

IUFRO

# CANOPY PROCESSES 2006 Regional Forest Responses to Environmental Change

A Traveling Workshop October 6-13, 2006







#### Sponsors:

International Union of Forest Research Organizations, Canopy Processes Working GroupBartlett Experimental ForestBlack Rock Forest ConsortiumBoston UniversityHarvard Forest, Harvard UniversityNational Science FoundationNortheastern Ecosystem Research CooperativeUSDA Forest Service, Northeastern Research Station

#### **Regional Forest Responses to Environmental Change** A Traveling Workshop

The goal of the meeting is to compare, contrast, and synthesize research on regional forest responses to environmental change. How environmental change impacts forests at the regional scale is a question of intense current interest, for both fundamental and applied reasons: *Regions* are defined both as natural biogeographic units that exhibit some degree of uniform response to environmental change, and political units that are critical for issues like carbon accounting and water resources. Yet, many questions remain as to the magnitudes and causes of regional forest change in this region and other regions of the globe, because of complexity of scaling the structure, function, and environmental response of forests from leaves to landscapes. This workshop focuses on assessing the state of knowledge of the tools and experiments needed to predict regional responses of forests to global and regional environmental change.

Scientific presentations are interspersed with visits to Bartlett Experimental forest in the White Mountains, New Hampshire; Harvard Forest in Massachusetts; and Black Rock Forest in the Hudson River Valley, New York. Selected papers from the meeting will be published in a special issue of an appropriate peer-reviewed journal.

### **Organizing Committee:**

Nathan Phillips, Boston University, coordinator Chris Beadle, CSIRO - ENSYS Sharon Billings, University of Kansas Jiquan Chen, University of Toledo Kevin Griffin, Columbia University Julian Hadley, Harvard Forest, Harvard University Jim Lewis, Fordham University Scott Ollinger, University of New Hampshire Mike Ryan, USDA Forest Service Marie-Louise Smith, USDA Forest Service



## Regional Forest Responses to Environmental Change October 6-13, 2006

# SOME IMPORTANT AND USEFUL INFORMATION

Welcome to the northeastern United States! This document contains some important and useful information, which we hope will make your stay comfortable and pleasant. Please take the time to read it.

# Registration

Pick up your registration packet and name tag at the designated reception area at the New England Center (Durham, NH) on October 6, between 1700 and 2300. Your packet will contain:

**Program Booklet** (General information, Program at a Glance, Program, Abstracts, Keynote Biographies, Participant Addresses, and Handouts for Field Trips)

**Other Material:** Maps of Massachusetts, New Hampshire, and New York; Excerpted material on natural history of northeastern forests; Participant List, and Meeting Evaluation Form. Material specific to each field trip will be provided as separate handouts on the Oct. 7<sup>th</sup>, 10<sup>th</sup>, and 11<sup>th</sup>.

Tickets for Drinks at the New England Center Reception

#### **Room Assignments**

**Field Trip Groups** for field trips on the 7<sup>th</sup>, 10<sup>th</sup>, and 11<sup>th</sup>. **Last names beginning with A through McCarthy form group 1; from Medhurst through Z form group 2.** If you need to switch, please find someone to switch with you, in order to maintain balanced group sizes.

# **Registration Fee**

The Registration Fee, which you have already paid, covers the following:

- Attendance at all sessions
- Workshop handouts
- Special Issue of Tree Physiology from the Workshop
- Accomodation and meals from the Reception on Friday, October 6 to breakfast on Friday, October 13
- Transport to and from Boston Logan or NY area airports on October 6 and 13.
- Field trips to Bartlett Experimental Forest, Harvard Forest, and Black Rock Forest
- Transportation between venues

# **Traveling Between Venues**

Please make sure your bags have identification, and have them ready early.

## Venues

In **Durham, New Hampshire**, all participants will be staying at the **New England Center**, located on the campus of the University of New Hampshire.

New England Center 15 Strafford Avenue University of New Hampshire Durham, New Hampshire 03824 603-862-0545 www.newenglandcenter.com

In **Petersham, Massachusetts**, some participants will be staying at the **Clamber Inn** and the **Winterwood Inn**, which are 2 and 3 miles, respectively, from our meeting site at Harvard Forest. Transport by van to and from Harvard Forest and these inns will be provided as needed. Many participants will be staying in one of several group housing facilities on Harvard Forest (Community House, Fisher House, Lyford House, Raup House).

#### **Harvard Forest**

324 North Main Street Petersham, MA 01366 (978) 724-3302 http://harvardforest.fas.harvard.edu/index.html

#### The Inn at Clamber Hill

111 North Main St. Petersham, MA 01366 978-724-8800 www.clamberhill.com

#### Winterwood Inn

19 N Main St PO Box 176 Petersham, MA 01366 978-724-8885 http://www.winterwoodinn.net/index.htm

In **Black Rock Forest**, New York, some participants will stay at the Fort Montgomery Holiday Inn Express, located 9.4 miles from Black Rock Forest. Vans will transport these participants between the Holiday Inn and Black Rock Forest as needed. Forest Lodge/Stone House are at Black Rock.

Holiday Inn Express, Fort Montgomery 1106 Route 9W Fort Montgomery, NY 10922 845-4464277 <u>www.ichotelsgroup.com/h/d/hi/1/en/hd/ftmny</u>

# **Room Assignments**

Room assignments have been made based on payments made at the following three levels as previously posted at <u>http://people.bu.edu/nathan/iufro\_info.htm</u>. If you believe an error was made in your room assignment based on your payment level, please contact Nathan Phillips immediately.

Venue	Low	Medium	High				
New England	Shared	Single at	Single at New England Center				
Center, Durham,	double at	New England	(www.newenglandcenter.com)				
New Hampshire	New England	Center					
	Center						
Harvard Forest,	Shared	Shared	Single at the Inn at Clamber Hill				
Massachusetts	double or	double, on-	(clamberhill.com) or Winterwood Inn				
	triple, on-site	site	(www.lanierbb.com/inns/bb7325.html)				
Black Rock	Multiple	Multiple	Single at Holiday Inn Express				
Forest, NY	occupant	occupant	(www.ichotelsgroup.com/h/d/hi/1/en/hd/ftmny)				
	dorm	dorm					
Fee	\$1475	\$1595	$(1895)^{1}$				
	$(\$1375)^1$	$(\$1495)^1$					
<sup>1</sup> Fees if payment is received by <b>June 30, 2006</b> .							

#### 1. Durham, New Hampshire

**New England Center**. Note: Room Number designated here will be different from the actual hotel room number. Your hotel room number will be provided on arrival to the New England Center.

Room# (#beds)	Occupants
#1 (2)	Alexander Olchev, John Bradford
#2 (2)	Diane Pataki, Sung Bae Jeon
#3 (2)	Jane Medhurst, Minna Pullkinen
#4 (2)	Remko Duursma, Qingling Zhang
#5 (2)	Julian Hadley
#6 (2)	Nathan Phillips, Mike Daley
#7 (2)	Georgianne Moore
#8 (2)	Sonia Wharton, Danielle Way
#9 (2)	Kristine Crous, Heather McCarthy
#10 (2)	Maurizio Mencuccini, Jose L Stape
#11 (2)	Frank Sterck, Matthias Peichl
#12 (2)	Sampo Smolander
#13 (2)	Louis Iverson, Jim Lewis
#14 (2)	Qingmin Han, Darius Culvenor
#15 (2)	Roman Zweifel, Abe Miller-Rushing
#16 (2)	Matthew Turnbull, Kevin Griffin
#17 (1)	Cory Pettijohn/Trish Pettijohn
#18 (1)	Tony O'Grady, Marrti Peramaki
#19 (1)	Jiquan Chen
#20 (1)	Rodney Foster
#21 (1)	David Ellsworth
#22 (1)	Yukihiro Chiba
#23 (1)	Barry Logan
#24 (1)	David Clark
#25 (1)	Michael Ryan
#26 (1)	David Whitehead
#27 (1)	James Cleverly
#28 (1)	Satoshi Kitaoka
#29 (1)	John Butnor
#30 (1)	Jenny Carter
#31 (1)	Olevi Kull
#32 (1)	Ingo Ensminger
#33 (1)	Brent Ewers

**2. Petersham, Massachusetts.** Note: At Raup, Lyford, Fisher, and Community House, name tags will be posted on room doors so that you can find your room. At Clamber and Winterwood, the host will show you to your room.

Building	Room# (#beds)	Occupants
Raup House	#1 (1)	S. Billings
•	#2 (4)	D. Pataki, S. Wharton
	#3 (2)	M. Pullkinen
	#4 (3)	K. Crous, H. McCarthy
	#5 (1)	Jane Medhurst
Lyford House	#1 (1)	O. Kull
	#2 (1)	J. Chen
	#3 (1)	R. Foster
	#4 (1)	F. Sterck
	#5 (1)	D. Ellsworth
Fisher House (floor 1)	#1 (1Q)	J. Medhurst/ A. O'Grady
	#2 (1)	Q. Han
	#3 (1)	L. Iverson
	#4 (1)	D. Way
Fisher House (floor 2)	#5 (3)	R. MacLean, A. Olchev, J. Bradford
	#6 (3)	D. Culvenor, D. Hollinger
	#7 (3)	J. Lewis, M. Peramaki
	#8 (1)	M. Peichl
	#9 (1)	S. Smolander
	#10(1)	B. Ewers
	#11 (1)	R. Zweifel
	#12 (1)	I. Ensminger
	#14 (2)	J. Carter, G. Moore
	#15 (3)	D. Tissue, B. Logan
Community House	#1 (3)	N. Phillips, C. Pettijohn, Q. Zhang
	#3 (1)	E. Traister
	#4 (1)	E. Cate
	#5 (3)	M. Daley, A. Miller-Rushing, Q. Thomas
	#6 (1)	S. Jeon
Clamber Inn	#1 (1)	D. Clark
	#2 (1)	M. Ryan
	#3 (1)	Y. Chiba
	#4 (1)	M.L. Smith
Winterwood Inn	#1(2)	D. Whitehead/ M. Mencuccini
	#2 (1)	J. Cleverly
	#3 (1)	S. Kitaoka, R. Duursma
	#4 (1)	J. Butnor
	#5 (2)	K. Griffin, M. Turnbull
	#6 (2)	J.L. Stape, P. Megonigal

Building	Room#	Occupants
Forest Lodge	(#Deus)	I Engminger P Zwiefel
Porest Louge	$\frac{\#1}{3}$	D. Datahi I. Cantan M. Dulllin an I. Madhumat
	#2 (4)	D. Pataki, J. Carter, M. Pulikinen, J. Mednurst
	#3 (4)	P. Megonigal, R. Duursma, J. Hadley, K. Griffin
	#4 (4)	JL Stape, F. Sterck, B. Ewers, J. Bradford
	#5 (3)	G. Moore, D. Way, H. McCarthy
	#6 (4)	Q. Han, D. Culvenor, L. Iverson, R. MacLean
	#7 (4)	J. Lewis, S. Smolander, A. Olchev
	#8 (3)	M. Peichl, Y. Chiba, R. Foster
	#9 (3)	M. Turnbull, S. Kitaoka, D. Tissue
	#10 (3)	A. O'Grady, M. Peramaki
Stone House	#1 (6)	N. Phillips, M. Daley, C. Pettijohn, Q. Zhang, A
		Miller-Rushing, Q. Thomas
	#2 (4)	E. Cate, S. Wharton, S. Jeon, E. Triaster
Holiday Inn	#1(1)	M. Ryan
	#2(1)	J. Cleverly
	#3 (1)	J. Butnor
	#4 (1)	D. Clark
	#5 (1)	O. Kull
	#6 (1)	D. Whithead
	#7 (1)	M. Mencuccini (day 1 only)

#### 3. Black Rock Forest, Cornwall-on-Hudson, New York

# Meals

Meal and break times are in the program. Breakfast is from 0700 - 0800. On Saturday the 7<sup>th</sup> Breakfast and Lunch will be in boxes that you should pick up from the lobby at 06:45, prior to boarding the bus at 07:00 for our field trip to Bartlett Experimental Forest. On Friday Oct. 13<sup>th</sup> breakfast will be 'rolling' to facilitate varying departure time needs. Lunches will generally be from 12:30 – 13:30. On Saturday the 7<sup>th</sup>, make sure to pick up your boxed lunch prior to departure on the Bartlett Field Trip. On Saturday the 7<sup>th</sup>, we will have boxed lunches from 13:00 – 13:30. On Wednesday, October 11, make sure to pick up a boxed lunch prior to departure to Black Rock Forest. These lunches can be eaten on the bus whenever you'd like. Dinner times are variable; consult the program for specific dates and dinner times.

# Time

New Hampshire, Massachusetts and New York are on Eastern Standard Time, GMT – 4.

# **Posters and Poster Presentations**

There will be 11 poster stations per session at Harvard Forest on Monday, October 9, and 12 poster stations at Black Rock Forest on Thursday, October 12. Poster presenters should have their posters up before the start of the session. This means that those in session A can put them up over the lunch break and will need to remove them immediately after the session, and those in session B will need to put them up during the break. We will have ~5 minute 'formal' presentations at each poster every 15 minutes during the session. Questions and discussion will take up the rest of the 15 minutes. Those not presenting please distribute yourselves so there are no more than 5-6 people per poster for each presentation, and please move to your next station when the bell rings!

# **Oral Presentations**

Oral presentations will have 20 minutes for presentation and questions. Keynote presentations will have 50 minutes for presentation and 10 minutes for question and discussion. The schedule will be strictly followed. We will have computer projectors, and an IBM laptop computer for powerpoint or pdf files. Please bring talks on USB memory or on CD/DVD. Because potential incompatibility problems cause program delays, YOU WILL NOT BE ALLOWED TO PLUG IN YOUR COMPUTER TO THE PROJECTOR. Please see your session moderator <sup>1</sup>/<sub>2</sub> hour before the session starts to give her/him your files.

# Publication of papers as a Special Issue of *Tree Physiology*

The Editor of *Tree Physiology* has agreed to the publication of papers resulting from this workshop in a Special Issue of the journal. David Whitehead will lead an editorial group appointed by the

organisers of the workshop to oversee the publication process. To enable us to work towards a publication date by late 2007, we will need to keep to strict deadlines

- 1. To register your intention to submit a paper to be considered for publication, send your provisional title and brief abstract of the content to David Whitehead at by **31 October 2006**. Please indicate if you intend to include colour images in your paper.
- 2. Full papers should be sent to David Whitehead before **1 February 2007**. This will be a strict deadline to avoid delays in publication. Please send your paper by e-mail in pdf format.
- 3. Papers must be prepared in accordance with *Tree Physiology*'s guide for contributors that can be found at <a href="http://heronpublishing.com/tpguide.html">http://heronpublishing.com/tpguide.html</a>
- 4. The editorial group retains the right to refuse manuscripts that are not formatted correctly or do not align with the themes of the workshop. If the number of contributed manuscripts exceeds the limits for an issue of the journal then selection of papers will be at the discretion of the editorial group. Papers will be screened by the editorial group and authors whose papers do not meet the specifications will be informed by **1 March 2007**.
- 5. Selected papers will be put through the regular journal review process, with comments requested from at least two reviewers. Manuscripts and comments will be sent to authors as soon as they are received.
- 6. Following revision, papers that are judged acceptable for publication by the editorial group will be sent to the Editor of *Tree Physiology* for consideration for final acceptance.

For further information, contact

David Whitehead Landcare Research Gerald Street, PO Box 40 Lincoln 7640 New Zealand Tel: +64 3 321 9862 Fax: +64 3 321 9998 e-mail: whitehead@landcareresearch.co.nz

## **Workshop Committee**

Nathan Phillips, Boston University, Coordinator Sharon Billings, University of Kansas Chris Beadle, CSIRO-ENSIS Jiquan Chen, University of Toledo Kevin Griffin, Columbia University Julian Hadley, Harvard Forest, Harvard University Jim Lewis, Fordham University Scott Ollinger, University of New Hampshire Mike Ryan, USDA Forest Service Marie-Louise Smith, USDA Forest Service

# Sponsors

- International Union of Forest Research Organizations (IUFRO) Canopy Processes Working Group, S 2.01.12
- Bartlett Experimental Forest and USDA Forest Service, Northeastern Research Station
- Black Rock Forest Consortium
- Boston University
- Harvard Forest, Harvard University
- National Science Foundation
- Northeastern Ecosystem Research Cooperative
- University of New Hampshire

# **Program Cover Photo Credits**

Thanks to John O'Keefe and David Lee

Friday	13-04		president (	and	departures	I							pepartures																						
Thursday	12-04			Breakfast			Oral	Session 4		Tools and	Physiology				Lunch		Poster	Session 2								Dinner		Keyerote	Address						
Wed	11-Oot			Breakfast		Travel to	BlackRock	Forest							lunch on site		BlackRock	Forest	Pield	Trip							Dimmer								
Tuesday	100-01-			Breakfast			putoutoje	Forest	F bid	Trips					L unch			Option	Session 3		Remote	Sensing				Dinner									
Monday	5-O4			Breakfast			001	Session 2		Forest	Structure,	Function,	Composition		runch U		Poster	Session	10		Poster	Session	æ			Dinner				sseup ne	meding				
Sunday	8-0d			Breakfast			Oral	Session 1		Regional	Carbon	Pools,	Fluxes,	Allecation	Lunch			Travelto	Hervard	Forest								000	Dinner and	Checklin					
500	7-04			Burtlett	Field Trip		(includes	breakfast	on bus	and lunch	at Bartlett)													Dinner	at Eagle	Mountain	House		Return to	Durham	Ŧ				
Fri	6-00t																			Registration								Evening	micre						
		Time	630	700	730	880	808	906	800	1000	1030	1100	1130	1200	1230	1300	1330	1400	1430	1500	1520	1600	150	1700	1730	1800	1830	1900	1830	2000	2020	2,100	2130	2200	2200

# Schedule at a Glance

# Program: Fri. Oct. 6 – Fri. Oct 13, 2006

#### Friday, October 6, 2006, Durham, NH

- 1200 2200 Registration, New England Center, University of New Hampshire, Durham
  1000 – 2200 Registration and Minute
- 1900 2200 Reception and Mixer

#### Saturday, October 7, 2006, Durham, NH

- 0700 12:00Travel to Bartlett Exp. Forest (boxed breakfast on bus)12:30-16:00Tour#1 of field research sites (group A)<br/>Tour#2 of field research sites (group B)<br/>Lunch17:00-19:00Dinner at Eagle Mountain House, Jackson, NH
- **19:30 22:00 Return to Durham**

#### Sunday, October 8, 2006, Durham, NH, traveling to Harvard Forest

0700 - 0800	Breakfast
0830 - 1210	Oral Session #1, New England Center Moderator: Phillips
	Subtheme: Regional Carbon Pools, Fluxes, and Allocation
0830 - 0930	<b>Keynote Address: David Hollinger</b> . New frontiers in understanding canopy processes at the regional level and beyond: Eddy covariance
	data, model parameter estimation, and data assimilation.
0930 - 0950	Talk #1: <b>John Bradford</b> : Spatial variability of carbon pools and fluxes: consequences for landscape-level estimates
0950-1010	Talk #2: <b>Minna Pulkkinen</b> : Developing an empirical model of GPP
	with LUE approach: results from an analysis of eddy covariance data at
	five contrasting sites in Europe
1010-1030	Break
1030-1050	Talk#3: <b>David Clark</b> : Landscape-scale leaf area distribution across a tropical rain forest land-use gradient
1050-1110	Talk#4: Mike Ryan: Carbon Allocation in Forest Ecosystems
1110-1210	<b>Keynote Address: Scott Ollinger</b> Effects of multiple environmental stressors on northeastern forest carbon and nitrogen dynamics.
1230-1330	Lunch
14:00-18:30	Travel to Harvard Forest
19:00 - 21:00	Check-in and BBQ dinner at Harvard Forest

#### Monday, October 9, 2006, Harvard Forest

0700 - 0800	Breakfast
0830 - 1210	Oral Session #2, <i>Moderator:</i> Julian Hadley Subtheme: Forest
	Structure, Function, Composition, and Environmental Change
0830 - 0930	Keynote Address: Maurizio Mencuccini: The Carbon Cycle of Forest
	Chronosequences
0930 - 0950	Talk#1: Julian Hadley: Differences in carbon/water cycling between
	early-successional deciduous forest and late-successional conifer forests:
	Implications for long-term effects of invasive hemlock woolly adelgid
0950 - 1010	Talk#2: : Louis Iverson: Regional modeling of potential effects of
	climate change on tree species habitats
1010 - 1030	Break
1030 - 1050	Talk#3: Matthias Peichl: Carbon and water fluxes in a temperate pine
	forest chronosequence during a warm, dry summer in southern Ontario,
1050 1110	
1050 - 1110	Talk#4: Sonia Wharton: The Impact of Water Stress on Net Carbon
1110 1010	Exchange at the Wind River Old-growth Forest, Washington, USA
1110 - 1210	<b>Keynote Address: Jose Luiz Stape</b> Landscape-scale studies of
	plot level studies
1230 1330	Junch
1230 - 1330	
1330 - 1500	Poster Session #1A, Harvard Forest, <i>Moderator:</i> Mike Ryan
	1245 1400 1415 1420 and 1445 Quantians and discussion will take
	1345, 1400, 1415, 1430, and 1445. Questions and discussion will take
	vourselves so there are no more than 5.6 people per poster for each
	presentation and <i>please</i> move to your next station when the hell rings
Station 1	Sharon Billings: Dendrochronological indicators of northern red oak
Station	suscentibility to red oak horer
Station 2	Abraham Miller-Rushing: Effects of winter temperatures on flowering
~ ~ ~ ~ ~	times in birch trees
Station 3	Jane Medhurst: Spring photosynthetic recovery of boreal Norway
	spruce at the shoot- and tree-level under conditions of elevated $[CO_2]$
	and air temperature
Station 4	Barry Logan: Physiological impacts of eastern dwarf infection and
	developmental responses of host white spruce
Station 5	Satoshi Kitaoka: Seasonal changes of photosynthetic production of
	larch plantation in Northern Japan
Station 6	Kevin Griffin: Seasonal variation in the temperature response of leaf
~ -	respiration in <i>Quercus rubra</i> at the Black Rock Forest
Station 7	Ingo Ensminger: Spring recovery of photosynthesis in conifers is
Station 0	modulated by soil temperature and intermittent frost
Station 8	Jennier Carter: water use of an agrotorestry system measured at
Station 0	Oingmin Hon: Effect of loof ago on seasonal variability of
Station 9	<b>Vinghin Han</b> . Effect of leaf age on seasonal variability of

	photosynthesis parameters and leaf nitrogen within a <i>Pinus densiflora</i> crown
Station 10	Kristine Crous: Nutrient and CO2 Interactions in Tree Photosynthesis
Station 11	<b>Pamela Templer:</b> Effect of calcium availability on nitrogen uptake by sugar maple and beech trees
Station 12	<b>Vikki Rodgers:</b> Impacts of <i>Alliaria petiolata</i> invasion on nutrient
	cycling and native plant diversity in southern New England forests
1500 - 1530	Break
1530 - 1700	Poster Session #1B, Harvard Forest, <i>Moderator:</i> Sharon Billings
	Presenters will give a 5-10 minute overview of their poster at 1530,
	1545, 1600, 1615, 1630, and 1645. Questions and discussion will take
	up the rest of the 15 minutes. Those not presenting please distribute
	yourselves so there are no more than 5-6 people per poster for each
	presentation, and <i>please</i> move to your next station when the bell rings!
Station 1	Jiquan Chen: Ecosystem Water Use of Forests - A New Concept for
~	Understanding C&H2O Cycles
Station 2	David Whitehead: Environmental regulation of ecosystem carbon
	exchange and water balance in a mature rainforest in New Zealand
Station 3	Frank Sterck: Scaling up water relations in trees: Can we predict
Q4-4: 4	drought responses from underlying mechanisms and traits?
Station 4	<b>Roman Zweifel</b> : Species-specific stomatal response of trees to
	dynamics
Station 5	uynamics Nothen Dhilling: Nocturnal Transpiration in Norway Spruce Tracs is
Station 5	Consistent with the Nutrient Supply Hypothesis
Station 6	Corv Pettijohn: A comparison of long-term irrigated and non-irrigated
Station	red maple transpiration
Station 7	Anthony O'Grady. Constraints on transpiration in irrigated and rainfed
Station /	<i>Eucalyptus globulus</i> trees in southern Tasmania
Station 8	<b>Georgianne Moore</b> : Nocturnal transpiration in <i>Tamarix</i> : A mechanism
	for temporal incongruence between sapflow and eddy covariance
Station 9	Brent Ewers: Quantifying Spatial Patterns of Transpiration across
	Environmental Gradients using Plant Hydraulics and Geostatistics
Station 10	James Cleverly: A long-term, regional flux network for evaluating
	climate, canopy processes, and evapotranspiration along the Mid Rio
	Grande, NM
Station 11	David Ellsworth: Acclimation to light in a pine canopy under long-term
	elevated atmospheric CO <sub>2</sub>
1800 - 2000	Dinner
2000 - 2100	IUFRO Canopy Processes S2.01.12 Business Meeting

#### Tuesday, October 10, 2006, Harvard Forest

0700 - 0800	Breakfast
0830 - 1230	Tours of Harvard Forest research sites
1245 - 1345	Lunch
14:00-17:30	<b>Oral Session #3,</b> <i>Moderator:</i> <b>ML Smith Subtheme: Remote sensing</b> of Forest Structure and Function
1400 - 1500	<b>Keynote Address: Darius Culvenor</b> Advances in remote sensing for forest structure assessment
1500 - 1520	Talk#1: <b>Sampo Smolander</b> : Current state of canopy spectral invariants in remote sensing
1520 - 1540	Talk#2: <b>John Butnor</b> : Estimating Decay Volumes in Living Trees with Ground-Penetrating Radar
1540 - 1610	Break
1610 - 1630	Talk#3: <b>Olevi Kull</b> : Reflection of Experimental Drought and Warming at European Shrublands
1630 - 1650	Talk#4: <b>Qingling Zhang</b> : From Landscape Snapshots to Regional Portraits of Forest Change: Extending Traditional Remote Sensing Analyses
1650 - 1710	Talk#5: <b>Alexander Olchev</b> : Responses of CO2 and H2O fluxes on land- use change in a tropical rain forest margin area in Central Sulawesi (Indonesia)
1710 - 1730	Talk#6: <b>Sung Bae Jeon</b> : The Effects of Land-use Change on the Terrestrial Carbon Budgets of New England
1800 - 2000	Dinner

# Wednesday, October 11, 2006, Harvard Forest, traveling to Black Rock Forest

0700 - 0800	Breakfast
0800 - 1330	Travel to Black Rock Forest Includes bagged lunch en route
14:00-18:00	Tour Black Rock research sites
18:30-20:00	Dinner

#### Thursday, October 12, 2006, Black Rock Forest

0700 - 0800	Breakfast
0830 - 1140	Oral Session #4, <i>Moderator:</i> Jim Lewis Subtheme: Tools and Physiological Responses to Environmental Change
0830 - 0930	Keynote Address: <b>Diane Pataki</b> The isotopic composition of forest canopies: New issues and applications
0930 - 0950	Talk#1: <b>Andrew Martin</b> : Response of Tsuga canadensis photosynthetic rate to changes in temperature and N-form
0950 - 1010	Talk#2: <b>TBA</b>
1010 - 1040	Break
1040 - 1100	Talk#3: Matthew Turnbull: Thermal Acclimation of Leaf Photosynthesis and Respiration in Populus Deltoides x Nigra
1100 - 1120	Talk#4: <b>Danielle Way</b> : High growth temperatures reduce photosynthesis, respiration and growth in black spruce
1120 - 1140	<i>Talk#5:</i> <b>Heather McCarthy</b> : Interaction of ice storms and management practices on current carbon sequestration in forests with potential mitigation under future CO2 atmosphere
1230 - 1330	Lunch
1330 - 1530	Poster Session #2, Moderator: Kevin Griffin
	Presenters will give a 5-10 minute overview of their poster at 1330, 1345, 1400, 1415, 1430, 1445, and 1500. Questions and discussion will take up the rest of the 15 minutes. Those not presenting please distribute
	yourselves so there are no more than 5-6 people per poster for each presentation, and <i>plagsa</i> move to your next station when the bell rings!
Station 1	<b>Jim Lewis</b> : Indirect effects of the hemlock woolly adelgid on oak seedling growth through effects on mycorrhizal richness and abundance.
Station 2	<b>David Tissue</b> : Spatial and temporal scaling of intercellular CO2 concentration in a temperate rainforest dominated by <i>D. cupressinum</i> in New Zealand
Station 3	Abby Sirulnik: Infestations of hemlock woolly adelgid are associated with changes in eastern hemlock ectomycorrhizal fungal communities and soil conditions
Station 4	<b>L. Rubino</b> : Hemlock woolly adelgid density affects net photosynthetic rates but not respiration rates or needle biochemistry in eastern hemlock
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TBA Breakfast

TBABuses to NYC area airports or Boston Logan airport

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#### Dendrochronological indicators of northern red oak susceptibility to red oak borer

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Oak-dominated forests in northwestern Arkansas have recently experienced an unprecedented outbreak of an endemic insect, the red oak borer, Enaphalodes rufulus, that has induced significant oak mortality across much of the region. We used a suite of dendrochronological parameters to determine whether northern red oak (Ouercus rubra) most susceptible to E. rufulus attack experienced greater drought stress than apparently healthy trees. We sampled Q. rubra experiencing various levels of E. rufulus infestation from areas with distinct site quality differences and examined their tree rings from 1954 to 2002, a period encompassing four severe drought and three relatively wet periods. We hypothesized that  $\delta 13C$  of  $\alpha$ -cellulose from tree rings, intrinsic water use efficiency (Wi), basal area increment (BAI), ring-width indices, early- and latewood widths, and lignin concentrations would reveal evidence of drought stress in trees most heavily attacked by E. rufulus. Five decades prior to oak mortality induced by E. rufulus, growth measurements exhibit reduced BAI and earlywood widths in Q. rubra most heavily infested with E. rufulus. This suggests that the most heavily attacked trees, though dominant in the canopy and apparently never suppressed compared to their counterparts, were at a competitive disadvantage for a significant time period. Lignin concentrations revealed no significant trends with level of E. rufulus infestation, water availability, or site quality. Parameters describing tree water relations ( $\delta$ 13C and Wi) responded to drought prior to the 1970s; after this time, all study trees ceased exhibiting a response to drought via these parameters. This time period is also associated with an increase in E. rufulus activity in a nearby forest, which later induced significant oak mortality similar to that observed in the current study. Latewood widths were sensitive to water availability, but exhibited no trend with level of E. rufulus infestation. These data imply that drought stress may not have been a dominant factor governing Q. rubra susceptibility to E. rufulus attack, though we cannot be sure due to lost sensitivity of water use parameters in later study years.

# Developing a method to characterize the response of a mountainous ecosystem to variations in climate using stable carbon isotopes of respired CO<sub>2</sub> in nocturnal cold-air drainage

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At least 20% of the terrestrial surface of the earth is covered by mountains, which contain many of the world's most productive ecosystems. Do such mountainous ecosystems respond differently to climate change than flat ecosystems by virtue of their topography? There are many reasons to think they might; however, most of the tools used to measure and monitor metabolic processes in ecosystems are difficult or impossible to use in complex, mountainous terrain. In a project we call the "Andrews Airshed project", located in western Oregon Cascades, we are measuring the stable carbon isotope composition of ecosystem-respired  $CO_2(\delta^{13}C_{R-eco})$  in nocturnal cold-air drainage systems, with the eventual aim of "inverting" this understanding to monitor intra- and inter-annual responses of ecosystem metabolism to environmental variation on a basin scale. We are characterizing patterns of airflow, quantifying the CO<sub>2</sub> concentration in the flow, and measuring  $\delta^{13}C_{R-eco}$  as well as the fluxes and isotopic composition of respiration from soils and foliage. We have found that the characteristics of the cold air drainage system are nearly ideal for our sampling. Nocturnal air drainage from the basin is very well-mixed and deep, and the air samples we collect appear to contain a well-mixed sample from the entire basin. We estimate that up to 100% of nocturnally-respired CO<sub>2</sub> exits the 96 ha basin advectively. Weekly samples (June-Sept, 2005; May-Sept 2006) of  $\delta^{13}C_{R-eco}$  reveal more than 3 per mil variation seasonally; this variation was more closely associated with soil moisture depletion than with humidity, and unlike previous investigations we found no temporal lag between environmental conditions and  $\delta^{13}C_{R-eco}$ . This may be due, in part, to a larger contribution of foliage, rather than soil, to total ecosystem respiration in this ecosystem. Soil-respired CO<sub>2</sub> was isotopically enriched compared with above-ground air, and also enriched on the north-facing relative to the south-facing slope. Soil samples also reveal seasonal variability, but not to the same degree as the air samples. Analyses of isotopes in foliarrespired CO<sub>2</sub> are currently underway. Our results to date show that  $\delta^{13}C_{R-eco}$  can be measured with great precision and accuracy in cold-air drainage from a small, deeply-incised watershed, and that variations in  $\delta^{13}C_{R-eco}$  are a sensitive indicator of metabolic change on the basin-scale in response to environmental variation.

#### Spatial variability of carbon pools and fluxes: consequences for landscape-level estimates.

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Terrestrial ecosystems hold substantial carbon which may impact atmospheric carbon concentrations, potentially influencing climatic conditions. Consequently, quantifying carbon dynamics in forest systems at large scales is a central goal for ecosystem ecologists. Previous studies have characterized carbon pools and fluxes at plot scales, and other work has linked these estimates to remote sensing or simulation modeling efforts. However, few studies have quantified large-scale carbon pools and directly from plot measurements. This study addressed two questions: 1) How much do forest structure, carbon pools and fluxes vary across landscapes? and 2) How many plots are necessary to accurately characterize these processes over landscapes?

We established 36 nested plots (circular with 8-meter radius) in each of three subalpine rocky mountain forests. Within each plot, we quantified stand structure (height, leaf area index, basal area and density), carbon pools (aboveground live, aboveground dead, forest floor and mineral soil) and carbon fluxes (live biomass increment, litterfall, forest floor decomposition and net ecosystem carbon balance).

Our results indicate that stand structure displays the least variability whereas carbon fluxes display the most variability. These differences imply that stand structure requires the least effort to quantify (24 plots for 1 km2), carbon fluxes require the greatest effort (39 plots for 1 km2) and carbon pool require an intermediate sampling level (29 plots for 1 km<sup>2</sup>). These results suggest that characterizing carbon fluxes at landscape scales may require greater sampling intensity that traditionally used for forest inventories. In addition, we found that site history and vegetation structure influence the magnitude and scale of spatial variability and consequently impact the required sampling intensity and optimal spatial sampling design. These results have implications for numerous studies of regional to global scale carbon dynamics, which often rely on extremely limited field plots.

#### Estimating Decay Volumes in Living Trees with Ground-Penetrating Radar

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Decomposition by saprophytic organisms of wood in living tree stems contributes substantially to disease loss in U.S. forests, causing destruction or decreased value of usable timber and the depletion of carbon reserves in forest stands. Precise methods that predict rot volume are lacking. Estimating rot volume via external visual cues, (i.e. conks, broken branches, stem bulges, or stem discoloration) is often restricted to a certain species and site. Also, visual cues of rot in stems usually do not appear until the decay process is well underway. Our objective was to test and apply ground penetratingradar (GPR) to non-destructively estimate active and inactive rot volumes in living trees. GPR is a geophysical tool which uses an antenna to propagate short bursts of electromagnetic energy in solid materials and measure the two-way travel time and amplitude of the reflected signals. When the transmitted energy contacts a layer of material with different electromagnetic properties (i.e. resistivity) a portion of the energy is reflected back to the antenna and discriminated. For this study we used the Tree Radar Unit (TRU) and TreeWin software developed by TreeRadar Inc. (Silver Spring, MD). The TRU consists of a commercially available SIR-3000 radar unit and a specially configured 900 MHz antenna (GSSI, North Salem, NH). In March 2005, with the assistance of a USDA Forest Service, hazard tree felling crew, we selected 10 trees of three different species for evaluation, followed by destructive verification: Pseudotsuga menziesii, Thuja plicata, and Tsuga heterophylla. Prior to felling, the circumference of each tree bole was scanned at several heights with the TRU (0-2 m). Once on the ground, partial circumferential scans (~50%) were collected every 2 - 5m, depending on the length of the bole. Cross-sectional "cookies" were sawed from each scanned location. Each cookie was photographed to preserve any visual information, and two perpendicular strips were sampled from each cross-section. In the laboratory, specific gravity and water content were measured at regular intervals from bark to pith. Using TreeWin we estimated rot volume at each elevation and compared it to physical and photographic data. GPR successfully detected abrupt changes in moisture content caused by decay, voids and wetwood. We found that near-surface decay and air-filled voids had unique electromagnetic signatures, which could be separated from other defects. Detection of incipient decay was possible, but it was difficult to grade levels of decay. We are currently working to understand non-target detections of water gradients and wood density in healthy material and separate it from actual defects. This work should allow more precise estimation of rot volumes in forest ecosystems and enable better prediction of losses to harvestable timber and carbon reserves.

#### Water use of an agroforestry system measured at different spatial scales

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Following the clearing of deep-rooted native vegetation for agriculture in southern Australia, trees are now being planted back into the landscape in an attempt to control rising groundwater and protect against dryland salinity. We measured the water use of widely-spaced belts of Eucalyptus kochii trees and inter-bays of annual crop, as part of a project parameterising models of tree growth and water use to predict impacts on hydrology. Tree transpiration and response to the environment was measured by leaf gas exchange and heat pulse sap flow sensors, while crop and whole system evapotranspiration was measured through water balance calculations and with eddy covariance.

Eucalyptus kochii had high rates of transpiration, and stomata were relatively insensitive to vapour pressure deficit, particularly when trees had access to groundwater. On a projected canopy area basis, trees with access to groundwater had transpiration rates that were similar to Priestley-Taylor potential evapotranspiration, which was approximately five-fold greater than evapotranspiration of the annual crop. Trees without access to groundwater had transpiration rates approximately double that of the annual crop.

Despite these differences in water use of trees and crop, eddy covariance measurements did not detect differences between parts of the landscape where trees did or did not have access to groundwater, or even between the crop (or bare soil) alone and the crop plus the tree belts. This may have been partly due to the fact that tree belts only occupied 5% of the landscape, with annual crop occupying the remainder. In the part of the system where trees had access to groundwater this proportion of tree planting was sufficient to prevent recharge, with an increase in whole-system evapotranspiration of 25%. However, over the entire study area integrating trees with and without access to groundwater, the belts increased the whole-system evapotranspiration by less than 10%. These results demonstrate the need for multi-scale measurements of water use when designing agricultural system aimed at incorporating hydrological benefits.

#### Ecosystem Water Use of Forests - A New Concept for Understanding C&H2O Cycles

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Compared to ecosystem carbon exchange, the dynamics and controls of ecosystem water balance have received relatively less attention. Yet, these two fluxes are tightly interdependent, with water availability having a direct effect on the carbon budget. Using direct measurements (eddy flux towers) of net ecosystem exchange (NEE) of water and carbon from over several ecosystem types in North America, I examined the magnitude and rate of change in ecosystem water use (WUEe, defined as the mass ratio of NEE of carbon to NEE of water). In addition to constructing the empirical relationships for estimating WUEe that incorporate disturbance and stand age, as well as the biophysical regulations such as vapor pressure deficit (VPD), solar radiation, and soil moisture conditions, I will demonstrate the use of this new concept in understanding ecosystem water consumption and needs. WUEe varied little throughout the growing season (June through September) in both regions, but there were notable differences in WUe with stand age. In northern Wisconsin, WUe was higher in mature stands (4.5 mg C g H2O) than in the younger, recently disturbed stands (2.1 mg C g H2O); yet WUe was much higher in 20 and 40 year-old stands (0.34-5.57) than in a 450-year-old stand (0.38-1.59) in the Pacific Northwest. The lowest WUe was found in a recent clearcut, where leaf area index was also the lowest. VPD is found to be a significant predictor of WUe in many ecosystems. Given the broad network of eddy flux towers currently collecting NEE data across the United States (e.g., Fluxnet), we expect that in the future we will be able to make further generalizations about WUe in ecosystems of different ages and under various disturbance regimes.

#### **Reconstruction of Canopy Profile Using DBH and Tree Height**

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Forest stands respond to environmental changes through physiological processes: such as energy capture, carbon gain, and resource allocation. Canopy components of foliage and branches contribute to such physiological processes to a great extent, so that one should quantitatively describe the 3D distribution of a forest canopy to understand forest dynamics and productivity in relation to canopy and stand structure. However, it would be laborious and time-consuming to get through tree harvest and data processing for reconstructing canopy structure. The objective of this study is to develop a simple and useful method to reconstruct vertical distributions of individual tree crowns in a forest stand, and then a canopy profile of the stand by summing up all of the trees. Several architectural tree form models provided theoretical bases for developing a new method.

Vertical distribution of leaves of a forest tree would strongly depend on branching architecture, as is pointed out in the pipe model (Shinozaki et al. 1964, Chiba 1990). Thus tree trunks that consist of branches flowing into should be affected by stand density. Let the weight densities of leaves, branches, and stems at position z along the stem be  $\Gamma(z)$ , B(z) and S(z), respectively. The mutual relationship can be formulated as

 $dS/dz = 1/b (\Gamma(z) + B(z) + S(z)),$  (1) where *b* is a constant (Chiba 1991). Employing this equation, stem form can be modeled by a hyperbolic function with two asymptotes of exponential functions. Examining the parameters included in these equations as related to the stem form and crown architecture, strong interdependencies were found with tree size: i.e. DBH and tree height. Using the stem form model, therefore, the vertical profile of leaves and branches ( $\Gamma(z) + B(z)$ ) of an individual tree can be reconstructed in combination with Equation (1).

The interrelationships among tree height H, height at crown base HB, and diameter at breast height DBH can easily be expressed by empirical formulae whose parameters are specific to the stand. Employing these formulations mentioned above, it is possible to reconstruct canopy structure (or profile) representing the vertical distributions of leaves and branches in a forest stand as related with stand structure.

#### Landscape-scale leaf area distribution across a tropical rain forest land-use gradient

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Current estimates of tropical rain forest (TRF) carbon stocks and fluxes are poorly constrained due to a variety of technical issues. The TOWERS project is using multiple approaches to develop independent estimates of GPP, NPP, and NEE over a TRF landscape with multiple land use histories at the La Selva Biological Station, Costa Rica. A critical need for these estimates is the distribution of leaf area and biomass across the landscape. We focused on upland old-growth tropical rain forest using a random design stratified by soil nutrients and slope conditions. A GIS was used to map 515 ha of old growth into 10 x 10 m blocks of high, medium, or low conditions of slope and total soil P, resulting in a 9 x 9 matrix with approximately 5700 blocks in each cell. Within each of the 9 categories five sites were selected using random coordinates, and a walk-up canopy tower was erected. Within the 1.86 x 2.45 m tower footprint all plant biomass was harvested, stratified by tower section (height above ground) and plant functional group. Secondary forests of 17, 27 and 44 years were also sampled using the same tower-based approach.

In old growth mean landscape-level Leaf Area Index (LAI) was  $5.99 \pm 0.33$  (1 SEM). Trees (55%), palms (22%) and lianas (13%) accounted for 90% of total LAI, while herbaceous epiphytes and climbers, understory herbs and ferns accounted for the remainder. At the tower footprint scale (ca. 5 m<sup>2</sup>), LAI was not related to soil P or slope and forest height explained only 12% of the variation in total LAI. The weak relation of forest height to total LAI is partially explained by the rarity of low canopy sites in a random sample. In a sample of additional sites selected to span canopy heights from 0 - 20 m, total LAI was highly correlated with canopy height (r<sup>2</sup>=0.70), reaching the landscape average LAI at 17 m.

In secondary forests LAI increased from 4.21 in the 17 year-old abandoned pastures to levels comparable to old growth in the 27 and 44 year-old forests (6.37 and 6.45 respectively).

We discuss the implications of these results for analyses of TRF landscape canopy structure at large spatial scales and across gradients of different land use. We also show how we will incorporate the results into carbon exchange modeling and on-going canopy research using high-resolution remotely-sensed data.

#### A long-term, regional flux network for evaluating climate, canopy processes, and evapotranspiration along the Middle Rio Grande, New Mexico

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The Middle Rio Grande (MRG) in New Mexico provides habitat for a wide diversity and of vegetation: from low-stature grasslands and xeroriparian shrublands to dense forests and thickets of native and non-native species. This paper presents the long-term record of riparian canopy flux processes using eddy covariance measurements of water, energy, and carbon fluxes collected from representative riparian forests: (1) native Populus deltoides ssp. wislizeni (Rio Grande cottonwood), (2) native P. deltoides with a dense non-native understory of Tamarix chinensis (saltcedar) and Elaeagnus angustifolia

(Russian olive), (3) T. chinensis-Distichlis spicata (saltgrass) mosaic woodland, (4) dense, monospecific T. chinensis, and (5) early successional E. angustifolia and Salix exigua (coyote or sandbar willow). Energy balance closure (75-90%) was invariant from year to year and did not improve following standard flux corrections. Evapotranspiration (ET), ranging from 69 to 134 cm/yr, was not different between T. chinensis, P. deltoides, and E. angustifolia and the highest seasonal ET rates were measured from a mixed stand of all three species. On a daily basis, average ET fluxes were higher in P. deltoids forests (5.5 mm/day) than in T. chinensis thickets (4.8 mm/day), reflecting the shorter growing season observed in the southern reaches of the MRG due to local topographic effects. Daytime carbon dioxide flux ( $-0.33 \pm 0.01 \text{ mg/m2 s}$ ) was decoupled from water fluxes during flooding at the T. chinensis site due to delayed leaf-out, and the response of nighttime CO2 flux to cessation of flooding was dependent upon the local history of soil saturation during flooding. Because of the episodic nature of meteorological and hydrological events like flooding and drought, long-term monitoring of fluxes provides a more complete understanding of canopy-atmosphere interactions than typical short-term studies. *Key words*: Drought, canopy water use, micrometeorology, eddy covariance, evapotranspiration, energy balance, Middle Rio Grande, saltcedar, cottonwood, Russian olive,

Tamarix chinensis, Populus deltoides ssp. wislizeni, Elaeagnus angustifolia

#### Nutrient and CO2 Interactions in Tree Photosynthesis

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Theory and measurements suggest that when tree growth is significantly limited by resources like nutrients, then the CO<sub>2</sub>-induced enhancement of net photosynthesis is reduced. In a mature loblolly pine forest at a N-limited site under elevated atmospheric CO<sub>2</sub> (560  $\mu$ l l<sup>-1</sup>) in FACE, I previously observed photosynthetic adjustments to long-term CO<sub>2</sub> enrichment (FACE) in one-year old needles of *Pinus taeda*. I hypothesized that with N addition at the Duke FACE experiment, the reduction in net photosynthesis in one-year old needles would be alleviated. The experimental treatments at this site are three replicates of elevated  $CO_2$  (560 µl l<sup>-1</sup>) exposure treatments in FACE, which has been ongoing for ten years. Within each CO<sub>2</sub> replicate, half of each plot received N addition at 110 kg N ha<sup>-1</sup> in a split-plot design with ambient and elevated levels of N. Gas-exchange measurements and CN elemental analysis were done for each leaf sample in upper and lower canopy of *Pinus taeda*. We found that the slope of the photosynthesis-nitrogen relationship was significantly reduced by long-term elevated CO<sub>2</sub>. The slopes of photosynthesis vs. nitrogen and carboxylation vs. N were both significantly reduced in elevated CO<sub>2</sub> in one-year old needles but not in current year needles, suggesting a reduction in nitrogen-use efficiency in long-term elevated CO<sub>2</sub>. In the second year of N fertilization, there was a significant effect of N addition, particularly in the elevated CO<sub>2</sub> treatment. The nitrogen content of needles support this finding. The results suggest that the previously found reduction of net photosynthesis in one-year old needles is alleviated by the N addition in elevated CO<sub>2</sub> due to increased N content as well as increased carboxylation rates.

# Changes in Ecohydrological Function due to the Loss and Replacement of Eastern Hemlock in a New England Forest

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Eastern hemlock (*Tsuga canadenssi* (L). Carr.) is a foundation species found across the northeastern United States that is currently threatened by the exotic pest hemlock woolly adelgid (HWA, *Adelges tsugae* Annand). The disturbance currently occurring across the northeastern United States from HWA provides a unique opportunity to study the impact of community structure change on ecosystem ecohydrological function. To gain an understanding of ecohydrological response due to the loss and replacement of a core species, this research considered whole-tree hydraulic controls while indicating the potential effects of these controls at the ecosystem scale. Whole-tree resistances, capacitances, and time constants were examined in eastern hemlock and the expected replacement species, black birch. Through a series of environmental perturbations, whole-tree resistances, capacitances, and time constants were determined from time series sap flux data. With knowledge of whole-tree resistance, capacitance and time constants, these hydraulic controls can be extended to examine potential alterations in the cycling of water due to a shift in the plant physiological characteristics of the watershed.

# Summary models for irradiance interception and light-use efficiency of non-homogenous canopies

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The application of detailed models of canopy photosynthesis relies on the estimation of attenuation of irradiance in the canopy. This attenuation is readily estimated with the Lambert-Beer law when the canopy is homogenous. In reality, forest canopies are far from homogenous, and this has led to the use of very detailed irradiance models that account for grouping of foliage between and within trees. Because such models require detailed parameterization and are therefore impractical in larger scale applications, interest is in simplified models that can be readily parameterized. We developed two equations that can be used to estimate irradiance interception by single unshaded trees, and subsequently interception by stands of trees when these are Poisson distributed. Interception by single trees is a function of crown surface area, the ratio of leaf area per crown surface area, the extinction coefficient in a homogenous canopy which can be determined separately, and one empirical parameter that depends on solar angle when irradiance is direct only. The summary model is tested against a very detailed model of interception, and shows good agreement, although slightly biased. The errors do not depend on crown shape (ellipsoids, cones, and height/width ratios). We also test whether canopy photosynthesis is proportional to irradiance interception across canopies with different structure and leaf area index, and find that the light-use efficiency is influenced by canopy structure. The model is useful in larger scale applications because it can be parameterized with available data without the need for additional empirical parameters. It can also be used in studying the effect of stand structure on interception and productivity.

#### Acclimation to light in a pine canopy under long-term elevated atmospheric CO<sub>2</sub>

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Experimental evidence of increases in whole-forest net primary productivity under CO<sub>2</sub> enrichment suggest that there are increases in canopy light-use efficiency (LUE) that underlie these increases. In closed-canopy mature forests, the acclimation of photosynthesis to light in the lower canopy may be affected by elevated atmospheric CO<sub>2</sub> which may serve to increase LUE and increase the depth to which foliage can be maintained. To date, few studies have quantified within-canopy leaf photosynthesis along with light environment in an elevated CO<sub>2</sub> experiment. I measured leaf physiological properties and light environment by hemispherical photography in loblolly pine (Pinus *taeda*) canopies exposed to elevated atmospheric CO<sub>2</sub> in the Duke FACE experiment to determine the degree of photosynthetic acclimation to light and CO<sub>2</sub> at three different stages of the experiment (3<sup>rd</sup>, 5<sup>th</sup> and 8<sup>th</sup> years of elevated CO<sub>2</sub> exposure). Loblolly pine canopy foliage typically survives to 14% full sun, and there was no effect of elevated CO<sub>2</sub> treatment on the overall minimum light environment in which needles are maintained, although LAI was slightly greater in elevated CO<sub>2</sub>grown stands. There was greater N invested in shaded needles under elevated CO<sub>2</sub>, and a shallower height profile for leaf N in elevated versus ambient CO<sub>2</sub>, which suggests a trade-off between foliage quantum efficiency and nitrogen-use efficiency. Acclimation to light and elevated CO<sub>2</sub> appears to involve changes in the photosynthetic apparatus in a way that increases canopy LUE via changes in the electron transport capacity of pine needles.

# Spring recovery of photosynthesis in conifers is modulated by soil temperature and intermittent frost

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In evergreen conifers the onset of photosynthesis in spring is triggered by increasing temperatures. Using controlled environments, we assessed the effects of cold or frozen soil or intermittent frost events on the recovery process of photosynthesis in Scots pine (Pinus sylvestris (L.)) seedlings under controlled environmental conditions. We first acclimated one-year-old seedlings to simulated winter conditions and then followed the response of photosynthesis after transfer to a range of different simulated spring conditions, viz (i) warm air and warm soil (both at 15 °C), (ii) warm air and warm soil with intermittent spells of sub-zero temperatures, (iii) warm air (15 °C) and cold soil (+1°C) and (iv) warm air (15 °C) with frozen soil (-2°C). Compared to the control (15 °C air and 15 °C soil) treatment cold or frozen soil slowed the rate of recovery of photosynthetic electron transport from PSII to PSI and net CO2 uptake but did not completely inhibit it. Low rates of photosynthesis in seedlings exposed to cold or frozen soil were associated with very low stomatal conductances while the water content of the needles was not severly affected. Light absorption was not reduced for needles on seedlings growing in the cold or frozen soils, thus a greater fraction of excessive excitation energy was associated in these treatments with increased thermal energy dissipation via xanthophylls. Intermittent frost events during the simulated spring recovery resulted in a decrease in photosynthetic activity but only as long as seedlings were exposed to sub-freezing air temperatures. Within a few days of the completion of each frost event, photosynthetic capacity had recovered rapidly to pre-frost levels. After 18 days under spring conditions no differences in the maximum quantum yield of photosynthesis between the frost and non-frost treated seedlings were observed. We conclude that intermittent frost events should delay but not severely inhibit photosynthetic recovery in evergreen conifers during spring. Cold and/or frozen soils exert much stronger inhibitory effects on the recovery process, but they do not totally inhibit it.
### **Quantifying and Explaining Spatial Patterns of Transpiration Across Environmental Gradients Using Plant Hydraulics and Geostatistics**

### Brent E. Ewers, University of Wyoming

Our knowledge of plant controls over transpiration has dramatically increased in the past two decades through testing plant hydraulic theory with continuous estimates of tree transpiration via sap flux. As sap flux measurements have become routine, the sample size of sap flux studies has dramatically increased. These large sample sizes (>100 trees in one stand) now provide sufficient data to quantitatively test scaling methodologies in time and space. This study tested 1) whether center-of-stand approaches to scale sap flux measurements to stand and landscape level transpiration are sufficient 2) whether geostatistical techniques provide the information necessary for quantifying important stand and landscape level gradients and 3) what environmental and biological variables explain spatial autocorrelation dynamics in time. Spatially explicit sap flux measureds were made in three contrasting forests: one dominated by lodgepole pine (Pinus contorta) in Wyoming, another dominated by trembling aspen (Populus tremuloides) in Wisconsin, and a third codominated by black spruce (Picea mariana), trembling aspen, and jack pine (Pinus banksiana) in northern Manitoba. In all three forests, a cyclic sampling technique in space was utilized that maximized quantifying spatial patterns of transpiration with minimal sample points. Variogram analyses were used to quantify the spatial patterns of transpiration at half-hourly time scales. Spatial range of autocorrelation in time was linearly and inversely correlated to vapor pressure deficit (VPD) in both Wyoming and Wisconsin. At low VPD (<0.6 kPa VPD), no trees limited their transpiration to maximize photosynthesis. As a result, transpiration rates were fairly uniform so spatial autocorrelation ranges were long (> 150 m in Wisconsin and 50 m in Wyoming). As VPD increased (> 1.5 kPa), individuals and species began regulating minimum leaf water potentials through stomatal closure at different levels of VPD. As a result, transpiration was less uniform between individuals and species so spatial ranges of autocorrelation were short (< 100 m in Wisconsin and 30 m in Wyoming). These results show that center-of-stand approaches are not sufficient for characterizing stand transpiration because transpiration becomes more variable in space with increasing vapor pressure deficit and spatial autocorrelation ranges were always much larger than traditional sap flux plot sizes. The results suggest easily measured variables, such as vapor pressure deficit in time and tree diameters in space, combined with geostatistics and plant hydraulic theory, improve temporal and spatial scaling of transpiration from trees to landscapes.

#### Environmental control of the onset of photosynthesis in spring in a balsam fir ecosystem

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Global warming may increase photosynthetic production in early spring and thereby increase annual net ecosystem production. Predicting the impact of warming on springtime photosynthesis requires identifying the environmental control of the onset of photosynthesis and also of photosynthetic rates in early spring. We report on the environmental control of the springtime onset of photosynthesis in a balsam fir (Abies balsamea (L.) Mill) forest in New Brunswick, Canada. Net ecosystem exchange (NEE) of carbon dioxide (CO<sub>2</sub>), water vapor and energy has been measured in this forest using the eddy covariance method since August 2003. We identified three periods during the winter-early spring period, before the initiation of shoot growth by trees that we used to assess the springtime onset of photosynthesis. The winter dormant period was characterized by a soil temperature  $(T_s)$ throughout the rooting zone colder than the 0°C isotherm; as well, soil temperature varied with depth and over time. During this period, daytime NEE had the same relationship with air temperature as nighttime NEE and there was no apparent response of daytime NEE to light. The second period was characterized by soil temperature near 0°C, with no diurnal variation or variation with soil depth of soil temperature, and snow cover for the entire time. During this period the response of daytime NEE to air temperature differed from that of nighttime NEE and the response of daytime NEE to light indicated that photosynthesis was occurring. In addition, the soil moisture content increased during this period. The date marking the beginning of this period varied among years, being March 27, March 28 and March 24 respectively in 2004 - 2006. The third period begins when soil temperature first rises above 0°C; soil temperature begins to vary with soil depth and display diurnal variation, and there is a large increase in soil moisture content. During this period, the nighttime NEE varies strongly with temperature at higher rates than observed during the second period, the daytime NEE does not have a simple relationship with air temperature, and daytime NEE responds to light as observed in the second period. We define the second period as the time of soil thawing, during which time soil temperature remains constant because ice and liquid water coexist in the soil profile. Moreover, the rise in soil temperature to the 0° isotherm at the beginning of the second period marks the first appearance of liquid water in the rooting zone. Ecosystem photosynthesis began as soon as liquid water became available in the root zone in each year. Global warming will initiate soil thawing earlier in spring than would otherwise occur and therefore, should cause photosynthetic uptake in this balsam fir forest to begin at earlier dates in the future. This may increase annual photosynthetic uptake of CO<sub>2</sub>.

## Seasonal variation in the temperature response of leaf respiration in *Quercus rubra* at the Black Rock Forest

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Leaf respiratory temperature responses of *Quercus rubra* were measured throughout the 2003growing season in a deciduous forest in northeastern USA, in the upper and lower portions of the canopy at two sites with different soil water availability. Consequently, stand-level canopy foliar carbon loss  $(R_{canopy})$  was modeled for a virtual *Quercus rubra* monoculture in these two sites. The base leaf respiration rate ( $R_0$ , respiration at 10 °C) of Q. rubra was significantly affected by season, site water availability, canopy height and their interactions. Upper canopy leaves generally had higher  $R_0$  than lower canopy leaves. At the drier site, a more significant seasonal pattern in  $R_0$  was observed, while at the more mesic site, a stronger canopy position effect was detected. By contrast, the temperature coefficient ( $E_0$ , the activation energy of respiration as a single reaction) was constant  $(52.5 \pm 5 \text{ kJ mol}^{-1})$ . Leaf reducing monose could partially explain the seasonality in respiration (32%) - 79%), and leaf nitrogen ( $N_{area}$ ) was well correlated to the canopy position effect.  $R_{canopy}$  of Q. rubra was first estimated by a "full distributed physiology model", which. integrates the effects of season, site, and canopy position on  $R_0$ . Sensitivity examination indicates that neglecting the season, site and canopy height effects on leaf respiration resulted in up to a 130% error on the estimation of  $R_{canopy}$ , but canopy level model parameterizations could be simplified by assuming a constant  $E_0$  (error < 5%). From June 8<sup>th</sup> to October 28<sup>th</sup> of 2003, the modeled  $R_{canopy}$  of the virtual Q. *rubra* monoculture was 6.3 mol  $CO_2$  m<sup>-2</sup> ground, and 13.5 mol  $CO_2$  m<sup>-2</sup> ground, at the drier and the more mesic site respectively. These results suggest that the temporal and spatial heterogeneities of  $R_0$  need to be considered in ecosystem models, but it is potentially predictable from well understood leaf properties. Meanwhile, simplifications can be made in *Q. rubra* by assuming a constant temperature coefficient ( $E_0$ , e.g. 52.5 kJ mol<sup>-1</sup> in this study)

### Differences in carbon and water cycling between early- to mid-successional deciduous forests and late-successional conifer forests: Implications for long-term effects of the invasive hemlock woolly adelgid

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Carbon budgets of forests have become the subject of great interest throughout the world due to the twin realizations that increasing atmospheric CO2 is changing the earth's climate, and that forests may have major effects on the global carbon budget. Water use by forests is also an important element in regional hydrologic budgets, affecting water availability for other forms of life, including humans. We present evidence that biosphere-atmosphere exchange of both carbon and water differ strongly between the latest-successional forest type in the northeastern United States (eastern hemlock, Tsuga canadensis, forest) and early to mid-successional forests. Mass mortality of eastern hemlock trees due to an invasive insect, the hemlock woolly adelgid (Adelges tsugae) may therefore result in significant changes in carbon and water cycling.

Eddy covariance measurements showed that the evapotranspiration (ET) rate of red oak (Quercus rubra)-dominated deciduous forest (around 4 mm per day) was nearly twice as great as ET of eastern hemlock forest during in early to mid-summer in 2004 and 2005. This difference decreased later in the growing season, but nevertheless deciduous forest had about 100 mm greater ET than hemlock forest during June through October 2004. This differential was only partially canceled by hemlock forest ET during the leafless period for deciduous trees. Higher summertime deciduous forest ET was correlated with a higher maximum carbon storage rate (about 25 µmol m-2 s-1 for deciduous forest versus 12 µmol m-2 s-1 for hemlock) and higher estimated annual carbon storage (x.x Mg C ha-1 for deciduous forest versus x.x Mg C ha-1 for hemlock forest for July 2004 through June 2005). The differences in water use and carbon storage at the ecosystem level paralleled differences in leaf-level photosynthesis and conductance to water vapor: Maximum photosynthesis was about 20 µmol m-2 s-1 for oak and 10 µmol m-2 s-1, while peak leaf conductance was near 0.15 mol m-2 s-1 for oak and 0.08 mol m-2 s-1 for hemlock.

Large areas of eastern hemlock from southern and eastern Massachusetts southwestward to Tennessee have been killed by the hemlock woolly adelgid since the 1970's, and this insect is expected to continue to spread through the rest of New England, especially if the winter climate becomes milder. Most of the dead hemlock in New England have been replaced by black birch (Betula lenta). Physiological measurements of black birch showed that its early-summer leaf conductance was much higher than in eastern hemlock, and closer to leaf conductance measured in red oak. Sapflow rates in black birch were also much higher than in hemlock, especially in early and mid-summer. Thus, when mature, black birch forests that replace hemlock are likely to transfer water from soil to atmosphere at much higher rates, resulting in lower soil water content and less streamflow in summer.

## Effect of leaf age on the seasonal variability of photosynthesis parameters and leaf nitrogen content within a *Pinus densiflora* crown

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In many evergreen conifers, the age-related decrease in the rates of photosynthesis may be spread over many years and a significant proportion of forest carbon fluxes is accounted for by old and/or aging foliage because canopies retain several cohorts of foliage. Therefore, the process of aging is likely especially important for conifers. Most of the studies on the effect of leaf age on photosynthesis and nitrogen content were conducted during growing season making a compromise with the same photosynthetic capacity and thus the effect of temporal scale was not taken into account. However, leaf nitrogen concentration exhibits dynamic changes in accompany with sprouting of current-year leaf, especially in conifers that need long period of leaf mature. In addition, photosynthetic capacity had a seasonal change and its correlation with nitrogen concentration often has a seasonal pattern. Therefore, it is imperative to elucidate the effect of leaf age on seasonal fluctuations of both photosynthesis and leaf nitrogen content.

A representative tree was selected in an approximately 80-year-old *P. densiflora* forest ( $35^{\circ}45'$  N,  $138^{\circ}80'$  E; elevation 1,030 m). The photosynthetic response curves to intercellular CO<sub>2</sub> concentration was measured in situ in needles from both the upper and lower crowns every other month during the whole growing season, under constant temperatures and light conditions. Needles were harvested after the gas exchange measurements and their nitrogen content was determined with a gas chromatograph after combustion with circulating O<sub>2</sub> using an NC analyzer.

Leaf mass per area (LMA) and leaf nitrogen content per area ( $N_a$ ) in mature needles of all age classes exhibited seasonal fluctuation in both upper and lower crowns. In general, LMA had a decreasing trend during the development of current-year needles. The difference in  $N_a$  among different ages became null in July and had different trends afterward depending on the crown position and leaf age. Seasonal trends of photosynthetic parameters including light-saturated photosynthesis, the maximum rate of carboxylation and electron transport differed between leaf ages and crown positions. These results suggest that storage proportion of nitrogen, which reflexes translocation, resorption and accumulation, caused its seasonal fluctuation, and photosynthesis parameters were less affected by leaf ages but its changes mirrored to the climatic acclimation. New frontiers in understanding canopy processes at the regional level and beyond: Eddy covariance data, model parameter estimation, and data assimilation.

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Measurements of carbon, water, and energy exchange over forests integrate canopy and soil processes in ways that were once unimaginable. There are presently hundreds of sites worldwide continuously collecting data using the eddy flux technique, and over 400 site-years of data are readily available for analysis. At some sites, multi-year records now exceed 10 years in length. These data represent an extraordinary resource for understanding canopy processes, but carry with them their own demands. The integrative nature of these data means that their use in analyzing specific processes can be complicated. Synthesizing results across sites can be a challenge due to the volume of data; a multi-year record at one site may consist of  $>10^6$  values. A third challenge relates to understanding the interplay between rapid changes in ecosystem function driven by diurnal and annual environmental variation and slower changes mediated by adjustments in long-lived carbon and nutrient pools or the species present brought about by management or natural processes.

Examination of flux data from forested sites shows that net annual carbon exchange depends upon forest type, age, management, and the climate. Year-to-year variations in carbon exchange show that the impact of natural climate variations can be substantial, exceeding several tons C per hectare per year. Determining the specific causes of year-to-year variations in carbon uptake can be difficult. In a Northeastern U.S. spruce-hemlock forest, for example, warmer than average spring and fall conditions lead to enhanced C uptake but warmer than average summer temperatures lead to reduced C uptake.

More recently researchers have started comparing carbon sequestration at "clustered" eddy flux sites where monitored stands experience the same regional climate but differ in age, species composition, or management. This has the great promise in teasing apart the role of these factors. Generally, carbon sequestration rates increase from north to south but may be profoundly affected by forest management.

Flux data are probably most useful for constraining outputs and establishing parameter values of models of canopy processes and surface-atmosphere exchange. Using data to determine the most likely model parameters ("inverse analysis") can increase our understanding of canopy processes. A variation of this approach utilizes other existing data to constrain the results of these analyses in what are known as Bayesian syntheses. Using these techniques, investigators can assess whether the data are consistent with the functional response of the model to environmental change, if parameter estimates are consistent with smaller-scale studies, or how much complexity is justified by the data. Different models of the same process can be compared to determine how well they replicate observed responses and the "best" models selected for further study.

### Regional modeling of potential effects of climate change on tree species habitats

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Global climate change will increasingly impact species distributions. In the northeastern United States, there will likely be simultaneous movement of species habitat into the region from the south and out of the region to the north. Our research uses a regression tree ensemble method to assess current species-environment relationships as well as model potential suitable habitat under a variety of global climate change scenarios. We find that this variety of tools – regression tree analysis, bagging, random forest – each have their value in our analysis. As such, regression tree analysis creates a single regression tree that can be used to map where a species, within its range, is controlled by certain variables; bagging with ~30 trees can provide statistics on the constancy and reliability of the model; and random forest tends to provide the best prediction. We are using these methods on 135 of the most common trees of the eastern United States. We are using 38 variables of climate, soil characteristics, elevation, and landform to create models from 100,000+ Forest Inventory and Analysis plots which are used to map current habitat (as importance values) for each species at a 20 x 20 km scale. We then change the 7 climate variables according to two recent and tested climate GCM models under low and high emission scenarios to estimate suitable habitat for the year ca. 2100. We also evaluate 'hot spots' of importance for the species and assess the potential changes of these zones under climate change. Within the defined suitable habitat estimated for ca. 2100, we then simulate migration of selected tree species through that suitable habitat. This cellbased model depends on abundance of the species within its range, habitat availability in the unoccupied, but suitable habitat, and the distance propagules must travel between cells. In general, we find that generally 5% or less of the newly available habitat (mostly north of current range) has at least a 20% chance of getting colonized within 100 years, so that there is a serious lag of migration in the absence of humans physically aiding migration. We find that this modeling approach to empirically derive relationships and then map potential habitat changes is appropriate as long as the majority of the species range is included and sufficient organism and environmental data are available to populate the model. The migration modeling can then follow in a more stochastic manner. Together, we envision what might happen under climate change. Keywords: regression tree, random forest, climate change, eastern United States, tree species distribution, migration

### The Effects of Land-use Change on the Terrestrial Carbon Budgets of New England

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The objective of this research is to quantify the effects of land-use change, particularly with respect to forests on the terrestrial carbon budget of New England. A well-developed carbon model with remote sensing estimates of rates and kinds of land-use change will determine the net fluxes of carbon from this region due to land-use change. Regrowth of forests in New England over the past century has resulted in significant storage of carbon. It is difficult to assess the magnitude of carbon sinks and sources resulting from land-use change in New England, however, as current trends in forest clearing and regrowth remain unknown. This study investigates changes in land use in New England for the past 20 years in order to estimate regional carbon budgets. In addition, this research projects the magnitude of the effects of ongoing forest clearing for development purposes on the carbon budget for the next 15 years in New England. The results will quantify the effects of human-induced land-use change on the regional carbon budget, which has implications for the greenhouse effect and future climates.

### Seasonal changes of photosynthetic production of larch plantation in Northern Japan

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Larix species are broadly distributed in eastern Eurasian Continent and characterized by their high photosynthetic rates and high growth rates. Therefore, Larix is one of the candidate species for moderating global warming through CO2 fixation. It is an urgent subject for us to evaluating the carbon fixation character of Larix forest. In northern Japan, we have huge Japanese larch (Larix kaempferi) plantations located in the southern edge of Eurasian Continent. Most of the Larix plantations in this region have mixed with invaded broad-leaved tree seedlings. We predicted that invaded broad leaved tree seedlings would also play an important role of carbon fixation in leaf-less period of Larix trees. To test our expectation, we monitored seasonal changes of leaf phenology, photosynthetic rates of both Larix and invaded four seral broad leaved tree seedlings, and we estimated photosynthetic production of Larix and the invaded tree seedlings by light dependent model (Revised the Monsi-Saeki model). Leafly period of both short and long shoot needles of Larix were mid May to October. Photosynthetic rates of both needles increased toward August, then it gradually decreased to October. There were no marked differences in photosynthetic rates between short and long shoot needles. Relative light intensity in the Larix forest floor (rPPFD), gradually decreased as canopy closing, finally it reached 10% then as Larix needles shedding it increased. The mid-successional and gap phase species Magnolia hyporeuca had short leafy period and high Psat. In contrast, two late successional tree species, Prunus ssiori, which performed leaf flush their leaves before Larix, and Carpinus cordata, which maintained green leaves until frost come, both had low photosynthetic rates but exploited the opportunity for the growth during the period of when the Larix canopy trees were leaf less. Quercus mongolica, a mid-late-successional species had values of photosynthetic parameters between those of the gap-phase and late-successional species. Estimated photosynthetic production values of Larix canopy showed highest value in July. Results of the photosynthetic production of invaded broad leaved tree seedlings, especially in both P.ssiori and C. cordata, suggest that these seedlings would utilize the leaf-less period of Larix trees.

### Leaf Level Acclimation to Light at Elevated CO<sub>2</sub>: Poplar Plantation in EUROFACE

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The aim of this study was to investigate leaf level acclimation in photosynthetic parameters and stomatal morphology and conductions to light conditions generated by canopy profile of PPFD in EUROFACE poplar plantation to see how elevated CO<sub>2</sub> would influence this acclimation. *Methods*: We measured leaf photosynthesis-CO<sub>2</sub> response curves according to the using portable gas exchenge system CIRAS-2. Leaves were sampled from three height levels (upper, middle and lower canopy). In situ stomatal conductance was measured using AP4 porometer. Two leaves from three height levels from each sub-plot were monitored throughout the field campaign; from each of the leaves, both adaxial and abaxial stomatal conductance was recorded. Hemispherical photographs were taken from the locations of these leaves. At the end of the field campaign, all leaves from the stomatal conductance sample were collected. From each leaf, stomatal imprints were taken, as well as wet-extraction Chl sample; the remaining leaf was analysed for N content.

*Results:* Our analysis of data collected in 2003 showed only slight and statistically non-significant down-regulation of photosynthetic capacity of leaves grown under elevated CO<sub>2</sub>. We detected somewhat increased  $J_{max}/V_{cmax}$  ratio under FACE treatment, suggesting nitrogen re-alloration, and evidence for increased non-photosynthetic N partition. No fertilisation-related changes in photosynthesic apparatus were detected.

The data collected in autumn 2004, again, did not show clear down-regulation of photosynthetic capacity. Correspondingly, assimilation in growth concentration was considerably stimulated by elevated CO<sub>2</sub>. Contrary to previous year, we detected fertilization-induced changes in the distribution of photosynthetic apparatus: fertilized trees of all species showed increase in their photosynthetic capacity in upper and decrease in middle canopy.

In situ stomatal conductance of *P. alba* was substantially reduced under elevated  $CO_2$  in 2004; for other species, same trend was present but insignificant. This contrasts with our measurements in 2003, when FACE-induced decrease in stomatal conductance was always clear and most pronounced in case of *P. x euramericana*.

We conclude that substrate induced increase in photosynthesis accounts for all increase in productivity and there was no down-regulation in photosynthetic capacity in this non-limited system. *Keywords*: canopy, chlorophyll, nitrogen, photosynthesis, stomata

### **Reflection of Experimental Drought and Warming at European Shrublands**

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We examined plant response to warming and drought at shrubland ecosystems of six European sites (UK, Denmark, Netherlands, Hungary, Spain, Italy). We used ground based canopy reflectance measurements in visible/near-infra-red wavebands for evaluation of the method to use in early detection in canopy composition and structure with possible implication in remote sensing technology. Reflectance index NDVI revealed expected relationship with green biomass data (obtained from point quadrat measurements) with strong tendency to saturate at high biomass conditions. Differences in reflectance indices between treatments were considerably smaller than differences between sites. Cross-sites comparison showed that in general effect of warming treatment was positive on NDVI, whereas drought treatment had negative effect. Green biomass data showed similar trends. Reflectance index PRI had no tendency to saturate at high biomass values suggesting that this parameter works better than NDVI in high biomass conditions. PRI showed a good agreement with leaf-level photochemical efficiency measurements. Plot level PRI measurements suggested that photochemical efficiency of plants was mainly influenced by the warming treatment. Reflectance proves to be a useful means for detecting changes in vegetation while reflectance is easier to measure and has better averaging ability than direct measurements of biomass or physiological status of vegetation.

# Indirect effects of the hemlock woolly adelgid on oak seedling growth through effects on mycorrhizal richness and abundance

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Invasive, non-native phytophagous insects have led to widespread declines in many dominant tree species. The loss of these foundation species may lead to cascading effects on non-target plant species through indirect effects on the mycorrhizal fungal community. In this study, we examined the roles of ectomycorrhizal abundance and diversity on the response of a non-target species, Northern red oak (Quercus rubra), to the decline of eastern hemlock (Tsuga canadensis) following infestation by the hemlock woolly adelgid (HWA; Adelges tsugae), an invasive, non-native aphidlike insect. To address this issue, we grew red oak seedlings for one growing season in hemlockdominated stands infested with the HWA and in adjacent oak-dominated stands. Soil cores indicated that ectomycorrhizal abundance and richness were significantly lower on hemlock trees in the infested hemlock stands compared to oak trees in the oak stands. Similarly, ectomycorrhizal abundance and richness were significantly lower on oak seedlings grown in the infested hemlock stands compared to oak seedlings grown in the oak stands. In addition, oak seedlings in the hemlock stands were significantly smaller than oak seedlings in the oak stands. Over 90% of the variation in oak seedling growth could be attributed to differences in ectomycorrhizal abundance and richness. These results indicate that reduced ectomycorrhizal abundance and richness in hemlock stands infested with the HWA negatively affect oak seedling growth in these stands. Further, these results suggest that the indirect effects of the HWA on the growth of replacement species through effects on ectomycorrhizal abundance and richness may negatively affect forest recovery following hemlock decline associated with HWA infestation.

# Physiological impacts of eastern dwarf infection and developmental responses of host white spruce

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Along the coast of Maine, intensive livestock grazing in the middle and latter part of the nineteenth century followed by land abandonment led to the replacement of red spruce and fir-dominated forest stands with those dominated by white spruce. White spruce is acutely vulnerable to infection by eastern dwarf mistletoe, a native xylem- and phloem-tapping plant parasite. In the 1980s, white spruce forest stands began to experience severe damage and increased mortality largely caused by eastern dwarf mistletoe infection. Our objective is to quantify the direct impacts of infection and the indirect developmental responses to infection, and in doing so, to understand how and why white spruce succumbs to mistletoe infection. One of the most visually obvious effects of mistletoe infection is a  $\sim$ 50% reduction in the size of host white spruce needles distal to infection. Since infection also reduces sapwood area-specific hydraulic conductivity by  $\sim$ 50%, this developmental response to infection may serve to re-establish the balance between the demand for water and the ability of infected branches to deliver water to distal foliage. Needle function, e.g., leaf area-based rates of photosynthesis and stomatal conductance, were not significantly affected by infection. Branch xylem tension was similarly unaffected by infection. Host developmental responses to infection (i.e., reductions in needle size) appear to preserve needle-and branch-scale function and longevity. Whole tree survival may be negatively impacted by these responses, as they prolong the survival of infected branches with presumably poor or negative carbon balance and also allow infected branches to serve as a source of parasite seed for further infection.

### Abiotic immobilization of nitrite in forest soils: a double label approach

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Anthropogenic sources of reactive nitrogen (N) have become an important source of N to natural systems in the industrialized world. A thorough understanding of how N cycles through ecosystems is required to predict how a given system will react to anthropogenic N addition, and there is still uncertainty left to be resolved. One possible mechanism which may further complete understanding of the N cycle is abiotic immobilization of nitrite (NO2-); the chemical reaction of nitrite, an intermediate in both nitrification and denitrification, with phenolics in the humic portions of the soil. This reaction has been demonstrated in vitro using both extracted and artificial humic compounds. There have also been previous studies which used direct isotope labeled nitrite (15NO2-) applications with live and sterilized soils. However, critics argue that while in vitro studies may indicate the possibility of the reaction they cannot demonstrate its plausibility in soils, that soil sterilization methods are not effective enough to eliminate biotic interactions with an experimental treatment, and that direct application of nitrite may not represent realistic availability in soils. This proposed study will attempt to demonstrate abiotic immobilization of nitrite in soil samples while avoiding the alterations critiqued in previous studies. Using double labeled nitrate (15N18O3-) and incubation under anoxic conditions, double labeled nitrite (15N18O2-) will be produced from the labeled nitrate during denitrification by the soil microbiota. This should prevent artifacts created during soil sterilization and introduce the labeled nitrite through natural processes. The humic portion of each soil sample will be extracted following the treatment for analysis of label content with GC mass spectrometry and presence of indicator compounds, described during previous in vitro studies, with proton NMR. Abiotic immobilization should leave isotope ratios consistent with binding of the double label as nitro and nitroso groups, while biotic immobilization would cleave the labeled oxygen to produce water. Presence of 15N labeled guinone monoximes and ketoximes in the proton NMR will also indicate abiotic immobilization. Success using this double label technique will open the door to quantification of the abiotically immobilized pool of N in both the lab and the field. Demonstration of abiotic immobilization of nitrite in soil will help shed new light on the current understanding of the N cycle and the understanding of ecosystem reactions to anthropogenic N.

#### Response of *Tsuga canadensis* photosynthetic rate to changes in temperature and N-form

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Two environmental changes associated with urbanization are the increase in ambient temperature and nitrogen deposition. Understanding plant responses to changes in temperature and nitrogen source will be critical to predicting distributions in areas subject to urban sprawl. In this study, changes in net photosynthetic rates of eastern hemlock (Tsuga canadensis) seedlings were observed in response to short-term, seasonal, and sustained changes in temperature, as well as changes observed with different ratios of inorganic nitrogen forms. Photosynthetic responses to seasonal changes in temperature of field-grown seedlings were examined over an annual cycle. Separately, photosynthetic responses to sustained changes in temperature were examined on seedlings in growth chambers at day/nighttime temperatures of 27/22°C and 20/15°C over 6 weeks. Photosynthetic responses of seedlings in both experiments, to rapid increases in temperature (+10°C within 15 minutes), were also measured. A separate greenhouse experiment examined the changes in net photosynthesis and growth of seedlings regularly watered with solutions containing equal concentrations of N, but in differing NO<sub>3</sub><sup>-</sup>:NH<sub>4</sub><sup>+</sup> ratios of 1:0, 3:1, 1:1, 1:3 or 0:1 over the course of five months. Net photosynthetic rates of field grown seedlings were abruptly lower between late-November and mid-March, when temperatures were at or below 3°C, but relatively constant throughout the rest of the year. Photosynthetic rates varied positively to increased seasonal temperature and moisture. In growth chamber studies, net photosynthetic rates (at the same temperature) of trees grown at 27/22°C were initially lower than those grown at 20/15°C, but samples in later weeks showed the seedlings grown at higher temperatures had a higher rate of net photosynthesis, suggesting that net photosynthetic rates of T. canadensis may acclimate to increased temperature, and should acclimate to temperature changes associated with environmental change, providing moisture levels remain constant. T. canadensis showed the greatest growth and net photosynthesis response to a 1:1 mixture of  $NO_3$ :  $NH_4^+$ , with large decreases in both parameters when  $NH_4^+$  concentration was reduced. Results suggest that *T. canadensis* is unable to use  $NO_3^-$ .

## Interaction of ice storms and management practices on current carbon sequestration in forests with potential mitigation under future CO<sub>2</sub> atmosphere

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Ice storms are periodic disturbance events with potential impacts on carbon sequestration. Common forest management practices, such as fertilization and thinning, can change wood and stand properties, and thus may change vulnerability to ice storm damage. At the same time, increasing atmospheric CO<sub>2</sub> levels may also influence ice storm vulnerability. Following a severe ice storm across the southeastern US, we estimated carbon transfer across the entire storm area and investigated the effects of fertilization, thinning and elevated CO<sub>2</sub> in determining susceptibility to ice damage. This was achieved by combining data from a statewide forest damage survey of North Carolina and federal Forest Inventory and Analysis reports with measurements of storm effects in a free air CO<sub>2</sub> enrichment (FACE) experiment in a *Pinus taeda* forest and an adjacent thinned *P. taeda* stand. Drawing on weather and damage survey data from the entire storm cell (southern Maryland to northeastern Georgia; ~23.4 million ha), the amount of C transferred from the living to the dead biomass pool was 26.5 +/- 3.3 Tg C. In the area with the thickest ice accumulation, conifers were three times more likely to be killed. Of the C transferred to detrital biomass pools, we estimated that 50% would be decomposed and returned to the atmosphere by the end of the eighth year. In the Duke Forest case study, the unthinned, ambient CO<sub>2</sub> pine stand experienced a  $\sim 250$  g C m<sup>-2</sup> reduction in living biomass during the storm, >30% of the annual net ecosystem carbon exchange of the system. Nitrogen fertilization had no effect on storm induced carbon transfer from the living to detrital pools, while thinning increased carbon transfer threefold. Elevated CO<sub>2</sub> reduced the storm induced carbon transfer to a third. Due to the lesser leaf area reduction, plots growing under elevated CO<sub>2</sub> also exhibited a smaller reduction in biomass production the following year. Our analysis reveals that major ice storms can have significant effects on regional and national carbon balances, where one storm event transferred to the dead biomass pool the equivalent of ~10% of inventoryestimated U.S. annual C sequestration. Further, these results suggest that forests may suffer less damage during each ice storm event of similar severity in a future with higher atmospheric CO<sub>2</sub>.

## Spring photosynthetic recovery of boreal Norway spruce at the shoot- and tree-level under conditions of elevated [CO<sub>2</sub>] and air temperature

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The pattern of recovery of photosynthetic capacity each spring is strongly climate-dependent for boreal forests. Climate changes are predicted for high northern latitudes with increases in gas pollutants causing concomitant increases in surface air temperatures. The predicted changes in climate may alter both the timing and rate of photosynthetic recovery in boreal forest stands. An understanding of the climatic controls over photosynthetic recovery is essential for improving the parameterisation of process-based models and predicting carbon balance of boreal forests under altered climate scenarios.

The effect of elevated atmospheric CO<sub>2</sub> concentration and temperature on the photosynthetic recovery of field-grown Norway spruce was assessed using whole-tree chambers. Shoot- and tree-level daily maximum CO<sub>2</sub> assimilation rates ( $A_{max}$ ), apparent quantum efficiency ( $\phi$ ) and needle starch accumulation were measured throughout late winter and early spring.

Elevated air temperature produced an earlier onset of  $A_{\text{max}}$  and greater  $\phi$  while elevated CO<sub>2</sub> did not alter the timing of recovery. Elevated CO<sub>2</sub> increased  $A_{\text{max}}$  once recovery commenced but did not alter  $\phi$ . Combined elevated temperature and CO<sub>2</sub> produced both earlier recovery and greater  $A_{\text{max}}$  values. Within treatments there was agreement in the timing of photosynthetic recovery at shoot- and tree-levels but some differences in pattern and magnitude were evident.

Our results suggest that rising air temperatures will lead to earlier spring recovery of boreal Norway spruce forests. Differences in recovery patterns observed at the shoot- and tree-level highlight the importance of accurate temporal and spatial up-scaling for annual carbon gain estimates.

### Methane Cycling in Upland Forests: New Findings and Implications for Forest-Climate Interactions

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Methane is an important greenhouse gas that accounts for about 20% of current global warming. Anaerobic environments, such as wetland soils, are abundant sources of the gas, contributing 40% of annual methane emissions even though they cover just 10% of Earth's surface. Methane cycling in upland ecosystems has been largely overlooked, yet they have the potential to impact atmospheric methane concentrations because their low exchange rates are scaled across large areas of land. For example, upland soils are weak methane sinks per unit area, but they scale up to contribute 5-10% of the global methane sink. Recent studies have shown that methane is also produced in upland soils, showing that forests can no longer be considered strictly aerobic environments.

A surprising recent report is that forest canopies may emit small amounts of abioticallyproduced methane that are globally significant when scaled upward (Keppler et al., 2006, *Nature*, 439:187-191). The authors estimated that upland ecosystems emit 150 Tg CH<sub>4</sub> yr<sup>-1</sup> globally, or up to one-third of all global sources. A misinterpretation of this estimate led to exaggerated headlines in the popular press such as "Cutting down the rain forests may actually be a way of preventing global warming!". More thoughtful analyses (including one by Keppler and colleagues), suggested that methane emissions would offset between 1 and 10% of the sequestration gains made through reforestation.

Keppler et al. (2006) may have overestimated global methane emissions from uplands due to the scaling approach they chose. Scaling according to leaf biomass and considering self-shading in the canopy produced mean emission rates of 27 and 43 Tg CH<sub>4</sub> y<sup>-1</sup> (Megonigal, unpublished data) compared to the mean Keppler et al. (2006) estimate of 150 Tg CH<sub>4</sub> y<sup>-1</sup>. Scaling according to known rates of methanol emissions yields a range of about 4 to 31 Tg CH<sub>4</sub> y<sup>-1</sup> (Guenther, Per. Comm.). Finally, the Model of Emissions of Gases and Aerosols from Nature (MEGAN), which estimates VOC emissions from vegetation, gave a range of 34 to 56 Tg CH<sub>4</sub> y<sup>-1</sup> (Guenther, Per. Com.).

Methane is produced and consumed in upland forests by both biotic and abiotic mechanisms. Because of their large areas, even low rates of methane cycling in upland ecosystems have the potential to influence methane concentrations in the atmosphere. It appears that methane emissions will offset only a negligible amount of the decrease in radiative forcing achieved by sequestering carbon in planting forests. Nonetheless, it is clear that the details of methane cycling in upland forests deserve more attention.

### Effects of winter temperatures on flowering times in birch trees

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Changes in flowering times are one of the most sensitive biological responses to climate change. However, it is clear that not all flowering times are changing at the same rate. In some cases, the flowering times of closely related species respond quite differently to climate change. It is not clear what mechanisms might be responsible for these differences. I examined the effects of temperature on flowering times in two mixed populations of Betula lenta (black birch) and B. populifolia (gray birch). According to historical records, the flowering times of B. lenta are sensitive to winter temperatures, whereas the flowering times of B. populifolia are not. During the winter of 2006, the male inflorescences of B. lenta were subject to high mortality from frost damage relative to B. populifolia. In addition, B. lenta was subject to a greater loss of hydraulic conductivity in the xylem of branches due to freezing-induced embolisms than was B. populifolia. The freezing damage to flowers and xylem in B. lenta could lead to delayed flowering in this species relative to B. populifolia in springs following cold winters. I am currently investigating if these differences may be the result of an ecological trade-off.

# Nocturnal transpiration in *Tamarix*: A mechanism for temporal incongruence between sapflow and eddy covariance

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Like other phreatophytes, *Tamarix*, an exotic riparian tree common to the Southwestern US, is capable of high transpiration (T) rates, but direct measures are discrepant at larger scales. Moreover, the potential for high nocturnal T has not been addressed in this species. Focusing on nocturnal water fluxes, we investigated temporal congruence between sapflow and eddy covariance, both seasonally and following rain events. We then conducted a second study to track detailed canopy processes over a 24-hour period. In the first study, measurements were taken in central New Mexico in 2004 near the end of the growing season. Total evapotranspiration (ET) declined more rapidly through the senescent period than did T. The contribution of nocturnal sapflow increased progressively over time and immediately following rain events, corresponding with temporal trends in ET. The second study was conducted in west Texas in May 2006 to determine if nocturnal sapflow was used to refill stem capacitance or for immediate T, a potential explanation for inconsistencies between eddy covariance and sapflow data at night. Sapflow, stomatal impressions, stem water content, leaf water potential, and leaf gas exchange measurements were taken at 3-hour intervals. Stomatal impressions revealed that a considerable proportion of the stomata were partially open at night, coinciding with minimal rates of stomatal conductance, sap flux, and leaf T. Additionally, stem water content was significantly higher at 2:00 am compared to 2:00 pm. Results from both studies suggest that *Tamarix* is indeed transpiring at night, but a significant amount of nocturnal sapflow contributes to refilling stem capacitance, especially following rain events. Furthermore, efforts to quantify *Tamarix* ET or T using eddy covariance or sap flux techniques must consider the potential for positive water fluxes at night.

# Constraints on transpiration in irrigated and rainfed *Eucalyptus globulus* trees in southern Tasmania

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The constraints on transpiration were studied in *Eucalyptus globulus* trees over the summer at a research site in southern Tasmania. Diurnal patterns of leaf water potential and tree water use, measured using heat pulse techniques, were examined monthly in rain-fed and irrigated trees growing under similar atmospheric conditions. Soil matric potential declined during the summer in rain-fed plots but remained high in irrigated plots. Pre-dawn and midday leaf water potentials decreased in rain-fed trees and this was associated with increasing soil water deficit. Furthermore, transpiration and canopy conductance were lower in rain-fed trees than irrigated trees and the decline in transpiration and canopy conductance was related to pre-dawn leaf water potential. There was a marked hysteresis in the relationship between transpiration and D in both rain-fed and irrigated trees. Hysteresis was also observed in the relationship between transpiration and leaf water potential, however this was only evident in rain-fed trees. In the case of transpiration vs. D, hysteresis was larger at high D's than at low D's in both rain-fed and irrigated trees and was not related to whole tree hydraulic conductance, estimated as the slope of the relationship between transpiration and leaf water potential. Whole tree hydraulic conductance of rain-fed trees declined in response to decreasing pre-dawn leaf water potential. We propose that loss of hydraulic conductance is an important mechanism for explaining increasing stomatal control of transpiration under progressive soil drying.

# **Responses of CO2 and H2O fluxes on land-use change in a tropical rain forest margin area in Central Sulawesi (Indonesia).**

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Deforestation of tropical rainforests results in changes of heat, water and CO2 budgets of land surfaces, and hence, in changes of local and regional climatic conditions. Most recent FAO statistic data indicated that South-Eastern Asia is currently characterised by the highest deforestation rate (more than 5% of the total area per 10 years). To predict potential effects of deforestation on the heat, water and carbon balances of land surfaces in the rain forest margin area, two process-based SVAT models (Mixfor-SVAT and SVAT-Regio) were applied to the area of the Lore Lindu National Park (LLNP) in Central Sulawesi (Indonesia). LLNP is an unique area which contains one of the largest intact forests in Indonesia. Increased economic activity of a very rapidly growing population in and around LLNP, result in serious pressure to forest ecosystems.

The applied SVAT models - Mixfor-SVAT for local and SVAT-Regio – for regional scales - are based on the multi-layered representation of the canopy and soils and use aggregated descriptions of the physical and biological processes on the different spatial scales (Olchev et al., 2002, 2006). The more sophisticated Mixfor-SVAT was used to describe the effect the conversion of tropical forest to corn, cacao and rice fields at local scale. SVAT-Regio was used to describe responses of energy, water and CO2 fluxes on land-use changes at the regional scale. In our study we used a relatively extreme deforestation scenario, assuming the strong decrease of the areas covered by tropical rain forests by about 20% and increase of agricultural and urban areas.

The present land-use pattern was described from LANDSAT ETM+ data. The spatial LAI pattern was derived from NDVI data and field measurements at key experimental plots. The regional meteorological patterns were reconstructed using the measurements from 10 meteorological stations. The modelling experiments showed that 20% deforestation results in a decrease of regional NEE of CO2 by about 12% and but only in a unexpectedly small decrease of monthly evapotranspiration (about 2%). The latter can be explained by the relatively high transpiration of the planted agricultural crops (e.g. corn) and increased soil evaporation (about 21%).

The accuracy of the presented trends in energy, water and CO2 flux changes, is mostly limited by lack of required biophysical data, model simplifications like, e.g., the limited representation of the variability of actual forest conversion and the lacking feedback of the fluxes to local atmospheric conditions.

#### The isotopic composition of forest canopies: New issues and applications

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The application of isotopic tools to the study of ecological change has greatly expanded in recent years. Stable isotopes in biomass, water, and atmospheric trace gases provide a great deal of information about the physical, chemical, and biological processes that affect forests over varying temporal and spatial scales. Potential applications of these methods are numerous, but here I will focus on recent work in: 1) interpreting commonly measured stable carbon isotopes of plant material and respired CO2, 2) isotope-based partitioning of canopy fluxes, and 3) using isotopes to trace multiple aspects of environmental change in highly disturbed and human-dominated forests. I will include results from recent advances in the application of high resolution, optically based measurements of isotopic composition in addition to traditional IRMS methods, as well as the potential for combining multiple environmental for coordination in environmental monitor networks and for regional scaling, particularly when combined with eddy covariance, atmospheric monitoring, GIS databases, and other methods discussed at this workshop.

## **SPP** - a model to estimate the photosynthetic production of forest stands applied to several pine stands across Europe

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Although the instantaneous response of leaf or shoot photosynthesis to environmental factors is quite well understood, the upscaling of shoot level photosynthesis to canopy level and over longer time periods still remains subject to study.

We have developed a model to calculate the photosynthetic production of a forest stand. The model combines a detailed canopy light (direct and diffuse) attenuation model and different mechanistic shoot level photosynthesis models. The forest stand can be heterogeneous: it can consist of several species and trees of different size and crown form. Photosynthetic parameters can be derived directly from leaf-level measurements. Meteorological data is used as input; time step is 30 min. Because SPP is flexible and easy to parameterise, it can readily be used for different sites.

We have applied SPP to calculate gross primary production (GPP) for several years of four pine-dominated stands (three Scots pine stands and one Maritime pine stand) located across Europe with marked variation in climate and water availability. We show the comparison of the results against GPP estimates obtained with eddy covariance. The results show generally very good agreement, and indicate that variation in climate across years and sites is much more important than fine-scale variation in leaf physiology.

SPP is a tool to analyse canopy photosynthesis and its dependence on environmental driving variables in heterogeneous stand structures and under different meteorological conditions.

## Carbon and water fluxes in a temperate pine forest chronosequence during a year with a warm and dry summer in southern Ontario, Canada

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Human activities in eastern North America have significantly altered the land surface. During the last 100 years a substantial portion of these cleared land have come under natural succession and managed plantation forests. These forests are in various stages of their development. Few studies have investigated how environmental change and stand-age affects the carbon dioxide (CO<sub>2</sub>) and water vapour exchange capacity in these stands, particularly in temperate conifer forests. We initiated year-round observations of energy, water vapour and CO<sub>2</sub> fluxes in a chronosequence (3, 16, 31, and 66 year-old) of temperate conifer plantation forests (white pine) in southern Ontario using the eddy covariance technique. These sites are known as the Turkey Point Flux Station. We will present results of CO<sub>2</sub> and water vapour flux measurements over the warm, dry year of 2005. Evapotranspiration rates during the growing season were highest at the 16-year-old stand (3 - 5.5 mm day<sup>-1</sup>) followed by the 66- and 31-year old forests (1.5 - 4 and 1.5 - 3.5 mm day<sup>-1</sup>). Net ecosystem productivity (NEP) was highest in the 16-year-old stand with 494 g C ha<sup>-1</sup> y<sup>-1</sup>, followed by 196, 18, and -103 g C ha<sup>-1</sup> y<sup>-1</sup> in the 31-, 66-, and 3-year-old stands. Compared to previous years, the warm, dry summer of 2005 resulted in a decreased NEP by 100 - 200 g C ha<sup>-1</sup> y<sup>-1</sup> at each site due to increased ecosystem respiration. We found that radiation and temperature were the two dominant controls on NEP. Seasonal patterns of CO<sub>2</sub> uptake were further influenced by soil moisture. Our results indicate that carbon uptake and forest productivity peaks within the first 25 years after plantation establishment. The correlation between climate variables and CO<sub>2</sub> exchange is important to understand impacts of future climate change on forest productivity and carbon cycling.

### A comparison of long-term irrigated and non-irrigated red maple transpiration

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Indirect methods of quantifying evapotranspiration ( $\lambda E_a$ ) are sought since regional estimations of  $\lambda E_a$ require prohibitive instrumentation or highly parameterized and data intensive land surface models (e.g., involving temporally and spatially-varying soil moisture, soil hydraulic properties, and vegetation properties). Complementary relationship (CR) models, based on Bouchet's heuristic hypothesis, are one such method of estimating  $\lambda E_a$  from routinely-measured meteorological variables. The treatment of vegetation in existing CR applications varies from neglecting physiological controls on transpiration to indirectly accounting for such regulatory mechanisms through recalibration of Penman's empirical wind function. Moreover, the leading theoretical models (e.g., Morton, Granger, Szilagyi) of the coupled land surface – atmosphere mechanisms responsible for CR focus primarily on vertical humidity (vapor pressure) profiles while assuming that vegetative and/or atmospheric diffusivities play an insignificant role in regulating CR. As such, we conducted CR evaluations at both temperate grassland (FIFE) and mixed-deciduous forest (Harvard Forest) ecosystems to investigate how vegetative and atmospheric diffusivities regulate CR-type behavior. Our field campaign at Harvard Forest involved an intensive irrigation program to investigate the underlying CR assumption that  $\lambda E_p$  is synonymous with unlimited water availability. Root-zone soil moisture of a red maple (Acer rubrum L.) sample set was elevated using a pulseirrigation system. Whole-tree transpiration of the `potential` (water-unstressed) and a reference (water-stressed) set of maples was monitored at high frequency using heat-dissipation Granier-type sap flux sensors. Preliminary results suggest the following: (1) the absence of an unstressed canopy conductance in the Penman equation results in violation of fundamental CR assumptions for both FIFE and Harvard Forest; (2) unlimited root-zone water availability does not reduce the leaf-level stomatal resistance enough to yield a Penman-type  $\lambda E_p$  signal, suggesting that the complementarity of the  $\lambda E_p$  signal is also a function of other environmental stresses, *e.g.*, vapor pressure deficit; and (3) eddy covariance measurements demonstrate that wind speed, and thus atmospheric conductance, increases with a reduction in regional moisture availability. In summary, our results yield valuable insight into how vertical atmospheric and vegetative diffusivities should not be neglected in theoretical advancements of Bouchet's heuristic CR hypothesis.

# Nocturnal Transpiration in Norway Spruce Trees is Consistent with the Nutrient Supply Hypothesis.

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A long-term nutrient optimization experiment in a nutrient-deficient, boreal forest afforded an excellent opportunity to evaluate whether nocturnal transpiration is associated with soil nutrient limitation. Using sap flux methods, we have determined that nutrient-limited Norway spruce trees transpire at night at rates exceeding twice that of fertilized trees, when nocturnal transpiration is expressed as a percentage of total (24- hour) tree water flux. Minimum nocturnal sap flow velocities reached up to nine percent of maximum daytime velocities in nutrient-limited trees, but stayed below three percent of daytime maxima in fertilized trees. Total nocturnal transpiration in all trees increased as day length shortened by two hours over a 1.5 month interval of measurements, indicating that stomata in Norway Spruce trees are relatively insensitive to growing season variation in diurnal light variation, so that transpiration responds primarily to evening-to-morning variation in evaporative demand. While fertilized trees always showed substantially less nocturnal transpiration than nutrient-limited trees, fertilized trees did display a relatively larger increase in nocturnal transpiration from the early to late growing season than nutrient-limited trees. This coincided with an increase in soil moisture in the fertilized stand when soil moisture either declined or remained constant in plots containing nutrient-limited trees. Together, these results are consistent with a hypothesis that nocturnal transpiration acts as a physiological process supporting nutrient acquisition, while it exacts differential costs on the water economy of trees, depending on soil moisture availability. Because nutrient availability, water availability, and atmospheric humidity represent potentially co-occurring aspects of environmental change

in the boreal region, our results suggests the potential for large change in the nocturnal function of this widespread boreal tree species.

### Developing an empirical model of GPP with LUE approach: results from an analysis of eddy covariance data at five contrasting sites in Europe

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Gross primary production (GPP) is the origin of carbon in all ecosystem fluxes, and therefore a key component of the carbon balance between the biosphere and the atmosphere. While its biological basis is well understood, its quantification for different biomes is not straightforward, because of its dependence on a variety of environmental and internal drivers at several time scales.

The objective of this study was to develop an empirical model consistent with current process knowledge for the GPP of coniferous forests, using daily values of environmental driving variables and information about canopy leaf area as input. Daily values of GPP estimated from five European eddy covariance measurement towers during 2-5 years each were used as the independent variable. The model applied the idea of light use efficiency (LUE) reduced with modifying factors: a linear dependence was assumed between GPP and absorbed photosynthetically active radiation (APAR) estimated with the Lambert-Beer law from canopy leaf area, and this relation was modified with multiplicatively applied functions of APAR, temperature, vapour pressure deficit (VPD) and soil water content, the statistical and practical significance of which were then analyzed. It was hypothesized that the same parameterization could be applied to all sites and years, and this was tested by comparing the site-specific parameters to those of the pooled data, and by testing the model in independent data from two AMERIFLUX stations.

The model with APAR, temperature and VPD modifiers did well in almost all the site-year combinations, whereas incorporating the soil water modifier improved the fit significantly only in few cases. The LUE parameter values varied between the sites: in pine stands, LUE decreased from north to south, and in the only spruce stand LUE was larger than in the pine stands. The modifier parameterization obtained in the pooled data appeared very adequate compared to site-specific parameterizations: most of the differences in GPP between the sites could be explained by the differences in LUE, leaf area and environmental conditions (PAR, temperature, VPD); this finding was corroborated by model testing in the independent AMERIFLUX data. The model with such parameterization could not, however, capture year-to-year variability in GPP, which together with the regional variation of LUE impede its use for actual prediction.

# Impacts of *Alliaria petiolata* invasion on nutrient cycling and native plant diversity in southern New England forests

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The impact of invasive species on the biological diversity and ecosystem function is one of today's most pressing global environmental problems. *Alliaria petiolata* (garlic mustard, family Brassicaceae) was introduced to the US in 1868 from Europe, and it is now found widely distributed throughout the US and Canada. It is an herbaceous biennial that is shade tolerant and can invade intact native forest ecosystems. *A. petiolata* produces glucosinolates, a group of secondary compounds which release isothiocyanates upon enzymatic degradation. The release of these organic cyanides into the soil, either through litter decomposition or root exudation, may confer a competitive advantage to *A. petiolata* by altering fungal and microbial communities or by influencing nutrient cycling processes. The spread of *A. petiolata* may therefore affect the composition of forest communities as a direct consequence of changing N & P availability or as an indirect response of altering soil microbial communities. The effects of *A. petiolata* invasion on nutrient cycling are currently unknown.

## Hemlock woolly adelgid density affects net photosynthetic rates but not respiration rates or needle biochemistry in eastern hemlock

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Invasive, non-native insects and pathogens are a significant threat to native forests. Currently, forests from North Carolina to Massachusetts are experiencing striking declines in eastern hemlock (Tsuga canadensis) associated with the invasion of the hemlock woolly adelgid (Adelges tsugae). Although this invasion may dramatically alter carbon and nutrient cycling in affected forests through effects on resource uptake and allocation within infested trees, relatively little is known about the effects of the hemlock woolly adelgid on hemlock physiology. This study examined the effects of differences in hemlock woolly adelgid density on photosynthesis, nitrogen uptake and allocation, and needle biochemistry. Net photosynthetic rates declined by 30% as the average adelgid density increased from zero to 0.5 adelgid per needle. However, net photosynthetic rates did not significantly vary as adelgid density increased from 0.5 to two adelgid per needle. Adelgid infestation was associated with reductions in total protein concentrations in needles, but needle nitrogen and chlorophyll concentrations did not significantly vary with adelgid density. Similarly,  $\tilde{N}^{15}$  tracer analysis indicated that the adelgid did not significantly affect nitrogen allocation to needles. Quantum yield, light compensation points, and daytime respiration rates did not significantly vary with adelgid density. These results suggest that even low densities of the adelgid lead to significant reductions in net photosynthetic rates. Further, these results suggest that adelgid effects on net photosynthetic rates are driven by effects on nitrogen allocation within needles rather than by effects on nitrogen allocation to needles.

### **Carbon Allocation in Forest Ecosystems**

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Carbon allocation plays a critical role in forest ecosystem carbon cycling by shifting the products of photosynthesis between respiration and biomass production, ephemeral and long-lived tissues, and aboveground and belowground components. We reviewed existing literature and compiled annual carbon budgets for forest ecosystems to test a series of hypotheses addressing the patterns, plasticity, and limits of three components of allocation: *biomass*, the amount of material present; *flux*, the flow of carbon to a component per unit time; and *partitioning*, the fraction of gross primary productivity used by a component. Hypothesis testing focused on four key questions:

- *Can annual carbon flux and partitioning be inferred from biomass?* We found that biomass was poorly related to carbon flux and partitioning.
- Are component fluxes correlated and, if so, why? All component fluxes (leaf NPP, wood NPP, aboveground respiration and total belowground) were correlated and increased linearly with increasing gross primary productivity (a rising tide lifts all boats).
- *How does carbon partitioning respond to variability in resources and environment?* Within sites, partitioning to aboveground wood production and belowground sinks responded to changes in stand age and resource availability, but not to competition. Increasing resource supply resulted in increased partitioning to aboveground wood NPP and decreased partitioning to belowground. Partitioning to foliage NPP was much less sensitive to changes in resources and environment. Changes in partitioning in response to resource availability and forest age within a site were <15% of gross primary productivity, but much greater than those inferred from a relationship across all sites.
- Do priorities exist for the products of photosynthesis? The data do not support the concept of "priorities" for the products of photosynthesis, because increasing GPP increased all component fluxes. Our analysis does support several intriguing ideas about how carbon is partitioned in forest ecosystems. Respiration and foliage appear to use constant fractions of GPP–partitioning to both was very conservative across forests that represent a broad range of gross primary productivity. Partitioning to aboveground wood production and to belowground were the most variable. Conditions that favored high gross primary productivity decreased partitioning to wood.

# Infestations of hemlock woolly adelgid are associated with changes in eastern hemlock ectomycorrhizal fungal communities and soil conditions

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In the northeastern United States, populations of eastern hemlock (Tsuga canadensis) are declining due to defoliation by the introduced invasive insect, the hemlock woolly adelgid (Adelges tsugae). Ectomycorrhizal fungal communities, soil chemistry, and soil nutrient cycling associated with eastern hemlock may be affected by adelgid-induced defoliation. To make predictions for changes in eastern US forests after eastern hemlocks die, it is important to understand how the ectomycorrhizal fungal communities and soil conditions that are associated with healthy hemlock stands are changing as a result of infestation of hemlock woolly adelgid. In Black Rock Forest of southern New York, ectomycorrhizal fungal communities and soil chemistry variables were compared between eastern hemlock stands that were infested with hemlock woolly adelgid with those that were relatively healthy. Results of this study showed that hemlock defoliation associated with hemlock woolly adelgid infestations results in lower ectomycorrhizal fungal richness and root tip density. Results of Sørensen's quantitative index suggest that the decline in ectomycorrhizal fungal richness and root tip density does not result in a very different ectomycorrhizal fungal community composition, but that all morphotypes decline in number, though some of the rarest species are eliminated. Hemlock woolly adelgid infestation also results in higher soil C/N, higher soil NO3- concentrations, higher soil NH4+ concentrations, and faster net nitrification. Changes in ectomycorrhizal fungal communities and soil chemistry show that the decline of the eastern hemlock could have a large impact on the soil ecology of eastern forests.

### Current state of canopy spectral invariants in remote sensing

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The spectral invariant approach aims at separating canopy reflectance to terms that depend only on canopy structure, and to terms that depend only on wavelength. The wavelength dependent part is simply leaf optical properties (leaf reflectance and transmittance in different wavelengths). The spectral invariants are wavelength independent and describe canopy geometrical structure. The aim is to find a small set of parameters that describe the effect of canopy structure on the multiple scattering of light inside the canopy. I present the current state in developing this set of parameters. (i) Canopy interception. The probability that a photon entering the canopy from above will not pass straight through to the ground. Depends on leaf area index (LAI), the degree of grouping, and the angle of incidence. (ii) Recollision probability. The probability that an at-least-once reflected photon flying inside the canopy will collide again with a canopy element. Depends on LAI and grouping, but seems quite insensitive to the angle of incidence. Recollision probability is simple and powerful. Using it and leaf spectrum, we can predict canopy absorption in all wavelengths. It also seems possible to express recollision probabilities separately for each hierarchy level of grouping in canopy (shoots, branches, crowns) and to combine these in a nested expression giving the whole canopy recollision probability. (iii) Upward and downward escape probabilities. If a photon is not absorbed, it will escape from canopy. For canopy reflectance models, the upwards escaping part is of interest. Of course, the non-absorbed part not going up will go down, so parameterization for one solves for both. Currently there is a one-parameter model for escape probability that does not work well beyond simple homogeneous leaf canopies, and some more complicated models requiring several parameters. These work better but seem like curve fitting, and there is no simple physical interpretation for the parameters. However the rules governing photons to escape upwards or downwards may not be too complicated, and I hope that a simple parameterization (one or two parameters) could be found. Some more work is needed. This set of parameters describes the effect of canopy structure on how the incoming radiation is partitioned into reflection, canopy absorption, and soil absorption. It may as such be useful in global climate and ecosystem models. In order to use models to invert canopy parameters from remote sensing data, also (iv) a parameterization for the directional distribution of upwards escaping photons is needed.

# Landscape-scale studies of ecosystem response to management: lessons for better interpretation of plot-level studies

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Knowledge about ecosystem processes is most often desired at the landscape level, but experiments are almost always conducted at the plot level to gain a mechanistic understanding of process. Researchers take great care to locate the experimental sites as being 'representative' of what might be expected for a landscape response. We used a novel 'twin-plot' approach to assess forest growth response to optimal silviculture (fertility, weed and pest control) across a wide variety of planted *Eucalyptus* forest estates in Brazil capturing a broad range of climates and soils. Two-year growth responses to optimal silviculture for ~800 control-optimal pairs in these highly productive forests ranged from 0-100% increase in wood production. The distribution of responses was very broad, even for similar climate and soils. The sampling design showed that the response to optimal silviculture varied with water availability and soil chemical composition. However, even considering these factors, variability remained, and no single site would have predicted the landscape response. We conclude that: 1) the approach was easy to implement because it was linked with the existing inventory networks; 2) it offered a true landscape perspective: that there was a wide range of responses, not all of which could be predicted from climate and soil; 3) annual or bi-annual measurements also offered insights into temporal variability with stand age and climate; 4) Even though the approach could not explain all of the variability in the response to optimal silviculture, the network of twin plots helped map areas to locate more intensive studies and also guided management application. We suspect that the same variable response would apply for any ecosystem characteristic and response and encourage researchers to consider implementing such an approach across landscapes, in addition to the typical plot-level studies.

## Scaling up water relations in trees: Can we predict drought responses from underlying mechanisms and traits?

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Human-induced climate change results in rising temperatures and influence rainfall intensities and distributions worldwide. It is evident that morphological, physiological and developmental traits respond to climate. How these traits jointly influence tree growth remains unclear. We developed a new 3D plant growth model to integrate the drought effects on hydraulic architecture, water flow, carbon gain, and biomass allocation and 3D growth between environments differing in microclimate and soil water supply.

The current model version is based on a number of assumptions: trees consist of crown layers with similar dimensions and leaf density; trees are in steady state for the vertical distribution (over the layers) in leaf temperature, water potential and associated water fluxes, and internal leaf  $CO_2$  concentration; leaf area production is linked to secondary thickening growth, according pipe theory; growth is limited by the carbon economy. Eco-physiological relationships are thus coupled to hydraulic architecture, carbon economy and 3D growth. Based on environment factors (air temperature, light intensity, wind speed, air humidity, soil water potential) and tree status (e.g. 3D dimensions, leaf density, wood anatomy), the model predicts the steady state for the vertical distribution of water potential, leaf temperature, leaf  $CO_2$  concentration, stomatal conductance, and photosynthesis.

The first simulation results focus on the eco-physiological behavior of the model. We simulated the eco-physiological patterns of trees on two days, during a wet and dry period, respectively, in the Wallis Valley of Switzerland. The wet day (7 june 2002) was relative cool (midday temperature =  $20^{\circ}$ C) and humid (RH>90%), and the dry day (17 june 2002, only dry days in between) was warm (midday temperature =  $35^{\circ}$ C) and dry (RH~50%). The model predictions for diurnal responses in leaf temperature, water flow relationships, stomatal conductance, transpiration, and carbon gain are compared with measured eco-physiological parameters for pines and oaks, on a 10 minute basis for the same two days.

### Effect of calcium availability on nitrogen uptake by sugar maple and beech trees

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In this study, we examined the effect of calcium (Ca) depletion on inorganic nitrogen (N) uptake by mature sugar maple (Acer saccharum Marsh) and American beech (Fagus grandifolia Ehrh.) trees, two common tree species of the northeastern United States (U.S.). Acid deposition, caused by human activities, has led to significant base cation depletion in forests throughout the northeastern U.S. Depletion of soil Ca in forests has been linked to sugar maple mortality. However, it is not known whether Ca depletion is leading to a reduction in N uptake by sugar maple and other dominant tree species, which could potentially contribute to reduced vigor of trees. To determine whether Ca depletion has led to a decline in N uptake by mature trees, we measured N uptake by intact roots in two watersheds at the Hubbard Brook Experimental Forest in New Hampshire in the summer of 2006. Watershed 1 (W1) was fertilized with Wollastonite in 1999 to increase base saturation of the soil to pre-industrial levels. We also examined N uptake in the watershed directly west of the reference Watershed 6 (WW6), an undisturbed watershed. We utilized the N depletion method in the field to determine uptake rates of  $NH_4^+$  and  $NO_3^-$  at varying ratios of  $NH_4$ :  $NO_3$ . The response of N uptake to Ca depletion by mature individuals of sugar maple and beech differed. Roots of beech tended to take up less N when exposed to greater amounts of Ca, while roots of sugar maple took up more. Our preliminary results indicate that dominant tree species vary in their response to Ca depletion and that there may be some positive feedbacks between acid rain, soil Ca depletion, reduced N uptake by sugar maple and possibly greater losses of Ca from northeastern forests.
# The importance of heterogeneity: integrating lidar remote sensing and height-structured ecosystem models to improve estimation forest carbon stocks and fluxes.

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Lidar remote sensing data have been shown to effectively represent forest structure, constrain estimates of carbon stocks and, when used to initialize a height-structured ecosystem model fluxes, constrain fluxes. Here we use large-footprint lidar data from the NASA Laser Vegetation Imaging Sensor (LVIS) to initialize the height-structured Ecosystem Demography (ED) model to study forest structure and dynamics at Hubbard Brook Experimental Forest (HBEF). HBEF is in the White Mountains of New Hampshire and includes heterogeneity in elevation dependent abiotic factors (i.e. temperature, precipitation, and soil depth), which are important drivers in a well documented decline in biomass and species change with elevation. We produced an estimate of the forest structure and fluxes in 1999 across all elevations at HBEF by first spinning up the model with elevation dependent climate and soil characteristics and then initializing the model using 1999 LVIS canopy height data. We validated the initialized model estimates against extensive field data and demonstrated that above ground carbon stocks, basal area, and species composition were within 1, 5 and 7%, respectively, of the field data at all elevations. Model projections were validated using data from a second LVIS acquisition obtained in 2003, accounting for the effects of both model uncertainty and lidar uncertainty. The additional constraint provided by including elevation dependent abiotic heterogeneity in the model initialization suggests that the forest is closer to a mature state than when initialized without the heterogeneity. We conclude that together lidar data and a height-structured ecosystem model give more information about forest structure and dynamics because together they account for critical fine scale heterogeneity.

# Spatial and temporal scaling of intercellular CO2 concentration in a temperate rainforest dominated by *Dacrydium cupressinum* in New Zealand

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Seven methods, including measurements of photosynthesis (A) and stomatal conductance  $(g_s)$ , carbon isotope discrimination, ecosystem CO<sub>2</sub> and water vapour exchange using eddy covariance, use of a multi-layer canopy model and ecosystem Keeling plots, were used to derive estimates of intercellular  $CO_2$  concentration ( $C_i$ ) across a range of spatial and temporal scales in a low productivity rainforest ecosystem dominated by the conifer Dacrydium cupressinum Lamb. in New Zealand. Estimates of shoot and canopy  $C_i$  across temporal scales from minutes to years were remarkably similar (range of 274 to 294  $\mu$ mol mol<sup>-1</sup>). The gradual increase in shoot C<sub>i</sub> with depth in the canopy was more likely attributable to decreases in A resulting from lower irradiance (Q) than to increases in  $g_s$  due to changes in air saturation deficit (D). The lack of marked vertical gradients in A and  $g_s$  at saturating Q through the canopy, and the low seasonal variability in environmental conditions, contributed to the efficacy of scaling  $C_i$ . However, the estimate of canopy  $C_i$  calculated from the carbon isotope composition of respired ecosystem  $CO_2$  ( $\delta^{13}C_R$ ; 236 µmol mol-1) was much lower than other estimates of canopy  $C_i$ . Partitioning  $\delta^{13}C_R$  into four components (soil, roots, litter and foliage) indicated root respiration was the dominant (> 50%) contributor to  $\delta^{13}C_{R}$ . Variable time lags and differences in isotopic composition during photosynthesis and respiration make the direct estimation of canopy  $C_i$  from  $\delta^{13}C_R$  problematic.

#### Thermal Acclimation of Leaf Photosynthesis and Respiration in Populus Deltoides x Nigra

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There is a good deal of consensus that changes in temperature will alter rates of photosynthesis and respiration under future climates. Previous research also supports the notion that the thermal response of these processes acclimates in plants exposed to temperature change. However, the extent and rate of acclimation in tree species is still poorly understood. In this study we examined the extent and rate of thermal acclimation in photosynthesis and respiration in pre-existing and new leaves of *Populus deltoides* x nigra ('Veronese') saplings exposed to both increasing and decreasing temperatures. Trees were grown at both low and high levels of N availability to test the hypothesis that leaf N content limits the rate and extent of thermal acclimation. The response of respiratory and photosynthetic parameters was observed in pre-existing leaves transferred to the new temperature environment and in new leaves which expanded following transfer. Strong acclimation in rates of photosynthesis for both high-N and low-N plants were observed in pre-existing and newly expanded leaves, as the plants were transferred to warmer treatments. However, the transfer of plants from a warm to a cooler environment resulted in a more limited degree of acclimation. Thermal acclimation of respiration was also very strong in both pre- existing and new leaves and was determined almost solely by changes in respiratory capacity  $(R_{10}, R_{25})$  rather than by changes in thermal sensitivity  $(Q_{10})$ . There were no significant changes in the  $Q_{10}$  of leaf respiration following the transfer of plants to either higher or lower temperatures. We conclude that pre-existing leaves are capable of significant levels of thermal acclimation and thus growth of new leaves is not necessarily required to re-establish a new thermal response in poplar. In addition, N status of leaves may be an important determinant of the extent of acclimation.

#### High growth temperatures reduce photosynthesis, respiration and growth in black spruce

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The response of black spruce (Picea mariana (Mill.) B.S.P.) to predicted climate warming will have significant effects on the structure and functioning of the North American boreal forest. We investigated the growth, net CO2 assimilation and dark respiration rates of black spruce seedlings grown at cool (22:15°C) and warm (30:23°C) temperature regimes. Cool-grown seedlings were taller and heavier than warm-grown trees and had significantly lower mortality. Photosynthesis of warm-grown seedlings was unable to acclimate, leading to reduced carbon assimilation at high temperatures; however, dark respiration showed significant temperature acclimation. This study suggests that higher future temperatures will reduce the growth and carbon uptake of black spruce.

# The Impact of Water Stress on Net Carbon Exchange at the Wind River Old-growth Forest, Washington, USA

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One traditional ecological paradigm predicts that after a serious disturbance, forest systems start as a strong carbon source to the atmosphere, shift into a strong sink after a few years, peaking after some decades, and then decline as a sink until reaching carbon equilibrium. Conversely, some studies have demonstrated that older ecosystems under favorable climate conditions continue to be significant carbon sinks. The regional implications of this variation derived from limited surface data (e.g., eddy covariance

flux sites) is critical for identifying and quantifying the role of terrestrial ecosystems in climate change and the converse, the effect climate change on terrestrial ecosystems.

Here we present six years of eddy-covariance carbon and water fluxes at the Wind River Canopy Crane Research Facility (WRCCRF), a 500 year old coniferous forest in southern Washington, USA (45.821, -121.952, 365 m asl). Long-term flux data show exceptionally high interannual variability in atmosphere-ecosystem carbon exchange, implying that this old-growth forest ecosystem may not be in "steady state" conditions. In this paper we focus on the relationship between water availability and carbon sequestration at WRCCRF with the objective of quantifying the impact of water stress on net carbon exchange. While this forest has high biomass and a complex canopy, it experiences water stress during the regular, summer drought. Our results show that mean dry-season water use efficiency (WUE) varied from 1.8 mg g-1 in 1999 to 3.9 mg g-1 in 2003. WUE in 1999 was significantly lower than any other year (P < 0.0001) coinciding with very wet, La Niña conditions. We found evidence that summertime soil respiration is attenuated  $\sim 40$  to 50% during the summer drought compared to respiration in late spring/early summer. When modeling ecosystem respiration, a respiration attenuation factor based on soil moisture and understory net ecosystem exchange (NEE) data had to be derived for the years with the greatest water stress in order to not overestimate respiration for this ecosystem. Links between carbon exchange and precipitation suggest that water availability is an important factor in determining whether or not the old-growth forest becomes an annual carbon sink, source, or is at equilibrium. However restrictions on water availability can limit respiration during the driest years and therefore moderate the impact of drought on the annual carbon balance. Implications of this work may be significant considering that the region is predicted to have more extreme and prolonged drought periods.

# Environmental regulation of ecosystem carbon exchange and water balance in a mature rainforest in New Zealand

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The extensive indigenous rainforests of South Westland, New Zealand are dominated by the ancient conifer *Dacrydium cupressinum*. The age of the trees ranges from 150 to 200 years, but the productivity is attributable to low nutrient supply, resulting from the soils being highly leached, acid and frequently saturated in the high rainfall environment (3000 mm year<sup>-1</sup>). Measuring small rates of carbon input and loss to estimate annual net carbon balance is challenging, but necessary to quantify changes in carbon storage by these forests and predict the impacts of future climate change.

Results from detailed measurement and modelling of canopy architecture, photosynthesis by trees and understorey species, respiration from foliage, stems and soil, and transpiration and evaporation, combined with scaling approaches using stable isotope have been published independently. Here, we bring together the available data combined with a process-based canopy model to develop carbon and water balances for the site, then test these using independent net carbon exchange data from continuous eddy covariance measurements.

Leaf area index and photosynthesis are low at the site and attributable to low nutrient supply and low internal transfer conductance. Respiration, 40% of which is derived from the trees, is almost equivalent to canopy photosynthesis. An additional small net input of carbon from photosynthesising bryophytes on the forest floor leads to an overall annual net uptake of 1.3 Mg C ha<sup>-1</sup>. Measurements of net carbon exchange from eddy covariance in summer varied between +2.9 to -3.2 g C m<sup>-2</sup> day<sup>-1</sup> with short-term variability attributable principally to changes in irradiance. Net carbon uptake in this nutrient-limited ecosystem is highly sensitive to the ratio of direct to diffuse irradiance.

# From Landscape Snapshots to Regional Portraits of Forest Change: Extending Traditional Remote Sensing Analyses

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Forest change plays a very important role in the terrestrial carbon budget. Deforestation, forest harvest, and reforestation have significant impact on carbon dynamics. Dating back to 1972, Landsat imagery has provided a unique and invaluable data source for tracking change in forest. However, traditional methods of using Landsat data for monitoring forest change in large areas are limited. Less time-consuming and less cost-intensive methods need to be explored in order to take full advantage of the high spatial resolution Landsat data. New methods for forest change monitoring using Landsat TM imagery in the Blacksea region is explored based on the Generalization concept. The idea of generalization is to build classifiers based on a set of sample training sites at one place or at one time and apply them to other places or a larger extent or a different time frame. Results show that the Neural Network Classifiers trained locally have the potential in detecting forest change, but with significant comission errors. Large confusion happened between forest and agriculture. Primary results from the Partially Supervised Maximum Likelihood Classification show that forest are successfully differentiated from agriculture, which indicates it as a better way to reach generalization over a large area. Cross-scene classification of the later method needs to be explored in future.

# Species-specific stomatal response of trees to microclimate – a functional link between climate change and vegetation dynamics

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Over the last 20 years, the mortality of Pinus sylvestris has increased dramatically in the Wallis, a dry inner-Alpine valley of Switzerland. This mortality has led to a decrease in the abundance of P. sylvestris and to an increase in the abundance of Quercus pubescens. In parallel to this vegetation dynamic, a significant increase in mean annual temperature occurred, while precipitation showed no significant trend over the past decades. Obviously, these parallel trends are related, but is there causality?

If we assume causality between climate change and vegetation dynamic, a climate-sensitive physiological process must be found which can be measured under field-conditions and which reflects how strongly a species benefits from the predominating climatic environment in relation to its neighbours. Our study compared relative stomatal aperture values ( $\theta$ ) in a 10-min interval of four co-occurring species (Q. pubescens, P. sylvestris, Juniperus communis, and Picea abies) at two south exposed sites over a period of four years. Values of  $\theta$  were deduced from the ratio between measured twig sap flow rate and calculated potential transpiration. Relative species-specific  $\theta$  were placed in relation with microclimatic conditions of air and soil.

Our results distinctly show different species-specific stomatal response patterns to climatic conditions: Juniperus communis had more opened stomata under extreme dry and hot conditions than the co-occurring species. Q. pubescens was second best in tolerating drought stress. On the one hand, P. sylvestris was strongly affected by dry conditions which led to a distinct stomatal closure in parallel with decreasing soil water potentials on the other hand, it had an advantage over the others when the weather was relatively wet and cool. Picea abies was hardly competitive during the two measured very dry years 2003 and 2004 and it closed its stomata almost completely during the summer months.

These results are evidence for a causality between climate change and the observed change in species abundances but they do not rule out the many other factors contributing to this process in the Wallis. P. sylvestris grows in this valley close to the limitations set by its physiological capabilities. Every climatic change which results in warmer and drier conditions weakens the position of this tree species in comparison to Q. pubescens. Therefore, with the rise in temperature the probability of further pine decline increases and a further shift towards oaks is to expect.

## **Biographies of Keynote Speakers**

Note: Some verbatim biographical text below is excerpted from Keynote Speakers' institutional web pages.

**Dr. Darius Culvenor** is Research Scientist/Engineer with Ensis, a joint venture between Australia's CSIRO and New Zealand's Scion, two of Australasia's leading forest research organizations. Dr. Culvenor is a leading developer of the ECHIDNA® Validation Instrument, a prototype device aimed at improving the accuracy and efficiency of forest structural measurements. The ECHIDNA® concept uses scanning laser rangefinding (lidar) technology to capture details of forest structure, such as canopy height, the number and location of trees and their basal area, up to a radius of 110 metres from its survey point.

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**Dr. David Hollinger** is a Senior Research Scientist with the USDA Forest Service. He started his career in the Forest Research Institute (FRI) of the New Zealand Forest Service in Christchurch in 1984. In 1993, Dr. Hollinger joined the Northeastern Research Station of the USDA Forest Service in Durham, New Hampshire, as a Plant Physiologist. Dr. Hollinger's research focuses on the interaction between plants and their environment. This work has taken the form of understanding how different foliage and canopy characteristics affect CO2 uptake (photosynthesis) and loss (respiration). Several themes have carried through this work, including using simple physiological models, and considering biological systems from the principals of optimality.

Dr. Hollinger has been carrying out long-term studies of CO2 exchange and carbon sequestration in a spruce-hemlock forest near Howland, Maine since 1995. One of the results from these studies is that forest C sequestration is far more variable than anticipated. With colleagues from the Woods Hole Research Center, the University of Maine, and other universities, the original studies at Howland have been augmented by several large-scale forest manipulations. The first of these is designed to test whether low-level nitrogen inputs (anthropogenic N deposition) may be enhancing forest carbon uptake and storage, and the second study is investigating the impact of forest management (shelterwood harvest) on carbon sequestration. Support for these studies have come from the Forest Service, the Department of Energy, NASA, and the NSF. More recent interests include quantifying and using information about the uncertainty in flux exchange measurements.

David Hollinger USDA Forest Service PO Box 640 Durham, NH 03824 Phone: 603-868-7673 Fax: 603-868-7604 email: dhollinger@fs.fed.us Website: RWU NE-4104 **Dr. J. Patrick Megonigal** is Senior Scientist at the Smithsonian Environmental Research Center. Dr. Megonigal's research concerns carbon biogeochemisty with an emphasis on belowground processes in wetlands. He is currently studying the effects of elevated CO2 on plant productivity, soil carbon storage, and methane emissions. In addition, Dr. Megonigal is studying a variety of plant-microbe interactions including the contribution of root exudates to the metabolism of methaneproducing microbes and the role of rhizosphere iron-oxidizing bacteria to a root-associated wetland iron cycle. Dr. Megonigal's research has been supported by agencies including the US National Science Foundation and the US Department of Energy. Dr. Megonigal carries membership in the Ecological Society of America, American Geophysical Union, Association of Southeastern Biologists, Soil Science Society of America, and Society of Wetland Scientists.

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**Dr. Maurizio Mencuccini** is Senior Lecturer in the Institute of Atmospheric and Environmental Sciences, School of GeoSciences, University of Edinburgh. Dr. Mencuccini has published widely in the areas of vegetation scaling and allometry, xylem and phloem water relations, ecosystem fluxes and stocks, phenotypic plasticity in hydraulic properties, and ageing in trees. Dr. Mencuccini has held research appointments at the Boyce Thompson Institute for Plant Research at Cornell University; the Institute of Forest Ecology, University of Florence; and the Forest Research Institute, Arezzo, Italy. Dr. Mencuccini's research has been sponsored by organizations including the European Science Foundation; the Royal Society; the Leverhulme Trust; the Scottish Forestry Trust, and UK's National Environmental Research Council. Dr. Mencuccini serves on the Editorial Boards of the journals *Tree Physiology* and *Forest Ecology and Management*, and has been deeply involved with the CARBO-EUROFLUX network of European flux towers.

Maurizio Mencuccini Institute of Atmospheric and Environmental Sciences School of GeoSciences University of Edinburgh Darwin Building, Mayfield Road EH9 3JU, Edinburgh (UK). 0131 650 5432 m.mencuccini@ed.ac.uk; http://www.geos.ed.ac.uk/abs/research/forestsci/homepage.htm **Dr. Scott Ollinger** is Assistant Professor of Natural Resources in the Institute for the Study of Earth, Oceans and Space at the University of New Hampshire. Dr. Ollinger has research interests in and has published widely in the fields of forest productivity and biogeochemistry, ecological effects of air pollution, carbon and nitrogen cycling in forest soils, disturbance and land use history, ecosystem modeling and remote sensing, forest response to multiple environmental stressors, landscape ecology, and regional ecological analysis. Dr. Ollinger's research has been sponsored by organizations including the US National Aeronautic and Space Agency (NASA), the Environmental Protection Agency, the USDA Forest Service, and the US Department of Energy. Dr. Ollinger is Associate Editor of the journal *Biogeochemistry*, and has advised and contributed to international scientific bodies including UNESCO and the Intergovernmental Panel on Climate Change.

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**Dr. Diane Pataki** is Assistant Professor, Earth System Science, in the School of Physical Sciences, and Assistant Professor, Ecology & Evolutionary Biology, in the School of Biological Sciences, at the University of California, Irvine. Dr. Pataki has research interests in and has published widely in the fields of physiological plant ecology, ecosystem ecology, and global change biology. Her specific interests are in the processes that control the exchange of gases between the terrestrial land surface and the atmosphere. Dr. Pataki studies these processes with plant physiological and meteorological measurements, including measurements of sap flow and whole plant transpiration; isotopic tracers as integrators of the processes that influence plant gas exchange; and biogeochemistry. Dr. Pataki's lab conducts these measurements in a variety of ecosystems ranging from natural areas and wildlands to urbanized and highly disturbed areas. Dr. Pataki's stated goal is to improve our ability to quantify the role of terrestrial ecosystems in the earth system, as well as the effects of global change on ecosystems and the services they provide to society. Dr. Pataki has held previous appointments at the University of Utah, the Desert Research Institute, Nevada, and was a Program Officer in the Global Change and Terrestrial Ecosystems (GCTE) core project of the International Geosphere-Biosphere Programme (IGBP).

Diane Pataki University of California 3313 Croul Hall Mail Code: 3100 Irvine, CA 92697 Phone: (949) 824-9411 Fax: (949) 824-3874 Email: dpataki@uci.edu **Dr. José Luiz Stape** is Professor in the Department of Forest Sciences at the University of São Paulo. Dr. Stape has research interests in and has published widely in the areas of forest productivity, forest nutrition, ecological consequences of invasive species, plantation forestry, forest carbon allocation, and forest resource use efficiency. With more than 95 national and international colleagues, Dr. Stape has published more than 90 articles, eight book chapters, and one book. Dr. Stape currently participates in six major research programs in Brazil and throughout the world, acting as lead coordinator for five. In addition to Dr. Stape's research, he teaches and mentors graduate students at the University of São Paulo.

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## Bartlett Experimental Forest, New Hampshire IUFRO Field Tour Saturday, October 7, 2006

Time	Site	Speaker	Торіс
7:00 AM	Leave Durham		
@ 9:00 AM	Arrive	Rest stop, snacks, tour historic house & site	
	Passaconway		
9:50-10:10 AM	Passaconway	Tom Wagner, WMNF	Welcome
		supervisor	Plan for the day
		ML Smith, NRS	
10:10-10:30 AM	Passaconway	Christy Goodale,	History of WMNF
		Cornell	
10:30-10:50 AM	Passaconway to 2 <sup>nd</sup> overlook	Load bus, take Bear Notch Road to second overlook	
11:00AM-11:20AM	2 <sup>nd</sup> overlook	ML Smith, NRS	Orientation to WMNF
			landscape, history of BEF
			Forest, group picture?
11:20-11:40 AM	2 <sup>nd</sup> overlook to	Load bus, take Bear Notch Road to Powder House.	
	Powder House		
11:45 AM-12:45 PM	Flux Tower &	Dave Hollinger, Julian	Flux Tower
	NACP plot	Jenkins	
	(2 groups, 30		
	minutes each)	Scott Ollinger,	North Am. Carbon Program
		ML Smith	study site
12:45 – 1:00 PM	Powder House to	Walk to Bear Notch Road, take bus to 3 <sup>rd</sup> overlook	
	1 <sup>st</sup> overlook	OR take bus to 1 <sup>st</sup> overlook, drive through forest	
1:00 – 1:30 PM	1 <sup>st</sup> overlook	Lunch	
1:30 – 2:00 PM	1 <sup>st</sup> overlook	Mary Martin,	RS of forest composition &
	at	Jeanne Anderson	structure
2:00 PM – 2:15 PM	1 <sup>st</sup> overlook to	Load bus, drive to hairpin turn (upper road)	
	hairpin turn		
2:15PM – 3:15 PM	2 groups, 30 min	Scott Bailey, Rich	Cation depletion
	each	Hallett	
		~ ~ ~ ~ ~ ~ ~	
		Scott Ollinger, ML	Old growth, Forest NPP, RS
		Smith	estimation
3:15-3:30	Hairpin turn to	Load bus, drive to middle road-Bear Notch junction	
	Hemlock site		
3:30-4:30	2 groups, 30 min. each	Wally Shortle	Cation cycling by fungi
		Rich Hallett	Hemlock wooly adelgid, canopy chemistry
4:30-5:00PM	Load bus, travel to Eagle Mountain House		
5:00PM- 7:30(?) PM	Dinner at Eagle Mountain House		
7:30 PM- 9:30 PM	Load Bus, travel back to New England Center		

## Preliminary schedule for IUFRO field tours at Harvard Forest, October 10, 2006:

1. Introduction to Harvard Forest and its history – John O'Keefe (for all IUFRO participants)

2. Divide into 3 groups for visits to EMS tower, Hemlock tower and small hurricane-simulating pulldown

- Group 1 visits EMS eddy flux tower for presentation by John Budney and Kathryn McKain, Research Associates, Earth and Planetary Sciences Department, Harvard University.
- Group 2 visits Hemlock eddy flux tower; presentation by Julian Hadley, Plant Ecophysiologist, Harvard Forest
- Group 3 visits Hurricane Simulation Pulldown; presentation by Audrey Barker Plotkin, Research Associate, Harvard Forest
- 3.
- Group 1 visits Hemlock eddy flux tower
- Group 2 visits Hurricane Simulation Pulldown
- Group 3 visits EMS eddy flux tower
- 4.
- Group 1 visits Hurricane Simulation Pulldown
- Group 2 visits EMS eddy flux tower
- Group 3 visits Hemlock eddy flux tower

5. Break (at Shaler Hall; all participants reassemble

6. Divide into two groups for visits to Soil Warming and Hemlock Forest Logging / Girdling experiments; Ride to respective sites.

7. Group 1 visits Soil Warming Experiment: Presentation by Jacqueline Mohan, Postdoctoral Research Associate with Marine Biological Laboratory (Woods Hole, MA), Ecosystems Center

8. Group 1 leaves Soil Warming Experiment

9. Group 1 walks into Hemlock Forest Experimental sites for presentation by Aaron Ellison, Senior Research Scientist, Harvard Forest (15 minute walk in and out).

- 10. Group 1 returns to Shaler Hall.
- 11. Group 2 walks into Hemlock Forest Experimental sites for presentation by Aaron Ellison
- 12. Group 2 leaves Hemlock Forest Experiment sites
- 13. Group 2 visits Soil Warming Experiment
- 14. Group 2 returns to Shaler Hall

## **Autumn Foliage Color**

(excerpted from John O'Keefe's Autumn Colors project on the Harvard Forest Website).

## 1. The Biological Significance of Leaf Color Change

Not long ago the consensus was that autumn leaf colors were the result of the unmasking of the carotenoid or anthocyanin pigments, and could have no function. We now know that the anthocyanins are not un-masked, but are made. There is growing evidence that these colors may have clear functions, assisting plants during the autumn. However, the riddle is explaining such function in leaves that are dying. Such a functional role must benefit the plant well beyond the short life of the leaf, and must extend into the following year. How might plants be benefited? Physiological Explanations - especially anthocyanins in red leaves

Anthocyanins may be physiologically important in aging leaves in two ways. First, anthocyanins are very strong anti-oxidants. There is growing evidence for the nutritional importance of anthocyanins in diet in retarding the beginning of some symptoms of aging.

Secondly, anthocyanins act as a sun-screen, protecting chloroplasts that are vulnerable as they take the chlorophyll molecules apart under autumn conditions of cold temperatures and bright sunlight. The pay-off for the plant is that this protection could increase the efficiency of resorbing the nitrogen that is released from the breakdown of chlorophyll and the enzymes of photosynthesis, taking it from the leaves and putting it back into the branches and trunk to be used the next spring. The evidence (documented in the scientific bibliography) is that the redder leaves have less nitrogen when they fall from the trees, compared to leaves without anthocyanin.

### **Biological Explanations**

Changes in pigments during leaf aging changes their appearance to animals. Animals might not recognize the leaves, or might recognize them more easily, depending on their color sensitivity. Thus, changes in leaf color could have the following functions.

\* Leaf Camouflage: a red or yellow color might camouflage leaves so that animals might not recognize-and eat-them. Theory proposed by Barry Juniper

\* Fruit Flag: bright leaf color might attract animals to consume less colorful fruit and increase the dispersal of seeds to other locations.

\* Leaf Apparency: a red or yellow color might make the leaves more apparent to animals. If the signal is associated with a toxin or poor palatability, color might repel the insects and "dissuade" them from laying eggs on the plant, thus reducing damage to the plant in the following year.

\* Avoiding Camouflage: Bright leaf color might repel animals that would otherwise eat leaves because they would be poorly camouflaged and more likely to be picked off by their natural predators. Theory Proposed by Simcha Lev-Yadun

## **Northeastern US Natural and Human History**

Excerpted pages from Field Guide to New England, by Peter Alden et al., 1998 National Audobon Society

12 OVERVIEW

## Topography

Inland New England is dominated by the Appalachian mountain range. Elevations increase gradually northward from the Connecticut shore through the Berkshire Hills of western Massachusetts and Vermont's Green Mountains. The highest clusters of peaks-several over 5,000 feet in elevation-are in the White Mountains of New Hampshire. Other ranges extend northcastward through Maine. A relatively flat glacial outwash plain covers parts of Rhode Island and southeastern Massachusetts, meeting the sea in sweeping sand beaches. Farther north the coast turns mainly rocky, and along its entire length there are many peninsulas and islands. The Connecticut River is New England's longest, but the Merrimack in New Hampshire and Massachusetts and the Penobscot, Kennebec, Saco, and Androscoggin in Maine are also extensive. Vermont's Lake Champlain is the largest lake, followed by Lake Winnipesaukee in New Hampshire and Moosehead Lake in Maine. Thousands of smaller lakes and ponds dot the landscape.

#### 1. Lake Champlain

This large freshwater lake, on the Vermont-New York border, is 125 miles long and up to 14 miles wide, with a maximum depth of 399 feet. Whale bones discovered near its shores in 1848 provide evidence that the lake was once filled with seawater.

#### 2. Mount Washington At 6,288 feet, Mount

Washington, in the Presidential Range of New Hampshire's White Mountains, is the Mt. Frissel 2.380 tallest peak in New England. Formed 380 million years ago, the ridge is composed of very compacted and resistant schist.

pringfield Hartford CONNECTICU Block ong Island Sound Island

#### TOPOGRAPHY 13

#### 3. Quabbin Reservoir

The largest inland body of water in Massachusetts and an important source of water for Boston and other Massachusetts cities, the Quabbin Reservoir was formed in 1939 by the damming of the Swift River. Its 120-square-mile watershed comprises hilly woodlands, marshes, and fields. The towns and hamlets of Enfield, Greenwich, Dana, and Prescott were abandoned and demolished so the waters of the reservoir could fill the river valley.

> 4. Mount Desert Island Most of Acadia National Park is on Mount Desert Island, at 104 square miles the largest island off the coast of Maine. Glaciers sculpted the island's features: a chain of rounded granite peaks, boulders deposited on mountainsides, long, narrow lakes, and a fjord.

#### 5. Narragansett Bay

Cape

Nantucket

nusett

Bay

Martha's

Vineyard

Vinalhaver

Gulf of Maint

Island

Narragansett Bay is part of a coastline that was flooded when sea levels rose as the glaciers melted at the end of the last ice age. The bay's numerous inlets and passages are mainly aligned in a north-south direction, the result of glacial drainage guided by the original bedrock structure.

#### 6. Connecticut River

The Connecticut River rises in a series of lakes in New Hampshire near the Canadian border and flows southward along old fault lines, forming the state line between New Hampshire and Vermont. It then cuts through Massachusetts and Connecticut and empties into Long Island Sound, amid vast salt marshes, at Old Saybrook-flowing a total of 407 miles. The Connecticut River drains approximately 11,000 square miles, nearly one-third of New England's landscape.

HABITATS 31

#### OVERVIEW 30

## Northern Conifer Forests and Alpine Regions



New England's coniferous woods are so dark and thick in parts that all animal sound seems to issue from the only open areas available, the treetops. Cape May, Blackpoll, and Blackburnian Warblers sing their high-pitched songs from the tips of spruces in early summer, and Red Squirrels fuss at almost everything in their arboreal territories. Generations of Moose have traveled the well-worn trails. At the

higher elevations, on the Mount Katahdin tableland and in the Green and White Mountains, isolated populations of glacial-era plants and animals-such as Bigelow's Sedge and the Mount Katahdin race of the Polixenes Arctic butterfly-exist in a glorious and fragile alpine environment.



Spruce forest, Cathedral Woods, Monhegan Island, Maine

#### Spruce-Fir Forests

Growing in the coolest, wettest corners of New England, spruce-fir forests (often called boreal forests) occupy three distinct regions: high mountains from northwestern Maine to southern Vermont, boggy peatlands in the same range, and the fog-shrouded coast of eastern Maine. The coastal forests are dominated by Red and White Spruces, those surrounding bogs by Black Spruces and Tamaracks, and the mountain forests by Balsam Firs and Red Spruces. These dark coniferous woodlands-foresters call conifers "softwoods"are almost devoid of ground cover vegetation, as little light penetrates the thick evergreen groves. The attractive Bunchberry is one species that thrives in the highly acidic soil in these low-light surroundings. Spruce Grouse survive in these dark groves by eating conifer needles, while wood warblers and insects abound in summer. No New England forest is more fragrant.



#### Krummholz

Krummholz, Mount Washington, New Hampshire

Krummholz (German for "crooked wood") is the very tangled, stunted, low-growing forest that exists on mountain slopes in a narrow belt just below the tree line. Krummholz grows only as tall as the insulating snow layer permits, usually only a few feet; high winds and bitter winter temperatures prevent growth above this level. Few birds inhabit the krummholz, a harsh environment for much of the year. One that nests here exclusively is Bicknell's Thrush; from late May through July its song is the characteristic. sound of this forest type. Higher peaks in all three northern New England states have trails leading up into the krummholz.

#### Alpine Zone

Once you pass the tree line, you are in the alpine zone. Sedges, lichens, and dwarf wildflowers abound in this most hostile of New England environments. The animals here are mainly invertebrates that spend most of their lives in hibernation, with perhaps a fewweek summer breeding period. New Hampshire's Presidential Range has nearly 8 square miles above timberline, including Mount Washington's Alpine Gardens, where hardy wildflowers and the blackish-grayish White Mountain race of the Melissa Arctic butterfly can be seen. Other alpine areas occur atop Vermont's Mount Mansfield and Camel's Hump and on Maine's Mount Katahdin.



#### HABITATS 33

#### OVERVIEW 32

## Northern Broadleaf Forests



Northern broadleaf forest covers most of Maine and Vermont, two-thirds of New Hampshire, and the Berkshire Hills in western Massachusetts. Dominated by maples, birches, and American Beech-broadleaf trees for which the forest is named-it commonly includes such conifers as Eastern Hemlocks, Eastern White Pines, and spruces. One of the great glorics of the New England scene is its fall foliage,

and this is the forest that produces the most spectacular display. From mid-September through mid-October, maples take on brilliant orange and red hues, while birches and beeches turn radiant yellow and gold (see page 102 for a description of how leaves turn color and a map of fall foliage periods in New England). Those who know the northern broadleaf woods visit them at other seasons as well, for they are marvelous year-round.



Maple-birch-beech woods along Howe Brook Trail, Baxter State Park, Maine

Maple-Birch-Beech Woods

The forest floor beneath this deciduous woodland holds a dark, fertile soil rich in minerals and humus. A comparatively open canopy allows sunlight to stream down upon the thick mat of forest leaf litter, establishing a rich, open environment perfect for the growth of numerous shrubs, wildflowers, and tree seedlings. Woodland butterflies such as the White Admiral can be abundant in summer. This forest is home to a full complement of vertebrates, from Red Efts (Eastern Newts) to Yellow-bellied Sapsuckers to Common Porcupines. Black Bears, White-tailed Deer, and Moose forage extensively here.



White Pine Woods Eastern White Pines grow scattered about the northern broadleaf forest, especially in New England's central regions, and often occur in quite extensive stands on drier, sandier soils. Do not expect a richness of

Fostern White Pine

plant diversity here, for the pine needles that carpet the forest floor are low in phosphorous, calcium, and potassium, elements essential to plant growth. A few species adapted to this acidic environment, such as the Canada Mayflower, occur in abundance. Eastern White Pines provide perfect nest sites for several hawk, owl, and woodpecker species, and food for the immature stages of hundreds of species of beetles, moths, and other insects.

#### Hemlock Woods

Whereas Eastern White Pines prefer sunnier, drier, sandier sites, Eastern Hemlocks reach their greatest abundance in cool, moist areas, and commonly occur throughout most regions of the northern broadleaf forest. Near the southern reaches of the forest, however, Eastern Hemlocks are much more common in cold, dark ravines and on shaded hillsides. The inquisitive, noisy Red-breasted Nuthatch may be heard among the hemlock boughs. Hemlocks can grow to majestic size if spared the ravages of fire, which is much more devastating to them than it is to broadleaf trees such as Red Maples and oaks, which easily sprout back to life from burned stumps; a serious fire will wipe out hemlocks for decades.



Eastern Hemlock woods in spring, Petersham, Massachusetts

#### HABITATS 35

**Oak-Hickory** Forests

Spreading across Connecticut, Rhode Island, eastern Massa-

chusetts, and a bit north along

the coast, this is a modern for-

cst, grown up on post-agricul-

tural land in the 20th century.

Various oaks and hickories

dominate the open, relatively

dry woods canopy, while Sas-

safras is common in the un-

derstory. Ground cover

includes native ferns, wild-

flowers, shrubs, and, in places,

#### OVERVIEW 34

## Southern New England Forests

Transition Forests Oak-Hickory Forests Pine-Oak Woods

Hike through any of the forests of southern New England and chances are you eventually will find your path blocked by a lichen-covered stone wall. The trademark New England stone walls that cross untold miles of upland woodlands speak of the drama of the changing landscape-of the innumerable fieldstones left by the scouring glaciers, of the clearing of the original forests by farmers, of the sub-

sequent abandonment and regrowth of the land. These woods, which are primarily a mixture of broadleaf and coniferous trees, are a patchwork of southern and northern species, comparatively short and open in places, tall and dense in others. Mushrooms of every description and reintroduced Wild Turkeys are two features of the landscape. As their name suggests, these forests cover almost all of Rhode Island, Connecticut, and Massachusetts, except for the Berkshire Hills, as well as a few low-lying, southern areas of Vermont, New Hampshire, and Maine.



Great Bay National Wildlife Refuge, Newington, New Hampshire

**Transition Forests** A transition forest is just what its name implies, a transitional blend zone between southern and northern New England forest types. Oaks, birches, maples, and Eastern White Pines grow in different parts of the forest, which occurs in a diagonal band from northwestern Connecticut to southwestern Maine, with northward tongues well up the Merrimack and Connecticut River valleys. Resident White-tailed Deer, Common Raccoons, and Eastern Gray Squirrels abound. The songs of the Black-throated Green Warbler, Black-throated Blue Warbler, and Solitary, Red-eyed, and Yellowthroated Vireos, which glean arboreal insects and their larvae, may be heard throughout these woods from May to July.



invasive introduced species. Japanese Barberry, armed Chestnut Oaks, Barkhamsted, Connecticut with spincs and doggedly aggressive, forms an impenetrable shrub layer in some parts of this forest. Eastern Screech-Owls find deer mice, Southern Flying Squirrels, woodland moths, and carthworms aplenty for feeding their broods. Virginia Opossums-active, like owls, mainly at night-may sometimes be glimpsed padding along woodland paths.

#### Pine-Oak Woods

An impoverished, sandy soil keeps the variety of trees to a minimum in the pine-oak woodlands that are characteristic of Cape Cod and that also spread across much of southeastern Massachusetts and north-central Rhode Island. Tall Pitch Pines and small, multibranched Bear Oaks often occur together and greatly outnumber all other species. The name Pitch Pine refers to the high resin content of the knotty wood; the American colonists produced turpentine and tar they used for axle grease from this species. The Eastern Towhee and the Fowler's Toad race of Woodhouse's Toad share the woodland floor with the Trailing Arbutus, or Mayflower, whose pinkish-white blossoms herald the New England spring.



#### 8 OVERVIEW

## The Effects of Humans

New England's primeval forests, with their soaring Eastern White Pines and magnificent American Chestnuts, thrived until 400 years ago. Since the first Europeans set foot here, this corner of the continent has undergone cataclysmic change. In a matter of generations, European settlers transformed, completely and irrevocably, lands the Native Americans had scarcely altered in 10,000 years. The fields that replaced the forests, the wildflowers that grow in the fields, the insects that visit the wildflowers—in these and myriad other features, New England's landscape, fauna, and flora have been greatly transfigured. The effects of human activities shown here are but a few of thousands.



#### The Beaver and Man

Beaver lodge, Holderness, New Hampshire

American Beavers were once abundant in New England. From 1631 to 1636, some 12,500 pounds of beaver pelts were shipped to England from the Plymouth colony alone. However, overtrapping took its toll: by 1700 beavers were virtually eliminated from all but the northernmost areas of New England. One result: the ponds that drained when thousands of unmaintained beaver dams collapsed became fertile land for farming. Today tens of thousands of beavers have returned to New England from adjoining regions, and once again beaver dams are part of the landscape.

#### The Gypsy Moth

Number 27 Myrtle Street, Medford, Massachusetts, was home to Leopold Trouvelot, introducer of the Gypsy Moth to North Amer-

ica. Experimenting with the European moths in the 1860s, he allowed some to escape, and the rest, as foresters and homeowners throughout the region know, is sad history. Gypsy Moth caterpillars, unlike most lepidopterans, feed on an enormous range of plants—they can strip hundreds of species of trees, vines, shrubs, wildflowers, and even aquatic plants of their foliage. If an outbreak of the moths is severe, trees may be killed within a year or two.



Gypsy Moth caterpilla



#### CONSERVATION AND ECOLOGY 49

Introduced Plants and Animals New England's successfully introduced species of plants and animals have arrived over the course of four centuries. The plants are perhaps best thought of as "alien" rather than "introduced," as they generally came as stowaway seeds that took root along roadsides and train tracks and near ports, then natu-

ralized in open country over the years.

European Skipper

Most New England alien plant species, including many clovers, the Oxeye Daisy, dandelions, hawkweed, Queen Anne's Lace, and Yarrow, are European in origin. Some escaped garden flowers, and trees such as the Blue Spruce and the Apple, have also spread across the region. Nearly 1,000 introduced plant species have become naturalized in New England. Many animals were deliberately introduced, often to be hunted (Ring-necked Pheasant) or fished (Largemouth Bass), or to eat city insects (European Starling and House Sparrow), or to benefit growers (Honey Bee). Unintentionally introduced animals include the abundant European Skipper and the Japanese Beerle.

#### The Effects of Introduced Species

Introduced species of animals and plants tend to change the landscape, sometimes dramatically and often for the worse. The European Starling is arguably New England's most common bird, and its aggressiveness has made life more demanding for smaller species such as Eastern Bluebirds. Purple Loosestrife, with its tenacious root system, is crowding out native wetland plants and changing the face of many freshwater marshes by turning



Purple Loosestrife

them into biologically unproductive monocultures. Other invasive exotics may feed on native species or carry diseases and parasites for which local organisms have few or no defenses.

#### The Felling of the Forests

The rigors of the New England environment, coupled with an unromantic, theological view of man's place in the wilderness, put early European settlers to work clearing the land and imposing an Old World landscape of orderly fields and town commons. The cutting of trees for fuel, but one element of the process, consumed a quarter billion cords of wood by 1800. In the 19th century, the advance of the railroads and invention of the stearn sawmill sounded the death knell of New England's great surviving primeval forests. The last large stand of such forest, a 300-acre broadleaf tract in Colebrook, Connecticut, was cleared in 1913.

#### WEATHER 55

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#### Weather

New England's location at an atmospheric crossroads—halfway between the equator and the North Pole and at the meeting of landmass and sea—is the dominant factor controlling its climate. Arctic cold waves, mild breezes from the distant Pacific (modified by their long journey across the continent), moist subtropical air off the nearby Gulf Stream, and fog-laden air from the North Atlantic all converge on the region to breed a great variety of weather.



warm and cold air into vast wind patterns, including the prevailing westerlies, a broad west-to-east air current that flows over the United States and southern Canada. Most of New England's weather approaches from the west, even its notorious nor'easters.

#### Highs and Lows

Embedded in the prevailing westerlies are a succession of whirls and eddies: systems of high pressure (fair weather) and low pressure (cloudiness, high humidity, stormy weather) that form and dissipate along fronts, which are the boundaries between warm and cold air masses. Winds blow in a circular pattern around the center of Northern Hemisphere weather systems: either counterclockwise (as seen from above) in a low-pressure system or clockwise in a highpressure system. In New England, low-pressure systems often form along a front between arctic air to the north and subtropical air from the Gulf Stream to the south. High-pressure systems may arrive from the arctic reaches of Canada and Siberia, bringing bitter cold in winter and refreshing air in summer, or cross the continent from the Pacific Ocean, bringing milder weather. During autumn months, a mild high-pressure system may become entrenched over New England, bringing pleasant "Indian summer" days.

#### How Storms Come and Go

While most New England storms arrive from the west, including the Canadian midwest (in the form of Alberta clippers, named for their rapid motion), and from the southern plains (Colorado lows), they may also approach from the Gulf of Mexico and the Caribbean. "Back-door" fronts, cold fronts that slip southwest from the North Atlantic, can bring sudden chill and fog in spring and relief from the heat in summer. In late summer and fall, New England is occasionally hammered by hurricanes from the south. Nor'easters, so named because northeasterly winds blow onshore from a low off the coast, may form off New England's coast or they may originate over the Gulf of Mexico, the Appalachians, or even far inland, around Colorado. Several nor'easters pound New England in an average year.

#### Tracing a Nor'easter

A nor'easter can dump many inches of rain (or a foot or more of snow) across much of New England and whip the coastline with gale-force winds (39 mph or much higher).

THE STAGE IS SET

All nor'easters feature an arctic high from the north and warm subtropical

air (a low) from the south, with ;

front separating them. Before the storm system develops the front ma

remain stationary for a while, producing light rain or snow or heavy thus



### THE STORM BUILDS

As the storm system starts spinning in a counterclockwise direction, a warn front to the east marks the leading edge of northbound warm air. As it rise over the colder, denser air to its north, the gently rising warm air produce

derstorms.

steady rain or snow. Meanwhile, west of the center, arctic air plunges south behind a cold front, along which heavier cold air shoves like a wedge beneath the warm and usually moist air. Forced upward, the warm air expands and cools, its moisture condensing into clouds, rain, or snow.



along the coast (but with lingering precipitation and clouds over the mountains and east of the Great Lakes), one or more days of fair skies, and eventually southerly winds ahead of the next storm.



#### THE END OF THE STORM

After several hours, the center of low pressure passes, generally to the east or northeast, followed by the cold front, which may set off brief but heavy showers, squalls, and thunderstorms. As the storm departs, in-flowing high pressure brings clearing, colder weather