A MAESTRO Retrospective

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Introduction

It is sometimes said that the measure of a good scientist is not how much work they themselves do, but how much they stimulate in others. Accordingly, the MAESTRO model may be cited as one piece of evidence for the importance of Paul Jarvis' contribution to plant ecophysiology. The model was fostered by Paul throughout its development and its subsequent use in an extraordinary variety of applications. One may easily argue that it has strongly influenced the way in which we think about forest canopy processes.

The occasion of Paul's retirement provides an opportunity for reflection on the development of forest tree ecophysiology over the last few decades and the history of the MAESTRO model embodies many aspects of this development. In this article I review the history of MAESTRO. I revisit the ideas leading to the development of the model and survey the wide range of applications for which it has been used. The history of the model takes us on a fascinating tour through forest tree ecophysiology during the last three decades.

Development of MAESTRO

Although the name 'MAESTRO' first appeared in print in Ying-Ping Wang's thesis in 1988, the model had a very long gestation period stretching back to the early 1970s, and involving work in several different countries. Inextricably associated nowadays with Edinburgh, the model's development also owes much to researchers in the US and New Zealand.

The 'twinkle in the eye' that eventually led to the birth of MAESTRO, however, may be said to have taken place in Aberdeen, where John Norman came to do a postdoctoral associateship with Paul Jarvis from March 1971 to May 1972. They were studying light interception by shoots of Sitka spruce with the aim of modeling the photosynthesis and transpiration in conifers. John Norman writes:

"From a model of shoot light interception that we never published, we knew that the distribution of light surrounding a spruce shoot was very important to predicting the photosynthesis and stomatal conductance of that shoot. Therefore we needed to model the light distribution in the spruce canopy in order to get a good estimate of what shoots were doing." (Norman 2001, person. comm.)

The work they did led to two of the publications in the well-known “Photosynthesis of Sitka spruce” series (Norman and Jarvis 1974, 1975). Contemporary models of canopy radiation transmission generally represented canopies as either arrays of solid geometric objects or as a horizontally homogeneous layer of randomly distributed elements (Lemeur & Blad 1974). The major advance contributed by Norman & Jarvis (1974, 1975) was to measure and characterise non-randomness in forest canopy structure and to incorporate this in a model. Reviews of radiation models of the time were strongly critical of ‘armchair’ models developed at the desk while field observations were almost non-existent (Lemeur & Blad 1974, Norman 1975). The work of Norman & Jarvis (1974, 1975) met this criticism with detailed measurements of shoot, whorl and crown structure (despite the “arduous and self-defeating” nature of the task; Norman (1975)). This work laid the foundation for a continued emphasis on empirical validation of theoretical results throughout the development of MAESTRO (Grace *et al*. 1987a; Wang & Jarvis 1990a).

Returning from Scotland, John Norman took up a position at Penn State in the US, where together with an M.Sc. student, Jon Welles, he developed the model feature that was to distinguish MAESTRO from other models of its time, namely the treatment of the canopy as a three-dimensional array of ellipsoidal tree crowns (Figure 1). Jon Welles describes how this came about:

> “I was a masters student at Penn State, looking for a thesis topic and an advisor, and somehow got connected with John Norman, one of the two faculty members (of about 15) there who did actual field work in micrometeorology. John did a good sales job on me, and we set out to do a radiative model of a heated orchard. This was in the days when it was not uncommon to protect orchards from frost damage by interspersing fuel oil powered heaters among the trees. There were controversies about the most efficient heater arrangements and protocols (the first oil embargo having recently happened), and we thought we could provide some answers. The model was an exercise in geometry; one had an array of isolated tree canopies, each containing foliage at some density and orientation distribution. Interspersed among the trees was an array of heaters. The model computed foliage temperature distributions based on the radiation balance of foliage elements, which was determined by the element's relative view of the cold sky, hot heaters, ground, and other foliage. There were three publications that came out of that work, in addition to the thesis: "An orchard foliage temperature model" (Welles *et al*. 1979); "Modelling the radiant output of orchard heaters" (Welles *et al*. 1981); and "Radiative transfer in an array of canopies" (Norman and Welles 1983). I believe it was the material in this third publication that went into the model that came to be known as Maestro.” (Welles 2001, person. comm.)

The model was known as GAR (General Array Model). Welles went on to develop the model further for his PhD, on bidirectional reflectance and transmittance, and renamed it BIGAR (Welles and Norman 1991). Later he joined Li-Cor and notes that his experience in radiation modelling served him well when developing the LAI2000 Plant Canopy Analyzer.

Paul Jarvis remained in touch with Norman and was aware of the work that he and Welles were doing. Around 1982, Paul went to visit Forest Research in NZ for a period of several months. At that time the tree physiology section at Forest Research had as a goal:

“To model the impact of silviculture on crown and stem growth in radiata pine stands with the objective of providing the silviculturist with a predictive tool for managing his crop through pruning / thinning / fertilisation / disease control to optimise the desired timber product.”

Paul suggested the model of Norman and Welles (1983) would be a useful way to examine effects of thinning and pruning on forest tree growth, and a copy of the code was duly obtained from Welles. Jenny Grace was a post-doc at Forest Research at the time and was given the job of modifying the model for *Pinus radiata*. She made many improvements that came to be fundamental to the model, including (Figure 2): the specification of individual tree crown positions and dimensions; the introduction of non-random foliage distributions within the crown; modelling of crowns as truncated ellipsoids, useful for simulating pruning; and the use of gridpoints evenly spaced through the crown for calculating photosynthesis (Grace *et al*. 1987a,b). The model at this time was known as radiate.

Although Grace’s work modifying the model was successful, she notes that the overall aim of the project, to develop a process-based growth model, was not achieved. She writes:

“[The aims of the model] were really in direct competition with those of mensurational models, and these could be developed far quicker and included data from a wide range of sites. The geology and climate within New Zealand is far too variable for data from one site to hold for all other sites.” (Grace 2001, person. comm.)

The aim of developing a good predictive process-based growth model was very ambitious and remains something of a holy grail today.

Grace’s background was in empirical forest modelling and she was enthusiastic to work on a process-based model in order to bring more physiology into her work. This emphasis continues to influence her work: since 1991 she has been studying branch development in radiata pine and has made a deliberate attempt to include elements of both empirical and process models.

Meanwhile, Paul Jarvis had returned to Edinburgh and was on the lookout for someone to continue building on Grace’s work in his lab. Russ Sinclair, of Adelaide University, was on study leave in Edinburgh during the second half of 1983. He hoped to use the model as part of his study on whole-tree transpiration rates, but notes that the program was very involved and he made little progress. The model evidently needed some dedicated hard work. The man for the job arrived in Edinburgh in early 1985. Fresh from China, Ying-Ping Wang was planning to do a thesis on water relations with Paul. Instead, Paul managed to convince him to work on modelling radiation use efficiency in Sitka spruce. Armed with a copy of Grace’s model on tape, and a Fortran textbook translated into Chinese, Wang set about reprogramming the model to make it work on the university mainframes. Andrew Sandford, a postdoctoral associate in the lab at the time, played an important role as day-to-day supervisor, computer adviser and interpreter for Wang. John Norman also returned to visit at this time and was influential in helping Wang to test the model, suggesting such experiments as observing model behaviour with the leaf reflectance set to one.

Wang developed a new method to describe the distribution of leaf area density within canopies using two-dimensional beta functions (Wang *et al*. 1990), and implemented leaf incidence angle distributions (Wang & Jarvis 1988) (Figure 3). However, Wang's main contribution was in developing the model to the point where it could be carefully validated against measurements of PAR transmittance in the field. Wang spent several weeks camped in Tummel Forest making these measurements. He also empirically validated the leaf area estimates. Andrew Sandford recalls:

> "I remember Paul breaking the news that YP [Wang] had to validate the leaf area estimates manually which involved a lot of work in harvesting several trees and feeding them through a Li-Cor leaf area meter. Sitka spruce has rather sharp needles and that was not a fun thing to have to do! This was one of the few periods I remember YP lost that enthusiastic smile he had (and still has to this day). I seem to recall Paul disappeared on a sabbatical or something similar during this process, so missed most of the mess of having several trees spread across the lab." (Sandford 2001, person. comm.).

Paul soon realised that the model Wang was developing had great potential. When he went to Australia for several months in 1986, he took Wang with him to apply and validate the model against the highly detailed dataset from the Biology of Forest Growth experiment in Canberra (Wang *et al*. 1990). During this visit Wang worked with another major influence, Ross McMurtrie, who was developing the BIOMASS model at the time.

Wang's thesis appeared in 1988. Several papers from this thesis were published soon after (Wang & Jarvis 1990b,c) including the key paper Wang and Jarvis (1990a), in which MAESTRO was fully described and validated. The exact origin of the name MAESTRO is now lost in time, but it seems likely that it emerged from the Jarvis household. The name is, in fact, an acronym, although the acronym is generally conveniently forgotten, since it's unlikely to go down well with funding bodies. However, I can here reveal that it stands for: Multi Array Evaporation Stand Tree Radiation Orgy.

Having developed this useful tool, the Jarvis lab were not slow to put it to use, and published applications of the model followed very soon after. In 1989 Jarvis *et al*. used the model to estimate effects of water stress on *Eucalyptus globulus* plantations in Portugal, while Dick *et al*. (1990) used the model to look at the effect of cone-bearing on photosynthesis in *Pinus contorta*. These two early papers are indicative of the diversity of applications in which the model has proved useful. Wang notes that the most curious application he heard of was that of a landscape architect in Sheffield who wanted to predict shading of buildings by street trees.

Although the structure of the model essentially remained the same as that described by Wang and Jarvis (1990a), it continued to be developed during the years that followed. Craig Barton and Jon Massheder, working in collaboration with Bob Teskey of the University of Georgia, added responses to ozone and a water balance to the model. Bart

Kruijt added responses to CO_2, foliar nitrogen, and acclimation to PAR. As part of an EU-funded collaborative project, ECOCRAFT, I rewrote the model to make it easier to use, and set up a website to disseminate the code. As I was working with an Italian student, Sabina Dore, at the time, we jokingly renamed the rewritten model to MAESTRA.

The continuing success of the model is somewhat surprising to those who worked on it in the early days. Wang reflects that it may be attributed to several factors – perhaps not least of which being Jarvis's ability as a salesman! But also, Wang notes, the core of the model has stood the test of time because it is based on sound physical principles describing radiation transmission through canopies. The model was unique when developed because of the three-dimensional description of the canopy, making it a versatile tool to study canopy processes in detail. Its use as a research tool was strongly encouraged, and it was flexible enough for a very wide variety of applications, all of which made it attractive to many researchers. In what follows, I survey some of the major fields of application of the model.

Applications of MAESTRO

Canopy structure

Perhaps the most important feature of the MAESTRO model is the level of detail it uses to represent the canopy. This level of detail makes it possible to explore in a concrete way the interactions between canopy structure and canopy processes. The obvious application of this detailed model is to examine the direct influence of canopy structure on radiation interception and photosynthesis. Thus, one of the first exercises with the model that came to be known as MAESTRO was to examine the sensitivity to stocking, foliar density and crown shape (Rook *et al*. 1985). Similarly, an inaugural application of the newly named MAESTRO (Wang and Jarvis 1990b) was a detailed investigation of the importance of crown shape, leaf area, leaf area distribution, and leaf inclination angles for crown radiation interception and photosynthesis. Wang and Jarvis (1990b) were able to show that total leaf area and leaf area distribution were the most important properties for canopy processes. Using a variant of Grace's model, Whitehead *et al*. (1990) came to a similar conclusion, that within-crown leaf area distribution had an important effect on radiation interception.

An important, related practical application was the investigation of the importance of changes in canopy structure due to silvicultural treatments. Hence, Grace's main applications of her model were to examine effects of thinning, pruning, tree arrangement and defoliation by insects. Grace *et al*. (1987a) illustrated that pruned *Pinus radiata* stands intercepted more radiation than thinned stands with the same leaf area index. Grace (1988b) showed that green crown pruning led to an exponential reduction in intercepted PAR and photosynthesis, and estimated the maximum effect on canopy photosynthesis of defoliation by a major pathogen. Grace (1990b) investigated the effects of tree spacing and arrangement on radiation interception, a study with important implications for agroforestry.

Silvicultural applications have been less common since Grace's work, although the model was recently applied by Ibrom (1999) to examine thinning strategies for Sitka spruce. As Grace and colleagues state many times, the model only calculates radiation interception and photosynthesis, not growth, owing to a lack of understanding of allocation patterns. Hence long-term responses to silvicultural treatments cannot be predicted, a major limitation to model application. I return to this problem of linking photosynthesis and growth later in this chapter.

Agroforestry

The three-dimensional representation of the canopy in MAESTRO also had obvious relevance to agroforestry, and several attempts have been made over the years to use the model to predict or interpret radiation interception, photosynthesis and water use in agroforestry systems. An early example was given by Grace (1988a), who showed that while row orientation had little effect, alternative arrangements of trees could vary annual canopy photosynthesis by up to 11% in a *Pinus radiata* system with 100 stems ha^{-1}.

In the early 90's, as part of the Agroforestry Modelling Project, MAESTRO was coupled to a crop model, PARCH, to provide a representation of the entire agroforestry system (Lawson *et al*. 1995). The coupled model was used to predict crop yield of a maize/eucalyptus system in different climates. The coupled model predictions differed from those of a second model assuming a horizontally homogenous canopy, in that at the driest site the spatial distribution of PAR interception and evapotranspiration allowed small areas distant from the tree sufficient water to produce a modest yield, while the second model predicted complete crop failure. However, these model predictions were not followed up with experimental tests. Levy (1994) noted several problems with the approach taken in this project, including the difficulty of evaluating tree-crop competition for water because of lack of information on root spatial distribution. As Grace (1988a) commented, "the full potential of process-based model will not be realised until there is a sound theory for allocation of carbon … At present the model is most suited to research studies."

The use of the model as a research tool is exemplified in the study by Broadhead (2000) on agroforestry systems involving two contrasting indigenous tree species in Kenya. MAESTRA (the model had undergone its sex-change by this time) was first validated against quantum sensor measurements made beneath the tree canopies. The model was then used to scale leaf level measurements to estimate canopy-scale photosynthesis and transpiration, which could be compared for the two different systems. The model thus played an important role in synthesis and interpretation of field data. Broadhead (2001, person. comm.) wrote: "MAESTRO was a Godsend because I had collected a lot of data not really thinking that the models available would be so constraining with respect to the high level of aggregation of data they required."

Physiology

Many researchers have found MAESTRO to be a highly useful tool to integrate measurements of leaf physiology over the canopy, thus obtaining canopy-scale responses. Applications of MAESTRO along these lines include the effects of water, nutrient, and low temperature stress; elevated ozone levels; elevated atmospheric [CO_2]; and climate change. The first such study was relatively simplistic: Jarvis *et al.* (1989) simulated water, nutrient and low-temperature stress by halving the quantum efficiency, the stomatal conductance and the carboxylation efficiency, singly and in combination, depending on the type of stress. This exercise gave a basic understanding of the sensitivity of canopy photosynthesis to each of these leaf photosynthetic parameters.

The studies that followed generally adopted a more detailed approach. Modelling of canopy photosynthetic responses to ozone, for example, was based on long-term field studies of branch-scale ozone responses in loblolly pine (Teskey *et al.* 1991). These studies were used to characterise responses of leaf phenology and physiology to light, temperature, VPD, predawn water potentials, and ozone levels. MAESTRO was then used to estimate the effect of ozone on annual canopy photosynthesis, and to investigate interactions with incident PAR and water stress (Jarvis *et al.* 1990; Dougherty *et al.* 1992).

There have also been numerous studies in which MAESTRO has been used to examine effects of elevated atmospheric [CO_2] and elevated temperature on canopy photosynthesis. McMurtrie *et al.* (1992) and McMurtrie & Wang (1993) first illustrated how leaf-level responses to [CO_2] and temperature could be incorporated into models of canopy photosynthesis. They estimated the responses of canopy photosynthesis to changes in [CO_2] and temperature and showed how these could be interpreted in terms of the proportions of light-saturated and non-saturated foliage. These papers were extremely important in showing how information from small-scale experimental studies on elevated [CO_2] could be extrapolated to the canopy. Two important limitations to the use of MAESTRO were noted, however. First, the absence of nutrient cycling in the model means that long-term nutrient feedbacks could not be estimated. McMurtrie *et al.* (1992) overcame this limitation by using a hierarchy of models; the detailed model MAESTRO was used to develop a simple relationship that could be fed into a simpler model of plant carbon and nutrient cycling. This strategy is an example of hierarchical modelling, a common use of MAESTRO, to which I return below.

A second shortcoming noted by McMurtrie and Wang (1993) was that the model did not incorporate phenomena of acclimation of photosynthesis to [CO_2]. This shortcoming was addressed in papers following soon after. Medlyn (1996) used MAESTRO to investigate how the response of canopy photosynthesis to elevated [CO_2] was modified by down-regulation due to reduced leaf nitrogen content or leaf Rubisco activity, both acclimatory responses which had been observed in high-[CO_2] experiments. Kruijt *et al.* (1999) included feedbacks from changes in leaf phenology, leaf area and nutrition in their study of the sensitivity of canopy photosynthesis and transpiration to changes in atmospheric [CO_2] and climate. In this study, two tree species with contrasting canopy structure were considered, *Picea sitchensis* and *Betula pendula*. It was found that canopy photosynthesis in *B. pendula* was more sensitive to the hypothesised feedbacks, owing to the deciduous nature of the canopy.

The above studies on elevated [CO_2] were theoretical studies designed to investigate implications of responses measured in experimental studies to mature forest canopies. The model has also proved extremely useful in directly interpreting results of experiments. Wang *et al* (1998) reported an analysis of data collected on a study of birch trees grown for four years in ambient and elevated [CO_2]. Using an extensive dataset on plant structure, leaf area development, photosynthesis, stomatal conductance and respiration measured during the final year of the experiment, Wang *et al*. constructed a carbon balance for both ambient and elevated-[CO_2] grown trees. They showed that net canopy photosynthesis was increased by 110% in elevated [CO_2], as a result of the direct effect of increased [CO_2] on photosynthesis plus to the indirect effect of enhanced leaf area; but that biomass increment only increased by 59% over the year, implying substantial losses of carbon to fine-root turnover and mycorrhizae in the elevated [CO_2] treatment.

The approach used by Wang *et al*. (1998) was applied by Laitat *et al*. (1999) to analyse a series of four other experiments. Responses of aboveground biomass to elevated [CO_2] in these experiments varied from zero to a 140% increase. The MAESTRA model was used to analyse the reasons for the different responses in different experiments; it was found that canopy structure (single trees vs. plant canopies) and allocation patterns played key roles in determining the observed responses.

Finally, a similar study is under way on the Duke Forest FACE (Free-Air CO_2 Exchange) experiment. Luo *et al*. (2001) used MAESTRA to scale up from leaf-scale physiology measurements to estimate canopy carbon uptake in both ambient and elevated [CO_2] treatments. Eddy-flux measurements were available to validate the estimates in the ambient treatment. It was estimated that treatment with elevated [CO_2] increased gross primary productivity by 35 – 40%; it remains to compare these estimates to biomass measurements to determine elevated [CO_2] effects on partitioning.

Acclimation to PAR

In addition to studies that integrate leaf physiology over the canopy, MAESTRO has also been used to study the distribution of leaf physiological properties within the canopy. A question of particular interest is whether or not the distribution of leaf nitrogen content and photosynthetic capacity are related to the distribution of intercepted PAR. Many so-called "big-leaf" models of forest canopies rest on this assumption (e.g. Sellers *et al*. 1992). Kruijt *et al*. (1999) modified MAESTRO such that photosynthetic capacity followed intercepted PAR averaged over a given time frame and showed that, under this assumption, the "big-leaf" simplification held even for a complex canopy.

However, other studies which compared measured distributions of leaf nitrogen content with the distribution of intercepted PAR modelled using MAESTRO generally concluded that the two distributions were not correlated (Leuning *et al*. 1991, Livingston *et al*. 1998). Livingston *et al*. (1998), for example, showed that while leaf nitrogen content declined consistently with height, there was a strong azimuthal variation in intercepted radiation, implying that the distribution of leaf nitrogen was influenced by other factors, potentially including the sink strength of the leader. Bart Kruijt used MAESTRO to investigate the potential error involved in making the "big-leaf" assumption of perfect correlation between leaf nitrogen and intercepted PAR; however, these results were never published.

Analysis of flux data

An area of forest ecophysiology that has gained dramatically in momentum over the last ten years is the use of eddy covariance to measure carbon uptake rates by forests. Naturally MAESTRO has been brought in to this area as well. In several studies the eddy covariance data has simply been used to validate baseline model estimates of canopy carbon exchange (or the other way round, as some modellers might claim!) (Jarvis 1995, Rayment 1998, Ibrom 1999, Luo *et al*. 2001). However, the model also has great potential for interpreting eddy covariance measurements in terms of underlying physiological processes, particularly for sparse canopies (Levy *et al*. 1997). For example, work is under way to use MAESTRA to analyse reasons for measured differences in carbon sequestration between contrasting forest stands (Medlyn *et al*., in prep.).

Model hierarchies

MAESTRO is a highly complex and detailed model and is thus inappropriate for many studies involving large spatial scales or long time scales. Simpler models with fewer parameters must be used in such cases. However, MAESTRO has still proven highly useful in studies on such scales, being used either to develop or to test the simplifications used. One example already mentioned above is the work of McMurtrie *et al*. (1992), who used MAESTRO to develop relationships between light-use efficiency, leaf nitrogen concentration and atmospheric CO_2 concentration. These relationships were then fed into the nutrient cycling model G'DAY to predict long-term forest responses to elevated [CO_2]. The light-use efficiency model is a good example of a simple model, useful at large spatial and time scales, which can readily be calibrated using MAESTRO (e.g. Wang *et al*. 1991, 1992, Kirschbaum *et al*. 1994). The validity of the light use efficiency approach was also thoroughly analysed using MAESTRO (Medlyn 1998).

Other examples of the use of MAESTRO to test or calibrate the canopy component of larger scale models include the work of Wang and Polglase (1995), who developed a long-term model of forest carbon balance under climate change, and Luxmoore *et al*. (2000), who attempted to assess forest response to environmental change at the regional scale. Finally, there have also been several studies where output from MAESTRO has been used to develop models of tree growth (e.g. Ludlow *et al*. 1990, Baldwin *et al*. 2001). The issue of modelling tree growth has been one which has troubled MAESTRO modellers throughout the history, so I examine it in more detail in the following section.

Modelling Forest Growth

As described above, much of the early development of the MAESTRO model was carried out by the New Zealand Forest Research Institute, who were ultimately aiming to produce a process-based model of forest growth. MAESTRO was to be one component of this model (Rook *et al*. 1985). However, although Grace *et al*.'s (1987a,b) work with MAESTRO was highly successful, the aim of producing a predictive process-based forest growth model was never achieved, largely because of the difficulty of modelling carbon partitioning. The realisation of the magnitude of this obstacle may be traced in the series of published articles. Grace *et al*. (1987b) wrote blithely: "The addition of routines for respiration, allocation of carbon from photosynthesis, and tree dimensional growth will improve our understanding of the factors controlling tree growth." Compare this with Grace (1990a): "to make full use of the potential of process models will require a long commitment to ecophysiological research". Although predictions of canopy photosynthesis were correlated with measurements of aboveground net primary productivity (Grace *et al*. 1987b), these correlations were specific to forest types, and hence the goal of being able to apply the model to predict growth in any given forest stand was unattainable (Goulding 1994).

The group in Edinburgh faced the same problems. Andrew Sandford writes:

"At the time I thought it probably a little premature trying to implement more detailed photosynthesis models when the program (or model) was weak in other areas. I guess other groups with expertise in partitioning and growth have now improved those sections, so by now it should be pretty good?" (Sandford, 2001, person. comm.)

However, despite Jarvis' continuing efforts to have allocation routines added to MAESTRO, the model remains without them. I suspect that most modellers would find that it would be unbalanced to incorporate our sketchy, empirical understanding of allocation processes into the highly detailed, complex (and yes, still time-consuming) radiation transmission scheme of MAESTRO. The best alternative seems to be the hierarchical approach whereby MAESTRO is nested within a growth model. Baldwin and colleagues (Baldwin *et al*. 1993, 1998, 2001) have made the most progress using this approach. They linked MAESTRO with a distance-dependent, individual tree model, PTAEDA2, and obtained a coupled model system able to predict changes in forest stand growth and yield in response to environmental changes. The linkage was achieved by passing tree and stand descriptive information from PTAEDA2 to MAESTRO, and changes in canopy photosynthesis and thus stand index back the other way. The coupled system gives reasonable results for the system for which it was developed, namely loblolly pine stands (Baldwin *et al*. 1998), but considerable effort would be required to adapt it for other forest stands.

Conclusion: Maestro – Past and Future

From this overview it is clear that, despite the failure to create the hoped-for process-level growth model, MAESTRO has been a highly successful model. Its most important role has not been as a predictive model, but rather as a research tool, allowing a generation of workers to explore ideas and refine thinking in many different areas of research.

And what of the model's future? MAESTRA is currently provided free of charge on the World-Wide Web (see bibliography). Despite concerted efforts to make the model more user-friendly, it remains highly complex, a fact likely to deter the casual user. However, good documentation is provided, and, with its well-established core of radiation transmission, it seems likely that the model will continue to see application in the future. The year 2000 bug was recently fixed; one wonders if the year 2050 bug that was thereby introduced will ever need to be corrected!

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Maestro Bibliography

Website:
http://www.maestra.unsw.edu.au/

Model Development:
Norman, J.M. and Jarvis, P.G. (1974) Photosynthesis in Sitka spruce (*Picea sitchensis* (Bong.) Carr.) III. Measurements of canopy structure and interception of radiation. *Journal of Applied Ecology* 11, 375-398.

Norman, J.M. and Jarvis, P.G. (1975) Photosynthesis in Sitka spruce (*Picea sitchensis* (Bong.) Carr.) V. Radiation penetration theory and a test case. *Journal of Applied Ecology* 12, 839-878.

Norman, J.M. and Welles, J.M. (1983) Radiative transfer in an array of canopies. *Agronomy Journal* 75, 481-488.

Welles, J.M. and Norman, J.M. (1991) Photon transport in discontinuous canopies: a weighted random approach. In: Myneni, R.B. and Ross, J. (ed.) *Photon-Vegetation Interactions*. Springer-Verlag, Berlin, pp. 389-414.

Grace, J.C., Jarvis, P.G. and Norman, J.M. (1987a) Modelling the interception of solar radiant energy in intensively managed stands. *New Zealand Journal of Forest Science* 17, 193-209.

Grace, J.C., Rook, D.A. and Lane, P.M. (1987b) Modelling canopy photosynthesis in *Pinus radiata* stands. *New Zealand Journal of Forest Science* 17, 210-228.

Wang, Y.P. (1988) Crown structure, radiation absorption, photosynthesis and transpiration. PhD thesis, University of Edinburgh, Scotland, U.K.

Wang, Y.P. and Jarvis, P.G. (1990a) Description and validation of an array model – MAESTRO. *Agricultural and Forest Meteorology* 51, 257-280.

Model components:
Daylength calculation

Barkstrom, B. (1981) What time does the sun rise and set? *BYTE* July 1981, 94-114.
Partitioning of direct and diffuse radiation

Spitters, C.J.T., Toussaint, H.A.J.M. and Goudriaan, J. (1986) Separating the diffuse and direct component of global radiation and its implications for modeling canopy photosynthesis. I. Components of incoming radiation. *Agricultural and Forest Meteorology* 38, 217-229.

Weiss, A. and Norman, J.M. (1985) Partitioning solar radiation into direct and diffuse, visible and near-infrared components. *Agricultural and Forest Meteorology* 34, 205-213.
Irradiance on slopes

Steven, M.D. and Unsworth, M.H. (1979) The diffuse solar irradiance of slopes under cloudless skies. *Quarterly Journal of the Royal Meteorological Society* 105, 593-602.
Leaf angle distribution

Campbell, G.S. (1986) Extinction coefficients for radiation in plant canopies calculated using an ellipsoidal inclination angle distribution. *Agricultural and Forest Meteorology* 36, 317-321.

Wang, Y.P. and Jarvis, P.G. (1988) Mean leaf angles for the ellipsoidal inclination angle distribution. *Agricultural and Forest Meteorology* 43, 319-321.

Campbell, G.S. (1990) Derivation of an angle density function for canopies with ellipsoidal leaf angle distributions. *Agricultural and Forest Meteorology* 49, 173-176.
Crown shape

Baldwin, V.C. Jr and Peterson, K.D. (1997) Predicting the crown shape of loblolly pine trees. *Canadian Journal of Forest Research* 27, 102-107.
Leaf area density distribution (beta functions)

Wang, Y.P., Jarvis, P.G. and Benson, M.L. (1990) Two-dimensional needle-area density distribution within the crowns of *Pinus radiata*. *Forest Ecology and Management* 32, 217-237.

Baldwin, V.C. Jr, Peterson, K.D., Burkhart, H.E., Amateis, R.L. and Dougherty, P.M. (1997) Equations for estimating loblolly pine branch and foliage weight and surface area distributions. *Canadian Journal of Forest Research* 27, 918-927.

Porté, A., Bosc, A., Champion, I. and Loustau, D. (2000) Estimating the foliage area of Maritime pine (*Pinus pinaster* Ait.) branches and crowns with application to modelling the foliage area distribution in the crown. *Annales des Sciences Forestières* 57, 73-86.

Model Applications:
Baldwin, V.C. Jr, Burkhart, H.E., Dougherty, P.M. and Teskey, R.O. (1993) Using a growth and yield model (PTAEDA2) as a driver for a biological process model (MAESTRO). USDA Forest Service Southern Forest Experiment Station Research Paper, No.276, p.U1 *et seq.*

Baldwin, V.C. Jr, Dougherty, P.M. and Burkhart, H.E. (1998) A linked model for simulating growth processes and stand development of loblolly pine. In: Mickler, R.A. and Fox, S. (eds.) *The Productivity and Sustainability of Southern Forest Ecosystems in a Changing Environment*. Springer-Verlag, New York, pp. 305–325.

Baldwin, V.C. Jr, Burkhart, H.E., Westfall, J.A. and Peterson, K.D. (2001) Linking growth and yield and process models to estimate impact of environmental changes on growth of loblolly pine. *Forest Science* 47, 77-82.

Broadhead, J.S. (2000) The Ecophysiology of Indigenous trees in Agroforestry Systems in the Semi-Arid Tropics. PhD Thesis, Nottingham University, U.K.

Dick, J.M., Jarvis, P.G. and Barton C.V.M. (1990) Influence of male and female cones on assimilate production of *Pinus contorta* trees within a forest stand. *Tree Physiology* 7, 49-63.

Dougherty, P.M., Teskey, R.O. and Jarvis, P.G. (1992) Development of MAESTRO, a process based model for assessing the impact of ozone on net carbon exchange of loblolly pine trees. In: Flagler, R.B. (ed.) *The response of southern commercial forests to air pollution: Transactions 21.* Air and Waste Management Association, Pittsburg, PA, pp. 37-48.

Grace, J.C. (1988a) Effect of tree arrangement on intercepted radiant energy and photosynthesis. In: Ek A.R., Shifley, S.R. and Burk, T.E. (eds.) *Forest Growth Modelling and Prediction*. US Department of Agriculture Forest Service General Technical Report NC-120, pp. 285-292.

Grace, J.C. (1988b) Effect of foliage distribution within crowns on intercepted radiant energy and photosynthesis. In: Werger M.J.A., van der Aart P.J.M., During H.J. and Verhoeven J.T.A. (eds.) *Plant Form and Vegetation Structure: adaption, plasticity and relation to herbivory.* SPB Academic Publishing The Hague, The Netherlands, pp. 153-159.

Grace, J.C. (1990a) Modeling the interception of solar radiant energy and net photosynthesis. In: Dixon, R.K., Meldahl, R.S., Ruark, G.A. and Warren, W.G. (eds.) *Process Modeling of Forest Growth Responses to Environmental Stress*. Timber Press, pp. 142-158.

Grace, J.C. (1990b) Process-level models for investigating alternative spacing patterns. In: James, R.N. and Tarlton, G.L. *New Approaches to Spacing and Thinning in Plantation Forestry*. Ministry of Forestry, FRI Bulletin No. 151, pp. 229-232.

Ibrom, A. (1999) Simulation of CO_2 and water vapour fluxes in a young Sitka spruce (*Picea sitchensis* (Bong.) Carr.) plantation. Internal Report, Institute of Ecology and Resource Management, University of Edinburgh.

Jarvis, P.G. (1995) The role of temperate trees and forests in CO_2 fixation. *Vegetatio* 121, 157-174.

Jarvis, P.G., Wang, Y.P., Borralho, N.M.G. and Pereira, J.S. (1989) Simulation of the role of stress on radiation absorption, assimilation, transpiration and water use efficiency of stands of *Eucalyptus globulus*. In: Pereira, J.S. and Landsberg, J.J. (eds.) *Biomass Production by Fast-Growing Trees.* Kluwer Academic Publishers, Dordrecht, pp. 169-179.

Jarvis, P.G., Barton, C.V.M., Dougherty, P.M., Teskey, R.O. and Massheder, J.M. (1990) Development and use of tree and forest response models: MAESTRO. In: *Acidic Deposition: SOS/T Vol III*. The U.S. National Acid Precipitation Assessment Program, Washington D.C., pp. 167-179.

Kirschbaum, M.U.F., King, D.A., Comins, H.N., McMurtrie, R.E., Medlyn, B.E., Pongracic, S., Murty, D., Keith, H., Raison, R.J. and Khanna, P.K. (1994) Modelling forest response to increasing CO_2 concentration under nutrient-limited conditions. *Plant, Cell and Environment* 17, 1081-1099.

Kruijt, B., Barton, C.V.M., Rey, A. and Jarvis, P.G. (1999) The sensitivity of stand-scale photosynthesis and transpiration to changes in atmospheric CO_2 concentration and climate. *Hydrology and Earth System Sciences* 3, 55-69.

Laitat, E., Ceulemans, R., Medlyn, B.E., LeFevre, F., Forstreuter, M., Jach, M.E., Rey, A., Strassemeyer, J. and Jarvis, P.G. (1999) Carbon uptake and allocation. In*: ECOCRAFT: Predicted Impacts of Rising Carbon Dioxide and Temperature on Forests in Europe at Stand Scale*. Final Report to the EU. Coordinator: Jarvis, P.G., Edinburgh University. Pp. 87-96.

Lawson, G.J., Crout, N.M.J., Levy, P.E., Mobbs, D.C., Wallace, J.S., Cannell, M.G.R. and Bradley, R.G. (1995) The tree-crop interface - representation by coupling of forest and crop process-models. *Agroforestry Systems* 30, 199-221.

Leuning, R., Wang, Y.P., Cromer, R.N. (1991) Model simulations of spatial distributions and daily totals of photosynthesis in *Eucalyptus grandis* canopies. *Oecologia* 88, 494-503.

Levy, P.E. (1994) Application of MAESTRO to tropical agroforestry systems. Internal Report, Institute of Ecology and Resource Management, University of Edinburgh.

Levy, P.E., Moncrieff, J.B., Massheder, J.M., Jarvis, P.G., Scott, S.L. and Brouwer, J. (1997) CO_2 fluxes at leaf and canopy scale in millet, fallow and tiger bush vegetation at the HAPEX-Sahel southern super-site. *Journal of Hydrology* 189, 612-632.

Livingston, N.J., Whitehead, D., Kelliher, F.M., Wang, Y.P., Grace, J.C., Walcroft, A.S., Byers, J.N., McSeveny, T.M. and Millard, P. (1998) Nitrogen allocation and carbon isotope fractionation in relation to intercepted radiation and position in a young *Pinus radiata* D. Don tree. *Plant, Cell and Environment* 21, 795-803.

Ludlow, A.R., Randle, T.J. and Grace, J.C. (1990) Developing a process-based growth model for Sitka Spruce. In: Dixon, R.K., Meldahl R.S., Ruark, G.A and Warren, W.G. *Process Modeling of Forest Growth Responses to Environmental Stress*. Timber Press, pp. 249-262.

Luo, Y., Medlyn, B.E., Hui, D., Ellsworth, D., Reynolds, J. and Katul, G. (2001) Gross primary productivity in the Duke forest: modeling synthesis of CO_2 experiment and eddy-flux data. *Ecological Applications* 11, 239-252.

Luxmoore, R.J., Hargrove, W.W., Tharp, M.L., Post, W.M., Berry, M.W., Minser, K.S., Cropper, W.P. Jr, Johnson, D.W., Zeide, B., Amateis, R.L., Burkhart, H.E., Baldwin, V.C. Jr and Peterson, K.D. (2000) Signal-transfer modeling for regional assessment of forest responses to environmental changes in the South-Eastern United States. *Environmental Modeling and Assessment* 5, 125-137.

McMurtrie, R.E., Comins, H.N., Kirschbaum, M.U.F. and Wang, Y.P. (1992) Modifying existing forest growth-models to take account of effects of elevated CO_2. *Australian Journal of Botany* 40, 657-677.

McMurtrie, R.E. and Wang, Y.P. (1993) Mathematical models of the photosynthetic response of tree stands to rising CO_2 concentrations and temperatures. *Plant, Cell and Environment* 16, 1-13.

Medlyn, B.E. (1996) The representation of photosynthetic productivity in an ecosystem model used to assess plant responses to climate change. PhD Thesis, University of New South Wales, Australia. 206 pp.

Medlyn, B.E. (1998) Physiological basis of the light use efficiency model. *Tree Physiology* 18, 167-176.

Medlyn BE, Berbigier P, Clement R, Grelle A, Loustau D, Linder S, Wingate L, Jarvis PG, Sigurdsson BD, McMurtrie RE (2005) The carbon balance of coniferous forests growing in contrasting climatic conditions: a model-based analysis. Agricultural and Forest Meteorology, in press.

Rayment, M.B. (1998) Carbon and water fluxes in a boreal forest ecosystem. PhD Thesis, University of Edinburgh, 145 pp.

Rook, D.A., Grace, J.C., Beets, P.N., Whitehead, D., Santantonio, D. and Madgwick, H.A.I. (1985) Forest canopy design: biological models and management implications. In: Cannell, M.G.R. and Jackson, J.E. (eds.) Attributes of trees as crop plants. Institute of Terrestrial Ecology, Natural Environment Research Council, Abbots Ripton, Huntingdon, pp. 507-524.

Wang, Y.P. and Jarvis, P.G. (1990b) Influence of crown structural properties on PAR absorption, photosynthesis, and transpiration in Sitka spruce – application of a model (MAESTRO). *Tree Physiology* 7, 297-316.

Wang, Y.P. and Jarvis, P.G. (1990c) Effect of incident beam and diffuse radiation on PAR absorption, photosynthesis and transpiration of Sitka spruce – a simulation study. *Silva Carelica* 15, 167-180.

Wang, Y.P., Jarvis, P.G. and Taylor, C.M.A. (1991) PAR absorption and its relation to aboveground dry-matter production of Sitka spruce. *Journal of Applied Ecology* 28,547-560.

Wang, Y.P., McMurtrie, R.E. and Landsberg, J.J. (1992). Modelling canopy photosynthetic productivity. In: Baker, N.R. and Thomas, H. (eds.) *Crop Photosynthesis: Spatial and Temporal Determinants.* Elsevier, Amsterdam, pp. 43- 67.

Wang, Y.P. and Polglase, P.J. (1995) The carbon balance in the tundra, boreal and humid tropical forests during climate change - scaling up from leaf physiology and soil carbon dynamics. *Plant, Cell and Environment* 18, 1226-1244.

Wang, Y.P., Rey, A. and Jarvis, P.G. (1998) Carbon balance of young birch trees grown in ambient and elevated atmospheric CO_2 concentrations. *Global Change Biology* 4, 797-807.

Whitehead, D., Grace, J.C. and Godfrey, M.J.S. (1990) Architectural distribution of foliage in individual *Pinus radiata* D. Don crowns and the effects of clumping on radiation interception. *Tree Physiology* 7, 135-155.

Additional References

Goulding, C.J. 1994: Development of growth models for *Pinus radiata* in New Zealand – experience with management and process models. *Forest Ecology and Management* 69, 331-343.

Lemeur, R. and Blad, B.L. (1974) A critical review of light models for estimating the shortwave radiation regime of plant canopies. *Agricultural Meteorology* 14, 255-286.

Norman, J.M. (1975) Radiative transfer in vegetation. In: deVries, D.A. and Afgan, N.H. *Heat and Mass Transfer in the Biosphere. Part I: Transfer Processes in the Plant Environment.* Scripta Book Company, Washington, DC, pp. 187-205.

Sellers, P.J., Berry, J.A., Collatz, G.J., Field, C.B. and Hall, F.G. (1992) Canopy reflectance, photosynthesis, and transpiration .3. A reanalysis using improved leaf models and a new canopy integration scheme. *Remote Sensing of Environment* 42, 187-216.

Teskey, R.O., Dougherty, P.M. and Wiselogel, A.E. (1991) Design and performance of branch chambers suitable for long-term ozone fumigation of foliage in large trees. *Journal of Environmental Quality* 20, 591-595.

Welles, J.M., Norman, J.M. and Martsolf, J.D. (1979) An orchard foliage temperature model. *Journal of the American Society for Horticultural Science* 104, 602-610.

Welles, J.M., Norman, J.M. and Martsolf, J.D. (1981) Modeling the radiant output of orchard heaters. *Agricultural Meteorology* 23, 275-286.

Figure Captions

Figure 1: Representation of the canopy in the Norman & Welles (1983) model. The canopy consists of an evenly spaced array of ellipsoidal tree crowns. The pathlength of radiation through crowns (S1 + S2) is calculated from geometrical considerations. Radiation transmission along the pathlength is calculated using Beer's Law.

Figure 2: Representation of the canopy in the Grace *et al*. (1987a,b) model. Positions and dimensions of each crown are now specified. Grid volumes within the target crown are used for crown photosynthesis calculations. Inner ellipsoids within crowns are used to specify leaf area distribution.

Figure 3: Representation of the canopy in MAESTRO (Diagram courtesy of Bart Kruijt). Tree crowns can now be cones. The leaf area distribution, for several different age classes, is specified both horizontally and vertically. Leaf physiological properties can be specified by age class and foliage height.

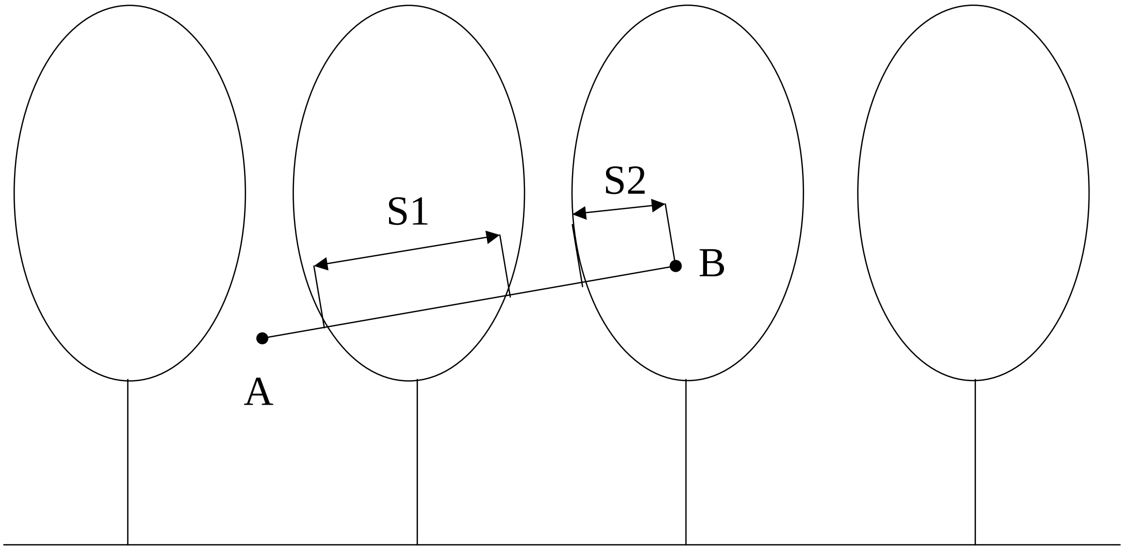

Fig. 1

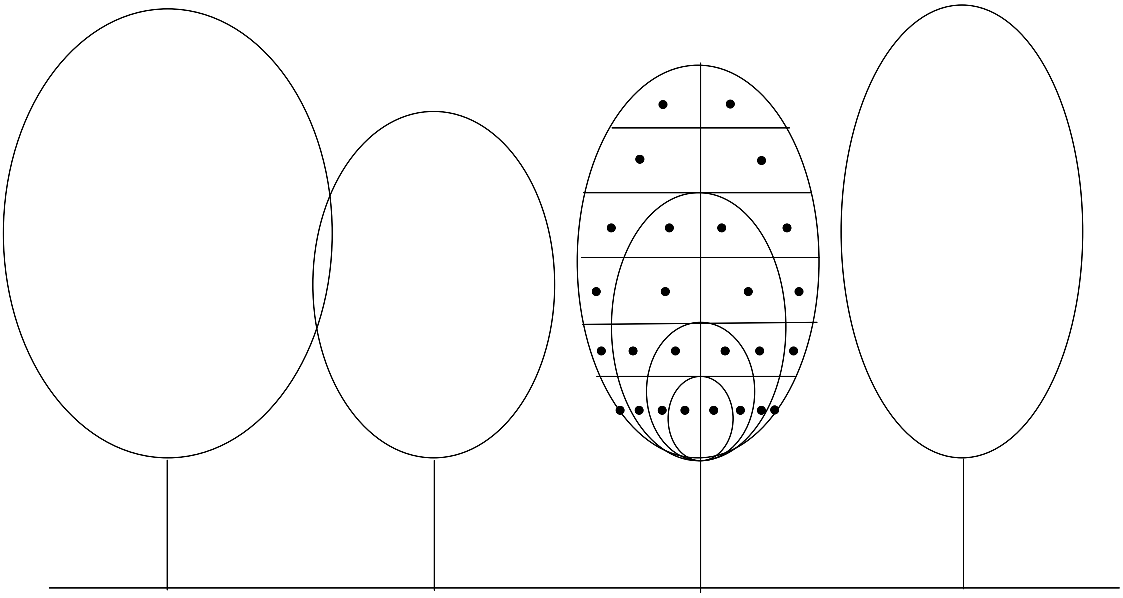

Fig. 2

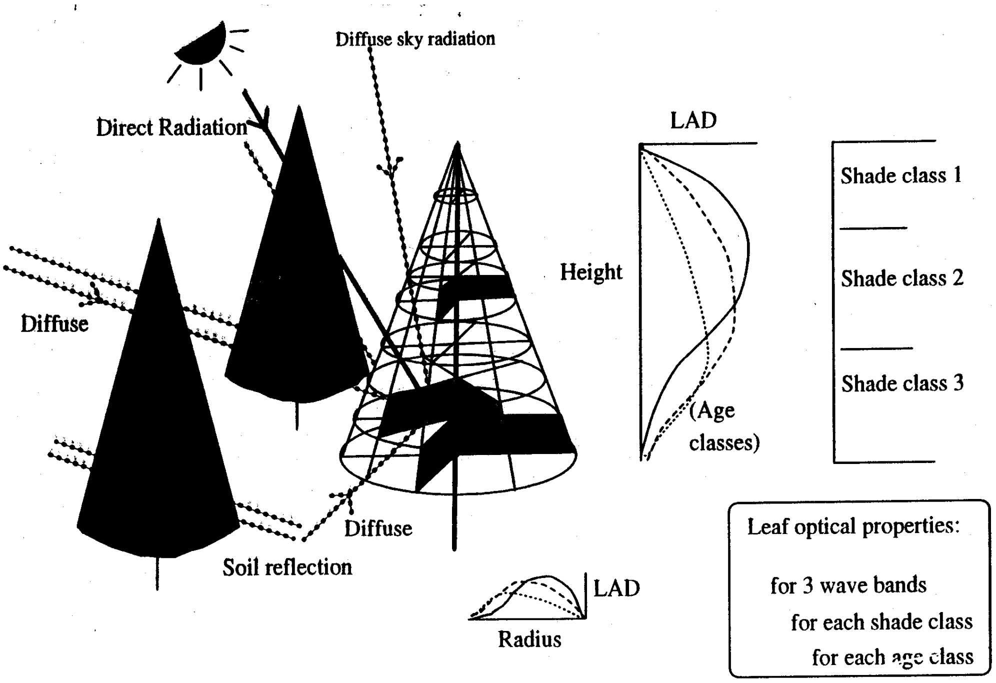
Diffuse sky radiation
Direct Radiation
Diffuse
Diffuse
Soil reflection
LAD
Height
(Age
classes)
Shade class 1
Shade class 2
Shade class 3
LAD
Radius
Leaf optical properties:
for 3 wave bands
for each shade class
for each age class

Fig. 3