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Perspectives of forest ecophysiological research in the context of Mediterranean Basin

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Abstract

The mediterranean-climate regions are linked to the presence of the unusual global conditions of cool rainy winters and warm dry summers. Thus, the common drought periods, frost nights, summer heat and fires and soil erosion disturb plants life. These regions have a global significance by their floristic richness. Nevertheless, these areas have been more heavily impacted by human activities than almost any other ecosystem. The foreseeable global change will most likely influence plant life, and the Mediterranean Basin will be specially affected (e.g. a decrease in spring and winter rainfalls, an increase in mean annual temperature), affecting the delicate equilibrium of these ecosystems. Ecophysiology is a powerful tool to examine the controlling mechanisms behind the functioning, distribution, abundance, and productivity of forest tree species and their response to a changing environment. This science discipline can help to the forest management by physiological approaches of the response of plant processes to the biotic and abiotic constraints imposed by the environment.

Key words: Tree research, forest ecosystems, plant physiological ecology.

Resumen

Perspectivas en la investigación ecofisiológica forestal en el contexto de la cuenca mediterránea

Las regiones de clima mediterráneo se caracterizan por presentar las precipitaciones concentradas en la época fría y veranos secos y calurosos. Ello conduce a la frecuente aparición de períodos de sequía, heladas, altas temperaturas estivales, fuegos forestales y fenómenos de erosión edáfica que afectan la vida de las plantas. Estas regiones poseen una alta riqueza florística de importancia mundial, pero son ecosistemas altamente influenciados por la actividad humana a lo largo de la historia y su delicado equilibrio puede verse afectado aún más si se cumplen las previsiones de cambio climático (aumento de temperaturas, disminución de precipitaciones, oscurecimiento global, etc.). Por tanto, la gestión y manejo de los sistemas forestales precisa de un mayor conocimiento del funcionamiento de las especies y de la respuesta de éstas ante las nuevas condiciones ambientales venideras, así como del resto de factores bióticos y abióticos que limitan el crecimiento de las plantas. Para ello la ecofisiología, a través del mejor conocimiento de los procesos fisiológicos vegetales, permitirá conocer el funcionamiento, distribución, abundancia y productividad de los ecosistemas forestales mediterráneos.

Palabras clave: ecofisiología vegetal, investigación forestal, ecosistemas mediterráneos, investigación en especies arbóreas.

The Mediterranean-climate regions

The five mediterranean-climate regions (Mediterranean Basin, California, central Chile, Southwestern Australia, the Cape Region of South Africa) are linked to the presence of the unusual global conditions of cool rainy winters and warm dry summers. These contrasting weather conditions during the year have apparently contradictory consequences in terms of environmental stress and disturbance. In addition to soil water deficits, the vegetation is prone to catastrophic fires in summer; erosion is important in

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bare soils due to heavy rains; and human occupation with agriculture and deforestation have exacerbated these tendencies (Pereira and Chaves, 1993). Although these regions collectively comprise only slightly more than 2% of the world's land area, they are home to 16% of the total vascular plant flora of the world, but despite this global significance, these areas have been more heavily impacted by human activities than almost any other ecosystem (Rundel, 2004; Valladares *et al.*, 2004b). The characteristic paradigm of mediterranean-climate ecosystems as being dominated by evergreen sclerophyllous shrublands is misleading. Woodlands and closed canopy forests cover more of the land area in most of the mediterranean-climate regions than do shrublands, except for South Africa region, the smallest of the regions (Rundel, 2004).

Ecophysiology

Plant ecophysiology (or physiological plant ecology) is a meeting point where ecology and physiology overlap and join forces to solve problems (Lassoie and Hinckley, 1991). Physiological plant ecology is primarily concerned with the function and performance of plants in their environment and tries to understand the underlying physiological, biochemical and molecular attributes of plants with respect to performance under the constraints imposed by the environment. It is also concerned with understanding the distribution and success of plants measured in terms of the factors that promote long-term survival and reproduction in the environment. So, we need to consider whole-plant physiology and the interaction among plants in competition for resources (Fitter and Hay, 2002), as the organism itself is the key level of organisation, the root of population and community responses whose dynamics determine the functioning of the entire ecosystem. The spatial environment of plants are hydrosphere, atmosphere and pedosphere together, however a plant's environment is determined also by all the physical and chemical factors characterising habitats, and by the influences of other co-occurring organisms. Throughout their lives, plants are subjected to multiple abiotic (low light intensities, drought, flooding, extreme temperatures, low soil fertility, salinity, wind, fire) and biotic (insects, pathogens and herbivory, human activities) stresses of varying intensity and duration that, by influencing physiological processes, modify their growth (Kozlowski and Pallardy, 1997; Larcher, 2003) and development (Fitter and Hay, 2002).

Tree research and field research

Field research in ecophysiology is heavily dependent on appropriate methods and instrumentation. It includes both measurements of the environment and of the physiological and morphological responses of the plants. In some cases, for example stable isotope measurements, these are done in the laboratory but on samples collected under field conditions and with the primary objective of understanding the ecological behaviour of plants in the field. The techniques used must provide the basis of evaluating the acquisition of resources (e.g. carbon, light, water, mineral nutrients) and the use of this resources for plant growth and development. The available laboratory equipment is either unsuited or much more difficult to operate under field than laboratory conditions. Therefore, it was necessary to adapt sophisticated instruments (e.g. microprocessors, infrared gas analyser, micrometeorology sensors, remote sensing) to characterise plan physiology and plant environment in the field (Pearcy *et al.*, 1989; Lassoie and Hinckley, 1991). Considerable advances have been reached with the new low-voltage high-precision electronic instruments recording variables under field conditions during a long period of time. Stable isotopes (e.g. ^{13}C, ^{18}O, ^{15}N, ^{2}H) techniques have also mean an important help in ecophysiological research, which have been matched by technical development in mass spectrometry and theoretical understanding of discrimination process (Griffiths *et al.*, 1999; Unkovich *et al.*, 2001).

It is probably more common for two or more factors to contribute simultaneously to the limitation of plant growth and development in the field, and the analysis of responses can also be complicated if limiting factors vary with time (Fitter and Hay, 2002; Valladares *et al.*, 2004c). An additional obstacle we could find if we try to study forest trees in the field due to its great size (it is difficult to access to all parts of the tree over and under the soil surface). Although forest research deals with several groups of plants (i.e.: trees, shrubs, grasses) tree species occupy an outstanding place among them. A knowledge of physiology of forest trees is useful for coping many practical problems. These include dealing with poor seed germination, low productivity, excess plant mortality, potential effects of increasing CO_2 concentration and global warming, environmental pollution, loss of biodiversity, plant competition and succession, and control of abscission of vegetative and reproductive structures (Kozlowski and Pallardy, 1997).

Trees are dominant species in stature but not different from other cormophytes in physiology. They have, however, some peculiarities (e.g. longevity, late ability for sexual reproduction) that do not make them the more suitable objects for research on the fundamental processes of plant physiology (Ziegler, 1997): they have to be handled under controlled conditions mostly in very young status and in a relative small number only; they are difficult to analyse due to the large amounts of substances (e.g. lignin, phenols, terpenoids, resins); one can hardly await manifestation of genetic markers in the subsequent generations; in important tree taxa (e.g. Pinaceae, Fagaceae, Cupressaceae) the chromosome number is relatively large and at present there are no attempts made to analyse a tree species genom in total. Although in the experiments in nursery or greenhouse conditions we can control some environment variables (temperature, soil humidity, nutrient supply, etc.), it is almost impossible to simulate natural conditions and the long-term effects of these factors is still unknown. So, it is necessary to increase experimental studies under natural conditions to separate the effect of each factor (Valladares *et al.*, 2004c).

Global change

The photochemical reduction of CO_2 via photosynthesis is the material and energetic origin of all higher life on earth. Thus a change in the CO_2 availability will most likely influence plant life and consequently the biosphere in multiple ways. We are currently witnessing an increase in atmospheric CO_2 concentration that is unprecedented in recent geologic times. Specifically, for the Mediterranean Basin, the UK Meteorological Office forecasts a decrease in spring and winter rainfalls, and an increase in mean annual temperature by 1,5 to 4,5 °C (1,4 to 5,8°C in 2100, according to the Intergovernmental Panel on Climate Change) at the same time to the duplicate of CO_2 concentration. Although during the next centuries physicochemical interactions between the oceans and the atmosphere will gradually equilibrate this striking deviation of atmospheric CO_2, in the near future (i.e. 100-200 years) the biosphere will have to cope with this «new diet» (Körner, 2003).

One of the highest priorities on the research agenda in scientific ecophysiology is to elucidate and understand the mechanisms associated with current and predicted atmospheric changes (Camarero *et al.*, 2004). Atmospheric CO_2 enrichment may also induce climate warming, with equally important implications for ecological processes (e.g. species adaptation and/or migrations of plant species to the North and to higher altitudes if they have a pathway to do that), and future climate will be characterised by combinations of temperature and precipitation that are not replicated in the modern landscape (Smith and Hinckley, 1995; Peñuelas *et al.*, 2004). Studies of plant-environments interactions implicitly must recognise the intimate coupling and attempt to consider reciprocal interactions (Bazzaz, 1996; Richardson, 1998). For example, the CO_2 assimilation rate will increase and plants will need less photosynthetic enzymes, plants will reduce their stomatal apertures and thereby lower water loss, without a simultaneous loss in photosynthetic yield and with the resulting influence on soil water content and nutrient availability (Körner, 2003). Additionally, harvesting schedules and silvicultural practices should be considered because they could affect the response of stands to climatic conditions (Rodá *et al.*, 1999; Sabaté *et al.*, 2002; Imbert *et al.*, 2004).

In terms of carbon sequestration into biomass, forest ecosystems play a significant role, as they form more than 80% of the global plant mass (Körner, 2003). Thus, in our studies we must consider not only growth rates of species but also the long-term residence time of carbon per unit of land area, because the life span of trees could be reduced without changing the mean pool size of biomass carbon in a given region (e.g. faster transitions between diameter classes and shorter rotations). Predictions of the effects of increasing CO_2 concentration on plants and ecosystems cannot be based on CO_2 responses alone, it has to be considered the availability of soil resources, the age of plants and stands, and species composition.

State of the art and future objectives

The global change, the pollution and the response of species to a changing environment are new problems added to the characteristics ones of the forest ecosystems in the Mediterranean Basin (drought, frost, degraded soils, plant regeneration, pests and diseases, perturbations, human activity, etc.). The traditional aspects of forest activity have been considered by ecophysiological approaches. Seedlings survival tests have been used for screening large number of plants for tolerance of drought, cold, heat, salt, shade, poor nutrient soils or other stresses. In addition, rapid screening tests have been successfully used in breeding for disease and pest resistance. Attributes for which screening can be carried out fall into four classes, i.e. morphological and anatomical, compositional, process rates and process control. The current studies and tendencies deal with comparative analysis of individuals, families, species, populations, etc., at different environmental constraints and their evolution patterns in time. The more numerous approaches have specially been in:

— Carbon assimilation: principally at leaf level, but tending to include other organs and subcellular attributes in order to predict the effect at whole-plant level.

— Water relations: water potential, relative water content, transpiration, stomatal aperture, stem and petiole hydraulic conductance, microoscillation of stem diameter, etc. Investigators try to elucidate the relationships between these parameters, and their effect on plant fitness and stress (drought, pathogen) resistance (Fig. 1).

— Tree architecture, morphology and anatomy of stems and leaves as interaction effects of heredity and environment.

— Biomass distribution (e.g. leaves, stems, roots, reproductive organs) and other compounds (mineral nutrients, starch, defences, etc.) allocation and concentration. Their short- and long-term variations, as well as their relationships with whole-plant growth and development and with the present and future environmental conditions of the habitats.

— The relationships between resources acquisition and maintenance cost at different time scales (e.g. stable isotopes techniques are useful tools for this interpretation) and environmental constraints.

Photosynthesis efficiency is one of the most actual and extended aspects of the ecophysiology research in diverse facets, being able to highlight:

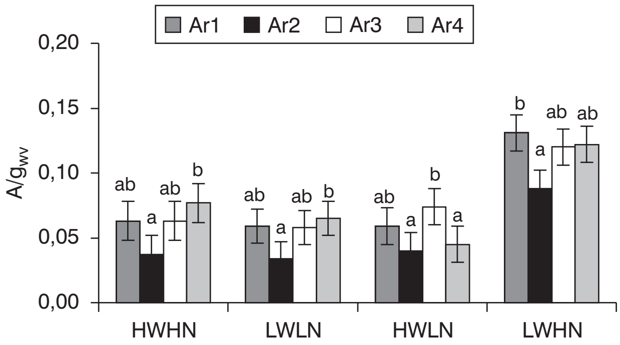

Figure 1. Mean value ± SE of intrinsic water use efficiency (A/g_{wv},$\mu molCO_2/mmolH_2O$) of four *Pinus pinaster* open families, Arenas de San Pedro provenance (Ar1, Ar2, Ar3, Ar4) growing during 62 days under four culture treatments (Hight or Low water —W— and nutrient —N— availability). Different letters indicate significant differences within each treatment. (Fernández *et al.*, New Forests, accepted for publication).

— Quantity of pigments in the leaves in relation to age, crown position (sun or shade) and global plant status.

— Chlorophyll status, a valuable tool to evaluate the photosynthetic system status of the plant under different environmental conditions (water stress, nutritional deficiencies, frost, pest, pollutants, etc.) (Fig. 2). In this line, in the future, the chlorophyll fluorescence evaluation can be combined with the rapid light curves (White and Critchley 1999, Rascher et at

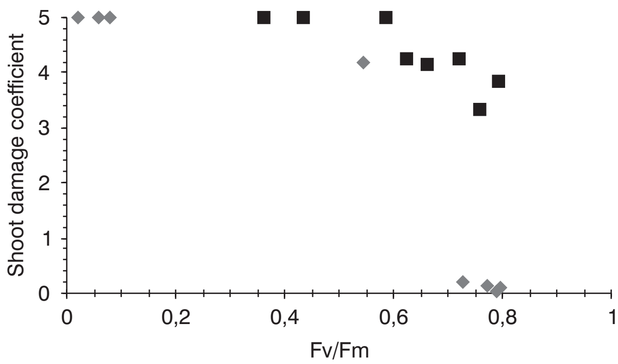

Figure 2. The relationship between chlorophyll fluorescence values (Fv/Fm) after 2 weeks and the shoot damage coefficient (after 2 months) for the drought resistance test (■, $y = -7.8577x^2 + 5.643x + 4.027$, $r^2 = 0.79$). And the relationship between Fv/Fm values (after 1 day) and shoot damage coefficient (after 2 months) for the freezing test (◆, $y = -18.307x^2 + 8.386x + 4.642$, $r^2 = 0.97$). Control and tested seedlings are included. Each point is the mean of 5 to 15 *Pinus halepensis* seedlings. (Fernández *et al.*, 2003).

the 2000) which represent the relationship between electron transport rate (ETR) and photosynthetically active photon flux density (PPFD).

— The photosynthetic response to irradiance of the species under different environments (light, water, temperature, etc.) in order to determine the characteristic points, as a possible tool to explain the shade-tolerance of species (Fig. 3). The information on the light available in Mediterranean ecosystems and its remarkable spatial and temporal heterogeneity is scant and the studies of plant responses to light are incomplete. Different individuals of a given species growing in the sun and in the shade exhibit contrasting morphologies and physiologies due to the phenotypic plasticity observed in all plants (Valladares *et al.*, 2004a; Fernández y Tapias, 2005).

— Study of photoprotectors cycles and their balance in the sprouting stage, water stress period or in winter vegetative stage in evergreen species, so much under high as low irradiances. The proportion of photoprotectors compounds (e.g. ascorbato, zeaxantina, violaxantina, luteina) may inform about some photosynthetic instability related to photo-oxidative damage and allow assessing plant status (Gamón *et al.*, 1997; Peñuelas and Llusia, 2002; Peñuelas *et al.,* 2004).

— The influence of CO_2 concentration has been very studied in other species and climates (Špunda *et al.*, 2005). Photosynthesis and transpiration, with the possible exception of respiration, are the physiological process by with plants sense directly, and respond to, the rising atmospheric partial pressure CO_2 (Long, 1999). All other changes in plants growing in elevated CO_2 are, therefore, an indirect response to changes in these leaf-level processes. Nevertheless, it has not been sufficiently approached for the main Mediterranean species.

— Balance in the light-absorption process, keeping in mind that a part is reflected and another is absorbed by different leaf tissues and elements before reaching the photosynthetic apparatus. The measures with spectroradiometer, covering the whole visible spectrum and part of the Ultraviolet and the Near Infrared ones, carried out in complete leaves or in split tissues are the way to approach this point and to follow the light attenuation process. These works permits to distinguish the apparent quantum efficiency of photosynthesis to true efficiency that consider only the absorbed radiation by leaf (Peñuelas *et al.*, 2004).

Another, and broadly studied, aspect in the forest ecosystems of the Mediterranean Basin is the availability of water and the use of this by the plants. Nevertheless, much of the work carried out to study plant responses to soil water status has been performed with single plants or even with detached plant parts in

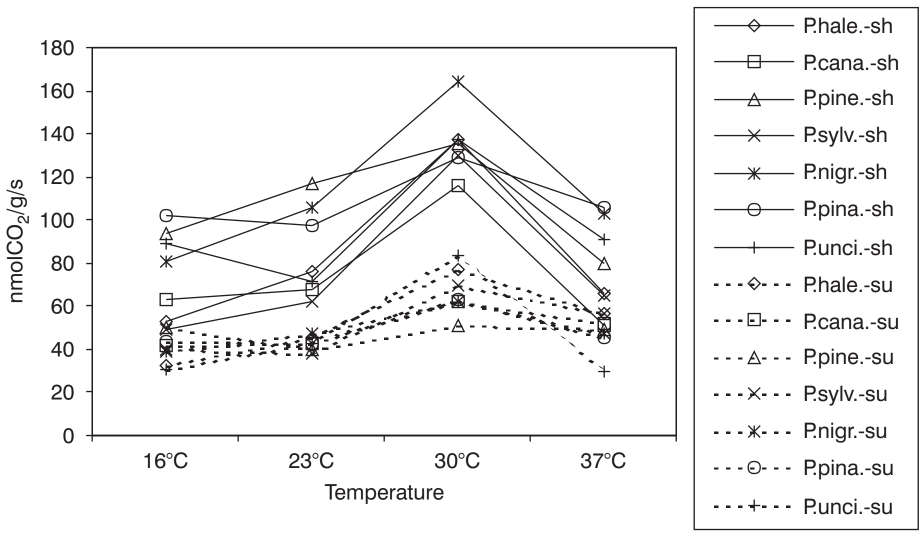

Figure 3. Mean values of maximum photosynthetic rate (nmolCO_2/g/s) at four temperatures of seven Spanish pines young seedlings cultivated under sunny (su) or shade (sh) conditions. Each point in the mean of 4 to 5 measurements (unpublished data).

the laboratory (Davies and Gowing, 1999; Fernández *et al.*, 1999; Pita and Pardos, 2001). To place these results properly in an ecological context more field studies must be considered (Gil *et al.*, 1999; Villar-Salvador *et al.*, 2004b; Pardos *et al.*, 2005). The evidence for a chemical signalling (e.g. Abscisic acid) in the regulation of the functioning of natural vegetation must be considered as well, because there have been comparatively few field-based studies of plants in communities. In spite of a wealth of physiological information in water relations (e.g. water potential, osmotic adjustment, elastic adjustment, hydraulic conductance, water movement, loss of water), the ecological significance of a plant's ability to respond to drying soil have been relatively little explored. It would appear that the control of water use via root-to-shoot communication would be a fundamentally conservative response, employing different strategies different species. Besides, studies of gas diffusion in the mesophyll (e.g. determination of the role of aquaporin in the O_2 and CO_2 diffusion under closed stomas conditions) can have certain relevance in forest species subjected to long water-stress periods.

Water relation parameters, as well as mineral nutrition, gas exchange, temperature and,something less, photoperiod have been used to evaluate plant quality of nursery forest seedlings in order to reduce possible plantation failures (Royo *et al.*, 2003; Fernández *et al.*, 2003; Puértolas *et al.*, 2003; Villar-Salvador *et al.*, 2004a). Linking readily measured morphological and physiological attributes to survival and growth will be essential for a proper evaluation. However, more research is needed about the effect of genetic factors, nursery practices and environmental conditions on survival and growth in forest plantations for Mediterranean forest tree species.

The studies of mineral nutrition take up another important chapter. In general, they assume the complexity of a global evaluation of the content of a wide range of elements that plants extracts of soil and uses in its metabolism (availability and absorption, interactions, translocation, transport across membranes). In most of the cases, the works evaluates these contents globally and they carried out comparative studies among more and less fertile soils (Oliet et al., 2004). They would be desirable a higher number of studies focused in individual elements, in interaction with other limiting factors for the plants (Villar-Salvador *et al.*, 2004a) since many of our species are not sufficiently studied even in laboratory. A lack of integration is observed some times between forest cycle studies and those of nutrition. The ecologists of soils study how vegetation affects to the soil and the ecophysiologist the effect of water and nutrients availability on plants, without keeping in mind the reciprocal relationships. The problem of climatic change is propitiating global studies but they would be desirable higher integration that allows us to understand the distribution of certain groups of species associated to very low fertility soil, abundant in the Mediterranean regions, and the application to forest management (Zavala *et al.*, 2004).

Acquire special relevance the knowledge of the interaction plant / symbiotic microorganisms such as mycorrhizas and some other related with the nitrogen acquisition. Valuables contributions have been carried out on synthesis and effect of mycorrhiza in laboratory and nursery (Parladé *et al.*, 2004; Buscot and Herrmann, 2004) but the state of knowledge of transfer to field is insufficient for most species, except for those that have a commercial value as the truffles and some other edible. It should be deepened in mycorrhiza autoecology and in functional aspects as the role that they carry out in the water and nutrient capture, as well as in the nitrogen acquisition through certain bacteria. The mechanisms of regulation of the formation of nodules have been approached for agronomic species and it would be interesting their broadening other forest/pasture species.

Roots perform two primary functions, anchorage and resource acquisition. Other root functions such as synthesis and storage are considered secondary. Anchorage depends largely on proprieties of the root nearest the stem base and is most significant as a root function install plants, notably trees (Fitter, 1999; Sudmeyer *et al.*, 2004). The ability to acquire resources from soil is a fundamental requirement for all plants, and is determined by four features of root systems: their architecture, their interactions with microorganisms, their ability to influence the rhizosphere by exudation, and their systems for transporting material across membranes. Only the last two of these are instantly recognisable as physiological ecology, but the others are certainly as important. Using techniques utilised in the study of the transport of ions across cell membranes is now possible to undertake studies to measure the molecular plasticity of uptake systems. Molecular biology also provides new tools to investigate another of the major components of root function, namely the development of roots and the consequent architecture of root systems.

Pest and disease have a great repercussion in plant health and production. Ecophysiologycal contributions are interesting in three aspects:

— To describe the infection/attacks process in terms of plant water status (Fig. 4), gas exchange parameters and secretion of defence substances (e.g. phenols, tannins), allowing to improve the knowledge of the process and the relationships with plant status(Luque *et al.*, 1999; Sánchez *et al.*, 2004).

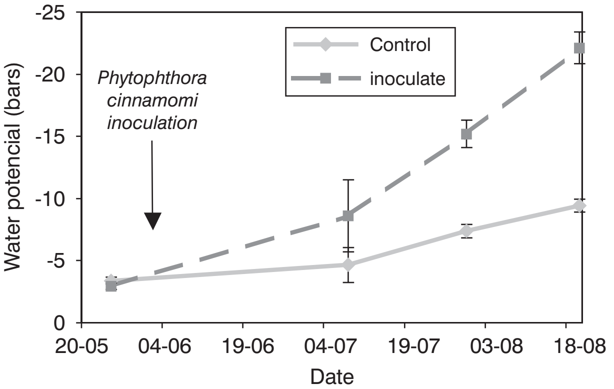

Figure 4. Water potential in holm oak (*Quercus ilex*) inoculated and not inoculated seedlings with *Phytophthora cinnamomi* inoculation. (Tapias *et al.*, 2005b)

— Monitoring ecophysiological variables before and during the attack (Fig. 4), it can detect more susceptible / tolerant situations. In this sense, they are specially relevant those related with the entrance way of pathogen like the water status of different stem tissues (Fig. 5) for borer insects, the size and hydraulic conductivity of vessels xylem (for vascular fungus) and the content of protectors compounds (phenols and tannins).

— Comparative studies of the two previous aspects among genotypes can be very useful to show eventual genetic differences that can be use in breeding programs (Fernández *et al.*, 2004).

In the integrated pest management context, it would be interesting to assess the host/parasite (insect) relationships, especially the mechanisms that allow to parasite locate adequate host (Picket *et al.* 1998). The

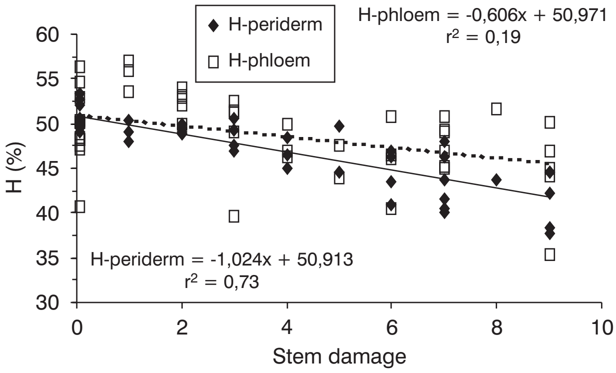

Figure 5. Relationships between «stem damage» with H-periderm (black rhombuses, continuous line) and H-phloem (open squares, dashed line) in four clones of eight years-old *Eucalyptus globulus*. Stem damage: 0 = very affected tree by *Phoracantha semipunctata*, 10 = no affected tree. (Fernández *et al.*, 2004).

presence of certain volatiles compounds or the relative proportions among them can point out species or individuals more appropriate for insect feeding or for larvae survival. The current techniques of study, take advantage of the electric properties of diverse organs of insect, overalls antennas (electrophysiolgy) to quantify the magnitude of perception of certain compound (monoterpenes, monoterpenic alcoholic, triterpenes, GLV, phenols, etc.). Compounds emissions depend of species, weather and plant status. Multidisciplinary works with biochemical, ecophysiological and ethological dimension have started to approach agronomic plagues and some forest ones (Sánchez-Osorio, 2005) but they even have a wide perspectives in the future.

In the field of parametric autoecology it has become an important contribution for the managing and planning of existent forests and new plantations of the main species (Pinaceae and Fagaceae) (Gandullo and Sánchez Palomares, 1994). The advantage of this methodology is that results can incorporate easily to computer software that provides an estimation of suitability of site for certain species. The limitations are imposed by the precision and resolution of some variables, as the coming from an insufficient meteorological station net. In a future, would be contemplated secondary species, the genetic variability of species at several levels (provenances, population) and the use of information coming from remote sensors integrated in geographical information systems.

Disturbances, with the current focus of the ecology, integrated in the dynamics and in the essential processes of the ecosystems, have been broadly approached in studies with an ecological dimension more than ecophysiological. The main strategies of survival of species are known (seeds banks, vegetative banks, protection from the adverse effects of disturbance agent, Table 1 for *Pinus*) but the degree of knowledge is not enough at population level. Neither they are completely clear the internal mechanisms that allow these strategies (e.g. longevity, starch and defences compound accumulation for resprouting, fruit retention and dehiscence, large viability of some seeds, early fructification and reproductive effort). Fire has been the disturbance more studied as corresponds for its preponderant role in the Mediterranean ecosystems (Velez 2000; Ferrandis *et al.*, 2001; Tapias *et al.,* 2001, 2004; Martínez-Sánchez *et al.*, 2003; Climent *et al.,* 2004; Madrigal *et al.*, 2005).

Some other studies of interest but less extended in Mediterranean forest research could be:

— The role of hormones in the regulation of growth and development of a wide range of plant species have been studied. There is, however, comparatively little information on the mechanism of action of hormones in any of those processes.

— Combined effect of shade and drought and the relationship of water stress and the mitochondrial respiration.

— Evaluation of oxidative status at cellular level as indicator of plant status under various environmental stresses and as balance of the biochemical and energetic stability of photosynthetic apparatus (problematic in situations of lack of CO_2 diffusion for closing of stomas for drought).

— The pollutants, both in soil and in atmosphere, among them the tropospheric ozone.

— The ultraviolet radiation.

Predicting the future response of plants and ecosystems

Because biological systems are so complex, one can rarely achieve complete mathematical descriptions of their behaviour. It is necessary, therefore, to make simplifying assumptions about the system behaviour and concerning the relevant components for inclusion in any study. This selection of variables is perhaps the most difficult task in the development of any mathematical model (Jones, 1992). Another problem, as ever, is that it is difficult to scale up from processes investigated at a small scale

Table 1. Life-history traits related to disturbances in the seven Spanish pines. (Tapias *et al*., 2004). (^ Summary data for Spanish pines (Gandullo and Sánchez-Palomares 1994). Drought: periods of relative drought (months with rainfall, in mm < mean monthly temperature, in 2x°C). % of burnt area: area burnt during 1968-1990/total area of species (%)

	Pinus						
	uncinata	**sylvestris**	**nigra**	**pinaster**	**pinea**	**halepensis**	**canariensis**
Mean annual temperature (°C) ^	5.5	8.5	11.0	11.4	14.3	13.8	14.5
Annual rainfall (mm)^	1000	919	882	618	594	503	519
Drought (months)^	0.6	0.8	2.1	2.6	4.9	3.2	5.1
% of burnt area during 1968-1990 (DGCONA 1994)	0.6	24.1	6.0	38.4	10.2	34.1	38.0
Bark thickness (mm, Martínez-Millan *et al.,* 1993	11	24	31	35	33	30	35
Sprouting capability	no	no	no	no	no	no	yes
Seed weight/Wing length	0,75	0,76	1,14	1,70	222,00	1,06	6,82
Age of first flowering (years)	>18	10-20	15-20	4-10	10-20	4-8	15-20
Serotinous cones (%)	0	0	0	2-82	0	40-80	0-60
Cone persistence in canopy (years)	1-3	1-3	1-3	2-40	1-3	5-20	2-10

(e.g. cell or leaf) and make predictions at higher scales (e.g. whole plant, plant population and beyond). Nowadays, the design and analysis of multifactorial experiments with plants are, however, possible and their role in developing predictive models will increase rapidly, but (Bazzaz, 1996):

— Predictions of the structure of specifically short-lived communities are possible if the environment, especially soil conditions and temperature, are known.

— Features of behaviour under specific conditions that are predictive for one species may not be equally predictive for other species in the same system.

— In order to the relative degree of competitive superiority to be predictive, the environmental conditions under which competitive interactions take place must be specified.

— Especially for long-term predictions, we must consider the genetic structure of the populations and its significant role in community dynamics.

— There is no reason to suspect that predictions based on physiological, demographic, and other life history features cannot be made about the structure of more complex communities, such as late-successional ecosystems.

Traditionally, physiological ecology of plants has developed two approaches: the *in vivo*, in which physiological processes were studied at the whole-plant or organ level, in field and laboratory; and the *in vitro*, in which cellular and subcellular processes were dissected in order to understand the mechanisms underlying physiological responses. Nowadays it is possible to include a third approach, the *in silico*, in which computers simulation and graphics modelling provide tools for the study of past and future plants and processes (Stewart and Schmidt, 1999).

Quantitative information on understory light is crucial to understand many aspects of forest ecology and dynamics. However, only scant information is available for Mediterranean shrublands and forests despite its increasing importance with land abandonment in Southern Europe. The study of light heterogeneity within crowns and in woody ecosystems (specially for abandoned Mediterranean ecosystems) together with the predicted global dimming will give us useful information about predictions of whole-plant photosynthesis and ecosystem dynamic (Pearcy and Valladares, 1999; Valladares 2004). We do not know enough information to make predictions of the responses of Mediterranean forests to dim in conjunction with increased temperatures and droughts. This is essential for understanding plant performance in temperate-Mediterranean forests, emphasising the need for detailed studies of the adaptive value of phenotypic plasticity in response to co-occurring stresses (Chambel *et al.*, 2004; Sánchez-Gómez *et al.*, 2004). Since management of forests is to a large extent the management of light, the combination of results and predictions from studies on forest plant ecophysiology, light heterogeneity and dynamics, and global change represents a meeting point for ecology and management (Valladares, 2004).

Gap models have been applied to a wide range of ecosystems, but mainly in temperate and boreal forests ecosystems. However, there is no gap model that can be appropriately used for predicting the long-term dynamics of Mediterranean ecosystems. Any model for Mediterranean Basin ecosystem dynamics should take into account different life forms (trees, shrubs, scrubs, grasses), resprouting ability, fire-germination interactions, underground structures and post-fire conditions, and anthropogenic influence. Current trends in modelling include more physiological-based approaches, however the lack of data for Mediterranean species and the importance of disturbance processes may require other approaches, such as the based on functional groups (Pausas, 1999).

In the coming decades, interactions between photosynthesis, nutrition and water relations must be understood. The link between molecular biology and ecology will be strengthened and, by using molecular tools, much progress can be made beyond simply correlative evidence. Species-specific interactions in ecosystem function will remain a major challenge (Schulze and Caldwell, 1995). It is necessary more experimental evidence on plant response at high CO_2 under a range of a field conditions. And the challenges of scaling up from plants to canopies, landscapes, and even a global level will drive many efforts in modelling and innovative approaches of these models.

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