The response of the Amazonian rain forest
Gas exchange to reduced rainfall

by

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Thesis
Submitted to the University of Edinburgh
for the degree of
Doctor of Philosophy

School of GeoSciences
January 2005
Declaration

I composed this thesis, the work is my own
No part of this thesis has been submitted for any other degree or qualification

Rosie A. Fisher, 06 June, 2005
Acknowledgements

During the course of my PhD, I have been fortunate enough to have been assisted along the way by many wonderful colleagues and friends. However, my greatest thanks must go to my supervisor, Mat Williams, who initially inspired me to start my PhD, and whose endless patience and good humour have seen it through to its completion. One could not ask any more of a PhD supervisor and I feel very lucky to have had his exceptional guidance both as a student and a friend.

My second thanks go to Patrick Meir for his astonishing levels of empathy, tact and kindness and for coming all the way to Brazil to check I was OK. I would also like to thank Yadvinder Malhi for his infectious enthusiasm for travel and rain forests and the quest for the 'zen' tower.

I would like to thank also the many people who have helped me in the field in Brazil and slowed my gradual decline into insanity. The Brazilian students, Rafael Costa, João Athaydes, Paulinho Gonçalves and Alan Braga, and the staff of the Estacaö Cientifica Ferreira Penna, especially the trabaladores, obrigada! My fellow PhD students, Raquel, Luiz, Virginie, Dan and Eleneide, and the various wierd and wonderful visitors to the Estacao Cientifica Ferreira Penna who kept us all amused. The fieldwork in Brazil and the whole Esecaflor experiment would really not have been possible without the help of Antonio 'Lola' da Costa, to whom we are all very grateful.

Back in Edinburgh, I am have been kept thoroughly entertained by my office mates in the BAMG, Tim, Lorna, Luiz, Rui, Luke and Mark. The support of the EUBAP group, John, Maurizio, Caroline, Lisa, the 2 Keiths, Mark, Rob, Jordi, Emiliano and all the others has been invaluable for checking that my ideas were not crazy and providing much entertaining lunchtime chat.

My thesis was supported financially by an Edinburgh University PhD scholarship, several NERC grants, the Natural Resources Council and the Elizabeth Sinclair Fund. I am hugely grateful to all these institutions for allowing me to enjoy many amazing trips to the awesome Brazilian rain forest.
I owe many of the happy times I have had here to the Edinburgh University Mountaineering Club, for allowing me to escape from the city and do countless crazy things in wild, far off places. As well as this, I owe a special debt to the many occupants of 34 Arden Street, but in particular to Erica, Naomi and Susie for the legendary times in our girlie flat, and to Huw and Steve for their constant quest for mind mincing satire. I would like to thank Rik for being the guardian of my sanity for the last 14 months, and for not letting me become too much of a hermit, and my Mum, Dad, Tom and Laura for looking after me and for being the best family I could wish for. I would like to dedicate my thesis to Gandhi and Sindbad, who will be sorely missed.
I went too far too soon. I didn't know you had to follow a good idea with loads more little good ideas. I'm sorry. I'm going to sleep in the spare room.

(Father Dougal McGuire, 'Father Ted', Channel Four Television, 1998)
Abstract

In the next 50-100 years, most global climate models predict that the Eastern Amazonian rain forest may be subject to reductions in rainfall of up to 50%. Existing measurements of rain forest gas exchange during the dry season suggest that forests vary in their responses to drought stress for reasons that are not well understood. Improvements in understanding of forest responses to hydraulic stress are therefore necessary to predict the future of the Amazon basin.

We tested two interlinked hypotheses involved with forest responses to hydraulic stress from data collected at a through-fall exclusion (artificial droughting) experiment at Caxiuanã in Eastern Amazonia. Firstly, we tested the ‘isohydric’ hypothesis, that stomatal conductance, in water stressed conditions, operates to maintain leaf water potential above a certain critical threshold limit. We use the soil-plant-atmosphere (SPA) model to predict the expected ecophysiological behaviour of the trees, and test these predictions against intensive diurnal cycle measurements of leaf water potential, stomatal conductance, sap flow and stem water potential. The data and the model predictions were largely consistent, indicating that isohydric stomatal control may be the prevailing mechanism controlling water use of rain forest trees in drought stressed conditions.

Analysis of the stem water potential data indicated that water use was mainly constrained by below-ground hydraulic resistivity. To investigate this further, we made measurements of soil hydraulic properties, including unsaturated hydraulic conductivity, of the soil at the experimental site. We used the soil hydraulics data to parameterise a geometric model of soil water transport and root water uptake, coupled to the SPA model. The model predicts a priori the changes in soil-to-root hydraulic resistance occurring over time. We ran the model for 3 years. In the dry seasons, the plot exposed to artificial soil drying developed large soil-to-root hydraulic resistances, causing a constraint to soil-to-leaf water supply, stomatal closure and restrictions on tree water use (sap flow). These modelled predictions were tested against sap flow data, scaled from a sample of 24 individual trees, and soil
water content time-series data from both the droughted and control plots. The sap flow data showed restrictions of the same timing and magnitude as those predicted by the model in the droughted plot ($r^2 = 0.75$) and the prediction of seasonal changes in atmospheric demand in the control plot was also in good agreement with the data ($r^2 = 0.81$). The model was parameterised using independent measurements of ecosystem properties and as such required no fitted parameters. The implication of this is that the response of rain forest ecosystems to drought may be predicted using soil, rooting and vegetation properties.

The SPA model is both computationally and data requirement intensive. We assimilated the model and produced a set of empirical equations which replicate the daily modelled gas exchange predictions from daily model inputs. We extrapolated this model 100 years into the future using the latest Amazonian climate predictions and found that after ~50 years, a threshold was reached when all the rainfall falling on the plot was evaporated by interception, soil surface evaporation or evapotranspiration. This represents a threshold beyond which rain forests will interact with the regional climate system to further reduce rainfall, therefore accelerating the decline towards loss of the forest and conversion to savannah vegetation. Further modelling at larger scales, and fieldwork to better define root and soil properties is necessary to refine predictions of this 'threshold' in climate change.
Contents

1 Introduction

1.1 Empirical data on Amazonian rain forest gas exchange ....... 4
1.2 Through-fall exclusion experiments ...................... 5
1.3 Existing modelling approaches .......................... 6
1.4 Recent Modelling Developments ....................... 8
1.5 Deep rooting hypothesis ............................... 8
1.6 Overview of Thesis .................................... 9
1.6.1 Chapter 2. Evidence from Amazonian forests is consistent
with isohydric control of leaf water potential ............. 10
1.6.2 Chapter 3. The Hydraulic Properties of a Sandy Eastern
Amazonian Oxisol: Estimation of Unsaturated Hydraulic Con-
ductivity using Tension Infiltrometry and Instantaneous Pro-
fileing ......................................................... 11
1.6.3 Chapter 4: A process-based simulation of the response of rain
forest to drought stress .................................. 12
1.6.4 Chapter 5. A simple model of rain forest drought tolerance. 13
1.7 Publication Status of thesis contents .................... 14
1.8 Appendix 1.1: A review of the representation of drought stress in
commonly used vegetation models ......................... 15
1.8.1 1. The Terrestrial Ecosystem Model (TEM) ............... 15
1.8.2 2. MOSES/TRIFFID ..................................... 16
1.8.3 3. IBIS model .......................................... 17
1.8.4 4. Water budget method .............................. 18
1.8.5 5. GEOS GCM method .................................. 18
1.9 References ............................................... 19

2 Evidence from Amazonian forests is consistent with isohydric con-
viii
trol of leaf water potential.

2.1 Abstract .................................. 25
2.2 Introduction ................................ 26
2.3 Methods .................................. 28
  2.3.1 Site ................................... 28
  2.3.2 Through-fall Exclusion Experiment ............... 29
  2.3.3 Tree Physiology measurements .................. 30
2.4 Results ................................... 32
  2.4.1 Meteorology ................................ 32
  2.4.2 Sap Flow ................................ 33
  2.4.3 Stomatal Conductance ......................... 33
  2.4.4 Leaf Water Potential ......................... 34
  2.4.5 Stem Water Potential ......................... 34
  2.4.6 Branch resistivity ......................... 35
2.5 Modelling .................................. 35
  2.5.1 Justification of Modelling Exercise ............... 35
  2.5.2 The SPA model .......................... 42
  2.5.3 Model inputs ........................... 43
  2.5.4 Processing of model output for comparison with data .... 45
  2.5.5 Model sensitivity to wet-dry season input changes .......... 46
  2.5.6 Model Verification ........................ 46
2.6 Discussion ................................ 48
2.7 Conclusions ................................ 51
2.8 Acknowledgements ................................ 52
2.9 Appendix .................................. 52
2.10 References ................................ 53

3.1 Abstract .................................. 60
3.2 Introduction ................................ 60
3.3 Methods .................................. 63
  3.3.1 Site ................................... 63
  3.3.2 Water Retention Curve Measurement ............... 63
  3.3.3 Unsaturated Hydraulic Conductivity Measurement ......... 64
3.3.4 Tension Infiltrometer ........................................ 64
3.3.5 Instantaneous Profile Method ................................. 65
3.3.6 Soil moisture sensor calibration ............................ 65
3.3.7 Model Extrapolation of Hydraulic conductivity .......... 66
3.3.8 Parameter Fitting ............................................. 70
3.3.9 Prediction of Water Retention Curves from soil texture .. 71
3.3.10 Prediction of Hydraulic Conductivity from water retention curves and soil texture ...................... 71

3.4 Results ......................................................... 72
3.4.1 Soil Moisture Sensor Calibration ............................. 72
3.4.2 Water Retention ............................................... 72
3.4.3 Hydraulic conductivity ....................................... 76
3.4.4 Prediction of Water Retention Curves from soil texture .. 77
3.4.5 Prediction of Hydraulic Conductivity from water retention curves and soil texture ...................... 77

3.5 Discussion ..................................................... 79

3.6 Acknowledgements ............................................... 82

3.7 References ..................................................... 82

4 A process-based simulation of the response of rain forest to drought stress. 86
4.1 Abstract ......................................................... 87
4.2 Introduction ...................................................... 87
4.3 Methods .......................................................... 90
4.3.1 Site .......................................................... 90
4.3.2 Meteorology ................................................... 90
4.3.3 Sap flow ....................................................... 91
4.3.4 Soil water content .......................................... 92
4.3.5 Vegetation Characteristics .................................. 92
4.4 Results .......................................................... 92
4.4.1 Meteorology ................................................... 93
4.4.2 Sap Flow ....................................................... 93
4.4.3 Soil water ..................................................... 96
4.4.4 Vegetation Characteristics .................................. 96
4.5 Modelling ........................................................ 101
4.5.1 Canopy Parameterisation ...................................... 102
4.5.2 Below-ground parameterisation ............................................. 103
4.5.3 Through-fall exclusion ......................................................... 105
4.5.4 GPP Predictions ..................................................................... 106
4.5.5 Model sensitivity tests ............................................................. 106
4.5.6 Modelling results ................................................................. 107
4.5.7 Sensitivity Test Results .......................................................... 115
4.6 Discussion ................................................................................. 117
4.7 Conclusions ............................................................................... 121
4.8 Acknowledgements ................................................................. 121
4.9 Appendix ................................................................................... 122
4.10 References ............................................................................... 123

5 A simple model of rain forest drought tolerance. ............................ 129
5.1 Abstract .................................................................................... 130
5.2 Introduction ............................................................................... 131
5.3 Methods .................................................................................... 133
  5.3.1 Generation of response surface using the SPA model .......... 133
  5.3.2 Aggregation of SPA model ................................................... 134
  5.3.3 Evapotranspiration Model ..................................................... 136
  5.3.4 Soil water uptake model ....................................................... 136
  5.3.5 SWAT model inputs ............................................................. 138
  5.3.6 Model extrapolation to future climate states ....................... 139
5.4 Results ....................................................................................... 141
  5.4.1 Response of SPA model to inputs ........................................ 141
  5.4.2 GPP simulation by ACM-GPP ............................................. 146
  5.4.3 ET simulation by ACM-ET ................................................. 146
  5.4.4 Fit of ACM-SWAT model to forest data ............................... 146
  5.4.5 Extrapolation to future climate ........................................... 147
5.5 Discussion .................................................................................. 152
  5.5.1 What reduction in model accuracy is found if it possible to
      reproduce the behaviour of the detailed half hourly soil-plant-
      atmosphere model with a simple aggregated model? ............... 152
  5.5.2 Is it possible to explain the heterogeneous responses of forests
      to low rainfall using only measured changes in soil, root or
      vegetation characteristics? ...................................................... 152
5.5.3 At what point in the next century will predicted climate drying begin to have an impact on rainforest gas exchange? 153

5.6 Acknowledgements ............................................ 154
5.7 Appendix 1- GPP model ........................................... 155
5.8 Appendix 2: Soil water uptake .................................... 156
5.9 References .......................................................... 156

6 Discussion .......................................................... 161
6.1 Main Findings and their implications ............................. 162
6.2 Possible further studies ........................................... 172
  6.2.1 Amazonian Extrapolation ...................................... 172
  6.2.2 Coupling to GCM model ....................................... 174
  6.2.3 Application in other ecosystems ............................... 174
  6.2.4 Integration of alternative stomatal control hypotheses .......... 175
  6.2.5 Data Assimilation ............................................. 175
  6.2.6 Effects of phenology and allocation ........................... 176
  6.2.7 Anisohydric behaviour ....................................... 177
  6.2.8 Use of light aircraft technology to investigate drought in Amazonia ........................................ 177
6.3 Concluding Remarks .............................................. 178
6.4 References .......................................................... 179
Chapter 1

Introduction
Interactions between the biosphere and the climate have profound effects on the functioning of the Earth system. One of the most important area of biosphere-atmosphere interaction is the Amazon basin, which plays an important role in the global cycles of carbon, water and energy (Werth and Avissar 2002). Changes in the functioning of the Amazon basin are threatened as the result of climate change, deforestation and development. Many recent studies have highlighted the potential for these factors to interact and reinforce each other through the effect of drought stress on forest evapotranspiration (Cox et al. 2000; Laurance and Williamson 2001; Laurance et al. 2004; Nepstad et al. 2004). All these analyses hinge on the interaction between reduced rainfall and reduced precipitation. Very little is known about the response of rain forest evapotranspiration to reduced rainfall. This thesis is concerned with observing, understanding, modelling and extrapolation of the response of Amazonian rain forest ecosystems to drought stress.

The Amazon basin covers more than 5 million km² of land area in nine countries (Lucas et al. 2000). This is at least four times larger than either of the next largest areas of tropical broadleaf forest which exist in the Congo and Indonesia (Davison, 2004) and contains about 40% of the world's remaining tropical rain forest (Laurance, 2001). The Amazon basin accounts for 10% of global terrestrial primary productivity and biomass (Fearnside, 1997; Mellilo et al. 1996; Botta, 2002), discharges 15-20% of all the world's fresh water (Davison, 2004) and has a substantial impact on global cycles of water, carbon and energy.

The Amazon basin is thought to act as a large sink of carbon dioxide. Studies of the carbon dioxide uptake of rain forests using the eddy covariance technique (Grace et al. 1996, Malhi et al. 1998) indicated that Amazonian forests may be substantial sinks of carbon dioxide of the order of 0.56 Gt C year⁻¹ (Grace and Malhi, 1999). These representativness of these initial findings have been the subject of much discussion and subsequent measurements at other sites have produced variable results (Carswell et al. 2002; Goulden et al. 2004; Saleska et al. 2003). However, measurements of above-ground carbon stocks from long-term forest plots have indicated an increase in carbon storage over the last few decades, amounting to an estimated basin-wide sink of 0.6 Gt carbon per year (Malhi and Phillips, 2004). In addition, inverse modelling of atmospheric carbon dioxide concentrations has indicated that the biotic carbon dioxide sink of South America, taking into account emissions from deforestation, is in the order of 0.8 Gt C year⁻¹ (Bousquet et al. 1998) or 1.1 Gt C
year\(^{-1}\) (Rayner et al. 1998). In the light of estimates of fossil fuel emissions of 5.5 Gt C year\(^{-1}\) and accumulation rates of carbon dioxide in the atmosphere of 3.3 Gt C year\(^{-1}\) (Malhi and Grace, 2000) present evidence suggests that uptake of CO\(_2\) by the Amazon basin at present causes a considerable deceleration to the rate of climate change.

In recent years it has been suggested that the size of the Amazonian carbon sink is limited by water availability. Early modelling studies of the carbon balance of the Amazon basin suggested that, at present, rain forest gas exchange is subject to interannual variability coinciding with the El-Niño Southern Oscillation (ENSO) (Tian et al. 1998, Botta et al. 2002). In Amazonia, El Niño events are related to lower than average precipitation and high temperatures. The initial modelling results of Tian et al. (1998) suggested that this would cause a reduction in the carbon dioxide uptake of the forest due to a reduction in tree growth caused by drought stress. The drought effect is more pronounced towards the Eastern and Northern parts of the basin, where rainfall is lower in general (Sombroek, 2002).

In the future, hot, dry, El Niño-like conditions are likely to become more frequent. Cubash et al. (2001) found that ‘most but not all’ global climate model predictions anticipated that the Amazon region would become warmer and drier in the next 50-100 years as the result of increasingly frequent and severe El Niño events (Cowling et al. 2004, Huntingford et al. 2004, Cox et al. 2004). To investigate the resulting feedback between climate change and vegetation cover, Cox et al. (2000) simulated the response of the Amazon forest carbon cycle to climate change, using the first example of a dynamic global vegetation model embedded within a global climate model. They found that the drying of the climate resulted in the conversion of the Amazon rain forest to savannah and an associated loss of soil and vegetation carbon. Reduced evaporation from the savannah vegetation resulted in a regional feedback which further reduced Amazonian precipitation. The acceleration of carbon accumulation in the atmosphere, caused in part by the Amazonian deforestation, caused a global feedback, intensifying the El Niño activity and further reducing the rainfall over Amazonia. Cox et al. (2004) predict, using the coupled climate-carbon cycle HadCM3LC model, that the magnitude of the reduction in rainfall may be up to 50% by 2100.
1.1 Empirical data on Amazonian rain forest gas exchange

However, the problem with model predictions such as those presented by Cox et al. (2000) and Tian et al. (1998) is that empirically, we know very little on how rain forests respond to drought stress and reduced rainfall. Information from other ecosystems cannot be applied here as rain forests differ substantially from other ecosystems on account of their stature, the prevailing hot and humid climate and the unique tropical soils on which they stand (Tomasella and Hodnett, 1996). Conducting controlled lab experiments into drought responses of forest ecosystems is also impossible, as the factors controlling evapotranspiration (rooting depth, hydraulic architecture, soil type) act at the scale of the whole ecosystem. Field studies are rare, due to the logistical difficulties of operating in remote forested areas. Estimates of whole ecosystem gas exchange using the eddy covariance technique (Moncrieff et al. 1997) have only been made at a small number of locations. The majority of these eddy covariance measurements appear to show no forest gas exchange limitation in the dry season (Saleska et al. 2003; Goulden et al. 2003; Carswell et al. 2002; da Rocha et al. 2004). Only one set of published data show a reduction in gas exchange in the dry season, those made by Malhi et al. (1998) at a rain forest near Manaus, in central Amazonia. At the site, at the height of the dry season, evapotranspiration was reduced by up to 50% (Malhi et al. 2002) with canopy conductance linearly related to soil moisture. Existing data on the response of Amazonian forests to the existing dry season therefore indicate some heterogeneity in forest behaviour, with a propensity towards the absence of severe hydraulic stress in the dry season. However, satellite image analysis by Asner, Townsend and Braswell (2000) indicated that the South-Eastern half of Amazonia experienced seasonal declines in normalised difference vegetation index (NDVI) a measure of canopy 'greenness' or leaf area. Empirical evidence of the impact of the current dry season on forest gas exchange is therefore ambiguous. This means that, inevitably, current predictions of the response of the forest to climate change are subject to high levels of uncertainty, owing to the lack of opportunity for model testing or parameterisation.

Given the severity of the rainfall reduction demonstrated by Cox et al. (2004) and the key role of Amazonia in the global climate system (Werth and Avissar, 2002), it is extremely important that we improve our ability to predict the resilience of
the forests of Amazonia to reduced rainfall.

Some key questions we seek to answer are
1. How resilient are rain forest ecosystems to periods of low rainfall.
2. What are the key factors controlling forest responses to soil drying?
3. Are there threshold reductions in rainfall which will trigger forest-climate feedback?
4. How can we represent detailed soil-plant-atmosphere interactions within global scale models?

1.2 Through-fall exclusion experiments

In order to investigate the role of drought in constraining forest gas exchange, two experimental rainfall manipulations were implemented by the LBA (Large Scale Biosphere Atmosphere Experiment in Amazonia) project (Avissar and Nobre, 2002). Two sites, Tapajos and Caxiuanã, (see Fig. map) were selected in Eastern Amazonia, the area most at risk from reduced rainfall (Cox et al. 2000, 2004). At both sites, a system of plastic panels and guttering intercepts the rainfall at 2 m height, and channels the intercepted water away from the plot, thereby reducing the quantity of water hitting the soil by ~50% (see Chapter 4). The experimental apparatus is shown in figure (1.2). This thesis presents analyses of data collected within the Caxiuanã through-fall exclusion experiment. Using this experimental set up, we can impose on the forest much more severe droughts than occur at present, even under El-Niño conditions, and therefore simulate the quantity of rainfall which is predicted by the Hadley Centre GCM at the end of this century.

Because through-fall exclusion is a costly process, it is not possible to establish experimental sites across the range of forest types found in the Amazon basin. Neither is it possible to replicate the experiment at the site, because the size of plot required to avoid edge effects, from cutting of lateral roots, is large (100 x 100 m). Therefore, the construction of a substantial empirical data set on the response of forest gas exchange to soil drying is not possible. For this reason, we must use the information we obtain from the through-fall exclusion, to test and refine models of forest function and physiology. These models may then be used to predict the behaviour of forests under differing soil, vegetation and climatic conditions and to
inform researchers of the data collection strategies which might best improve the accuracy of the model predictions.

Figure 1.1: Map of the Amazon basin, showing annual rainfall and the location of the three sites mentioned in this thesis. Caxiuanã, the location of the discussed through-fall exclusion experiment, Tapajos, the location of the other through-fall exclusion experiment, and Manaus, the location of the eddy covariance data collection discussed in chapter 5. Rainfall map reproduced from Sombroek (2001)

1.3 Existing modelling approaches

The majority of existing soil-vegetation-atmosphere-transfer (SVAT) models used to predict the behaviour of vegetation under dry conditions contain very little physiological understanding. A review of several widely used models can be found in Appendix 1.1. In brief, the general approach of most SVAT models is to simulate the drainage of water to different soil layers, and calculate, each day, a 'soil moisture
factor' using a simple equation, typically including one or two parameters determining the soil water availability. For example, the MOSES model (Essery, Best and Cox, 2001), which was used in the analysis of Cox et al. (2000) uses the following equation to calculate the moisture stress factor $\beta(\theta)$,

$$\beta(\theta) = \frac{\theta - \theta_w}{\theta_c - \theta_w} \quad (1.1)$$

where $\theta_c$ and $\theta_w$ are the critical and wilting water content, respectively, with values corresponding to the water content at $-0.033$ and $-1.5$ MPa respectively. The 'moisture stress factor' is used either to modulate the modelled stomatal conductance or photosynthesis rates. These models typically include empirical parameters controlling the interaction between soil moisture stress and gas exchange. However, in the absence of a substantial data set from which to calibrate these parameters (the only appropriate data available are the Malhi et al. (1998) data from Manaus), the applicability of all these model functions is unknown and therefore the errors
propagated from their use are potentially very large.

1.4 Recent Modelling Developments

At present, the mechanistic information included in the majority of soil-vegetation-atmosphere-transfer (SVAT) models does not reflect an explicit mechanism for the limitation of plant gas exchange by low soil moisture. However, recent modelling developments have allowed the inclusion of water transport mechanisms in SVAT models for the first time. Williams et al. (1996) developed the soil-plant-atmosphere (SPA) model in which stomatal conductance is sensitive to leaf water potential during dry periods. The leaf water potential is simulated as the balance of supply of water to the leaves from the soil and evaporative demand from the atmosphere. This development allows the effect of alterations in the soil-to-leaf water supply on gas exchange to be intensively interrogated. In addition, it allows, for the first time, the development of a model of drought stress from the 'bottom up'. That is, the parameters of the model are derived from independent measurements of soil, root and plant properties. The SPA model of drought stress has only previously been tested at a Ponderosa Pine site in Oregon, where some of the key parameters, such as rooting depth and plant hydraulic conductivity, were unknown. In this thesis, I have attempted to parameterise the SPA model as far as possible using independent measurements of canopy and soil properties, to provide a unique and comprehensive test of the mechanisms embedded in the SPA model at multiple scales, from leaf to stand level. Should the model test prove successful then we may determine that process-based SVAT models of drought stress might provide better means of predicting the effects of climate change on rain forest water and carbon exchange.

1.5 Deep rooting hypothesis

The majority of soil-vegetation-atmosphere transfer models described in appendix 1.1 use a parameter for the maximum rooting depth of rain forest trees of 3 metres or less (see Appendix 1.1). However, there is substantial evidence that within Amazonia, water uptake occurs at least as deep as 10 m. The first example of this was published by Nepstad et al. (1994). They found evidence of rooting down to
at least 8 m at sites in Paragominas in Eastern Amazonia, Trombetas, near Manaus, and Santa de Araguaia in South Eastern Amazonia. They also measured water extraction at 8 m depth at the Paragominas site. Nepstad et al. then produced a map indicating the regions of Amazonia where rainfall is less than 1.5 mm day\(^{-1}\) for at least three months and where normalized difference vegetation index (NDVI) did not display a seasonal depression. They ‘deduced’ that these forests would probably have to use deep roots (>2 m) to access sufficient water to maintain evapotranspiration and evergreen canopies throughout the dry season. The area calculated to require deep rooting was 1.8 \(\times\) 10\(^6\) km\(^2\), mainly in Southern and Eastern Amazonia. Further experiments measuring the uptake of water from deep soils around Manaus (Hodnett et al. 1996a) showed that water was removed from at least 3.6 m depth at sites near Manaus, at Ji-Paraná, in Rondonia (S.W. Amazonia) and at Marabá in Eastern Amazonia. Hodnett et al. (1996b) then used a simple model of unstressed forest evapotranspiration to predict that, given the available soil moisture per metre soil depth at the Manaus site, extraction of water down to 9 m would be necessary to maintain evapotranspiration in the dry season. More recently, water extraction from deep soil has been indicated by Moreira, Sternberg and Nepstad (2000) using isotope labelling methods and Sternberg et al. found roots down to at least 4 m at Fazenda Vitória in Eastern Amazonia, (Pará State). In each case, water extraction was observed at the maximum depth measured, and no counter-example of shallow rooting depths and water extraction has been published, to our knowledge. Compared to the vast size and potential heterogeneity of the Amazon basin, the number of sites described here is low, but the weight of evidence suggests that Amazonian tree have roots which are substantially deeper than the \(~3\) m assumed by most widely used vegetation models. Nepstad et al. (2004) calculate that the average rooting depth estimated by current studies is 10 m.

1.6 Overview of Thesis

The overall aim of this thesis is to use the results of the Caxiuanã through-fall exclusion experiment to improve mechanistic understanding of rain forest gas exchange responses to soil drying. We have used a simulation modelling approach to test specific hypotheses concerning the functioning of rain forest ecosystems. The thesis is designed as a series of four stand-alone chapters which have been prepared for publication as scientific papers (see “Publication Status of thesis contents”).
Each chapter is based around a series of key science questions, and the discussion of each chapter pertains to answer each of these science questions in turn. Here, I summarise the content of each chapter and list the science questions which will be tackled therein and give a brief summary of the main results obtained.

1.6.1 Chapter 2. Evidence from Amazonian forests is consistent with isohydric control of leaf water potential.

The first paper is an analysis of diurnal tree physiology data. In this paper, we test the hypothesis that stomatal conductance (the main regulator of tree water use) is responsive to leaf water potential, so that, when leaf water potential reaches a critical minimum, stomata shut to avoid further water loss. This mechanism creates constant water potentials in the leaves under hydraulically stressed conditions, and therefore is referred to as the 'isohydric hypothesis'. We use a simulation model of the soil-plant-atmosphere continuum (the SPA model, Williams et al. 1996) to represent the predictions of the isohydric hypothesis, and compare the predictions to diurnal cycles of leaf water potential, stomatal conductance, sap flow and stem water potential.

Key science questions

1. Are the leaf water potential, sap flow and stomatal conductance data consistent with the hypothesis that stomata function to maintain isohydric conditions within the plant under water stressed circumstances?
2. Are changes in soil-to-leaf water supply dominated by changes in soil water potential or soil-to-leaf hydraulic resistance?
3. If there is a major change in soil-to-leaf hydraulic resistance between seasons, is the change in resistance located above or below ground?

We conclude that leaf water potential does appear to exert control over stomatal conductance on account of the existence of marked plateaux leaf water potential throughout the day in the majority of trees studied. We found that soil-to-leaf hydraulic resistance increased by a factor of 7.6 between wet and dry seasons, while
the change in soil-to-leaf water potential gradient increased by a factor of 2.2. The changes in tree water use simulated from these data were consistent with tree water use, leaf water potential and stomatal conductance data, and therefore we conclude that changes in soil-to-leaf hydraulic resistance are the main factor responsible for the changes in tree hydraulics between seasons. Measurements of stem water potential showed that the main increase in hydraulic resistance between seasons was located below ground.


The existence of a large measured increase in below-ground resistance in chapter 2 indicates that the hydraulic resistance of either the soil-to-root pathway or the root xylem has increased during droughting. It is unclear which is resistance responsible for the altered tree water use. To estimate soil-to-root hydraulic resistance demands some knowledge of the soil hydraulic properties, in particular the unsaturated hydraulic conductivity. In the absence of a database of the hydraulic conductivity of Amazonian soils (Tomasella and Hodnett, 1997), we collected data on the hydraulic properties of the Caxiauana soil, which is a sandy oxisol. The second paper presents this data, and an analysis of four soil hydraulics models used to represent the data. We also tested the ability of pedo-transfer functions derived from Amazonian or Brazilian soils to predict the observed water retention curve and hydraulic conductivity curve respectively.

Key science questions

1. Which soil hydraulic model provides the most appropriate representation of the water retention curve and hydraulic conductivity data collected?
2. What is the uncertainty placed on predictions of hydraulic conductivity in dry soils (−8 to −1500 kPa) involved in extrapolating hydraulic conductivity measurements beyond field capacity using models?
3. Is the water retention curve typical of Amazonian soils of this texture with reference to an Amazonian water retention curve pedo-transfer function (PTF)
4. Does the soil exhibit the same high hydraulic conductivity found in the Manaus soil, with reference to the PTF of Tomasella and Hodnett, 1997?

In this chapter, we conclude that all the soil hydraulics models produced similar fits to the soil hydraulics data and that they gave largely similar predictions when extrapolated into dry soil and that the data show a water retention curve of drastically different shape to that predicted by the pedo-transfer function of Tomasella and Hodnett (2000). The soil appears to exhibit higher than expected hydraulic conductivity in some layers, but not in others. Hydraulic conductivity reduces by around four orders of magnitude between field capacity and \(-100\) kPa, and therefore may be able to explain the increase in below-ground hydraulic resistance measured in Chapter 2.

1.6.3 Chapter 4: A process-based simulation of the response of rain forest to drought stress.

In the third paper we present three years of sap flow and soil water content data from the through-fall exclusion experiment. In this instance, we use a modelling approach to test the hypothesis that changes in soil hydraulics (soil-to-root hydraulic resistance and soil water potential) are responsible for the observed changes in sap flow during dry periods. We use the SPA model, whose stomatal conductance algorithm is tested in Chapter 2, linked to a soil water model, which predicts changes in soil-to-root hydraulic resistance from geometric equations developed by Newman (1969). The soil water model is parameterised using the data collected in Chapter 3. This creates a fully coupled model of the development of drought stress through time, driven only using climatological and phenological data. The model does not require any calibrated parameters to run, and all the model inputs may be measured using small amounts of independent data.

**Key science questions**

1. Are the observed seasonal changes in evapotranspiration consistent with the hypothesis that gas exchange is limited by changes in soil-to-root water supply?
2. What is the simulated reduction in photosynthesis associated with the observed
reduction in sap flow?

3. Which ecosystem properties are most critical in controlling the sensitivity of the ecosystem to reduced rainfall?

Our findings indicate that the model hypothesis, that water use is constrained solely by soil-to-root water supply, is consistent with the sap flow and soil moisture data in both the control and through-fall exclusion plots. The model predicts the changes in sap flow of the control plot, where no hydraulic stress was observed, and the through-fall exclusion plot, where the timing and magnitude of the sap flow declines during dry season periods was well simulated. Using the SPA model thus verified, we use the simulated stomatal conductance values to predict that the drought treatment resulted in a decline in photosynthesis of 15% over two years of treatment. Using a sensitivity test approach, we find that the sensitivity of the ecosystem to rainfall reduction is controlled mainly by rooting depth and soil texture. Both these properties are poorly defined for the Amazon region and point to the clear need for intensified data collection in these areas.

1.6.4 Chapter 5. A simple model of rain forest drought tolerance.

The SPA model is the first fully mechanistic representation of the development of a drought to have been verified against whole ecosystem time series data. However, the SPA model requires half hourly meteorology, and is computationally expensive due to the intensive iterations required to calculate many dynamic processes. In this chapter, we construct a simplified model, which works on a daily time-step, yet still maintains realistic representations of the processes controlling drought responses and canopy physiology. We followed the aggregation procedure described by Williams et al. (1997), whereby the detailed SPA model is run over a wide array of meteorological and vegetation inputs to create a response surface of the model to daily input variables. A set of simple equations is developed which describes the response surface. We developed aggregated canopy models (ACM's) of evapotranspiration (ET) and gross photosynthetic productivity (GPP) using existing meteorological data from across Amazonia. To enable the model to predict drought stress, we created a simple daily time-step soil water model (SWAT) which provided estimates of the soil-to-root hydraulic conductivity and soil water potential dynamics. The cou-
ple ACM-SWAT model was tested against the eddy covariance data from Manaus and the sap flow results from the Caxiuana through-fall exclusion experiment. This new model provides a lower data requirement, faster computational speed and more user friendly means by which to simulate the development in drought stress from rain forest soil, root and meteorological properties.

Key science questions

1. What reduction in model accuracy is caused if the behaviour of the detailed half hourly soil-plant-atmosphere model is reproduced using a simple aggregated daily model?
2. Is it possible to explain the heterogeneous responses of forest gas exchange to low rainfall using only measured changes in soil, root or vegetation characteristics?
3. At what point in the next century will predicted climate drying begin to have an impact on rainforest gas exchange?

The model assimilation resulted in an $r^2$ value of 0.872 and 0.870 between the predictions of the SPA and ACM models of evapotranspiration and GPP respectively. Coupling of these daily timestep models to a soil water transport model allowed a good prediction of the forest gas exchange under drought stressed circumstances for both the Caxiuana and Manaus forest datasets. This indicates that it is possible to simulate the variation in forest drought responses via consideration of the underlying water supply properties of the roots and soil. Extrapolation of the model into the future, simulated by a gradual reduction in rainfall, indicated that the severity of the initial forest-atmosphere feedback was dependant on rooting depth and soil texture. However, when rainfall was reduced past $~70\%$ of current levels, the total amount of rainfall was less than evaporative demand, therefore predicted evapotranspiration declined, irrespective of ecosystem properties.

1.7 Publication Status of thesis contents

Chapter 1 is in press at Plant, Cell and Environment. May 2005.

Chapter 2 has been conditionally accepted for publication by the European Journal of Soil Science. February 2005.
Chapter 3 has been submitted to Global Change Biology.

Chapter 4 will also be submitted to Global Change Biology.

1.8 Appendix 1.1: A review of the representation of drought stress in commonly used vegetation models.

To understand both the response of the Amazon forest to reduced rainfall, and to estimate the carbon dioxide uptake of the Amazon basin, to help with global carbon inventories, several teams have using existing ecosystem models to predict the gas exchange of Amazonian forests. However, the majority of existing models used to predict the behaviour of vegetation under dry conditions contain very little physiological understanding. Here I will review previous Amazonian modelling studies, and detail the mechanisms by which existing ecosystem models link reduced soil moisture to reduced gas exchange.

1.8.1 1. The Terrestrial Ecosystem Model (TEM)

Tian et al. (1998) used the Terrestrial Ecosystem Model (TEM) developed by Melillo et al. (1993) to predict the interannual variability in the carbon storage of the Amazon basin. They noted three main effects. Firstly, that, as the result of CO₂ fertilisation, the Amazon basin appeared to be a net sink of carbon over the period 1980-1994. Secondly, they noted that interannual variability was large and correlated with the ENSO cycle. The basin was a sink of CO₂ in La Niña years and a source in El Niño years. Thirdly, they noted that the changes in carbon storage were related to precipitation reductions causing drought stress and therefore lowering photosynthesis. The drought stress model in TEM is therefore critical to the overall conclusions of the paper.

The drought stress model of TEM is detailed by Vorosmarty et al. (1989). They determine evapotranspiration (ET - mm day⁻¹) as

\[ ET = SM \frac{\ln FC}{(1.1282FC)^{1.1276}} PET \]  

(1.2)
where $SM$ is the soil moisture content over the whole rooting zone and $FC$ is the field capacity over the rooting zone. $PET$ is the potential evapotranspiration (mm day$^{-1}$), the maximum rate of evapotranspiration possible in the absence of water stress. The rooting depth varies with soil texture, but the maximum value for a forest ecosystem (sandy soil) is 2.5 m. A clay soil has a rooting depth of 1.2 m. The field capacity values also varied with soil type and were 14.1% for sand to 48.5% for clay. Photosynthesis was modulated according to the ratio between actual and potential evapotranspiration.

1.8.2 2. MOSES/TRIFFID

MOSES/TRIFFID is the model developed by the Hadley Centre for Climate Change at the UK met office. MOSES is the soil-vegetation-atmosphere-transfer model, which calculates the basic ecophysiological processes involved in land-atmosphere interaction, and TRIFFID is a dynamic-global-vegetation-model (DGVM) which calculates the shifts in vegetation types and the movement of biomes over time. MOSES/TRIFFID has been coupled to the HadCM3LC global climate change model to produce a fully coupled climate change-carbon cycle model, which estimated that feedbacks from the carbon cycle, caused in part by the drying of Amazonia and a conversion to savannah, would accelerate the rate of global warming. Again, the connection between soil moisture and forest gas exchange is of critical importance to the conclusions of this model.

The MOSES model (Essery, Best and Cox, 2001) includes the effects of soil moisture as a direct effect on leaf assimilation rate ($A$), rather than as an influence on stomatal conductance.

$$A = A'\beta(\theta)$$  \hspace{1cm} (1.3)

Where $A'$ is the rate of photosynthesis without the effect of hydraulic stress. The soil water limitation, $\beta(\theta)$, is defined as

$$\beta(\theta) = \frac{\theta - \theta_w}{\theta_c - \theta_w}$$  \hspace{1cm} (1.4)

where $\theta_c$ and $\theta_w$ are the critical and wilting water content, respectively, with values corresponding to the water content at $-0.033$ and $-1.5$ MPa respectively. The parameters of the model are therefore set using soil hydraulic data, but depend on
assumptions of the above equations, which are untested. The rooting depth for the tropical evergreen forest vegetation type used in MOSES is 3 m.

MOSES/TRIFFID has been used to explore Amazonian climate change in a series of modelling investigations subsequent to Cox et al. (2000). Of these, only one has tested the outcome of the model against existing data. Harris et al. (2004) tested MOSES against the only existing data set showed drought stress in the Amazon basin (Malhi et al. 1998). They re-calibrated the soil water retention parameters, \( \theta_e \) and \( \theta_w \), and the parameters determining stomatal conductance to the Manaus eddy-covariance data. However, the re-calibrated version of the model predicted severe hydraulic stress during the wet season periods at the Manaus site, as well as correctly predicting the drought limitation in the dry season, towards the beginning of the data set. In addition, the MOSES model was not able to predict the observed difference in canopy conductance between seasons owing to the impact of soil moisture directly on photosynthesis and not stomatal conductance. Huntingford et al. (2004) analyse the impact of the re-calibration of the MOSES parameters for predictions of Amazon-wide gas exchange in the coming century using an 'analogue' model of the coupled climate-carbon cycle HadCM3LC model. They predicted a faster decline in vegetation using the new calibrated parameters than predicted by the standard MOSES calibration. However, given that the soil at Manaus has a particularly low water retention capacity (5% below 1 m, Tomasella and Hodnett, 1996) and that the MOSES model only uses a rooting depth of 3 m, it is likely that both the Manaus and whole-Amazon drought stress impact would be over-estimated.

1.8.3 3. IBIS model

The IBIS model, (Foley et al. 1996, Kucharik et al. 2000) was used to predict the inter-annual variability of Amazonian forest gas exchange by Botta et al. (2002). Botta et al. attribute the variation in NPP of the Amazon basin to the ENSO cycle and water stress reducing forest NPP. Again, the conclusions of this paper are critically based on the relationship between soil water and gas exchange. However, Foley et al. (1996) state that “owing to a lack of clear understanding of the mechanism by which water stress influences photosynthesis and growth, we have adopted a simple heuristic approach to represent this influence”. They first calculate a ‘stress factor’
based on soil moisture given by

\[
\frac{1 - e^{-2.5\left(\frac{\theta - \theta_{\text{wil}}}{1 - \theta_{\text{wil}}}\right)}}{1 - e^{-2.5}}
\]  

(1.5)

where \( \theta \) is the soil water content and \( \theta_{\text{wil}} \) is the wilting point (both in fraction of ice-free pore space). The value of the function ranges between 0 and 1. Photosynthesis is directly reduced by this factor. Clearly, this model formulation has no mechanistic input and no empirical calibration to existing data, and therefore there is not reason to imagine that the prediction of drought stress will be realistic.

1.8.4 4. Water budget method

Wilmott et al. (1985) estimated global forest evaporation by multiplying the potential evapotranspiration by another water stress coefficient \( \beta \), but on this occasion the stress is calculated as

\[
\beta = 1 - \exp\left(-6.68\theta/\theta^*\right)
\]  

(1.6)

where \( \theta^* \) is the capacity of the soil.

1.8.5 5. GEOS GCM method

The Goddard Earth Observing System (GEOS) GCM (Werth and Avissar, 2004) models the effect of soil water on stomatal conductance as

\[
\beta = (\psi_1 - \psi_2)/\left(\psi - \psi_2\right)
\]  

(1.7)

where \( \psi_1 \) and \( \psi_2 \) are the critical and wilting point water potentials. The GEOS model has a rooting depth of 1 m. In a review of the evapotranspiration predictions of several models of Amazonian vegetation gas exchange Werth and Avissar conclude that “there is substantial uncertainty concerning the degree to which drought stress limits ET during the dry season in Amazonia”, and that more experimental data is required to rectify this situation. In this thesis, we will tackle both the uncertainty in the magnitude of the natural annual cycle, and the effect of drought stress on gas exchange.
1.9 References


Chapter 2

Evidence from Amazonian forests is consistent with isohydric control of leaf water potential.

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2.1 Abstract

Climate modelling studies predict that the rain forests of the Eastern Amazon basin are likely to experience reductions in rainfall of up to 50% over the next 50 to 100 years. Efforts to predict the effects of changing climate, especially drought stress, on forest gas exchange are currently limited by uncertainty about the mechanism controlling stomatal closure in response to low soil moisture. At a through-fall exclusion experiment in Eastern Amazonia, where water was experimentally excluded from the soil, we tested the hypothesis that plants are isohydric, i.e. that when water is scarce, stomata act to prevent leaf water potential dropping below a critical threshold level. We made diurnal measurements of leaf water potential ($\Psi_l$), stomatal conductance ($g_s$), sap flow and stem water potential ($\Psi_{stem}$) in the wet and dry seasons. We compared the data with the predictions of the soil-plant-atmosphere (SPA) model, which embeds the isohydric hypothesis within its stomatal conductance algorithm. The model inputs for meteorology, LAI, soil water potential and soil-to-leaf hydraulic resistance ($R$) were altered between seasons, in accordance with measured values. No optimisation parameters were used to adjust the model. This 'mechanistic' model of stomatal function was able to explain the individual tree level seasonal changes in water relations ($r^2 = 0.85, 0.90$ and $0.58$ for $\Psi_l$, sap flow and $g_s$ respectively). The model indicated that the measured increase in $R$ was the dominant cause of restricted water use in the dry season, causing a modelled restriction of sap flow four times greater than that caused by reduced soil water potential. Higher resistance in the dry season resulted from an increase in below-ground resistance (including root and soil-to-root resistance) to water-flow.
2.2 Introduction

Over the next 50-100 years, most, but not all, global climate models predict that increasingly El Niño-like climate conditions will cause reduced rainfall over Eastern Amazonia (Cox et al. 2000; Cubasch et al. 2001; Cowling et al. 2004; Cramer et al. 2004). Cox et al. (2004) suggested that the reduction in rainfall over Amazonia may be as great as 50% by 2100. Reductions in rainforest evapotranspiration during the dry season have been observed using the eddy-covariance technique at Manaus, in relatively wet and humid Central Amazonia (Malhi et al. 1998, 2002). However, more recent eddy covariance studies in Eastern Amazonia have not shown any limitation in forest evaporation during the dry season, even though these forests experience more intense dry seasons than the Manaus forest (Carswell et al. 2002; da Rocha et al. 2004; Goulden et al. 2004; Saleska et al. 2004). The lack of a simple correlation between limitation of forest evapotranspiration and dry season intensity implies we cannot simply extrapolate the results of a small number of experiments uniformly across the Amazon region. A more sophisticated understanding of the drought physiology of rain forest trees is necessary before we can predict the responses to the predicted drier conditions.

To investigate the mechanisms underlying the response of forest evapotranspiration to reduced rainfall, we conducted a one hectare manipulation study at Caicivaná, in Eastern Amazonia. Rain passing through the canopy (through-fall) was intercepted by a system of plastic panels, and drained away from the plot, thereby artificially reducing soil moisture. Within this through-fall exclusion site and an adjacent control, we collected diurnal cycles of leaf and stem water potential, stomatal conductance and sap flow from a sample of trees in both the wet and dry seasons.

We use the tree physiology data to investigate three areas of uncertainty: the mechanism by which stomata sense and respond to soil water status; whether leaf water supply is controlled by changes in soil water potential or soil-to-leaf hydraulic resistance and whether the major resistance to water uptake is located above or below ground.

The first part of our investigation involved testing the hypothesis that stomata sense reduced soil moisture via 'hydraulic signalling' between soil water potential and leaf water potential (Jones, 1998; Salleo 2000; Chaves, Maroco and Pereira 2003). In this hypothesis, low soil moisture affects stomatal conductance and gas exchange via its influence on leaf water potential. It has been repeatedly observed that some plants act to maintain leaf
water potentials above a critical minimum value, or 'isohydric' conditions, under hydraulically stressed circumstances (Field and Holbrook, 1989; Tardieu et al. 1993; Saliendra et al. 1995; Cochard et al. 1996; Comstock and Mencuccini, 1998; Sperry et al. 1998; Oren et al. 1999; Bonal et al. 2000; Salleo et al. 2000; Hubbard et al. 2001; Sperry et al. 2002). This does not mean that the water potential is constant all of the time, but that there is a definite minimum value below which it does not drop, owing to stomatal closure. The primary supposed role of this mechanism is the avoidance low water potential, leading to xylem cavitation (Jones and Sutherland, 1991) and the possibility of runaway cavitation (Tyree and Sperry, 1988). It has yet to be demonstrated that this isohydric behaviour is common in tropical forest trees, or that it can act as the sole explanation of altered whole tree water use between seasons.

We used a modelling approach to investigate the ability of the isohydric hypothesis to explain the physiology of whole trees, as a complement to empirical testing. In the field, stomatal conductance is high when both energy and water are abundant and stomata close due to either due to a lack of water, or due to a lack of energy (when the increase in photosynthesis to be gained by opening stomata is very small (Farquhar et al. 1980)). Using a model allows us to dynamically link the stomatal conductance, leaf water potential and energy availability to account for the multiple factors that determine stomatal conductance. The model we have used is the soil-plant-atmosphere (SPA) model (Williams et al. 1996). The SPA model is a multi-layer soil-vegetation-atmosphere transfer model, the stomatal conductance algorithm of which is based on the isohydric hypothesis. We parameterised the SPA model using measured estimates of hydraulic parameters, and compared the diurnal predictions of the model with the tree physiology data to test the isohydric hypothesis embedded in the model.

The second area of uncertainty investigated was whether soil water potential ($\Psi_s$) or soil-to-leaf hydraulic resistance ($R$) was the factor limiting the soil-to-leaf water supply under water stressed conditions. Soil-to-leaf water transport, along with atmospheric demand, determines leaf water status, but it is not clear whether $\Psi_s$ or $R$ is the major factor constraining water uptake in the dry season. Some previous modelling studies in tropical and seasonal temperate forests (Williams et al. 1996; Williams et al. 2001) suggest that dry season changes in ecosystem water use could only be explained through changes in soil-to-leaf hydraulic resistance, as only small changes in soil water potential were observed. However, other studies have found very large seasonal changes in soil water potential between seasons (Misson Panek and Goldstein, 2004). In this paper, we
use measured estimates of soil water potential and soil-to-leaf hydraulic resistance, and the description of soil-leaf water transport in the SPA model, to isolate the relative importance of both transport factors in constraining evapotranspiration during the dry season.

The third area of uncertainty investigated in this paper is the distribution of hydraulic resistance within the soil-to-leaf continuum. Soil-to-leaf hydraulic resistance consists of several hydraulic resistances in series in the leaves, branches, trunks, roots, root-soil interface and soil matrix. Much information exists describing the resistance of excised branch segments under different water potentials (Mencuccini, 2002), but little information exists on the relative magnitudes of branch, trunk and below ground resistance components (Sperry et al. 1998; Sperry et al. 2002). It is impractical to obtain enough information to model the dynamics of every resistance in the soil-plant-atmosphere continuum and therefore it is more efficient to deduce where the major resistance to water transport is located. In this paper, we split the resistance of the soil-to-leaf pathway into above- and below-ground components using stem psychrometry measurements, and thus determine the location of the greatest resistance to water transport.

Three key questions are addressed in this paper, as follows:
1. Are the leaf water potential, sap flow and stomatal conductance data consistent with the hypothesis that stomata function to prevent leaf water potential declining below a minimum critical value under water stressed circumstances?
2. Are changes in soil-to-leaf water supply dominated by changes in soil water potential or soil-to-leaf hydraulic resistance?
3. If there is a major change in soil-to-leaf hydraulic resistance between seasons, is the change in resistance located above or below ground?

We first address how the data alone may be used to answer these questions, then we investigate what additional conclusions we may draw by comparing the data to the predictions of the SPA model.

2.3 Methods

2.3.1 Site

The experimental site is located in the Caxiuanã National Forest, Pará, Brazil, (1° 43' 3.5" S, 51° 27' 36" W). The forest is a lowland terre firme rainforest. Mean annual rainfall is 2272 mm (± 193 mm), but with a pronounced dry season between July and
December, when only 555 mm (± 116 mm) of rainfall occurs on average (data from 1999 to 2003). The soil is a yellow oxisol (Brazilian classification latosol), with a 0.3-0.4 m thick stony/laterite layer at 3-4 m depth. The soil texture (0.0-0.5 m) is 75-83 % sand, 12-19 % clay and 6-10 % silt (Ruivo and Cunha, 2003). The soil consists of mainly kaolin in the clay fraction and quartz in the sand fraction (Ruivo and Cunha, 2003). The site elevation is 15 m above river level, and the water table has been observed at a depth of 10 m during the wet season.

2.3.2 Through-fall Exclusion Experiment

To investigate the limitation of soil water on forest gas exchange in drier conditions than those normally experienced, an artificial soil drought was created using through-fall exclusion (TFE). This work was carried out as part of the LBA (Large Scale Biosphere Atmosphere Experiment in Amazonia) Ecology program (Avissar and Nobre, 2002). Two 160 x 100 m plots, a control and a treatment ‘through-fall exclusion’ (TFE) plot were established, and the borders trenched to a depth of 1 m to reduce the lateral flow of water. In the TFE plot, a roof of transparent plastic sheeting and wooden guttering was installed at approx. 2 m height in November 2001, with the purpose of excluding rainfall from the soil.

A 30 m tall canopy access tower was installed in each plot. Nine trees were accessible from each tower. Of these trees, five in the TFE plot and four in the control plot were equipped with sap flow monitoring equipment. The species, canopy heights and diameter at breast height (DBH) were recorded (Table 2.1). The sap flow equipped trees were the tallest trees accessible from the towers, and their leaves ranged in height from 11 to 28 m in the control plot and 16 to 28 m in the TFE plot. Trees were measured up to the top of the canopy. A meteorological station (Campbell Scientific, Loughborough, UK) installed on a 55 m tall tower 700 m from the experimental site, recorded climatic conditions (wet and dry bulb temperatures, rainfall, wind speed and direction, incoming and outgoing photosynthetically active radiation (PAR), short-wave and long-wave radiation) every 15 minutes.
Table 2.1: Details of the intensively studied trees (those equipped with sap flow and accessible from the canopy tower) including tree codes and species names, height of measurement of leaves, total canopy height range, DBH and the ‘critical’ leaf water potential ($\psi_{\text{crit}}$) the lowest value of leaf water potential measured for each tree. ‘C’ trees are in the control plot, and ‘T’ trees are in the through-fall exclusion plot.

<table>
<thead>
<tr>
<th>Tree Code</th>
<th>Species</th>
<th>DBH (m)</th>
<th>(\psi_{\text{crit}}) (MPa)</th>
<th>Measurement ht (m)</th>
<th>Canopy height (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>C1</td>
<td>Mezilaurus mahaho</td>
<td>0.156</td>
<td>-1.9</td>
<td>11</td>
<td>6-21</td>
</tr>
<tr>
<td>C2</td>
<td>Licaria heteromorpha</td>
<td>0.187</td>
<td>-0.9</td>
<td>19</td>
<td>18-26</td>
</tr>
<tr>
<td>C3</td>
<td>Manilkara bidentata</td>
<td>0.515</td>
<td>-4.3</td>
<td>28</td>
<td>21-30</td>
</tr>
<tr>
<td>C4</td>
<td>Manilkara bidentata</td>
<td>0.439</td>
<td>-2.7</td>
<td>27</td>
<td>23-31</td>
</tr>
<tr>
<td>T1</td>
<td>Licaria ameniacaca</td>
<td>0.159</td>
<td>-2.2</td>
<td>16</td>
<td>10-22</td>
</tr>
<tr>
<td>T2</td>
<td>Hirtela bicornis</td>
<td>0.295</td>
<td>-2.1</td>
<td>20</td>
<td>15-30</td>
</tr>
<tr>
<td>T3</td>
<td>Lecythis confertiflora</td>
<td>0.366</td>
<td>-2.9</td>
<td>25</td>
<td>21-32</td>
</tr>
<tr>
<td>T4</td>
<td>Swartzia racemosa</td>
<td>0.485</td>
<td>-3.2</td>
<td>27</td>
<td>22-32</td>
</tr>
</tbody>
</table>

2.3.3 Tree Physiology measurements

Canopy leaf area index (LAI) was measured with an LAI-2000 Plant Canopy Analyser (LI-COR, Inc., Lincoln, NE, USA) on a 10 m x 10 m grid in both plots, in May 2003 and November 2003. The grid covered the full extent (100 m x 100 m) of each plot. Diurnal courses of leaf water potential (\(\psi\)) were monitored using a digital pressure bomb (Skye Instruments, Llandrindod Wells, UK) on the 17th and 19th May 2003 (late wet season) and the 19th and 20th November 2003 (late dry season). On each of these days, four to five leaves were sampled from each of the intensively studied trees at 0600, 0900, 1100, 1300, 1500 and 1630 hours, and \(\psi\) was determined for each leaf using the pressure bomb. Sap flow rates were measured for each of the intensively studied trees using the trunk segment heat balance method (Cermak, Deml and Penka, 1973; Cermak et al. 2004) (Environmental Measuring Systems (EMS), Brno, Czech Republic). The heat balance sensors measure sap flow over an entire sector of circumference, therefore do not require calibration for xylem depth, if the sensors (which are 30 - 50 mm long), penetrate through all of the active xylem tissue. Xylem depth was estimated in wood cores both visually, and using dye previously injected below the point of measurement, to confirm that water was not transported beyond 30 mm depth. Xylem depth measurements of 47 trees ranging from 0.1 m to 1.3 m in diameter, indicated that the xylem rarely extended beneath 20 mm depth, irrespective of tree size (data not shown), therefore the 30 mm long sap flow sensors cut through all of the conductive tissue. Water flux was logged every 15 minutes.
throughout each day.

The heat balance sap flow measurement method suffers from calibration errors around zero, such that when there is zero flow, a slight positive flow is recorded and a calibration is necessary. This is typically achieved by taking the minimum point over a period of several days and subtracting it from the raw data, so that the minimum becomes the zero point. This method is problematic if sap flow data are used to establish that the trees and soil have reached equilibrium, based on the achievement of zero sap flow during the night. However, if flow continues through the night as the leaves refill, then the flow will constantly decline as the soil-leaf water potential gradient becomes smaller. If flow were to stop altogether then the apparent flow would be constant. For all of the trees studied the refilling period appeared to last only until between 2200 and midnight. Thereafter, sap flow values remained constant to within 0.002 kg s$^{-1}$ cm$^{-1}$. This constant value was used as the zero point in all cases, and the existence of unchanging sap flow for several hours was used as evidence of the existence of zero flow.

Stomatal conductance ($g_h$) was measured using an LI-1600 leaf porometer (LI-COR, Inc., Lincoln, NE, USA). Diurnal measurements of the ambient transpiration rates, stomatal conductance and other associated meteorological variables (humidity, photon flux density, leaf and cuvette temperature) were made in the control plot on the 27th May and 31st Oct 2003, and in the TFE plot on the 23rd May and 2nd November 2003 (May dates are late wet season and Nov/Oct dates are late dry season). Four to five leaves were sampled from each of the intensively studied trees. Measurement times were 0900, 1030, 1200, 1330, 1500 and 1630 hours. Prior to 0900, very high (>90 %) humidity prevented accurate readings being obtained from the porometer, due to low transpiration rates. Leaves were not divided into shade and sun leaves, on the basis that the sun/shade definition of a mid-canopy leaf changes very frequently as the position of the sun shifts throughout the day. It was assumed that at a given canopy level, all leaves experienced a similar proportion of sun and shade conditions.

Stem psychrometers (Plant Water Systems, Guelph, Ontario, Canada) in conjunction with a manual microvoltmeter (Wescor, Logan, Utah, USA) were used to measure the water potential of the xylem at the base of each of the intensively studied trees. We collected these measurements at the same time as the leaf water potential measurements, in order to compare the water potentials of the leaves and stem. Prior to installation, the psychrometer sensors were calibrated against pressure bomb measurements of leaf water
potential. Nine leaves were collected from trees at different levels in the canopy at midday. From each leaf, a piece of the lamina was removed and measured with the psychrometers, according to the Wescor protocol, while the water potential of the remaining leaf was measured using the pressure bomb. After calibration, we installed the sensors between 0.2 and 0.3 m height at the base of the intensively measured trees. The sensors were insulated using a depth of ~ 0.1 m of foam, and an aluminium foil radiation shield. This insulation was highly effective at removing temperature gradients between the two thermocouple junctions - the main source of error in psychrometer measurements - and the voltage gradient was never higher than 0.1 µV, which was within the range recommended by the manufacturers.

We measured the ambient hydraulic resistance of excised segments of terminal branches during November 2002, May 2003 and November 2003 as another means of observing changes in above-ground hydraulic resistance. Four branches were collected from each intensively measured tree over several days. Branches were collected between 1400 and 1500 hours to ensure that embolism risk was maximal. The leaves and petioles were removed immediately, to prevent further water loss, and measurements were made within three hours of collection to minimise the effects of cavitation recovery (Zwieniecki and Holbrook, 2000). Measurements of hydraulic resistance were made with a low-pressure hydraulic resistance measurement system, similar to that described by Sperry et al. (1988). Branch segments were between 0.09 and 0.15 m in length and 10 to 14 mm in diameter. Leaf area distal to each measured segment was found by measuring the area/mass ratio of a subset of leaves from each branch, using digital photography and Scion image software (Scion image, Frederick, MD, USA).

2.4 Results

2.4.1 Meteorology

Average meteorology changed between the wet and dry season measurement days (Fig. 4.1). Average air vapour pressure deficit (VPD) between saturation and the atmosphere over 24 hour period was higher in the dry season (0.5 kPa) than the wet season (0.38 kPa). Average short wave radiation increased from 183 in the wet season to 216 W m\(^{-2}\) in the dry season. Average temperature was higher in the dry season (25.3°C) than the wet season (24.6°C).
2.4.2 Sap Flow

In the control plot, sap flow was 44% higher in the dry season than in the wet season. However, in the through-fall exclusion plot, sap flow was 15% lower in the dry season than in the wet season (Fig. 2.2 and Table 2.2). The majority of the change between seasons occurred in the upper canopy trees (C3, C4, T3 and T4). In particular, tree T3 showed a very large decline from 1134 to 16 kg day\(^{-1}\). The sap flow data in Fig. 2.2 are normalised for tree leaf area (see modelling section), so differences between the trees are due to factors other than size.

Table 2.2: Average daily sap flow value for the wet and dry seasons for the control plot (C) and through-fall exclusion plot (T) trees.

<table>
<thead>
<tr>
<th>Plot</th>
<th>Tree Code</th>
<th>Wet Season</th>
<th>Dry Season</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>C1</td>
<td>27</td>
<td>40</td>
</tr>
<tr>
<td></td>
<td>C2</td>
<td>13</td>
<td>13</td>
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<tr>
<td></td>
<td>C3</td>
<td>184</td>
<td>285</td>
</tr>
<tr>
<td></td>
<td>C4</td>
<td>438</td>
<td>777</td>
</tr>
<tr>
<td>TFE</td>
<td>T1</td>
<td>40</td>
<td>45</td>
</tr>
<tr>
<td></td>
<td>T2</td>
<td>34</td>
<td>45</td>
</tr>
<tr>
<td></td>
<td>T3</td>
<td>134</td>
<td>16</td>
</tr>
<tr>
<td></td>
<td>T4</td>
<td>157</td>
<td>134</td>
</tr>
</tbody>
</table>

2.4.3 Stomatal Conductance

In control and TFE plots, the stomatal conductance of 6 out of the 8 trees measured remained high (>100 mmol m\(^{-2}\) s\(^{-1}\)) for the majority of the day during the wet season (Fig. 2.3). Average maximum stomatal conductance was 184 mmol m\(^{-2}\) s\(^{-1}\) and the only period with low (<100 mmol m\(^{-2}\) s\(^{-1}\)) stomatal conductance occurred at 1630 in the TFE plot, corresponding to a period of low radiation and temperature (Fig. 4.1). In the dry season, \(g_s\) was 35% and 39% lower than the wet season in the control and TFE plots respectively. In the dry season, \(g_s\) declined gradually between 0900 and 1530 in the control plot, but no diurnal pattern was observed in the TFE plot, and \(g_s\) remained between 45 and 85 mmol m\(^{-2}\) s\(^{-1}\) for the whole day.
2.4.4 Leaf Water Potential

We found that the daytime leaf water potentials were lower in the dry season than the wet season in both plots (Fig. 2.4). The average minimum leaf water potential reached was $-1.71$ MPa in the wet season, and $-2.47$ MPa in the dry season. For each measurement period, there was no significant difference in daytime leaf water potential values between plots ($p>0.05$). In the dry season, $\Psi_l$ declined quickly each morning in all trees, reaching a plateau around a minimum value by 0900 or 1100 and remaining within 0.5 MPa of the minimum value for the majority of the day (from 0900 or 1100 until at least 1500). The exception to this was tree C1, which showed gradual recovery in leaf water potential throughout the afternoon on the 20th November. However, this tree did display a minimum plateau around $-1.7$ MPa on the 19th November, below which it did not decline at any other time. Between 1500 and 1630, leaf water potential recovered slightly in 6 out of the 8 trees studied. We found large differences in the minimum leaf water potential values reached by the different trees (Table 2.1). The minimum leaf water potential reached was negatively correlated with height ($r^2 = 0.74$). In the wet season, none of the trees reached the same minimum level observed in the dry season (with the exception of tree T2).

2.4.5 Stem Water Potential

The calibration procedure showed that the psychrometers provided an unbiased estimate of stem water potential. Regression analysis of the data showed indicated that very little calibration was necessary, as the slope of the psychrometer/pressure bomb relationship was 1.03 and the intercept was 0.092 MPa with an $r^2$ value of 0.94, thus indicating that the psychrometers provided a reliable estimate of leaf water potential compared to those of the pressure bomb. In other investigations, stem psychrometers have been calibrated against sections of wood subject to drying (Irvine and Grace, 1997). In this instance, the variability of tree species, and the logistics of felling large rain forest trees meant that this approach was not possible. We were therefore limited to calibration against leaf laminar measurements. In this case, however, virtually no calibration correction was applied to the psychrometer outputs as the result of the calibration, indicating that the calibration was not actually necessary in the first place. It is feasible that an error in the psychrometer measurements could have been introduced as the result of measurements being made on woody stems instead of leaf laminae. In the wet season, the stem water potential values were consistently higher than $-0.5$ MPa, close to the soil water potential values estimated from pre-dawn leaf water potential ($-0.08$ to $-0.09$ MPa). In the dry season, the stem
water potential data show similar plateaux to the leaf water potential measurements (Fig. 2.6), with the levels of the plateaux being slightly (0.7 MPa average difference) wetter than the leaf water potential values. The average dry season stem water potential was —1.69 MPa in the control and —1.53 MPa in the TFE plot.

2.4.6 Branch resistivity

We found no difference in the ambient resistivity of the excised terminal branch segments between seasons (Fig. 2.7), but there were large differences between the resistivity values for the different trees. The largest resistivity (0.37 m$^2$ s MPa mmol$^{-1}$), for tree C1, was 9.4 times larger than the smallest resistivity (0.04 m$^2$ s MPa mmol$^{-1}$) for tree C3.

2.5 Modelling

2.5.1 Justification of Modelling Exercise

The data presented here indicate, from initial analysis, that they are broadly consistent with the ‘isohydric’ hypothesis, that stomata respond to leaf water potential in order to prevent leaf water potential decreasing below a critical threshold value under water limited conditions. A persistent minimum leaf water potential plateau was observed in the dry season in all trees. When the leaves were at their minimum leaf water potential in the dry season, the stomatal conductance was consistently low. During the wet season, high stomatal conductances were observed and the leaf water potential was not near the minimum value.

However, the leaf water potential data alone do not actually confirm the existence of an isohydric mechanism. The plateaux in $\Psi_l$ could potentially have been due to the meteorological conditions, e.g. low atmospheric demand for moisture may have caused the fortuitous maintenance of stable leaf water potentials. To exclude this possibility, we must establish the atmospheric demand at all the different canopy levels, was high enough to reduce leaf water potentials below the measured values, in the absence of stomatal control. Therefore, construction of the predictions of the isohydric model necessitated the use of a dynamic simulation model. We chose to use the soil-plant-atmosphere (SPA) model (Williams et al. 1996). The specific reasons for choosing the soil-plant-atmosphere model to simulate the predictions the isohydric hypothesis, for each data set, were as follows.
Figure 2.1: Diurnal courses of vapour pressure deficit, short wave radiation and air temperature at 30 m height on intensive measurement days in the wet season (left hand panels) (15th May, 17th, 23rd May, 27th May) and dry season (right hand panels) (19th November, 20th November, 31 October, 2nd November) 2003.
Figure 2.2: Measured (symbols) and modelled (lines) sapflow per m² leaf area for individual trees in the control (top four panels) and through-fall exclusion (TFE) (bottom four panels) plots for wet and dry seasons. C1-C4 are trees in the control plot and T1-T4 are trees in the through-fall exclusion plot. Note change in scale between control and through-fall exclusion plot figures.
Figure 2.3: Measured (symbols) and modelled (lines) stomatal conductance for individual trees in the control (top four panels) and through-fall exclusion (TFE) (bottom four panels) plots for wet and dry seasons. C1-C4 are trees in the control plot and T1-T4 are trees in the through-fall exclusion plot.
Figure 2.4: Measured (symbols) and modelled (lines) leaf water potential for individual trees in the control (top four panels) and through-fall exclusion (TFE) (bottom four panels) plots for wet and dry seasons. C1-C4 are trees in the control plot and T1-T4 are trees in the through-fall exclusion plot.
1. The isohydric hypothesis proposes that leaf water potential is the dominant control over stomatal conductance and water use in water limited conditions. Leaf water potential is the balance of soil-to-leaf water supply and atmospheric loss. To generate 'expected' leaf water potential values, we must simultaneously model both atmospheric demand and soil-to-leaf water supply. Both these processes are explicitly simulated by the SPA model.

2. Stomatal conductance may be limited either by hydraulic stress, or by low light energy levels. We therefore need simulations of both the leaf water potential and the availability of light energy to the leaves, to predict the model expectations of stomatal conductance. The SPA model includes a radiative transfer scheme and a model of leaf water potential to allow both the factors determining stomatal conductance to be simulated.

3. Tree-level predictions of sap flow must be constructed from leaf level estimates of evapotranspiration. Leaves at different heights in the canopy of a single tree have different rates of sap flow depending on their respective energy supply and hydraulic limitation. The SPA model includes a multi-layer model of the forest canopy, and a radiative transfer model, so it is possible to scale from leaf-level evapotranspiration predictions to tree-scale sap flow predictions, therefore producing patterns of sap flow consistent with the 'isohydric' hypothesis.

4. Prediction of stem water potential from leaf water potential is difficult, as water
Figure 2.6: Measured (symbols) and modelled (lines) stem water potential for individual trees in the control (top four panels) and through-fall exclusion (TFE) (bottom four panels) plots for wet and dry seasons. C1-C4 are trees in the control plot and T1-T4 are trees in the through-fall exclusion plot.
Figure 2.7: Resistivity of excised branch segments in the November (dry season) of 2002 and 2003 and May (wet season) of 2002. Measured using the method of Sperry (1988) for branch segments 0.09 to 0.15 m long and 10 - 14 mm in diameter. Error bars are standard deviation of four measurements.

storage, or capacitance, in the tree leads to a lag between the leaf water potential and the stem water potential measured at the base of the tree in the morning as water is supplied from above ground water stores, and not drawn from the soil. Estimates of stem water potential dynamics consistent with the hypothesis can be made using the a dynamic model of the interaction between capacitance and resistance incorporated into the SPA model.

2.5.2 The SPA model

The SPA model is a multi-layered soil-vegetation-atmosphere-transfer (SVAT) model, designed to represent processes that are common to vascular plants, so that ecosystem-atmosphere exchange may be understood in terms of similar processes in different locations. The model has previously been tested in temperate deciduous and evergreen forests, arctic tundra and tropical rain forest ecosystems (Williams et al. 1996, 1998, 2000, 2001a, 2001b).

SPA is ideally suited to investigating the impact of drought on forest ecosystems due to its explicit modelling of water transport to leaves. In the model, stomatal conductance is controlled such that photosynthesis is maximised while not allowing leaf water potential
to drop below a critical minimum value. If $\psi_1$ reaches the critical minimum leaf water potential ($\psi_{\text{crit}}$), $g_s$ decreases and further water loss is prevented, therefore causing isohydric model behaviour under water stressed conditions. Leaf water potential is determined from the balance of atmospheric demand, simulated using the Penman-Monteith equation (Jones, 1992) and leaf water supply, as

$$\frac{\delta \psi_1}{\delta t} = \frac{\psi_s - \rho g h - E R - \psi_1}{CR}$$

(2.1)

where $\psi_s$ is the soil water potential, $\rho$ is the density of liquid water (kg m$^{-3}$), $g$ is gravitational acceleration ($9.8$ m s$^{-2}$) and $h$ is the height (m) of the canopy layer. Strictly, this should be the distance between the point of water uptake and the leaves. Strictly, this should be the vertical distance between the point of water uptake and the leaves. However, we are, at this stage, unsure of the height of the water uptake, and therefore are not able to correct for these changes. However, a 10 m difference in height causes only an 0.1 MPa difference in gravitational leaf water potential, so this is thought to be of little consequence in relation to the observed changes in leaf water potential in all trees. $E$ is the rate of evapotranspiration (mmol m$^{-2}$ s$^{-1}$), $C$ is the capacitance (mmol m$^{-2}$ MPa$^{-1}$) and $R$ is the soil-leaf hydraulic resistance (m$^2$ s MPa mmol$^{-1}$). To solve this equation, we must first define the hydraulic properties determining water supply to leaves, $R$, $C$ and $\psi_s$. All these parameters are physical properties of trees or ecosystems and can be estimated either independently or, in the case of $R$, from a sub-set of the data. The hypothesis underlying the SPA stomatal conductance algorithm has not previously been tested against high resolution diurnal time series tree physiology data as presented here.

2.5.3 Model inputs

We ran the SPA model for each tree for each of the intensively measured days. All parameters in SPA remain as given by Williams et al. (1996) unless otherwise stated. Of those inputs that were changed to reflect local observations, some were common to all trees, plots and seasons, and others were varied according to available data (Table 2.3).

Capacitance ($C$) was estimated as 2300 mmol MPa$^{-1}$ m$^{-2}$ from measurements made by Goldstein et al. (1998) for a seasonal tropical forest in Panama, the only published estimate of $C$ for tropical forest trees (see appendix) and was assumed to be constant between seasons. Soil water potential ($\psi_s$) was determined from the averaged pre-dawn
Table 2.3: Characteristics of the control and through-fall exclusion plot used as input to the SPA model. Some parameters were constant between seasons (canopy height and capacitance, and some varied between seasons according to measured values (LAI, soil water potential).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Units</th>
<th>Control Wet</th>
<th>Control Dry</th>
<th>TFE Wet</th>
<th>TFE Dry</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Canopy height</td>
<td>m</td>
<td>30</td>
<td>2300</td>
<td></td>
<td></td>
<td>Meas. from tower.</td>
</tr>
<tr>
<td>Capacitance</td>
<td>mmol m⁻² MPa⁻¹</td>
<td>30</td>
<td>2300</td>
<td></td>
<td></td>
<td>Goldstein et al. (1998)</td>
</tr>
<tr>
<td>Soil water potential</td>
<td>MPa</td>
<td>-0.09</td>
<td>-0.17</td>
<td>-0.08</td>
<td>-0.66</td>
<td>Pre-dawn ψₜ</td>
</tr>
<tr>
<td>LAI</td>
<td>m³ m⁻³</td>
<td>5.0</td>
<td>5.8</td>
<td>4.3</td>
<td>4.6</td>
<td>LAI 2000</td>
</tr>
</tbody>
</table>

leaf water potential measurements (Fig. 2.4), for each plot and season. Sap flow decreased to zero during the night (Fig. 2.2), indicating that equilibrium between the soil and tree had been reached, so pre-dawn leaf water potential should be a reasonable estimate of soil water potential (Donovan et al. 2001). Leaf area index was determined from the LAI-2000 measurements (Table 2.3). ψ_crit was determined for each tree from the minimum observed leaf water potential (Table 2.1) and was kept the same between seasons.

Soil-to-leaf hydraulic resistance \( R, \text{ m}^² \text{ s MPa mmol}⁻¹ \) varies between trees and seasons, and was calculated as

\[
R = \frac{A(\Psi_t - \Psi_s)}{S}
\]

(2.2)

where \( S \) is tree level sap flow (mmol s⁻¹). \( A \) is tree leaf area (m²) calculated from tree diameter. Diameter was assumed to be proportional to leaf area since we found no relationship between xylem depth and tree diameter. The ratio between diameter and leaf area was derived from tree survey data and canopy leaf area index. We estimated \( R \) from each measurement of \( \Psi_t \). The 0900 estimates of \( R \) were very high, since the release of stored water from plant tissues above the sap flow sensor allowed \( \Psi_t \) to drop without causing a corresponding increase in sap flow rate and thus creating a high apparent resistance. Thereafter \( R \) reached a plateau stable to within 1 m² s MPa mmol⁻¹. We took the average value of this post 0900 plateau and used it as the \( R \) parameter in the model (Table 2.4).

The SPA model inputs were independent of the verification data, with the exception of three parameters, \( \Psi_{crit}, \Psi_s \) and \( R \). However, all three of these parameters were found deterministically, using the methods previously described. Critically, these parameters were determined without reference to the fit between the model and the data and therefore
they are not 'fitted' or 'optimised' parameters, but representations of real physical or biological properties.

Table 2.4: Values of $R$ (soil-leaf hydraulic resistance) calculated using equation 2.2, $b$, the proportion of resistance located below ground, fitted to the $\Psi_{stem}$ data, and the above- and below-ground resistance, $R_{ag}$ and $R_{bg}$ calculated from $R$ and $b$.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Units</th>
<th>Season</th>
<th>Control Plot</th>
<th>TFE Plot</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>C1  C2  C3  C4</td>
<td>T1  T2  T3  T4</td>
</tr>
<tr>
<td>$R$</td>
<td>$m^2 \cdot \text{s MPa mmol}^{-1}$</td>
<td>Wet</td>
<td>2.0  3.0  1.1  0.6</td>
<td>1.1  3.7  0.5  0.8</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Dry</td>
<td>2.8  3.0  4.1  2.5</td>
<td>2.1  3.5  19.7  6.1</td>
</tr>
<tr>
<td>$b$</td>
<td></td>
<td>Wet</td>
<td>0.1  0.1  0.2  0.1</td>
<td>0.1  0.1  0.1  0.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Dry</td>
<td>0.6  0.2  0.9  0.8</td>
<td>0.3  0.1  0.7  0.6</td>
</tr>
<tr>
<td>$R_{ag}$</td>
<td>$m^2 \cdot \text{s MPa mmol}^{-1}$</td>
<td>Wet</td>
<td>1.8  2.7  0.9  0.5</td>
<td>1.0  3.3  0.5  0.6</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Dry</td>
<td>1.1  2.4  0.4  0.5</td>
<td>1.5  3.1  5.9  2.4</td>
</tr>
<tr>
<td>$R_{bg}$</td>
<td>$m^2 \cdot \text{s MPa mmol}^{-1}$</td>
<td>Wet</td>
<td>0.2  0.3  0.2  0.06</td>
<td>0.1  0.4  0.05  0.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Dry</td>
<td>1.7  0.6  3.7  2.0</td>
<td>0.6  0.3  13.8  3.7</td>
</tr>
</tbody>
</table>

2.5.4 Processing of model output for comparison with data

The SPA model provides predictions of gas exchange and physiology for layers of leaves at different heights in the canopy. Leaf water potential and stomatal conductance data were compared directly to the model output at the height at which they were measured. To allow comparison of the tree level sap flow data with the model output, the leaf level model predictions were scaled to the tree level. We again allocated a total leaf area to each tree ($A$), and distributed it evenly between the lowest and highest canopy layers occupied by each tree (Table 2.1). Sap flow was estimated for each layer from the SPA model predictions, and the tree level sap flow was the sum of the sap flow from individual layers (see appendix for full details of scaling approach).

To compare the predictions of the isohydric hypothesis, as embedded in the SPA model, with the stem water potential data, we used the SPA model output of $\Psi_t$ to create estimates of modelled stem water potential for each tree. However, stem water potential depends upon not only $\Psi_t$ and $\Psi_s$, but also upon the distribution of hydraulic resistance above and below ground, $b$ where

$$b = \frac{R_{bg}}{R}$$

$R_{bg}$ is the leaf-specific hydraulic resistance located below ground, in the roots and soil,
and $R$ is the total soil-to-leaf hydraulic resistance (both $m^2 \text{ s MPa mmol}^{-1}$). To find the value of $b$ which best explained the stem water potential data, we created several different scenarios of modelled stem water potential, with values of $b$ ranging from 0 and 1, in increments of 0.1. We calculated modelled stem water potential as

$$\psi_{\text{stem}} = (b(\psi_1 - \psi_s)) + \psi_s$$

(2.4)

where $\psi_1$ and $\psi_{\text{stem}}$ are modelled leaf and stem water potential respectively and $\psi_s$ is the soil water potential estimated from pre-dawn leaf water potential. We then determined which value of $b$ gave rise to the smallest root mean square error (RMSE) between the modelled and measured $\psi_{\text{stem}}$ values. The value of $b$, fitted in this manner, is therefore an estimate of the proportion of the soil-to-leaf resistance which was located below ground in each season. We then estimated the absolute values of the above- and below-ground resistance ($R_{\text{ag}}$ and $R_{\text{bg}}$ respectively) by multiplying the total soil-leaf resistance, $R$, by the proportion located below ground ($b$) or above ground ($1-b$).

### 2.5.5 Model sensitivity to wet-dry season input changes.

Water supply to leaves, at a given leaf water potential, depends on soil-to-leaf hydraulic resistance ($R$) and soil water potential ($\psi_s$). It is unclear which of these two factors changes most between seasons and which has the greatest impact on water supply within the range experienced. In addition, sap flow rates are influenced by meteorology and LAI changes. We used the SPA model to investigate which of these factors was the dominant cause of altered sap flow between seasons by generating SPA output for each plot six times. For the 'baseline' run, we used wet season input values of $b$, $\psi_s$, $R$ and meteorology data (Table 2.4). For the second run, we altered the meteorology data to its dry season value to test the impact of increasing temperature, VPD and solar radiation. The remaining four model runs tested the impact of altering the LAI, $\psi_s$ and $R$ to their dry season values (Table 2.5, column 1). In each instance, we estimated the canopy sap flow, averaged for the two modelled days in each season and for the four tree specific parameterisations. This allowed us to create a step-wise estimate of the effect of the different variables on the total sap flow.

### 2.5.6 Model Verification

The isohydric hypothesis, as incorporated into the SPA model, showed good agreement with the data in the majority of cases. The model accounted for an average of 85% of the
Table 2.5: Modelled average daily sap flow in mm day$^{-1}$. 'Baseline' refers to the predictions made using wet season meteorology data and parameters. The model inputs were then sequentially changed to their dry season values to identify which factor was the main cause of inter-season variation in water use. Differences between plots in the baseline values are due to differences in wet season LAI.

<table>
<thead>
<tr>
<th>Variables Included</th>
<th>Control Plot</th>
<th>TFE Plot</th>
</tr>
</thead>
<tbody>
<tr>
<td>Baseline</td>
<td>3.4</td>
<td>3.7</td>
</tr>
<tr>
<td>Met</td>
<td>4.2</td>
<td>4.6</td>
</tr>
<tr>
<td>Met+LAI</td>
<td>4.3</td>
<td>4.7</td>
</tr>
<tr>
<td>Met+LAI+$\Psi_s$</td>
<td>4.2</td>
<td>4.4</td>
</tr>
<tr>
<td>Met+LAI+$R$</td>
<td>4.0</td>
<td>3.6</td>
</tr>
<tr>
<td>Met+LAI+$\Psi_s$+$R$</td>
<td>3.9</td>
<td>3.1</td>
</tr>
</tbody>
</table>

variation of $\Psi_t$, of 83% of the variation of sap flow, 57% of the variation in $g_s$ and 98% of the variation in $\Psi_{stem}$ (Table 2.6). In the wet season, stomata were fully open, leaf water potential did not drop down to the minimum value and sap flow values were high (Fig. 2.4). In the dry season, as the result of changes in model inputs ($R$, $\Psi_s$ and LAI) and meteorological drivers, the SPA model captured the reduction in leaf water potential to the minimum value in all trees (Fig. 2.4), and the resulting reduction in stomatal conductance (Fig. 2.3). The reduction in $g_s$ in the through-fall exclusion plot was strong enough to cause a large reduction in the sap flow of the TFE plot trees, in agreement with the data (Fig. 2.2). In the control plot, the stomatal closure necessary to maintain the minimum leaf water potential was not sufficient to cause a major decline in sap flow rates, and in fact, the rising VPD meant that sap flow increased in the control plot in the dry season, again in agreement with the data. Other features of the data which were well described by the model include the reduction in the rate of sap flow in the evening (this is co-dependent on the resistance and capacitance values) and the difference in leaf area specific sap flow between trees, which occurs as the result of their different illuminations at different heights in the canopy. Predictions of the magnitude of reduction in leaf water potential in the wet season, when no hydraulic limitation is present, show good agreement with the data.

One inconsistency between the model hypothesis and the data is the modelled increase in stomatal conductance found for several of the trees at 1630 in the dry season (Fig. 2.3), when no increase in stomatal conductance is observed in the data. This coincides with a recovery in leaf water potential in both the model and the data (Fig. 2.4). This indicates
Table 2.6: $R^2$ and slope, values for the relationship between data and the SPA model predictions of leaf water potential, sap flow, stomatal conductance and stem water potential for individual trees. Data for different seasons are combined.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Tree</th>
<th>$\Psi_1$</th>
<th>Sap flow</th>
<th>$g_s$</th>
<th>$\Psi_{stem}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$R^2$</td>
<td>C1</td>
<td>0.78</td>
<td>0.90</td>
<td>0.39</td>
<td>0.98</td>
</tr>
<tr>
<td></td>
<td>C2</td>
<td>0.83</td>
<td>0.90</td>
<td>0.74</td>
<td>0.92</td>
</tr>
<tr>
<td></td>
<td>C3</td>
<td>0.80</td>
<td>0.92</td>
<td>0.29</td>
<td>0.93</td>
</tr>
<tr>
<td></td>
<td>C4</td>
<td>0.89</td>
<td>0.90</td>
<td>0.90</td>
<td>0.97</td>
</tr>
<tr>
<td></td>
<td>T1</td>
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<td>0.72</td>
<td>0.70</td>
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<tr>
<td></td>
<td>T2</td>
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<td>0.81</td>
<td>0.38</td>
<td>0.99</td>
</tr>
<tr>
<td></td>
<td>T3</td>
<td>0.94</td>
<td>0.72</td>
<td>0.87</td>
<td>0.99</td>
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<tr>
<td></td>
<td>T4</td>
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<td>0.75</td>
<td>0.30</td>
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<td>Slope</td>
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<td>1.34</td>
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<tr>
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<td>0.91</td>
<td>1.24</td>
<td>1.11</td>
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<tr>
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<td>C3</td>
<td>0.92</td>
<td>0.79</td>
<td>0.49</td>
<td>1.11</td>
</tr>
<tr>
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<td>0.85</td>
<td>1.05</td>
<td>0.98</td>
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<tr>
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<td>1.02</td>
<td>0.53</td>
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<td>0.26</td>
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<tr>
<td></td>
<td>T3</td>
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<td>0.71</td>
<td>0.71</td>
<td>1.00</td>
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<tr>
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<td>0.81</td>
<td>0.88</td>
<td>0.42</td>
<td>0.99</td>
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</table>

that, in the model, the energy available was sufficient to justify some stomatal opening in the late afternoon. However, the data show that the trees did not respond to the removal of hydraulic limitation in the same manner. The data therefore indicate that some further stomatal closure mechanism may be necessary to explain the observed stomatal behaviour.

2.6 Discussion

Are the leaf water potential, sap flow and stomatal conductance data consistent with the hypothesis that stomata function to maintain isohydric conditions within the plant under water stressed circumstances?

The isohydric hypothesis, as embedded in the SPA model, produced results broadly consistent with the data. Importantly, the SPA model contains no 'optimised parameters', or parameters whose value is adjusted to minimise the model-data error. A minimum plateau of leaf water potential was observed during the dry season in the majority of cases, at the same time as reduced stomatal conductance was observed. The SPA model analysis indicates that these patterns are consistent with a hypothesis of hydraulic limitation and not
reduced atmospheric demand or light availability. Because the model is based on underlying physical factors, we have been able to use it to test the physiological hypothesis underlying stomatal function with encouraging results.

The main consistent exception to the isohydric hypothesis was the afternoon stomatal opening which the SPA model predicts for some trees in the dry season, but is not observed in the data. There are at least two possible explanations for the observed lack of afternoon stomatal reopening in the absence of hydraulic stress. Firstly, that there is a direct response of stomata to VPD, such that the VPD observed at 4 pm in the dry season (1.2-1.5 kPa) causes stomatal closure even in the absence of actual hydraulic stress. This sort of response is implicit in Jarvis type stomatal conductance models, and the implied mechanism is a direct response of the guard cells to vapour pressure deficit. A second possible explanation, invoked by Tardieu (1993) involves chemical signalling of soil water status, whereby abscisic acid is produced in root tissue in dry conditions and transported to the stomata, where it invokes stomatal closure (Zhang and Davies 1989). The sap flow velocities measured in this study were sufficient to allow the transport of abscisic acid at a rate of 8-15 m day⁻¹, around the height of the smallest trees. This is not sufficient to allow abscisic acid to be the cause of afternoon stomatal closure or any sort of subdiurnal pattern. It is possible that the afternoon stomatal closure may be explained by an interaction between chemical and hydraulic signals, as described by Tardieu (1993), but as we did not measure ABA concentrations, and because the discrepancy is only minor, the integration of additional hypotheses into the model is not a research priority at this stage.

We have shown here that it is possible to model leaf water potential dynamics, stomatal conductance and sap flow, given a knowledge of the soil water potential and soil-leaf hydraulic resistance. However, modelling the dynamics of the soil-to-leaf hydraulic resistance is a further challenge (Misson et al. 2004; Sperry et al. 1998; Tuzet, Perrier & Leuning, 2003; Williams et al. 2001). We recommend that efforts are concentrated on the estimation of soil and plant hydraulic resistance dynamics to reduce uncertainty in the modelling of leaf water potential.
Are changes in soil-to-leaf water supply dominated by changes in soil water potential or soil hydraulic resistance?

We tested the impact of changing the model input variables from their wet to dry season values, to investigate which factor had the greatest impact on gas exchange. Water supply to leaves is proportional to both the $\Psi_s$ to $\Psi_l$ gradient and to $1/R$ (Equation 4.4). $R$ appears to be more sensitive to changes in ecosystem water status and therefore was the dominant cause of reduced water use in the dry season. The change in the $\Psi_s$ to $\Psi_l$ gradient was small (an average factor of 2.2) while the change in $1/R$ between seasons was large (an average factor of 7.6). (Table 2.3). Altering the model input meteorology and LAI from wet to dry season caused an increase in SPA simulated sap flow (Table 2.5). Subsequently decreasing $\Psi_s$ to dry season values caused only a very small reduction of 0.07 mm day$^{-1}$ in the control plot, and a larger decrease of 0.26 mm day$^{-1}$ in the TFE plot. However, setting $R$ to its dry season values caused simulated sap flow to decrease by 0.23 and 1.07 mm day$^{-1}$ in the control and TFE plots respectively. Some authors (Donovan et al. 2001) have criticised the use of pre-dawn leaf water potential as a proxy for soil water potential, using plants from desert ecosystems which are prone to night-time transpiration. In this instance, we believe that sap flow reaches zero during the night, and that night time transpiration is unlikely. In addition, if errors were introduced by the dis-equilibrium between soil and leaf water potential, correction of this would have the effect of reducing the estimated soil water potential. In this case, this would decrease the impact of soil water potential on model predictions even further, and reinforce the conclusions already drawn.

In addition, this analysis indicated that very little restriction on sap flow occurred in the control plot even in the height of the dry season. The maximum unstressed sap flow in the control plot was 4.2 mm day$^{-1}$, compared to 3.9 mm day$^{-1}$ when resistance and soil water potential were changed to their dry season values. This finding mirrors that of Carswell et al. (2002) who found no seasonality in the eddy covariance gas exchange measurements, made at a flux tower 1 km from the through-fall exclusion experiment, at Caxiuana.
If there is a major change in soil-to-leaf hydraulic resistance, is the change in resistance located above or below ground?

We have shown that ecosystem sap flow is sensitive to soil-to-leaf hydraulic resistance \( (R) \) and that \( R \) is highly variable both between trees and through time. If simulation of the supply of water to leaves is a realistic and accurate means of simulating tree and forest sap flow, as demonstrated here, then the next goal of the development of hydraulic limitation simulation must therefore be to develop a process-based model for the \textit{a priori} prediction of \( R \) from other ecosystem level data. To achieve this goal, we must first deduce which part of the soil-plant-atmosphere continuum provides the greatest resistance to water movements under hydraulically stressed conditions.

We found that, in the wet season, the stem water potential measurements were very close to the soil water potential measurements, indicating that most of the soil-to-leaf hydraulic resistance was located above ground. However, the main change in resistance between seasons was below-ground. The optimization of the parameter \( b \) indicated that an average of only 13\% of the resistance was located below-ground in the wet season, increasing to 45\% in the dry season. Between seasons, the total soil-leaf resistance increased in all trees except C2 and T2. The total above-ground resistance did not change by more than 0.5 s MPa m\(^{-2}\) mmol\(^{-1}\) between seasons for all trees except T3 and T4. These results suggest that under control or ambient conditions, changes in \( R_{bg} \) were the factor dominating the dry season response of the trees. Under some more extreme dry conditions in the TFE plot, some increase in \( R_{ag} \) was triggered by the low system water potential. Branch resistivity values indicated no change in above-ground resistance between seasons.

We have therefore found that changes in below-ground resistance are the likely cause of stomatal limitation in the dry season. It remains to be determined whether this is due to increases in root xylem or soil-to-leaf hydraulic resistance.

### 2.7 Conclusions

We tested the hypothesis that stomata function to maintain isohydric conditions in rainforest trees under hydraulically stressed situations. We tested this hypothesis against diurnal time series in leaf water potential, stomatal conductance, sap flow and stem water potential from a tropical rain forest. The hypothesis, as embedded in the SPA model and including no optimised parameters, is in broad agreement with the data. Further model
analyses indicate that variations in soil-to-leaf resistance are the major factor limiting water use in the dry season and that very little hydraulic limitation of sap flow occurred in the control plot in the dry season. Stem psychrometer measurements indicate that the major change in resistance between seasons is located below ground, and we suggest that advances in understanding the response of tropical forests to gas exchange will result from intensification of research on the dynamics of soil-to-leaf hydraulic resistance.

We expect that increasing confidence in process-based representations of drought stress will eventually allow identification of the critical factors controlling forest vulnerability to drought stress. This will allow integration of our increasing understanding of forest hydrology and gas exchange processes, with concern about the effect of drier climates on biosphere-atmosphere interactions, both within Amazonia and in other drought threatened ecosystems.

2.8 Acknowledgements.

This work was supported by a University of Edinburgh faculty research Scholarship, several Natural Environment Research Council (UK) research grants, European Framework Programme 5 funding, a Natural Resources International Foundation Fellowship and the Elizabeth Sinclair fund (School of Geosciences, University of Edinburgh). R.A.F would like to thank Sandra Patino, Yadvinder Malhi, John Grace and Mike Dixon for help with experimental methods, planning and logistics, Rafael Ferreira da Costa, Alan Braga, João Athaydes and Paulo Gonçalves for their field assistance and the Museu Paraense Emilio Goeldi for the use of their field station and laboratory facilities.

2.9 Appendix

We used an estimate of $C$ derived using the data of Goldstein et al. (1998) for a seasonal tropical forest in Panama, the only published estimate of $C$ for tropical forest trees. Goldstein et al. (1998) found a relationship between tree basal area and tree capacitance by measuring the lag between sap flow in terminal branches and at the base of the trunk. We converted these estimates of $C$ to the units required for SPA using the following equation:

$$C = \frac{1}{n} \sum_{i} \frac{c_i}{r \psi \text{min}_i}$$

(2.5)
where \( C \) is the new value of capacitance \((\text{mmol MPa}^{-1} \text{ m}^{-2} \text{ (leaf area)})\), \( c_i \) is the value of capacitance \((\text{mmol m}^{-2} \text{ (basal area)})\) calculated by Goldstein et al. (1998) for the \( i \)th tree. \( \psi_{\text{min}} \) is the minimum value of \( \psi \) reported by Goldstein et al. for the \( i \)th tree (MPa). \( n \) is the number of trees sampled and \( \tau \) is the ratio between basal area and leaf area calculated for our site \((5.5 \text{ m}^2 \text{ m}^{-2})\). The sensitivity of SPA to \( C \) is low, except at the extremes of the ranges (Williams et al. 1998), so this method of calculation, using data from elsewhere in the tropics, is a tolerably level of uncertainty, given that there are no other data sets available for tropical species. Using this method, we find a mean value of \( C \) of 2300 mmol m\(^{-2}\) MPa\(^{-1}\).

The simulated sap flow \((S_j)\) in mm h\(^{-1}\) was calculated as

\[
S_j = \sum_{i=1}^{h} \frac{s_i L_{(i,j)}}{l_i}
\]

(2.6)

where \( j \) is a given tree and \( i \) is one of 10 modelled canopy layers. \( s_i \) is the SPA simulated sap flow (mm h\(^{-1}\) m\(^{-2}\) - ground area) of layer \( i \). \( l_i \) is the modelled leaf area (m\(^2\)) in layer \( i \) per m\(^2\) of ground area. \( L_{(i,j)} \) is the leaf area estimated for layer \( i \) of tree \( j \) (m\(^2\)).

### 2.10 References


in CO$_2$ and H$_2$O flux at an eastern Amazonian rain forest. *Journal of Geophysical Research*, 107(D20), 8076.


Chapter 3

3.1 Abstract

Estimates of unsaturated hydraulic conductivity ($K_{\text{unsat}}$) are rare for tropical soil and in particular for Amazonia. This lack of data causes large uncertainties in the estimation of land surface evapotranspiration within global climate models. We present unsaturated hydraulic conductivity data for a sandy oxisol in Eastern Amazonia measured using tension infiltrometry and the instantaneous profile method, in addition to water retention curves for the same soil. This is the second published data set of $K_{\text{unsat}}$ for Amazonian soils. We tested the ability of four soil hydraulic models to represent the data and found that there was little variation between the model fits. We used the soil hydraulics models to extrapolate the $K_{\text{unsat}}$ data from the measurement limit, $-8$ kPa, to $-1500$ kPa and found that the choice of van Genuchten, Campbell or Brooks-Corey model caused differences in $K$ of only $0.58$ orders of magnitude at $-1500$ kPa. We tested the ability of a Brazil-specific pedo-transfer function to predict the water retention curve from soil texture. The range of volumetric water content values was over predicted by the PTF, and the model incorrectly predicted the shape of the relationship. We also tested a relationship between the water retention and hydraulic conductivity curves developed specifically for Brazilian soils. The model generally underestimated hydraulic conductivity, indicating, in common with previous measurements, that Amazonian soils may exhibit anomalously high hydraulic conductivity values.

3.2 Introduction

The hydraulic properties of soils - water retention capacity, water potential, and hydraulic conductivity, are key controls of land surface energy balance, ecosystem evaporation, infiltration, runoff and drainage. For temperate soils, there are large databases of soil hydraulics data, but for tropical soils, data are very limited (Hodnett and Tomasella, 2002). In the Amazon basin, a key component of the global weather system (Werth and Aviszar 2002, 2004), soil hydraulic properties are poorly understood, especially with respect to unsaturated hydraulic conductivity, for which measurements have been made at only one site near Manaus, in central Amazonia (Tomasella and Hodnett, 1996).

During the dry season, where atmospheric demand for evapotranspiration is higher than rainfall, evapotranspiration depends on stored soil water. The majority of the rain-
forests of Southern and Eastern Amazonia experience, in an average year, periods, sometimes exceeding three months, during which rainfall is less than 0.3 mm day\(^{-1}\). (Sombroek 2001), therefore many Amazonian forests probably rely on deep (>2m) soil water to maintain evergreen canopies and correspondingly high levels of evapo-transpiration (Hodnett et al. 1998; Nepstad et al. 1994). More intensive dry seasons are forecast by the majority of climate change models (Cubash et al. 2001; Cox et al. 2000) and it is unclear whether soil water storage will be sufficient to maintain the functioning of a closed canopy under such circumstances (Werth and Avisar 2002).

The rate of extraction of soil water by plants depends upon the water potential gradient between the soil and the leaves, and the soil and plant hydraulic conductivity. As soils dry and water content decreases, both soil water potential and soil hydraulic conductivity decrease. Therefore, both soil water potential and hydraulic conductivity may potentially limit the rate of extraction of water by roots if leaf water potential remains constant (Comstock and Mencuccini, 1998; Hubbard et al. 2001; Sperry et al. 2002). It is necessary that we know both the soil water retention and hydraulic conductivity properties to predict the limits of soil water extraction by plants.

Hydraulic properties of soils are usually described as empirical functions relating soil water content to soil matric potential and hydraulic conductivity (van Genuchten, 1980; Campbell, 1974; Brooks and Corey, 1964). Soil hydraulic properties are generally a function of soil texture, among other factors, since grain size determines the distribution of pore sizes and, thus, the tension at which water is released from the soil.

Soil hydraulic properties have been measured for a large number of temperate soils, and for most soils, the parameters of soil hydraulics models may be predicted from soil texture using empirical equations called pedo-transfer functions (PTFs). However, tropical soils are poorly represented in global data sets (Hodnett and Tomasella, 2002). In the IGBP-DIS data-set, of 131,472 horizons, only 785 horizons with sufficient data to produce a water retention curve were found for tropical soils. Hodnett and Tomasella (2002) constructed a PTF to predict the van Genuchten parameters (van Genuchten, 1980) of tropical soils from texture using these data. They found significant differences in the van Genuchten parameters of given soil textures between the tropical and temperate soils, especially for clay soils, which were poorly represented by the temperate database. Tomasella et al. (2000) showed that a Amazon-soil-derived PTF predicted the water retention characteristics of an independent set of Amazonian soils better than temperate soil derived PTFs. This was
attributed to the bi-modal pore structure of the highly weathered tropical oxisols, which resemble a clay at low water potential and sand at high water potentials.

Tomasella and Hodnett (1997) developed a means of predicting unsaturated hydraulic conductivity from water retention properties using all the data available from Brazilian soils. However, the only hydraulic conductivity measurements available from the Amazon rain forest - those made for a clay oxisol near Manaus (Tomasella and Hodnett, 1996) - exhibited unusually high hydraulic conductivity for a soil containing 75% clay owing to biogenic macropores present in the clay structure. These Amazonian soils data were an outlier to the otherwise consistent relationship between saturated conductivity and porosity found for other Brazilian soils. However, as only a single set of hydraulic conductivity experiments has been conducted in Amazonia, it is unclear how widely this atypically high conductivity occurs among all rainforest soils. Hodnett and Tomasella (1996) suggest that the high conductivity is a function of the abundance of biogenic macropores, derived from the intensive root and macroinvertebrate activity in rainforest soils. It is therefore possible that all rain forest soils exhibit high conductivity in the macropore range, but no data are yet available to test this hypothesis.

In this paper, we present a second set of data on the unsaturated hydraulic conductivity of Amazonian soils, that was collected using similar methodology to that used by Tomasella and Hodnett (1996), for a highly weathered sandy oxisol (U.S. Department of Agriculture Soil Taxonomy), located in Eastern Amazonia. The methods used did not provide estimates of soil hydraulic conductivity (K) for soils drier than field capacity. Ultimately, these data will be useful for modelling plant water uptake, which occurs at water potentials lower than field capacity. It was therefore necessary to use soil hydraulic models to extend the K data into drier soil, to allow the representation of soil processes in drier conditions. We tested the impact of using a range of models to predict K in dry soil, and compared our measured data to the predictions of existing pedo-transfer functions. We asked the following questions:

1. Which soil hydraulic model provides the most accurate representation of the water retention curve and hydraulic conductivity data collected?
2. What is the impact of model choice on predictions of hydraulic conductivity in dry soils (−8 to −1500 kPa) when extrapolating K measurements beyond field capacity?
3. Is the water retention curve typical of Amazonian soils of this texture with reference
to an Amazonian water retention curve pedo-transfer function (Tomasella et al. 2000)?

4. Does the soil exhibit high hydraulic conductivity with reference to the Brazilian soil-specific relationship between water retention and hydraulic conductivity described by Tomasella and Hodnett (1997)?

3.3 Methods

3.3.1 Site

The experimental site is located in the Caxiuanã National Forest, Pará, Brazil, (1° 43’ 3.5" S, 51° 27’ 36" W). The forest is a lowland terra firme rainforest. Mean annual rainfall is 2272 mm (± 193 mm), but with a pronounced four month dry season between July and November, when only 310 mm (± 127 mm) of rainfall occurs on average (data from 1999 to 2002).

The soil is a yellow oxisol (Brazilian classification latosol), with a 0.3-0.4 m thick stony/laterite layer at 3-4 m depth. The soil texture (0.0 to 0.5 m) is 75-83% sand (>0.05 mm particle diameter), 12-19% clay (<0.02 mm) and 6-10% silt (0.05 - 0.02 mm) (Ruivo and Cunha, 2003). The soil consists of mainly kaolin in the clay fraction and quartz in the sand fraction. (Ruivo and Cunha, 2003). The site elevation is 15 m above river level.

3.3.2 Water Retention Curve Measurement

Pressure plate analyses were conducted on intact samples, collected in April 2002 inside 55 cm³ soil cores, at depths corresponding to soil horizons identified by Ruivo and Cunha (2003) in two 5 m deep soil trenches. The trench locations were chosen at random from within a 220 x 100 m plot located 500 m north of the Caxiuanã research station. Water contents were gravimetrically determined at —6, —10, —30, —100 and —1500 kPa. The water retention curve for tensions between —6 kPa and —1 kPa was determined by in-situ measurements of soil water potential (ψ) and soil water content (θ) by the instantaneous profile method described below. The water retention curve for tensions between —1 and —0.1 kPa was determined from the water retention curve constructed from the soil calibration experiment also described below.
3.3.3 Unsaturated Hydraulic Conductivity Measurement

The measurement of hydraulic conductivity at tensions below field capacity is inherently difficult, since gravity does not provide a hydraulic gradient sufficient to cause the measurable movement of water. Water movement must therefore be driven by gradients in matric potential, which are difficult to implement for in-situ soil (Dirksen, 2000). Given the logistical constraints imposed by the remote location of the field site, measurement of the hydraulic conductivity was therefore possible only at tensions wetter than field capacity. We used two field based methods, tension infiltrometry (Ankeny et al. 1991) and the instantaneous profile method (Dirksen, 2000) to obtain estimates of $K$ over different ranges of tension.

3.3.4 Tension Infiltrometer

Measurements of unsaturated conductivity of soils in the macropore region ($-0.1$ to $-1$ kPa tension) were made using a tension infiltrometer (TI) with a 0.2 m disk (Soil Measurement Systems, Tucson, AZ, USA). Measurements of infiltration rates were made for every 0.1 kPa of tension between $-0.1$ and $-1$ kPa. It is necessary to correct the TI measurements for the increase in apparent flow caused by the three-dimensional capillary flow. To achieve this, we applied the correction method suggested by Reynolds and Elrick (1991).

Eight hydraulic conductivity $K$ vs. water potential $\psi$ curves were measured on the surface soil. Measurements were randomly located within the chosen 220 x 100 m plot. In addition, three TI measurement profiles, also randomly selected, were made by removing the soil sequentially and measuring $K$ vs. $\psi$ at four different depths (0.1, 0.35, 0.5 and 0.9 m). The tension infiltrometer measurements for each profile were not located immediately below one another to prevent possible impacts of compaction of the soil column by the instrument. To infer the water content ($\theta$) from the water potential ($\psi$) at which measurements were made, we used the simultaneous measurements of these parameters made during the soil core calibration procedure (below) to allow continuous $K$ vs $\theta$ functions to be derived.
3.3.5 Instantaneous Profile Method

The instantaneous profile method (IPM) measured the vertical flow of water through soil by isolating a monolith of soil, 1 m diameter by 1 m depth and wrapping it in plastic sheeting to prevent lateral water movement. Soil water content and water potential were measured at 0.05, 0.3, 0.6 and 0.9 m using CS615 probes (Campbell Scientific, Loughborough, UK) and mini tensiometers (Skye Instruments, Llandrindod Wells, Wales) respectively, and readings were logged each minute using a Campbell Scientific CR10X datalogger (Campbell Scientific, Loughborough, UK). Water was poured on top of the monolith until the mini-tensiometers gave readings above —0.2 kPa, indicating that saturation had been achieved. The monolith was covered to prevent evaporation from the soil surface, and allowed to drain. The flow past the sensors \((q)\) was calculated at each depth as the loss in storage of the soil above the sensor in mm h\(^{-1}\). Using this estimate, the hydraulic conductivity \(K\) (mm h\(^{-1}\)) was calculated as

\[
K[\theta, z, t] = \frac{q[z, t]}{d(H)/d(z)[z, t]} \tag{3.1}
\]

where \(z\) is depth (mm), \(t\) is time (h), and \(H\) is the hydraulic head (mm) (Dirksen 2000). The tensiometers, located at the same depth as the CS615 probes, also allowed the construction of in-situ water retention curves. The monolith was left to drain until the water potential of all the sensors was below —6 kPa.

3.3.6 Soil moisture sensor calibration.

In the sandy soil at the Caxiuana site, the applicability of the calibration functions of the CS615 soil moisture sensors used in the IPM method was unknown, so we conducted a gravimetric calibration to assess how the sensors respond to varying soil moisture in the sandy latosol soil. We removed three 0.3 m long, 0.15 m diameter cores of soil kept intact within PVC piping. We took two cores from the surface soil (0.05 to 0.35 m depth) and one from 0.35 to 0.65 m depth. The locations were chosen at random (avoiding large roots) with the 220 x 100 m plot.

Each core was instrumented with a CS615 probe and a mini-tensiometer. The cores were continuously saturated until the automatic moisture readings were stable for 30 minutes, and the tensiometer readings were less than —0.02 kPa, indicating that saturation had been reached. The cores were allowed to drain and placed inside a light box at (at
~60°C) and simultaneous measurements of soil mass, and moisture sensor output were made at gradually increasing time intervals for ten days. At the end of the calibration period, the sensors were removed, and the cores were dried for 24 hours at 105°C and weighed to determine the mass of the dry soil.

Soil calibration curves were established by calculation of the volumetric water content \( \theta (m^3 m^{-3}) \) using the following relationship:

\[
\theta = \frac{M_w - M_d}{\rho V}
\]

where \( M_w \) and \( M_d \) are the masses of the wet and dry soils respectively (g) and \( \rho \) is the density of water (g m\(^{-3}\)) and \( V \) is the volume of the core in m\(^3\).

**3.3.7 Model Extrapolation of Hydraulic conductivity**

Given the difficulties inherent in the measurement of unsaturated hydraulic conductivity, four soil hydraulic models were used to extrapolate the \( K_{\text{unsat}} \) data into unsaturated soil. Several soil hydraulics models are in widespread use in the soil modelling community. We have used three of the most common - the Campbell (1974), van Genuchten (1980) and Brooks and Corey (1964) models - and a fourth model (Poulsen et al. 2003) designed to account for the behaviour of soils with multi-modal pore size distributions, to account for the possibility of the soil displaying similar bi-modal pore size distribution to other Amazonian oxisols (Tomasella and Hodnett, 1996).

**Campbell Model**

The Campbell (1974) model of hydraulic conductivity proposes that the water retention function is a single exponential relationship,

\[
\psi = \alpha_{cb}(\frac{\theta}{\theta_s})^{-b}
\]

where \( \alpha_{cb} \) is the air entry water potential (where saturation is approached and water content is effectively constant) in kPa, \( \theta_s \) is the saturated water content (m\(^3\) m\(^{-3}\)) and \( b \) is a shape parameter related to the pore size distribution. The related hydraulic conductivity equation is,

\[
K = K_{cb}(\frac{\theta}{\theta_s})^{2b+3}
\]
where $K$ is the hydraulic conductivity (mm h$^{-1}$), $K_{cb}$ is the saturated hydraulic conductivity (mm h$^{-1}$). The two relationships are linked by their common dependance on the shape parameter $b$.

**van Genuchten Model**

The van Genuchten et al. (1980) model describes the water release curve as,

\[
S_e = \frac{\theta - \theta_r}{\theta_s - \theta_r} = \left[1 + (\alpha_{vg} \psi)^n\right]^{1+1/n} \tag{3.5}
\]

where $S_e$ is the effective saturation, with $\theta_s$ and $\theta_r$ as the saturated and residual soil water contents (m$^3$ m$^{-3}$). $\alpha_{vg}$ is a scaling factor which determines the maximum pore size (kPa$^{-1}$), and $n$ is a dimensionless curve shape parameter. Hydraulic conductivity is given as,

\[
K = K_{vg} \frac{(1 - (\alpha_{vg} \psi)^n)^{-[1 + (\alpha_{vg} \psi)^n]^{-1}(1-1/n)^2}}{[1 + (\alpha_{vg} \psi)^n]^{1(1-1/n)}} \tag{3.6}
\]

A 'tortuosity factor' $l$, is required, to account for the influence of soil structure on conductivity. Therefore the shapes of the water retention and hydraulic conductivity curves are independent. $K_{vg}$ is the saturated hydraulic conductivity (mm h$^{-1}$).

**Brooks-Corey Model**

The Brooks-Corey model (1964) defines the soil hydraulic behaviour using the following two equations,

\[
S_e = \frac{\theta - \theta_r}{\theta_s - \theta_r} = (\alpha_{bc} \psi)^{-\lambda} \tag{3.7}
\]

\[
K = K_{bc} \cdot \psi^{N_{bc}} \tag{3.8}
\]

where $\alpha_{bc}$ (kPa$^{-1}$) is related to the air entry value and $\lambda$ is the shape parameter of the water retention curve. Two more parameters, the saturated hydraulic conductivity, $K_{bc}$ (mm h$^{-1}$), and the hydraulic conductivity shape parameter, $N_{bc}$, determine the hydraulic conductivity curve. $N_{bc}$ is related to $\lambda$

\[
N_{bc} = \frac{1.843}{\lambda} + 3.701 \tag{3.9}
\]

so the water retention curve and hydraulic conductivity curve are thus linked.
Poulsen et al., Three Region Model

All the above models assume that there is a unimodal frequency distribution of pore size within the soil. This assumption is frequently violated, especially in the case of structured, undisturbed soils that contain secondary pore systems, including cracks, fissures, biogenic macropores and microaggregates (Durner et al. 1994). The high abundance of both biogenic macropores and clay matrix micropores, and the resulting bi-modal pore size distribution, was cited as a possible explanation for the poor fit of the van-Genuchten model to the hydraulic conductivity data collected by Tomasella and Hodnett (1996) for the clay oxisol near Manaus. At Caxiuanã, it is possible that, due to the existence of rain forest ecosystems at the sites, that biogenic macropores may also alter the soil structure.

The Poulsen et al. (2003) model accounts for this possibility by incorporating different water retention characteristics for macro, meso and micro pore regions. The Poulsen et al. model describes both the Log $\theta$ vs. Log $\psi$ and the Log $\theta$ vs. Log $K$ relationships as a series of three straight lines, corresponding to the behaviour of the macro, meso and micro pore ranges ($\geq -1$ kPa, $-1$ to $-25$ kPa and $\leq -25$ kPa respectively) (Fig. 3.1). Poulsen et al. observed that, for a dataset of 168 European soils, in the meso and micro pore regions, there was a strong relationship between the slope of measured water retention curve and that of the hydraulic conductivity curve. Therefore, if the slope of measured water retention curve is known, in combination with a scaling value for the macro-mesopore region boundary ($K_{-1kPa}$), the hydraulic conductivity of the mesopore region may be estimated. The log-log slopes of the water retention curve in the macropore, mesopore and micropore zones are denoted as $b_1$, $b_2$ and $b_3$ and the log-log slopes of the hydraulic retention curve in the macropore, mesopore and micropore zones are denoted as $\alpha_1$, $\alpha_2$ and $\alpha_3$, where $b_2$ and $b_3$ are calculated as,

$$b_{2,3} = \frac{d(\log \psi)}{d(\log \theta)}$$

(3.10)

and the parameters $B_2$ and $B_3$ are calculated as,

$$B_{2,3} = 1.2b_{2,3} + 2.75$$

(3.11)

The $K$ vs. $\theta$ relationship of the mesoporous region is calculated from this estimate of its gradient ($B_2$) and $K_{-1kPa}$,

$$\log K = \log(K_{-1kPa} - B_2(\log \theta_{-1kPa} - \log \theta))$$

(3.12)
Figure 3.1: Generalised representation of the form of the Poulsen et al. (2003) three region soil hydraulics model showing the proposed models of the water retention curve (a) and the hydraulic conductivity curve (b).

Equation 3.12 is used to forecast the conductivity at $-25$ kPa, and this value is then used to scale the conductivity of the micropore region, using the value of $B_3$ calculated by equation 3.10.

$$\log K = \log K_{-25\text{kPa}} - B_3(\log \theta_{-25\text{kPa}} - \log \theta)$$ \hspace{1cm} (3.13)

The conductivity of the macropore zone ($0$ to $-1$ kPa) is expressed as a linear log-log relationship between $\theta$ and $K$. The intercept and gradient of the relationship between $\theta$ and $K$ may be determined from the tension infiltrometry data. The applicability of the Poulsen et al. (2003) model depends on the applicability of the temperate soil derived relationship in Equation 3.11 to this tropical soil data set.
Table 3.1: Summary of the available soil hydrology data

<table>
<thead>
<tr>
<th>Data Type</th>
<th>$\psi$ range (kPa)</th>
<th>Depth Range (m)</th>
<th>Hydraulic conductivity</th>
<th>Water Potential</th>
<th>Water Content</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tension Infiltrometer</td>
<td>-0.1 to -1</td>
<td>0 to 0.9</td>
<td>yes</td>
<td>yes</td>
<td>no</td>
</tr>
<tr>
<td>Pressure Plates</td>
<td>-6 to -1500</td>
<td>0 to 4.5</td>
<td>no</td>
<td>yes</td>
<td>yes</td>
</tr>
<tr>
<td>Soil calibration cores</td>
<td>-0.1 to -6</td>
<td>0 to 0.9</td>
<td>no</td>
<td>yes</td>
<td>yes</td>
</tr>
<tr>
<td>Instantaneous Profile</td>
<td>-0.8 to -7</td>
<td>0 to 0.9</td>
<td>yes</td>
<td>yes</td>
<td>yes</td>
</tr>
</tbody>
</table>

3.3.8 Parameter Fitting

The tension infiltrometer, instantaneous profile and pressure plate measurements were made at slightly different depths in all cases (Table 3.1). To allow comparison between the measurements, we grouped the data into four 0.1 m depth range categories. The depth categories used were 0.05-0.15 m, 0.25-0.35 m, 0.55-0.65 m and 0.85-0.95 m. By grouping together the data in this way we have assumed that each 0.1 m depth range is effectively homogeneous. This assumption is necessary because it is not practically possible to do all the measurements in the same location.

The Campbell, Brooks-Corey and van Genuchten models all required parameter optimisation. This was achieved using the simplex search method (Lagarias et al. 1998) embedded in ‘Matlab’ (MathWorks Inc., Natick, MA, USA). The parameters were fitted to minimise the error parameter $e$, the sum of the relative root mean square error between the observed and modelled water contents ($\theta_o$ and $\theta_m$), plus the sum of the relative root mean square errors between log of the $K$ data ($K_o$) and the log of the model $K$ prediction ($K_m$).

$$e = \sum \frac{(\theta_o - \theta_m)}{\theta_o} + \sum \frac{(\log K_o - \log K_m)}{\log K_o}$$  \hspace{1cm} (3.14)

The log transformation of $K$ is based on the assumption that the data error is constant on a log scale, and avoids bias of the fitting routine towards the larger values, as $K$ varies over many orders of magnitude. The Poulson model parameters were found using the water retention data, as described in the methods section.
3.3.9 Prediction of Water Retention Curves from soil texture

Hodnett and Tomasella (2002) found 'marked differences' between temperate and tropical soil water retention parameters. We therefore employed a PTF developed specifically for Brazilian soils by Tomasella and Hodnett (2000) (TH2000) to determine whether the Caxiuaná sandy oxisol was typical of soils of the region. The TH2000 model predicts the parameters of the van Genuchten equation from soil texture (coarse sand, fine sand, silt and clay). Tomasella and Hodnett (2000) provide four different pedo-transfer functions, differing in the amount of data required as inputs. We used the third level of complexity, which required inputs of course and fine sand, silt, clay, bulk density and organic carbon content. The inputs were derived from measurements made at the same site by Ruivo and Cunha (2003).

3.3.10 Prediction of Hydraulic Conductivity from water retention curves and soil texture

Tomasella and Hodnett (1997) provide an equation for predicting the hydraulic conductivity of the soil from soil porosity (the TH1997 model). The relationship was constructed using all the available \( K_{\text{sat}} \) within Brazil. They found a consistent relationship between the soil porosity index (defined as the water released between saturation and -33 kPa) and the saturated hydraulic conductivity (\( K_{\text{sat}} \)) for the Brazilian soil data set, with the exception of the Manaus clay oxisol which was the only Amazonian soil in the data set. This soil was an outlier, and had a significantly higher \( K_{\text{sat}} \) than that expected from the relationship derived from all the other soils. The TH1997 model also includes a Brazilian soil specific relationship between the parameter of the Brooks-Corey water retention curve (\( b \)) and the parameter of the Brooks-Corey hydraulic conductivity curve (\( N \)) using the whole data set. We applied the TH1997 model to the water retention curve data to predict the hydraulic conductivity values. We compared our data to the output of the TH1997 model, and to the Saxton (1986) pedo-transfer function, a standard temperate soil pedo-transfer function.
3.4 Results

3.4.1 Soil Moisture Sensor Calibration

The responses of the CS615 probes to water content were effectively linear (Fig. 3.2). The results for all cores were grouped together to produce the following calibration equation:

\[ \theta = 0.79P + (-0.59) \]

Where \( \theta \) is the volumetric water content (m\(^3\) m\(^{-3}\)) and \( P \) is the period output of the CS615 sensors in ms. We used this calibration to determine the water content values given by the CS615 sensors in the Instantaneous Profile Method.

![Calibration curve](image)

Figure 3.2: Calibration of CS615 sensor output against gravimetrically determined volumetric soil water content. Calibration line follows equation of best fit to all data: \( \theta = 0.79P - 0.59 \)

3.4.2 Water Retention

Three data sets were used to create the water retention curve; the soil calibration core water retention curves, the in-situ water retention curves from the IPM, and the pressure
Figure 3.3: Water retention curve data from pressure plates and in-situ measurements, plus model approximations to the data made using the van Genuchten (VG), Poulsen (PN), Campbell (CB) and Brooks Corey (BC) models. Data are shown for water potentials beneath the air entry value determined by the Campbell equation.
plate data. Where the ranges of measurement of the in situ and IPM methods overlapped at −1 kPa, estimates of water content ranged from 0.313 to 0.329 m$^3$ m$^{-3}$, and there was good agreement between the two data sets (Fig. 3.3). However where the IPM and pressure plate methods overlapped at −6 kPa there were, in two cases (0.05 and 0.90 m), slight offsets between the pressure plate water retention curves and the IPM water retention curves. The offsets were 4 and 7% for 0.05 and 0.90 m respectively. This result is probably due to heterogeneity between the soils sampled.

The water retention results show that the saturation values of the different soil depths were very similar and all were within 1% of 0.37 m$^3$ m$^{-3}$. Between saturation and field capacity (−6 kPa) and an average of 0.088 m$^3$ m$^{-3}$ was lost from the soil. This water is normally unavailable to plants as it is quickly drained away. Between field capacity and −100 kPa (a nominal limit of rapid plant water extraction) a further 0.137 m$^3$ m$^{-3}$ was lost, and between this value and −1500 kPa (water which is slowly extracted in drought stressed circumstances) another 0.062 m$^3$ m$^{-3}$ was available. This means that in the key region of plant availability, the soil has a high water retention. The Manaus soil had a field water range (after drainage) of only 0.05 -0.10 m$^3$ m$^{-3}$. This means that the Caxianã soils had substantially higher quantities of available water than those at Manaus, even though the Manaus soils are a clay and the Caxianã soils are a sand.

The best model fit for the water retention curves was provided by the van Genuchten (VG) model (Table 3.3) which had an RMSE of 0.0302 m$^3$ m$^{-3}$ for data below the air entry value. However, the RMS error values of the 4 models were very similar. The worst fit was the Poulsen (PN) model (0.0347 m$^3$ m$^{-3}$). The Brooks-Corey and Campbell models had intermediate RMS values. Given the uncertainty in the data, essentially there was very little difference between the model fits. This means that model choice does not have an impact on the ability to describe the water retention curve successfully.
Table 3.2: The best fitting parameter sets of the four soil hydraulics models at four depths.

<table>
<thead>
<tr>
<th>Model</th>
<th>Parameter</th>
<th>Depth</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>0.05-0.15 m</td>
<td>0.25-0.35 m</td>
<td>0.45-0.55 m</td>
<td>0.9-1.0 m</td>
</tr>
<tr>
<td>van-Genuchten</td>
<td>( \theta_r )</td>
<td>0.0003</td>
<td>0.0009</td>
<td>0.001</td>
<td>0.0004</td>
</tr>
<tr>
<td></td>
<td>( \theta_s )</td>
<td>0.397</td>
<td>0.371</td>
<td>0.372</td>
<td>0.382</td>
</tr>
<tr>
<td></td>
<td>( \alpha_{vg} )</td>
<td>1.83</td>
<td>0.636</td>
<td>0.720</td>
<td>0.586</td>
</tr>
<tr>
<td></td>
<td>( n )</td>
<td>1.15</td>
<td>1.23</td>
<td>1.17</td>
<td>1.12</td>
</tr>
<tr>
<td></td>
<td>( K_{vg} )</td>
<td>955</td>
<td>376</td>
<td>397</td>
<td>1292</td>
</tr>
<tr>
<td></td>
<td>( l )</td>
<td>0.12</td>
<td>-0.06</td>
<td>1.35</td>
<td>-0.08</td>
</tr>
<tr>
<td>Poulson</td>
<td>( b_1 )</td>
<td>45.8</td>
<td>45.8</td>
<td>45.8</td>
<td>45.8</td>
</tr>
<tr>
<td></td>
<td>( b_2 )</td>
<td>9.39</td>
<td>3.61</td>
<td>6.31</td>
<td>8.12</td>
</tr>
<tr>
<td></td>
<td>( b_3 )</td>
<td>3.01</td>
<td>11.4</td>
<td>8.72</td>
<td>9.63</td>
</tr>
<tr>
<td></td>
<td>( K_{1 kPa} )</td>
<td>1.39</td>
<td>1.51</td>
<td>2.66</td>
<td>5.06</td>
</tr>
<tr>
<td>Campbell</td>
<td>( \theta_s )</td>
<td>0.351</td>
<td>0.354</td>
<td>0.368</td>
<td>0.333</td>
</tr>
<tr>
<td></td>
<td>( \alpha_{cb} )</td>
<td>0.97</td>
<td>0.68</td>
<td>0.51</td>
<td>1.11</td>
</tr>
<tr>
<td></td>
<td>( b )</td>
<td>9.59</td>
<td>5.36</td>
<td>7.87</td>
<td>9.53</td>
</tr>
<tr>
<td></td>
<td>( K_{cb} )</td>
<td>2.4</td>
<td>65.3</td>
<td>84.2</td>
<td>20.0</td>
</tr>
<tr>
<td>Brooks-Corey</td>
<td>( \theta_s )</td>
<td>0.361</td>
<td>0.359</td>
<td>0.354</td>
<td>0.344</td>
</tr>
<tr>
<td></td>
<td>( \theta_r )</td>
<td>0.0012</td>
<td>0.0009</td>
<td>0.0012</td>
<td>0.0012</td>
</tr>
<tr>
<td></td>
<td>( \alpha_{bc} )</td>
<td>1.34</td>
<td>1.08</td>
<td>1.11</td>
<td>1.20</td>
</tr>
<tr>
<td></td>
<td>( \lambda )</td>
<td>0.104</td>
<td>0.19</td>
<td>0.135</td>
<td>0.105</td>
</tr>
<tr>
<td></td>
<td>( N_{bc} )</td>
<td>21.3</td>
<td>12.9</td>
<td>17.3</td>
<td>21.2</td>
</tr>
<tr>
<td></td>
<td>( K_{bc} )</td>
<td>90.7</td>
<td>4.02</td>
<td>4.85</td>
<td>103.9</td>
</tr>
</tbody>
</table>

Table 3.3: RMSE errors of water retention curve predictions, and log errors of hydraulic conductivity predictions, made using either both tension infiltrometer and instantaneous profile data, or only tension infiltrometer data.

<table>
<thead>
<tr>
<th>Model</th>
<th>VG</th>
<th>PN</th>
<th>CB</th>
<th>BC</th>
</tr>
</thead>
<tbody>
<tr>
<td>RMS (( \theta_{obs} - \theta_{model} ))</td>
<td>0.0302</td>
<td>0.0347</td>
<td>0.0310</td>
<td>0.0305</td>
</tr>
<tr>
<td>RMS (Log ( K_{obs} - Log K_{model} )): All data</td>
<td>0.1683</td>
<td>0.198</td>
<td>0.2286</td>
<td>0.2119</td>
</tr>
<tr>
<td>RMS (Log ( K_{obs} - Log K_{model} )): TI data only</td>
<td>0.30</td>
<td>0.19</td>
<td>0.29</td>
<td>0.2119</td>
</tr>
</tbody>
</table>
3.4.3 Hydraulic conductivity

There was generally good agreement between the two hydraulic conductivity measurement techniques, (tension infiltrometry and instantaneous profiling) where their ranges overlapped at —1 kPa. The maximum difference between the two techniques was 0.6 mm h$^{-1}$, hence continuous $K$ vs. $\theta$ relationships between —0.1 and —7 kPa were constructed for each depth using these two data sets (Fig. 3.4). The observed values of $K$ varied over 5 orders of magnitude over the measured range of water contents, between 844 mm h$^{-1}$ and 0.01 mm h$^{-1}$.

The van-Genuchten model provided the best description of the hydraulic conductivity data (Table 3.3). However the van Genuchten model responded in a highly unstable manner to the removal of the IPM data. The VG model has a large number of fitted
parameters, and when the parameters are fitted to a small dataset, several combinations of parameters explain the data equally well, and while searching for the optimum combination, these local minima are encountered. The log-log error between the VG model and the data increased from 0.16 to 0.30 m$^3$ m$^{-3}$ when the IPM data were excluded, hence the use of the VG model with limited data (e.g. studies where logistics preclude the use of the more labour intensive IPM method) may produce results with large extrapolation errors. The Campbell and Brooks-Corey produced slightly poorer fits to the hydraulic conductivity data as their shape parameters ($b$ and $N$, respectively) were constrained by the shape of the water retention curve. The van Genuchten model included the parameter $l$ which alters the shape of the hydraulic conductivity curve independently of the water retention data.

### 3.4.4 Prediction of Water Retention Curves from soil texture

The Brazilian specific pedo-transfer function (TH2000) overestimated the range of water content between saturation and $-1500$ kPa in all cases with an average net overestimate of 0.052 m$^3$ m$^{-3}$. There was no systematic over or under estimation of the actual water content values across all the layers. In addition to this, the TH2000 model substantially overestimated the loss of water between $-1$ and $-100$ kPa compared to the data. (Fig. 3.5). The RMSE error (0.078 m$^3$ m$^{-3}$) was more than double the average error of $\sim 0.035$ m$^3$ m$^{-3}$ reported by Hodnett and Tomasella for soils with less than 10% silt. Because of the difference in shape between the TM200 model and the data, the water availability between $-6$ kPa and $-100$ kPa is only 0.8 m$^3$ m$^{-3}$, compared to the actual value of 0.137 m$^3$ m$^{-3}$. This is an error of $\sim 40 \%$, which could substantially change the modelled ecosystem properties.

### 3.4.5 Prediction of Hydraulic Conductivity from water retention curves and soil texture

The TH1997 model under-predicted $K_{unsat}$ for the whole range of values for the 0.60 m and 0.90 m layers (Fig. 3.6). The values of $K$ for water contents wetter than the air entry value were better predicted for the top 2 layers, but hydraulic conductivity values approaching saturation were substantially under-predicted in all cases. There seems to be
Figure 3.5: Available water content as measured by pressure plate curves (Caxianá data) and as predicted from soil texture by the pedo transfer function of Tomasella and Hodnett (1998).
a general under-prediction of the hydraulic conductivity values by the TH1997 Brazilian soil relationship, in common with the conclusions of Tomasella and Hodnett (1997), who noted that the saturated hydraulic conductivity of the clay oxisol found at Manaus was also higher than the model predicted. This may potentially due to the possibility that Amazon rain forest soils display increased hydraulic conductivity on account of the existence of biogenic pores in the soil structure, resulting from intense biological activity found in the rain forest environment. However, as this is only a single set of data, general trends cannot be derived.

The Saxton model was a very poor predictor of hydraulic conductivity. While the TH1997 model accurately predicted the gradient, if not the intercept of the conductivity curve, the Saxton model underestimated the gradient and overestimated the intercept in all cases (Fig. 3.6). Neither model properly predicted the rapid change in K between saturation and −1 kPa shown in the data. This pattern reflects the change in the gradient of the water retention curve at low tensions (Fig. 3.3).

3.5 Discussion

Which soil hydraulic model provides the most accurate representation of the water retention curve and hydraulic conductivity data collected?

We found that the most accurate representation of the data overall was provided by the van Genuchten model, but that the fits of all the models to the water retention data were very similar, with RMSE errors of 0.03 m$^2$ m$^{-2}$. The Poulsen model, with its rigid structure of 3 straight line log (θ) vs. log(K) relationships, was not flexible enough to represent the data as well as the other three models. However, since the model fits were all very similar, it is not appropriate to suggest that one model is superior to another, given the uncertainty in the data.

What is the impact of model choice on predictions of hydraulic conductivity in dry soils (−8 to −1500 kPa) when extrapolating K measurements beyond field capacity using models?

The predictions of the Campbell, Brooks-Corey and van Genuchten models for $K_{unsat}$ at −1500 MPa were very similar at all four depths, and varied by only 0.58 orders of
Figure 3.6: Comparison of hydraulic conductivity data with the predictions made by the pedo-transfer function of Tomasella and Hodnett (1997).
magnitude (over a range of 9 orders of magnitude). The Poulsen model predictions were an average of 1.58 orders of magnitude higher than the next highest predictions. The divergence between the Poulsen model and the other models for the dry soil predictions of hydraulic conductivity are most likely due to the low applicability of the relationship between the gradient of the water retention curve and the gradient of the conductivity curve proposed by Poulsen et al. (2003) in tropical soils. Given the similarity of fit between the van Genuchten, Brooks-Corey and Campbell models, and the similarity of their predictions of $K$ in dry soil, there is no evidence to suggest that any of these models would provide a more accurate extrapolation than the others. We conclude that the uncertainty on predictions of $K$ at -1500 kPa derived from choosing between these models is low.

Is the water retention curve typical of Amazonian soils of this texture with reference to an Amazonian water retention curve pedo-transfer function of Tomasella et al. (2000)?

The comparison of the water retention curves predicted using the specific Brazilian pedo-transfer function (Tomasella and Hodnett 2000) and the data, showed that the TH2000 model over-predicted the range of water contents and that the shape of the water retention curve showed a much greater loss of water between $-1$ and $-10$ kPa than observed in the data. The TH2000 database was mainly created using soils with a high clay content; the average clay content was greater than 40%. While the texture of the Caxivanã soil was within the range of calibration of the TH2000 model, it is likely that the fitting was skewed towards clay soils with low silt and sand contents. It is possible that the low silt content of the Caxivanã soil caused the TH2000 model to produce predictions similar to the highly weathered low silt, high clay oxisols used to construct the PTF, therefore producing a steeper drop in water content in the silt pore size range than found in the data.

Does the soil exhibit the high hydraulic conductivity found in the Manaus soil, with reference to the Brazilian soil-specific relationship between water retention and hydraulic conductivity described by Tomasella and Hodnett (1997)?

The TH1997 model under predicted the hydraulic conductivity for the two lower soil layers by $\sim 2$ orders of magnitude for water contents drier than $-1$ kPa. The hydraulic conductivity of the two upper soil layers was better predicted by the TM1997 model, however, above
- 1 kPa the model failed to represent the change in gradient of the hydraulic conductivity curve. While we cannot conclude that higher than expected hydraulic conductivity is a universal feature of Amazonian soils, the data presented in this paper repeat the conclusions of Tomasella and Hodnett (1997) tropical rain forest soils unusual hydraulic features and that more measurements of the hydraulic conductivity of Amazonian soils are necessary to create a more thorough characterisation of these soils.

3.6 Acknowledgements

The work presented in this paper would not have been possible without the input of the late Dr Wim Sombroek, and the authors would like to dedicate this paper to his memory.

This work was supported by a University of Edinburgh Faculty Research Scholarship, several Natural Environment Research Council (UK) research grants, a Natural Resources International Foundation Fellowship and the Elizabeth Sinclair fund (School of Geosciences, University of Edinburgh). We would like to thank Martin Hodnett for advice and discussion on soil hydraulics methodologies, Edso Veldkamp for advice on soil moisture sensor calibration, Alan Braga, Joao Athaydes and Paulo Gonçalves for field assistance and the Museu Paraense Emilio Goeldi for the use of their field station and laboratory facilities. We would like to thank Keith Smith (Edinburgh University) and David Dent (ISRIC) for their helpful comments on the manuscript.

3.7 References


Chapter 4

A process-based simulation of the response of rain forest to drought stress.

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². Universidade Federal do Pará, Belém, Pará, Brazil
³. Universidade Federal de Campina Grande, Paraíba, Brazil
4.1 Abstract

Warmer and drier climates are expected over Eastern Amazonia as the result of climate change in the next 50 to 100 years. The possibility of positive feedback between changing climate and forest gas exchange means that we must develop a way of predicting how the Amazonian forest will respond to a drier climate. Data suggest that the response of Amazonian forest gas exchange to current levels of rainfall seasonality is heterogeneous, so simple cross-basin scaling from a few sites is inappropriate. Existing studies must therefore be used to obtain a process-level understanding of forest drought tolerance, which may assist us in scaling the small number of observations to the whole Amazon region. We used sap flow and soil moisture data from a simulated drought or 'through-fall exclusion' experiment in Eastern Amazonia to test our understanding of how ecosystem gas exchange responds to soil drying. The sap flow data show large seasonal declines in evapotranspiration in the through-fall exclusion experiment. We tested the hypothesis that the restriction of evapotranspiration in the dry season was controlled by limitation of soil-to-leaf water transport, caused by low soil water potential and high soil-to-root hydraulic resistivity. Implementation of this hypothesis using the soil-plant-atmosphere (SPA) model, driven by local measurements, provided a good explanation of both the magnitude and timing of the reduction in sap flow in the through-fall exclusion experiment and of the predominantly unstressed patterns of gas exchange in the control experiment. Rooting depth and soil hydraulic properties were identified as the major causes of varying sensitivity to reduced rainfall. The modelled stomatal conductance values were used to estimate that the ~50% reduction in rainfall experienced by the through-fall exclusion experiment caused a 16% decrease in gross photosynthetic productivity (GPP). The forest is expected to buffer any change in rainfall up to 40%, but rapid reductions in rain forest gas exchange are forecast beyond this limit. The forest was found to be relatively insensitive to the seasonality of rainfall reduction. We conclude that more measurement of soil and root properties would enable much better predictions of the response of the Amazon rain forest to reduced rainfall.

4.2 Introduction

Over the next 50-100 years, most, but not all, global climate models predict that increasingly El Niño-like climate conditions will cause reduced rainfall over Eastern Amazonia (Cox et al. 2000; Cubasch et al. 2001; Cowling et al. 2004; Cramer et al. 2004). Cox et
al. (2004) suggested that the reduction in rainfall over Amazonia may be as great as 50% by 2100. It is unclear what effect this will have on the gas exchange of Amazonian forests, but any change is likely to produce climatic feedback at both regional and global scales (Cox et al. 2000; Huntingford et al. 2004; Werth and Avissar, 2004). For this reason, many authors have identified that understanding the relationship between soil water content and the gas exchange of rain forest trees is critical if global climate model predictions for Amazonia are to be improved (Asner et al. 2004; Avissar, 2002; Cox et al. 2004; Gash et al. 2004; Huntingford et al. 2004; Nepstad et al. 1994; Potter et al. 2004; Tian et al. 1998).

Observations of rain forest gas exchange during the dry season, using the eddy-covariance technique, have shown that responses to climatic drying are heterogeneous. At Manaus, in relatively wet and humid Central Amazonia, evapotranspiration was reduced by up to 50% in the dry season (Malhi et al. 1998, 2002). However, more recent studies in Eastern Amazonia, at two sites in the Tapajos forest (da Rocha et al. 2004; Goulden et al. 2004; Saleska et al. 2004), and one study at Caxiquanã forest (Carswell et al. 2002) have not shown any limitation in forest evapotranspiration during the dry season, despite these forests experiencing a more intense dry season those in central Amazonia (Sombroek, 2002). The lack of a simple correlation between limitation of forest evapotranspiration and dry season intensity implies that the rain forests of the Amazon basin vary in their sensitivity to drought stress. It is important that we understand the reason for such heterogeneity to enable better predictions of the response of the region to reduced rainfall.

Efforts to understand Amazon forest responses to reduced rainfall are hindered by a lack of understanding of the biophysical mechanisms determining the response of stomata to soil drying (Werth and Avissar, 2004) as well as a complete lack of empirical data on the response of tropical tree ecophysiology and gas exchange to reduced soil moisture. Recently, a related study (Fisher et al. in review b) showed that detailed ecophysiological measurements of tree hydraulics made at Caxiquanã in Eastern Amazonia (the site of this study) were consistent with the idea that rainforest trees are isohydric, i.e. that stomata act to maintain a leaf water potential above a critical minimum value under hydraulically stressed circumstances. Gas exchange was limited in the dry season by changes in soil-to-leaf water transport. In this paper, we draw on the results of this study and assume that stomatal conductance is controlled by an isohydric mechanism. This allows us to investigate in more detail the soil-to-leaf water transport factors that control variation in
leaf water potential.

Soil-to-leaf water transport is equal to the soil-to-leaf water potential gradient divided by the total soil-to-leaf hydraulic resistance. Soil-to-leaf hydraulic resistance is the sum of soil-to-root hydraulic resistance and plant hydraulic resistance. Plant hydraulic resistance depends on the conductivity of plant xylem vessels, and decreases with decreasing water potential due to air entry (cavitation) into the xylem vessels, which breaks the water column and renders the vessels dysfunctional. Soil hydraulic resistance decreases with decreasing soil water potential, as the reduced number of water filled pores reduces the connectivity of the water in the soil. Therefore, under dry conditions, evapotranspiration may be limited by either soil-to-root or plant hydraulic resistance, but it is not known which of these factors is usually limiting (Williams et al., 1998, 2001; Sperry et al. 1998). Earlier studies at this site (Fisher et al. in review b) have indicated that the major changes in hydraulic resistance between seasons occur below ground, in either the roots or soil.

In this paper, we use a modelling approach to estimate the dynamics of soil-to-root hydraulic resistance from geometric equations (Newman, 1969) and soil physical properties including water retention and hydraulic conductivity curves. We test the hypothesis that the limiting resistance to water transport is located in the soil, and that changes in soil-to-leaf water supply, mediated by changes in soil-to-root hydraulic resistance and soil water potential alone, can account for the seasonal changes in sap flow observed in a through-fall exclusion experiment located in Eastern Amazonia. We implemented this hypothesis using the soil-plant-atmosphere (SPA) model (Williams et al. 1996), a multi-layer half-hourly model of forest gas exchange. The SPA model embeds the hypothesis that soil-to-leaf water transport varies according to soil water potential and soil-to-root hydraulic resistance. We parameterised the model, as far as possible, using independent measurements at our field site. To verify the hypothesis, we collected two years of sap flow and soil water content data, and used the data-model synthesis to answer the following questions.

1. Are the observed seasonal changes in evapotranspiration consistent with the hypothesis that gas exchange is limited by changes soil-to-root water supply?
2. What is the reduction in photosynthesis associated with the reduction in sap flow?
3. Which ecosystem properties are most critical in controlling the sensitivity of the ecosystem to reduced rainfall?
4.3 Methods

4.3.1 Site

The experimental site is located in the Caxiuanã National Forest, Pará, Brazil, (1° 43' 3.5" S, 51° 27' 36" W). The forest is a lowland *terre firme* rainforest. Mean annual rainfall is 2272 mm (± 193 mm), but with a pronounced dry season between July and December, when only 555 mm (± 116 mm) of rainfall occurs on average (data from 1999 to 2003). The soil is a yellow oxisol (Brazilian classification latosol), with a 0.3-0.4 m thick stony/laterite layer at 3-4 m depth. The soil texture (0.0 and 0.5 m) is 75-83 % sand, 12-19 % clay and 6-10 % silt (Ruivo and Cunha, 2003). The soil consists of mainly kaolin in the clay fraction and quartz in the sand fraction. (Ruivo and Cunha, 2003). The site elevation is 15 m above river level, and the water table has been observed at a depth of 10 m during the wet season.

To investigate the limitation of soil water on forest gas exchange in drier conditions than those normally experienced, an artificial soil drought was created using through-fall exclusion (TFE). This work was carried out as part of the LBA (Large-Scale Biosphere-Atmosphere Experiment in Amazonia) Ecology program. Two 100 x 100 m plots, a control and a treatment ‘through-fall exclusion’ (TFE) plot, were established and their boundaries were trenched to a depth of 1 m to reduce the lateral flow of water. In the TFE plot, a roof of transparent plastic sheeting and wooden guttering was installed at ~ 2 m height in November 2001, with the purpose of excluding rainfall from the soil.

4.3.2 Meteorology

Half-hourly meteorology data were measured by an automatic weather station located at the top (56 m) of a tower located 2 km from the research station. This weather station provided 60-80% coverage over the 3 years for wet and dry bulb temperature, incoming and outgoing short-wave radiation, photosynthetically active radiation (PAR), and long-wave radiation, wind speed and direction every 30 minutes. For the periods where no meteorological data were available, a gap filling procedure was used. The gap filling procedure is described elsewhere (Malhi et al. in prep). In the case of rainfall, the gaps were filled using daily rainfall data collected from a manual weather station located in a clearing 800 m from the drought experiment, so the coverage of rainfall data was 100%. There was good agreement between the manual and automatic precipitation data.
(r² = 0.87).

4.3.3 Sap flow

Sap flow rates were measured for between 12 and 24 trees, chosen using stratified sampling, to obtain the same diameter distribution in the sample as that found in the plot. Sap flow was measured using the trunk segment heat balance method (Cermak, Deml and Penka, 1973; Cermak et al., 2004) (Environmental Measuring Systems (EMS), Brno, Czech Republic). The sensors used in this technique measure sap flux velocity (kg s⁻¹ cm⁻¹) over an entire sector of circumference, therefore do not require calibration for xylem depth, if the sensors (which are 30 - 50 mm long), penetrate through all of the active xylem tissue. Xylem depth was estimated in wood cores both visually, and using dye previously injected below the point of measurement, to confirm that water was not transported beyond 30 mm depth. Xylem depth measurements of 47 trees ranging from 0.1 m to 1.3 m in diameter, indicated that the xylem rarely extended beneath 20 mm depth, irrespective of tree size (data not shown), therefore the 30 mm long sap flow sensors cut through all of the conductive tissue. Water flux was logged every 15 minutes throughout each day. The data collection period was January 2001 to December 2003, although power supply problems caused gaps in the data set in the first year.

We developed a protocol to estimate the stand-scale sap flow (total sap flow per unit ground area) from the tree-scale sap flow data. During the day, sap flux velocity (kg s⁻¹ cm⁻¹ circumference) was positively correlated with tree diameter (average daytime r² = 0.48). The larger diameter trees were taller and therefore placed their leaves higher in the canopy (data not shown), where they could access more light. For each plot, we obtained surveys of the diameters of all the trees larger than 0.1 m in diameter. The sap flux velocity s (kg h⁻¹) of each tree in the experimental plot was calculated as

\[ s_{t,i} = p_t d_i + q_t \]  \hspace{1cm} (4.1)

where \( p_t \) and \( q_t \) are the slope and intercept of the estimated linear relationship between sap flux velocity (kg s⁻¹ cm⁻¹ circumference) and diameter at time \( t \), and \( d_i \) is the diameter of the \( i \)th tree (m). The stand-scale sap flow \( Q \) (kg h⁻¹ m⁻² ground area or mm h⁻¹) was then calculated as

\[ Q = \frac{\sum s_{t,i} d_i}{a} \]  \hspace{1cm} (4.2)

where \( a \) is the area of the plot (m²).
4.3.4 Soil water content

To monitor the effect of the through-fall exclusion on soil moisture, we dug four 5 m deep soil pits in each plot and placed time domain reflectometry (TDR) sensors, (Jipp et al. 1998) at 0, 0.5, 1, 2, 3 and 5 m depths in each pit. We measured soil moisture with this network of sensors every two weeks between July 2000 and December 2003. The TDR sensors were monitored using a cable tester (Textronix 1502C). The waveforms produced by the cable tester were analysed using the WATTDR program (v. 3.11, Waterloo Groundwater Research, 1996).

We carried out a gravimetric calibration of the sensors by removing three 0.3 m tall by 0.15 m diameter cores of soil at 0.05-0.35 m and 0.30-0.60 m depth. We installed TDR probes in the 3 cores, then saturated the soil and allowed it to dry within a light box for 10 days. Mass and TDR waveforms were measured at gradually decreasing frequency throughout the experiment. The samples were then oven dried at 105 °C for 24 hours to calculate for the remaining water content. The best fitting calibration between the output of the TDR sensor (t) and the soil water content (θ, m³ m⁻³) obtained was

\[ θ = 16.61 \log t - 17.52 \] (r²=0.95).

We applied the calibration function to the output of the sensors and the calibrated values were averaged over the four soil pits.

4.3.5 Vegetation Characteristics

Leaf Area Index (LAI) was measured in Nov 2001, May 2002, November 2002, May 2003 and November 2003 using a LI-COR LAI-2000 plant canopy analyser (LI-COR, Inc., Lincoln, NE, USA). 100 measurements were made at every point on a 10 x 10 m grid in both the control and TFE plots. Root biomass was measured using samples obtained in 2001 during the construction of the soil access pits. From each of the four soil pits, all the soil extracted (6.25 m³) was sifted for roots, which were divided into diameter classes of 2-5 mm, 5-10 mm, 10-20 mm and >20 mm, then dried and weighed to find the total dry mass in each depth category.

4.4 Results

In this section we discuss the results of the field measurements, before going on to discuss the methods and results of the model hypothesis testing exercise in the next section.
4.4.1 Meteorology

The meteorological measurements show some seasonality in temperature, incoming short wave radiation, vapour pressure deficit (VPD) and rainfall (Fig. 4.1). In each of the three years studied there were high temperatures and vapour pressure deficits between August and December followed by a sharp decline to wetter cooler conditions in December as the wet season commences. The wet season occurred between January to July each year. Average wet season (Jan-Jul) rainfall was 9.4 mm day\(^{-1}\). Average dry season (Aug-Dec) rainfall was 3.0 mm day\(^{-1}\). Average daytime VPD increased from 0.34 kPa in the wet season to 0.50 kPa in the dry season. Mean incoming short-wave radiation increased from 322 W m\(^{-2}\) in the wet season to 378 W m\(^{-2}\) in the dry season. Average daily minimum temperature remained the same (23.0 - 23.1 °C) but maximum temperature was higher in the dry season (31.2 °C) than the wet season (29.6 °C).

4.4.2 Sap Flow

In the control plot, average sap flow in the wet season (2.6 mm day\(^{-1}\)) was 29% lower than the average rate of sap flow in the dry season (3.4 mm day\(^{-1}\)) (Fig. 4.2). In the TEE plot, through-fall exclusion began in November 2001, but no sap flow data were available until early 2002, when the wet season had begun. The TEE plot sap flow was an average of 0.7 mm day\(^{-1}\) lower than the control plot sap flow until mid-August 2002 when there was a very rapid reduction in TEE plot sap flow from ~4 to ~0.4 mm day\(^{-1}\) within 50 days. On the 4th November 2002, the panels were temporarily removed to allow decomposition of the leaf litter (marked * in Fig 4.2). A large rain event (44 mm) occurred on the 16th November. Sap flow responded immediately to the pulse of rainfall, on the 17th November, increasing from 0.4 to 1.8 mm, and then to 4.5 mm on the 18th November, two days later. The panels were replaced on the 21st November. The sap flow then quickly decreased again to the previous minimum value of ~0.4 mm day\(^{-1}\) once the panels were back in place and rainfall was again excluded. The sap flow remained low compared to the control plot until around the 20th March 2003 when rainy season inputs of precipitation occurred. A second decline in the TEE sap flow occurred in the dry season of 2003, starting on the 1st August 2003, and continuing until the end of the measurement period.
Figure 4.1: Daily averaged temperature, photosynthetically active radiation (PAR), vapour pressure deficit (VPD) and total daily rainfall for the period between 1st January 2001 to 31st December 2003.
Figure 4.2: Measured (symbols) and modelled (lines) stand-scale sap flow in the control (upper panel) and through-fall exclusion (lower panel) plot for three years using the standard SPA parameterisation. Sap flow data scaled to stand-scale from a sample of 12-24 trees. The vertical arrows indicate the beginning of the through-fall exclusion. The '*' symbol indicates the period when the panels were temporarily removed (explanation in text).
4.4.3 Soil water

The soil water content of the top 3 metres (Fig. 4.3) was initially slightly lower in the TFE plot, but the differences were not significant. In the control plot, seasonal oscillations in the water content of the top 3 m of soil occurred between a maximum value of 860-890 mm in the wet season and a minimum value of 570-610 mm in the dry season. This is equal to a change in average water content from 29.2% to 22.7%. In all years, the minimum soil water content was maintained only for a brief period in October. Major differences between the control and TFE plot arose at the beginning of the 2002 wet season. The control plot re-wetted from 609 to 870 mm whereas, in the TFE plot, soil water content did not rise above 645 mm during all of 2002, and did not rise above 655 mm (21.8%) in 2003. The minimum soil content reached in the three dry seasons declined gradually from 466 mm (15.5%) in 2001 to 439 mm (14.6%) in 2002 and 398 mm (13.3%) in 2003.

There were only slight differences in the behaviour of the different soil layers between 0 and 3.0 m depth in the control plot (Fig. 4.4), indicating that water was extracted down to at least 3 m even in the control plot. The average range of water content values was 0.046 m$^3$ m$^{-3}$ and there were no observable lags between the water contents of different layers. In the TFE plot, there were only slight differences between layers, with the exception of the top layer. Between 0.3 and 3.0 m the range of water contents was 0.041 m$^3$ m$^{-3}$, but the top layer (0.0 to 0.3 m - black circles in Fig. 4.4) showed a reduced water content, up to 0.098 m$^3$ m$^{-3}$ (9.8%) lower than the other soil layers. This difference was only apparent after the beginning of the exclusion.

4.4.4 Vegetation Characteristics

Leaf area index was initially 5.4 in both plots, and remained around this value until November 2002, when there was a large decline in both plots, the LAI decreasing to 4.1 in the control plot and 3.6 in the TFE plot (Fig. 4.5). After this, leaf area recovered gradually in both plots, with the control plot recovering to 5.8 and the drought plot recovering to 4.6 by November 2003. The inter-plot difference was 1.2 units at the end of the measurement period.

In the control plot, roots were found in each plot down to the maximum depth measured of 10 m (Fig. 4.6). However, in the through-fall exclusion plot, no roots were found beneath 5 m depth. The reason for this is unknown, but is potentially due to the differential
Figure 4.3: Total water content in the top 3 metres of soil in control plot (filled circles) and through-fall exclusion (open circles). Error bars are standard errors (n=4). The vertical arrows indicate the beginning of the through-fall exclusion.
Figure 4.4: Measured (symbols) and modelled (lines) soil water content in the control and through-fall exclusion plot for three years using the standard SPA model run. The vertical arrows indicate the beginning of the through-fall exclusion. Soil water data is the average of four measurements in each plot. Standard deviations were small (average 1.2%) but have been omitted here for the purposes of clarity.
Figure 4.5: Leaf area index (LAI) data for three years for the control (solid lines) and through-fall exclusion (dotted lines) (TFE) plots taken with LAI 2000 leaf area meter. Error bars show standard error where n=100. Line indicates linear interpolation between data points used as model input.
permeability of the stony laterite layer found at 3-5 m depth. This may prevent root growth beneath 5 m in the TFE plot. The smallest root class measured was 2-5 mm, leaving some fine roots unmeasured. The biomass in the 2-5, 5-10 and 10-20 mm categories was similar for all depths below 0.3 m, so we assumed that fine root biomass was the same as the 2-5 mm biomass. The total estimated fine root biomass was lower in the TFE plot, 513 g m$^{-2}$ compared to 865 g m$^{-2}$ in the control plot. These fine root biomass estimates are slightly larger than the average values for tropical forest given by Jackson et al. (1997) of 570 g m$^{-2}$. Root area ($A_r$) was determined from biomass as

$$A_r = \frac{b}{d\pi r^2} 2\pi r$$

(4.3)

where $b$ is the root biomass (g), $d$ is the density of the root material (g m$^{-3}$) and $r$ is the root radius (m). Jackson et al. (1997) give a mean value for tree fine root diameter of 0.58 mm. The root:shoot area ratio was 1.37, slightly greater than the range of values reported by Tyree, Velez and Dalling (1998), who reported values of 0.18 to 0.97 for tropical seedlings.
4.5 Modelling

The sap flow data in the dry seasons of 2002 and 2003 suggest a very strong limitation of evapotranspiration in the through-fall exclusion plot, presumably as the result of soil drying (Fig. 4.2). However, given the observed heterogeneity in the response of Amazonian forests to the dry season, it is clear that our results cannot be used in isolation for simple extrapolations across wider areas of the Amazon region. Instead, we have chosen to use the data from the through-fall exclusion experiment to test a mechanistic hypothesis, that the response of sap flow to soil drying is mediated primarily by changes in the soil water potential and soil-to-root hydraulic conductivity. If our hypothesis provides an adequate explanation of the data, then we may use soil and root information from other forests to predict responses to soil drying a priori.

Testing our hypothesis, that the response of sap flow to soil drying is mediated primarily by changes in the soil water potential and soil-to-root hydraulic conductivity, is complex. Construction of the predictions of the hypothesis requires the coupling of many dynamic processes: radiation distribution through the canopy; soil water transport; water loss from leaves and internal plant storage tissue; transport of water from the soil matrix to the leaf and simulation of potential rates of photosynthesis, to determine stomata opening times. For this reason, we have used a simulation model, the soil-plant-atmosphere (SPA) model (Williams et al. 1996, 1998, 2001). The SPA model is a multi-layer half hourly model of canopy gas exchange which incorporates all the necessary dynamic simulations. In the SPA model, reduced soil-to-leaf water supply is linked to forest gas exchange via 'isohydric' stomatal function as verified by Fisher et al. (in review, b). Leaf water potential dynamics are simulated as the balance between supply and demand as

\[ \frac{\delta \Psi_l}{\delta t} = \frac{\Psi_s - \rho g h - ER - \Psi_i}{CR} \]  

(4.4)

where \( \Psi_s \) is the soil water potential, \( \rho \) is the density of liquid water \((\text{kg m}^{-3})\), \( g \) is gravitational acceleration \((9.8 \text{ m s}^{-2})\) and \( h \) is the height \((\text{m})\) of the canopy layer. \( E \) is the rate of evapotranspiration \( (\text{mmol m}^{-2} \text{ s}^{-1}) \) calculated using the Penman-Monteith equation (Jones, 1992) for each canopy layer. \( C \) is the capacitance \( (\text{mmol m}^{-2} \text{ MPa}^{-1}) \) and \( R \) is the soil-leaf hydraulic resistance \( (\text{m}^2 \text{ s MPa}^{-1} \text{ mmol}^{-1}) \). Stomatal closure in water-limited situations occurs when leaf water potential is reduced down to the critical minimum threshold, \( \Psi_{\text{crit}} \).
The hydraulic properties determining soil-to-leaf water supply are therefore \( \Psi_s \), \( R \) and \( C \). \( \Psi_s \) is calculated from soil water content using the van Genuchten (1980) soil hydraulics model, which has been fitted to soil hydraulic conductance data from the Caxiuana site (Fisher et al. in review (a)). \( C \) is a canopy property, the sensitivity to which is very low (Williams et al. 1998) and \( R \) is the sum of the soil-to-root, root xylem and above-ground plant resistance. Of these three resistances, only soil-to-root resistance was dynamic in this version of the SPA model, as we are testing whether the changes in sap flow can be explained solely by changes in the soil-to-root resistance and soil water potential. The soil-to-root hydraulic resistance \( R_s \) (s m\(^{-2}\) MPa mmol\(^{-1}\)) is determined geometrically using the method of Newman (1969),

\[
R_s = \log \left( \frac{1}{2\pi L K \omega} \right)
\]  

(4.5)

where \( L \) is the total root length in the soil layer in question (m), \( r \) is the root radius (m) and \( K \) is the soil hydraulic conductivity (m s\(^{-1}\)). \( \omega \) is a scaling value to convert hydraulic conductivity from m s\(^{-1}\) to mmol m\(^{-1}\) s\(^{-1}\) MPa\(^{-1}\). The soil-to-root resistance is added to the root xylem resistance to obtain the resistance appropriate to each soil layer. Water is then extracted preferentially from the layers with low resistance and high water potential. The total root resistance is added to the total above-ground leaf area specific resistance to give the final value of \( R \) as an input to Equation 4.4 (see appendix for more detail).

### 4.5.1 Canopy Parameterisation

The canopy parameterisation of SPA has already been tested and verified against intensive wet and dry season measurements of leaf water potential, stomatal conductance, tree level sap flow and stem water potential in a related study (Fisher et al. in review b). \( V_{\text{max}} \) and \( J_{\text{max}} \), the photosynthetic capacity parameters, were measured at different heights in the canopy using an LI 6400 plant gas analyser (LI-COR, Inc., Lincoln, NE, USA) via measurement of photosynthetic response to varied CO\(_2\) concentrations (A-C\(_1\) curves) (Lobo do Vale, Maroco, , Carvalho & Chaves, in prep.). In the standard version of SPA, a constant critical leaf water potential of \(-2.5\) MPa is used (Williams et al. 1996). In a previous study (Fisher et al. in review b) we found that the leaf water potential minima of nine trees varied between \(-0.9\) and \(-4.1\) MPa. In addition, the minimum values were
maintained for several hours (from 11:00 to 16:00) during the dry season, indicating the presence of a critical minimum leaf water potential. In Fig. 4.7 we see that these values of \( \Psi_{\text{crit}} \) are negatively correlated with tree height \( (r^2 = 0.74) \), possibly reflecting the varying adaptations of the trees at different heights in the canopy to drought stressed conditions. We have therefore replaced the constant \( \Psi_{\text{crit}} \) with a value modulated by canopy layer height:

\[
\Psi_{\text{crit},i} = -0.0017 \log h_i^2 + 0.05 \log h_i - 0.61
\]  

(4.6)

where \( h_i \) is the height of \( i \)th canopy layer (m) and \( \Psi_{\text{crit},i} \) is the critical minimum leaf water potential of layer \( i \) (MPa). The impact of this change on the total sap flow is likely to be small, but the physiology of individual layers will be more accurate. Fisher et al. (in review b) found that the average above-ground resistance in the wet season was 1.43 s m\(^{-2}\) MPa mmor\(^{-1}\). The model parameter determining the incremental increase in photosynthesis necessary for stomata to open, \( \epsilon \), was set as 1.001, from a study using SPA by Misson et al. (2004), who calibrated the parameter against data from a Ponderosa Pine forest in Oregon. The canopy parameterisation values are described in Table 4.1.

Table 4.1: Parameters used in the SPA model run and their origins. Photosynthetic parameters \( (J_{\text{max}} \) and \( V_{c\text{max}} \) vary linearly with canopy height.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Units</th>
<th>Control</th>
<th>Drought</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Canopy height</td>
<td>m</td>
<td>30</td>
<td></td>
<td>Meas. from tower.</td>
</tr>
<tr>
<td>( J_{\text{max}} )</td>
<td>( \mu\text{mol m}^{-2} \text{s}^{-1} )</td>
<td>43-75</td>
<td></td>
<td>Vale et al. in prep</td>
</tr>
<tr>
<td>( V_{c\text{max}} )</td>
<td>( \mu\text{mol m}^{-2} \text{s}^{-1} )</td>
<td>24-44</td>
<td></td>
<td>Vale et al. in prep</td>
</tr>
<tr>
<td>Capacitance</td>
<td>mmol m(^{-2}) MPa(^{-1})</td>
<td>2300</td>
<td></td>
<td>Goldstein et al. (1998)</td>
</tr>
<tr>
<td>Through falls</td>
<td>fraction</td>
<td>1.0</td>
<td>0.6</td>
<td>Nepstad et al. (2002)</td>
</tr>
<tr>
<td>Above-ground resistance</td>
<td>m(^2) MPa mmol(^{-1})</td>
<td>1.43</td>
<td>1.43</td>
<td>Fisher et al. (in review).</td>
</tr>
<tr>
<td>Root resistivity</td>
<td>m(^2) MPa mmol(^{-1})</td>
<td>5.2</td>
<td>10.38</td>
<td>Fisher et al. (in review).</td>
</tr>
<tr>
<td>Iota</td>
<td>m(^2)</td>
<td>1.001</td>
<td>1.001</td>
<td>Misson et al. (2004).</td>
</tr>
<tr>
<td>( \Psi_e )</td>
<td>MPa</td>
<td>Fm of ht (Eqn 4.6)</td>
<td>Fisher et al. (in review).</td>
<td></td>
</tr>
</tbody>
</table>

### 4.5.2 Below-ground parameterisation

The parameters required to calculate soil-to-root hydraulic resistance are root length and its vertical distribution, the internal root resistivity, the soil hydraulic conductivity curve,
Figure 4.7: Relationship between minimum measured leaf water potential $\Psi_{\text{crit}}$ and measurement height ($h$) for nine trees. Symbols are data and solid line is line of best fit ($\Psi_{\text{crit}} = -0.0017 \log h + 0.051 \log h - 0.61$). In all cases, a plateau at the minimum leaf water potential was observed for the majority of the day time in the dry season.

and soil water retention curves (see appendix). Water uptake is assumed to occur only in fine roots (Tyree et al. 1998), so we used the estimated fine root biomass as the input biomass for SPA. Root length was calculated from biomass as

$$l = \frac{b}{d\pi r^2}$$

(4.7)

where $l$ is the root length (m), $b$ is the root biomass (g), $d$ is the density of the root material (g m$^{-3}$) and $r$ is the mean root radius.

We do not know the internal hydraulic resistivity of the tree roots, since data on this characteristic are very sparse in general and completely absent for tropical forest. Fisher et al. (in review) found that, in the wet season, the below-ground resistance of the measured trees varied between 0.05 and 0.37 s m$^{-2}$ MPa mmol$^{-1}$ with an average of 0.19 s m$^{-2}$ MPa mmol$^{-1}$ in both plots. In the wet season, soil hydraulic resistance is very low, since the soil is saturated and movement of water is very fast. We therefore assume that in the wet season, below-ground resistance is representative of the root resistance only. We fitted the root resistivity parameter ($\sigma$, see appendix) to give a value of wet season below-ground resistance of 0.19 m$^{-2}$ MPa mmol$^{-1}$. Fitted resistivity was 10 MPa g s mmol$^{-1}$ in the TFE plot and 5 MPa g s mmol$^{-1}$ in the control plot as a result of the differences in root biomass between plots. We assumed that the root tissue density was $0.5 \times 10^{-6}$ g m$^{-3}$.
The soil hydraulic properties were measured by Fisher et al. (in review, a). Water retention curves were measured between -0.1 and -2500 kPa. Soil hydraulic conductivity ($K$) measurements were made between -0.1 and -8 kPa. Four soil hydraulics models were used to extrapolate the data into drier soil. The best fitting model to the data was the van Genuchten model, so the parameters of this model were used as input to the SPA soil hydraulics model (Table 4.2). For the lower soil depths (1 to 5 m), no hydraulic conductivity data was available, so we used the soil hydraulics parameters of the lowest hydraulic conductivity measurements (1 m).

Table 4.2: Parameters of the Van Genuchten Soil Hydraulics Model used in the SPA simulations taken from Fisher et al. (in review a).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>0-0.1</th>
<th>0.1-0.5</th>
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### 4.5.3 Through-fall exclusion

We parameterised the SPA model using independent measurements as described, and ran the model with a 30 minute resolution for 3 years from 1st Jan 2001 to 31st Dec 2003 for both the control and TFE plots. The meteorology (Fig. 4.1) and linearly interpolated LAI data (Fig. 4.5) were used to drive the model. We simulated the effect of the through-fail exclusion experiment by including a dimensionless 'exclusion' parameter ($\epsilon$) controlling the amount of rainfall hitting the ground where

$$R_g = \epsilon (R_t - R_i).$$

($R_g$ is the rainfall reaching the ground (mm), $R_t$ is the total rainfall (mm) and $R_i$ is the rainfall intercepted by the canopy and evaporated before hitting the ground (mm). We did not measure $\epsilon$ directly due to logistical constraints, but instead compared our experimental...
design to a similar experiment in the Tapajos forest, also in Eastern Amazonia (Nepstad et al. (2002)). Nepstad et al. (2002) made physical measurements of the amount of water flowing through the drainage ditch system during rainstorms and report that, irrespective of the size of the rainstorm, the through-fall exclusion infrastructure excluded 48% of all incoming rainfall from the soil surface. We compared the Caxiuanã through-fall exclusion experiment to the Tapajos experiment by measuring the area of the forest covered by the panels. We found that in the Caxiuanã experiment the panel coverage was 80%, the same as that reported by Devison et al. (2004) for the Tapajos experiment. We concluded that the Caxiuanã experiment was similar to the Nepstad experiment, since the design, materials and panel coverage were all similar. Therefore in the model simulation, $c$ was set to 0.48.

### 4.5.4 GPP Predictions

The SPA model predicts photosynthesis rates from estimates of stomatal conductance, which are used to generate internal leaf CO$_2$ concentrations. Internal leaf CO$_2$ concentrations, in combination with canopy layer meteorology, are used to drive the photosynthesis model of Farquhar and Von Caemmerer (1982). We can therefore predict the effects of reduced stomatal conductance on gross photosynthetic productivity (GPP). We extracted the half-hourly GPP predictions from the SPA model output, and produced 5-day average GPP values to provide a clearer description of the seasonal patterns.

### 4.5.5 Model sensitivity tests

In a study of a global climate model, coupled to a vegetation carbon model, Cox et al. (2004) predicted a reduction in rainfall over Amazonia of $\sim$50%, from 3.5 mm day$^{-1}$ to 1.5-2.0 mm day$^{-1}$ by 2100. In this experiment, we have tested the effects of the current ambient (100%) rainfall (the control plot), and a $\sim$50% reduction in rainfall (the through-fall exclusion plot) on forest evapotranspiration. In isolation, these results only tell us the magnitude of evapotranspiration limitation 100 years into the future under severe climate change. A more useful result from this experiment would be an indication of the vulnerability of forest evapotranspiration to less extreme decreases in rainfall intensity, and an indication of the ecosystem properties determining forest vulnerability to reduced rainfall.
We investigated vulnerability using model sensitivity tests, to observe the behaviour of the model system with different climatic, soil and rooting properties. We investigated how changes in soil type, root biomass, rooting depth and rainfall seasonality affected the sensitivity of forest evapotranspiration to reduced rainfall. We ran the SPA model, for three years in each instance, with gradually reducing rainfall, from a value of \( \varepsilon \) of 1.0 (100% rainfall) reducing to 0.2 (20% rainfall). We conducted this set of model runs repeatedly for an array of model inputs, and found the average sap flow over the three years, each time starting with soil water content at field capacity.

For the first test, we varied root biomass between a multiple of 0.5 and a multiple of 4 of the original SPA input values. In the second test, we varied rooting depth between 1.0 m and 11.0 m, keeping root biomass the same between runs. In the third test, we investigated the consequences of altering the soil hydraulic properties from those measured for the sandy oxisol at Caxiuanã to those measured for the clay oxisol at Manaus (Tomasella and Hodnett, 1996).

For the fourth test, we altered the seasonality of rainfall. We constructed scenarios whereby the impact of rainfall reduction was concentrated entirely in the dry season, entirely in the wet season, or spread over both seasons, and tested how the altering seasonality affects the sensitivity of forest evapotranspiration to reductions in total annual rainfall. The seasonality was determined as a multiplication factor of the dry season rainfall (\( \alpha \)). Once the dry season rainfall was calculated, the wet season rainfall was estimated as the remaining rainfall, the once reductions in total annual rainfall (\( \varepsilon \)) were taken into account. Low values of \( \alpha \) indicate extreme rainfall seasonality.

### 4.5.6 Modelling results

The observed changes in soil water content were well simulated by the SPA model for the control plot (Fig. 4.4). \( r^2 = 0.90 \), slope = 1.07, RMSE= 0.020 m\(^3\) m\(^{-3}\) (Fig. 4.8). In the TFE plot, the \( r^2 \) value was 0.78 and the RMSE was 0.029 m\(^3\) m\(^{-3}\) but the slope and intercept of the model-data relationship were 0.61 and 0.06. This was caused mainly by model over-prediction of soil water content during the dry season (Fig 4.8). The major model-data errors were located in the dry season of 2002, when the model soil water content did not decrease down to the same level as the data. This is reflected in the over-prediction of sap flow during this time. This may reflect a minor inaccuracy in the soil water transport model, but because both the sap flow and soil water are overestimated
Figure 4.8: Measured vs. modelled soil water content for the control (filled symbols) and through-fall exclusion (open symbols) plots. Model values obtained using the standard SPA parameterisation. Solid line is 1:1 line, dashed line is regression of control plot ($y=-0.01+1.07x$) and dotted line is regression of TFE plot ($y=0.07+0.61x$).
there is no implication for the central physiological hypothesis. In both plots, simulated soil evaporation dried the top layer of the soil such that the soil water content was very low. This was reflected in the data for the through-fall exclusion experiment but not for the control experiment.

Modelled soil water potential was very low for the 0.0-0.1 m layer in both plots as the result of soil surface evaporation (Fig. 4.9). In the remaining soil layers, the soil water potential declined to a minimum of −0.1 to −0.2 MPa in the control plot each dry season, but in the through-fall exclusion plot soil water potential declined to −0.4 to −0.6 MPa in the dry season (Fig. 4.9). Fisher et al. (in review, (b)) found that the gravity corrected average pre-dawn leaf water potential of the TFE plot in the dry season of 2003 was −0.66 MPa. This independent agreement between the model predictions of soil water potential and the estimates from pre-dawn leaf water potential, provide a good test of the model predictions. The reduction in soil moisture also caused modelled increases in the soil-to-root hydraulic resistance. The model output showed a very large increase in soil-to-leaf hydraulic resistance ($R$) in the dry season in the through-fall exclusion plot (Fig. 4.10) peaking around 9 s m$^2$ MPa mmol$^{-1}$ in 2001 and 2002, and at 14 s m$^2$ MPa mmol$^{-1}$ in 2003 before decreasing to the ‘background’ constant resistance in the wet season, where soil-to-root resistance was negligible (1.7 s m$^2$ MPa mmol$^{-1}$). The control plot only experienced very slight increases in $R$ from 1.5 s m$^2$ MPa mmol$^{-1}$ in the wet season to 2.4 s m$^2$ MPa mmol$^{-1}$ in the dry season.

The SPA model also provided a good description of the sap flow data (Fig. 4.2). In the TFE plot, reduced soil-to-leaf water supply in the dry season was caused by the combination of low soil water potential and high soil-to-leaf resistance (Fig. 4.9 and Fig. 4.10). In combination with increased atmospheric demand (Fig. 4.1), slow soil-to-leaf water supply caused reductions in leaf water potential down to the minimum critical value. In accordance with the isohydric hypothesis, this low leaf water potential triggered reduced stomatal conductance and subsequent declines in sap flow during the dry season. The reductions in sap flow were of similar timing and magnitude to those observed in the data (Fig. 4.2). The $r^2$ values of the modelled vs. measured daily sap flow were 0.81 and 0.75 for the control and TFE plots respectively. The slopes of the model-data relationship were 0.80 and 0.93 (Table 4.3, Fig. 4.11), indicating a slight over-prediction by the SPA model, especially in the control plot. However, the model captures the seasonality of atmospheric demand, which controls sap flow in the control plot, and the reduction in sap flow caused by the through-fall exclusion experiment (Fig 4.2). Other minor features of
Figure 4.9: Modelled time-courses of soil water potential at 0.1 m (thick solid line), 0.5 m (thick dotted line), 1.0 m (thick dashed line), 2.0 m (thin solid line) and 3.0 m (thin dotted line). Symbols are the pre-dawn leaf water potential measurements, scaled for leaf height to estimate the effective soil water potential. The vertical arrows indicate the beginning of the through-fall exclusion. The log scale is to allow the very negative water potentials of the upper layer to be compared to the wet season water potentials of the other layers.
Figure 4.10: Top Panel: Daily Rainfall (mm day\(^{-1}\)). Bottom Panel: Modelled changes in soil to leaf hydraulic resistance in the standard SPA parameterisation. All changes in soil-leaf resistance were located in the soil as the result of decreased soil hydraulic conductivity according to the equations of Newman, (1969). The vertical arrow indicates the beginning of the through-fall exclusion.
the water flux dynamics are well simulated, in particular, the response to a large rainstorm during the period when the covers were removed in November 2002, and the dry down period in the dry season of 2003, including responses to small rain storms. The diurnal sap flow measurements both in the wet season and in the dry season of 2003 were also well simulated (Fig. 4.12). \( r^2 \) values of half hourly sap flow across all the days when data were collected were 0.82 and 0.75 for the control and TFE plots respectively. The implication of this is that the hypothesis integrated into the SPA model provides a good explanation of the data observed both at daily and hourly timescales, and for sap flow, soil water content and soil water potential data.

Table 4.3: Statistics of model-data comparison for sap flow and soil water content.

<table>
<thead>
<tr>
<th>Data Type</th>
<th>Units</th>
<th>Statistic</th>
<th>Control</th>
<th>Drought</th>
</tr>
</thead>
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<tr>
<td>Sap Flow</td>
<td>mm day(^{-1})</td>
<td>( r^2 )</td>
<td>0.74</td>
<td>0.77</td>
</tr>
<tr>
<td></td>
<td></td>
<td>RMSE</td>
<td>0.68</td>
<td>0.68</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Slope</td>
<td>0.80</td>
<td>0.93</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Intercept</td>
<td>0.40</td>
<td>0.44</td>
</tr>
<tr>
<td>Soil Water</td>
<td>m(^3) m(^{-3})</td>
<td>( r^2 )</td>
<td>0.90</td>
<td>0.78</td>
</tr>
<tr>
<td></td>
<td></td>
<td>RMSE</td>
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<td>0.03</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Slope</td>
<td>1.07</td>
<td>0.61</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Intercept</td>
<td>-0.01</td>
<td>0.07</td>
</tr>
</tbody>
</table>

The use of the model allows annual totals of sap flow to be estimated (estimation of annual totals directly from the data is impossible due to gaps). The annual totals of sap flow were similar for 2001, 2002 and 2003 in the control plot (1316, 1253 and 1223 mm) but declined gradually in the TFE plot (1258, 953 and 805 mm). The control plot evaporated 54-58% of the incoming rainfall in all years. In the TFE plot, 58% of the rainfall was evaporated in 2001, rising to 91% in 2002 and 85% in 2003 as the amount lost from the plot through drainage declined.

Reduced stomatal conductance caused decreases in gross photosynthetic productivity (GPP) (Fig. 4.13). Reductions in daytime bulk average stomatal conductance (of sun and shade leaves over all ten canopy layers) were reduced from \( \approx 150 \) mmol m\(^{-2}\) s\(^{-1}\) to \( \approx 60 \) mmol m\(^{-2}\) s\(^{-1}\) during both dry periods in the TFE plot, while in the control plot, conductances remained high >200 mmol m\(^{-2}\) s\(^{-1}\) during the dry season. In the wet season,
Figure 4.11: Measured vs. modelled daily total sap flow for the control (open symbols) and through-fall exclusion (filled symbols) plots. Model values obtained using the standard SPA parameterisation. Solid line is 1:1 line, dashed line is regression of control plot \( y=0.4+0.80x \) and dotted line is regression of TFE plot \( y=0.44+0.93x \).
five day average modelled canopy GPP is very similar between plots (Fig. 4.13), but in the dry season, the GPP of the TFE plot drops to a minimum of 55-60% of the GPP of the control plot in response to a modelled draw-down of internal leaf CO$_2$ concentration. GPP was 3094 g in the control and 2678 g in the TFE in 2002, and 3138 g in the control and 2661 g in the TFE in 2003. The average difference in total GPP between the control and the TFE plots was 13% and 15% in 2002 and 2003 respectively.

4.5.7 Sensitivity Test Results

We conducted a series of two way sensitivity tests, between reduced rainfall, and four factors which are likely to differ between ecosystems, root biomass, rooting depth, soil type and the seasonality of rainfall reduction. We therefore identified how these ecosystem properties affect the sensitivity of the forest to reduced rainfall.

Increasing the root biomass had very little impact on the sensitivity of the model to reduced rainfall (Fig. 4.14a). In contrast, rooting depth had very large impacts on sensitivity to rainfall reduction (Fig. 4.14b). Under ambient rainfall, reducing the rooting depth to less than 3 metres caused a large restriction in sap flow. A rooting depth of 3 m buffered rainfall reduction up to 30%, but a rooting depth of 10 m allowed a reduction in rainfall of up to 60% with no change in sap flow at all, over two years. The rooting depth observed in the TFE plot (5 m) buffered reductions in rainfall of up to 40%.

Changing the soil type from the Caxiuanã sandy oxisol to the Manaus clay oxisol decreased sap flow under ambient conditions, and increased the sensitivity of the ecosystem to reduced rainfall due to the reduced water holding capacity of the Manaus soil (Fig. 4.14c). The Caxiuanã soil buffered changes in rainfall up to 30%, while there was an immediate decline in sap flow with the Manaus soil when rainfall was reduced below ambient conditions. If only the first year was considered, the difference between the Manaus and Caxiuanã soils was greater, as the effect of differential soil moisture storage is less noticeable over the span of three years.

Changes in the seasonality of rainfall had a little effect on the sensitivity of the model response to reduced rainfall (Fig. 4.14d). There was only a noticeable effect when the rainfall in the dry season was reduced to 20% of ambient, and the rest of the rainfall fell in the wet season. The buffering capacity of the soil appeared to be sufficient that extra rain falling in the wet season could be stored until the dry season. This may be changed
Figure 4.13: Upper panel: Daily rainfall (mm day$^{-1}$). Middle panel: five day average daytime average stomatal conductance (weighted average of sun and shade leaves at 10 canopy layers between 0600 and 1800) for the control (dotted line, open symbols) and through-fall exclusion (solid line, filled symbols). Bottom panel: Simulated GPP for the control (dotted line, open symbols) and through-fall exclusion (solid line, filled symbols). 5 day average values from half hourly simulations by the SPA model. The vertical arrows indicate the beginning of the through-fall exclusion.
Figure 4.14: Response of averaged stand-scale sap flow to reduced rainfall as the result of incrementally reducing the through-fall parameter ($\epsilon$) from 1 to 0.2. Model runs over 3 years. Different lines indicate variation in model input parameters for a) root biomass (multiple of original data), b) rooting depth and c) soil type and d) rainfall seasonality index ($\alpha$) (Low values of $\alpha$ indicate extreme rainfall seasonality.).

if the rooting depth was shallower.

4.6 Discussion

Are the observed seasonal changes in evapotranspiration consistent with the hypothesis that gas exchange is limited by changes soil-to-root water supply?

Simulation of the reduction in evapotranspiration, using the hypothesis that water use is constrained by soil-to-root water supply, provided a convincing explanation of both
the sap flow and soil water content over three years for both ambient and manipulated conditions (Fig. 4.2 and Fig. 4.4). Both the seasonal and diurnal sap flow patterns were well simulated by the model. We have not found that it is necessary to invoke any other changes in soil-to-leaf resistance, such as xylem embolism, to explain the change in water dynamics in the dry season. The SPA model predictions of sap flow and soil water content were generated without the need to optimise any parameters to the data. The model parameters were either standard SPA parameters used in other investigations, those generated from independent measurements at the Caxiuana forest, or in the case of above ground and root resistance, calculated from a small subset of the data by Fisher et al. (in review b). The implications of this study are that, given knowledge of the soil hydraulic properties, root biomass distribution and some canopy properties, it is possible to predict the short term response of the rainforest ecosystem to reduced rainfall.

The data are consistent with the hypothesis that the major resistance to water transport is the soil-to-root resistance. This result contrasts with that of Sperry (1998), who deduced, from a modelling analysis, that the major limiting factor in soil-to-leaf water supply was usually increased plant xylem resistance due to embolism. In the SPA model, plant xylem resistance was maintained as a constant, and it was not necessary to invoke changes in plant xylem resistance to explain the data. However, at the Caxiuana forest, the root biomass was spread out over several metres of soil depth, therefore effectively reducing the root length density. Sperry (1998) assumed that all the roots were concentrated in 0.3 m$^3$ of soil. Deeper rooting, via the consequential reduction of rooting density, is more likely to encourage the formation of major soil-to-root resistances. Also, the soil at Caxiuana is very sandy (75% sand) and therefore more likely to experience very low hydraulic conductivity at low soil water content (Fisher et al. in review a). We therefore expect that in this forest soil-to-leaf resistance is likely to be located mainly in the soil in hydraulically stressed circumstances.

The control plot results indicate that there is very little limitation of evapotranspiration during a normal dry season. Unless there are very occasional droughts of much greater magnitude than the ‘normal’ dry season, there is no need for the forest to invest heavily in a larger root system. It is clear that a deeper root system would be necessary to allow high rates of evapotranspiration during the through-fall reduction. However, the lack of hydraulic stress in a ‘normal’ year (Fig. 4.14d) means that such a root system is unlikely to develop,
What is the reduction in photosynthesis associated with the reduction in sap flow?

Extrapolation of the estimated stomatal conductance values, using the photosynthesis model of Farquhar and von Caemmerer (1982) indicated that a 13-15% drop in GPP occurred as a result of the through-fall exclusion experiment, with a reduction of 40-45% during the driest periods (Fig. 4.13). GPP fluxes are comparable to those found at an eddy covariance tower 1 km from the through-fall exclusion experiment Carswell et al. (2002). Carswell et al. found that night time NEE was $\sim 8 \mu\text{mol m}^{-2} \text{s}^{-1}$, with peak daytime NEE of $19 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the wet season and $21 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the dry season. If the daytime NEE values are added to the night time average NEE, GPP estimates of 27 and $29 \mu\text{mol m}^{-2} \text{s}^{-1}$ are found for the wet and dry seasons. The modelled maximum rate of GPP in the control plot, was $27.1 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the wet season and $27.4 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the dry season. The similarity between the eddy covariance and model generated GPP estimates reinforces our confidence in the sound mechanistic basis of the SPA model and the validity of scaling from leaf level photosynthesis capacity measurements to stand scale GPP estimates using this approach.

Studies of carbon stocks within the through-fall exclusion experiment show that stem growth in the TFE plot effectively ceased over the course of the experiment (data not shown) and that there was a decline in leaf area. Both of these observations are consistent with a significant decrease in carbon input from GPP, but the quantification of the carbon balance of the ecosystem, and the effect of through-fall exclusion on net ecosystem exchange is beyond the scope of this paper.

Which ecosystem properties are most critical in controlling the sensitivity of the ecosystem to reduced rainfall?

Soil hydraulic properties were found to be a key control over ecosystem responses to reduced rainfall (Fig. 4.14b). Simulations of the response of sap flow to altered rainfall showed that if the Manaus soil properties were used, an immediate decline in evapotranspiration occurred when rainfall was reduced from 100% of ambient, therefore there was no capacity for buffering climate change. This was in contrast to the Caxiuanã soil, where reductions in rainfall of up to 40% were possible before any major change in sap flow. Eddy covariance studies have shown that a rain forest near Manaus displayed reduced latent energy flux in the dry season (Malhi et al. 1998; Williams et al. 1998). Both eddy
covariance and sap flow measurements at Caxiuanã indicate that no seasonality occurs in
the gas exchange of this forest. The plant available water of the Manaus soil is 0.05-0.10
m$^3$ m$^{-3}$, whereas, at the Caxiuanã site, the water content of the control plot varies by
0.12 m$^3$ m$^{-3}$ without causing any reduction in gas exchange. These results indicate that
soil hydraulic properties are a critical factor controlling rain forest responses to climate
change, and may explain the different behaviour of the Caxiuanã and Manaus ecosystems
in the dry season. However, we do not know the extent to which the soil properties used
here are indicative of the range of soil textures found in Amazonia as a whole. Very little
information exists on the hydraulic resistivity of rainforest soils. The only measurements
other than those made at the Caxiuanã site were at the Manaus soil (Tomasella and Hod-
nett 1996). It is clear that more information on soil hydraulic resistivity is necessary to
extend this analysis further.

Rooting depth appears to be a very strong control on the sensitivity of sap flow to
reduction in rainfall (Fig. 4.14a). Nepstad et al. (1994) found root biomass down to at
least 8 m at three sites, Paragominas in Eastern Amazonia, Trombetas, near Manaus, and
Santa de Araguaia in South Eastern Amazonia. They also measured water extraction at
8 m depth at the Paragominas site. Nepstad et al. (1994) also generated a map of the
regions of Amazonia where rainfall is less than 1.5 mm day$^{-1}$ for at least three months,
and normalized difference vegetation index (NDVI) does not display a seasonal depression
(according to satellite data). They ‘deduced’ that these forests would probably have to
use deep roots to access sufficient water to maintain evapotranspiration and evergreen
canopies throughout the dry season. However, the method of deduction and in particular
the method for allocating plant available soil water was not discussed. The area calculated
to require deep rooting was 1.8 x 10$^6$ km$^2$, mainly in Southern and Eastern Amazonia.
Nepstad et al. (1994) determined that deep rooting (>2m) was necessary for the majority
of Amazonian forests to maintain full canopies throughout the dry season. We find that
under ambient conditions, if rooting depth is reduced to 2 m, some restriction of sap flow
is apparent, and that a depth of 3 m is necessary to allow unrestricted transpiration. It
is clear that this ecosystem property is a crucial control on ecosystem behaviour. The
majority of existing studies have found that Amazonian forests have deep rooting systems
and deep soil water uptake (Nepstad et al. 1994, Hodnett 1996; da Rocha et al. 2004;
Nepstad et al. 2002) but information is still scarce and the collection of more information
on rooting depth throughout Amazonia should be a high research priority (Potter et al.
The buffering of the system to rainfall reductions of up to 40%, with a rooting depth of 5 m (Fig. 4.14a) might lead us to conclude that the forest is not very sensitive to reductions in rainfall, and that no significant reduction in forest gas exchange is likely over the next 100 years. However, the major issue here is what reduction in evapotranspiration can be considered 'significant'? It is possible that very small changes in evapotranspiration could cause strong feedbacks to atmospheric humidity, cloudiness, rainfall and fire risk (Betts et al. 2004). Therefore these results should ideally coupled to an atmospheric circulation model or be used in the context of a coupled meso, regional or global scale forest-atmosphere interaction model.

4.7 Conclusions

Measurements over 2 years in an Eastern Amazonian rain forest indicate that sap flow is higher in the dry season than the wet season under normal circumstances, and there is little evidence for limitation of water use during the dry season. However, experimental through-fall exclusion, removing an estimated 48% of the rainfall, caused soil drying and a resultant decrease in sap flow of 41% over the course of two years, with the most severe drought periods causing 80% reduction in sap flow compared to the control.

The observed reductions in sap flow and soil moisture were consistent with the hypothesis that changes in soil hydraulics are the major control of evapotranspiration under reduced soil water conditions, as embedded in the soil-plant-atmosphere (SPA) model. Further modelling analyses indicated that a 15% decrease in GPP resulted from the through-fall exclusion experiment, and GPP predictions were consistent with eddy covariance-based GPP predictions made at an adjacent site in 1999. We find that the modelled ecosystem vulnerability to reduced rainfall is sensitive to variations in rooting depth, soil properties and rainfall seasonality, all of which are poorly quantified for Amazonian ecosystem. Therefore, we suggest that field measurements to determine soil and root properties are intensified.

4.8 Acknowledgements

This work was supported by a University of Edinburgh faculty research Scholarship, several Natural Environment Research Council (UK) research grants, a Natural Resources Inter-
national Foundation Fellowship and the Elizabeth Sinclair fund (School of Geosciences, University of Edinburgh). We would like to thank Yadvinder Malhi and John Grace for help with experimental methods, planning and logistics. Raquel Lobo do Vale and João Maroco for providing leaf photosynthetic capacity data. Alan Braga, João Athaydes and Paulo Gonçalves for their field assistance and the Museu Paraense Emílio Goeldi for the use of their field station and laboratory facilities.

4.9 Appendix

Soil-to-root resistance for each soil layer is calculated as

\[ R_s = \log \left( \frac{\sqrt{\frac{L}{2\pi r}}}{LR_k \omega_q} \right) \]  \hspace{1cm} (4.9)

where \( L \) is the total root length in the soil layer in question (m), \( r \) is the root radius (m) and \( K \) is the soil hydraulic conductivity (m \( s^{-1} \)). \( \omega \) is a scaling value to convert hydraulic conductivity from m \( s^{-1} \) to mmol m \(^{-1} s^{-1} MPa^{-1} \). The total resistance of water within one soil layer \( R_{st,i} (m^2 MPa s mmol^{-1}) \) is found by adding the soil-to-root to the internal root transport resistance for the \( i \)th layer.

\[ R_{st,i} = R_{s,i} + \frac{\sigma}{b_i} \] \hspace{1cm} (4.10)

where \( \sigma \) is the inverse of the conductivity of root xylem per unit biomass (MPa s g mmol\(^{-1}\)) and \( b_i \) is the total root biomass in each soil layer (g). The cumulative conductance of all the soil layers is then calculated and multiplied by the fraction of leaf area \( l \) in a given canopy layer \( i \).

\[ R_{bg} = \frac{1}{\sum_{i=1}^{10} R_{st,i}} \] \hspace{1cm} (4.11)

\( R_{bg} \) is then added to the above-ground resistance \( R_{ag} \) to give the total resistance as input to Equation 4.4.
4.10 References


change and rate of deforestation. *Philosophical Transactions of the Royal Society of London Series B-Biological Science* 359 (1443), 331-343.


124


Chapter 5

A simple model of rain forest drought tolerance.

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5.1 Abstract

The Amazon rain forest may be subject to reduced rainfall and increasing temperature over the next 100 years, if the results of global climate simulations are accurate. This poses a challenge to ecosystem modellers, as current models for predicting the impacts of drought are highly simplified and largely untested. Recent studies at a drought simulation (or through-fall exclusion’ experiment in Eastern Amazonia have suggested that the use of a state-of-the-art process based soil-plant-atmosphere (SPA) model may allow accurate simulation of drought responses. However, such a model requires hourly meteorological data, a rare commodity in Amazonia, and is computationally expensive. In this paper we present an aggregated daily version of the SPA model- the Aggregated Canopy Model (ACM) coupled to a soil water transport model (SWAT). The ACM model represents the response surface of the process-based SPA model to input data ($r^2 = 0.86$) and the SWAT model is a simple model of the water movement through soil and the hydraulic resistance between the soil matrix and the root surface. The ACM-SWAT model can predict the onset of drought periods using only basic ecosystem properties and daily meteorological inputs. We were able to predict the behaviour of two drought affected Amazonian ecosystems at Caxiuana and Manaus by changing only the soil hydraulic properties between ecosystems. Using the ACM-SWAT model, we extrapolated ecosystem behaviour 100 years into the future in accordance with the rainfall predictions of the HadCM3LC model for Amazonia using a range of rooting depths and soil hydraulic properties. We found that for rainfall reduction less than 30% there was no effect on forest evapotranspiration if rooting depth was more than 10 m using the Manaus clay soil properties, or 4 m using the Caxiuana sandy soil properties. However, there was a threshold rainfall reduction of 30%, beyond which all of the available rainfall was evaporated by the ecosystem irrespective of the rooting or soil properties. Climate simulations by the Hadley Centre HadCM3LC model suggest that external forcing would reduce rainfall by 25% in the next 100 years. A small amount of biosphere-atmosphere feedback (e.g. from deforestation) in addition to this external forcing would shift the climate system beyond the 30% rainfall reduction required to provoke a positive biosphere-atmosphere feedback loop in the Amazon region, potentially leading to the conversion of much of the basin to savannah type ecosystem.
5.2 Introduction

In the next 50-100 years, most GCM models predict reductions in precipitation and increased temperatures over the Amazon basin (Cubasch et al. 2001) as the result of a shift towards a more El-Niño like mean state of the climate. There is likely to be a feedback between this climate drying and rain forest gas exchange which may affect both regional weather patterns and global carbon budgets (Cox et al. 2000, 2004; Laurance and Williamson, 2001; Higgins, Mastrandrea and Schneider, 2002). The magnitude of this feedback depends upon the sensitivity of rain forest gas exchange to a drying climate.

In a recent investigation, (Fisher et al. in review, c) we found that a detailed model of plant water uptake could accurately simulate the response of an Eastern Amazonian rain forest to an imposed artificial drought. The model tested was the SPA model (Williams et al. 1996), a half-hourly multi-layer model of forest gas exchange which incorporates an explicit simulation of the movement of water from the soil to the leaf, and optimises stomatal conductance to prevent leaf water potential dropping below a critical minimum value. The SPA model was parameterised using soil, root and vegetation data collected at the Caxiuanã through-fall exclusion site. The model was driven with local climatology data and provided a convincing description of the dynamics of the stand-scale sap flux data over 3 years in both the through-fall exclusion plot and the control plot. We are therefore confident that the SPA model contains an appropriate representation of the processes underlying forest gas exchange responses to reduced rainfall. It is therefore possible that, in the presence of soil, root and vegetation data, the model could predict a priori the vulnerability of different areas of rain forest to climate drying.

We are therefore potentially able to extrapolate the findings of the Caxiuanã through-fall exclusion experiment throughout Amazonia without the need to establish many more flux data collection sites. However, the SPA model requires hourly meteorological data to run, because of large sub-diurnal variation in leaf physiology and water transport processes and the resulting necessity to run the model at high temporal resolution. Hourly meteorological data is very uncommon in Amazonia. In addition, the computation time is high, owing to the need to do optimising calculations on several layers of leaves and soil. These two factors make the SPA model somewhat unsuitable for use in large regional-scale studies.

In this paper, we used model aggregation to produce a simplified version of the SPA model, with reduced data requirements and improved computational speed. Model
aggregation involves running the half-hourly process-based SPA model under a multi-
dimensional array of representative input variables (soil hydraulics, vegetation and me-
teorological conditions), and recording the daily gas exchange output. This generates
a response surface between the daily input variables and the daily gas exchange (latent
energy flux (LE) and gross primary productivity (GPP)). A series of equations is then
derived, from consideration of the underlying physiology, which describe the response sur-
face. The tunable parameters of these equations are fitted to maximise the agreement
(minimise the root-mean-square error) between the response surface and the resulting
empirical model.

Williams et al. (1997) previously conducted an aggregation procedure on the SPA
model, to produce the Aggregated Canopy Model (ACM) which predicts daily GPP from
daily input variables. In this paper we extend this analysis. Firstly, we re-aggregate
the SPA model using real meteorology data from across the Amazon basin, to create an
Amazon specific aggregated canopy model of GPP (ACM-GPP). Secondly, we develop a
new aggregated canopy model to predict daily evapotranspiration from daily meteorology
(ACM-ET). Thirdly, we develop a simple model of soil water transport and root water
uptake (SWAT) with which to predict the soil hydraulic inputs to the ACM models.
We coupled the ACM and the SWAT models to produce a stand-alone model which can
predict the onset of drought and its effect on forest evapotranspiration and GPP. We
test this model against data from the Caxiuanã and Manaus forests, then extrapolate
the model 100 years into the future to predict the timing of severe restrictions on forest
evapotranspiration and GPP under current global climate model forecasts (Cox et al.
2004). Model aggregation allows the construction of a faster model, which allows better,
more thorough exploration of response surfaces. In addition, model aggregation also helps
isolate the critical factors that control the processes of interest, e.g. the factor which
are most critical in determining forest gas exchange under a range of climate, soil and
vegetation conditions.

These analyses address three key questions:
1. What reduction in model accuracy is found if it is possible to reproduce the behaviour
   of the detailed half hourly soil-plant-atmosphere model with a simple aggregated daily
   model?
2. Is it possible to explain the heterogeneous responses of forest gas exchange to low
   rainfall using only measured changes in soil, root or vegetation characteristics?
3. At what point in the next century will predicted climate drying begin to have an impact
5.3 Methods

5.3.1 Generation of response surface using the SPA model

The SPA model is a multi-layer soil-vegetation-atmosphere-transfer (SVAT) model. It uses half-hourly meteorology, vegetation properties (LAI, N content) and information on soil and plant hydraulics to produce estimates of GPP and LE flux of the whole canopy, as the sum of the individual canopy layers. The SPA model explicitly simulates the supply of water from soil to leaf, and then models the leaf water potential, to determine whether stomatal closure due to hydraulic stress is necessary. For model structure detail see Williams et al. 1996, for structure of the below-ground soil water model see Williams et al. (2001) and for model testing in Amazonian ecosystems see Williams et al. 1998 and chapters 2 and 4.

Our testing of the SPA model at Manaus (Williams et al. 1998) and Caxivanã (Chapter 4) has provided some confidence that the model contains accurate representations of the critical processes controlling tropical forest gas exchange. We therefore use the SPA model to extrapolate the resulting physiological understanding to a range of other meteorological and vegetation conditions which could potentially be found within the Amazon basin. This is an alternative method to that used by Williams et al. (1997) who developed an Aggregated Canopy Model by constructing a hypercube of all possible inputs, with the meteorological variables being independent of one another. In this paper, we use real Amazonian meteorological data so that the fitting process accounts for any cross-correlation between the meteorological variables.

SPA requires inputs of hourly meteorology, vegetation properties (leaf area index and total canopy Nitrogen) and soil hydraulics (soil water potential and soil-to-root hydraulic resistance). We sampled meteorological data from four sites across the Amazon basin, Tapajos and Caxivanã in the East, Manaus in the centre, and Rondonia in the South West. The precise location of the weather stations is described elsewhere (Carswell et al. 2002 for Caxivanã, Malhi et al. 1998 for Manaus, Saleska et al. 2004 for Tapajos and von Randow et al. (2002) for Rondonia). One to three years of radiation, temperature, vapour pressure deficit and wind speed data were available from each site. We constructed meteorological inputs for SPA from the 2503 days when all the meteorological measurements were present.
The vegetation (LAI and foliar nitrogen) and hydraulic (total soil-to-leaf resistance $R$ and soil water potential $\Psi_s$) inputs were unknown, and thus assigned randomly at the beginning of each day, within a given range (Table 5.1). The ranges were chosen to represent values typical of rain forest ecosystems. The range of values of soil-to-leaf resistance ($R$) (1 to 20 MPa s m$^{-2}$ mmol$^{-1}$) was determined from the values of $R$ inferred using the SPA model at Manaus (Williams et al. 1998) and Caxiuanã (Fisher et al., in review c). The range of values of soil water potential was between soil saturation and the lowest measured value of pre-dawn water potential found in Amazonia by Williams et al. (2001), which was $-1.5$ MPa. The minimum leaf water potential was set at $-2.5$ MPa. The ranges of LAI and N were typical of those normally found in Amazonia. We ran the SPA model for each of the 2503 days of real meteorology data, and randomly assigned the soil-to-leaf resistance, soil water potential, leaf area index and leaf Nitrogen at the beginning of each day. The hourly output of the SPA model was summed to give daily estimates of evapotranspiration (ET) and gross photosynthetic productivity (GPP).

Table 5.1: Ranges of the input variables to SPA and ACM

<table>
<thead>
<tr>
<th>Input parameter</th>
<th>Units</th>
<th>Low</th>
<th>High</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperature</td>
<td>°C</td>
<td>16</td>
<td>37</td>
</tr>
<tr>
<td>Max. VPD</td>
<td>kPa</td>
<td>0.07</td>
<td>2.9</td>
</tr>
<tr>
<td>Short wave radiation</td>
<td>W m$^2$</td>
<td>2</td>
<td>29</td>
</tr>
<tr>
<td>Temperature</td>
<td>°C</td>
<td>16</td>
<td>37</td>
</tr>
<tr>
<td>$R$</td>
<td>MPa s m$^2$ mmol$^{-1}$</td>
<td>0.1</td>
<td>20</td>
</tr>
<tr>
<td>$\Psi_s$</td>
<td>MPa</td>
<td>$-0.01$</td>
<td>$-1.5$</td>
</tr>
<tr>
<td>LAI</td>
<td>m$^2$ m$^{-2}$</td>
<td>4</td>
<td>6.5</td>
</tr>
<tr>
<td>N</td>
<td>g m$^{-2}$(ground area)</td>
<td>6</td>
<td>12</td>
</tr>
</tbody>
</table>

5.3.2 Aggregation of SPA model

Our goal was to produce a simple set of equations which describe the response surface of the SPA model forest gas exchange outputs to variations in input variables with the lowest possible RMSE. Two aggregated models were necessary. One to predict GPP and one to predict latent energy (LE). The methodology for both models was similar, in that a heuristic process was used to develop the model structure, then the model parameters were fitted to minimise the RMSE error between the SPA and ACM predictions. The opti-
misation routine used the quasi Newton method and a finite difference gradient (UMINF, IMSL Math Library).

GPP model

The model used to predict GPP from daily input variables is similar in structure to that developed by Williams et al. (1997), and consists of a series of equations, each of which account for a factor which may limit photosynthetic uptake. The model structure is described in Appendix 1 and is similar to the Williams (1997) model structure, except for the calculation of stomatal conductance ($g_c$). In the original Williams et al. (1997) aggregated canopy model, $g_c$ was found using

$$g_c = \frac{\Psi_d e^{\phi_1 T}}{p_2 H + DT}, \tag{5.1}$$

where $\Psi_d$ is the difference between minimum leaf water potential and soil water potential (MPa). $p_1$ and $p_2$ are fitted parameters. $DT$ is the daily temperature range ($^\circ$C) and $H$ is canopy height (m). The stomatal conductance calculation was modified for use the in tropics and in severely drought stressed ecosystems. The new method of calculating $g_c$ is as follows:

$$g_c = \frac{\sqrt{\Psi_d}}{b_1 R^{b_2} + 0.5 V^{b_3} I^{b_4}} \tag{5.2}$$

In this new method, $g_c$ is increased by large soil-leaf water potential difference, $\Psi_d$. When the soil is wet, the soil water potential is high and the leaf water potential is low (−2.5 MPa) so the water potential gradient is large and water transport is fast. When soil dries, $\Psi_d$ approaches $\Psi_l$ and the water potential gradient ($\Psi_d$) declines limiting water uptake. $g_c$ is limited by high soil-to-leaf hydraulic resistance, $R$ and by high atmospheric demand, which is represented here as the product of vapour pressure deficit, $V$ (kPa), and irradiance, $I$ (Wm$^{-2}$). Higher atmospheric demand means that the supply of water to the leaves is more likely to be insufficient, leading to reduced leaf water potential and stomatal closure. It was necessary to include this evaporative demand term, since the output of the SPA model for Amazonia indicated large declines in GPP when both irradiance and VPD were high, behaviour which was not captured by Equation 5.1. The parameters $b_1$, $b_2$, $b_3$ and $b_4$ determine the relative weighting of $R$, $V$ and $I$ on the stomatal conductance. This gives a total of eight fitted model parameters (Table 5.3). The model parameters were fitted to the SPA GPP output values to minimise the root-mean-square error (RMSE) between the ACM and SPA model outputs.
5.3.3 Evapotranspiration Model

Evapotranspiration was modelled as the product of the atmospheric demand and the stomatal limitation. The atmospheric demand \( D \) was modelled using the Penman-Monteith Equation (Jones, 1992)

\[
D = \frac{d_1 \left( s(I - d_2) + c_p g_a V \rho_a \right)}{s + \lambda (g_a / g_c)}
\]  

(5.3)

Where \( I \) is average daily radiation (Wm\(^{-2}\)), \( V \) is average daily vapour pressure deficit (kPa) and \( g_a \) is canopy conductance. \( \lambda \) is the psychrometric constant (0.066 kPa°C\(^{-1}\)), \( c_p \) is the specific heat of air (1010 J Kg\(^{-1}\) K\(^{-1}\)) and \( \rho_a \) is the density of air (1.2 Kg m\(^{-3}\)). \( d_1 \) is a correction between the average daily radiation and the effective radiation observed. \( d_2 \) is the intercept of the relationship between radiation and evapotranspiration. These fitting parameters are necessary because the Penman Monteith equation is an instantaneous equation, but the input parameters are daily averages or maxima. \( s \) is the change in slope of the saturation vapour pressure curve in with temperature (kPa °C):

\[
s = 6.166 e^{1733/7 + 273 + T}
\]

(5.4)

Stomatal conductance is defined as

\[
g_c = e_1 L \Psi_d e^{e_2 I / \sqrt{R}}
\]

(5.5)

where \( \Psi_d \) is difference between the minimum leaf water potential \( \Psi_l \) and the soil water potential \( \Psi_s \) (MPa), \( R \) is the soil-to-leaf hydraulic resistance (s m\(^{-2}\) MPa mmol\(^{-1}\)), \( L \) is the leaf area index and \( I \) is the irradiance (W m\(^2\)). Again, \( g_s \) is increase by high LAI and \( \Psi_d \) values, and limited by high irradiance and hydraulic resistance terms. \( e_1 \) and \( e_2 \) are the fitting parameters.

5.3.4 Soil water uptake model

The ACM model requires inputs of soil-to-leaf hydraulic resistance \( R \) and soil water potential \( \Psi_s \) to determine stomatal conductance. These are both functions of soil moisture, which varies over time and with the development of drought stress. A dynamic model of ecosystem hydraulics is necessary to predict these model inputs. In the SPA model implementation tested by Fisher et al. (in review, c), the SPA canopy model was coupled with a soil water transport model, which was used to predict the dynamics of soil water content \( \theta \), \( R \) and \( \Psi_s \) from soil hydraulic properties and meteorological data. The SPA soil-water transport model is a complex model with >10 soil layers and detailed soil
surface evaporation, water drainage and infiltration routines. In this paper, we present a simplified daily two layer daily resolution soil water transport model (SWAT), which may be driven with daily climate data and used to predict $R$ and $\Psi_s$ for input into the ACM model. Coupling the ACM and SWAT models creates a tool which may be used to probe the behaviour of rainforest ecosystems under a wide range of possible scenarios.

The SWAT model has two soil layers, 0.0 - 0.3 m and 0.3 m - $R_m$, where $R_m$ is the maximum rooting depth. Root biomass is assigned to these layers as measured in the field. Rainfall is added at the beginning of each day and infiltrated into the two layers. 80% of the rainfall is infiltrated into the second soil layer, reflecting the drainage of water through macropores present in rain forest soils (Chauvel, 1991). Soil water potential, $\Psi_s$ (kPa) and hydraulic conductance, $K$ (m s$^{-1}$), are then calculated from the soil water content, $\theta$ (m$^3$ m$^{-3}$), using the van Genuchten (1980) equation:

$$S_e = \frac{\theta - \theta_r}{\theta_s - \theta_r}$$  \hspace{1cm} (5.6)

$$\Psi_s = \left( \frac{S_e^{\alpha/(1-n)}}{(1-n)^{1/n}} - 1 \right)^{1/n}$$  \hspace{1cm} (5.7)

$$K = K_s \frac{(1 - (1. + (\alpha \Psi_s^n)^{(1-1/n)})^2}{(1. + (\alpha \Psi_s^n)^{(1-1/n)})^2}$$  \hspace{1cm} (5.8)

where $S_e$ is the effective saturation, with $\theta_s$ and $\theta_r$ as the saturated and residual soil water contents (m$^3$ m$^{-3}$). $\alpha_v$ is a scaling factor which determines the maximum pore size (kPa$^{-1}$), $n$ is a dimensionless curve shape parameter and $K_s$ is the maximum hydraulic conductivity (m s$^{-1}$). Values of the parameters of equations 5.6 - 5.8 were derived from measurements in chapter 1, for the Caxiuanã site and from Tomasella and Hodnett (1996) for the Manaus site. Water is drained into the next layer if the soil water potential is higher than $-6$ kPa (field capacity). This is in accordance with the water potential reached after 3 days of drainage by a saturated monolith measured in Chapter 1.

After drainage, soil-to-root hydraulic resistance, $R_{s,i}$, of each of the two soil layers (i), is calculated from the new hydraulic conductance. The basic geometric equations for simulating the soil-to-root hydraulic resistance were defined by Newman (1969). Soil-root resistance for each soil layer is calculated as

$$R_{s,i} = \log \left( \frac{\sqrt{L_i / \gamma}}{2\pi L K_{i,g}} \right)$$  \hspace{1cm} (5.9)

137
where $L$ is the total root length in the $i$th soil layer (m), $r$ is the root radius (m) and $K$ is the soil hydraulic conductivity (m s$^{-1}$) in the $i$th layer. $g$ is a scaling factor (0.009807) to convert hydraulic conductivity from m s$^{-1}$ to mmol m$^{-1}$ s$^{-1}$ MPa$^{-1}$.

The total below ground resistance to water uptake within one soil layer $R_{s,i}$ (m$^2$ MPa s mmol$^{-1}$) is found by adding the soil-to-root resistance to the internal root transport resistance

$$R_{i,i} = R_{s,i} + \frac{\sigma}{b_i}$$

where $\sigma$ is the inverse of the conductivity of root xylem per unit biomass (MPa s g mmol$^{-1}$) and $b_i$ is the total root biomass in each soil layer (g). The methodology for converting soil-to-root resistance into soil-leaf leaf area specific resistance $R_s$ is in Appendix 5.2.

The evapotranspiration estimate produced by the ACM-ET model, $E$, is used to extract water from both soil layers according to the relative ease of doing so. An additional soil water loss from the top layer was added to simulate soil evaporation. The average modelled soil evaporation for each day was 0.08 mm day$^{-1}$ (standard deviation 0.11 mm). The model is insensitive to variation of this magnitude, and so the soil evaporation remained constant at 0.08 mm day$^{-1}$. In addition, evaporation of intercepted rainfall from leaf surface was included in the model, derived from the results of Ubarana et al. (1996) who measured canopy storage at two Amazonian forest sites. Their estimates for the rain stored in the canopy in each rainstorm were 1.03 and 1.25 mm. We used an average between these two values of 1.14 mm.

Again, we parameterised the leaf surface evaporation using the output of the SPA model, which contains a detailed process based simulation of the process. We found that the SPA model predicted canopy evaporation of an average of 1.0 mm on days when there was rainfall. This figure was not related to the size of the rainstorm in question, as it depends mainly on the capacity of the canopy to store water.

### 5.3.5 SWAT model inputs

The ACM-SWAT model was tested against the two sets of Amazonian gas exchange data which have shown an indication of drought stress. These are the eddy covariance data collected at the ZF2 Cuieiras site near Manaus (Malhi et al. 1998) (hereafter referred to as the 'Manaus' data) and the data from the Caxiuanã through-fall exclusion plot presented
The models were driven with the daily meteorology data acquired for the Manaus and Caxiuanã forests. Root biomass data was available at the Caxiuanã sites. Soil hydraulic properties for Manaus were taken from Tomasella and Hodnett (1996) and for Caxiuanã from Chapter 3. The other input data were derived from those used in the SPA modelling analysis in Chapter 4. The input data for the SWAT model are shown in Table 5.2. The model was tested against scaled sap flow data from the Caxiuanã site (Fisher et al. in review c) and eddy covariance data from the Manaus site (Maihi et al. 1998). Predictions of canopy LE flux were the simulated sap flow plus the soil evaporation and interception rates.

Table 5.2: Parameters of the Soil-Water-Transport-Model.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Units</th>
<th>Layer 1</th>
<th>Layer 2</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Layer depth</td>
<td>m</td>
<td>0.3</td>
<td>4.7</td>
<td>-</td>
</tr>
<tr>
<td>Drainage limit</td>
<td>kPa</td>
<td>-6</td>
<td>-6</td>
<td>Chapter 3</td>
</tr>
<tr>
<td>Root resistivity</td>
<td>MPa s kg mmol⁻¹</td>
<td>10</td>
<td>10</td>
<td>Chapter 4</td>
</tr>
<tr>
<td>Root biomass</td>
<td>g m⁻³</td>
<td>200</td>
<td>6</td>
<td>Chapter 4</td>
</tr>
<tr>
<td>( \Psi_{\text{crit}} )</td>
<td>MPa</td>
<td>-2.5</td>
<td>-2.5</td>
<td>Williams et al. 1996</td>
</tr>
<tr>
<td>Root diameter</td>
<td>mm</td>
<td>0.58</td>
<td>0.58</td>
<td>Chapter 4</td>
</tr>
<tr>
<td>Soil evaporation</td>
<td>mm day⁻¹</td>
<td>0.08</td>
<td>-</td>
<td>Chapter 4</td>
</tr>
<tr>
<td>Rainfall interception</td>
<td>mm</td>
<td>1.0</td>
<td>-</td>
<td>Chapter 4</td>
</tr>
<tr>
<td>( R_{\text{plant}} )</td>
<td>MPa s m² mmol⁻¹</td>
<td>1.2</td>
<td>-</td>
<td>Fisher et al. (in press)</td>
</tr>
</tbody>
</table>

5.3.6 Model extrapolation to future climate states

Cox et al. (2004) used the Hadley Centre “HadCM3LC” Global Climate Model (GCM) to produce predictions of future climate over the Amazon region. The HadCM3LC model includes a representation of the global carbon cycle within the “TRIFFID” dynamic global vegetation model (DGVM) (Cox 2001). The first simulation of the HadCM3LC model produced a very significant amplification of global warming owing to the feedback between land carbon stock and climate change (Cox et al. 2000). This acceleration of climate change was due mainly to loss of carbon from soil reservoirs, but also due to the dieback of the Amazon rainforest in response to hotter drier conditions and subsequent modelled conversion from forest to savanna. Cox et al. (2004) provide greater levels of detail
concerning the predicted changes in climate over the Amazon basin. These predictions are dependant on the assumptions and parameterisation of the MOSES model (Essery, Best and Cox, 2002) which controls the land-atmosphere interactions in HadCM3LC. In particular, the MOSES model assumes that rooting depth is 3 m for rain forest, and that stomatal conductance is linearly related to soil water content between the wilting and critical water contents. Huntingford et al. (2004) tested the predictions of the MOSES model against the eddy covariance data collected at Manaus, the same data used in this paper to test the ACM-SWAT model. They found that the MOSES model, parameterised using site specific soil hydraulics data (Tomasella and Hodnett, 1996) predicted significant hydraulic limitation during the dry season, which was not evident in the data (Malhi et al. 2002). Therefore, the MOSES model was not successfully validated. Nevertheless, these predictions represent the state-of-the-art in Amazonian climate predictions.

The information provided by Cox et al. (2004) give the trajectory of rainfall decline over the next 100 years (until 2100) for an average value over the Amazon basin. We used these trajectories to drive the ACM-SWAT model from the present 100 years into the future using a daily time-step. We ran the model with the 2003 climate repeatedly, and scaled the rainfall according to a multiplier derived from the results of Cox et al. (2004). The rainfall reached 50% of the original total by 2100, so the multiplier was reduced from 1 to 0.5 over this time. In Chapter 4, we found that seasonality had very little effect on the total sap flow over a whole year, so we did not include any change in the seasonality of rainfall. We ran the model continuously for 100 years, changing the climate at the beginning of each year. The advantage of running the model with continuously decreasing rainfall is that the sequential decreases in soil moisture can be properly simulated. If only individual time slices are considered, the effects of gradual soil moisture decline are ignored.

We conducted a sensitivity test to soil type and rooting depth inputs, as both these parameters are a) poorly quantified and b) are key controls on forest drought resilience. We ran the 100 year model extrapolation for rooting depths ranging from 0.5 m (very shallow) to 18 m (the maximum depth at which roots have been reported, Nepstad et al. 2004). We conducted this analysis using both the soil hydraulic properties measured at Manaus by Tomasella and Hodnett (1996), and those measured at Caxiuana (Fisher et al. in press).

Betts et al. (2004) suggested that 50% of the precipitation reduction predicted by
Cox et al. (2004) was due to 'combination of physiological forcing and biogeophysical and global carbon cycle feedbacks'. This means that, in the absence of land-atmosphere feedbacks, the reduction in precipitation would only be half that suggested by the HadCM3LC model. We ran a second set of model simulations with the reduction in precipitation reaching only 25% in 100 years time.

5.4 Results

5.4.1 Response of SPA model to inputs

All the input variables, soil-to-leaf hydraulic resistance ($R$) radiation, VPD and temperature had strong effects on SPA modelled evapotranspiration (Fig. 5.2). The most limiting variable was soil-to-leaf hydraulic resistance. When $R$ was set at values higher than 10, evapotranspiration was limited to less than 2.3 mm day$^{-1}$. In contrast, the simulation of GPP responded most strongly to radiation inputs (Fig. 5.1). Soil-to-leaf resistance also had a strong effect, with temperature and VPD having lesser effects. All the meteorological variables (radiation, VPD and $T_{\text{max}}$) appeared to have threshold values above which carbon assimilation decreased. This corresponded to the point at which atmospheric demand was high enough to cause stomatal closure. The decline in GPP at high radiation values is due to correlation between VPD and radiation in the input data and the resulting stomatal limitation from high atmospheric demand, rather than due to direct limitation of GPP by high radiation (photoinhibition can result in reduced GPP at high radiation, but SPA does not incorporate non-stomatal photoinhibition).

Evapotranspiration and GPP have differing responses to variation in soil-to-leaf hydraulic resistance ($R$). Evapotranspiration has a very extreme decline when $R$ is increased, decreasing by 80% between 0.1 m$^2$ s MPa mmol$^{-1}$ and 20 m$^2$ s MPa mmol$^{-1}$. The response of GPP to $R$ is less extreme than the response of evapotranspiration, and a decline of only 50% over the same range. The maintenance of relatively high evapotranspiration when GPP is very low is potentially due to the carbon dioxide which is be assimilated in the morning. Even when $R$ is very high, the water stored above-ground is refilled overnight, allowing a brief stomatal opening in the morning before leaf water potential declines to the critical value and stomata close. The CO$_2$ assimilated into the leaves in this period is sufficient to allow 5 gC day$^{-1}$ m$^{-2}$ of photosynthesis, but evapotranspiration is low (< 1 mm day$^{-1}$) due to the low vapour pressure deficits in the morning.
Table 5.3: Fitted ACM parameters and values.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Symbol</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
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<td>Stomatal restriction exponent</td>
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Figure 5.1: Responses of the ACM (open circles) and SPA (filled circles) GPP predictions to driving variables. a) Soil-to-leaf resistance ($R$) b) Incoming short-wave radiation, c) Maximum Daily Temperature and d) Vapour Pressure Deficit.

Figure 5.2: Responses of the ACM (open circles) and SPA (filled circles) sap flow predictions to driving variables. a) Soil-to-leaf resistance ($R$) b) Incoming short-wave radiation, c) Maximum Daily Temperature and d) Vapour Pressure Deficit.
Figure 5.3: Daily sap flow rates modelled using the detailed SPA model, vs. daily sap flow modelled using the simple ACM model. The solid line is the 1:1 line. $r^2 = 0.87$

Figure 5.4: Daily GPP modelled using the detailed SPA model, vs. daily GPP modelled using the simple ACM model. The solid line is the 1:1 line. $r^2 = 0.87$
Figure 5.5: The error between the ACM and SPA model predictions of GPP, vs. the driving variables a) Soil-to-leaf resistance (R) b) Incoming short-wave radiation, c) Maximum Daily Temperature and d) Vapour Pressure Deficit.

Figure 5.6: The error between the ACM and SPA model predictions of daily sap flow, vs. the driving variables a) Soil-to-leaf resistance (R) b) Incoming short-wave radiation, c) Maximum Daily Temperature and d) Vapour Pressure Deficit.
5.4.2 GPP simulation by ACM-GPP

The ACM model development and fitting procedure described above resulted in good agreement between the daily GPP predictions of the complex high resolution SPA model, and the daily GPP predictions of the simplified, empirical ACM model ($r^2 = 0.87$) (Fig. 5.4). The fitted parameters are shown in Table 5.3). The response of the ACM model to variations in the input parameters was similar to the SPA response to input parameters (Fig. 5.1). In particular, the ACM model captures the reduction in GPP when stomatal conductance is decreased by high evaporative demand (short wave radiation and VPD). The dominant constraint on GPP, over the ranges tested, was solar radiation. In contrast, temperature and soil-to-leaf water potential gradient ($\Psi_d$ and hydraulic resistance ($R$) had less of an impact. The model-data residual errors did not show a relationship with any of the varied model inputs which varied, (temperature, short-wave radiation, VPD, $R$, LAI, $N$ and $\Psi_d$) suggesting that the model is an unbiased predictor of GPP (Fig. 5.5). The RMS error was 0.56 g C day$^{-1}$ m$^{-2}$ and the average relative error was 4.5%.

5.4.3 ET simulation by ACM-ET

The parameter fitting exercise for ET was similar to the GPP exercise, but, since evapotranspiration is affected by fewer biological factors than photosynthesis, there were fewer fitted parameters (5 compared to 8 for GPP, Table 5.3). The model fit was similar to that for GPP (Fig. 5.3) ($r^2 = 0.872$) but the relative error was higher (13.4%). The model errors did not correlate with any of the input variables (Fig. 5.6) and the responses of the ACM model to the input variables were similar to those of the SPA model (Fig. 5.2). The RMS error was 0.39 mm day$^{-1}$.

5.4.4 Fit of ACM-SWAT model to forest data

We tested the ability of the coupled ACM-SWAT model to predict the response of two different ecosystems, Caxivanã and Manaus, to drought stress, changing only the hydraulic properties of the soil between sites. The model provided a good explanation of the timing and magnitude of the reductions in soil water and sap flow found in the Caxivanã through-fall exclusion experiment. The predictions of the ACM-SWAT model were very similar to those of the SPA model ($r^2=0.87$), so the simple rapid daily ACM-SWAT model can be
used as a proxy for the SPA model at Caxiuanā. A similar pattern was found at Manaus, where the output of the ACM-SWAT model provided a good explanation ($r^2 = 0.77$) of the measured LE fluxes. The main feature of the Manaus data set was a reduction in the measured latent energy flux at the beginning of the measurement period (1st September 1995) (Malhi et al. 1998, 2002) until mid-December 1995. The model predicted a decline in stomatal conductance and evaporation of the same magnitude and timing as that shown in the data. To test whether the different soil types actually explained the behaviour of the two sites, we reversed the soil texture/climate combinations. For the Manaus climate, no drought stress was simulated using the Caxiuanā soil, and for the Caxiuanā climate, severe restrictions occurred, even in the wet season (data not shown).

5.4.5 Extrapolation to future climate

The vulnerability of the model to reductions in rainfall in the first 50 years was highly dependent on rooting depth and soil type. The sensitivity analysis showed that, at Caxiuanā, if roots are present down to 4 m, the sensitivity of the forest to reduced rainfall is low, no change in evapotranspiration occurring as the result of drought stress for the first 50 years (corresponding to a decrease in rainfall of 25%) (Fig. 5.9). Rooting depths shallower than the 4 m threshold were subject to increasing levels of drought stress and declines in evapotranspiration. The soils of the Manaus site, with their lower water storage capacity, required that rooting depths of 10 m were necessary to avoid drought stress in the first 50 years of simulation (Fig. 5.10). After 60 years, (30% decline in rainfall) a threshold was reached, whereby all the rainfall is evaporated either through interception, soil surface evaporation or evapotranspiration. The soil never refills during the wet season, and the dry season droughting becomes more and more intense. The properties of the ecosystem are unimportant past this threshold and all the simulations eventually converge.

The simulations run with only half of the decline in rainfall, simulating the external forcing of the Amazonian climate according to the Betts et al. (2004), do not reach the 30% threshold, therefore resemble the first 50 years of the initial simulations.
Figure 5.7: Time series data from the ACM-SWAT model at Caxiuanã. a) Measured sap flow (filled symbols) and sap flow estimated with the ACM-SWAT model (open symbols). b) Soil-to-leaf hydraulic resistance estimated with the ACM-SWAT model. c) \( \log_{10} \) of the uptake resistance of the 0.0-0.3 m soil layer (dashed line) and the 0.3-5.0 m soil layer (solid line). d) Modelled soil water content of the 0.0-0.3 m soil layer (dashed line) and the 0.3-5.0 m soil layer (solid line). e) Daily precipitation.
Figure 5.8: Time series data from the ACM-SWAT model at Manaus. a) Measured latent energy (LE) flux (filled symbols) and LE estimated with the ACM-SWAT model (open symbols). b) Soil-to-leaf hydraulic resistance estimated with the ACM-SWAT model (solid line) and by the SPA model (dashed line). c) Log₁₀ of the uptake resistance of the 0.0-0.3 m soil layer (dashed line) and the 0.3-5.0 m soil layer (solid line). d) Modelled soil water content of the 0.0-0.3 m soil layer (dashed line) and the 0.3-5.0 m soil layer (solid line). e) Daily precipitation.
Figure 5.9: Future evaporation scenarios for 100 years into the future modelled with ACM-SWAT using an array of rooting depth inputs and Caxiuana soil properties. Rainfall decreases to 50% of current rate by 2103.

Figure 5.10: Future evaporation scenarios for 100 years into the future modelled with ACM-SWAT using an array of rooting depth inputs and Manaus soil properties. Rainfall decreases to 50% of current rate by 2103.
Figure 5.11: Future evaporation scenarios for 100 years into the future modelled with ACM-SWAT using an array of rooting depth inputs and Caxiuana soil properties. Rainfall decreases to 25% of current rate by 2103.

Figure 5.12: Future evaporation scenarios for 100 years into the future modelled with ACM-SWAT using an array of rooting depth inputs and Manaus soil properties. Rainfall decreases to 25% of current rate by 2103.
5.5 Discussion

5.5.1 What reduction in model accuracy is found if it possible to reproduce the behaviour of the detailed half hourly soil-plant-atmosphere model with a simple aggregated model?

We have here described how the soil plant atmosphere model was aggregated into two daily time-step models, ACM-ET and ACM-GPP to predict evapotranspiration and GPP from daily drivers. The correlation between the SPA model and the ACM models is good, 0.870 and 0.872 for ACM-GPP and ACM-ET respectively (Fig 5.3 & 5.4). The average relative errors were 4.5% and 13.5%. However, this error is unbiased, as it was not correlated with any of the input variables (Fig. 5.5 and Fig. 5.6). Therefore over longer time scales the errors will be small. This result has important consequences, as it means that detailed understanding of forest drought physiology, including soil-to-leaf water transport and complex stomatal optimisation, can be captured by a simple model requiring only daily meteorological drivers, and operate ~600 times faster than the detailed model. This opens up much larger possible applications where only daily data is available. The use of aggregated models is uncommon in ecosystem studies, but we are of the opinion that in certain circumstances, such as this, where processes may be accurately simulated, but at the cost of high computational time and data requirements, model aggregation could provide an ideal solution.

5.5.2 Is it possible to explain the heterogeneous responses of forests to low rainfall using only measured changes in soil, root or vegetation characteristics?

In this analysis, we attempted to explain the behaviour of two different ecosystems, Caxiuanã and Manaus, with the same model. The only changes made to the model between the two runs was a change in the soil hydraulic properties from those measured on the Caxiuanã sandy oxisol by Fisher et al. (in review a) and those measured for the clay oxisol at Manaus by Tomasella and Hodnett (1996). When run with the correct soil hydraulics properties, the fit between the model and the data was good (Fig. 5.7 & 5.8), and the model predicted hydraulic stress at the same time as that identified in earlier
studies (Williams et al. 1998, Fisher et al. in review). When the two soil parameter sets
were reversed (data not shown), the Caxiquaná forest had much more drought stress than
observed in the data, and no drought stress was observed at the Manaus forest. These
results indicate that the differences in response to rainfall of the two sites are due
to differences in underlying soil hydrology and not climatological differences. Without
knowledge of the soil hydraulic properties, it would therefore be impossible to predict the
response of either forest to reduced rainfall.

When testing the MOSES model against the Manaus eddy covariance data, Harris et
al. (2004) used local measurements of soil hydraulics (Tomasella and Hodnett, 1996) to
parameterise the soil moisture deficit component of the model. Using this parameterisa-
tion, major stomatal limitation occurred from January to March, a phenomenon which
was not observed in the eddy covariance data (Fig. 5.8). Also, the model failed to
capture the inter-season dynamics in observed stomatal conductance. This test therefore
did not validate the hypothesis embedded in the MOSES model, which is the only other
mechanistic model of drought tolerance to be tested against forest gas exchange data in
this manner. The ACM-SPA model is therefore the only mechanistic model of drought
stress to have been successfully verified against time-series data from Amazonian forests.
As such, it would be an ideal model with which to scale up the information acquired in
the through-fall exclusion experiment. Further work is required to obtain sufficient soil
hydraulics data with which to achieve this. The testing of the model against other Ama-
zonian forest gas exchange data-sets, in particular those displaying drought sensitivity,
would allow further testing of the model hypothesis that soil water transport is the main
constraint of gas exchange in drought limited circumstances.

5.5.3 At what point in the next century will predicted cli-

mate drying begin to have an impact on rainforest gas
exchangen

When the model was run using the Cox et al. (2004) rainfall predictions, with a 50%
reduction in rainfall by 2100, a threshold in the response to rainfall reduction was observed
(Figs. 5.9 and 5.10). When the rainfall was reduced such that the forest no longer
achieved field capacity during the wet season, no water was drained out of the system,
and the forest effectively evaporated all of the water which was supplied by rainfall (via
evapotranspiration, interception or soil surface evaporation). This means that after 50-60
years, irrespective of the soil and root properties, the ecosystem will no longer be able to support the current evapotranspiration rate, which is a function of leaf area index, and it is likely that conversion to savannah will occur.

Betts et al. (2004) suggest that 50% of the precipitation reduction in HadCM3LC was due to biosphere-atmosphere feedback in the model. Our model predicts that no biosphere-atmosphere feedback is likely before rainfall is reduced below 30% if the rooting depth is more than 10 m (with the Manaus soil) or 4 m (with the Caxiuanã soil). Rooting depth in Amazonia was estimated to average 10 m by Nepstad et al. (2004), based on deep rooting studies located in Paragominas (Nepstad et al. 1994), Tapajos (Nepstad et al. 2002), Manaus (Hodnett et al. 1995), Jipp et al. (1998) and Moreira et al. (2000). This means that, over 100 years, if the forest is subject to only the external climate forcing, no biosphere-atmosphere feedback is likely to occur. However, there only needs to be a small quantity of biosphere-atmosphere feedback in the system to reduce rainfall from 75% to 70% of current rates. This could easily be caused by reduced evapotranspiration from deforested areas. It is therefore highly feasible that in the next 100 years the threshold of rain forest drought tolerance will be exceeded and a positive regional feedback between drought and evapotranspiration will occur.

Nevertheless, the predictions of this model are more conservative than those of Cox et al. (2000, 2004) who predict that rainforest carbon stocks begin to decline around 2030, with only a 15% rainfall reduction. This is likely to be due to the low rooting depth in the MOSES model (3 m), or potentially due to the effects of climatic heterogeneity, which may set up feedback cells in the drier parts of Amazonia, which have a subsequent effect on the whole basin. Investigations of deforestation rates, model scaling and forest and soil heterogeneity are likely to yield a more accurate estimate of the threshold climate change beyond which the rain forest of the Amazon basin will become unsustainable.

5.6 Acknowledgements

This work was supported by a University of Edinburgh faculty research Scholarship, several Natural Environment Research Council (UK) research grants, a Natural Resources International Foundation Fellowship and the Elizabeth Sinclair fund (School of Geosciences, University of Edinburgh). The author would like to thank Yadvinder Malhi and John Grace for help with experimental methods, planning and logistics, Rafael Ferreira da
5.7 Appendix 1- GPP model.

The Aggregated Canopy Model structure is similar in structure to the Williams et al. (1997) ACM model. The limiting factors considered are leaf Nitrogen concentration, temperature, leaf area index, atmospheric CO₂ concentration, stomatal conductance and light availability. Firstly, the maximum Nitrogen limited rate of photosynthesis (\(P_N\)) is determined by leaf nitrogen content, \(N\) (g m\(^{-2}\)), leaf area index, \(L\) and maximum temperature \(T\) (°C).

\[
P_N = e^{(a_2T)a_1NL} \tag{5.11}
\]

\(a_1\) and \(a_2\) are fitted parameters. The Nitrogen limited photosynthesis rate was then assumed to be further limited by the internal leaf CO₂ concentration, \(C_1\). An asymptotic function was used to describe the relationship between \(C_1\) and the CO₂ diffusion limited photosynthetic rate, \(P_C\).

\[
P_C = \frac{P_N(C_1 - \theta)}{k + (C_1 - \theta)} \tag{5.12}
\]

where \(k\) is a fitted parameter and \(\theta\) is the compensation point, also a fitted parameter.

The CO₂ diffusion limited photosynthetic rate, \(P_D\), was calculated as the gradient between the internal (\(C_1\)) and atmospheric (\(C_a\)) CO₂ concentrations multiplied by the stomatal conductance \(g_c\).

\[
P_D = g_c(C_a - C_1) \tag{5.13}
\]

\(C_1\) was found by equating Equations 5.12 and 5.13, assuming a steady state so that \(P_C = P_D\).

\[
C_1 = \frac{1}{2} \left(C_a + q - p + \sqrt{(C_a + q - p)^2}\right) \tag{5.14}
\]

where \(q = \theta - k\) and \(p = \frac{P_N}{g_c}\). The value of \(C_1\) was substituted into Equation 5.13 to find the value of \(P_D\). The light limitation, \(P_L\), was determined as

\[
P_L = \frac{E_0IP_D}{E_0I + P_D} \tag{5.15}
\]

where \(I\) is the \(E_0\) is the canopy level quantum yield, a function of LAI:

\[
E_0 = \frac{c_1L^2}{L^2} \tag{5.16}
\]

This leaves the canopy conductance, \(g_c\), undefined.
5.8 Appendix 2: Soil water uptake.

Total below ground resistance to water uptake within one soil layer $R_{b,i}$ ($m^2 \text{MPa s mmol}^{-1}$) is found by adding the soil-to-root resistance to the internal root transport resistance

$$R_{b,i} = R_{a,i} + \frac{\sigma}{b_i}$$

(5.17)

where $\sigma$ is the inverse of the conductivity of root xylem per unit biomass (MPa s g mmol$^{-1}$) and $b_i$ is the total root biomass in each soil layer (g).

The cumulative conductance of both soil layers is then calculated and multiplied by the fraction of leaf area $i$ in a given canopy layer $j$ to give the total leaf-area specific below-ground resistance ($R_{bg}$).

$$R_{bg} = \frac{1}{\sum_{j=1}^{10} \frac{1}{R_{bg,i}}}$$

(5.18)

$R_{bg}$ is then added to the above-ground resistance, $R_{ag}$, to give the total leaf area specific soil-to-leaf hydraulic resistance $R$.

The soil water potential of both soil layers was then weighted to reflect the layer where the most soil water uptake occurred by calculating the evaporative demand for the critical minimum leaf water potential ($\Psi_{crit}$).

$$\Psi_{w} = \sum_{i} \Psi_{i}(\Psi_i - \Psi_{crit})$$

(5.19)

The weighted soil water potential, $\Psi_{w}$, and the total soil-to-leaf hydraulic resistance, $R$, were then used as input to the ACM-GPP and ACM-ET models. The evapotranspiration estimate produced by the ACM-ET model, $E$, was then used to extract water from each soil layer. The fraction of the water removed from each layer was determined as

$$f_i = \frac{(\Psi_i - \Psi_{crit})/R_{bg,i}}{\sum (\Psi_i - \Psi_{crit})/R_{bg,i}}$$

(5.20)

and the water was removed from each layer according to this fraction

$$\Delta \theta_i = E f_i$$

(5.21)

5.9 References


Chapter 6

Discussion
6.1 Main Findings and their implications

In the introduction, I outlined how a lack of fundamental understanding of drought physiology has lead to an absence of mechanistic understanding and the use of very simplified models of forest responses to soil drying. The lack of understanding was due partly to a lack of appropriate data against which to test physiological models, and to a lack of appropriate physiological models containing sufficient detail on plant hydraulic functions.

The main contribution of this thesis has been to show how detailed physical consideration of the mechanisms of drought physiology can lead to an accurate simulation of the behaviour of a whole ecosystem under hydraulically stressed conditions. Over the course of the four experimental chapters a series of scientific questions were asked. Here I review the answers to these questions derived from the completed studies and the implications of the findings. The wider applications and limitations will be discussed in the following sections.

1.1. Are the leaf water potential, sap flow and stomatal conductance data consistent with the hypothesis that stomata function to maintain isohydric conditions within the plant under water stressed circumstances?

Homeostasis of leaf water potential (isohydric behaviour) provided a convincing explanation of diurnal plant physiology under drought stressed circumstances in a tropical rain forest. The concept has many advocates in the plant hydraulics community (Field and Holbrook, 1989; Tardieu et al. 1993; Saliendra et al. 1995; Cochard et al. 1996; Comstock and Mencuccini, 1998; Sperry, 1998; Oren et al. 1999; Bonal et al. 2000; Salleo et al. 2000; Hubbard et al. 2001; Sperry et al. 2002) on the strength of both empirical evidence, and the argument that xylem disfunction is inevitable at very negative leaf water potentials and the need for stomata to close to avoid runaway cavitation (Tyree and Sperry, 1988). However, the isohydric hypothesis has been disregarded by the stomatal modelling community on the basis of evidence which suggested that some plants do not regulate their leaf water potential. Dewar (2002) suggest that the difference between isohydric and anisohydric plants may be explained by alteration of the stomatal response to leaf water potential by abscisic acid, but this theory is awaiting more thorough tests against data sets. All the species observed at the Caxiuaná forest appeared to display isohydric behaviour as demonstrated by the maintenance of a plateau in leaf water potential for the
majority of the daylight hours in the dry season.

**Chemical Signalling of soil water status**

Some biochemical studies have demonstrated that stomatal conductance may respond to changes in root and soil water status independently of changes in leaf water potential. During drying, roots increase production of the plant signalling hormone abscisic acid (ABA) in root tips (Zhang and Davies 1989). It is therefore hypothesised that the ABA is transported through the transpiration stream to the leaves, where it has also been shown to increase stomatal closure (Gowing et al. 1993). The 'chemical signalling' hypothesis proposes that ABA is the signal by which stomata sense soil drying, as opposed to the 'hydraulic signalling' mechanism tested in this paper. However, the chemical signalling hypothesis alone, when formally described in a model by Tardieu (1993) was unable to recreate the observed homeostasis of leaf water potential found in many species.

The chemical and hydraulic mechanisms for signalling between soil and stomata signalling are not mutually exclusive and Tardieu (1993) also investigated the possibility that stomatal sensitivity to ABA was increased under reduced water potential (as experimentally demonstrated for maize by Tardieu Zhang and Gowing (1993), thus integrating the two hypotheses). Tardieu (1993) compared this 'integrated' model of chemical and hydraulic signalling to a purely hydraulically based model. Both models produced similar predictions of plant hydraulics, since they both predicted homeostasis of leaf water potential. However, the purely hydraulic model predicted an increase in stomatal conductance in the afternoon, similar to that observed in the SPA model predictions. The combined hydraulic and chemical model, in agreement with the data presented here, did not predict stomatal opening in the later afternoon, since the high levels of ABA produced in the soil prevent this from occurring. In addition, the combined model predicted that the observed minimum leaf water potential depended on the evaporative demand, and was variable, whereas the purely hydraulic model had a static minimum leaf water potential. Tardieu (1993) concluded that it was possible for a purely hydraulically based model to provide a good explanation of general observed trends in stomatal behaviour, but that the combined model of chemical and hydraulic signals could explain the lack of afternoon stomatal opening and variable leaf water potential minima. It is therefore possible, as with all models, that the good fit of our model is fortuitous and that the implied mechanism of stomatal control is not exactly correct. To distinguish whether either the purely hydraulic, or the combined hydraulic and chemical model is correct, assuming that the
results are Tardieu (1993) are universal, it is clear that we require minimum leaf water potential data collected at different evaporative demands. During the course of the project, no such data was collected. However, at this point, we must make a practical distinction between model correctness and model adequacy. The hydraulic model tested here and the combined chemical and hydraulic model proposed by Tardieu (1993), work by using similar mechanisms and both use leaf water potential to determine stomatal conductance. There is only a small discrepancy between the purely hydraulic SPA model and the data presented.

In terms of implementation, both models require modelling of the leaf water potential dynamics, but chemical signalling models require, in addition to this, the modelling of abscisic acid concentration, which involves several unknown tunable parameters. In light of the lack of data on the ecophysiology of Amazonian trees, these tunable parameters may be very difficult to constrain. Also, the increased model-data agreement is likely to be restricted to the late afternoon stomatal conductance values, which will have little effect on the overall vegetation gas exchange. Soil-vegetation-atmosphere models which use a large number of optimised parameters produce descriptions of the current response surface of ecosystem processes to external input, but do not inform us about the potential responses of the ecosystem to major perturbations outside of the calibration range. Therefore the representation of processes which require multiple optimised parameters, such as chemical signalling, should be discouraged unless deemed entirely necessary.

We have shown here that it is possible to model leaf water potential dynamics, stomatal conductance and sap flow, given a knowledge of the soil water potential and soil-leaf hydraulic resistance. However, modelling the dynamics of the soil-to-leaf hydraulic resistance is a further challenge (Fisher et al. in prep; Misson et al., 2004; Sperry, 1998; Tuzet Perrier and Leuning, 2002; Williams et al., 2001). We recommend that efforts are concentrated on the estimation of soil and plant hydraulic conductance dynamics to reduce uncertainty in the modelling of leaf water potential, rather than concentrating on additional chemical signalling hypotheses.

We also recommend the planning of experiments so as to distinguish between disparate hypotheses which give similar results, such as those described here. In this case, it is likely that, measuring leaf water potential time series under several different evaporative demands will establish whether the minimum leaf water potential is variable or static, and therefore distinguish between the two hypotheses.
1.2. Are changes in soil-to-leaf water supply dominated by changes in soil water potential or soil-to-leaf hydraulic resistance?

The changes in supply of water to leaves appeared to be dominated by differences in the soil-to-leaf hydraulic resistance, and not by changes in leaf water potential. The importance of soil-to-root hydraulic resistance is not often considered in studies of drought stress, the most common predictor of drought stress being pre-dawn leaf water potential, which is associated with soil water potential. The dominance of soil-to-root resistance was also indicated by the SPA model sensitivity analysis, when changes in $R$ caused a response in evapotranspiration four times greater than that caused by altering soil water potential from wet to dry season values. It is quite possible for limiting soil-to-root hydraulic resistances to co-exist with high pre-dawn water potentials. High pre-dawn leaf water potential values may occur during periods of drought stress due to night-time refilling from lower, wetter soil layers, which have few roots. This appears to be the case at the Caxiuana site. The change in soil water potential from ~0 MPa to ~0.6 Mpa only altered the soil-leaf water potential gradient from ~2.5 Mpa to ~1.9 MPa, a factor of 2.1. Soil-to-leaf hydraulic resistance increased by an average factor of 7.6. Therefore, it is clear that $R$ should be the dominant variable. This conclusion is important as it makes it clear that we should consider the hydraulic conductivity of soil, rather than just the water retention curve.

1.3. If there is a major change in soil-to-leaf hydraulic resistance between seasons, is the change in resistance located above or below ground?

Between seasons, we measured an increase in soil-to-leaf hydraulic resistance. The change in soil-to-leaf hydraulic resistance was located mainly below ground in the majority of trees measured using stem psychrometers. In the wet season, the stem psychrometer values were close to zero, but in the dry season, they were close to leaf water potential, indicating that there is a large increase in below-ground resistance between seasons. These types of measurements are very rare in the literature. Comstock and Mencuccini (1998) found that, *Hymenoclea salsola* 49% of the resistance between soil and leaf was located below ground. Irvine and Grace (1997) also determined that for *Pinus sylvestris* L., the resistance of above- and below-ground components was approximately equal. In our experiment, we found that, in the wet season, only 12.5% of the resistance was located below ground. However, the trees in our study are substantially taller than those measured
We remain unsure as to whether the resistance is located in the soil matrix (soil-to-root hydraulic resistance) or in the root tissue. Experiments to measure root xylem conductance were attempted using a High Pressure Flow Meter (HPFM). Using this instrument, which pushes water back into the root system and measure the ratio of flow to pressure gradient, we were able to measure the maximum conductance of the root systems, but since emboli caused by drying would have been compressed, allowing previously cavitated vessels to again be usable (Sperry, J, pers. comm.). We were therefore unable to make measurements of unsaturated hydraulic conductance in droughted conditions. In addition, we were only able to measure the whole root systems of sapling trees, as the only accessible roots of large trees were surface roots, which grew at angles too extreme to be measured by the instrument. Therefore, to test that the main resistance to water transport, and therefore the main impedance to plant water supply, was in the soil, it was necessary to use a sophisticated model of soil-to-root water transport instead. This required measurement of the site-specific soil hydraulic properties.

2.1. Which soil hydraulic model provides the most appropriate representation of the water retention curve and hydraulic conductivity data collected?

We found that all the soil models provided very similar fits to the soil water retention curve, but that the van Genuchten model marginally provided the best description, presumably as the result of having a larger number of fitted parameters than the Campbell and Brock-Corey models, and a more flexible form than the Poulsen model. The hydraulic conductivity was estimated substantially better by the van Genuchten model than the other models, for similar reasons. This result has important ramifications, as the better fit by the van Genuchten model than the Poulsen model means that the Caxivanã soil did not display the same bi-model porosity structure observed by Tomasella and Hodnett (1996) for the clay oxisol at Manaus.
2.2. What is the uncertainty placed on predictions of hydraulic conductivity in dry soils (−8 to −1500 kPa) involved in extrapolating $K$ measurements beyond field capacity using models?

Despite the similar fits between the various models and the data, the different soil hydraulics models produced markedly different results when extrapolated into the dry soil zone down to −1500 kPa. The main features of the extrapolated results were that the van Genuchten model consistently produced the lowest values of hydraulic conductance. The Poulsen model produced the highest values, for all four soil depths. The range over predictions was large, 2.56 orders of magnitude averaged between the layers. However, sensitivity tests on the results of the SPA model to use of different soil models showed that changes of only 5% in total annual transpiration were caused by the use of the four different soil hydraulics models.

2.3. Is the water retention curve typical of Amazonian soils of this texture with reference to an Amazonian water retention curve pedo-transfer function (PTF) (Tomasella et al. 2000)?

The predictions of the Campbell, Brooks-Corey and van Genuchten models for 1500 MPa were very similar at all four depths, and varied by only 0.58 orders of magnitude (over a range of 9 orders of magnitude). This result is encouraging, as it suggests that a subjective choice of soil model would not have a major impact on the estimation of unsaturated hydraulic conductivity.

2.4. Does the soil exhibit the high hydraulic conductivity relative to the relationship between water retention and hydraulic conductivity derived for Brazilian soils by Tomasella and Hodnett, (1997)?

The hydraulic conductivity of the Caxiuanã soil was generally under-predicted by the Tomasella and Hodnett (1997) model, especially near to saturation. The two lowest soil depths display high conductance relative to the model predictions for low soil water contents, but are under-predicted by the model at values approaching saturation and the two higher depths conform to the model predictions, except for when the soil approaches saturation, when the model underestimates hydraulic conductance. This indicates that the Caxiuanã soil may exhibit the same elevated hydraulic conductivity values displayed by the Manaus clay oxisol, potentially as the result of the elevated biological activity of rain
forest ecosystems and the resulting frequency of biogenic macropores in the soil (Chauvel, 1991).

3.1. Are the observed seasonal changes in evapotranspiration consistent with the hypothesis that gas exchange is limited by changes soil-to-root water supply?

The increase in soil-to-root hydraulic resistance as soil dries can provide a convincing explanation for the decreasing use of water by trees during the dry season. It was not necessary to invoke any other mechanisms (e.g. chemical signalling between roots and stem (Tardieu, 1993; Tardieu et al. 1996, Gowing et al., 1993) or embolism of plant xylem vessels under low water potentials (Sperry, 1998)) to explain the data we obtained. This is the first occasion where an explicit model of soil-to-leaf water transport and its effect on gas exchange has been tested against a seasonal time-series of tree water use such as this, where all input parameters are known (Williams et al. 2001, tested the model at a site in Oregon, but they were not able to measure rooting depth or biomass and used optimised values instead). The results of the exercise are encouraging, and provide substantial impetus for further tests of this forest drought response model in other ecosystems and climate regimes.

We also found that the SPA model of radiation transfer, evaporation and photosynthesis provided a realistic explanation of canopy gas exchange under non-drought stressed conditions in the control plot and in the droughted plot during the wet season. This reflects the conclusions of Williams et al. (1998) who found that the model provided a good description of canopy gas exchange measured by the ZF2 eddy covariance tower near to Manaus in Central Amazonia in the wet season.

Our grounds for concluding that the SPA model provided an adequate explanation for the data were that the model was parameterised without reference to the time-series of sap flow data, using a combination of soil and vegetation characteristics. The data set is complex, and consists of several types of data (sap flow, soil water, leaf physiology) and it at different time (half hourly, daily, annual) and spatial (leaf, tree and stand) scales. It is unlikely that a model which did not include a sufficiently realistic mechanism would simulate each type and scale of data with similar levels of confidence as described by the work in this thesis. However, owing to the complexity of the data set, and the variety of different data types, a full statistical analysis of the ‘confidence limits’ of the model has
not, yet, been possible. In a later section, we discuss the use of data assimilation to rectify this situation and it remains a future goal.

3.2. What is the reduction in photosynthesis associated with the reduction in sap flow?

The SPA model, verified against the sap flow data, indicated that the reduction in gross photosynthetic productivity (GPP) in response to decreasing stomatal conductance, was 15% over in the final third year. The model has been verified against eddy covariance data of Carswell et al. (2002) in the wet season and found to give output of a similar magnitude to the GPP estimated from the eddy covariance data. Malhi et al. (1998) estimated that the carbon dioxide uptake of an Amazonian rain forest near Manaus was 30 tonnes per hectare per year. If respiration were to remain unchanged, then the reduced photosynthesis calculated here would produce a carbon source in the order of 4.5 tC per hectare, which would equate to 2.5 Gigatonnes if scaled to the entire Amazon basin following the methodology of Grace and Malhi (1999). However, the assumption that respiration will not change is probably incorrect, as respiration rates are likely to depend on the input of labile carbon and therefore it is probable that they will decrease as photosynthesis decreases. The consideration of the carbon balance of the entire ecosystem is not within the scope of this study but will be investigated in future collaborative studies.

3.3. Which ecosystem properties are most critical in controlling the sensitivity of the ecosystem to reduced rainfall?

The sensitivity tests using the SPA model showed that the model had little response to either rainfall seasonality, or to root biomass, all other things being constant. The lack of sensitivity to rainfall seasonality is the result of the use of a rooting depth of 5 m. At this depth, it is possible that enough rainfall is stored in the soil to last even the most severe dry seasons. When rainfall gets to 70% of the ambient value, the total rainfall is less than the annual evaporative demand, so the water storage is not refilled in the wet season, resulting in declines in sap flow irrespective of seasonality.

The lack of sensitivity to root biomass indicated that increasing root density did not substantially effect the amount of water available. Increasing root biomass would only allow extra water uptake if it allowed more soil water to be removed per unit soil volume.
However, changing root biomass by a factor of 2 has little effect. This effectively halves the distance water must travel to the root surface, but soil hydraulic conductivity changes rapidly on a log scale, and so alterations of a factor of 2 in path length are negligible compared to the changes in conductivity of a factor of 10, which occur on average every 2% of soil water content. The doubling of root water content is therefore likely to increase the volume of extractable water by less than 1%.

The model showed high levels of sensitivity to both soil hydraulic properties and to rooting depth. It is not possible to say which variable is 'dominant', as this would depend on having a well defined range over which the water holding capacity and rooting depth varied, which is not the currently possible in Amazonia. Another problem is that conducting sensitivity tests to reduced rainfall over short time frames such as 3 years is that the impact of reduced rainfall is greatest in the 3rd year as the limitation on soil recharge comes into effect. It is therefore more appropriate to conduct these sensitivity tests over realistic climatic change time spans, as shown Chapter 5.

4.1. What reduction in model accuracy is found if the detailed half hourly soil-plant-atmosphere model is replaced by a simple aggregated daily model?

In order to run simulations over larger spatial and temporal scales, we aggregated the SPA model to create two Aggregated Canopy Models, one for evapotranspiration and one for GPP. These models represented the outcome of SPA with $r^2$ values of 0.870 and 0.872. The relative errors between the ACM and SPA predictions of daily gas exchange were 10.5% and 4.5% for ET and GPP respectively. However, more importantly, the parameter optimisation routines produced an unbiased fit, and the SPA-ACM error was not correlated with any of the input variables, therefore, over longer time periods, the relative errors should gradually decrease. This approach allows us to represent the predictive capacity of the mechanistic SPA model but with significant lower data input and computational requirements.
4.2. Is it possible to explain the heterogeneous responses of forest gas exchange to low rainfall using only measured changes in soil, root or vegetation characteristics?

The new daily canopy gas exchange model was coupled to a model of soil water transport and soil-to-root water movement, simplified from the version in the SPA model. This new ACM-SWAT model was tested against gas exchange data from the Caxiuana and Manaus sites. The only change made to the model inputs between sites was an alteration in the soil hydraulic properties parameterised from measured data. The model thus parameterised provided a good explanation of both data sets. This is an important result, as it indicates that the model may be used to calculate the inter-site variability in vulnerability to rainfall reduction without the need to make additional measurements of canopy gas exchange. Notwithstanding the need for further model testing, this methodology may be an effective tool for scaling the information gathered in intensive experiments to wider spatial scales.

4.3. At what point in the next century will predicted climate drying begin to have an impact on rainforest gas exchange?

The predictions of the ACM-SWAT model for the next 100 years revealed several points of interest. Firstly, when the model was run using the Cox et al. (2004) predictions of a 50% reduction in rainfall by 2100, the evapotranspiration of the forest between 2050 and 2100 was completely independent of the forest properties and entirely dependant on the incoming rainfall. In the first 60 years, the response of forest evapotranspiration was co-dependent on soil properties and rooting depth, with rooting depths more than 4 m with the Caxiuana soil and 10 m with the Manaus soil proving sufficient to guard against hydraulic limitation of any sort in the first 60 years. After 60 years, when rainfall declined to 70% of its current value, the rainfall was less than the evaporative demand, and a decline in evaporation occurred.

However, the predictions of Betts et al. (2004) who suggest that only half of the decline in forest evapotranspiration predicted by Cox et al. (2004) was due to external climatic forcing. In this scenario, rainfall does not reach 70% of the current rate in before 2100. Therefore there is no change in evapotranspiration if the rooting depth, again, is more than 4 m at Caxiuana and 10 m at Manaus. These results indicate that forest ecosystems may cope with a rainfall reduction of up to 30%, but beyond this there is an inevitable decline in gas exchange, presumably accompanied by leaf area loss and conversion to savannah.
The threshold of forest survival (70% of current rainfall) lies between the predictions of Cox et al. (2004) who included biosphere-atmosphere feedback and Betts et al. (2004) who calculated the drying predictions without biosphere-atmosphere feedback. If we assume that rooting depths are more than 10 m, as suggested by the existing data, we find that there is no biosphere-atmosphere feedback, so the system appears to remain about 70% rainfall and ecosystem collapse does not occur. However, even if there is no feedback of the pristine forest ecosystems to rainfall reduction, there will still be biosphere-atmosphere feedback resulting from deforestation and forest fragmentation (Laurance and Williamson, 2001; Nepstad et al. 2004). It may well be the case, therefore, that land use change reduces precipitation past the rainfall threshold of required to maintain rain forest ecosystems. If so, then these findings could have major policy implications for the economic development of Amazonia (Laurance et al. 2004).

6.2 Possible further studies

6.2.1 Amazonian Extrapolation

As it stands, the 100 year predictions of ecosystem behaviour are only really applicable to the Manaus and Caxiuanã ecosystems, due to the site specific parameterisations. Clearly, in order to make globally applicable conclusions, the model must eventually be scaled up to the regional/Amazonian level. Here we discuss the practical difficulties and possible solutions which could accompany such an investigation.

Other forests in Amazonia are likely to differ in their soil hydraulic properties, root biomass profiles, leaf area indices and canopy photosynthetic capacity. We have shown that, in particular, the rooting depth and soil moisture content have a strong influence on the drought stress response. However, data on both rooting depth and soil hydraulic properties are extremely rare. Presently, estimates of rooting depth are based on a small number (~8) of locations. The majority of these studies have found either water uptake or root biomass at the deepest levels observed in their respective soils. These range between 2 and 10 m. The only exception to this is in fact this study, which did not find roots deeper than 5 m in the experimental plot, potentially due to the local thickness of the stony laterite layer found between 3 and 5 m in the droughted plot. There is therefore a reasonable
consensus that rooting depths in Amazonia are much deeper than initially imagined when the majority of large modelling studies were published with rooting depths between 2 and 3 m. Further field work is still necessary to determine what the actual limit of rooting depth might be, and to estimate the spatial variability of rooting profiles. In order to capture the regional-scale responses to climate drying and the feedbacks therefrom, it will be necessary to improve the estimates of rooting depth by means of additional field campaigns and the digging of access shafts to make more measurements of root biomass. Such field campaigns would not be expensive or difficult, and would add substantially to or ability to predict the response of the rainforest to the changes in climate likely over the next century.

Data on the water retention curve of soils is reasonably abundant for Amazonia (Tomasella, 2000) and the prediction of the water retention curve by the Brazilian pedo-transfer function undertaken in chapter 3 produced a similar range of water contents to those shown in the data. However, the SPA model depends heavily on predictions of soil hydraulic conductivity, and the lack of existing hydraulic conductivity data for Amazonian soils, even with the additions made by this study, do impinge on the ability of the modelling community to improve model confidence. One approach may be to use the range of relationships between water retention and hydraulic conductivity derived from the measurements made here and by Tomasella and Hodnett (1997) to conduct a sensitivity test of the results of the ACM-SWAT model to the observed range of variability. Nevertheless, a preferable solution would be to undertake inexpensive field campaigns which conduct a series of instantaneous profile experiments and made pressure plate measurements of the water retention curve would significantly improve this situation at little extra cost.

Provision of daily data for Amazon wide modelling studies is also an issue. Daily inputs of rainfall, solar radiation, temperature and humidity or vpd are necessary to run the ACM-SWAT, and indeed any soil-vegetation-atmosphere-transfer model. Daily rainfall data are available from the Tropical Rainfall Monitoring Mission (TRMM), gridded at 0.5° from 1998 to 2001. Monthly minimum and maximum temperature data, gridded at 0.5° between 1900 and 1995, is available from the Climate Research Unit (CRU) database (New et al., 2000) as as monthly estimates of vapour pressure deficit. Monthly average solar radiation data is available for the whole globe at 1° resolution from the ISLSCP project (Stackhouse et al. 2000).

In addition, because the ACM model is an empirical model, with fitted parameters, it
is only applicable across the range of input variables used to calibrate the model initially. These ranges were taken from contemporary Amazonian weather stations, and as such do not extend either to more arid areas outwith the basin or into future hotter drier climates. Re-calibration of the ACM model to a wider range of climatic inputs, including future climatic states generated by GCM models, would therefore be necessary.

6.2.2 Coupling to GCM model

The development and testing of both the SPA and ACM models in drought limited environments allows a potentially very wide sphere of application. However, the highest priority is the application of the model within a coupled model of climate change. The MOSES/TRIFFID model, the model currently being used for the majority of coupled climate-carbon cycle studies, has been shown to produce erroneous predictions for the Manaus site, and therefore there is little basis on which to assume that the drought stress mechanism contained therein is reasonable. As discussed in the introduction, the links between soil drying and forest gas exchange in all the major ecosystem models employed in Amazonia are simplistic and, except for the MOSES/TRIFFID model, untested against field data from tropical rain forests. We are therefore of the opinion that it would be advantageous to include the SPA/ACM model as the land surface routine within a GCM model. The main difficulty in this case is that ACM, acting on a daily time-step, is not compatible with the hourly time-step employed by GCM models and the SPA model, with multiple canopy layers and optimisation routines, may prove too computationally expensive to use in a GCM model. At present, work is planned on a new UK based land-surface model (Meir P., Levy P. pers comm.), and the most beneficial course of action would be to integrate the new understanding of drought stress provided by this thesis into the new land-surface model.

6.2.3 Application in other ecosystems

It would be greatly advantageous to test the SPA model predictions against gas exchange fluxes in other ecosystems, but even more so for other ecosystems which have been observed to be subject to hydraulic limitation. Ideally, it would be beneficial to test the model against the parallel LBA Tapajos through-fall exclusion experiment (Nepstad et al., 2002), but owing to logistical difficulties with data analysis, this is not yet possible.
It also is feasible that the mechanistic model of drought stress presented in this thesis could be applicable to a wide range of hydraulically stressed ecosystems elsewhere in the world (Mediterranean, savanna etc.) as well as the Ponderosa Pine ecosystems studies by Williams et al. (2001). Application of the model to such ecosystems, which have much more frequent and intense dry seasons, could possibly improve our ability to predict the impact of increasingly severe droughts such as those experienced in Europe in recent years. The application of the model to other ecosystems will enable testing of the key model hypotheses.

6.2.4 Integration of alternative stomatal control hypotheses

The SPA model provides a convenient framework in which to test mechanisms of stomatal conductance, as it accounts for temporal and vertical variations in meteorology which are difficult to model in any other manner. This allows real-time predictions of leaf level physiology which are not possible without the use of such a detailed SVAT model. In Chapter 2 we have only tested a single stomatal control mechanism, but the system would be ideally suited to a comparison of competing stomatal models, such as the combined chemical/hydraulic signalling hypothesis of Tardieu et al. (1993) described in an earlier part of the discussion chapter and the Sperry (1998) model which explicitly models xylem embolism over a series of spatially explicit xylem segments, while assuming that stomata act to maintain maximum evapotranspiration rates.

6.2.5 Data Assimilation

In any study which attempts to compare a model to several different data sets at different temporal and spatial scales, difficulties are encountered in assigning confidence in the overall model, and in determining the uncertainty in the state of the system resulting from the combination of both data and model results. In particular, the effects of uncertainty in parameters and verification data are difficult to reconcile. In addition, the comparison with different data sets may yield different conclusions about model certainty. In the absence of a technique for weighting the contribution of different data sets to the testing of the whole model, it is not clear how conclusions of different verification data sets should be interpreted. One solution to these problems is the data assimilation technique. Data assimilation is a set of statistical techniques designed to deal with the issues described
here. One data assimilation technique, the ensemble Kalman filter (Evenson, 1994) employs an array of many model runs, parameterised within the confidence limits of the input data. This generates confidence limits around to the model predictions, which are compared to the confidence limits around the verification data. In this way, the degree of agreement between the model and data may be analysed and a best guess of the true state of the system achieved. The Kalman filter requires that models are expressed as transition matrices acting on state variables. The method of conversion of the SPA model to a matrix is not yet clear, but the data assimilation method may provide a better means than presented here of comparing model predictions and multiple data sets at varying temporal and spatial scales.

6.2.6 Effects of phenology and allocation

The modelling approach presented in this paper allows us to predict the effect of hydraulic stress on GPP in a fully mechanistic manner, a methodology which has not previously been available. However, this prediction of GPP does not lead, in itself, to predictions of the carbon storage of ecosystems, the growth of trees, or the conversion between different sorts of vegetation. The leaf area and rooting biomass are strictly inputs of the SPA model framework, not outputs. It is intended that the GPP model acts as an input to other models which may generate phenological changes. In order to determine the proportions of photosynthate which are assigned to different fates by the plant, an allocation model is required, which uses a set of empirical parameterisations to determine where the photosynthate should go. The underlying empirical nature of the majority of allocations is problematic, if the intention is to construct models for extrapolation into the future, and where empirical datasets do not exist. A mechanistic approach with a similar philosophical basis would be ideal. For example, Magnani, Mencuccini and Grace (2000) proposed a model whereby allocation to different plant organs (roots, leaves, stem) was determined to maintain functional homeostasis in the plant. To avoid excessive hydraulic limitation, the plant will develop root and stem material at a rate sufficient to maintain water potentials within ‘safe’ limits to prevent excessive stomatal closure, and when hydraulic stress is absent, greater allocation to leaves will result. The model is optimised so that maximum leaf area is produced within this safe limit. Coupling with an optimal allocation model such as this may provide a feasible means by which to integrate the SPA model with dynamic vegetation modelling techniques.
6.2.7 Anisohydric behaviour

The SPA model only applies to isohydric plants, and would require integration of additional regulation mechanisms (i.e. response to chemical signals) to explain the behaviour of anisohydric species. This must be noted for future applications in other drought stressed ecosystems. It would be helpful if some index of isohydric and an-isohydric species could be developed but on the strength of the existing quantity of data available, this does not seem very likely. Establishment of isohydric behaviour is labour intensive, as leaf water potential measurements must be taken repeatedly throughout the course of a day to establish the persistence of a plateau in leaf water potential. This study is the only one of which we know which has measured leaf water potential at suitable temporal frequency. Further meteorological data is required to establish that decreasing patterns atmospheric demand did not artificially cause a plateau in leaf water potential. Ideally, measurements should be taken throughout the dry season, to establish that the minimum leaf water potential is consistent (this was not possible in this study). Canopy access is also an issue for this technique, as frequent access to large numbers of trees must be facilitated. In this study, canopy access towers were used, which limited leaf access to a small sample of trees. Leaf shooting techniques are more flexible, but do not allow accurate estimates of height to be taken (a critical factor in leaf water potential measurements). Current developments in rope based canopy access techniques may facilitate access to substantially larger numbers of tree individuals without the need for the complex logistics of tower installation. This could provide another means of verifying the central hypothesis of the SPA model.

6.2.8 Use of light aircraft technology to investigate drought in Amazonia

The work in this thesis has supplied a 'bottom up' mechanism by which to predict drought stress in rain forest ecosystems. However, 'top down' measurements will arguably be necessary if further verification is required. The problem with top down measurements is that they are spatially limited by the need to establish either eddy covariance towers or sap flow measuring systems. Current measurement sites are limited by funding availability, access and logistical considerations and therefore are not necessarily located in the sites of greatest scientific interest. Replication is very low and the time taken to establish measurements (several years) means that it is not possible to measure areas thought to be experiencing short term drought stress. A solution to this limitation may be to employ
small environmental research aircraft (SERA's), (Hacke and Schwerdtfeger, 1997) with on board eddy covariance technology. These systems can record diurnal cycles of water and carbon dioxide fluxes over large spatial scales, and are therefore ideally suited to rainforest environments, where continuous forest is the normal situation. These platforms are not appropriate for measuring the annual carbon dioxide budget of a rain forest ecosystem. However, a single day of flight over a forest in both the dry and wet seasons could, in tandem with meteorological data, indicate the existence or otherwise of drought stress. Since, at present, we do not know the extent of drought limitation for more than four or five sites in Amazonia, this methodology, combined with ground truthing of root soil and leaf area index properties, could substantially improve our understanding of forest drought resilience.

6.3 Concluding Remarks

The Amazon basin appears to be at risk from a drying climate and a reduction in the viability of the rain forest ecosystem. The loss of the Amazon rain forest, for both the climate system and for humanity, would bear an enormous cost, not only in terms of the reduced size of the carbon sink, but also in terms of biodiversity, landscape and culture.

In this thesis, we have found that rooting depths in the field are much greater than those initially supposed vegetation models, including the Hadley Centre MOSES model, the predictions of which provided the main impetus for the study. The forest therefore potentially has much greater resilience to dry periods than initially supposed. So it may be the case that the forest may be able to withstand a modest reduction in rainfall with no direct effect on growth or gas exchange. There are, however, three sets of caveats to this broad conclusion. Firstly, the forest properties we have identified as the key controls over resilience to drought, soil hydraulics and rooting depth, are exceptionally poorly documented for the whole Amazon region. The likelihood that these properties are highly heterogenous means that a uniform response of the whole basin is unlikely. Areas of forest vulnerable to drought may set up local feedbacks resulting in regionally reduced precipitation, which may cause the whole basin to shift towards a drier state. Secondly, there is a need to consider the impact of processes outwith the scope of this study. For example, changes in rainfall rates may not impact on forest gas exchange due to high water storage capacity, but they may have an effect on water table depths, seasonally flooded forests and evaporation rates from standing water. There is therefore a pressing need
to understand the integration of the atmospheric, biological and hydraulics systems at a larger scale than considered here before some predictions of the fate of the Amazon basin can be determined. Thirdly, the model predictions indicated that, under conditions equal to a \( \sim 30\% \) decline in rainfall, rainforest became unviable due to the basic disequilibrium between supply and demand of water. This is in-between the reduction predicted by 2100 by Cox et al. (2004) and Betts et al. (2004) with or without the interaction of vegetation in the climate system. This scenarios is not extreme, and it is highly possible that it will come about in the next 100 years, irrespective of the ability of rainforest ecosystems to store water to last through the dry season.

Climate change discussions are increasingly influenced by the idea of 'thresholds' - degrees of climate change beyond which systems become at risk. In this thesis, we have provided a mechanism by which such thresholds of forest tolerance may be interrogated. This is a substantial increase in our level of understanding. The new information acquired must now be integrated into larger scale simulations to allow detailed investigations of the regional scale biosphere-atmosphere feedback, thus enabling determination of the risk of forest collapse under future drier climate scenarios.

6.4 References


180


