Tree-related research at Wytham Woods

The following notes provide background to some of the work going on in Wytham Woods, focussed particularly on changes in the tree and shrub layer and its function. It has been developed for and from a workshop held at the Wytham Field Station on November 21st 2013. We are grateful to those who attended and contributed material to this compendium.

Contents

The Dawkins Plots .................................................................................................................................................. 3
  Introduction .......................................................................................................................................................... 3
  Main trends......................................................................................................................................................... 3
Paviour-Smith/Mihok Regeneration study ............................................................................................................. 5
Environmental Change Network (ECN) - seedling abundance, tree height and tree DBH ......................... 6
  ECN - Lichen study.......................................................................................................................................... 6
Canopy Research at Wytham .................................................................................................................................. 7
  Key results ......................................................................................................................................................... 7
  References ....................................................................................................................................................... 7
Deer exclosures ....................................................................................................................................................... 8
Other references to complement other reports ..................................................................................................... 8
The Smithsonian Forest Dynamics Plot in Wytham ............................................................................................. 9
  Measuring trees in 2009 (Butt et al. 2009)....................................................................................................... 9
  References ....................................................................................................................................................... 9
Flux Tower and Carbon Cycling Research at Wytham ......................................................................................... 10
Patterns of oak death in Wytham Woods ............................................................................................................ 12
Forest fragmentation and carbon cycling in Wytham Woods ............................................................................... 14
  Background .................................................................................................................................................... 14
  Research........................................................................................................................................................ 14
  Major findings ............................................................................................................................................... 14
  References .................................................................................................................................................... 15
FORESTPRIME: Predicting carbon release from forest soils through priming effects. ......................... 16
  Summary ......................................................................................................................................................... 16
Earth Observation at Wytham Woods ..................................................................................................................... 17
Drilling down from stand to leaf level: the application of airborne remote sensing for studying biomass, leaf chemistry and the impact of tree diseases in British woodlands .................................................. 19
Plant Virology ....................................................................................................................................................... 21
Spatial components of plasticity in tit phenology: adaptation, constraints and amelioration ...................... 22
  Key references ............................................................................................................................................... 23
Other potential resources for researchers interested in work at Wytham ....................................................... 24
  Past publications relating to Wytham Woods. ............................................................................................... 24
Historic aerial photographs ........................................................................................................ 24
Management plans .................................................................................................................. 24
Elton Notebooks ..................................................................................................................... 25
Woodland history ................................................................................................................... 25
The Dawkins Plots
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Introduction
Between 1973 and 1976 (hereafter referred to as the 1974 survey), 164 10x10m quadrats were established at alternate points of a 100x100m grid by Dawkins and Field (1978). Various measures of tree and shrub cover were made as follows:

- The occurrence of all woody species in the plot was noted
- Diameters (breast height) of the four largest trees in the plot were measured;
- Canopy cover (>2.5m) (split by species) and shrub cover (all species) (0.5-2.5m) was estimated across the plot diagonal;
- The basal area of the trees in the plot and its surroundings was estimated by relascope sweeps;
- Regeneration (seedlings and saplings up to 1m tall) were noted in 13 0.1m² circlets positioned evenly along the two diagonals of the plot.

A partial survey of these plots was carried out in the 1980s and a full re-survey was completed in 1991-92 (the ‘1991 resurvey’), 1999-2002 (the ‘1999 resurvey’) and 2011-12 (the ‘2012 resurvey’) (Horsfall and Kirby, 1985, Kirby et al., 1996, Kirby, 2004, Savill et al., 2010).

![Distribution of plots of different origins and treatments](image)

Figure 1. The distribution of the plots across Wytham Woods and their stand type: a.i pre-1800 woodland, still semi-natural; a.ii pre-1800 woodland disturbed by planting; b.i 19th C. colonisation, still semi-natural; b.ii 19th C. colonisation, replanted 1945-60; c 19th C. plantations; d. 20th C. plantations; e. rides and open grassland.

Main trends
Aerial photographs taken in the 1940s show the canopy was very open in places, with large gaps, probably a consequence of wartime felling, and that large areas that have now become wooded, were rough grazing or fields. By 1974 (when the plots were first surveyed), the average canopy cover was around 80% across the whole wood with a dense understorey as a consequence of both
planting and natural regeneration. Most trees were young; the largest tree in the plot was most likely to be in 11-20 cm diameter class.

Since 1974 there has been relatively little change in the canopy layer cover but the understorey cover has declined markedly. The number of species records also dropped between 1974 and 1991. The basal area of trees has more than doubled (shrubs were not included in this part of the recording process). The increase in basal area is reflected also in the increase in the mean size of the largest trees in the plots and the shift in the median size class for the largest trees in the plots to 31-40 cm. This equates roughly to trees about 40-60 yrs old in 2012. The main tree species tended to show one of two patterns in diameter distribution: *Fraxinus excelsior* and *Acer pseudoplatanus* had a pulse of regeneration (part planted but mostly natural) that was released in about the 1950s; *Fagus sylvatica* and *Quercus robur* contribute most of the large-diameter stems and much of their younger growth is in the plantations.

*Fraxinus excelsior* has increased across all measures using all measures of abundance. *Acer pseudoplatanus*, *Quercus robur* and *Fagus sylvatica* had slight declines or no change in occurrence, little change in their contribution to the canopy cover and slower basal area growth than *F. excelsior*. *Betula spp* and *Ulmus spp*. declined, particularly in terms of plot occurrences, but also in terms of their relative contributions to canopy cover and basal area. There were fewer conifers in 2012 than in 1974, but their basal area had increased. *Ilex aquifolium* was unusual in showing a marked increase in plot occurrences, although as yet its contribution to canopy and basal area overall was very small.

Shrubs other than *Crataegus spp.* and *Prunus spinosa* declined after 1974, contributing to the overall loss of understorey cover, but there were indications of possible recovery by 2012 for *Corylus avellana* and *Euonymus europaeus*.


Paviour-Smith/Mihok Regeneration study
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This study investigates changes in the composition of part of Wytham Woods (southern England), between the 1960s and 2007. The study focussed on an area of about 4 ha shown on a 1961 aerial photograph, part former open common, part ancient woodland. Changes in the canopy appearance were considered using a recent (1999) aerial photograph. Trees and shrubs were recorded in a 200 m x 10 m transect to illustrate current stand structure across the historic management division. In the north-east corner of the area tree diameters and understorey abundance from 1968 were compared with the current stand structure.

Since the 1950s *Fraxinus excelsior* has colonised the open areas. Tree growth was estimated from comparison of diameter/girth measurements from 1968 and 2007. *Fraxinus excelsior* diameter increment was greater than that of *Acer pseudoplatanus* and both showed faster growth than *Quercus robur*. Some canopy trees died, but no large gaps formed in the closed woodland. The abundance of understorey stems declined. The current stand structure reflects effects of past management, browsing pressure and climatic stresses over the last four decades. Multiple causes of change are probably commoner than single factors in explaining woodland structure.

The aerial photograph of the sampling site (grid reference SP 461086) from 1961 (left) (Elton 1966) and 1999 (right). The photographs have been re-orientated to run south-north compared to the version in Elton (1966). Note the increased canopy closure and abundance of small canopied trees in the south of the area by 2007.

The ECN monitors changes in vegetation throughout the woods and farm, in woodland, grassland and managed fields. In a small number (currently 14) of plots vegetation is recorded annually (10x10m plots). Vegetation is also recorded every nine years in 45 plots (2x2m). Where these plots occur in woodland or scrub, a 10x10m plot, centred on the 2x2m plot is used to record the presence of woody trees and shrubs every three years. Ten smaller plots (40x40cm) were randomly selected within the plot and the species and number of woody seedlings were recorded. In each smaller plot the tree nearest the centre of the plot with a DBH of greater than 5 cm was measured, DBH, height and number of stems. These smaller plots were marked and resurveyed.

The results show that the growth rate of 11 tree species have shown a general downward trend, although there are yearly fluctuations. For *Fraxinus excelsior*, tree DBH had increased by an average of 1.3cm between 1993-96, but by only 0.67cm between 2008-2012.

The most abundant seedling in the plots has been *F. excelsior*. In 1993 there were 101 seedlings and this increased to 760 in 2005, however there was a drop in 2008 to 424 and 443 in 2011. In contrast, for *Acer pseudoplatanus* there was a rise in the number of seedlings between 2005 (n=12) and 2008 (n=150), followed by a decrease to 6 seedlings in 2012.

*ECN - Lichen study*

As part of the ECN we have a sandwich student working with us each year, and each year they carry out a small research project. This year Joe Rowland, an Environmental Sciences student from the University of Aberystwyth, is looking at the abundance of lichen on oak and sycamore trees in three areas of the wood, classified by intervention; natural, semi–natural and managed. This is planned to start in the next couple of weeks.
Canopy Research at Wytham
Mike Morecroft

The canopy of the forest and its effects on microclimate, carbon and water cycle processes has been better studied at Wytham than almost anywhere else in the world. The canopy walkway which was put up in 1993 under the TIGER programme (mainly for studying food webs) was stimulus for a series of research projects looking at leaf scale carbon and water dynamics in situ. Other sampling has been carried out using cherry pickers at a variety of forest edge sites. Microclimate, including soil water has been monitored at the walkway, in Ten Acre Copse at the ECN Target Sampling Site, the flux tower site and a variety of forest edges.
A wider variety of data are potentially available for further analysis including leaf nitrogen contents, leaf area index, specific leaf area, carbon isotope ratios (d13C), photosynthesis and transpiration rates.

Key results
Slow development (approximately a quarter of the growing season to reach maximum rates) of photosynthetic capacity, particularly of oak leaves, in the spring
Interspecific differences in photosynthetic capacity of canopy leaves of different species
Higher water loss at forest edges
Quantification of the buffering effect of a forest canopy on temperatures
Description of vertical profile in canopy characteristics

References
Deer exclosures
In 1997 we started an exclosure experiment to test the effects of deer grazing on ground flora and trees. 3 exclosures were set up in areas of ancient woodland (abandoned hazel coppice with standards), each containing 3 10m square monitoring plots of the same design as the ECN woodland plots. This shows that the changes in the woods that were recorded in the 1980s and 90s which have been ascribed to deer are, as would be expected, reversed by exclosure.

Draft manuscript - contact Mike Morecroft for further information

Other references to complement other reports

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The Smithsonian Forest Dynamics Plot in Wytham

In collaboration with Earthwatch, in 2008 an 18 ha Forest Dynamics plot was established in Wytham Great Wood, which has been regularly censused since then following both the CTFS and RAINFOR protocols (Marthews et al. 2012). Several other research projects are running alongside this, utilising the base data of the tree census to look at all aspects of forest dynamics.

Measuring trees in 2009 (Butt et al. 2009).

- All tree stems down to 1 cm diameter have been measured and mapped across all 18 ha.
- Continuous measurement of CO₂, water and energy fluxes is underway at the flux tower in the NW of the plot (in partnership with CEH).
- Direct measurements of soil and stem CO₂ efflux from the trees and soil surface are also taken regularly.
- Ground cover survey

References


Flux Tower and Carbon Cycling Research at Wytham
Yadvinder Malhi. OUCe.

The intensive carbon cycle plot is a 1 ha plot situated in the NW corner of the 18 ha plot. Over the period 2006-2009, comprehensive measurements of the major components of net primary productivity and autotrophic and heterotrophic respiration were conducted by CEH/Oxford DPhil student Katie Fenn. Since 2009 measurements have continued at this plot at a lower intensity, led by Nathalie Butt, Terhi Ruitta and Martha Crockatt.

The flux tower monitors fluxes of carbon dioxide, water and energy above the forest canopy, and is operated by CEH and ECI. Data from the years 2008-2010 were published by Thomas et al (2010). Over 2012-2013 data have been intermittent through lack of a dedicated project, but from Nov 2013 an modem transmission system is being installed so the data can be checked on a daily basis.

There is also a full automatic weather station on top of the tower, and an soil and ground layer weather station operated (monitoring light levels at the ground, and soil temperature and moisture)

Net primary productivity, respiration and gross primary product at the carbon plot.

Net carbon fluxes from the 18 ha plot (net change in biomass) and from the flux tower (which includes net soil and necromass fluxes). Blue indicates net uptake of CO2 by the canopy (in the daytime and in summer), and red net release of CO2.

A comparison of net biomass increase in the 18 ha plot, which is in close agreement with the net carbon balance measured by the flux tower. The plot is increasing in biomass because it is still aggrading, with little mortality to offset the growth. The agreement with the tower suggests that net soil and necromass carbon fluxes are relatively small.


![Graph](image)

**Fig. 5.** The Net Ecosystem Exchange (NEE) “pulse” of Wytham Woods showing diurnal (x-axis) and seasonal (y-axis) CO₂ fluxes in μmol CO₂ m⁻² s⁻¹, generated using CarboEurope’s online partitioning tool.
Patterns of oak death in Wytham Woods
Ella F. Cole, Ben Sheldon Department of Zoology.

During February 2011 all oak trees in Wytham Woods (384ha) with a diameter at breast height (dbh) of 30cm or above were mapped using handheld GPS equipment. The dbh of all mapped oaks was recorded, as well as the health of each tree’s crown. Health was scored on a scale of 1-5 (where 1 = 0-24% crown dieback, 2 = 25-49%, 3 = 50-74%, 4 = 75-99%, 5 = completely dead). In total 5748 oaks were mapped, 323 of which were dead. The dbh of oaks ranged from 30–202cm (mean = 63.8, s.e = 0.325).

Oak trees which were completely dead or dying (75-100% dieback) were, on average, larger than healthy trees (less than 25% dieback), but smaller than trees with intermediate health scores (25-75% dieback, see figure 1 & 2). The fact that dead trees appear to be intermediate in size suggests that the observed pattern of oak death is not solely caused by very old trees dying, or the self-thinning of small trees. Indeed the majority of oaks found in dense plantation areas, which generally had a dbh between 30-40cm, had minimal crown dieback (see the first panel of figure 1). However, it is possible that there is a bias in these data, as small trees tend to have very small concentrated crowns; making it more challenging to score dieback (especially when the branches are bare). This would result in the number of small, healthy oaks being inflated. To attempt to rule out this possibility, the accuracy of these dieback scores will be assessed by carrying out spot checks once the oaks are in leaf. To establish whether self-thinning may be contributing to the observed patterns in oak death, more detailed analysis is needed that accounts for oak spacing.

As part of this oak survey Wytham was split into 122 discrete compartments, usually bounded by linear features. Compartment size ranged from 0.07 - 14.1 ha (mean = 3.15, s.e = 0.263). The percentage of oak trees that were dead or dying (75-100% dieback) was calculated for each compartment. These data suggest that the distribution of oak death across Wytham appears to be non-random (figure 3). As the boundaries to the compartments used here usually coincided with changes in woodland structure, the compartments will loosely correspond to different management areas (e.g. beech plantation vs. mature oak woodland). This means that the observed patterns in oak death could be the result of cohort effects, or something particular to the management of certain compartments. Information from the plantation records and woodland management records could be used to establish whether this is the case. Alternatively these patterns could be caused by spatially heterogeneous environmental factors, or the spread of some sort of infectious disease. The relative importance of these different
factors could be established by analysing oak death distribution on a finer scale, testing for
correlates with environmental gradients, and examining the proximity of dead and dying trees to
one another.

Figure 2. Differences in average oak size (dbh) between the different crown dieback categories
(Mean ± standard error, N=5748).

Figure 3. Map showing the distribution of oak death across Wytham, measured as the proportion of
oaks in each woodland compartment that have more than 75% crown dieback. Percentage
categories: ≥ 21% (red), 13 – 20% (orange), 7 – 12% (yellow), 1 – 6% (dark green), 0% (light green),
and compartments that were excluded as they contained fewer than 5 oaks (white).
Forest fragmentation and carbon cycling in Wytham Woods
Martha Crockatt, Earthwatch, November 2013

Background
Woodland across the UK and much of western Europe has been fragmented through agriculture, urbanisation and road building, e.g. in England 64% of woodland is within 100 m of the forest edge (Riutta et al., 2011). Forest edges are generally warmer and drier, with greater fluctuations of temperature and moisture, than the forest core. This altered microclimate is expected to alter carbon cycling through impacts on tree growth, physiology and community structure, as well as similar impacts on decomposer function and communities.

In 2008 – 2009 a network of permanent sampling plots were established, with funding from the HSBC Climate Partnership, to investigate the impacts of fragmentation on temperate forest carbon cycling. This was part of a larger, global programme run by Earthwatch, with University of Oxford leading the research in Wytham (Dr Terhi Riutta, in Prof Yadvinder Malhi’s group at Environmental Change Institute). Mike Morecroft (Natural England) and Jill Thompson (CEH) were also partners. The research is supported by groups of volunteers, generally from corporate partners, who contribute significantly to data collection (Butt et al., 2013).

Research
There are 9 plots (1 ha each), based in the core and north/south facing edges of the main body of the woods, and in six fragments of varying sizes around Wytham. Within each plot a number of metrics have been measured:

- Tree biomass: initial census established co-ordinates, species and diameter of all stems ≥ 5 cm DBH; the census is repeated bi-annually to look at population trends (dead trees, new trees) and changes in carbon stocks through diameter change. This year we have finished the third complete census.
- Intra-annual stem growth: dendrometer bands were installed on a subset of trees by size class and species in 2010; monthly measurements of these provides data on intra-annual growth patterns.
- Dead wood: line intersect sampling for dead wood was conducted in all plots between 2008 – 2011, and repeated in 2013.
- Soil respiration: measured in all plots 2010 – 2011; core plot only since 2012.
- Leaf litter: collected in all plots in 2010, then core plot only (gap in 2012). Sorted by date, species and litter fraction.

There have also been a number of stand alone experiments on leaf litter decomposition (Riutta et al., 2012; Slade and Riutta, 2012), soil faunal feeding (Simpson et al., 2012; Riutta et al., in prep.), volunteer data quality (Butt et al., 2013), canopy structure (McMahon et al., in prep) and edge effects on decay of coarse woody debris (ongoing).

Major findings
- Decomposition of both leaf litter (Riutta et al., 2012) and dead wood (Crockatt et al., in prep) is slower at the forest edge than core, with likely impacts on not only carbon, but also nutrient cycling. This is at least partly due to edge effects on soil fauna feeding activity, which is lower at the forest edge than core (Simpson et al., 2012; Riutta et al., in prep.), but may also be significantly related to edge effects on decomposer fungi (Crockatt, 2012).
• Core and edges / fragments vary in terms of species composition and carbon stocks, as well as canopy structure, the latter being more related to management history than plot “edginess” (McMahon et al., in prep);

• Although there is more error in data collected by volunteers than scientists, the error is acceptable given the larger sample sizes we’re able to collect (Butt et al., 2013).

References

In preparation:

Crockatt, M.E., Bebber, D.P. In preparation. Wood decomposition is slower at the forest edge than core.


Riutta, T., Clack, H., Crockatt, M.E., Slade, E.M. In preparation. Landscape scale implications of the edge effect on soil ecosystem processes in fragmented temperate forests.
FORESTPRIME: Predicting carbon release from forest soils through priming effects.

**Principle investigator:** Emma J. Sayer, Lecturer in Environmental Sciences, The Open University, UK.

**Funding:** European Research Council Starting Grant

**Project duration:** 60 months (Dec 2012 – Nov 2017)

**Summary**

Forest soils represent the largest terrestrial pool of carbon (C) in the world: they contain more C than the atmosphere and up to twice as much C as the aboveground vegetation. Interactions between plants and soils can have a major impact on the C balance of forests and play a decisive role in determining whether C is stored in the soil or released to the atmosphere. To date, it is unclear how increased plant inputs to the soil, as a result of enhanced tree growth or extreme weather events such as droughts or storms, will affect soil carbon dynamics. Recent work has shown that increased inputs of fresh organic matter (such as plant litter and root exudates), can stimulate the microbial decomposition of older, stored soil C, releasing CO$_2$ to the atmosphere via ‘priming effects’. Despite the potential of plant-soil interactions, such as priming effects, to impact upon soil C storage under future environmental change, we still know surprisingly little about the underlying mechanisms.

The first aim of this project is to redress current knowledge gaps to significantly advance our understanding of priming effects and provide essential data to improve predictions of the future carbon sequestration potential of forest soils. Priming effects are essentially *microbially-mediated responses to changes in plant inputs with consequences for biogeochemical cycling*; the study of priming effects in natural ecosystems therefore not only requires tools from different disciplines (microbial ecology, plant ecology and biogeochemistry) but also the harmonization of methods across scales differing by several orders of magnitude. The second aim of the project is therefore the reliable integration of results across scales.

FORESTPRIME takes a multidisciplinary multi-scale approach, combining the precision and detail of small-scale laboratory studies with large-scale field plots, to answer the following questions:

1) What controls the occurrence of priming effects in forest ecosystems?
2) Are there general patterns in soil C release by priming across different forest types?
3) Can the results of small-scale lab studies be reliably extrapolated to larger scales?

Soil C released by priming effects will be measured in response to experimental amendments of plant C inputs (leaf litter and root exudates) in temperate woodland at Wytham Woods, UK and in tropical forest in the Barro Colorado Nature Monument in Panama. The experiments are nested across three scales: the largest scale involves experimental plots (c. 600 m$^2$) at one temperate and one tropical forest site; the intermediate scale uses *in situ* ‘mesocosms’ (c. 0.3 m$^2$) in three forest stands along an age-gradient within each forest type. Finally, small-scale (c. 0.1 m$^2$) laboratory ‘microcosms’ involve >20 forest soils collected worldwide. The nested design makes it possible to compare results across scales and to test the validity of the extrapolation at each scale-step. The successful development of this scaling approach for experiments will deliver a new tool for investigating other microbial processes in the field.

FORESTPRIME represents the first comparative field study of priming effects to date and will deliver a comprehensive dataset on soil carbon dynamics under change in tropical and temperate forests.

**Website:** [www.forestprime.com](http://www.forestprime.com)
Earth Observation at Wytham Woods
France Gerard (ffg@ceh.ac.uk) and Charles George (ctg@ceh.ac.uk), EO team at Centre for Ecology and Hydrology, Wallingford; Clare Rowland (CEH Lancaster).

The CEH study was setup to investigate how the leaf phenology in Wytham woods and its temporal and spatial variability is observed through remote sensing. The work started in 2008. Our initial aim, developed jointly with Mike Morecroft (NE), was to establish if impacts of drought on the leaf canopy of trees were detectable by remote sensing through changes in leaf water content, and if we could see the difference in drought impact between the woodland edge and the centre. We have been waiting for a drought event ever since the study started. We now have moved on to a more generic study, trying to establish how the start and end of season in Wytham manifests itself in remotely sensed data, linking up flux tower observations, webcams and radiometry. We are still on standby for when a drought event occurs.

We have build up a good set of point based time series of radiometer, webcam and soil moisture observations and are committed to continue and expand these observations. Below are a summary of the measurements and a map locating the observations (Fig1).

Webcams
ECN regular long term camera snapshot of understorey.
One on flux tower capturing a panorama of woodland canopy
One aimed at an individual Oak tree which is also being measured by radiometer. This is to match up the radiometer measured reflectances with plant development stage.

Radiometers
2 Cropscan 16 channel radiometers measuring reflectance of an oak and a sycamore; footprint of measurement has 1m radius (canopy walkway).
Skye instruments NDVI and PRI sensor focussing on same oak (walkway).
2 more Cropscans to be deployed before next season (2014), one looking at an ash tree, one to record below canopy ground flora greening.

In-situ (drought study)
Used cherry picker to sample leaves for leaf water content (LWC) and nutrients and measure photosynthesis (IRGA) in the tree canopy (locations on map).
Neutron probe soil water measurements every month since 2005
Logged top 15cm soil moisture at 4 locations throughout the woodland since 1999.
Airborne data processing is ongoing – this will result in a (tree) species map of Wytham which we need as an input to upscale and match up the flux tower observations, radiometer observations with satellite observation.

Our radiometer data and flux tower data are being used by Anne Verhoef (Univ Reading) as part of a collaborative study aiming at evaluating the outputs of a radiative transfer, energy and carbon balance model (SCOPE) parameterised for a forest (Wytham) canopy.

Fig2. below shows a comparison between the phenological observations taken at Wytham Woods from the ground based ECN camera observing the understorey (weekly photo), the webcam on a fluxtower (fluxcam) observing the forest canopy from a wide angle, a radiometer (Oak radiometer) observing 1m² area of an Oak canopy and a MODIS 250m pixel, observing a mixture of forest, grasslands and cropland. The NDVI from the radiometer and MODIS pixel were compared with the Excess Green Index (Richardson et al., 2007) and the NDVI-red Index. These were calculated for the whole image, in the case of the weekly photos, and for sub areas of interest within the photo, in the case of the Fluxcam. The NDVI-red (Green – Red)/(Green + Red) is plotted below.
Drilling down from stand to leaf level: the application of airborne remote sensing for studying biomass, leaf chemistry and the impact of tree diseases in British woodlands
Minerva Singh, University of Cambridge

Temperate woodlands are recognised as important reservoirs of biodiversity, functioning ecosystems and carbon sinks and are increasingly being managed to protect ecosystem services. Airborne LiDAR methods provide an effective way of mapping forest structure over large spatial scales. The standard method of estimating forest biomass from LiDAR imagery involves using plot-based summary statistics. The objective of this study is to explore whether using image segmentation to identify individual trees offers an improved, more rigorous method of estimating above-ground biomass (AGB).

We worked with LiDAR imagery collected from Wytham Woods, Oxfordshire (UK). These data were collected in 2005-06 and has a low point density (approx. 1-2 points/m²). This woodland is mainly comprised of ash, oak and sycamore trees. Two approaches were used to estimate AGB from LiDAR imagery: (a) a standard approach of deriving descriptive statistics at a 100 x 100 m and 40m x 40m and 20m x 20m scale and (b) a segmentation approach in which individual trees were identified and biomass was estimated for each tree. Height and crown metrics were extracted from the LiDAR data and used in conjunction with field measurements of AGB to derive LiDAR predicted AGB both at 1ha and 20m scale. At the 1ha scale, a week correlation (Pearson’s correlation r =0.18) was obtained between field observed AGB and LiDAR predicted AGB. When we repeated the calculations at 20m scale, no correlation was found between field and LiDAR AGB. Three LiDAR-based models were derived from the segmented individual trees. One model used only LiDAR-derived height variables, one used only crown variables, and one used a combination of LiDAR-derived crown and height variables. Of these three models, the model based on the combination of height and crown variables performed the best and with R² values of 0.95, 0.92 and 0.88 for ash, oak and sycamore, respectively, when correlated with ground AGB values, and R² values of 0.98, 0.96 and 0.88 for ash, oak and sycamore, respectively, when correlated with ground DBH values. LiDAR-derived height and crown variables were used to construct LiDAR-based allometric equations for each tree species. The LiDAR-derived variables were also used to estimate the tree DBH. In turn, these LiDAR derived DBH values were used in allometric equations to estimate AGB at the plot level. The AGB estimated from LiDAR-derived DBH data strongly correlated with the AGB from field measurements at both the 1ha, 40mx40m, 20mx20m scale (r=0.32, 0.54 and 0.58 respectively).

Synthesis: Segmentation approaches can be used to generate species-specific allometric equations. These can be used to estimate LiDAR derived DBH which can be substituted into allometric equations to produce improved estimates of AGB at different spatial scales. This technique can allow for a more accurate landscape-scale assessment of AGB compared to a correlational plot-level approach.

Proposed future work: In the summer of 2013, a NERC flight will be carried out over Wytham Woods. It will collect LiDAR and Hyperspectral data. This flight will be carried out as a part of the ongoing NERC flights over British woodlands which are collecting LiDAR and Hyperspectral data with the view of studying the spread of ash die back disease. It is proposed: Using Hyperspectral data for carrying out mapping of tree species and producing tree species location/distribution maps. It is expected such a mapping exercise will facilitate the monitoring of trees, spread of tree diseases at a landscape scale. A preliminary analysis was done with multispectral CASI data and ground location information of trees.
CASI Based Map showing the Location and Distribution of 3 Major Tree Species (Oak, Ash, Sycamore) in Wytham Woods

The efficacy of different algorithms was tested (such a comparison of PCA based methods with Support Vector Machine based classification) and a preliminary map of tree species distribution was produced over Wytham Woods. It is expected that Hyperspectral data will improve the mapping results.

A combination of lab spectra and lab based analysis will be carried out to measure to concentration of leaf chemicals such as chlorophyll, specific leaf area index. Note: such an analysis is already underway with data collected over other British woodlands such as Madingley. It is expected this study will help broaden the understanding of how leaf chemistry and concentration of different leaf chemicals and consequently spectral responses vary across seasons. Further we hope to establish a baseline of leaf chemistry of healthy trees. Machine learning algorithms have been successfully implemented with lab spectra to identify wavebands that distinguish between different species (oak and ash) as well as leaves of the same species ranging from healthy to yellowing to showing early signs of ash die back disease. In the future we hope to scale these up to airborne Hyperspectral data.
A new small RNA based technology that detects host anti-virus gene silencing immunity provides an alternative route to the traditional approach that detects viruses themselves. The procedure consists of small RNA isolation, small RNA deep sequencing, de novo assembly of short reads, and a homologue-based database screen. Application of this technology in samples of ash trees (*F. excelsior*) situated at the edge of the wood and the yellow ant reserve, and along the road leading from the sawmill to the chalet, detected the prevalence of four previously undescribed viruses, infection rates were 20 to 100% in 2009-2011 (Wang, Pallett, et al., unpublished data). According to the partial genome sequences obtained, these viruses are distantly related to the *Blackcurrant reversion virus* (BRV), *Grapevine leafroll associated virus* - 1 (GLAV-1), *Raspberry bushy dwarf virus* (RBDV) and *Cassava vein mosaic virus* (CVMV).

For future work we would like to

- Determine the full-length genome sequences of ash tree viruses.
  - We propose to obtain the full genome sequences of these four viruses by using genome walking techniques. Infected RNA extracts have been obtained and stored in -70°C.

- Develop real time RT-PCR for measuring the virus load.
  - Transcripts of an Ash glucose-6-phosphate dehydrogenase (G6PD) will be used as internal control to measure the relative quantities of the viral RNAs by using the 2-ΔΔCT method (Bai et al., 2011). Primer sets will be designed and conditions will be optimized by using the infected and uninfected RNA extracts.

- Detection of salicylic acid accumulation in ash tree leaves.
  - The salicylic acid (SA) pathway is a major plant response to pathogen infection. Free SA is produced at the site of infection, it accumulates and is then transported systemically via the vascular system. The processes associated with the SA pathway result in developmental costs, therefore healthy plants do not normally accumulate free SA. We have a SA biosensor bacterium assay that can detect free-SA accumulations in fresh and dried leaves. We plan to apply the assay to leaf extracts from individual ash trees, to determine the SA accumulation level and to show if there is a correlation between virus load, SA accumulation and tree growth.
Spatial components of plasticity in tit phenology: adaptation, constraints and amelioration

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Recent studies suggest that phenotypic plasticity is a key process underpinning how animals respond to environmental change. However, our current understanding of the determinants of plasticity in natural populations is limited by the fact that studies often treat the environment as equivalent for all individuals within a population (e.g. temperature measured at a single location). Many animals use a restricted amount of space within the range of the population, suggesting that selection is likely to favour sensitivity to small-scale environmental variation.

Within Wytham, great tits (Parus major) show considerable spatial variation in breeding phenology. Like many woodland passerine birds, a key food resource for their offspring is the flush of lepidopteran larvae (e.g. winter moth Operophtera brumata) adapted to feed on the newly emerged foliage of deciduous trees (e.g. oak Quercus spp.). The timing of oak leaf development and the peak in caterpillar abundance also show marked within-population variation, at a spatial scale that is relevant to individual bird reproductive attempts. This variation provides a potential mechanism driving patterns of spatial variation in bird phenology, which is worthy of further exploration.

We have recently begun work on a three and half year NERC-funded project to explore small-scale spatial variation in phenology of trees, insects and birds in order to better understand the scale at which natural selection acts on plasticity in birds, and how this leads to matching between different trophic levels. We will use long term data on breeding behaviour and fitness, together with detailed environmental data to analyse the spatial scales at which variation in bird reproductive timing can best be explained, and to test hypotheses about the influence of scale on fitness and population dynamics. We will supplement these data with information on tree bud-burst and caterpillar abundance collected across a regular grid of 200 locations across Wytham (Figure 1). These data will be used to characterise the extent to which birds are able to match the timing of events in their environment at different scales. We also plan to experimentally test whether mis-matches in phenology between birds and the environment can be alleviated by breeding in more varied environments.

Collecting large-scale data on vegetation budburst is labour-intensive and cannot be obtained retrospectively. We are therefore testing the extent to which satellite images can be used to estimate vegetation phenology at scales that are relevant to individual animals. We will present data for a 14-year period that shows that nestbox-specific vegetation ‘green-up’ dates for Wytham, derived from MODIS satellites at 240*240m resolution, can predict small-scale variation in great tit phenology. We also present findings on the extent to which spatial variation in the mis-match between satellite-derived vegetation ‘green-up’ dates and observed bird phenology predicts individual fledging and recruitment success. We discuss how this approach could greatly broaden the scale and scope of studies exploring phonological matching between organisms and their environment.
Figure 1. Map showing the locations of 200 sampling points distributed across Wytham Woods. Throughout April to June we monitor temperature, tree bud-burst and caterpillar abundance at these sites.

**Key references**


Other potential resources for researchers interested in work at Wytham.

Past publications relating to Wytham Woods.
http://www.bodleian.ox.ac.uk/science/use/finding-your-way-around-the-rsl/rsl_collections/zoology/wytham_publications
This aims to contain all publications relating to Wytham and should include student project reports, dissertations and theses, but in practice there are some gaps. So please have a look and see if your work is included. If Wytham does not appear in the title, abstract or keywords it might not have got picked up. If you spot any omissions, please let Oliver Bridle oliver.bridle@bodleian.ox.ac.uk in the Radcliffe Science Library know.

The best ‘overviews’ are:

Historic aerial photographs.
There is good aerial photographic coverage of Wytham from the 1940s through to the end of the 1960s. The immediate post-war ones are particularly interesting in showing just how open parts of the woods were then.

Contact Nigel Fisher for more details nigel.fisher@admin.ox.ac.uk

Management plans

Detailed forestry management plans were produced in 1949 and 1959. These include general descriptions of the woods and also some information on their structure in terms of tree diameter distributions for some compartments (Keith Kirby has extracted some of this into excel spreadsheets) keith.kirby@bnc.oxon.org. Between 1960 and 1980s the Woods were also used for the management plan exercise that students on the Forestry MSc had to do. These also contain information and comments on the woods. They are held in the Radcliffe Science Library.
Elton Notebooks
From the early 40s to 1970 Charles Elton made notes on his regular visits to Wytham Woods. While these were often just where he had seen/collected a particular fly etc, others give impressions of the state of the Woods and its management (see below). These notebooks are stored in the Natural History Museum in Oxford, but are being converted to a digital facsimile by Caroline Pond at present. We hope they will be available on the Wytham Website sometime next year.

November 1956 notes
The lateness of leaf-fall is quite remarkable. Probitts cannot remember a year like it and says beech mast is also late and continues to fall. The individual trees vary greatly, but there are some of practically all species with a lot of leaf. Beeches are in wonderful yellow and brown colours. Osmaston says that all the old (and gorgeous low spreading and beautiful) beeches along the Singing Way (which is included in dedication agreement) will gradually be removed and replaced by groups of (mainly) other deciduous species. This policy needs some attention.

There are also some photographs of Wytham in the Elton material (separate to the notebooks). Many of these are only as small black and white negatives which are not very useful at present. However there are also some fascinating prints from the Field Courses that he ran in the 1950s at Wytham. As well as showing various ecologists ‘before they were famous’ they also give views of the Woods in the background. We are looking at making these more available (some are in his 1966 book, but not all.)

Woodland history