

Ecophysiology, a meeting point between function and management of forest ecosystems

J. A. Pardos

E.T.S. de Ingenieros de Montes. UPM. Ciudad Universitaria s/n. 28040 Madrid

Abstract

The paper begins with a brief history of botany leading to the first descriptions on plant life phenomena. It then moves on to plant physiology as a science with a proper identity in the XVIII century. The works by Duhamel du Monceau and the German forester Robert Hartig are pointed out as landmarks on the way to the future ecophysiology of trees. The Symposium «The Physiology of Forest Trees», held in 1957 at the Harvard Forest, is also remarked as a step forward in the incorporation of forest trees as experimental material and the application of modern techniques in Plant Physiology. Thereafter, some topics in Ecophysiology, relevant for process-based forest management, are briefly reviewed. Tree canopy as a radiation collector and primary production factory of forest stands, carbon balance and allocation in trees, water and mineral nutrition, and modelling are the matters dealt with.

Key words: tree physiology, ecophysiological parameters, forest ecosystem management.

Resumen

La Ecofisiología, nexo de unión entre el funcionamiento y la gestión de los ecosistemas forestales

Se hace un sucinto recorrido por la Botánica en su andadura a lo largo de los siglos para abocar a las primeras observaciones de fenómenos vitales de las plantas, que confluirán en la configuración con entidad propia de la Fisiología Vegetal en el siglo XVIII. Se destaca, por su específica referencia a los árboles, la obra de Duhamel de Monceau y, de manera especial, la del profesor de selvicultura Roberto Hartig, cuyas agudas descripciones del comportamiento funcional en monte de diversos especímenes forestales pueden enmarcarse en los prolegómenos de lo que mas de cien años más tarde constituirá la ecofisiología forestal. Se destaca, a continuación, el Simposio «The Physiology of Forest Trees» celebrado en 1957 en «Harvard Forest», que constituyó un paso importante en la incorporación de los árboles forestales como material experimental y aplicación de las técnicas modernas de fisiología vegetal a los mismos. Finalmente, se pasa revista a algunos aspectos actuales de Ecofisiología, destacando conceptos y aspectos de la misma y su proyección en la gestión de los ecosistemas forestales. Se subraya la especial significación del dosel arbóreo, receptor de la radiación y maquinaria primaria de la producción del rodal forestal, el balance de carbono y su reparto en los árboles, el papel del agua y la nutrición mineral y los modelos de estimación de la productividad forestal basados en procesos fisiológicos.

Palabras clave: fisiología, parámetros ecofisiológicos, gestión de ecosistema forestal.

In the beginning

La capacidad para comprender el mundo
depende del conocimiento acumulado
(Jorge Wagensberg, 2004)

Plant study is as old as humanity. Although Aristotle is considered the founder of Natural Sciences teaching,

it is his disciple Theophrastus (born c.370 B.C.) who transmitted two treatises about botany, «A natural history of plants» and «On the Causes of Plants». He did the first classification of plants in trees, bushes, shrubs and herbs and he wrote abundant observations about the parts of the plants (he distinguished between the external parts of plants, or organs, and the internal parts, or tissues); their propagation, especially of trees, devoting Book 3 to «Wild Trees». The detailed description on the peculiarity of some species «*which make three fresh starts in growth and produce three*

* Corresponding author: josealberto.pardos@upm.es
Received: 30-06-05; Accepted: 20-08-05.

separate sets of buds» (what we call today the phenomenon multimodality) and the observations on the role played in seed germination by the environmental conditions existing in their maturation process are two examples of the enormous contributions that the Greek philosopher made to botany (Hort, 1968).

Agriculture and pharmacology were the great promoters of botany in the classical Science. In Pliny the Elder's Natural History, agriculture and arboriculture have special relevance in the chapter devoted to botany (Beaujeu, 1988); something similar occurred in Arabic Science, which used Greek sources from agriculture, the *Geoponics*. In the early stages of medicine, specific attention was given to vegetal poisons.

The twelfth century was the period of the great translations. Spain became the great centre of culture, greatly enriched by Arabic sources. The first Universities and Encyclopaedias included botanical knowledge. In «*De naturis rerum*» by Tomás de Cantimpré and in «*De vegetabilibus et plantis*» by Albertus Magnus there is mention of the influence of light in plant growth and of the position of cotyledons inside the embryo. These may be included among the first steps in the future plant physiology. Practical advice on the fixation of sandy dunes with trees is also given in these works (Beaujouan, 1988).

The fifteenth and sixteenth centuries are the period of the exploration of nature by botanists, of species identification, herbarium-making and the origin of systematic botany. The taxonomic importance of the reproductive structures began to be recognised and developments made towards the future Linnaean classification.

In the Renaissance, Leonardo da Vinci made acute examinations of tree architecture, precursors to the study of hydraulic tree behaviour. In his «*De plantis libri*», Cesalpinus reduced to three (nutrition, growth and reproduction) the functional processes of plants and he conferred to the shoot and the root similar functions to those assigned to animals upside down (Davy de Virville & Leroy, 1988a).

In 1620, the Englishman Francis Bacon in his «*Novum organum*» developed the scientific method as an attempt to correct the deficiencies of classical Aristotelian theory, giving a procedure to make gradual and progressive inductions and a method for exclusion. He also advocated the institutionalization of science at

many activity levels, with participation of a great number of people working together through several generations (Encyclopaedia Britannica, 1979).

Structure and function acquire a proper entity in the frame of Botany

In the eighteenth century, the history of botany is dominated by the figure of Linnaeus, with whom Jussieu and Adamson share the glory of establishing the basis of natural classification. However, progress in techniques (microscope) and methodology (quantitative and experimental methods) led to new approaches. The studies on structure and function of plants and their relationship with the environment began to have proper entity. An Englishman, Robert Hooke, made the first description of a cellular tissue (a cork sample) seen under the microscope; the Dutchman Leeuwenhoek described different kinds of xylem vessels, while Grew marked the fundamentals of plant anatomy. At the same time, plant physiology took its first steps developing out of physics. The Frenchman Mariotte dealt with the rising of sap, mineral nutrition and development; the Italian Malpighi studied the upward and downward movement of sap; the German Ray tried to interpret the movements in Leguminosae, in terms of the mechanical tension of tissues, variable with temperature; plant sexuality was studied by Camerarius, setting the bases for the general theory of sexuality as a function common to plants and animals; Hales compared the rising of sap with that of water through capillaries and showed that sap was transported in vessels; Joseph Priestley discovered that green plants exposed to the sun's radiation vivified the atmosphere made foul by the air coming from them, that is, from their dark respiration; Ingenhousz discovered the chlorophyll assimilation; even Linnaeus made some experiments on «sleep movements» in plants (Davy de Virville & Leroy, 1988b).

Duhamel du Monceau paid special attention to trees. In the fourth and fifth books of his «*Physica de los árboles*, en la qual se trata de la Anatomía de las Plantas y de la Economía Vegetal, o sea Introducción al Tratado General de Bosques y Montes» (Spanish translation by Dr Casimiro Ortega, the first full professor in the Royal Botanic Garden in Madrid) the author raised some physiological and ecophysiological questions. He dealt with the light phototropic role and plant movements ...

«por acción del sol y de las lluvias, con cierta relación o semejanza con los movimientos de los músculos de los animales»... *«se insta a los Physicos a indagar si alguna porción de la tierra penetra hasta el cuerpo de las plantas y si todas las especies se alimentan de un mismo jugo nutricio o sabia»*. The author supported the link between sap movement and transpiration, but the question about sap movement still remained: *«quando lloran las plantas en tiempos en que carecen de hojas»*, suggesting *«practicar inyecciones»* in order to better examine the phenomenon. He made a reference to plant illnesses *«que proceden de un exceso de sequedad o humedad, heladas o calidad depravada del terreno, y también los insectos»* (Duhamel du Monceau, traducción española del Dr Ortega, 1722).

Plant physiology, a botanical science

The nineteenth century saw the birth of plant physiology as a science. The names of Liebig, de Saussure and Pfeffer, among others, will remain linked to the bases of plant nutrition science. The nitrogen cycle and atmospheric nitrogen fixation by bacteria (Boussingault and Winogradsky among others); the discovery of osmosis, the establishment of its laws and the development of measurement methods (Pfeffer, de Vries, Van't Hoff, Sachs) are keys to the furthering of knowledge about the water economy of plants (absorption, circulation, transpiration), later developed by Mohl, Dixon and Strassburger among others. Knowledge of photosynthesis and carbon assimilation was also greatly stimulated in this century: to Sachs is due the classic equation to express glucose formation, while to Blackman is due the distinction between light and dark phases. Both discoveries were better fixed years later by other scientists (Leroy, 1988a).

In the first third of the twentieth century the study of coleoptiles response to light, already observed by Darwin, led to the discovery of auxin and its role in growth (Went and Thimann, among others). New knowledge on other phytohormones, growth factors and synthesis compounds as well as other topics concerning growth and development (tropisms, nastic movements, photoperiodicity, flowering and fructification) were incorporated in subsequent decades. The work by Warburg on cellular metabolism, the oxidation phosphorylation processes and the Krebs cycle were important milestones in the understanding of plant

respiration. Radioisotopes were used as tracers and chromatographic techniques permitted the elucidation of the mechanisms involved in photosynthesis. Water photolysis (Van Niel), the role of chloroplasts (Hill), ATP production and the reduction of carbon dioxide (Arnon), glucose biosynthesis (the Calvin cycle) were key steps in the knowledge of the photosynthetic and carbon assimilation processes (Leroy, 1988b). The application of biochemical and molecular genetic techniques to research on signal perception and transduction (the phytochromes deserve a especial mention) has resulted in major advances in plant physiology.

The use of highly purified mineral solutions helped to further knowledge of plant mineral nutrition, while electrophysiological techniques improved knowledge of ionic transport through membranes. Their structure is better understood applying cryofracture and scanning electronic microscopy. The concepts and measurements of water potential (Boyer, 1995) and hydraulic conductivity (Tyree & Zimmermann, 2002) opened new ways to the study of absorption, movement and water loss in plants. The analogy between growth and fluid dynamics facilitated the application of mathematical methods from classical analysis to plant growth dynamics, providing useful computer graphic growth models (Raz, 1988).

The knowledge of changes in compounds (metabolism) and forms (growth and development) studied in plant physiology had a biochemical basis, hence the strong inter-connection between physiology and biochemistry, whose frontiers are not always easily delimited. The impact of molecular biology and genetics on the study of the vegetal kingdom contributed to this (Buchanan *et al.*, 2000).

The functional study of plant's behaviour in their environment linked ecology and physiology and a new discipline emerged, the ecophysiology. Early research was based on field observations and the application of rudimentary techniques while in the last half century work, using portable field measurement equipment, became more complex and precise (Lassoie & Hinckley, 1991). New greenhouses and growth chambers allowed different levels of environmental control. All this, with the help of accurate laboratory analytical techniques (Reigosa, 2001), provided information to improve understanding of physiological, biochemical and molecular plant attributes at an ecophysiological level (Lange *et al.*, 1981, 1982, 1983).

Trees and forest at the beginning of the twentieth century, an ecophysiological perspective

In the compendium «Anatomía y Fisiología de las Plantas y principalmente de los Árboles Forestales», Spanish version by Castellarnau (1906) of the book by the forestry professor Dr Hartig, there is a last part devoted to physiological themes, which is divided into four chapters: the action of environmental factors, nutrition, growth and reproduction. The approach given to the text is descriptive. The information does not seem to involve any complex experimental measurements since no detailed figures nor statistical inferences are shown, but the text is the product of a host of specific and insightful observations (with actual application) aimed at explaining order phenomena and behaviour of trees and forest.

Its ecophysiological implications and conclusions about the effect of thinning in the forest can be exemplified as follows: «... *que al facilitar la mayor penetración del sol y aumentar la temperatura, provocan se anticipe la actividad cambial de los troncos en primavera respecto a bosquetes no aclarados; y, si se trata de especies de ritidoma delgado, conducen a la producción de quemaduras por acción directa de los rayos solares*». The following paragraph also deserves special attention: «... *el efecto, llegada la primavera, de la menor temperatura en el suelo, que en los pies añosos provoca un retraso en el crecimiento en grosor de las raíces respecto al tronco; o la influencia de la hojarasca que, en invierno, al impedir la penetración del hielo en el suelo, protege las raíces de las plántulas, mientras que en primavera impide su rápido calentamiento y evita una brotación demasiado temprana*». Professor Hartig uses the concepts of osmosis and turgor to deal with trunk frost crack formation, wilting symptoms caused by dehydration and turgor recuperation, as well as (among other matters) the process of sudden leaf drop in the autumn following the early night frosts. The different sensitivity to extreme temperatures in saplings and mature trees and the use of plants as a thermometer (actual thermal time) to explain and predict tree phenology (he shows himself critical and elusive on this subject) are some phenomena that he discusses in the light of the behaviour of several forest tree species.

The effects of light on growth, tree crown shape and size and leaf histology, and their interaction with

temperature in thinned and unthinned stands; the effects of pruning, the distinction between sun- and shade-species, are dealt with by Hartig, who predicts with great intuition many of the experimental results obtained today with the modern tools now available to ecophysiology.

In the chapter devoted to evaporation (transpiration), the German forester warns of the harmful effect of exposing roots to air at transplanting and the benefits of using balled plants. He emphasizes the complexity of leaf transpiration control and its dependence on many external and internal factors, which, even today with the battery of available instruments, poses many questions.

The chapter devoted to water absorption, movement, its incorporation to tissues and evaporation occupies many pages. The loss of sapwood transport functionality in the old rings is analyzed, while the loss of water and substitution by air are suggested as causes of duraminization. The role of osmosis in water absorption and the existence of root pressure are noted. Simple field experiments led to reasoned inferences about the effects of species, age, vegetative state and site, but this is still a long way from water potential and other concepts essential to the present knowledge of water relations in trees. Soil fertility, nutrient absorption and roles, emphasizing nitrogen as the principal limiting growth factor, are also dealt with. The term Hartig net, of hyphae surrounding cortex cells in mycorrhized roots, was named after the German professor.

Observations on phloem function (the term *liber* is attributed to Hartig), biomass allocation within trees, growth ring structure in conifers and broadleaves, seed formation, germination and ecological implications complete the abundant information in the book, the reading of which is recommendable for modern tree ecophysilologists.

The 1957 Symposium at the Harvard Forest: a decisive step forward in Forest Tree Physiology

«*Few plant physiologists use trees for experimental material, and few professional foresters study plant physiology*». With this affirmation begins the Preface written by Kenneth V. Thimann to present the contributions made to the First International Symposium on Forest Tree Physiology that took place

on April 1957 at the Harvard Forest, Cambridge, Massachusetts. «*We should know much more than we now do about trees because their economic importance and botanical interest*» is said in the Introduction of the Proceedings. Its author, Mangelsdorf, goes on «*... the anatomy of trees has been studied for many years... but the physiology, which is concerned with their function, is a neglected subject partly because plant physiologists usually prefer to work with smaller plants which are more easily manipulated*». Half a century later, the names of the participants in the Symposium, such as Greenidge, Gibbs, Huber, Kozlowski, Leyton, Scholander, Thimann, Wareing and Zimmermann among others, are a reference in tree physiology, some of them specifically linked to ecophysiology and even today profusely cited. Actually, many more names shape a large list of prestigious and well known tree physiologists over the world, mainly in the occidental countries, who study how trees work and how their physiological processes, heredity and environment depending, determine growth and development, and at the end, they should guide silvicultural practices and forest management.

Trends in moisture uptake and patterns of the water-conducting system; the seasonal water content pattern related to taxons; water radial gradients in sapwood; the influence of using rings out of the transpiring trees (role of the tension) in the measurements of water loss; the explanation of the mechanism which produces surprising sap pressures and flows in maple stems; the effect of dew on the survival of *Pinus ponderosa* at the wilting point of the sunflower; photosynthesis of trees as affected by their environment; the influence of location on growth-nutrient relations and the use of radioactive isotopes instead of dyes injected into the tree to the research on nutrient translocation; the breaking of bud dormancy by low temperatures and root development in spring; together with some other topics (i.e. phloem transport, photo- and termoperiodism, reproduction) all of them were topics presented and deeply and hardly discussed in the Symposium by tree physiologists from USA, UK, Canada, Germany and New Zealand (Thimann, 1958).

Tree Physiology and Genomics

A great number of scientific contributions carried out on a wide range of functional aspects of forest trees

show the long way tree physiology has been running from the 1957 Symposium at the Harvard Forest. Further research should aim in understanding how structural and regulatory genes and gene products (i.e. proteomics) determine how cells function and how they form organisms, and how those organisms respond (i.e. adaptation) to their environment (Wulsschleger *et al.*, 2002). On the other hand, genome-wide research (i.e. QTLs analysis, functional expression of genes in the development of trees) can shed light on poorly understood basic physiological processes as well as lead to shorten the time required for tree improvement, specially concerning woody species used in forest plantations and their adaptation to abiotic stresses (pollution, climatic change).

Forest Ecosystems, Ecophysiology and Silviculture

A community of species occupying a site and interacting between them form an ecosystem. Ecosystems may be considered as levels of organization in nature studied in terms of structure (components quantification) and function (casual relations, type and quantity of matter and energy determining the structural model) (Ramos, 1987).

In forest ecosystems trees are the dominant vegetation, conditioning primarily the site where other plants live. Trees are the plants that have achieved the highest degree of the control of their environment, creating spatial heterogeneity in terms of fertility and other micro-environmental factors (Terradas, 2001). The scientific and practical management of tree stands is a responsibility of forestry. However, the forest ecosystem has a wider meaning when we refer to the Spanish word «monte», which is a natural space with any type of vegetation but with no agricultural use. The structure of the different forest ecosystems will be determined by bioclimatic factors and the main species composition.

Ecophysiology has been developed over the last hundred years, from its origins as descriptive phytogeography to an independent functional ecology of plants and animals (Lange *et al.*, 1981; Lambers *et al.*, 1998). Physiology enables the making of quantitative predictions of plant behaviour. At its interphase with ecology, and using the information obtained from genetics, ecophysiology studies the responses of plants to the environment and the causal

analysis of physiological mechanisms involved from organs (the leaf being the most representative) to individual grading to community and ecosystem (Fitter & Hay, 2002).

Understanding the structure and function of forest ecosystems is necessary for a sustainable conservation and use, as well as for forest preservation. The ecophysiological data are a useful tool in the hands of forest engineers for the evaluation, and to some extent the prediction, of responses to silvicultural practices. Because ecophysiology and ecosystems behaviour show complementary aspects, their interaction will be also productive in clarifying the complex responses of forest ecosystems to climatic change (Buchmann, 2002). Moreover, it will give guidelines for high seedlings quality production and forestation.

The forest canopy

The forest canopy regulates the exchange of energy, carbon and water between the ecosystem and the atmosphere. Understanding canopy processes is important for modelling forest production and determining how forests will respond to global change (Ryan, 2002). Forest productivity can be studied and predicted through the assessment of physiological processes, the development of models for the photosynthetic active radiation (Par) interception and the simulation of tree canopy photosynthesis (Landsberg & Gower, 1997). Patterns of absorption and penetration of radiation in several tree canopies, taking into account the proportion of diffuse to total light and the foliage exposed to direct solar radiation and shade, have been developed. When the only information available about canopy architecture includes height, stand density and leaf area index (Lai, leaf area to crown orthogonal projection on the soil), it is useful to express the decrease in radiation through the canopy by the Beer law (Larcher, 1995).

Canopy characteristics are under a strong genetic control at tree level, but they are also influenced by provenance (mainly latitude) and stand structure (site depending) (Zobel & Talbert, 1984). Two parameters, the specific leaf area (Sla, leaf area to leaf dry weight) and Lai, serve to characterize the canopy and monitor its temporal evolution in a stand. Sla is well correlated with ecophysiological factors, such as nutrient availability, atmospheric humidity and leaf longevity.

Sla facilitates the calculation of total foliar area, applying sapwood to leaf dry weight equations and to model processes at stand level. Lai facilitates the characterization of foliage distribution and the disposition defining leaf area density profiles per crown volume unity. This index shows different patterns in conifers, deciduous and evergreen broadleaf species, according to stand density and diameter class distribution (Landsberg & Gower, 1997).

Canopy closure, also dependent on the initial stand density, is a silvicultural reference in its evolution. It leads to the balance between the seasonal loss and renewal of leaves, which results in a relatively small variation in stand radiation interception and the LAI value (Waring, 1983). The so called « $-3/2$ power law» for self-thinning expresses the limitation imposed in monospecific stands by density (trees per ha) to maximum size (trunk biomass) reached by the trees, of whatever species and age and defines an isometric model (Drew & Flewelling, 1977). The allometric models that relate the self-thinning exponent with morphological traits, which are different among species, are a great step forward (Pittman & Turnblom, 2003). The «dehesas o montados» are an exception because other agroforestry factors prevail in the ecosystem and canopy closure is neither achieved nor sought (San Miguel, 1994).

The microclimatic parameters (temperature, vapour pressure, wind speed) are basic for calculations of radiation interception and evapotranspiration. On the other hand, the stand microclimate is also influenced by silvicultural treatments. Thinnings, in particular reproductive fellings, modify the stand structure and change the energy and water balance (Aussenac, 2000) with important effects on tree regeneration in monospecific stands and also in broadleaved species planted in mature conifer plantations to create mixed stands. Air pollution has also dramatic negative effects on the forest canopies. The physiological responses of trees to pollutants and to climate change are complex and only partially understood, Foresters thus require a solid scientific foundation for the development of a strategy to deal with forest ecosystems (Karnosky *et al.*, 2003).

Water relations

Physiological processes govern tree growth and depend on water availability and other soil properties; it

is thus important to understand the physical and ecological agents that affect forest ecosystems.

The hydrological balance of the stand, watershed or region they occupy influences tree growth and survival. Such balance depends on both meteorological and ecological factors and on the tree population. From that follows the strong connection between tree water relationships and forest hydrology, and the importance that forest canopy has on the hydraulic yield in a watershed (Bormann & Likens, 1979). In the same way, forest management (silvicultural regimes, fire breaks, felling, logging, skidding tracks) affects water balance and water content, soil erosion and compaction, and therefore exerts its influence on tree growth and, also, on water yield and quality in the watershed (Perry, 1994).

Transpiration is a component of the water balance. Transpiration rate is a function of stomatal conductance, which is a physiological parameter under plant control that responds to microclimatic factors and soil humidity (Taiz & Zeiger, 1998). Stomatal conductance as well as that of other water and gas exchange parameters are useful tools to compare different stands, species performance in mixed populations (Aranda *et al.*, 2000), and also in the study of provenances (Fernández *et al.*, 1999) and clonally selection for planting (Pita *et al.*, 2003).

The decrease in stomatal conductance, the hydraulic restrictions in water conductivity and the hormonal signals (ABA) in the soil-plant-atmosphere continuum may predict the effects of soil water shortage on growth in the longer term and on foliage maintenance and biomass production, i.e., on productivity, at a longer time. All this information is helpful for the forest technician in managing forests, including wood production and preservation (Landsberg, 1986).

At the same time, the measurement of variables and calculation of parameters related to water status concerning absorption, movement, storage, use and stomatal loss, (i.e. osmotic and pressure potential, hydraulic conductivity and capacitance, sap flow, isotopic carbon discrimination, water use efficiency), as well as parameters linked to canopy structure, have opened great possibilities to the water relations study in forest stands with regard to survival, growth and inter and intra-species competition (Pearcy *et al.*, 1989; Ehleringer, *et al.*, 1993). These methodologies are complemented with instrumentation to measure physical factors in the soil (water measurement by TDR

reflectometry, soil matric potential and temperature and some other edaphic proprieties) and in the atmosphere (air vapour pressure deficit, solar radiation), all of them useful when interpreting tree performance in an ecophysiological context (Kozlowsky *et al.*, 1991). Measurement of chlorophyll fluorescence and photosynthetic pigments are also helpful in studying the response of carbon assimilation to water deficits and other stresses, as well as for characterizing their seasonal variation in Mediterranean forest species (García-Plazaola *et al.*, 1997; Corcuera *et al.*, 2005).

Water potential and conductance measurements in thinned and unthinned stands make it possible to analyze tree responses in terms of water balance. The effects of thinning on the water table and run off in a *Eucalyptus marginata* stand (Stoneman, 1993), in the water relations and growth of *Quercus petraea* (Breda *et al.*, 1995) or in the water loss and gas exchange in beech (*Fagus sylvatica*) seedlings planted in a mature pine forest (Aranda *et al.*, 2001) are some illustrative examples.

Where water accessibility to roots and soil does not satisfy the atmospheric evaporative demand of the tree, stomata will close to avoid transpired water surpassing root water supply, because growth will then decrease or even stop. In terms of productivity it is worth to identifying the periods when this happens, in order to take this into account in the programming of silvicultural practices.

Nevertheless, the majority of plant water status measurements are instantaneous, they provide a value for the variable at the moment of measurement, but they do not provide much information on growth and different organ biomass allocation, processes that have acted in the past. The «water stress integral» is a useful contribution (Myers, 1988) to the solution of this problem concerning water status over a period under examination. This parameter integrates the products of differences between mean values of predawn water potential over an interval minus the maximum value measured (or calculated) during the period, multiplied by the number of days. This concept has led Landsberg and Gower (1997) to propose that growth may be estimated as dry mass increment per unit area per unit time expressed over a period as the product of a function depending on radiation and plant nutrient status multiplied by predawn water potential over time. The model, according to the authors, must distinguish between short- and long-term. In the first case, the

effects of stomatal conductance on water potential and hence on carbon assimilation will be reflected, while the effects of water potential in leaf expansion and stem diameter will be expressed over a longer term.

Water fluxes have been monitored and compared for several European forest ecosystems. In beech stands, transpiration reaches up to 80-90% of total evapotranspiration, with rates similar among sites because of the close canopy LAI and conductance values (Granier *et al.*, 2003). A different strategy has been found in *Pinus sylvestris* and *P. pinaster* populations in terms of water use strategy, and the existence of a maximum photosynthesis latitudinal gradient matched to stomatal conductance. It is emphasized that management practices are decisive in the differences in water and carbon fluxes found between ecosystems (Ceulemans *et al.*, 2003).

Water parameters have special relevance in the Mediterranean climate. Plants respond to the scarce and irregular precipitations with strategies to overcome water stress. Avoidance (i.e. adaptation of morphology and anatomy of roots and leaves) and tolerance (i.e. osmotic adjustment) to water stress make survival and growth possible under very limiting conditions (Valladares *et al.*, 2004).

Tree hydraulic architecture and its implications in water transport and tree height (Becker, 2000) are of special interest. Following the early hypothesis by Leonardo da Vinci that branches maintain the conducting area of the trunk, later confirmed by Hubber, the concepts of hydraulic conductance and conductivity have contributed to a better knowledge of water transport in trees and several methodologies have been developed to quantify these parameters and to explain the physiological basis of the phenomenon (Tyree & Zimmermann, 2002). Five architectural patterns have been identified as adjusted to the principle of the minimizing of energy; these coexist in countless combinations depending on the relationship between distal and proximal tubes. The major conduction efficiency in ring-porous species with respect to conifers and diffuse porous species is justified because in the first group the conducting area increases distally without any increase in xylem total area (Mc Culloh & Sperry, 2005). Hydraulic conductivity measurements have been also shown as a helpful tool to step forward in the assessment of hybrid variability, and in this sense they have been applied to sub-Mediterranean oak- hybrids (Himrane *et al.*, 2004)

Carbon balance and forest productivity

In the frame of sustainable development, forest productivity can be considered essentially in terms of biomass production and carbon fluxes in the ecosystem. The knowledge of the carbon balance in relation to physiological bases will improve the technical management of forests and the evaluation of the carbon fixed (Jarvis, 1995).

Photosynthesis is the first and main biological process in the productive chain. The net primary production is defined as the difference between CO₂ fixation and its loss by photorespiration and autotrophic respiration. Gas exchange measurements with the eddy-covariance technique permit the evaluation of forests as carbon sinks (Aubinet, 2000). This technique also makes it possible to evaluate the effects of climatic change and land use (deforestation and forestation) in the ecosystem and to provide data for land parameterization (Baldocchi *et al.*, 1996). The effects of leaf position and morphological characteristics, stomatal conductance and photosynthetic capacity have been quantified by means of the biophysical Canoak model (Baldocchi *et al.*, 2002): The authors foresaw a closer coupling between the biophysical models and the modules that compute the dynamics of canopy structure, function and composition, in order to obtain a more acceptable fidelity to predict fluxes of CO₂ and water vapour.

In the Euroflux network, six European beech forests have been monitored during six years. It has been found that the greater portion of net carbon exchange variation is due to respiration, 50% of which occurred in the soil. Increase in respiration leads to a decrease in carbon fixation. This fact is important in the perspective of climatic change (Granier *et al.*, 2003). Woody debris from silvicultural operations gives origin to heterotrophic respiration which affects carbon net change in the ecosystem (Nee). The authors concluded that differences between sites might be due to the intensity and silvicultural regime applied.

Euroflex results show that latitude (as indicative of radiation balance, vegetative season, etc.) is a high significant variable to explain Nee variation. The altitudinal gradient shows a high and less variable strength as carbon sink in low latitudes (up to 6,7 ton C/ha/year) and a higher variability in medium latitudes respect to climate (continental opposite to maritime),

soil and stand. It is suggested that interannual Nee variation recorded in boreal ancient forests can allow them to be converted in carbon sources. Gross primary production (GPP) is more conservative between latitudes and sites, that suggests the participation of other components in Nee variation. Ecosystem respiration, dominated by root and microorganism respiration, is considered conditioning of the Nee tendency (Valentini *et al.*, 2003).

The low respiration rates found in Mediterranean ecosystems are linked to limiting water availability, while in similar latitudes under Atlantic climate the different respiration rates are related to silvicultural practices regarding soil preparation and fertilization. Holm-oak stands, an example of Mediterranean forest ecosystems, show the ability to assimilate carbon during the whole year providing that low temperature in the winter and available water during the summer were not limiting factors. Photoperiod length becomes determinant for carbon balance. Respiration costs reach up to 70% GPP in the ecosystem and this increases in spring while Nee decreases. However, in the summer, in spite of the high temperature, respiration rates are lower because of water stress (Tirone *et al.*, 2003).

The carbon sink condition of boreal forests has been widely studied (Margolis & Ryan, 1997). In the last decade, a seasonal carbon absorption decrease has been recorded. This has been linked to the decreases in summer precipitations and relative humidity. This variation has been specially related to Lai, leaf nitrogen concentration and soil respiration rate. It is highly important to improve and extend field measurements in order to follow this tendency more closely (Wang *et al.*, 2004).

In summary, direct estimations of carbon exchange fluxes are a useful tool for understanding the global process of carbon balance in terrestrial ecosystems. Evaluations based on forest inventories would be examined at the light of carbon flux measurements taking into account respiration. Sinks may become sources under extreme conditions.

Carbon allocation

Allometric equations have been developed to express the relationship between the growth rates of leaves, stem and roots, and plant dry weight production

rate in tree seedlings. Biomass allocation coefficients between the different organs of the plant can also be derived from such equations (Mc Murtrie & Wolf, 1983). Water, light and available nutrients affect biomass allocation between the different organs of the plant. The «nitrogen productivity» concept (biomass produced per unit of nitrogen) has been employed to calculate the carbon allocation in the different organs. Thus, it has been useful to predict the responses in the root to shoot ratio to changes in the nitrogen supply. Such changes are related to the limiting effect of nitrogen over photosynthesis with respect to its effect over the root pool (Agren, 1983).

Quantification of the carbon stored in the aboveground biomass (AGB) and in the belowground biomass (BGB) is required in order to estimate carbon budgets of forest stands under different environmental and management conditions. Knowledge of biomass allocation and its modifications through silvicultural practices (thinning) or natural hazards (wildfires, pests, climatic changes, etc.) are essential for the modelling of stand productivity. In tree seedlings and young stands the BGB/AGB ratio increases as supplies of P and N become growth limiting, but nutrient requirements may change during stand development. In fact, as trees grow there is an increase in biomass partitioning towards shoots (Helmisaari *et al.*, 2002).

The BGB component is difficult to evaluate, but it constitutes a significant and highly variable proportion of total biomass in forest stands, not only in natural stands but also in plantations (Madeira *et al.*, 2002). A shift in nutrient availability increases carbon assignment to leaves to the detriment of roots (Gower *et al.*, 1992). The existence of a structural component that changes with the AGB pool and a second component highly responsive to nutrient availability has been hypothesized (Zerihun & Montagu, 2004).

The carbon allocation between coarse and fine roots is important to calculations of the carbon balance of the ecosystem. Fine root production represents a large production of total annual net primary production in forest ecosystems (Nadelhoffer & Raich, 1992). Under similar weather conditions, there is an inverse relationship between the biomass of the fine roots (< 2-5 mm) and nutrient availability. In this sense, the installation of minirhizotrons in the field has permitted the monitoring of the effects of thinning on carbon allocation in a holm-oak stand (López *et al.*, 2003).

Different water availability is another cause of the variation found in the BGB/AGB ratio (Madeira *et al.*, 2002). Carbon allocation to the fine roots decreases as water input increases (Comeau y Kimmings, 1989). Light and its possible interaction with water, plays an important role in the regeneration process of tree stands, differently so in light- and shade-species. Intense shading promotes the biomass allocation to leaves, while in poor or dry soils a higher amount of carbon is inverted in roots (Van Hees & Clerk, 2003). These results show the difficulty of morphological adaptation to climate when both circumstances are present (Valladares & Pearcy, 2002). Moreover, such process will presumably change under a shift in atmospheric CO₂, as has been shown in cork oak seedlings, which were able to live better under low light intensities when the CO₂ level was doubled (Pardos, M, pers.com.)

Organic matter decomposition and mineral nutrition

The incorporation of animal and vegetal detritus into the soil is followed by the decomposition of organic matter by invertebrates and microorganisms and its subsequent mineralization. Organic soil matter plays an important role in the nutrient biochemical cycle; it is a critical factor in forest nutrition and it affects the chemical, physical and hydrological properties of the soil. The amount of organic matter depends on latitude, season and forest type. It is closely related to nutrient availability (nitrogen especially) and is a limiting factor for microbial activity (Schlesinger, 1991). Litterfall does not appear to vary greatly between evergreen and deciduous forests under similar climate, climatic and edaphic conditions being more important than the type of species. (Landsberg and Gower, 1997).

In the decomposition process, respiration of microorganisms and plant roots is the origin of soil CO₂ flux, which plays an important role in the nutrient and carbon cycles, reaching between 20 and 40% of the carbon input in the atmosphere (Schimel, 1995). The use of IRGA analyzers and eddy-covariance systems have made possible the precise measurement of CO₂ flux from the soil (Baldocchi, 1996) and the study of the evolution of soil organic matter in different forests (Lankreijer *et al.*, 2003). Temperature and moisture content (in sites under water stress) have been shown to

be the most determining factors of soil carbon efflux. This has been positively related to net primary production, which suggests that site productivity is more important than local climate for the interpopulation differences in CO₂ efflux. Besides, higher litterfall C/N values tend to have a negative effect on the flux (Janssens *et al.*, 2003).

Forest management can modify the relationships between primary producers and decomposers, thus affecting organic matter production and long-term productivity (Johnson, 1992). Therefore, it is important to study the effects on edaphic respiration caused by prescribed fires, site preparation and fertilization in plantations (Nambiar, 1990).

Mineral nutrition is a key factor for the sustainable management of forests and nursery production of high quality plants. Some nutrients, nitrogen in particular, can be limiting. Thus, as the litterfall is the primary source of nutrients, its decomposition must be considered a fundamental step in the biogeochemical cycles in forest ecosystems. Stand canopy can determine the decomposition of litterfall. In a beech and melojo-oak mixed stand at Montejo de la Sierra (Sistema Central, Iberian Peninsula) the decomposition pattern for both species differed according to the canopy under which the process had been developed (Pardo *et al.*, 1997).

The basic processes in nutrient cycling are common to all forest ecosystems, but variations exist in time and speed among them. The control of nutrient dynamics in forest soils is rather incomplete and nutrient absorption by trees has only begun to be understood applying mechanistic models. Modelling concerning nitrogen and phosphorous availability and their interaction with water and other nutrients is considered especially important as nitrogen and phosphorous are principal determinants of productivity in many forests (Landsberg *et al.*, 1991).

A great controversy concerns the negative effects of silvicultural practices, fires, etc., on forest sustainability, as well as those related with the effects of wood harvesting on soil fertility, mainly in short rotation species (Boyle, Jr *et al.*, 1999). This topic requires experimental support in ecologically comparable conditions, which are not easy to ensure with accuracy. Ecophysiological results from stand measurements, even covering a period of some years is instantaneous reflection of the structure and species composition, which would change with the age of trees.

These changes are, both the consequence and the cause of changes in the functional characteristics of the stand, such as soil biogeochemical cycles and carbon and water fluxes. The changes provoked by perturbances such as pests and diseases, and selective deaths due to meteorological causes (Perry, 1994) must be added. Thus, the value of functional parameters in evaluating the consequences of these changes in terms of sustainability and productivity.

It is important to explain temporal changes in biogeochemical cycles, mainly in Mediterranean ecosystems, which support such different populations structure and ecological conditions. A ancient anthropogenic actions, the flora and fauna diversity, the erosion phenomena and the scarce organic matter, oblige us to pay special attention to nutrient cycles and to the way forest management has influenced and will influence these ecosystems (Imbert *et al.*, 2004).

Special importance can be attributed to the changes in leaf area and other leaf parameters such as *Lai*. An asymptotic tendency for leaf area when tree stands become older is admitted as a general pattern, but the causes and mechanisms involved in the process are far from fully understood. Possible limitations imposed by a decrease in nutrient availability, as suggested by Gower *et al.* (1994), may be opposed with a higher absorption efficiency with age (Gholz *et al.*, 1985). Besides, the tolerance versus intolerance to shade showed by the species or mixture of species influences the response. *Lai* is negatively affected by nutrient limitation and is well correlated with sapwood width. *Lai* is a good index for evaluating the recovery speed of a forest stand whose structure has been altered, for instance due to crown insect attacks or selective felling.

The changes in root systems are less known because of the inherent difficulty in their quantification and the shortage of data. There is some evidence for the existence of positive relationship between the amount of thick roots and stand development, but data concerning fine roots appear to be less conclusive (Vogt, 1987). Some contributions about the structure and dynamics of the root systems in evergreen oak forests (Canadell *et al.*, 1999; López *et al.*, 2001) are especially interesting for forestry in the Mediterranean basin.

Mycorrhizal associations play an important role in forestry. They occur in practically all native forests; they are essential for tree mineral nutrition and confer effectiveness to trees in drought responses (Harley &

Smith, 1983). The inoculation of seedlings in the nursery for planting purposes is a common practice providing the mycorrhizal fungi are ecologically adapted to the tree species and the planting site (Pera *et al.*, 1999).

Productivity and modelling

A high number of empirical models on tree growth have been fitted and conventionally applied to forest stands in forecasting productivity. Growth curves are statistically derived from tree diameter and height measurements carried out in situ (Cañadas *et al.*, 2002). Modelling spatial and vertical structure of the stand makes it possible to characterize changes in long periods of time (i.e. one rotation) and to make inferences for the future silviculture actions (Montes, 2005). Modelling tree growth can be also approached in forecasting the assimilation and allocation of carbon and other constituents. Carbon-based models of individual tree growth have been developed and a critical revision has been made by Le Roux *et al.* (2001). Bridging process-based and empirical approaches to modelling tree growth, in part by the use of a common model, have been recently formulated (Valentini & Mäkelä, 2005).

Net primary production (NPP) decreases as stands become older, independently of forest type. Causes are not well known. The decrease in nutrient availability (mainly nitrogen), the increase of the ratio of the woody fraction (less accessible to microbial decomposition in the soil) to total litterfall biomass, and the higher C/N in leaf detritus with age are several suggestions which have been made (Hart *et al.*, 1994). A more conservative hydraulic tree architecture as trees become older with higher resistance to water transport in the thicker branches has been suggested as an explanation of the lower nutrient availability with age (Yoder *et al.*, 1994). One hypothesis supports that NPP approximates to zero in the steady state and ancient forests as a result of the compensation between carbon accumulation in some stands and carbon losses in others (Landsberg & Gower, 1997).

Models based on physiological processes make it possible to incorporate nutrition and water status for predicting forest productivity (Pennig de Vries, 1983). These models are more versatile since they facilitate the evaluation of the consequences of changing

conditions and the probable effects of stimuli received. However, it is necessary to manage a great number of parameters, all too often difficult to obtain. The scale of operative time (from hours to years) and the degree of detail achieved (determined by the number of parameters set in play) condition the efficiency of the model. An extensive range of models has been applied to forest ecosystems. For instance, an operative scale of hours and the measurement of great amount of micrometeorological and physiological data characterize the MAESTRO model (Wang & Jarvis, 1990). Another concept inspires the CENTURY model (Parton *et al.*, 1993), which focusses on organic matter decomposition and recycling, with the assumption of proportionality between growth and available nitrogen, and operating on a scale of years, over a long time.

The FOREST-BGC model (Waring & Running, 1998) has been applied to simulate the daily range of Lai, GPP and NPP in several forest ecosystems and to estimate the carbon sinks in European forests (Mollicone *et al.*, 2003). The authors estimate that the values given for Mediterranean species were low because of poor adaptation to the model. The GOTILWA model has been used by GRACIA to estimate NPP in the forests of the Iberian Peninsula. The results (M.^o Medio Ambiente, 2005) show that these forests may increase the carbon sink effect for some decades, but in the second half of the XXI century they could change, to become atmospheric carbon sources.

Based-process models can be used together with geographic information systems (GIS) and remote sensing (Landsat TM) of radiance signals from vegetation. The reflectance of visible red and near infrared radiation permits the calculation of the normalized difference vegetation index (NDVI). The mathematical relationship between NDVI and Lai makes possible to use intercepted radiation to predict forest productivity at regional level. Spectral transmittance measurements are also helpful for assessing annual changes in structural attributes and functional variables determining forest productivity (Serrano & Peñuelas, 2005).

New long-term and large-scale data are available for the development and evaluation of process-oriented forest growth and ecosystem models. The future challenge, as has been suggested by Mäkelä & Hasenauer in the Preface of «Modelling Forest

Production» (2005), is the development of appropriate methods to convert these data into useful knowledge.

In conclusion, basic knowledge of the functional performance of forest ecosystems supplied by stand ecophysiological measurements is an important tool when putting into practice the principles of sustainability to the management of woodlands by forest engineers. The meeting of silviculture and ecophysiology is an appropriated starting point for a sustainable forestry guided by maintenance of the ecological equilibrium of forests.

Acknowledgments

I thank Prof Dr Luis Gil, Dr Ricardo Alía and Dr Marta Pardos for their comments and suggestions. Thanks also to Mr Farrel for checking the English version, highly improved by him.

References

- AGREN G., 1983. Nitrogen productivity of some conifers. *Can. J. For. Res.* 13: 494-500.
- ARANDA I., GIL L., PARDOS J.A., 2000. Water relations and gas exchange in *Fagus sylvatica* L. and *Quercus petraea* (Mattuschka) Liebl. In a mixed stand at their southern limit of distribution in Europe. *Trees* 14: 344-352.
- ARANDA I., GIL L., PARDOS J.A., 2001. Effects of thinning in a *Pinus sylvestris* L. stand on foliar water relations of *Fagus sylvatica* L. seedlings planted within the pinewood. *Trees* 15: 358-384.
- AUBINET M., *et al.*, 2000. Estimates of the annual net carbon and water exchange of European forests: the EUROFLOX methodology. *Adv Eco Res* 30: 113-175.
- AUSSENAC G., 2000. Interactions between forest stands and microclimate: Ecophysiological aspects and consequences for silviculture. *Ann Sci For* 57: 287- 31.
- BALDOCCHI D.D., VOGEL C.A., 1996. A comparative study of water vapour, energy and CO₂ flux densities above and below a temperate broadleaved and a boreal pine forest. *Tree Physiol* 16: 5-16.
- BALDOCCHI D.D., WILSON K.B., GU L., 2002. How the environment, canopy structure and canopy physiological functioning influence carbon, water and energy fluxes of a temperate broadleaved deciduous forest: an assessment with the biophysical model CANOAK. *Tree Physiol*. 22: 1065-1078.
- BEAUJEU J., 1988. La ciencia helenística y romana: Ciencias físicas y biológicas. En: *Historia General de las Ciencias*. Dirección R. Taton. Orbis, Vol.2, 414-424.

- BEAUJOUAN G., 1988. La ciencia en el Occidente medieval cristiano: La Ciencia, la Escolástica y las Universidades. En: Historia General de las Ciencias. Dirección R. Taton. Orbis, Vol 3, 643-653.
- BECKER P., MEINZER F.C., WULLSCHLEGER S.D., 2000. Hydraulic limitation of tree height: A critic. *Funct. Ecol.* 14: 4-11.
- BORMANN F.J., LIKENS J.E., 1979. Pattern and process in a Forested Ecosystem. Springer- Verlag.
- BOYER J.S., 1995. Measuring the water status of plants and soils. Acad. Press.
- BOYLE J.R., 1999. Planted forests: views and view points. *New Forests*, 17: 5-9.
- BREDA N., GRANIER A., AUSSÉNAC G., 1995. Effect of thinning on soil and tree water relations, transpiration and growth in an oak forest (*Quercus petraea* (Matt.) Liebl.) *Tree Physiol.* 15: 295-36.
- BUCHANAN B.B., GRUISSEM W., JONES R.L., 2000. Biochemistry and Molecular Biology of Plants. Amer. Soc. Pl. Phys.
- BUCHMANN N., 2002. Plant ecophysiology and forest response to global change. *Tree Physiol.* 22: 1177-1184.
- CANADELL J., DJEMA A., LÓPEZ B., SABATÉ S., SISCART D., GRACIA C., 1999. Structure and dynamics of the root system. En: Ecology of Mediterranean Evergreen Oak Forests. Ecological Studies, 137. Eds: Rodá F., Gracia C., Retana J. y Belló J. Springer, Chapter 4:163-180.
- CAÑADAS N., 2002. Modelización forestal a partir de los datos del Inventario Nacional. En: Bravo F. *et al.* (edits.) El Inventario Forestal Nacional. Elemento clave para la gestión forestal sostenible. M.º de Medio Ambiente, 133-148.
- CEULEMANS R., KOWALSKI A.S., BERBIGIER P., DOLAN H., GRELLE A., JANSSENS I.A., LINDROTH A., MOORS E., RANNIK U., VESALA T., 2003. Coniferous forests (Scots and Maritime pine): carbon and water fluxes, balances, and ecological and ecophysiological determinants. En: Fluxes of carbon, water and energy of European forests (Edit.: R. Valentini), Springer, 71-97.
- COMEAU P.G., KIMMINGS J.P., 1989. Above and below-ground biomass and production of lodgepole pine on sites with different soil moisture. *Canad. J. For. Res.* 19: 447-454.
- CORCUERA L., MORALES F., ABADÍA A., GIL-PELEGÍN E., 2005. Seasonal variations in photosynthesis and photoprotection in a *Quercus ilex* subsp. *ballota* woodland located in its upper altitudinal extreme in the Iberian Peninsula. *Tree Physiol.* 25: 599-608.
- DAVY de VIRVILLE A., LEROY J.F., 1988a. El siglo XVII. Las Ciencias de la Naturaleza: la Botánica. En: Historia General de las Ciencias. Dirección R. Taton. Orbis, Vol 4, 194-204.
- DAVY de VIRVILLE A., LEROY J.F., 1988b. El siglo XVIII. Las Ciencias de la Naturaleza: la Botánica. En: Historia General de las Ciencias. Dirección R. Taton. Orbis, Vol 7, 724-743.
- DREW T.J., FLEWELLING J.W., 1977. Some recent Japanese theories of yield-density relationships and their applications to Monterrey pine plantations. *For. Sci.*, 23:517-534.
- DUHAMEL de MONCEAU (traducción al castellano por Dr Casimiro Ortega), 1722. *Physica de los árboles*, en la qual se trata de la Anatomía de las Plantas y de la Economía Vegetal, o sea Introducción al tratado general de Bosques y Montes. Madrid, 1772, Real Compañía de Impresores y Libreros del Reyno.
- ENCYCLOPAEDIA BRITANNICA, 1979. Francis Bacon. Vol. 1, pp 715.
- EHLERINGER J.R., HALL A.E., FARQUHAR G.D., 1993. Stable isotopes and plant carbon- water relations. Academic Press.
- FERNÁNDEZ M., GIL L., PARDOS J.A., 1999. Response of *Pinus pinaster* Ait provenances at early age to water supply. I. Water relations parameters. *Ann. For. Sci.* 56:179-187.
- FITTER A.H., HAY R.K.M., 2002. Environmental physiology of plants. 3rd edit. Academic Press.
- GARCÍA-PLAZAOLA J.I., FARIA T., ABADÍA J., ABADÍA A., CHAVES M.M., PEREIRA J.S., 1997. Seasonal changes in xanthophyll composition and photosynthesis of cork oak (*Quercus suber* L.) leaves under Mediterranean climate. *J. Exp. Bot.* 48:1667-1674.
- GHOLZ H.R., PERRY C.S., CROPPER W.P., HENRY L.C., 1985. Litterfall, decomposition and nitrogen and phosphorous dynamics in a chronosequence of slash pine (*Pinus elliotii*) plantations. *For. Sci.* 31:463-478.
- GOWER S.T., VOGT K.A., GRIER C.C., 1992. Carbon dynamics of Rocky Mountain Douglas fir: Influence of water and nutrient availability. *Ecol. Monogr.* 62:43-65.
- GRANIER A., AUBINET M., EPRON D., FALGE E., GUDMUNDSSON J., JENSEN N.O., KÖSTNER B., MATTEUCCI G., PILEGAARD K., SCHMIDT M., TENHUNEN J., 2003. Deciduous forests: carbon and water fluxes, balances and ecophysiological determinants. In: Ecological Studies, Vol. 163 (Valentini R., ed.). Fluxes of carbon, water and energy of European forests. Springer-Verlag Berlin Heidelberg, pp. 55-70.
- HALL D.O., SCURLOCK J.M.O., BOLHAR-NORDENKAMPF H.R., LLEGUOOD R.C., LONG S.P., 1993. Photosynthesis and production in a changing environment. Chapman.
- HARLEY J.L., SMITH S.E., 1983. Mycorrhizal Symbiosis. Academic Press.
- HART S., NASON G.E., MYROLD D.D., PERRY D.A., 1994. Dynamics of gross nitrogen transformations in an old-growth forest: the carbon connection. *Ecology* 75: 880-891.
- HARTIG R., 1906 (traducción de J.M.^a Castellarnau). Compendio de Anatomía y Fisiología de las Plantas, y principalmente de los árboles forestales. Imprenta Alemana, 358 pp.
- HELMISAARI H.S., MAKKONEN K., KELLOMAKI S., VALTONEN E., MALKONEN E., 2002. Below- and

- above-ground biomass, production and nitrogen use in Scots pine stands in eastern Finland. *For. Ecol. Manage.* 165: 317-326.
- HIMRANE H., CAMARERO J.J., GIL-PELEGRIN E., 2004. Morphological and ecophysiological variation of the hybrid oak *Quercus subpyrenaica* (*Q. faginea* x *Q. pubescens*). *Trees* 18:566-575.
- HORT A.F., 1968. *THEOPHRASTUS Enquiry into Plants* (translation from the Greek. Harvard University Press.
- IMBERT J.B., BLANCO J.A., CASTILLO F.J., 2004. Gestión forestal y ciclos de nutrientes en el marco del cambio global. En: F. Valladares (edit.) *Ecología del bosque mediterráneo en un mundo cambiante*. M.º de Medio Ambiente, 479-506.
- JANSSENS I.A., DORE S., EPRON D., LANKREIJER H., BUCHMANN N., JARVIS P.G., 1995. The role of temperate trees and forests in CO₂ fixation. *Vegetatio* 121: 157-174.
- JARVIS P.G. (Edit.), 1995. *European forests and global change. The likely impacts of rising CO₂ and temperature*. Cambridge Univ. Press.
- JOHNSON D.W., 1992. Effects of forest management on soil carbon storage. *Water Air Soil Poll* 64: 83-120.
- KARNOSKY D.F., PERCY K.E., CHAPELKA A.H., SIMPSON C., PIKKARAINEN (Edit.), 2003. *Air pollution, global change and forest in the new millennium. Developments in Environmental Science* 3, Elsevier.
- KOZLOWSKY T.T., KRAMER P.J., PALLARDY S.G., 1991. *The Physiological Ecology of Woody Plants*. Academic Press.
- LAMBERS H., CHAPIN III F.S., PONS T.L., 1998. *Plant Physiological Ecology*. Springer.
- LANDSBERG J.J., 1986. *Physiological Ecology of Forest Production*. Academic Press.
- LANDSBERG J.J., KAUFMANN M.R., BINKLEY D., ISERANDS J., JARVIS P.G., 1991. Evaluating progress towards closed forest models based on fluxes of carbon, water and nutrients. *Tree Physiol.* 9:1-15.
- LANDSBERG J.J., GOWER S.T., 1997. *Applications of physiological ecology to forest management*. Academic Press.
- LANGE O.L., NOBEL P.S., OSMOND C.B., ZIEGLER H. (Edits.), 1981, 1982, 1983, 1983. *Physiological Plant Ecology* I (625 p), II (747 p.), III (799 p.) y IV (644 p.). *Encyclopedia of Plant Physiology*, Springer.
- LANREIJER H., JANSSENS I.A., UCHMANN N., LONGDOZ EPRON D., DORE S., 2003. Measurement of soil respiration. En: *Fluxes of carbon, water and energy of European forests* (Edit. R. Valentini), Springer, 37-54 pp.
- LARCHER W., 1995. *Physiological Plant Ecology*, 3rd edit., Springer.
- LASSOIE J.P., HINCKLEY T.M. (edits.), 1991. *Techniques and Approaches in Forest Tree Ecophysiology*. CRC Press.
- LEROY J.F., 1988a. El siglo XIX. *Las Ciencias de la Vida: Fisiología Vegetal*. En: *Historia General de las Ciencias*. Dirección R. Taton. Orbis, Vol 10, 503-522.
- LEROY J.F., 1988b. El siglo XX. *Las Ciencias de la Vida: Fisiología Vegetal*. En: *Historia General de las Ciencias*. Dirección R. Taton. Orbis, Vol 15, 794-820.
- LE ROUX X., LACOINTE A., ESCOBAR-GUTIÉRREZ A., LE DIZÈS S., 2001. Carbon-based models of individual tree growth: a critical appraisal. *Ann. Sci. For.* 58: 469-506.
- LONGDOZ B., BROSSAUD J., MONTAGNANI L., 2003. Climatic influences on seasonal and spatial differences in soil CO₂ flux. En: *Fluxes of carbon, water and energy of European forests* (Edit.: R. Valentini), Springer, 235-253.
- LÓPEZ B., SABATÉ S., GRACIA C., 2001. Vertical distribution of fine root density, area index and mean diameter in *Quercus ilex* L., forest. *Tree Physiol.* 21: 555-560.
- LÓPEZ B.S., SABATÉ S., GRACIA C.A., 2003. Thinning effects on carbon allocation to fine roots in a *Quercus ilex* forest. *Tree Physiol.* 23: 1217-1224.
- MCCULLOH K.A., SPERRY J.S., 2005. Patterns in hydraulic architecture and their implications for transport efficiency. *Tree Physiol.* 25: 257-267.
- Mc MURTRIE R.E., WOLF L.J., 1983. Above- and below-ground growth of forest stands: A carbon budget model. *Ann. Bot.* 52: 437-448.
- MADEIRA M.V., FABIAO A., PEREIRA J.S., ARAÚJO M.C., RIBEIRO C., 2002. Changes in carbon stock in *Eucalyptus globulus* Labill plantations induced by different water and nutrient availability. *For. Ecol. Manage.* 171: 75-85.
- MÄKELÄ A., HASENAUER H. (Edit.), 2005. Preface. In «Modeling Forest Production». *Tree Physiol.* 25.
- MARGOLIS H.A., RYAN M.G., 1997. A physiological basis for biosphere-atmosphere interactions in the boreal forest: an overview. *Tree Physiol.* 17: 8-9.
- M.º MEDIO AMBIENTE 2005. Principales conclusiones de la evaluación preliminar de los impactos en España por efecto del cambio climático, 39 pp.
- MOLLICONE D., MATTEUCCI G., KOBLE R., MASCI A., CHIESI M., SMITS P.C., 2003. A model-based approach for the estimation of carbon sinks in European forests. En: *Fluxes of carbon, water and energy of European forests* (Edit.: R. Valentini), Springer, 179-206.
- MONTES F., 2005. Estudio de la relación entre la silvicultura y la diversidad estructural en los montes Pinar de Valsain y Pinar de Navafria. Tesis Doctoral. E.T.S.I. Montes, Madrid, 125 pp.
- MYERS B.J., 1988. Water stress integral- a link between short term stress and long term growth. *Tree Physiol.* 4, 315-323.
- NAMBIAR E.K.S. (edit.), 1990. *Management of water and nutrient relations to increase forest growth*. *For. Ecol. Manag. Special Issue*, v.30.
- NADELHOFFER K.J., RAICH J.W., 1992. Fine root production estimates and belowground carbon allocation in forest ecosystems. *Ecology* 73: 1139-1147.
- PARDO F., GIL L., PARDOS J.A., 1997. Field study of beech (*Fagus sylvatica* L.) and melojo oak (*Quercus pyrenaica* Willd.) leaf litter decomposition in the centre of the Iberian Peninsula. *Plant & Soil* 191: 89-100.

- PARTON W.J., SCURLOCK J.M.O., OJIMA D.S., GILMANOV T.G., SCHOLLES R.J., SCHIMEL D.S., KICHNER T., MENAUT J., SEASTEDT T., GARCÍA MOYA E., KAMNALRUT A., KYINYAMARIO J.I., 1993. Observations and modelling of biomass and soil organic matter dynamics for the grassland biome worldwide. *Global Biogeochem. Cycles* 7: 785-809.
- PEARCY R.W., EHLENGER J.R., MOONEY H.A., RUNDEL P.W., 1989. *Plant Physiological Ecology. Field Methods and Instrumentation*. Chapman & Hall.
- PENNIG de VRIES F.W.T., 1983. Modelling of growth and production. En: *Physiological Plant Ecology IV*, Encyc. Plant Physiol. Vol 12D, pp 117-150.
- PERRY D.A., 1994. *Forest Ecosystems*. The John Hopkins University Press.
- PITA P., GASCO A., PARDOS J.A., 2003. Xylem cavitation, leaf growth and leaf water potential in *Eucalyptus globulus* clones under well-watered and drought conditions. *Funct. Pl. Biol.* 30: 891-899.
- PERA J., ÁLVAREZ I., RINCÓN A., PARLADÉ J., 1999. Field performance in northern Spain of Douglas-fir seedlings inoculated with mycorrhizal fungi. *Mycorrhiza* 9: 77-84.
- PITTMAN S.D., TURNBLOM E.C., 2003. A study of self-thinning using coupled allometric equations: implications for coastal Douglas-fir stand dynamics. *Can. J. For. Res.* 33: 1661-1669.
- RAMOS A. (Edit.), 1987. *Diccionario de la Naturaleza*, Espasa Calpe.
- RAZ R., 1988. El último cuarto de siglo. *Biología: Botánica*. En: *Historia General de las Ciencias*. Dirección R. Taton. Orbis, Vol 18, 133-138.
- REIGOSA J. (Edit.), 2001. *Handbook of Plant Ecophysiology Techniques*. Kluwer Acad. Pub.
- RYAN M.G., 2002. Canopy processes research. *Tree Physiol.* 22 (15/56): 1035-1044.
- SAN MIGUEL A., 1994. La dehesa española. Origen, tipología, características y gestión. Fundación Conde del Valle de Salazar.
- SCHIMEL D.S., 1995. Terrestrial ecosystems and the carbon cycle. *Global Change Biol* 1: 77-91.
- SCHLESINGER W.H., 1991. *Biogeochemistry: An analysis of global change*. Acad. Press.
- SERRANO L., PEÑUELAS J., 2005. Assessing forest structure and function from spectral transmittance measurements: a case study in a Mediterranean holm oak. *Tree Physiol.* 25: 67-74.
- SMITH J.A.C., GRIFFITHS H. (eds.), 1993. *Water deficits. Plant responses from cell to community*. Bios Sci Pub.
- STONEMAN G.L., 1993. Hydrological response to thinning a small jarrah (*Eucalyptus marginata*) forest catchment. *J. Hydrol* 150: 393-47.
- TAIZ L., ZEIGER E., 1998. *Plant Physiology*. The Benjamin/Cummings Publ. Co, Inc.
- TERRADAS J., 2001. *Ecología de la vegetación. De la ecofisiología de las plantas a la dinámica de comunidades y paisaje*. Omega.
- THIMANN K.V. (Edit), 1958. *The Physiology of Forest Trees. A Symposium Held at the Harvard Forest, April 1957*, The Ronald Press Company.
- TIRONE G., DORE S., MATTEUCCI G., GRECO S., VALENTINI R., 2003. Evergreen mediterranean forests: Carbon and water fluxes, balances, ecological and ecophysiological determinants. En: *Fluxes of carbon, water and energy of european forests* (Edit.: R. Valentini), Springer, 125-149.
- TYREE M.T., ZIMMERMANN M.H., 2002. *Xylem structure and the ascent of sap*. 2nd edit., Springer.
- VALENTINI R., MATTEUCCI G., DOLMAN A.J., SCHULZE E.D., 2003. Conclusions: the role of canopy flux measurements in global C-cycle research. En: *Fluxes of carbon, water and energy of european forests* (Edit.: R. Valentini), Springer, 257-266.
- VALENTINI H.T., MÄKELÄ A., 2005. Bridging process-based and empirical approaches to modelling tree growth. *Tree Physiol* 25: 769-779.
- VALLADARES F. *et al.*, 2004. Estrés hídrico: ecofisiología y escalas de la sequía. En: F. Valladares (edit.) *Ecología del bosque mediterráneo en un mundo cambiante*. M.º de Medio Ambiente, pp 163-190.
- VALLADARES F., PEARCY R.W., 2002. Drought can be more critical in the shade than in the sun: a field study of carbon gain and photo-inhibition in a California shrub during a dry El Niño year. *Plant Cell Environ.* 25: 749-759.
- VAN HEES A.F.M., CLERK P.M., 2003. Shading and root-shoot relations in saplings of silver birch, pedunculate oak and beech. *For. Ecol. Manag.* 176: 439-448.
- VOGT K.A., 1987. Conifer and angiosperm fine root biomass in relation to stand age and site productivity in Douglas-fir forests. *J. Ecol.* 75: 857- 870.
- WANG Y.-P., JARVIS P.G., 1990. Description and validation of an array model- MAESTRO. *Agric. For. Meteorol* 51: 257-280.
- WANG K.Y., KELLOMÄKI S., ZHA T.S., PELTOLA H., 2004. Component carbon fluxes and their contribution to ecosystem carbon exchange in a pine forest: an assessment based on eddy covariance measurements and an integrated model. *Tree Physiol.* 24: 19-34.
- WARING R.H., 1983. Estimating forest growth and efficiency in relation to canopy leaf area. *Adv. Ecol. Res.* 13: 325-354.
- WARING R.H., RUNNING S.W., 1998. *Forest ecosystems-analysis at multiple scales*. Academic Press.
- WULLSCHLEGER Stan D., TUSKAN G.A., DIFAZIO S.P., 2002. Genomics and tree physiology. *Tree Physiol* 22: 1273-1276.
- YODER B., RYAN M.G., WARING R.H., SCHOETTLE A.W., KAUFMANN M.R., 1994. Evidence of reduced photosynthetic rates in old trees. *For. Sci.* 40: 513-527.
- ZERIHUN A., MONTAGU K.D., 2004. Belowground to aboveground biomass ratio and vertical root distribution responses of mature *Pinus radiata* stands to phosphorus fertilization at planting. *Can. J. For. Res.* 34 (9): 1883-1894.
- ZOBEL B.J., TALBERT J.T., 1984. *Applied forest tree improvement* Wiley&sons, NY.