WatNitMED - management improvements of WUE [Water Use Efficiency] and NUE [Nitrogen Use Efficiency] of Mediterranean strategic crops (wheat and barley)

Slafer G.A., Karrou M., Karam F., Thabet C., Spiertz H.J., Dahan R., Foulkes J., Nogués S., Peltonen-Sainio P., Albrizio R., Ayad J.Y., Mellouli H.J.

in

Lamaddalena N. (ed.), Bogliotti C. (ed.), Todorovic M. (ed.), Scardigno A. (ed.).
Water saving in Mediterranean agriculture and future research needs [Vol. 3]

Bari : CIHEAM
Options Méditerranéennes : Série B. Etudes et Recherches; n. 56 Vol.III

2007
pages 291-299

WatNitMED - MANAGEMENT IMPROVEMENTS OF WUE AND NUE OF MEDITERRANEAN STRATEGIC CROPS (WHEAT AND BARLEY)

G. A. Slafer, M. Karrou, F. Karam, C. Thabet, H. J. Spiertz, R. Dahan, J. Foulkes, S. Nogues, P. Peltonen-Sainio, R. Albrizio, J. Y. Ayad and H. J. Mellouli *

[*] Authors are scientific coordinators and leaders of each WP ordered by number of WP of the project from Univ. Lleida – Spain; INRA – Morocco; LARI – Lebanon; ESHE Chott Meriem – Tunisia; Wageningen Univ. - The Netherlands; INRA – Morocco; Univ. Nottingham - United Kingdom; Univ. Barcelona – Spain; MTT – Finland; IAMB – Italy; Univ. Jordan – Jordan; INRAT – Tunisia; respectively.

Corresponding author: GA Slafer, Research Professor of ICREA at the Department of Crop and Forest Sciences, University of Lleida, Centre UDL-IRTA, Av. R. Roure 191, 25198 Lleida, Spain [slafer@pvcf.udl.es].

SUMMARY - Water is recognized as the most limiting factor in Mediterranean regions, though N shortages seem as important as water scarcity. The general objective of this proposal is to identify and transfer improvements in management of wheat and barley through increasing the capture and/or the use efficiency of water and N. The project is based on the premise that understanding the physiological bases of the responses to water x N shortages would allow the design of more consistent management practices to overcome the deficiencies explored, either by directly using the concepts in such strategic design or by being able to build up (or adapt an existing) robust simulation models based on this knowledge and then allowing the testing of different alternatives exploring a large degree of G x E interactions. We developed work-packages (WP) on plant and crop physiology (WP5-10, some more focus on root attributes, others on N/water economies of the canopy) designed to elucidate facts under the realistic (actual and near future) range of water x N deficiencies in the Region (established beyond the well known general pattern of “Mediterranean conditions” by WP1), so that the agronomic (WP11-12) and strategy design (WP4) works may be based on more solid bases, and the social impact and outreach activities (WP2) be made more confidently on the actual impacts of any proposed changes in management measured in the project.

Key words: Water, Nitrogen, Wheat, Barley, Management, Nitrogen use efficiency, Water use efficiency

CHARACTERISING THE SITUATION

Mediterranean climate is characterised by a high seasonal variability in rainfall, with soils characterised by their relatively low and variable nitrogen content, and simultaneously highly prone to wind and water erosion due to the presence of irregular steep slopes (López-Bellido *et al*., 2000). The environmental factors most strongly influencing crop grain yields in the region are soil moisture and nitrogen, the former of which depends on rainfall and its distribution during the growing season (*e.g.* Loss and Siddique, 1994; Araus et al., 2002). Although water is recognized as the most limiting factor in Mediterranean regions, N shortages seem as important as water scarcity (e.g. Passioura, 2002).

Breeding under Mediterranean conditions of South Europe and the West Asia and North Africa (WANA) has been consistently funded by the EU-INCO programme (MPCs). As crop productivity for a particular region is the consequence of the breeding x management x weather interaction, understanding the bases for improved management has been becoming increasingly important. The general objective of this proposal is to identify and transfer improvements in management of wheat and barley through increasing the capture and/or the use efficiency of water and N. As improvements in crop productivity in any environmental background are the result of the genetic by management interactions, the overall aim of the project is critical not only on its own but also to power any likely genetic improvement in attributes related to use more or more efficiently scarce resources.

In this context, WatNitMED is based on the premise that understanding the physiological bases of the responses to water x N shortages would allow the design of more consistent management practices to overcome the deficiencies explored, either by directly using the concepts in such strategic design or by being able to adapt a robust simulation model based on this knowledge and then allowing the testing of different alternatives exploring a large degree of G x E interactions.

PHYSIOLOGICAL BASES OF PRODUCTIVITY

Cereal productivity, the final goal of farmers determining their success (and fate), is the final outcome of the Genetic x Management interaction in a particular range of environmental backgrounds also interacting. To produce trustworthy advances, in either breeding or management, the determinants of productivity must be taken it account. The better the yield determination is understood the more likely the breeding or management strategies designed to raise productivity will efficiently apply (Austin, 1993; Richards, 1996; Slafer *et al*., 1996).

Whenever we think on the determination of yield a wide range of different ideas may come to our mind. This is because yield is the final outcome of crop growth and development processes occurring throughout a growing season: yield is being formed all the time from sowing to harvest (Slafer & Rawson, 1994), and therefore virtually any trait may be considered yield-determining. However, in an agronomic context the idea is mostly restricted to two groups of attributes: those conferring adaptation (through phenological adjustment or tolerance/resistance to abiotic or biotic constraints for yield) and those related more directly to the productivity (attributes determining yielding advantages beyond tolerance to stresses).

Some of the clearest examples of attributes controlling yield through the effect of major genes on adaptation are those related to phenology. Undoubtedly, the pattern of crop development is the single most important attribute largely determining its performance under field conditions (*e.g.* Passioura, 1996; 2002; Richards, 1996). For instance, improving yield due to a better adaptation to different regions has been possible in wheat due to modifications in its pattern of development to suit each particular combination of environmental conditions, being the key issue the fact that anthesis must occur when frost risks are small and that some water is still available during grain filling (Slafer & Whitechurch, 2001), for which the contributions of breeding and management have been both paramount.

However, in most realistic situations crops are exposed to a range of largely unpredictable combinations of stresses that requires the understanding of the attributes conferring higher productivity for a wide range of conditions. Although the most popular approach has been the dissection of yield into its “numerical components”, so that crop yield (in the case of wheat) is considered to be the product of plants per unit land area, spikes per plant, spikelets per spike, grains per spikelet, and average individual grain weight. Although this approach is eminently correct from the mathematical logic sustaining it, it has a major problem that makes it unsound from a physiological point of view, at least for predicting the effect of manipulating a component on crop yield (*e.g.* Fischer, 1984; Slafer *et al.*, 1996). The insolvable inconvenience has its roots in the fact that these yield components are, almost invariably, negatively related between each other (as illustrated in Slafer, 2003). Despite of being competition among growing grains the most commonly reported interpretation for the negative relationship between mean grain weight and grain number per unit land area, this is not true, at least for most of the conditions in which cereals are grown, even under stress (being the stress effects seemingly directly affecting grain size rather than through changes in assimilate availability e.g. Slafer & Miralles, 1992; Zahedi *et al*., 2003; Acreche & Slafer, 2006). Although for economy of space we could not develop the point with detail here (but see Slafer & Savin, 1994; Kruk *et al.*, 1997), it implies that we need to understand much more deeply the nature of the negative relationship between grain number and grain size in order to develop effective management strategies minimizing trade-offs among yield determinants.

The alternative, physiologically sound and agronomically trustworthy approach is that based in the ability of the crop to grow and partition the dry matter together with the efficiency in transforming these two attributes into grain number per unit land area (*e.g.* Fischer, 1984; Slafer *et al*., 1996); complemented by a more refined understanding of the actual (genetic and environmental) determinants of the final weight of the grains (Calderini *et al*., 2001).

In this context, to be able to design adequate management strategies (either by direct agronomic experimentation or through building/improving, and then using, simulation models) we need to improve our understanding on the way in which cereals do acquire their abilities to use more, and use more efficiently the water and N (the most limiting factors in Mediterranean agriculture) to produce their growth and partitioning (as the latest is strongly determined by the timing of growth; *e.g.* Fischer, 1984) and to what degree management may influence in the production of fertile spikelets and florets per unit of dry matter allocated to reproductive growth. WPs on plant and crop physiology (WP5-10) were designed to elucidate these facts under the realistic (actual and near future) range of water x N deficiencies in the Region (to be established beyond the well known general pattern of "Mediterranean conditions" by WP1 with contributions from WP3), so that the agronomic (WP11-12) and strategy design (WP4) works may be based on more solid bases, and the social impact and outreach activities (WP2) be made more confidently on the likely actual impacts of any proposed changes in management suggested from this project.

RESOURCE CAPTURE AND ROOT SYSTEMS

For wheat and barley crops grown in Mediterranean environments, the interactions between fertilizer N applications yield and water use are imperfectly understood, but since roots are the agents of both water and nutrient uptake their activity seems crucial. To be in a position to manage more effectively, an improved quantitative understanding of relationships between root traits and capture of water and nitrogen is required. The literature (Fischer, 1981) contains many suggestions of the type of root system likely to benefit capture during grain filling, but there are few measurements of root growth and activity.

The major phase of root growth in wheat and barley is during tillering and stem extension, a time when the canopy is also rapidly expanding. The total length of the root system increases until about anthesis (Gregory *et al.* 1978; Barraclough and Leigh 1984). The mechanisms controlling root:shoot weight ratio at anthesis are complex, involving the exchange of hormonal messages between roots and shoots. At present our understanding of root activity during grain filling, and the factors that influence it, is poor. The weight of the shoots and root systems, however, may not provide the best measure of their ability to capture resources. Arguably, more a appropriate measure would be the leaf area and root length density (Lv, cm cm^{-3}), respectively.

Field data sets of barley grown on stored water in Syria indicate a Lv of about 1 cm cm^{-3} is required for extraction of 90% of the available water, and about 2 cm cm^{-3} for complete extraction (Gregory and Brown, 1989). It is encouraging that this estimate, based on field measurements, is comparable to that predicted from theoretical considerations of water uptake by single roots for cereal root systems (Van Noordwijk 1983). The relationship between Lv and below-ground resource capture in cereal root systems has recently described in a quantitative model, jointly developed by University of Nottingham and other UK research institutes, linking the size and distribution of the root system to the capture of water and nitrogen during grain filling (King *et al*., 2003). The model uses only summarized concepts, relying on only a minimum number of parameters, each with a clear biological meaning.

It is possible that a larger investment in fine roots at depth in the soil and less proliferation of roots in surface layers, would improve yields in rain-fed environments, including those Mediterranean environments with moderate to high winter rainfall, by accessing extra resources (King *et al*., 2003). Further development of these concepts will provide the basis of the proposed work in the present project. The aim is to develop a framework for optimising roots in Mediterranean environments, including an investigation of interactions between early and later events during crop development.

MODELLING AND STRATEGY DESIGN

Optimization of crop management at tactical and strategic levels is complex due to the fact that crop response to different practices (*e.g*. sowing date, sowing rate, fertilization, etc.) interacts with other agronomic factors, and with soil type, genotype and particularly weather (Fischer, 1985). The generation of management guidelines for a particular region from experiments may require many experiments in several years and sites, at a high cost of time and money. A major inconvenience of using conventional experimentation is that interactions between cultivar, climate and soil management practices frequently have a greater impact on yield than their individual effects (Byerlee *et al.*, 1991). Therefore, extrapolating the results obtained from a limited number of environmental combinations to other environments is not only difficult but may be misleading. A complementary method of evaluating crop/soil/climate interactions is to use a validated crop simulation model in combination with an extended series of climatic data (Stapper and Harris, 1989).

Passioura (1973) pointed out the dangers in using complex mechanistic simulation models because of the difficulties inherent in testing them and the wide gap between crop growth and yield and processes taking place at relatively low organization levels. On the other hand, extremely simplistic, purely empiric models may not be sufficiently realistic to allow testing some hypotheses or sufficiently robust for meaningful application. Nevertheless, Fischer (1985) demonstrated that simulation models of intermediate complexity could be confidently useful agronomic tools. Angus (1991) emphasized the important contribution made trough the use of simulation models to the study of the effects of different management practices in a region when large series of climatic data are evaluated. There are some examples in the literature of the usefulness of this approach to the analyses of management decisions on final crop yield and other crop attributes with different simulation models (Stapper and Harris, 1989; Fischer *et al.*, 1990; Freebairn, *et al.*, 1991; Singels and de Jager, 1991) over a range of crop species (*e.g.* Fischer *et al.*, 1990; Muchow *et al.*, 1991; Parsch *et al.*, 1991).

Crop simulation models are increasingly being used to support local decision-making. Examples for management decision support systems are WHEATMAN, APSIM and ShowDevel. These systems are initiated from the awareness that growers need to be able to accurately identify crop growth stages and be aware of key crop characteristics or standards associated with high yields. In the Show Devel package, calculations are based on regional climatic data and photoperiod, which are included in the package for over 400 locations in the Australian wheat growing areas. The present project will look for ways to construct the model such that the output can be linked with these Decision Support type of models.

Until now the time courses of regulatory aspects of sink and source processes have been widely neglected in studies on yield under stress conditions. Traits related to organ formation and carbon partitioning (typical sink activity determining factors) and traits related to photosynthesis and remobilization of stored carbohydrates (source related processes) are usually studied as independent entities. This is one of the reasons why our continually improving understanding of plant physiology has made little impact on defining the attributes required for breeding for stress tolerance, despite the best efforts of plant physiologists to define which plant characteristics are important under stress conditions. In the foreseen new water/nitrogen-limited model, source- and sink-limited growth will be simulated independently as described in a mechanistic model that was developed for grasses (LINGRA) (Schapendonk, 1998). The model has been adapted for wheat in LINGRA-CC model (Rodriguez *et al.*, 2000). This model will serve as a basis for subroutines that include photosynthetic acclimation to water supply and changes in the canopy nitrogen profile. The model will include sink and source terms to keep track of the demand and supply of assimilates during different developmental stages.

THE PROJECT

WatNitMED specifically addresses a thematic priority to the Mediterranean region: improving management of Mediterranean wheat and barley to increase water/Nitrogen use and use efficiency. It is fully multidisciplinary, including in the consortium agronomists, physiologists, geneticists, crop modellers and sociologists together with farmers associations. It mobilises the strength, expertise and resources of European and non-European (Mediterranean) teams. It places a strong emphasis on the establishment of a coherent and optimised use of European research resources, developing synergistic interaction across the EU.

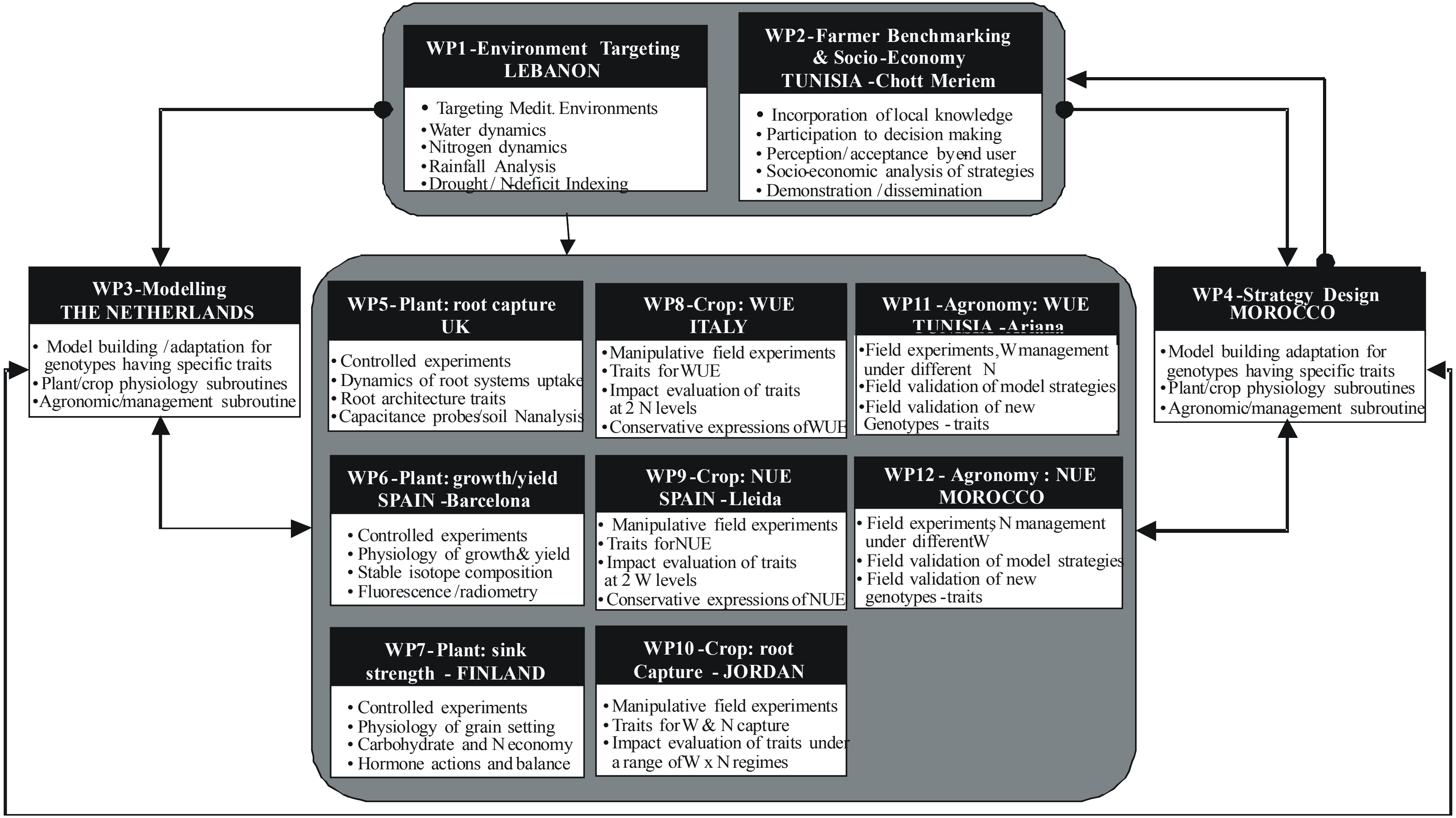
Too often, research programs on plant physiology result in extremely interesting information that in its current status is not relevant to practical crop management strategies. The project proposed will strengthen the links between discovery, deployment, production and end-use, by combining and exploiting the otherwise fragmentary information available at different research centres. The inclusion of modelling development/adaptation and simulation exercise will provide not only a powerful tool to design management strategies but also a framework in which the physiological-crop science-agronomic information produced as innovation of the specific WPs will be integrated to produce reliable outputs in form of management alternatives, as the main outreach activity of the proposed work of this consortium. In this context, the project proposed addresses a subject that is of high relevance for unlocking new developments in agriculture.

We aim to improve the understanding on the determinants of the crop ability to capture more water and/or to use water more efficiently (WUE) in a range of nitrogen availability conditions; as well as to capture more N and/or to use N more efficiently (NUE) in a range of water availability conditions. In this case, both ranges will be characterized and described within the context of the project, (i) identifying plant/crop characteristics that may confer superior ability to cope with insufficient water and nitrogen resources, (ii) constructing/adapting a simulation model to be friendly but reliably (with mechanistic basis, for which plant and crop physiological bases are to be established) used in the design of management strategies to improve capture and/or use efficiency of these resources, (iii) testing agronomic hypothetical management strategies improving the performance of cereals in these environments, and (iv) evaluating the socio-economic impact of the adoption of the improved strategies likely identified. We are also committed, within the project, in transferring the outcomes to the producers, with Farmers Associations in our partnership.

To satisfy the objectives the project have work-packages (WP) on plant and crop physiology (WP5-10, some more focus on root attributes, others on N/water economies of the canopy) designed to elucidate facts under the realistic (actual and near future) range of water x N deficiencies in the Region (established beyond the well known general pattern of “Mediterranean conditions” by WP1), so that the agronomic (WP11-12) and strategy design (WP4) works may be based on more solid bases, and the social impact and outreach activities (WP2) be made more confidently on the actual impacts of any proposed changes in management measured in the project.

The first WP is on Targeting Environments, aimed to characterise the main environmental conditions (weather and soils) of the Mediterranean region, particularly on the expected dynamics of water and N availabilities. The exercise will also include an assessment of the expected scenarios in the near future for these regions (in association with WP3). With the environments clearly characterised on which management strategies aimed to improve the capture and use efficiency of water and nitrogen clearly targeted the core WPs of the project, dealing collectively with the aim of designing better management strategies to improve profitability and sustainability of farmers in the region with a strong mechanistic basis. They are divided into WPs designed (*i*) to understand the whole-plant physiology of cereals grown in different ranges of water x N shortages, (*ii*) to identify the crop physiological characteristics of root systems to capture these resources and those determining grain setting and grain filling in conditions of water and nitrogen scarcity, (*iii*) to build up a simulation model able to capture the identified responses to water x N shortages at the plant and canopy levels, and (*iv*) to test agronomic responses to a range of management practices derived from the information of the plant- and crop-physiological studies and suggestions from running the model under different scenarios. The three Plant Physiology WPs will be focused in different aspects, though each would be equally committed to both water and N. One (WP5) will be focused on responses of the root systems, and on the changes in resource capture expected from different patterns of root growth and soil exploration. Other (WP6) will be more concerned with experiments analysing basic changes in growth capacity under water x N deficiencies, mostly based on stable isotope composition, photosynthetic gas exchange, chlorophyll fluorescence, and activities of N-metabolism enzymes. The third WP on plant physiological aspects (WP7) will be more focused on floret set/abortion in relation to carbohydrate/nitrogen translocation to developing ovaries under different water and N stresses and maybe also some hormonal studies in this context. One of the three Crop Physiology WPs is concerned with root systems under field conditions in Mediterranean environments attempting to assess to what degree different attributes of the root systems may be valuable for different growing areas of the Region (WP10). The other two Crop Physiology WPs are more concerned with the efficiency in using the resources captured; one of them would be more focused in WUE (WP8) while the other in NUE (WP9), though in both cases some degree of water x N interactions will be explored. In these studies manipulations of the environmental conditions will be imposed to determine whether the use efficiency of these resources may be improved by exposing the crop to particular conditions (which would then provide the basis for the design of strategies tested in the Agronomic WPs). Based on the results from the studies on plant and crop physiological responses to water x N deficiencies in terms of both resource capture and use efficiency, two Modelling WPs are proposed: one on building up (or adapting an existent) model (including parameterisation; WP3) and the other one on designing management strategies using a model for both the present prevalent conditions and for those expected in the near future (WP4). The core WPs are synthesised in the two Agronomy WPs, in which the final designed management strategies will be directly tested in one case more focused in water (WP11) while in the other in N issues (WP12), but in both considering the interactions. These Agronomic WPs will provide in addition feedback to the other WPs. The whole project concludes with a Socio-Economic WP (WP2) mainly in charge of answering whether the proposed strategies are actually applicable and acceptable by the farmers in each of the main regions of the cereal production area of the South Mediterranean Countries, and if so which is the economic-financial issues of the expected adoptions. This WP will also be in charge of the outreach activities of the consortium.

Management Improvement of WUE & NUE of Mediterranean Strategic Crops (Wheat and Barley) **WatNitMED**



REFERENCES

Acreche, M. and Slafer, G.A. 2006. Grain weight response to increases in number of grains in wheat in a Mediterranean area. *Field Crops Research*, **98**: 52-59.

Angus, J.F. 1991. The evolution of methods for quantifying risk in water limited environments. In: R.C. Muchow and J.A. Bellamy (Editors), Climatic risk in crop production: Models and management for the semiarid tropics and subtropics. C.A.B, U.K., pp. 39-54.

Araus, J.L., Slafer, G.A., Reynolds, M.P. and Royo, C. 2002. Plant breeding and water relations in C_3 cereals: what should we breed for? *Annals of Botany*, **89**: 925-940.

Austin, R.B. 1993. Augmenting yield-based selection. In 'Plant Breeding: Principles and Prospects'. (Eds M.D. Hayward, N.O. Bosemark and I. Romagosa.) pp. 391-405. (Chapman & Hall: London.)

Barraclough, P.B. and Leigh, R.A. 1984. The growth and activity of winter wheat roots in the field: the effect of sowing date and soil type on root growth of high yielding crops. *Journal of Agricultural Science* **103:** 59-74.

Byerlee, D., Triomphe, B. and Sebillotte, M. 1991. Integrating agronomic and economic perspectives into the diagnostic stage of on-farm research. *Exp. Agric*., **27**: 95-114.

Calderini, D.F., Savin, R., Abeledo, L.G., Reynolds, M.P. & Slafer, G.A. 2001. The importance of the immediately preceding anthesis period for grain weight determination in wheat. *Euphytica* **119**: 199-204.

Fischer, R.A. 1981. Optimizing the use of water and nitrogen through breeding of crops. In *Soil and water and nitrogen in Mediterranean type environments* (Ed. J.L. Monteith and C. Webb), pp. 249-278. The Hague : Nihoff/Junk.

Fischer, R.A. 1984. Wheat. In: WH Smith, JJ Banta (Editors), *Potential Productivity of Field Crops under Different Environments*. IRRI, Los Baños, pp. 129-154.

Fischer, R.A. 1985. The role of crop simulation models in wheat agronomy. In: Day, W. and Atkin, R.K. (Editors), Wheat Growth and Modelling. Plenum Press, NATO Scientific Affairs Division, New York, pp. 237-257.

Fischer, R.A., Armstrong, J.S. and Stapper, M. (1990). Simulation of soil water storage and sowing day probabilities with fallow and no-fallow in southern New South Wales: I. Model and long term mean effects. *Agric. Syst*., 33: 215-240.

Freebairn, D.M., Littleboy, M., Smith, G.D. and Coughlan, K.J. 1991. Optimising soil surface management in response to climatic risk. In: R.C. Muchow and J.A. Bellamy (Editors), Climatic Risk in Crop Production: Models and Management for the Semiarid Tropics and Subtropics. C.A.B, U.K., pp 283-306

Gregory, P.J., McGowan, M., Biscoe, P.V. and Hunter, B. 1978. Water relations of winter wheat. 1. Growth of the root system. *Journal of Agricultural Science* **91**: 91-102.

Gregory, P. J. and Brown, S. C. 1989. Root growth, water use and yield of crops in dry environments: what characteristics are desirable? *Aspects of Applied Biology* **22**: 235-243.

King, J., Gay, A., Sylvester-Bradley, R., Bingham, I., Foulkes, M.J., Gregory, P. and Robinson, R. 2003. Modelling cereal root systems for water and nitrogen capture: towards and economic optimum. *Annals of Botany* **91**: 383-390.

Kruk, B., Calderini, D.F. and Slafer, G.A. 1997. Source-sink ratios in modern and old wheat cultivars. *Journal of Agricultural Science* **128**: 273-281.

López-Bellido, L., López-Bellido, R.J., Castillo, J.E. and López-Bellido, F.J. 2000. Effects of tillage, crop rotation and nitrogen Fertilization on wheat under rainfed Mediterranean conditions. *Agronomy Journal* **92**: 1054-1063.

Loss, S.P. and Siddique, K.H.M. 1994. Morphological and physiological traits associated with wheat yield increases in Mediterranean environments. *Advances in Agronomy* **52**: 229-276.

Muchow, R.C., Hammer, G.L. and Carberry, P.S. 1991. Optimizing crop and cultivar selection in response to climatic risk. In: R.C. Muchow and J.A. Bellamy (Editors), *Climatic Risk in Crop Production: Models and Management for the Semiarid Tropics and Subtropics*, C.A.B., Wallinford, U.K., pp. 235-262.

Parsch, L.D., Cochran, M.J., Trice, K.L. and Scott, H.D. 1991. Biophysical simulation of wheat and soybean to assess the impact of timeliness on double-cropping economics. In: J. Hanks and J.T. Ritchie (Editors), Modeling Plant and Soil Systems., Am. Soc. Agron., Madison, Wisconsin, pp. 511-535.

Passioura, J.B. 1973. Sense and nonsense in crop simulation. *J. Aust. Inst. Agric. Sci*., **39**: 181-183

Passioura, J.B. 1996. Drought and drought tolerance. *Plant Growth Regulation* **20**:79-83.

Passioura, J.B. 2002. Environmental biology and crop improvement. *Functional Plant Biology* **29**, 537-546.

Richards, R.A. 1996. Defining selection criteria to improve yield under drought. *Plant Growth Regulation* 20, 157-166.
Rodriguez, D., van Oijen, M. and Schapendonk, A.H.C.M. 1999. LINGRA_CC: a sink/source model to simulate the impact of climate change and management on grassland productivity. *The New Phytologist*, **144**: 359-368.
Schapendonk, A.H.C.M., Stol, W., van Kraalingen, D.W.G. and Bouman, B.A.M. 1998. LINGRA, a sink/source model to simulate grassland productivity in Europe. *European Journal of Agronomy* **9**, 87-100.
Singels, A. and de Jager, J.M. 1991. Determination of optimum wheat cultivar characteristics using a growth model. *Agric. Syst.*, **37**: 25-38.
Slafer, G.A. 2003. Genetic basis of yield as viewed from a crop physiologist's perspective. *Annals of Applied Biology* **142**: 117-128.
Slafer, G.A. and Miralles, D.J., 1992. Green area duration during the grain filling period of wheat as affected by sowing date, temperature and sink strength. *Journal of Agronomy and Crop Science* **168**:191-200.
Slafer, G.A. and Rawson, H.M. 1994. Sensitivity of wheat physic development to major environmental factors: a re-examination of some assumptions made by physiologists and modellers. *Australian Journal of Plant Physiology* **21**:393-426.
Slafer, G.A. and Savin, R., 1994. Sink-source relationships and grain mass at different positions within the spike in wheat. *Field Crops Research* **37**: 39-49.
Slafer, G.A. and Whitechurch, E.M. 2001. Manipulating wheat development to improve adaptation and to search for alternative opportunities to increase yield potential. In: 'Application of Physiology in Wheat Breeding' (Eds M.P. Reynolds, J.I. Ortiz-Monasterio & A. McNab,) pp. 160-170. (CIMMYT, Mexico DF).
Slafer, G.A., Calderini, D.F. and Miralles, D.J. 1996. Yield components and compensation in wheat: opportunities for further increasing yield potential. In 'Increasing Yield Potential in Wheat: Breaking the Barriers' (Eds M.P. Reynolds, S. Rajaram and A. McNab.) pp. 101-133. (CIMMYT: Mexico, DF.)
Stapper, M. and Harris, H.C. 1989. Assessing the productivity of wheat genotypes in Mediterranean climate, using a Crop-Simulation Model. *Field Crops Res*earch, **20**: 129-152.
Van Noordwijk, M. 1983. Functional interpretation of root densities in the field for nutrient and water uptake. In Böhm W, Kutschera L, Lichtenegger E, eds. *Wurzelokologie und ihre Nutzanwendung.* Irdning: Bundesanstalt für alpenlandische Landwirtschaft, 207-226.
Zahedi, M, Sharma, R & Jenner, C.F. 2003. Effects of high temperature on grain growth and on the metabolites and enzymes in the starch-synthesis pathway in the grains of two wheat cultivars differing in their responses to temperature. *Functional Plant Biology* **30**: 291-300.