Leaf area, biomass and physiological parameterisation of ground vegetation of lowland oak woodland

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SUMMARY

Results of a complete ecological survey of the Straits Enclosure research site are presented for four time points during the 1999-2000 growing season. This survey has enabled four discrete understorey vegetation communities to be identified, covering the majority of the woodland block, based on the past management history. Biomass, annual growth increment and leaf area of understorey shrubs were estimated. Inputs are thus available for modelling the role of the understorey in photosynthetic CO_2 assimilation, specifically with regard to eddy correlation flux measurements that are being carried out within the forest.

INTRODUCTION

Detailed quantitative ecological survey data were needed for several different research investigations within the lowland oak stands of Alice Holt Forest, in Surrey. Management of the various forest blocks has resulted in wide variation in the structure of the understorey, dominated in some places by grasses and herbs, and in others by interlocking hazel stools with stems up to five metres high. A number of distinct vegetation communities have thus evolved. The one kilometre square forest includes an Environmental Change Network (ECN)site, with a 0.1 Ha TSS (Target Sampling Site) established in 1994, in which there has been no management or destructive sampling, leading to a dense hazel understorey. There is also a network of fixed quadrats for coarse and fine grain ecological monitoring. A comparison between the TSS and other plots within the Straits Enclosure would enable the impact of management on carbon stocks and fluxes to be identified. The ecological survey reported here provided the groundwork for this area of research and an assessment of biodiversity in the forest.

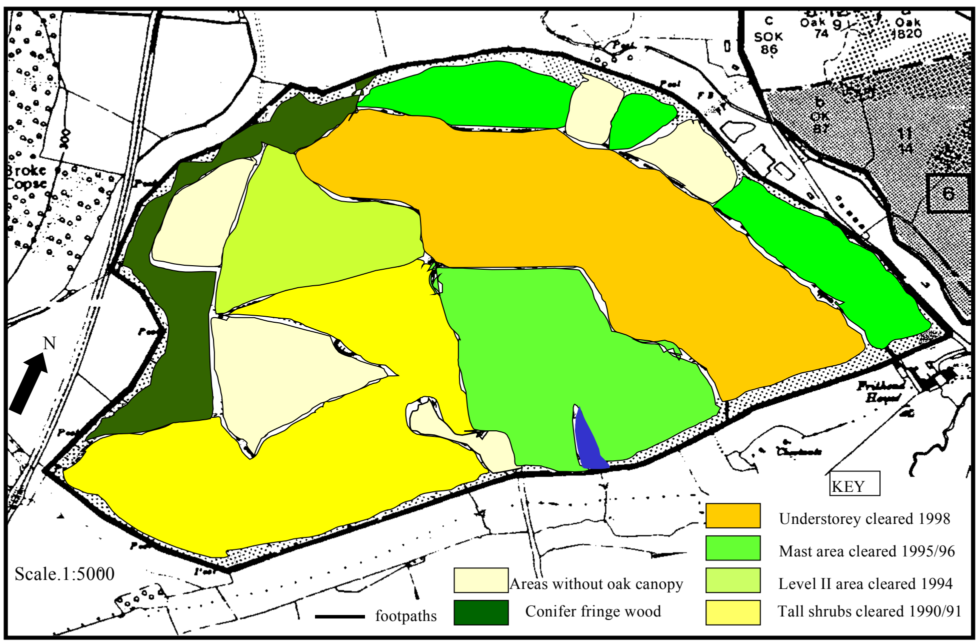
OBJECTIVES

- To classify the understorey vegetation of the Straits enclosure into characteristic communities
- To obtain species composition of the defined communities and monitor seasonal change
- To make a reliable leaf area assessment of each community at four time intervals in the year
- To produce similarly spaced estimates for the biomass of the understorey components

METHODOLOGY

An initial ecological survey was carried out in May 1999 to identify specific vegetation categories and to quantify their relative importance within the woodland block (Map1.) Four major communities were identified from the understorey components, and three 10x10m plots set up in each for random subsampling. Field data taken in three1 square metre ground quadrats in each plot recorded cover and abundance based on the BraunBlanquet system, taking additional notes on stem lengths (e.g. for *Rubus*), seedling and sapling heights, flowering and fruiting occurrence. Nomenclature of the species recorded in the Straits quadrats follows Rose (1981) *A Flora of Britain* and Fitter and Fitter (1984) Collins guide to *Grasses, Sedges, Rushes and Ferns of Britain and Northern Europe*. For ease of analysis, the plant list was grouped into categories of woody shrubs and trees, perennial climbers, soft stem herbs (both annual and biennial), grasses and sedge, rush and fern groups.

Biomass and leaf area estimates were then made for each of the four vegetation communities at four time points during the course of the 1999-2000 (May, July, October 1999, and February 2000). Above ground growth was harvested and dried for 48 hours at 70^0 C before weighting. Separate green samples were kept flat in a refrigerator for leaf area measurement on a Delta T system. SLA results were recorded for 25-30 species in each season to enable the calculation of leaf area from community biomass estimates (Table 1). Calculated leaf area index was compared with estimates of leaf area made through litter collection and analysis of ten 0.25 m2 quadrats in two of the vegetation communities in autumn 1999 and 2000. Foliar nitrogen concentrations were measured across a broad range of understorey species to allow the characterisation of photosynthetic parameters.



MAP OF TREATMENT AREAS IN STRAITS ENCLOSURE 1999 - 2000

RESULTS

The table below indicates the differing rates of leaf expansion between May and July 1999-note for instance the early development of Wood Millet grass and the later expansion of Soft grass at the same sites. It also highlights some species that maintained greencover throughout the winter 2000, notably several herbs like Stitchwort and Herb Robert, which regrow underneath a cover of leaf litter, along with newly shooting Wood sedge. New and old leaves were present on Bramble and some Honeysuckles, and some fern fronds were just viable in February, which was a mild winter month. Some of the May 2000 values are ahead of those in May 1999 due to a short spell of warm anticyclonic weather.

Table 1: Seasonal Specific Leaf Area Change Of Understorey Species ($cm^2\ g^{-1}$)

Species 1999	May mean	July	Sept/Oct	2000 Feb	May
Hazel	185.9	253.8	291.7		186.2
Hawthorn	97.03	185.0	195.0		171.7
Holly	52.8		65.35	76.3	
Ash		308.3	315.4		175.0
Wood Rose	101.5	284.7	253.4		241.4
Honeysuckle	163.3	315.4	275.9	228.9(old)	246.5
Ivy	132.9(new)	101.2	156.1	135.4	74.8
Bramble	133.9	256.3	191.7	144.7(old)	131.7
Grasses:					
Wood Millet	235.9	270.7	248.4		145.6
Deschampsia	100.7	98.0	89.7	93.8(old)	82.4
Soft grass	196.7	295.6	213.9	266.4	186.0
Sedge	132.3	220.5	158.2	185.6(new)	173.7
Ferns:					
Dryopteris dil.	63.5(Croz)	175.7	214.9	214.2(old)	
D. cristata	215.5	329.9	266.0	273.8(old)	
Herbs:					
Viola	174.7	268.9	317.9		
Stitchwort	103.2	144.7		108.3	
Nettle	252.0	423.9			280.9
Fragaria	235.0	397.6			
Stachys sylv.	318.6	458.8	604.5		287.7
Herb Robert	99.5	446.3		173.7(new)	

Characterisation of understorey hazel coppice

Hazel stools dominate the secondary canopy, and to calculate thes leaf area an allometric relation between stem diameter and subtended leaf area was defined from leaf weights on selected stems sampled from the plots.Leaf area estimates obtained from the ground litter collected are however, lower than those calculated using the allometric relationships, by at least 25 %. This difference is due to a combination of factors, particularly the speed with which hazel leaves decayed on the ground during the autumn on 2000 before the collection date, due to high rainfall. However, the general agreement between the two methods does indicate that these estimates are realistic, and thus, that the application of a leaf area: stem diameter relationship is an acceptable approach for determining the hazel contribution to the understorey canopy.

Formulae finally used in the calculations to estimate the Hazel growth in the plots:

Young hazel 0-10 years in Open, Mast and Level II plots:

Leaf area subtended from stem diameter (cm^{-1}) $y=2208.2x^{2.28}$

Standing woody biomass from stem diameter (g) : $y = 40.646x^{2.599}$

Old hazel 10 + years in Tall shrub plots:

Leaf area subtended from stem diameter (cm^{-1}) $y= 1446.6x^{2.567}$

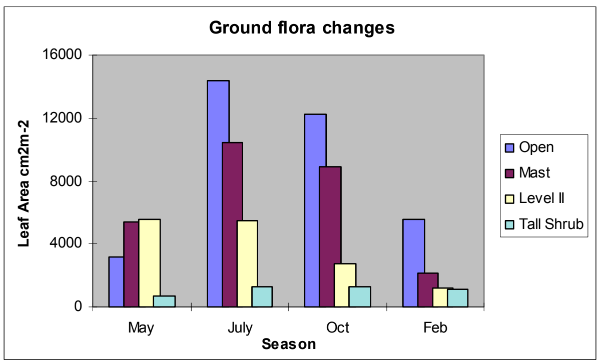
Standing woody biomass from stem diameter (cm^{-1}) $y = 41.07x^{2.58}$

Leaf area

Differences in leaf area between the four communities are apparent, with the contribution from hazel to total leaf area highest in the Tall shrub community. The effect of recent thinning in the remaining three communities is also apparent (Fig.1d), with leaf area in the Level II community twice that in both the Mast and open communities, reflecting thinning of the former in 1995, as opposed to 1997 for the latter two.

The summary data shown in Figs. 1a-d clearly demonstrate the seasonal patterns of leaf growth for each plant group and for each community, whilst Table 2 gives a total leaf area index for the understorey. Sampling that commenced in May 1999 was coincident with the leaf flush of hazel, such that the rapid expansion of this secondary canopy was reflected in its large contribution to the May data

Fig 1a)



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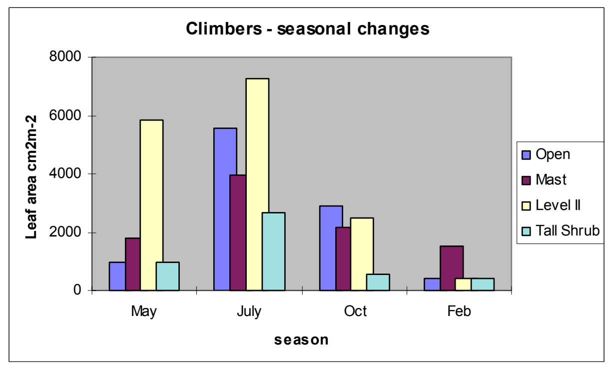

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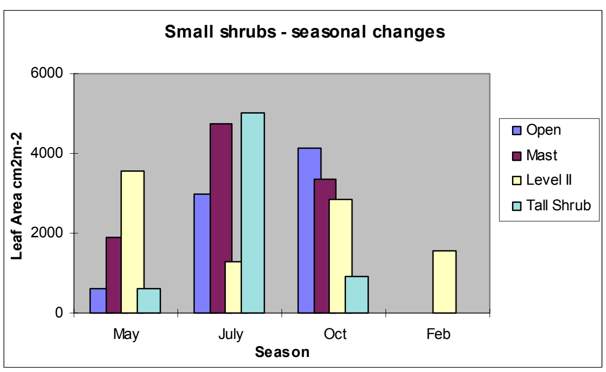

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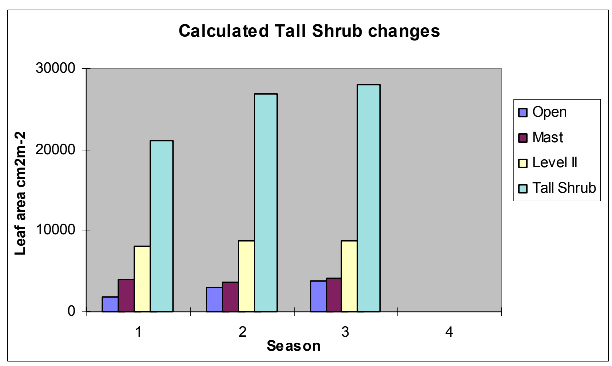

Fig. 1. Total contribution from (a) herbaceous ground flora, (b) climbers (c) woody ground flora and (d) secondary (shrub) canopy to green leaf area for each community and each sampling time.

Table 2. Understorey leaf area summary 1999-2000 (m^2 m^{-2})

	Open	Mast	Level II	Tall Shrub
May	0.66	1.31	2.30	2.34
July	2.58	2.27	2.29	3.58
October	2.31	1.96	1.61	3.08
February	0.61	0.37	0.32	0.16

Table 3 expresses the leaf area of each plant group as a percentage of ground flora and of total understorey vegetation. It is clear that the ground flora (grasses, herbs, ferns, sedges and rush), formed a significant proportion of the understorey in all communities except the Tall Shrub, making up over 40% of leaf area in the Open and Mast communities throughout the year, and between 15 and 20% in the Level II community. In the winter months, the proportion rose to over 80%, 55% and 35% in the Open, Mast and Level II communities, respectively.
Leaf area of the ground vegetation exceeded that of both climbers and short woody shrubs category, particularly in May and July. However, the dominant tall shrub species (i.e. hazel and hawthorn) formed between 20 – 90% of total understorey leaf area during the majority of the growing season, reaching $2.0 m^2 m^2$ in July in the Open, Level II and Mast plots, and $3.6\ m^2 m^2$ in the Tall shrub plots.

	Contribution to understorey leaf area (%)									
Community	herb	grass	fern	sedge	shrub	climber	herb	grass	fern	sedge
May										
open	22.2	61.1	0.8	15.9	36.6	15.0	10.7	29.6	0.4	7.6
mast	52.9	37.2	1.9	7.9	45.5	13.7	21.8	15.4	0.8	3.2
level II	71.7	19.4	2.6	6.3	50.4	25.3	17.4	4.7	0.6	1.5
tall shrub	13.1	73.9	9.1	3.9	93.1	4.2	0.4	2.0	0.3	0.1
July										
open	40.3	36.4	3.5	19.7	22.8	21.6	22.5	20.3	2.0	11.0
mast	51.4	27.2	10.8	10.5	36.7	17.5	23.6	12.5	5.0	4.8
level II	60.5	32.0	5.1	2.3	41.9	31.8	14.6	7.7	1.2	0.6
tall shrub	17.1	65.7	14.5	5.4	92.0	7.3	0.6	2.3	0.5	0.1
October										
open	18.0	79.1	2.2	1.0	34.5	12.6	9.6	42.1	1.2	0.5
mast	51.8	40.2	5.1	3.7	43.2	11.1	23.5	18.3	2.3	1.7
level II	51.1	36.4	8.6	4.0	67.7	15.5	8.6	6.1	0.5	0.7
tall shrub	5.1	49.8	45.1	4.4	94.4	1.7	0.2	1.9	1.7	0.2
February										
open	5.8	63.7	4.5	11.1	0.1	7.2	5.4	59.0	4.2	20.0
mast	22.1	41.8	10.1	26.1	0.0	41.1	12.9	24.6	5.9	15.4
level II	59.0	34.6	3.6	0.2	49.2	13.8	21.8	12.8	1.4	0.1
tall shrub	2.6	11.0	24.8	61.9	0.0	26.0	1.9	8.2	19.3	45.8

Table 3. Percentage contribution from each plant group to understorey leaf area for each community at each sampling point, expressed as a percentage of ground flora, or total understorey growth. Sedges and rushes are grouped together as ‘sedge’.

Biomass

Contribution of hazel to understorey biomass

The estimates of hazel standing biomass for each of the vegetation communities are based on the derived allometric relationships. Differences between communities reflect the effects of management strategies on the composition of the understorey, particularly the dominance of hazel coppice re-growth over all other species in areas in which no management intervention has been undertaken in the last 8 – 10 years (Tall shrub community). Table 4 summarises the annual incremental growth of hazel, including both woody stem/twig and green leaf (dry weight). The dominant position of hazel in the understorey is reflected in a contribution of almost 50% to the NPP, as determined by flux measurements.

Biomass of other woody shrubs and climbers

Incremental growth for other woody species are summarised in Table 4 – these species form a significant but highly variable proportion of understorey biomass in the Mast and Level II plots. In May 1999, woody shrubs (excluding hazel) constituted approximately 40 % of the standing understorey biomass in these communities, composed primarily of hawthorn, dog rose, blackthorn, guelder rose and saplings of ash, with small quantities of blackthorn, willow and beech. In the Tall shrub community only hawthorn was present in the quadrats and contributed 50% of the understorey biomass (excluding hazel).

	Shrub biomass(g m^2)				**Climbers** (g m^2)			**Total (g m^2)**
	Coryllus	*Crataegus*	*Rosa*	*Fraxinus*	*Rubus*	*Lonicera*	*Hedera*	
open	17.8	12.4	17.6	0.7	15	25.6	2.1	**93.5**
mast	40	18.3	4.4	21.7	5.8	0	0.8	**94.5**
Level II	64.2	17.9	4	2.3	23.5	11.1	0.3	**136.5**
tall shrub	178.3	25.8	3.8	0.8	7.1	9.6	0	**225.3**

Table 4. Incremental growth of woody shrubs and climbers in 1999 (May to October). Values include both wood and leaf material.

At the beginning of the year, the biomass of climbers is greatest in the Level II community followed by Mast plots and the Open community. The incremental growth of the climbers is largest in the Open community(Fig.3), as a result of the high solar radiation input maximum climber biomass was recorded at all sites in July.

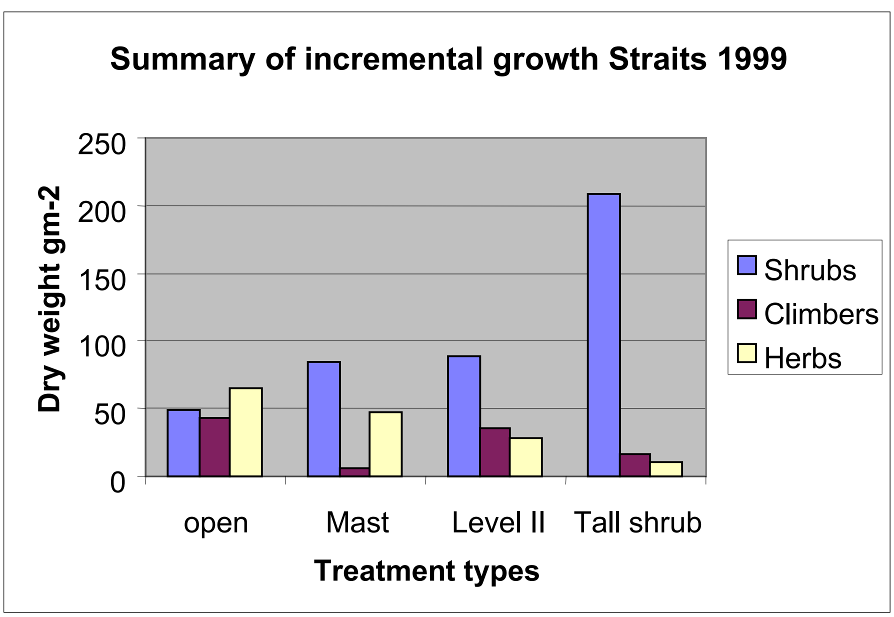

Fig. 3. Incremental growth for 1999-2000 of the three main plant groups in each of the four communities.

The persistence of bramble through the winter months is recorded from all sites, but was particularly noticeable in the Mast community in February 2000. It is noteworthy that the ratio of stem to leaf biomass for this species remained relatively constant (1:1) throughout the year. The Ivy as recorded here is largely a ground cover component, and is most significant in the Open community over clear or disturbed ground.

Contribution of non-woody species to understorey biomass
Low growing herbs and grasses form an important component of the understorey biomass in both the Open and Mast communities. In the former, the dominance of the grasses is evident, particularly *Deschampsia flexuosa*, with the late development of this species leading to maximum biomass recorded in October (43 g m^{-2}), and two thirds of its green biomass persisting through the winter.

Maximum biomass of other grass species common in the Mast and Level II sites was recorded in May and July (12-16 g m^{-2}), with these species presumably utilising the higher light levels prior to canopy closure in these less open communities. However, in both the Mast and Level II communities, total biomass of herbaceous species was almost equal to that of grass species in the Open community in May (20 – 23 g m^{-2}).

The biomass of the remaining categories of non-woody plants is small in all communities. However wood sedge is common throughout the Straits Enclosure and made significant contribution to understorey biomass of the Open Community throughout the year, with 'spring' growth commencing in late autumn/mid-winter. The contribution from each of the plant groups represented in the herbaceous ground vegetation is given in Fig. 4 with a summary of total incremental growth given in Table 5, including the proportion made up by foliage, compared to the production of woody biomass.

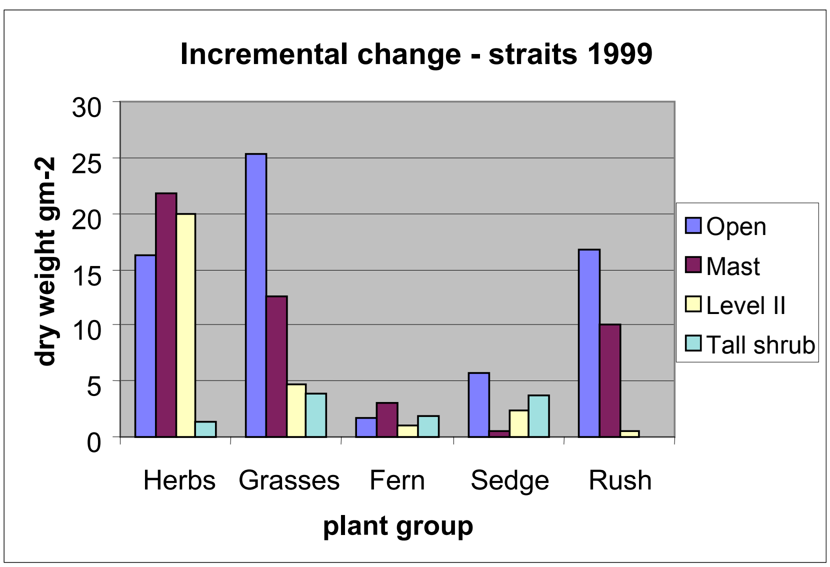

Figure 4

Table 5: Incremental growth of understorey Biomass in each community – Straits 1999 to 2000 (g m^{-2})

	Open	Mast	Level II	Tall Shrub
Woody shrubs/climbers	93.5	94.5	136.5	225.3
Soft green herbs /grasses	65.7	47.6	28.3	10.7
Total	**159.2**	**142.1**	**164.8**	**236.0**
Green % Biomass	68.3	56.6	61.7	53.6

Physiological assessment of understorey foliage

In order to evaluate the contribution of the understorey to stand carbon fluxes, and eventually NPP, photosynthetic and respiratory parameters are required for input to ForestFlux models. Most process models of forest growth and function rely on foliar nitrogen concentration to provide the basis for these parameters. A survey of the foliar nitrogen to determine intra-species variability was carried out round the mast plots in July, 1999. The data is summarised in Table 6, and the relation between SLA and N(mg g^{-1}) is shown in Fig. 5.

Two herbaceous species (nettle and woundwort) have the highest N values expressed per gram of plant material, but the lowest value when expressed on an areal basis. *Stachys sylvatica* is an understorey species adapted to deep shade, but plants found in mixed sun/shade patches, such as the grasses and *Rubus fruticosus*, have both higher N content per m^2 and lower SLA values. Of the climbing plants analysed, honeysuckle showed great variability in SLA, which results in a twofold varibility of N per m^2 - this reflects its growth habitin a range of radiation environments, on the forest floor but also up into the shrub cover. Ivy with the highest value N, has a niche as a sun exposed tree canopy climber. The N content of the grasses show some small variation between early and later developing species, and the low nitrogen content of the two overstorey species (oak and ash) sampled here as saplings is indicative of shade adapted leaves.

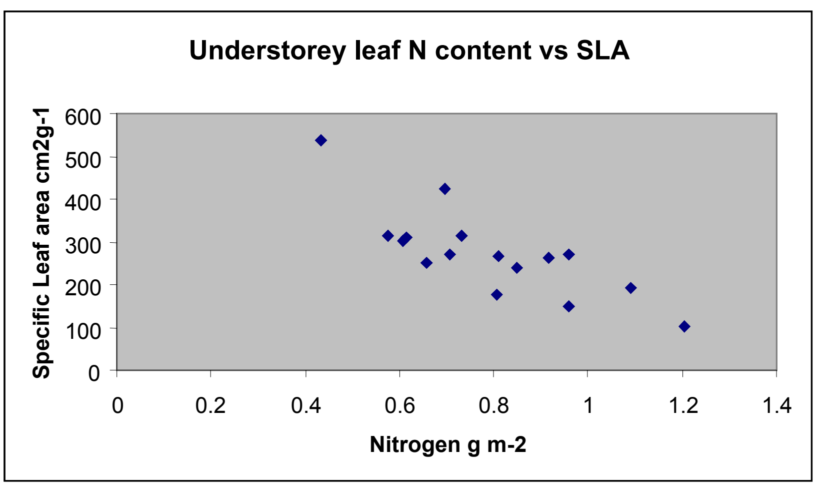

Figure 5: Relation of Specific leaf area to foliar nitrogen content by weight

Table 6: Nitrogen content of selected plants – Straits understorey 1999

Species	Na (g m^{-2})	N (mg g^{-1})	SLA (cm^2g^{-1})
Hedera helix	1.205	12.2	101
Quercus robur	1.090	21.1	194
Deschampsia flexuosa	0.960	19.1	150
Coryllus avellana	0.899	24.1	268
	0.931	26.0	264
Carex sylvatica	0.850	20.4	240
Millium effusum	0.733	24.9	339
Crataegus monogyna	0.605	15.3	253
	1.139	18.4	162
Rubus fruticosus	0.871	22.6	258
	0.748	18.8	251
Holcus cf lanatus	0.733	27.5	296
Dryopteris filix-mas	0.821	21.3	259
	0.592	16.5	279
Lonicera periclymenum	0.636	20.6	324
	0.472	20.0	424
	0.821	21.8	265
	0.915	22.5	296
	0.454	17.5	385
Fraxinus excelsior	0.616	19.0	308
Rosa arvensis	0.619	20.6	333
	0.649	24.6	379
	0.559	23.0	405
Urtica dioica	0.698	29.6	424
Viburnham opulus	0.577	18.1	314
Stachys sylvatica	0.508	28.7	564
	0.449	30.7	682
	0.338	26.6	603

CONCLUSIONS

The work carried out provided essential background data for several research projects underway in the oakwood of the Straits Enclosure. The analysis of biomass and leaf area by vegetation community has highlighted the need to approach a study of this nature from an ecological stand point. A random survey across the woodland block would introduce a very large error term as a result of the heterogeneous nature of the stand. Measurements of understorey leaf area index range from 2.3 and 3.6 m^2m^2 depending on the vegetation community, standing biomass values are between 2.0 and 8.3 t ha^{-1}, foliage turnover was0.8 to 1.3 t ha^{-1} and incremental woody growth varied from 0.5 to 1.1 t ha^{-1}. These size of these values (compared to an oak canopy above of LAI 5.5-6.0 m^2m^2) indicate the importance of the understorey to the stand carbon balance, particularly in relation to flux modelling and NPP studies. The common relationships that have been derived between the photosynthetic parameters and both foliar nitrogen and specific leaf area, suggest that either can be used as surrogates for input to process models, even across the range of species and growth forms reported here. Together, with the species and community specific values of leaf area index, these data-sets therefore provide the means to quantify the role of ground vegetation in carbon fluxes throughout the year. Furthermore, predictions can be made as to how this will change with time, as the varying makeup of understorey vegetation largely reflects the length of time since management intervention. The record of species occurrence in the various plots has set a base line for future biodiversity research.