soybean (GLYCIM), potato (POTATO), sunflower (OILGRO), alfalfa (SIMED), and sugarbeet (SUBGRO). They all differ for the input/output variables selected, but essentially they are generated to consider a wide range of detailed crop parameters to accommodate possible changes in cultivars. The reader is referred to Joyce and Kickert (1987) for an overview of these different models.

Multiple crop models can be used for resource management and decision making processes in agriculture. Among alternative multi-crop models are FLEXCROP (Halvorson and Kresge, 1982), NTRM (Shaffer and Larson, 1982), and CROPSYST (Stockle *et al.*, 1994). Here, one of the main multi-crop models (EPIC), on which the author of this article has first hand experience, is reported to illustrate an example of application.

EPIC (Erosion-Productivity Impact Calculator) is a dynamic, deterministic, mechanistic model originally developed to evaluate the impact of soil erosion on the productivity of agricultural lands as commissioned by the National Soil Erosion-Productivity Research Planning Committee of the United States (Williams et *al.*, 1984). In order to evaluate the erosion-productivity relationship, EPIC simulates comprehensively, on daily time-steps, the various processes involved in the soil-crop-atmosphere continuum through different interacting sub-models, each one focusing on a specific mechanism to simulate.

Those submodels are identified as: hydrology, weather, erosion, nutrients, crop-growth, soil balance, management. Other submodels concerning economics, pesticides, and climate changes, added on over time. Here, the crop-growth sub-model is discussed since of relevance to the crop-water relations modelling. For further details and tests on EPIC, the reader is referred to Williams et al. (1984, 1989), Sharpley and Williams (1990), Cabelguenne *et al.* (1988,1990), and Steduto *et al.* (1995).

Crop-growth in EPIC is simulated, on daily time-step, by: (a) first deriving the potential dry matter as function of leaf area index (LAI) of the previous day and of the climatic variables; (b) then calculating the corresponding water and nutrient demand to reach the potential growth; (c) evaluating the actual supply of water and nutrient from the soil, assigning a stress index (ranging from 0 to 1) to each potentially limiting resource; (d) selecting the minimum among these stress indexes as the most limiting one, and thus representing the stress factor for that day; (e) and lastly, using this stress factor to lower the potential growth of that day to the actual growth.

The core of the crop-growth submodel of EPIC, closely resembling the Monteith-type model of Fig. 3, is shown in Fig. 7.

While the physiological responses to water stress are considered of direct impact on harvest index and canopy growth, the stress factor algorithm lacks of the direct effect of water stress on leaf expansion. In other terms, the water stress factor for any day ($S_{w,i}$) is expressed as

$$S_{w,i}=\frac{u_i}{E_{p,i}} \qquad (10)$$

where: u_i is the soil supply estimated on the basis of the soil characteristics and rooting depth, the water extraction pattern along the soil depth, a partial compensation of water supply coming from layers other than the one considered, a water deficit compensation factor (function of the root ability to extract water), and the soil-water retention function (for detailed formulation, see Sharpley and Williams, 1990); and $E_{p,i}$ is the potential evapotranspiration, or demand, of the crop on a given day. The interpretation of $S_{w,i}$ is that a water stress effect is considered only when the supply (u_i) does not match the demand ($E_{p,i}$). This, however, is not sufficient during early vegetative growth of many crops (as previously discussed) when moderate water stress may slow down the expansive growth of leaves without affecting stomatal resistance. In such conditions, the demand is however satisfied by the supply independently from the effect of water status on leaf growth. Under these circumstances, EPIC overestimates leaf area development, biomass production, and consequently yield. Such overestimation has been observed in various tests (Steiner *et al.*, 1987; Cabelguenne *et al.*, 1990; Steduto *et al.*, 1995). Other crop-growth models implement algorithms which consider the direct effect of possible water stress on leaf expansion (e.g., CERES), or of VPD on stomatal resistance (e.g., CROPSYST).

Notwithstanding the apparent limitation of the EPIC crop-growth submodel, many algorithm modifications are being made to improve the performance of the model under variable agricultural conditions.

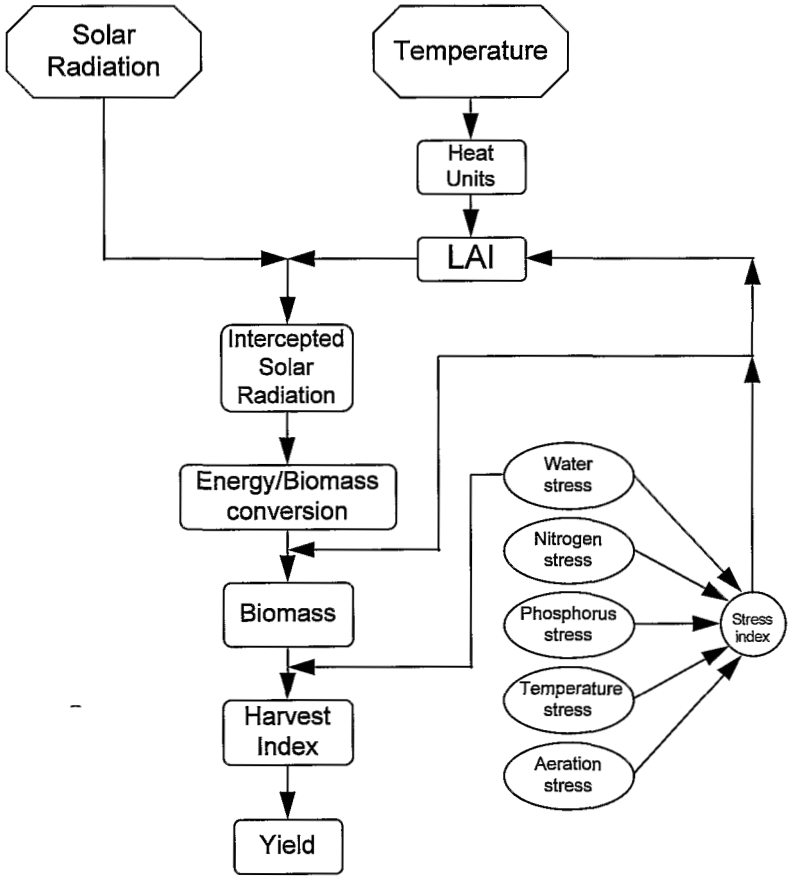

***Fig. 7** - Schematic diagram of the relationships among the variables influencing growth and productivity within the crop-growth submodel of EPIC (Erosion Productivity Impact Calculator). Redrawn and modified from Steduto et al. (1995).*

The adaptability and flexibility of EPIC as a multiple-crop model has been appreciated in the Commission of the European Communities for Agriculture and Agro-industry programme of research and technological development, so that a project on the impact of agricultural policy on the economic viability and environmental risks of various agricultural systems through Europe has been implemented using EPIC as a tool for generating 'engineering' production functions to be used as inputs for economic models. The project, named POLEN (Flichman, 1995), involved many institutions throughout Europe: some had to deal with economic aspects, some with social issues, and others with agronomic aspects; it expresses one of the basic features of modelling: the integrative tool of an interdisciplinary work.

LIMITS OF MODELLING IN THE MEDITERRANEAN BASIN

Despite the appealing peculiarities of crop models, two main limiting aspects need to be pointed out when dealing with the Mediterranean Basin: modelling tree crops and modelling under salinity conditions.

Tree crop modelling

The majority of crop models deal with annual species, preferably determinant, and with a growth behaviour which spans a typical three stage pattern (exponential growth, canopy closure, senescence). One or two dimensions of the crop architecture can be enough to represent the system (e.g., the big leaf approach may fit most of the field crops); the time scale of the processes is limited to the life span of the crop cycle; the partitioning of assimilates and resources among plant organs also presents relatively straightforward source-sink relationships; and the boundary and initial conditions of the systems are probably the least complicate. The system complicates when modelling row crops (which never reach complete ground cover, and start to show 2-dimensional space arrangement) or, even further, when modelling orchards. The complication of this latter case results from a 3-dimensional space representation and from a much more complex physiology (e.g., partitioning in the storage organs, wood growth, mutual shading, previous season *vs.* actual season assimilate allocation, *etc.*).

Attempts have been made to model fruit trees such as apple tree(e.g., Seem *et al.*, 1986) grapevine (e.g., Gutierrez *et al.*, 1985), oil palm (e.g., Kraanlingen, 1985) and olive tree (e.g., Abdel-Razik, 1989). They all tend to rely on the eco-physiological processes in a sort of deterministic way, but due to the incompleteness and the level of approximation introduced they are still far from the application level reached by the field crop-growth models. Consequently, where tree crops are involved in resources management, and production functions are needed, then statistically based, same-level experimental information may show to be much more reliable.

Salinity modelling

In arid and semiarid lands, the problem of salinity cannot be overlooked. Attempts to generate models including the effects of salinity on crop growth are present in the literature from quite a while, considering either the salinity in soil (e.g., Childs and Hanks, 1975) or the salinity in irrigation water (e.g., Yaron *et al.*, 1980). The principal assumption in these models is that salinity influences crop growth through its relative reduction of transpiration, due to the decrease in osmotic potential in the soil which in turn decreases the total water potential gradient between the plant and the soil. This means that specific ion toxicity is not considered.

More recently, models to generate crop-water production functions, including salinity in the irrigation water, are based on current understanding of the response of crops to water, salt tolerance of crops, and leaching processes have been conceptualized and implemented (e.g., Solomon, 1985; Letey *et al.*, 1985) and used to simulate production functions for several crops (Letey and Dinar, 1986). These models could easily take into account the effect of uniformity of distribution as well as for the effect on water use efficiency (Letey, 1993). They could also be used for irrigation management with waters of various quality. Though, the only implication of salinity on water use has been on crop production as it is affected by water stress, either from osmotic or matrix potentials. The major limitation of the existing models dealing with water quality aspects is that they do not take into account the effects of water quality on the physical characteristics of the soil. This is a very hard subject to be handled in modelling if one considers the difficulties linked to the long-time dependence of the processes involved. The toxicity aspects are substantially neglected as well.

CONCLUSIONS

To deal properly with the economic aspects of water management under limited resource availability, as it is the case of the Mediterranean Basin, there is no question that a feasible crop production 'function' is needed. Due to the complexity of the physiological aspects involved in the crop-water relationships, the route to generate such functions has struggled agronomists, experimentalists, and crop-physiologists so that the system has been subdivided into hierarchical or organizational levels, much easier to handle. But moving down in the hierarchy to explore the mechanisms explaining the observed behaviour leads to a reductionist approach which still does not predict the quantitative response of the complex system to variation in inputs. That is, interactions and integration among processes are needed to attempt an answer.

Whatever the attempt to generate a 'functional' relationship between inputs and outputs, though, it is a modelling effort. Depending, of course, on the proportion of integration and interaction between the processes of the various hierarchical system levels, two broad categories of crop models can be identified (Loomis *et al.*, 1979): (a) same-level models (also called empirical, descriptive, or correlative models), generally making use of statistics (multivariate regressions) where the degree of understanding of causality is quite low. Classical yield-response function to water falls in this category, accommodating average field and climatic conditions. They cannot be disregarded as they had, and still have, large relevance in many water management issues using existing same-level experimental results; (b) mechanistic models (also called multi-level, or explanatory models) where the degree of understanding of causality is substantially high. They generally tend to be predictive and provide quantitative explanation from the knowledge of the underlining physiological and morphological processes.

The mechanistic models differ from same-level models for including in their implementation at least one hierarchical level below the one at which predictions are to be made. It is evident, however, that there is always an ultimate hierarchical level, no matter how many are included, where the model stops and where the mechanisms described become empirical. Actually, it seems desirable to build a model at no more than one or at most two levels of hierarchy below the one of interest (Whisler *et al.*, 1986). In reality, however, depending on the objective and ultimate purpose for which the model is built or is being used (and on the data available, too), a 'user' may choose within a range of opportunities going from a very empirical to a very mechanistic model (Fig. 8).

What is not sufficiently indicated in the literature is that, as a tool, any model has some uncertainty associated to its predicted variables which generally need to be assessed before using it for a real world application. Tests, calibrations, validations and sensitivity analysis are hard jobs which have not yet properly permeated academic and scientific agricultural institutes. In economic analysis, for instance, economists should indicate the maximum values of uncertainty in output to be acceptable for a useful analysis. These uncertainties bounds assume a different significance depending on the objective.

Tree crops deserve particular attention in the yield response to water as they are relevant to the Mediterranean agriculture, while presenting a much higher degree of complexity than field crops. Similarly, salinity issues need to be necessarily included in research programs of crop response to water.

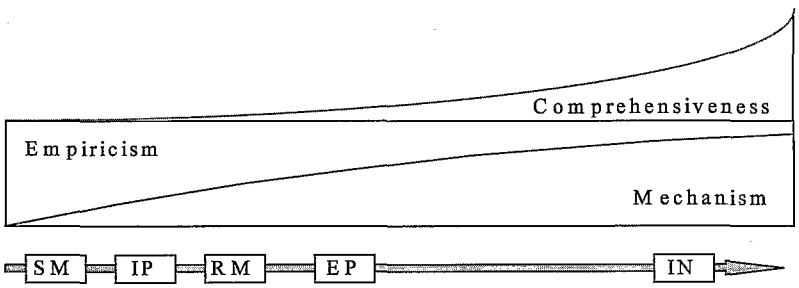

***Fig. 8** - Schematic representation of model types according to their relative empiricism and mechanism content. Some types of models may be indicated as: SM, summarizing data; IP, interpolative prediction; RM, research management; EP, extrapolative prediction; IN, interpretation and simulation of experimental results. Redrawn and modified from Whisler et al. (1986).*

A special feature of crops, belonging also to many other biological system, is 'plasticity' (the ability to adapt or acclimate to particular environmental conditions). This physiological aspect, similarly to the variation in plant populations, is not seriously introduced in crop modelling. These aspects, in fact, largely contribute to the variability observed at any hierarchical level. Some of the variations observed in crop systems, however, are constrained by some homeostatic mechanisms such as feedbacks and functional balances (Loomis *et al.*, 1979). This would encourage for a stochastic treatment of the crop models, with the possibility of introducing such a treatment for selected processes only. A large gap exists, anyway, in using this approach in mechanistic crop modelling due to their handling complexity.

Among the major mechanistic crop models described, the solar-driven growth-engine is the most used one, though its best performances are obtained when predicting potential productivity, i.e. when water is not limiting. In the Mediterranean Basin, the water-driven growth-engine is probably the most promising in predictive performance. Though, it needs additional research for normalizing the response in relation to the atmospheric vapour pressure deficit and for separating field evaporation from transpiration. In both types of models, though, dark respiration and assimilate partitioning are among the main sources of uncertainty in their predictive capability. CERES, EPIC, CROPSYST, and a few other mechanistic models may all be used for optimization, multiobjective, and decision support type of analysis, provided they are properly tested and thoroughly understood in their functionalities. Most of them, though, use the solar-driven growth-engine.

To conclude, a great deal of hard work is still to be done before crop models become the straightforward simulative tools to be easily plugged into any of the resource management analysis.

As pointed out by Loomis *et al.* (1979), in fact, the "initial enthusiasm about the potentiality of crop modelling must be tempered". They are not substitute for experiments, but they do help in interpreting the experimental results, as well as in guiding toward more effective research and experiments. Notwithstanding all the limitations that any one may envisage in crop modelling, no other means exist for progressing in attributing the proper significance to the various physiological aspects of growth, and in quantitatively integrating them into a productivity response function.

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