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Leaf area, biomass and physiological parameterisation of ground vegetation of lowland oak woodland; consequences for carbon flux modelling.

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Summary
A 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, and based largely on their past management history. Allometric relationships have been developed enabling the biomass, annual growth increment and leaf area of understorey shrubs to be estimated from non-destructive surveys of stem diameter. An analysis of understorey biomass and leaf area is presented for each of the sampling periods over which the ecological survey was carried out, and is broken down by both plant life form and vegetation community. Maximum understorey leaf area index was reached in July for all four communities, and varied between 2.3 and 3.6 with the understorey shrubs (secondary canopy) comprising between 23 and 92%. Woody climbers, herbaceous species and grasses also made up a significant proportion of total understorey leaf area in some communities with contributions of up to 32%, 24% and 20%, respectively. A comprehensive survey of specific leaf area for the majority of species present in the Straits Enclosure, including seasonal variation is also presented. Photosynthetic parameters for key species have been obtained from CO_2 response analysis, and common relationships have been derived relating these to foliar nitrogen concentrations and specific leaf area. Physiological 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 Straits Enclosure. Annual biomass turnover and increment has also been estimated for each of the plant life forms in each of the vegetation communites. Standing biomass of hazel alone, which dominates the understorey, varied between 0.3 and 3.8 t ha^{-1} at the start of the sampling period, and rose to 0.38 and 4.6 t ha^{-1} by the end of the 1999 growing season. Annual incremental growth was therefore between 80 and 810 kg ha^{-1} in terms of woody biomass, or between 1 and 11% of net ecosystem flux as measured by eddy correlation. The importance of the understorey in terms of carbon fluxes becomes more prominent when all species are included in this analysis: total biomass production of the understorey (excluding below-ground biomass) amounted to between 1.4 and 2.4 t ha^{-1}, of which between 0.5 and 1.1 t ha^{-1} (7% and 15% of NEF) was woody biomass increment. Furthermore, foliage turnover of between 0.8 and 1.3 t ha^{-1} must also be included in any modelling of stand scale fluxes. A critical analysis of understorey vegetation, both in terms of standing biomass and annual turnover is thus essential for closing carbon budgets in carbon flux studies, particularly in species rich woodland subject to management intervention. A corollary of this last observation is that process models of tree and forest growth can only be calibrated and validated by flux data if the role of the ground vegetation is assessed..

1. INTRODUCTION

Detailed quantitative ecological survey data from the Straits Enclosure are needed for several current research investigations already being carried out within this area of lowland oak forest. This is particularly important as a result of the heterogeneity of the canopy, due in part to past management practices and also natural factors such as windblow (1987 & 1990). Management of the various forest blocks in the Straits Enclosure has also 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. This variation in canopy structure across the woodland block will impinge upon the various research activities, many of which assume a homogenous overstorey and understorey. A comprehensive characterisation of this important research site is therefore essential to aid the interpretation of existing projects, but will also provide data on which to base future projects, utilising the heterogeneity of the woodland to investigate research areas such as carbon sequestration, rainfall interception and nitrogen deposition.

The interpretation of eddy correlation flux measurements and their application to the modelling of atmosphere-plant interactions using ForestFlux is reliant on an accurate quantification of both biomass and leaf area of primary and secondary canopies and also for the ground vegetation. These data are essential in providing information on their relative contribution to short term carbon fluxes, both photosynthetic and respiratory, and also to NPP on an annual basis. To date, these data have been provided solely for the overstorey by litter analysis in the Level II Intensive Forest Health Monitoring Plot. However, no quantification of leaf area index (LAI: leaf area per unit ground area) has been made for woodland blocks across the Straits Enclosure.. Furthermore, there has been no assessment of leaf area or biomass for the understorey or ground vegetation fractions. In particular, the role of the hazel understorey, which has not been cleared from some parts of the enclosure for over ten years, with respect to water and carbon balance needs to be established. It is thus apparent that these data must be collected in order to use the flux data to fully parameterise process models at this site.

Other long term monitoring projects using the Straits Enclosure include the Environmental Change Network (ECN). This includes 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, and is the subject of a project proposal. The ecological survey reported here would provide the groundwork for this area of research.

A 1 km grid-square centred on the Straits Enclosure has also been designated as one of two ground truthing stations in the UK for the *Global Terrestrial Observing System* (sponsored by FAO, UNESCO, WMO, UNEP and ICSU) NPP project. This project aims to validate models of NPP (net primary productivity and leaf area production using satellite imagery. A minimum commitment to submit data on NPP and LAI at an eight day time-step is due to be initiated in 2001, using flux data to estimate NPP. The comprehensive survey reported here will enable a protocol for the derivation of LAI representative of the forest block to be developed. The contribution of the understorey and ground vegetation is important in this context, particularly in spring, prior to development of the oak overstorey. The network of quadrats set up during the survey will also enable any measurements made to be scaled to provide data fully representative of the 1 km grid-square.

1.1 Ojectives

- **To classify the understorey vegetation of the Straits enclosure into characteristic communities**
- **To obtain species composition of the defined communities and monitor their 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**

1.2 Site description

The Straits Enclosure is a relatively homogeneous and mono-specific forest block planted in the 1930s and covering an area of approximately 70 ha (see Plate 1). The altitude is 80 m and the plot is situated within Alice Holt forest in south-east England (51°10'N; 0°51' W). Other species (mostly ash) make up 10% of the tree cover and the understorey is dominated by hazel (*Corylus avellana*), hawthorn (*Crataegus monogyna*), *Rubus* spp. and various grass and herbaceous species. The soil is a surface-water gley (Pyatt, 1982) with a depth of 80 cm to the C horizon of the cretaceous clay. The pH is 4.6 and 4.8 in the organic and mineral horizons respectively. Top height and DBH were 19.3 m and 25.9 cm respectively in 1995 at a density of 606 trees per hectare resulting in a basal area of 22 m^2 ha^{-1}; general yield class is 6 and the site was last thinned in 1995 (and 1991). A UK Environmental Change Network plot has also been set up within the forest block (ECN, 1996). Daily meteorological data are available from 1955 (within 5 km of the stand), and an automatic weather station was installed in 1994. Total nitrogen deposition was 9.1 and 7.4 kg ha^{-1} in 1996 and 1997 (calculated after Ulrich, 1983), respectively, and a continuous pollution record (hourly concentrations of SO_2, NO_x, O_3) is available from 1987 (and NH_3 from 1996). Mean annual rainfall is 780 mm, and mean annual temperature 10.6°C. The meteorology mast and instrumentation are located 200 m from the Intensive Monitoring Plot, at the centre of the plantation to provide a 500 m fetch for the micrometeorology measurements.

Plate 1. Straits Enclosure (a) Level II and (b) Mast vegetation communities.

2. METHODOLOGY

An initial ecological survey of the Straits Enclosure was carried out in May 1999 to identify specific vegetation categories (here termed ‘communities’), and to quantify their relative importance within the woodland block. This results of this survey are given in section 2.x, with the distribution of the four communities given in Plate 2. A detailed discussion of the choice of sampling locations (shown in Plate 3) is given in section 2.2 together with a description of the overall sampling strategy employed. Details of individual procedures and protocols are given in section 2.3.

2.1 Overview

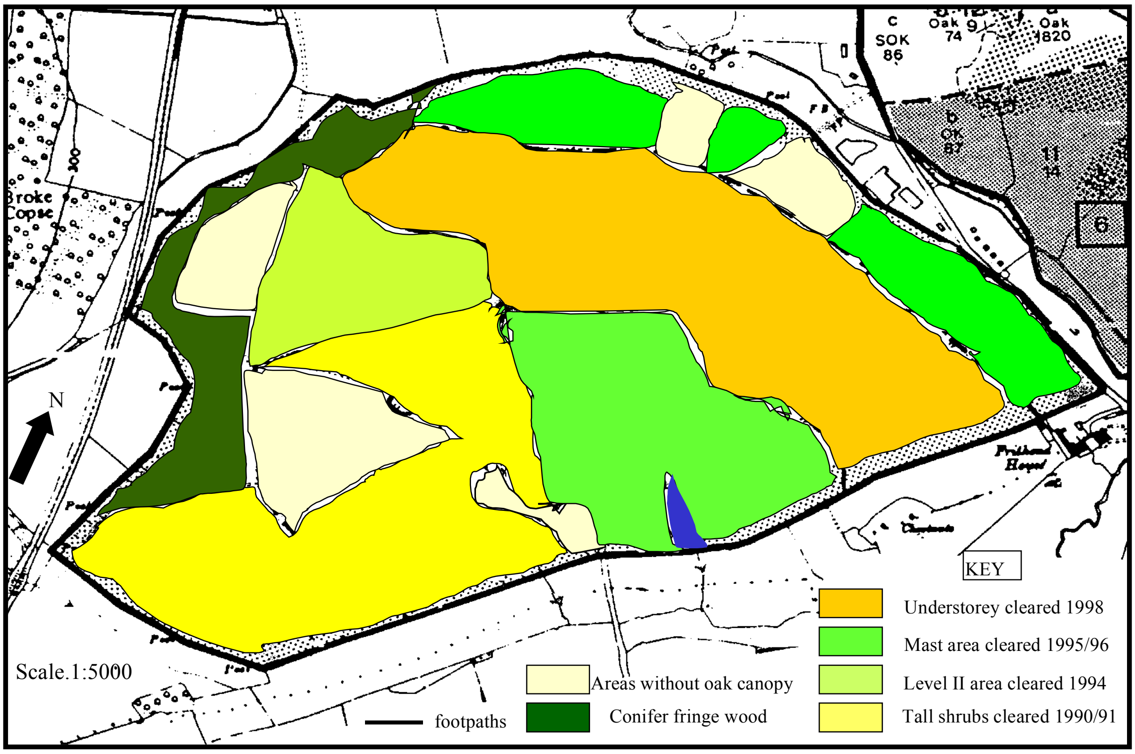
Biomass and leaf area estimates were made for each of the four vegetation communities present within the Straits Enclosure at four time points during the course of the 1999-2000 growing season (May, July, October 1999, and February 2000). This was achieved by clearing ten 1 m^2 quadrats of ground vegetation, climbers and small shrubs in each of the four communities, and analysing biomass on an individual species or plant group basis. A species specific survey of specific leaf area (SLA) during each sampling period (section 2.3.?) enabled the calculation of leaf area from biomass estimates. In the case of the large overhanging woody shrubs such as hazel and hawthorn which were present in some communities (particularly the Tall shrub community), direct biomass determinations were impractical, and thus a different approach was employed. Allometric relationships were developed between stem diameter and height, leaf area, ‘twig’ biomass and total biomass for both hazel and hawthorn, enabling the non-destructive analysis of these biomass components. The approach was validated though direct biomass determinations in a series of 10x10 m quadrats, and is summarised in section 2.3.y, with a more detailed description in Appendix 4. These allometric relationships also enabled the leaf area of the secondary canopy (hazel and hawthorn) to be calculated. Calculated leaf area index was compared with estimates of leaf made through litter collection and analysis of ten 0.25 m2 quadrats in two of the vegetation communities in autumn 1999 and 2000 (section 2.3.X).

Photosynthetic parameters (J_{max}, V_{max}, R_d and θ) of understorey species were derived from light and CO_2 response curves in June 1999 to provide process model inputs, thus enabling the contribution of the understorey to stand carbon fluxes to be made. These parameters were related to foliar nitrogen concentrations measured across a broad range of understorey species.

2.2 Strategy for biomass and leaf area analysis

There are many restrictions on the experimental design possible within the Straits Enclosure imposed by recent forest management, particularly the current understorey brashing and tree thinning (1998). Forest blocks reflect distinct re-growth communities with similar but patchy ground flora of herbs, but under varying secondary (shrub) canopies. This distribution therefore needs to be accommodated within the sampling plan, with the subdivision of the enclosure initially according to the characteristics of the secondary canopy, providing four main vegetation communities (Table 1, a-d), and three further sub-divisions. There was also a need to establish representative quadrats within each community in sufficient numbers to be statistically significant for ground cover estimates, but not in such large numbers that biomass estimates prove impractical. It should also be borne in mind that the primary role of the survey was to provide data relevant to the flux measurements, which are made within a block dominated by medium shrubs, although all four major communities occur within 100 m of the flux mast (see Plate 2).

An initial ‘walking’ survey was carried out in April 1999 placing each forest block into one of the four main communites (a-d) given in Table 1. A full description of each of these communities at each of the four sampling points (May, July, October 1999 and February 2000) is given in Table 2, whilst the distribution of these communities is shown in Plate 2, and the location of the sampling quadrats in Plate 3.



MAP OF TREATMENT AREAS IN STRAITS ENCLOSURE 1999 - 2000

Plate 2. Distribution of vegetation communities within the Straits Enclosure.

A completely random experimental design was not possible, largely as a result of the large number of plots already designated for current and ongoing ecological experiments (see Plate 3 for distributions of plots). In particular, material could not be removed from ECN or Biodiversity squares for biomass estimates. The large variation in both overstorey and understorey within each vegetation community also necessitated some subjectivity in the choice of quadrat location. All quadrats were representative of their respective community, and located away from rides and clearings.

vegetation description	**community**	**area (km^2)**	**% of total**
Blocks cleared of understorey 1998	Open	0.252	26.1
Short shrubs dominant (3/4 yr regrowth)	Mast	0.201	20.8
Intermediate regrowth (5/6 yr): Level II	Level II	0.070	7.3
Tall shrubs dominant (8 + yrs regrowth)	Tall shrub	0.275	28.5
Tall shrub with reduced tree canopy	-	0.07	7.3
Tall shrub with no tree canopy	-	0.014	1.5
Conifer fringe	-	0.084	8.7

Table 1. Area of forest blocks according to understorey characteristics.

There is then a need to establish representative quadrats within each block (treatment) in sufficient numbers to be statistically significant for ground cover estimates, but not in such large numbers that biomass estimates prove impractical. Although the Flux mast stands within a block dominated by medium shrubs, all four major treatments occur within 100m of the tower, particularly within the westerly quadrant (see Plate 2 for distribution).

A totally random distribution of quadrats within the blocks is however not possible, due to the large number of plots already designated for current and ongoing ecological experiments (see Plate 3 for distributions of plots). In particular, material must not be removed from ECN or Biodiversity squares for biomass estimates. Potential sampling quadrats do need to be positioned well within the remainder of the blocks away from the edge effects of rides, but not overlapping any of the existing plots – this leads to some subjectivity of distribution. Quadrat locations are marked on Plate 3.

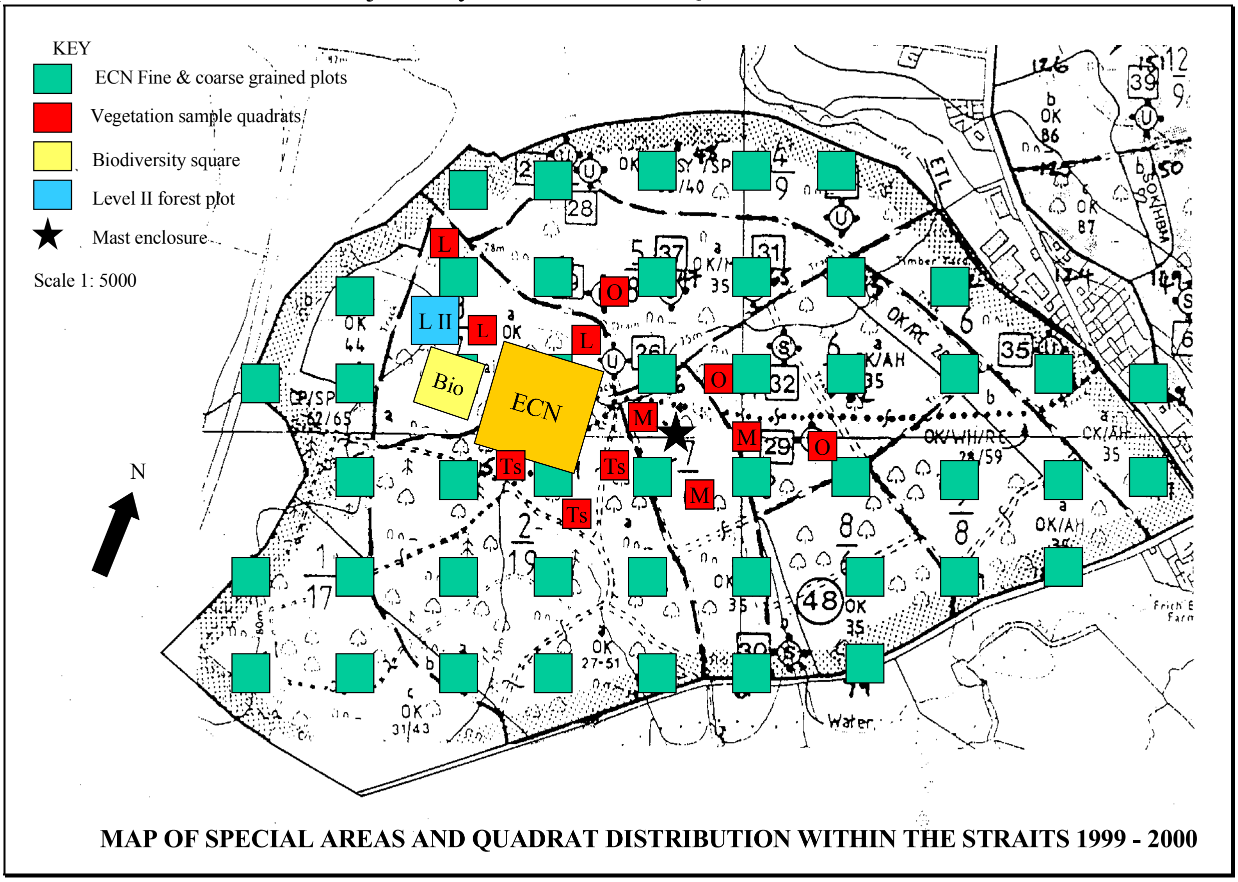


Plate 3. Distribution of existing monitoring plots and sampling quadrats used in this study.

2.3 Biomass sampling procedure

Three pairs of 10 m x 10 m permanent representative plots were established at three locations within each community. One of each pair of plots was used for the analysis of ground vegetation, and the second, for analysis of the secondary (shrub) canopy. For each ground vegetation plot, three 1 m x 1 m quadrats were placed at random at each sampling point for vegetation analysis (15 per community). For the shrub canopy plots, three 2 m x 2 m quadrats were established at each sampling point (9 per community). Analysis was carried out in May, July and October 1999, and February 2000. During sampling, each community was completed in turn to reduce development effects causing variation within the data-set for each community. However, as sampling continued for 2-3 weeks at each sampling point, differences will have been evident in developmental stage between communities, particularly for the spring May) analysis. Winter sampling in February was limited to an assessment of green leaf area and biomass only, without measurements of standing woody biomass. It is assumed that no change in standing biomass occurred between October and February.

Herbaceous species: Species cover and abundance was recorded, prior to total clearance. The vegetation was divided into six plant groups: grasses, herbs, ferns, sedges, rushes. Samples were oven dried at 70^{o}C to constant weight (48 hours). Prior to drying, a sub-sample was retained in a plastic bag containing moist tissue paper to prevent drying. Specific leaf area (SLA: area per unit weight) was determined for this sub-sample (see section 2.?). An estimate of the area of moss cover in each quadrat was made in the field, but no dry weight or leaf area measurements were attempted in the laboratory. Most moss growth was associated with the occurrence of fallen, decaying wood, from which it proved difficult to separate. Short woody shrubs, whose growth was contained within the metre square, were cut at ground level at the same time as the herbaceous vegetation. Overhanging branches of shrubs rooted outside the quadrat were noted and paint marked, but not cut. Alternative quadrats were sampled where first random choice resulted in the rootstocks of large woody shrubs (such as hazel stools) filling the entire sample square. Quadrats with partial cover of rooted shrubs were included and any herb or climber growth collected.

Shrub layer: Species cover and abundance was recorded for the ground vegetation quadrats, as for the herbaceous species. Overhanging woody branches were clipped above the quadrat boundary, and leaf biomass measured. The secondary canopy quadrats were cleared of all (shrub) woody material in May and October 2000, only.

Climbers: At ground level record climbers were recorded as for herbaceous species, although the biomass was assessed separately. Climbers rooted within the quadrat were destructively harvested. Since tree roots were specifically excluded from the quadrats, these estimates do not account for ivy climbing up tree trunks.

Tree canopy: Light interception was measured using a pair of Ceptometers (Delta-T Devices, Herts.), one located in a forest clearing, and the other sampled across a 10 m transect within each 10 m x 10 m quadrat. Leaf area index was calculated according to Gower and Norman (1987), assuming an effective light extinction coefficient (K_{eff}) of 0.38 (Broadmeadow et al., 2000). Sampling took place in late June and early July 1999.

2.4 Field measurement of secondary canopy allometric relationships

It became clear that the separate survey of large woody understorey shrubs necessary to complete the estimates of both leaf area and biomass of hazel could not be achieved by destructive means with the available time and manpower (although this was attempted for hawthorn in three quadrat locations). An allometric relationship for understorey hazel was therefore derived by subsampling 30 hazel stems in July and September from Level II and Tall shrub communities. Measurements of stem diameter were taken at ground level and the leaves stripped, dried and weighed. Current year ‘twig’ biomass was also separated from stem wood thus enabling the derivation of relationships between stem diameter and twig, stem, leaf and total woody biomass. A non-destructive survey of hazel stem diameter was undertaken in late October after leaf fall in each of the 10 m quadrats of the Tall shrub, Mast and Level II communities.

Leaf litter was collected in the Tall shrub and Level II communities in late November 1999 in order to validate the estimates of hazel leaf area derived using the allometric relationships. Ten small 50 x 50 cm quadrats were randomly cleared from the forest floor at each location, dried, sorted and weighed, following the procedure adopted for Litter traps at the Level II sites (see Pitman and Broadmeadow, 2001). An Ecological survey of the three critical Mast quadrats was also undertaken in May 2000 to quantify growth increment, and any change in leaf area over a whole year. The procedures followed those described above.

2.5 Laboratory procedure

At times when samples could not be analysed immediately from the field, whole quadrats in polythene bags were stored in a cold room overnight or leaf subsamples of specific species were stored flat in a refrigerator. This was necessary for many small herbs, such as wood sorrel, and the soft grasses such as *Holcus lanatus,* which curl up on drying. Specific Leaf Area (SLA) was analysed on a seasonal basis for the main species represented in the understorey (Table 2). During the sorting of leaf material, particularly for overwintering grasses such as *Deschampsia,* only live green lamina segments were included in the leaf area estimate. Mixtures of dead and live material on one stem were also a problem in some creeping herbs, such as stitchwort and cleavers, as they begin to senesce in July and September. The laminae of ferns were recorded whole and in all cases, data are expressed as projected leaf area, with no correction applied to three-dimensional leaves, such as those of *Juncus*.

The majority of leaf area measurements were made using a belt driven Delta-T area measurement system (Delta-T Devices, Herts). Measurements were made in static and automatic modes and compared with results from, a hand operated scanner (CI-201S) in June 1999. The data for entire large leaves compared well for all three systems. However, measurements for finely divided small leaves, such as those of stitchwort (*Stellari*a) were increasingly variable with decreasing leaflet size. This emphasises the need for careful analysis even for small plants, as carpets of this herb can comprise a major ground cover in some parts of the Straits enclosure.

	specific leaf area (cm^2 g^{-1})				
species	**May 1999**	**July 1999**	**October 1999**	**February 2000**	**May 2000**
woody species					
Corylus avellana	186	254	292		186
Crataegus monogyna	97	185	195		172
Ilex aquifolium	53		65	76	
Fraxinus excelsior		308	315		175
Rosa arvensis	102	285	253		241
Lonicera periclymenum	163	315	276	229	247
Hedera helix	133	101	156	135	75
***Rubus* spp/agg.**	134	256	192	147	132
Prunus spinosa		281			
Viburnum opulus		314			
Betula pendula		321			
herbs					
Viola riviniana	175	269	318		
Stellaria holostea	103	145		108	
Urtica dioica	252	424			281
Fragaria vesca	235	398			
Stachys sylvatica	319	459	605		288
Robertum geranianum	100	446		74	
Geum urbanum		300			
Mercuralis perennis		334			
Ajuga reptans		264			
Primula vulgaris		283			
Galium aparine		159			
grasses					
Millium effusum	236	271	248		146
Deschampsia caespitosa	101	98	90	94	82
Holcus mollis	197	296	214	266	186
***Carex* spp.**	132	221	158	186	174
ferns					
Dryopteris filix-mas	64	176	215	214	
Dryopteris dilata	215	330	266	274	

Table 2. Values of season specific leaf area (SLA) used in the calculation of total understorey leaf area.

Some species were ‘bulk weighed’ with no separation of leaf from stem, where sub-samples showed a consistent relationship between twig and subtended leaf biomass. This was particularly the case for *Rubus fruticosus*, where twig extension was matched by lamina increase throughout the year. By contrast, it was impossible to bulk any *Lonicera* samples, as the ratio constantly changed through early rapid growth of leaf, stem extension in summer and early leaf senescence in September. For soft but erect herbs with green stems, such as nettle and bugloss, leaves and stems were recorded as separate weights, although the green stem material may have a role in photosynthesis.

Table 2 also indicates differing rates of leaf development between May and July 1999 (see 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 green cover throughout winter 2000, notably several herbs such as stitchwort and herb Robert, which persisted underneath a cover of leaf litter, together with new wood sedge growth. New and old leaves were present on bramble and some honeysuckle, and some fern fronds were also viable in February. It is noteworthy that devopment of some species was advanced in May 2000 compared to 1999, reflecting a warm period in early May 2000.

2.6 Ecological survey of the understorey in the Straits Enclosure

Field data taken for measurements of cover and abundance in 1 square metre ground quadrats was based on the BraunBlanquet system taking additional notes on stem lengths (e.g. for *Rubus*), seedling and sapling heights, flowering and fruiting occurrence. The following ecological records are based on this survey from the 10 sampled quadrats (six in February 2000) from three different locations within each community. The results of the cover/abundance surveys in each season are summarised in Appendix 1. A further table of field notes on seasonal vegetation progression is also presented as Table 3.

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 has been grouped into categories of woody shrubs and trees, perennial climbers, soft stem herbs (both annual and biennial), grasses and sedge, rush and fern groups. *Rosa arvensis* thus falls within the woody shrub group, whereas bramble, *Rubus fruticosus* comes within the climber group, along with woody nightshade, *Solanum dulcamara*. A general bulked category of mixed herbs was adopted where small herbs occurred only sporadically in one sample period and were individually of both small leaf area and biomass. This bulking procedure was also occasionally used for grasses where the leaf area of individual species was low, particularly during winter.

Over 40 species appear on the list, and specific leaf area values were determined for between 25-30 of them at any one season (see Table 1), and recorded in a series of Key Sheets for the calculation of leaf area at each sampling point (May, July, October and February). The resultant data are recorded by species in Table 2, with the raw data grouped by plant group in Appendix 2.

2.6.1 Open community

The first sampling period in May was less than 4 months after the completion of brashing, canopy thinning and clearance of understorey shrubs in one third of the enclosure. This process caused several side effects:

- The creation of large amounts of fallen wood, occasionally in deep piles but more often remaining as poles scattered across the site.
- The creation of deep ruts through the use of heavy machinery, giving rise to areas of standing water and bare soil.

- Uneven cutting of the understorey, leaving behind large individual shrubs growing beside the remaining oak trees, which later posed problems in estimating average shrub regrowth.

The recent forest management thus created a very uneven microhabitat for understorey growth, and great variability in the consequent leaf area and biomass estimates from the limited number of quadrats that were assessed. Ten metre squares were located subjectively to minimise the inclusion of large individual shrubs, although their stem diameters were later measured for the estimation of total understorey biomass and leaf area based upon allometric relationships (see Appendix 4).

Bare soil estimates were occasionally as high as 60%, but in wetter areas, rushes and clumps of grasses (mostly *Deschampsia*) quickly recovered to provide 15-20% cover in the middle of the year, and seedlings of birch, ash and oak were encountered in several quadrats by October.

This Open community is characterised at ground level by the vigorous growth of the grasses, *Deschampsia flexuosa* and wood millet (*Millium diffusum*) in dryer areas with wood sedge (*Carex sylvatica*) and rush (*Juncus effusus*) in damper places. Small patchy carpets of stitchwort (*Stellaria*

holostea), with *Viola ,* herb Robert *(Geraninium robertium)* and wood avens are common, with short stems of bramble, honeysuckle and *Rosa arvensis* growing through. Ivy spreads sideways on the bare soil under the other herbs with moss on older decaying wood. Herbs such as enchanters nightshade, wild strawberry and geum grow between grass clumps, and on more bare areas, mullein and wood spurge have also been recorded.

2.6.2 Mast community

This community was cleared of understorey shrubs four years ago and is now characterised by re-growth of hazel (Corylus *avellana*), hawthorn (*Crataegus monogyna*), willow (*Salix capraea*) and blackthorn (*Prunus spinosa)* from the old stumps. Hazel is dominant with stem heights of 2m plus, but nowhere in this community is this understorey canopy closed. There are some locations where a distinct association of shrubs dominate at a small scale, such as on the floodplain of the brook, where blackthorn and new ash saplings 1-1.5 m high are common. In the dryer parts, dominated by hazel, there is guelder rose (*Viburnham opulus*), honeysuckle and *Rosa arvensis* as woody associates, and frequent bramble with stems up to 1.5-2.0 m in length. This open shrub understorey allows a variety of herbs to flourish, such as Viola*, Fragaria*, *Geranium, Stellaria, Mercurielis perennis, Stachys sylvatica* and *Urtica dioica* between the clumps of the dominant grasses species, including *Millium effusum*, *Deschampsia* and *Holcus lanatus* (soft grass). Tussocks of wood sedge and rush occur throughout, and are found associated with carpets of *Lysimachia nemorum (*Yellow Pimpernel) and the climber, woody nightshade (*Solanum dulcamara*) in the wetter areas. Well established clumps of fern, both *Dryopteris felix-mas* and *D. dilatata* are also common throughout this community.

	OPEN QUADRATS	MAST QUADRATS	LEVEL II QUADRATS	TALL SHRUB QUADRATS
MAY	New growth - Lonicera, Rubus, Rosa Show of herbs- Viola, W.Sorrel, figwort, Herb Robert & Ivy on ground	Leaf extension - hawthorn 50%, hazel 33% Ferns- crozier - flower heads on rush Forward growth - Lonicera, cleavers 50cm nettles 20cm stitchwort new leaves - Bugloss, Rubus, wood millet Sedge , Ench. Nightshade	Carpets of cleavers(30 cm) Primrose, Galeobdolon in flower Wood millet, Veronica& Sedge growing on New growth cuckoo pint, Holcus lanatus	Hazel out 3/4 leaves Oak 1/2 flush Herbs showing: Fragaria, cleavers, Wood Spurge & Honeysuckle leaves Ferns crozier
JULY	Noticeable forward moss growth, new hazel shoots on cut stools- still 15/20% bare ground Full extension of D.felix-mas clumps+ rush Developing herbs: Stachys,Circaea & Holcus l	Full development: nettle, Stachys, ferns(2m) Forward growth Rubus. Bugloss, Full flower on Herb Robert,Ench. Nightshade Flower spikes on Wood Millet & sedge Forward growth,Veronica- Hemp nettle Die-back on Cleavers	Full overcanopy of oak and shrubs - best dev. of honeysuckle leaf but few flowers Vigorous growth Deschampsia clumps Dev.on ground of Circaea, HerbRob,stitchwort Veronica, and D.dilatata-new spikes Rubus Dieback of cleavers(stems only)cuckoo pint	Overstorey fully developed -deep shade Cleavers dead, weak Rubus growth Short sedge and Deschampsia patches some flower heads on wood millet Occsasional Viola and Ivy plants and Hypericum in open spots,with birch seedlings
OCTOBER	Forward dev.of wood spurge,Mullein and Deschampsia clumps. Die back of cleavers, Circaea, Honeysuckle, Stachys and Holcus lanatus New seedlilngs of ash, blackthorn, birch and oak obvious now	Leaf fall starting in hawthorn, Rosa and honeysuckle- most hazel still green Nettles & Stachys yellowing, stems folding Deschampsia going moribund,cleavers dead Still carpets of wood sorrel,fragaria & Lysimachia	Oaks above yellowing in lower layers Ash leaves falling + hawthorn. Lots fungi Cleavers gone,dieback of stitchwort,circaea Stachys moribund but Betony still green!	D.dilatata Fern still vigorous, D.fm going moribund. Honey suckle loosing leaf, hazels yellowing and brown spotted.
FEBRUARY	Hazel catkins fully extended. New flush on Honeysuckle, Rubus & Wood millet grass Deschampsia still mostly green Under the litter, Fragaria,Geum, Stitchwort & Herb Robert are persisting green	Lots good litter cover on ground layer over moribund Deschampsia, broken fern pinnae New shoots on wood millet & Sedge presence still of Herb Robert, Fragaria, wood sorrel, stitchwort and viola in litter cover	Rubus stem dieback to 1/3 length,moribund ferns(esp. D. dilatata) and Deschampsia Honeysuckle leaf 1/2 out, new growth on wood millet, sedge(bright green) still in herb layer - Veronica, stitchwort + new leaf on cuckoo pint & primrose and I cm seedlings of cleavers & nettle	D.dilata fern hanging on-v.moribund Occasional Fragaria,Viola and odd spike of Deschampsia, Sedge and rare wood millet

Table 3. Field notes from the ecological survey of each of the four vegetation communities.

	May 1999				July 1999				October 1999				February 1999			
	Open	Mast	Level II	Tall shrub	Open	Mast	Level II	Tall shrub	Open	Mast	Level II	Tall shrub	Open	Mast	Level II	Tall shrub
Shrubs																
Oak									68			1				
Ash	69	271	714		949	478	321	14	1299	1422	503	14				
Hazel	66	868	1848		103	291		1735	1202	160						
Hawthorn	78	371	867	518	326	235	811	4914	1188	364	1645	898				
Blackthorn		282			478	709			873	1254	45					
Holly			69		1					2	533		8		1558	
Birch	62	33						15	11		26					
Rosa	135	69	50	37	110	325		60	722	132	107					
Guelder rose				55	30											
Rowan						85										
Beech							137									
Willow									2	11						
Climbers																
Honeysuckle	526	276	2659	668	2774	59	861	1223	344	44	471	142	48	25	65	49
Bramble	365	132	2580	281	2481	3709	6346	1421	2196	1936	1895	363	355	1379	364	301
Ivy	85	13	595	4341	309	36	63	26	358	70	122	53	24	105	33	54
Nightshade		181	6			95				111						
Herbs																
Buttercup		158	13		446				13	2933	49			167		
Cleavers	16	1050	891	85	13	787	224	10								
Stitchwort	20	428	974			15	391			182	175		174	68	25	3
Primrose			85		19				288				41			
Strawberry			82	10		37				28		12	23		161	
Herb Robert	146	31	29		3107	489			498	123	48		36	83		
Wood sorrel	5	117				51				130	14	7		31		
Viola	204	33			652	17			71	158	10	30	1	27	6	1
Enchanted nightshade	7	23	31		840	243	19		16	71	8					
Veronica							2351				955		37		449	
Nettle		302	1176	4		759				169			0		7	
Stachys	15	235	1580		938	556			1224	629	44		0		20	
Geum		41			48	18				63			7	15		6
Dogs mercury		102				145				100				70	19	20
Birdseye		158	129			73	90				5					
St.Johns wort		26	8					205								
Bugle						215					71	5	8	11	8	
Wood spurge	34	50		13	22				45	5		11	19	19		
Mixed herbs	266	1188	164		185	315	250		51							
Grasses																
Wood millet	313	215	281	148	2174	913	261	270	4228	1151	232		549	440	168	4
Soft grass		713	347		1862		382			798	222	23	61			
Rough grass	162	751	366	280	1376	1136	1045	558	5476	1617	326	369	2943	463	238	123
Mixed grasses	1468	336	444	49		786	57				45	250				
Sedge	411	202	330	25	1408	376	94	33	79	256	104	57	774	263		712
Rush	91	228			1175	720	36		82	85	8		649	300	3	
Ferns																
D. filix-mas	25	94	43	36	273			52		168	233	336				113
D. dilitata		10	101	22	237	1129	281	131	277	282		244	250	218	43	172
Total LAI (m^2 m^{-2})	**0.457**	**0.898**	**1.646**	**0.657**	**2.233**	**1.480**	**1.402**	**1.067**	**2.061**	**1.446**	**0.789**	**0.281**	**0.601**	**0.369**	**0.317**	**0.156**

Table 4. Leaf area for each species present in the biomass/leaf area analysis quadrats. Generic specific leaf area values have been used for many of the herb species.

2.6.3 Level II community

Understorey shrub re-growth in this treatment was five to six years old in 1999, having been cleared initially for the establishment Intensive Forest Health Monitoring site (Level II). The fallen, decaying wood has become colonised by mosses, notably *Rhytidiadelphus,* and in some quadrats up to 25% of the ground area was entirely moss covered with ivy trailing through. The hazel shrubs are commonly up to 2.5-3.0 metres in height in this community, with 10 plus live stems arising from each stool, although they do not form a closed secondary canopy. Hawthorn occurs in well-developed bushes 1.5 m high, but is less frequent than hazel, and a number of clumps of holly (1.5-2.0 m) and well-branched beech saplings (1.0-1.5 m high) are also present. Single stem ash seedlings occur throughout over a range of heights up to one metre. The growth of climbers in this community is good with honeysuckle both on the ground and up to the top of the shrub layer, particularly on hazel and hawthorn, and vigorous arching *Rubus* stems to 1.5 - 2.0 metres in length. *Rosa arvensis* is confined to the more open light patches. This community has the greatest diversity of ground flora of the whole Straits woodland. The abundance of grasses is lower than in the Mast quadrats, with *Deschampsia* less dominant, and wood millet and *Holcus lanatus* equally prevalent; tufts of the latter often show grazing damage, presumably by deer. Wood sedge is also widespread, but less wood rush is present compared with the other communities, except in ditchside locations. Both species of fern grow throughout. Herb species which have not been recorded elsewhere include primrose, yellow archangel (G*aleobdolon sp.*), hemp nettle (*Veronica hederifolia*), betony *(Betonica officinalis*) and cuckoo pint (*Arum maculatum*). Carpets of cleavers, stitchwort and enchanters nightshade replace the grasses, particularly in deeper shade and close to the base of trees. Herb Robert and trailing *Veronica* are also frequent as ground cover between the shrubs, and in areas with more ash and mature beech in the overstorey. *Veronica* seems to substitute for *Stachys sylvatica* here compared to the Mast community, where it damper soils are prefered. Coupled with the decreased incidence of *Juncu*s recorded in this community, there is some ecological indication of overall dryer ground conditions across the Level II plot.

2.6.4 Tall shrub community

The last period of management in this area appears to have been following the storms of 1990, and the largest hazel stems cut from the understorey show a maximum of 10/11 distinct growth rings. The average size stem (2.2 cm diam) has 7-8 rings and these stems are still over 4.0 m high and interlock to form a closed canopy over much of the area under. Although the hazel stools are still producing new side shoots, there is a considerable proportion of standing dead stem wood in the lower parts of the canopy, which had attained some three or four years growth (judging by stem diameter) before becoming moribund. No exact measure of this component has yet been attempted. The heavy shade cast by this under-canopy leads to the suppression of all other shrubs and herbs, and makes this community the most species poor in the Straits Enclosure.

Some hawthorn persists here, but the proportion measured (see Table 4), is less than one-third of the standing biomass recorded in the Mast and Open communities. Hawthorn is rarely more than 1.5 m high and other shrubs such as willow and blackthorn are completely absent. Beech saplings occur sporadically (3-4 years old), but in contrast to the other communities, ash seedlings are rare. The dominant climber is honeysuckle, which is also found as ground cover, whereas ivy is restricted to the oak trunks, and even the growth of bramble is suppressed and limited to etiolated short stems.

Ground cover is greatly reduced, with less moss than recorded in the Level II community, and large areas of bare soil, sometimes up to 90% of the total sample area. A few small clumps of grasses persist, mostly *Deschampsia* and wood millet, but even these become occasional to rare. There is similarly poor cover of wood sedge, and no occurrence of rush was recorded in any of the Tall shrub quadrats (though it can be found in major active ditch lines). Clumps of fern were recorded in almost every location, but it is noticeable that the smaller *D. dilata* becomes the dominant species over *D. felix-mas*. There are also rare, sporadic occurrences of herbs in the ground cover, notably wood spurge (*Euphorbia amygdaloides*), *Viola, Fragaria*, cleavers and *Hypericum*.

With the notable loss of *Juncus* from the species list, the lower incidence of mosses and the presence of butchers broom (*Ruscus)* in some other places within this community, there is good ecological evidence that ground conditions in this community are much dryer than other forest blocks in the Straits. As the entire Enclosure is established uniformly on Gault clay soils, this difference may relate to either the increased water demand and/or increased interception losses as a result of the dense closed canopy of understorey hazel shrubs.

2.7 Secondary canopy allometric relationships

2.7.1 Hawthorn

As this shrub is found sporadically in all parts of the Straits Enclosure, a methodology was developed to estimate its leaf area and biomass by clearing three complete ten square metre quadrats of bushes and trees, one from each of the Mast, Open and Tall shrub communities (Table 5). The methodology is based upon a non-destructive survey of stem diameter, similar to that developed for hazel (section 2.7.2), which is described in detail in Appendix 4. As the shrub has frequently been left standing during understorey clearance when growing next to retained overstorey trees, there are some data relating to large bushes/trees from a number of communities included in the relationships between leaf area and both stem diameter and stem biomass given in Fig. 1. A tight relationship is observed between stem biomass and stem diameter, although it should be applied with caution as a result of the limited number of data points. The relationships between leaf area, and both stem diameter and stem biomass show more scatter, as might be expected given the variation in light environment experienced in the four communities.

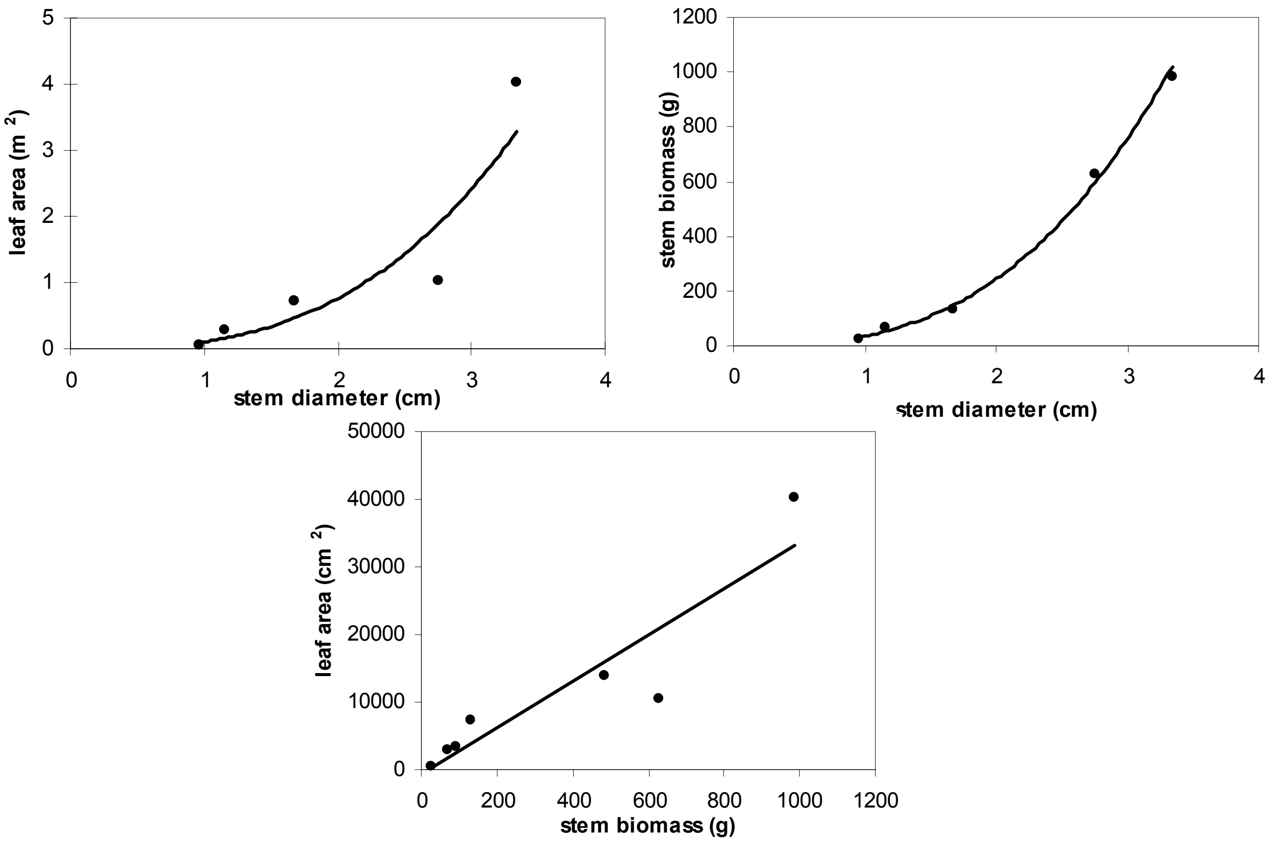


Fig. 1 Relationships between (a) leaf area and stem diameter ($y=1.05x^{2.86}$; $r^2=0.87$), (b) stem biomass and stem diameter ($y=35.1x^{2.80}$; $r^2=0.99$), and (c) leaf area and stem biomass ($y=34.3x-582$; $r^2=0.84$).

quadrat	stem biomass ($kg\ m^{-2}$)	leaf biomass ($g\ m^{-2}$)	twig biomass ($g\ m^{-2}$)	leaf area ($m^2\ m^{-2}$)
Mast 2	2.601	0.470	1.109	0.917
Open 2	2.323	0.368	0.859	0.718
Tall shrub 1	0.878	0.204	0.475	0.390

Table 5. Summary of hawthorn biomass and leaf area data used in the derivation of allometric relationships.

2.7.2 Hazel

Although data are available (FC, unpublished) which describe the relationship between stem diameter growth and biomass accumulation for hazel coppice grown in the open, there do not appear to be any extant data available on hazel growth as an understorey crop, either for biomass or leaf area estimates.

The following procedure was therefore adopted in order to make a realistic estimate of the leaf area and biomass of understorey hazel in the four vegetation communities represented in the Straits Enclosure:
Living stems from the understorey of the Tall shrub community were sampled during the growing season and basal diameter, wet and dry weight of stem wood, twig and leaf components were measured, together with leaf area, enabling the derivation of SLA.
Mathematical expressions describing the relationships between (a) twig and leaf biomass, (b)stem and combined twig/leaf biomass and (c) stem diameter and leaf area subtended, were derived.
The diameter and number of all stems in all vegetation quadrats were recorded, enabling estimates of leaf weight, leaf area and the biomass of each component to be made by applying the allometric relationships given below.
Hazel leaf litter was collected from ground level in autumn 1999, providing a direct comparison with, and validation of the allometric approach adopted for the determination of leaf area.

A more detailed description of this methodology is given in Appendix 4.

Allometric relationships used to estimate the Hazel growth in each vegetation community

Open, Mast and Level II communities:

Leaf area (cm2) subtended from stem diameter (cm)	**$y=2208x^{2.28}$**
Standing woody biomass (g) from stem diameter (cm)	**$y = 40.6x^{2.60}$**
Twig biomass (g) from stem diameter (cm)	**$y = 10.3x+4.1$**

Tall shrub community:

Leaf area (cm2) subtended from stem diameter (cm)	**$y= 1447x^{2.57}$**
Standing woody biomass (g) from stem diameter (cm)	**$y = 41.1x^{2.58}$**
Twig biomass (g) from stem diameter (cm)	**$y = 22.8x-32.9$**

3. Results

3.1 Leaf area of hazel

Total leaf area of hazel at the time of full canopy development in the four communities is summarised in Table 6, using data obtained from both litter analysis (see A4.3.6) and the application of the allometric relationships derived in section 2.7 and Appendix 4. It is clear that the estimates obtained from litter analysis are lower in both the Mast and Tall shrub communities compared to those calculated using the allometric relationships, by at least 25 %. This difference is probably due to a combination of factors including the rate at which the hazel leaves may be lost on the ground by decay during the autumn before collection (particularly in 2000, when rainfall was high). The allometric relationships may also overestimate leaf area in some communities because of the limited dataset. 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 allometric relationship is an acceptable approach for determining the contribution of hazel, which dominates the secondary canopy, to stand leaf area index.

	leaf area index (m^2 m^{-2})		
	allometry	litterfall analysis	
community		**1999**	**2000**
open	0.28	-	-
mast	0.45	-	0.31
Level II	0.80	0.4	-
tall shrubs	2.75	2.00	2.25

Table 6. Comparison of hazel leaf area as determined by allometric relationships (see section 2.7) in July 1999 and litterfall analysis in October 1999 and 2000 (see Appendix 4).

Difference between the four communities are apparent, with the contribution from hazel to total leaf area far higher in the Tall shrub community than the other three. The difference in timing of thinning and brashing between the remaining three communities is also apparent , 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. This re-growth of the shrub layer in the Level II community was attended to in winter 2000-2001 through shrub clearance.

3.2 Leaf area of the other shrubs and herbs

Table 7 summarises green leaf area recorded at each sampling time for the four communities, by plant group, with a more detailed analysis by species given as part of the ecological survey in Section 2.6. These estimates of leaf area are based upon the dry weight of green biomass collected in the 10 one metre square quadrats in each community, distributed between three replicate blocks, corrected for the species and season dependent values of specific leaf area (SLA: leaf area per unit area) given in Table 2. The raw data from which the life form category data (discussed in section 2.5) are summarised is also given in Appendix 2.

These data demonstrate the large variability that was evident, particularly within the Open community, where for every group, the standard deviation exceeded the mean. The data recorded here are thus indicative rather than absolute, and reflect a greater variability of regrowth in recently brashed communities, resulting from the heterogenous opening of the canopy. In both the Mast and Level II communities, the data become tighter and less variable, although in the Tall Shrub community the small amount of sporadic herbaceous ground cover again leads to high variability. However, if the leaf area within each community is expressed as a single cumulative value accounting for all ground vegetation (i.e. herbs, grasses, rush etc.), variability is reduced, leading to a reduction in potential error when the data are applied to NPP or carbon flux studies.

	leaf dry weight per unit ground area (g m^{-2})									
	climber	**herb**	**grass**	**fern**	**sedge**	**rush**	**shrubs (-hazel)**	**hazel**	**Total (-shrub)**	**Total**
MAY										
Open	8.0	7.6	17.4	0.3	3.3	1.3	2.7	6.0	37.9	46.6
Mast	12.2	20.4	13.3	0.4	1.6	4.5	7.9	14.8	55.5	78.1
Level II	11.5	23.7	8.0	0.7	2.3	0	11.5	31.7	63.6	106.8
Tall shrub	7.2	1.3	5.1	0.6	0.2	0	7.2	77.5	12.6	97.2
JULY										
Open	8.7	18.7	20.7	1.9	6.2	18.1	8.7	10.6	86.4	105.7
Mast	5.9	18.5	12.0	3.4	1.8	11.1	5.9	14.9	59.5	80.3
Level II	8.0	10.1	7.6	0.9	0.4	0.6	8.0	30.3	50.0	88.2
Tall shrub	23.5	0.1	3.8	0.6	0.1	0	23.5	104.7	13.8	142.0
OCTOBER										
Open	14.0	9.0	42.7	1.0	0.5	1.3	12.0	9.6	68.4	90.0
Mast	12.0	22.4	14.8	1.8	1.6	1.1	14.1	15.5	53.6	83.2
Level II	11.6	8.4	3.4	1.1	0.3	0.1	18.1	27.4	24.9	70.4
Tall shrub	2.7	0.2	3.1	2.5	0.7	0	9.0	97.6	9.2	115.8
FEBRUARY										
Open	2.9	2.4	33.6	0.9	4.2	9.8	0.1	0	53.9	57.1
Mast	11.7	2.4	6.6	0.9	1.4	4.4	0	0	27.4	27.4
Level II	3.3	3.8	3.3	0.2	0	0.1	20.4	0	10.6	35.6
Tall shrub	2.5	0.4	1.3	1.2	3.8	0	0	0	9.0	9.0

Table 7. Summary of leaf biomass by plant group and community.

3.2.1 Open community

Growth of the ground flora (notably the grasses) from July through to October was evident, with a large proportion (~50%) also persisting through the winter as green biomass (0.35 m^2 m^{-2}), possibly reflecting the mild winter (Fig. 2a). Maximum leaf area of the ground flora exceeds any other community (see Fig. 6a), totalling 0.58 m^2 m^{-2} for herbs and 0.52 m^2 m^{-2} for grasses (Fig. 2b). It is also noteworthy that in May 1999, leaf area of the ground vegetation was higher in both the Mast and Level communities (Fig. 6a), but this position had been reversed by February 2000, reflecting the more recent thinning of the open community and rapid growth of the understorey. Leaf area of both climbers and the ground flora increased rapidly in early summer, and then fell away towards the end of the growing season. This contrasts with woody shrubs, which show a more gradual increase in leaf area, throughout the growing season. Total understorey leaf area peaked July 2.3 m^2 m^{-2}), of which the total non-woody ground flora comprised 56%.

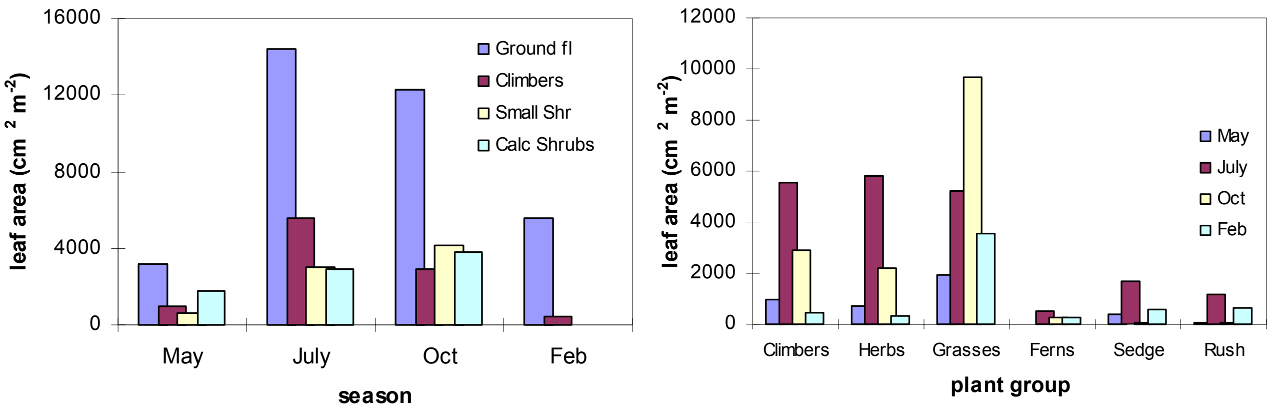


Fig. 2. (a) Seasonal change in leaf area represented by each of the four main plant life forms in the Open community. (b) Contribution from each plant group to total leaf area at each sampling point for the Open community.

3.2.2 Mast community
The seasonal pattern of foliage growth in the Open community was repeated in the Mast community but with a lower contribution from the grasses (0.28 m^2 m^{-2}: Fig. 3a) in July, reflecting the denser canopy of this community, whilst a more varied ground flora was also evident (Fig. 3b). The proportion of winter persistent climbers was also notable, with leaf area of nearly 0.2 m^2 m^{-2} due mainly to *Rubus fruticosus* and *Lonicera*. Woody shrubs also contributed significantly to total leaf area of the ground vegetation, peaking in July (0.47 m^2 m^{-2}), when it constituted 21% of total understorey leaf area (2.29 m^2 m^{-2}: Table 7).

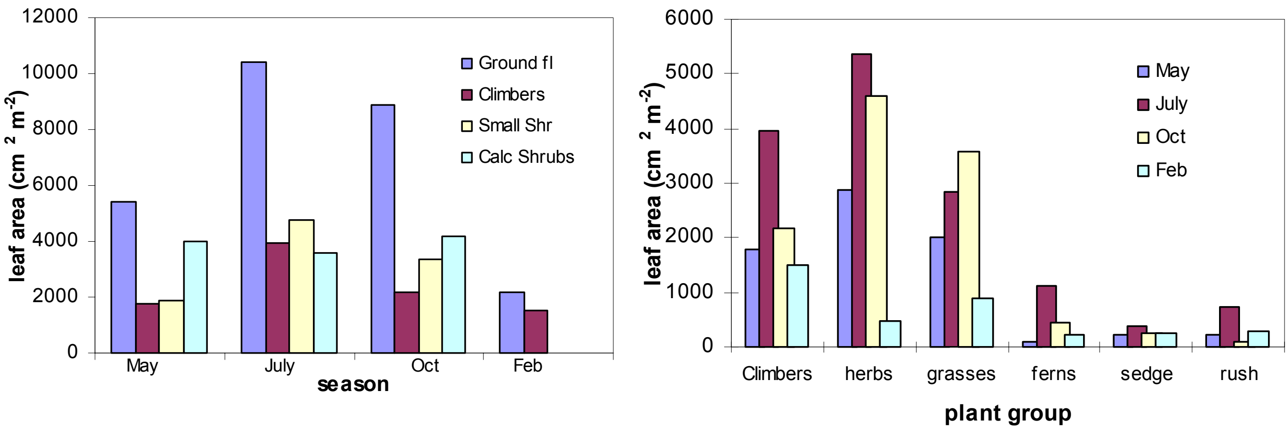


Fig. 3. (a) Seasonal change in leaf area represented by each of the four main plant life forms in the Mast community. (b) Contribution from each plant group to total leaf area at each sampling point for the Mast community.

3.2.3 Level II community
The Level II community showed a slightly different seasonal pattern of leaf area growth compared to the Open and Mast communities, largely as a result of the contribution of evergreen holly to the small shrub category, and the greater growth of climbers in the secondary canopy (0.73 m^2 m^{-2}). The small fall in total leaf area of the secondary canopy between May and July (Fig. 4a) is likely to be an experimental artefact, reflecting the high variability for this life form, rather than a real decline. The contribution from the ground flora to total understorey leaf area again peaked in July (0.3 m^2 m^{-2}), although as a lower proportion than for the Mast and Open communities (13%: Table 7), largely as a result of the limited quantities of grass recorded (0.18 m^2 m^{-2}: Fig. 4b).

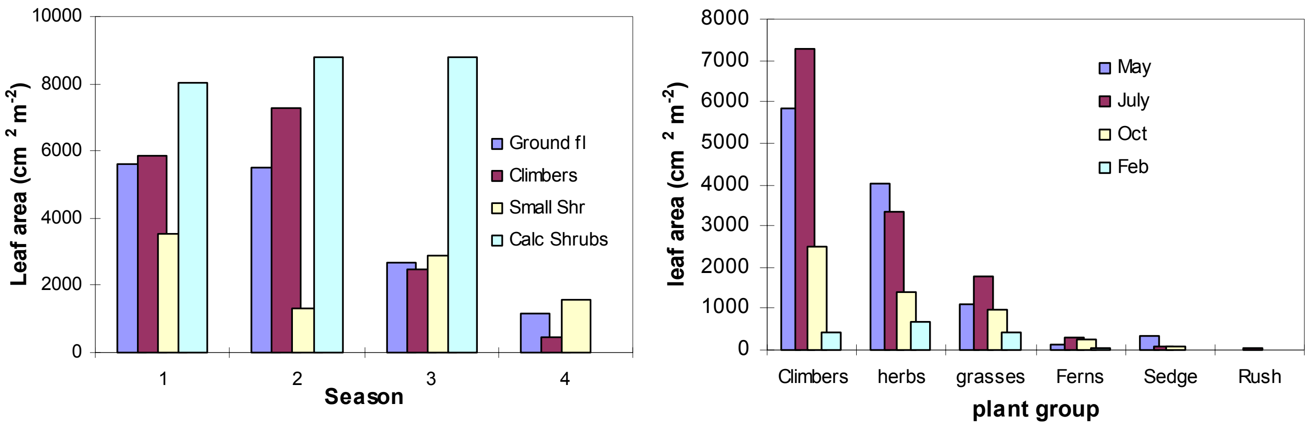


Fig. 4. (a) Seasonal change in leaf area represented by each of the four main plant life forms in the Mast community. (b) Contribution from each plant group to total leaf area at each sampling point for the Mast community.

3.2.4 Tall shrub community

Leaf area in the Tall shrub community was dominated by the secondary canopy, primarily comprised of hazel, with a maximum leaf area of 2.7 $m^2 m^{-2}$ in October. By contrast, the winter persistent green leaf area comprising some climber and sedge regrowth was less than 0.16 $m^2 m^{-2}$, and lower than that for any other community. In July, the climber leaf area was only 0.27 $m^2 m^{-2}$, whilst other small shrubs contributed a total of 0.5 $m^2 m^{-2}$, and herbs and grasses comprised less than 0.1 $m^2 m^{-2}$.

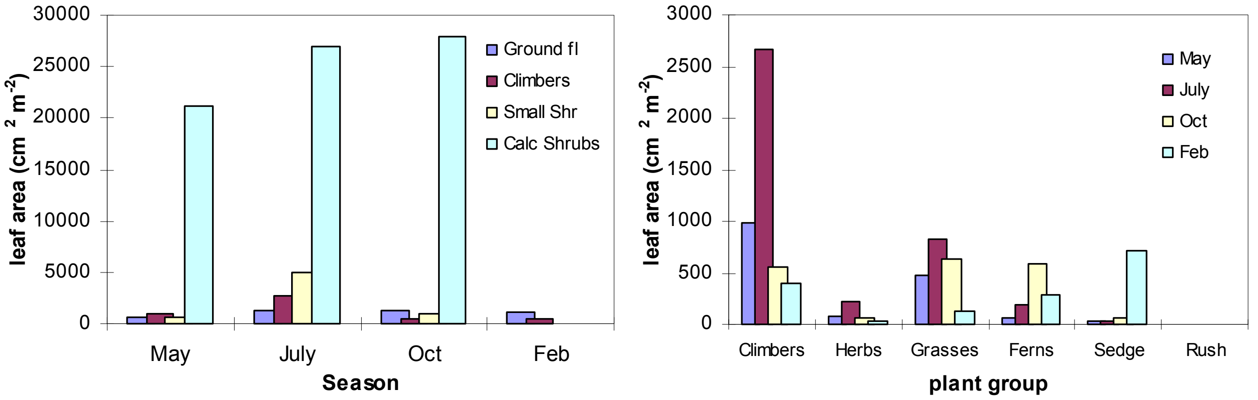


Fig. 5a. (a) Seasonal change in leaf area represented by each of the four main plant life forms in the Mast community. (b) Contribution from each plant group to total leaf area at each sampling point for the Mast community.

3.2.5 Summary data

The summary data shown in Figs. 6a-d clearly demonstrate the seasonal patterns of leaf growth for each plant group and for each community, whilst Fig. 7 and Table 8 give 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 for all communities.

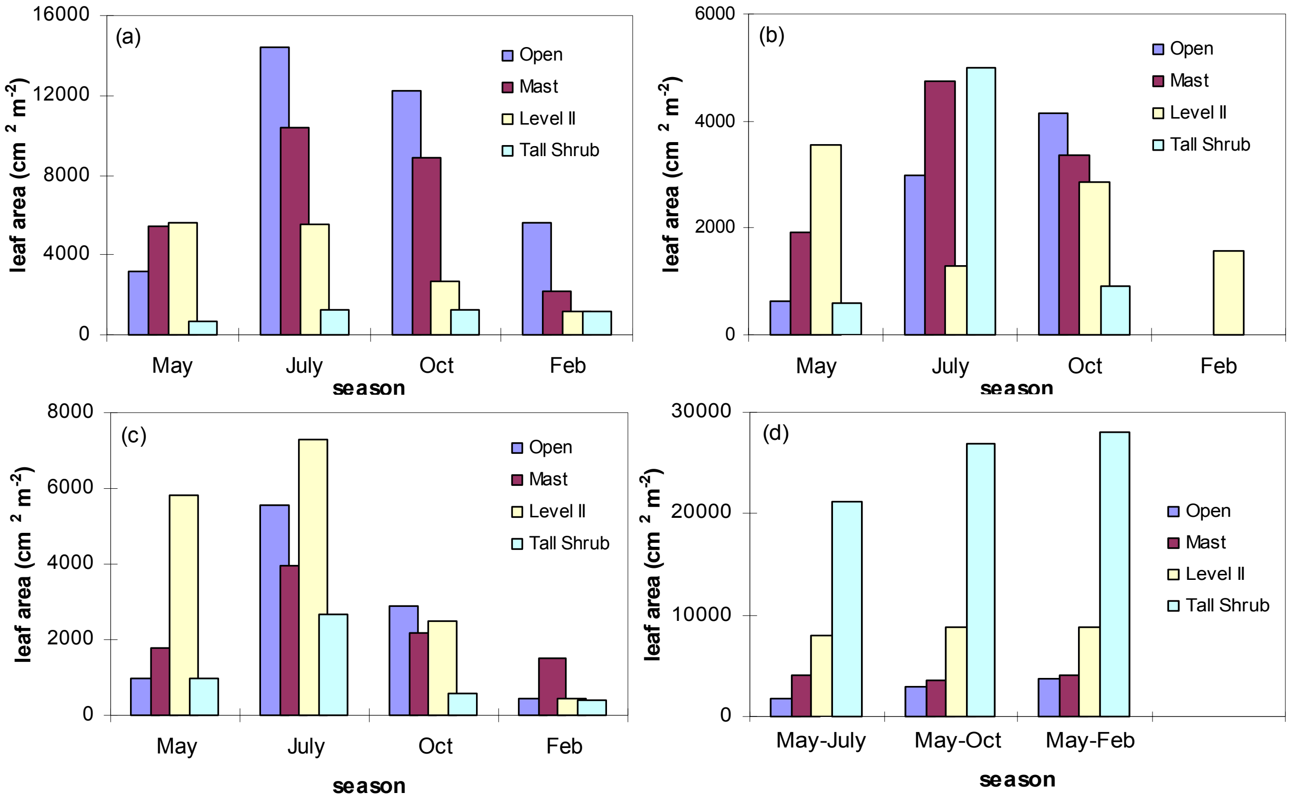


Fig. 6. Total contribution from (a) herbaceous ground flora, (b) woody ground flora (c) climbers and (d) secondary (shrub) canopy for each community and each sampling point.

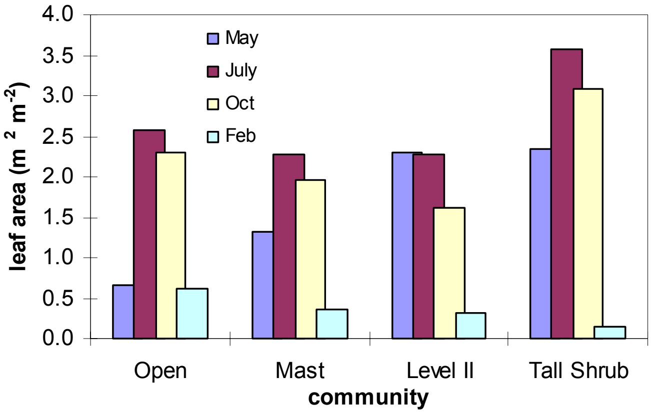


Fig. 7. Total green leaf area of the understorey of each community for each sampling period.

	understorey total leaf area (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 8. Total green leaf area of the understorey of each community for each sampling period.

Table 9 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.

	contribution to understorey leaf area (%)									
community	**herb**	**grass**	**fern**	**sedge**	**shrub**	**climb**	**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	45.4	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	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	26.0	1.9	8.2	19.3	45.8

Table 9. 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'.

Leaf area of the ground vegetation exceeded that of both climbers and short woody shrubs category, particularly in May and July, and in the winter months, was still significantly over 0.6 m^2 m^{-2} and just under 0.5 m^2 m^{-2} in the Open and Mast treatments respectively. 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, which reached a maximum of over 2.0 m^2 m^{-2} in July in the Open, Level II and Mast communities, and 3.6 m^2 m^{-2} in the Tall shrub community.

3.3 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. Most process models of forest growth and function rely on foliage nitrogen concentration to provide the basis for these parameters (see Broadmeadow *et al*., 2000; Medlyn *et al*., 2001). The following sections identify whether a common relationship between foliar $[N]_a$ and these parameters is valid across the range of species present in the understorey of the Straits Enclosure.

3.3.1 Foliar chemistry and structure

A survey of foliar nitrogen content and specific leaf area was carried out in the Mast community in July 1999, to provide an indication of inter and intra-species variability. The data are summarised in Table 10. Foliar nitrogen content was highest in two of the herbaceous species (nettle and woundwort), and lowest in ivy. The three woundwort samples showed a large degree of variation, which may be related to either their developmental state, or the microhabitat in which they were growing, particularly the radiation environment. The low [N] of ivy is likely to reflect the much thicker leaves, compared to all other species assessed.

species	SLA (cm^2 g^{-1})	[N] (mg g^{-1})	[n]a (g m^{-2})
Hedera helix (ivy)	101	12.2	1.205
Quercus robur (oak)	193	21.1	1.090
Deschampsia flexuosa (tufted hair grass)	150	19.1	0.960
Coryllus avellana (hazel)	268	24.1	0.899
	300	27.9	0.931
Carex sylvatica (wood sedge)	240	20.4	0.850
Millium effusum (wood millet)	339	24.9	0.733
Crataegus monogyna (hawthorn)	253	15.3	0.605
	162	18.4	1.139
Rubus fruticosus (bramble)	258	22.6	0.871
	251	18.8	0.748
Holcus lanatus (soft bent)	296	27.5	0.733
Dryopteris filix-mas (male fern)	259	21.3	0.821
	279	16.5	0.592
Lonicera periclymenum (honeysuckle)	324	20.6	0.636
	424	20.0	0.472
	265	21.8	0.821
	296	22.5	0.915
	385	17.5	0.454
Fraxinus excelsior (ash)	308	19.0	0.616
Rosa arvensis (wood rose)	333	20.6	0.619
	379	24.6	0.649
	405	23.0	0.559
Urtica dioica (nettle)	424	29.6	0.698
Virurnum opulus (guelder rose)	314	18.1	0.577
Stachys sylvatica (woundwort)	564	28.7	0.508
	682	30.7	0.449
	603	20.4	0.338

Table 10. Structural and chemical composition of foliage of selected understorey species.

[N] was relatively constant in the five samples of honeysuckle analysed, although the large variation in SLA resulted in an observed twofold variability in leaf nitrogen content when expressed on an area basis ([N]a). This variability may reflect the adaptability of this species, in growing in a range of radiation environments as a result of its growth form. Generally, [N]a was lower in thin leafed shade adapted species such as *Stachys sylvatica*, and this close relationship between nitrogen content expressed on an area basis and leaf thickness across all species is evident in Fig. 8. This tight relationship and has important implications for the generation of the photosynthetic parameters required for process modelling of carbon fluxes. The low nitrogen content [N] of the two overstorey species (oak and ash) is indicative of shade adapted leaves.

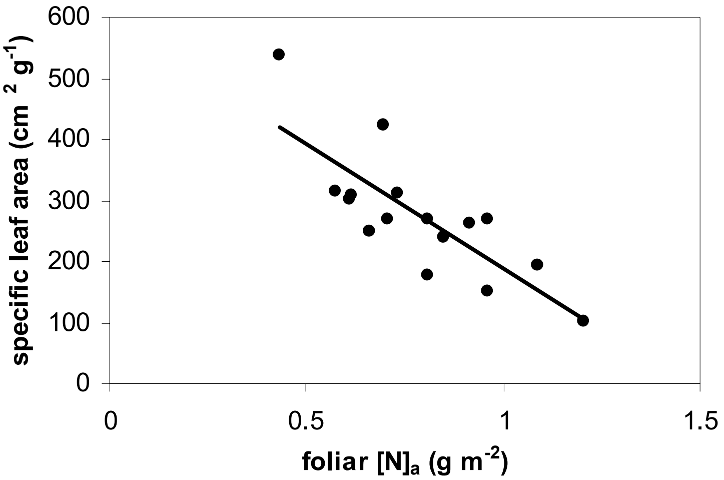


Fig. 8. Relationship between specific leaf area and foliar nitrogen content expressed on an area basis for selected understorey species given in Table 9. Line fitted by least sum of squares (y=594-406x; r^2=0.63).

3.3.2 Photosynthetic parameterisation

species	J_{max} (μmol m^{-2} s^{-1})	V_{max} (μmol m^{-2} s^{-1})	R_d (μmol m^{-2} s^{-1})	$[N]_a$ (g m^{-2})
Fraxinus excelsior	74	33	1.0	0.62
Viburnum opulus	78	36	2.0	0.58
Coryllus avellana	87	51	3.3	0.90
	74	36	1.9	0.61
Rubus spp.	90	36	1.6	0.74
Lonicera	76	36	1.9	0.64
	72	23	0.5	0.47
	74	32	1.4	0.45
	84	41	1.8	0.82
	84	35	1.8	0.92
Rosa arvensis	78	36	1.8	0.56
	62	30	1.3	0.62
Urtica dioica	61	25	1.7	0.70
Stachys sylvatica	53	20	1.1	0.34
	64	25	1.0	0.45
Dryopteris	67	28	1.0	0.51
	77	31	3.1	0.82

Table 11. Photosynthetic parameters for selected understorey species.

Light and CO_2 responses of selected understorey species were analysed according to De Pury and Farquhar (1998), generating the photosynthetic parameters which are required as inputs to process models. In general terms, the shade adapted herbaceous species (woundwort, nettle and male fern) had lower values of J_{max} (potential rate of electron transport), whilst the woody species which grow in more mesic environments tended towards higher values. A similar pattern was repeated for potential RuBisCO activity (V_{max}). Relationships between the three derived photosynthetic parameters and foliar nitrogen content expressed on an area basis were evident (Fig. 9), and given the range of species and growth forms represented, the relationships are surprisingly good.

Furthermore, they suggest that together with the relationship between SLA and $[N]_a$ shown in Fig. 8, photosynthetic parameters for a range of understorey species can be derived from a simple analysis of SLA.

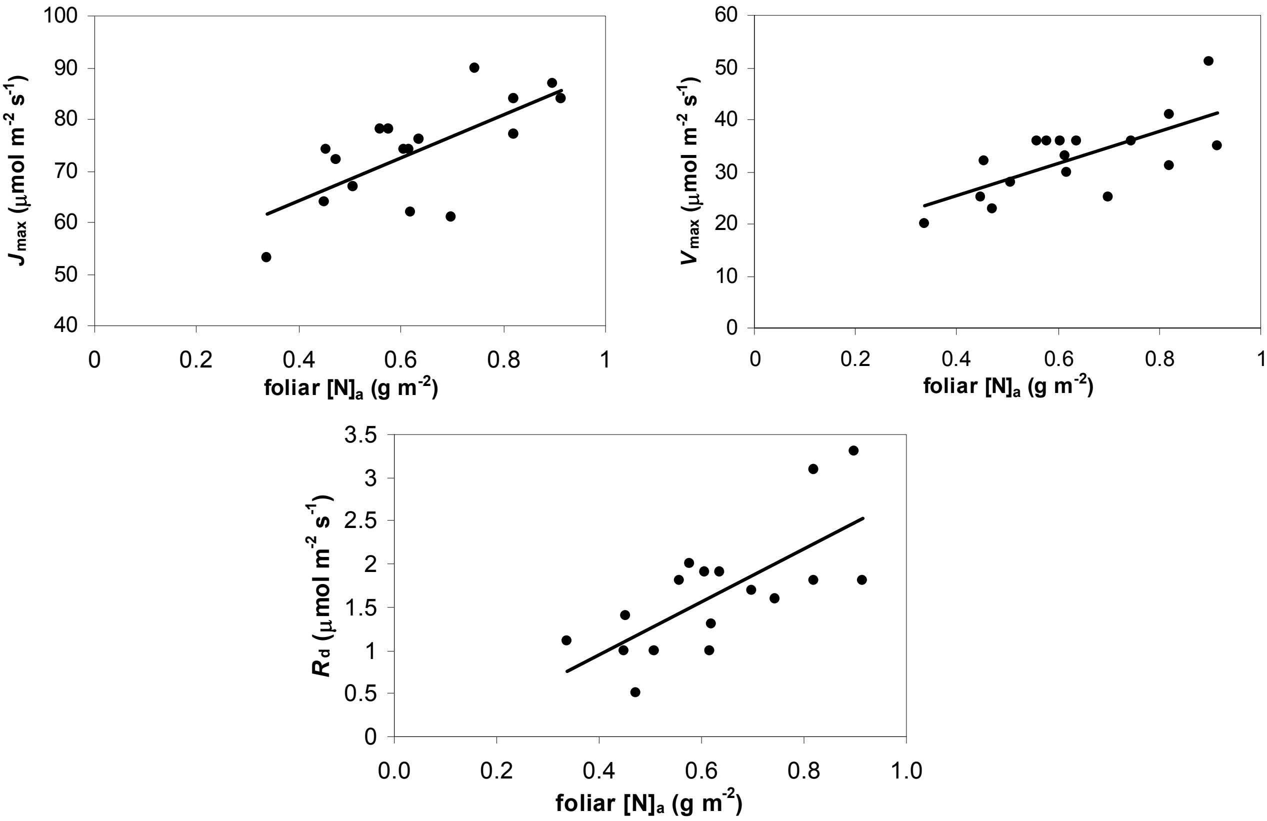


Fig. 9. Relationships between J_{max}, V_{max}, R_d and foliar nitrogen content, respectively. Lines were fitted by least sum of squares (y=47.3+41.9x, r^2=0.49; y=13.2+30.7x, r^2=0.48; y=0.358-0.164x, r^2=0.50).

3.4 Biomass of understorey vegetation 1999 – 2000.

3.4.1 Contribution of hazel to understorey biomass

A detailed description of the methodology behind the estimates of hazel standing biomass for each of the vegetation communities (Table 12) is given in Appendix 4. These estimates are based on the derived allometric relationships for stem diameter summarised in section 2.7.2. The differences between communities reflect the effects of past 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 for 8 – 10 years (Tall shrub community).

community	**standing biomass (g m^{-2})**		**incremental growth (g m^{-2})**		
	May	**October**	**wood**	**leaf**	**total**
Open	29.5 (31%)	37.6	8.2	9.6	17.8
Mast	45.8 (25%)	70.3	24.5	15.5	40.0
level II	86.7 (31%)	123.5	36.8	27.4	64.2
Tall shrub	380.0 (86%)	460.5	80.5	97.8	178.3

Table 12. Standing biomass and incremental growth of hazel in 1999. Figures in parentheses represent the percentage of woody understorey biomass made up by hazel in May 1999.

Table 12 also summarises the annual incremental growth of hazel, including both woody stem/twig and green leaf (dry weight). These data highlight the dominant position of hazel in the understorey, with leaf biomass in the Tall shrub community (~1 t ha-1), almost an order of magnitude greater than that contributed by the rest of the ground flora. In the Level II sites (four years re-growth) the biomass of hazel foliage is approximately equal to that of the herbaceous ground flora, whilst the contribution is smaller in both the Mast (25%) and Open Communities (12%). This high rate of incremental growth of hazel, amounting to almost 50% of NPP, as determined by flux measurements, should be confirmed by continued monitoring of hazel growth.

3.4.2 Biomass of other woody shrubs and climbers

Detailed data on seasonal changes in the biomass of the individual plant groups are given as Appendix 3 (excluding the contribution from the hazel secondary canopy), and are summarised as incremental growth for the woody species in Table 13. Other small woody shrubs sampled from within the metre square quadrats form significant but highly variable proportions of total understorey biomass in both the Mast and Level II communities. In may 1999, woody shrubs (excluding hazel) constituted 43 and 40 % of the standing understorey biomass in these two 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 all quadrats and contributed 50% of the understorey biomass (excluding hazel) in May.

	shrub biomass (g m^{-2})					**climbers (g m^{-2})**				**total**
	Coryllus	***Crataegus***	***Rosa***	***Fraxinus***		***Rubus***	***Lonicera***	***Hedera***		
Open	17.8	12.4	17.6	0.7	**48.5**	15.0	25.6	2.1	**42.7**	**93.5**
Mast	40.0	18.3	4.4	21.7	**84.3**	5.8	0	0.8	**6.5**	**94.5**
Level II	64.2	17.9	4.0	2.3	**88.4**	23.5	11.1	0.3	**34.8**	**136.5**
Tall shrub	178.3	25.8	3.8	0.8	**208.7**	7.1	9.6	0	**16.6**	**225.3**

Table 13. 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 with approximately 160 g m^{-2} of bramble and 118 g m^{-2} of honeysuckle. At the same time, these species contributed 73 and 13 g m^{-2} to understorey biomass respectively in the Mast community, and 17 and 58 g m^{-2} in the Open community. The incremental growth of both these climbers is largest in the Open community, presumably as a result of the high solar radiation input (see above) followed by the Level II sites, with maximum biomass recorded at all sites in July.

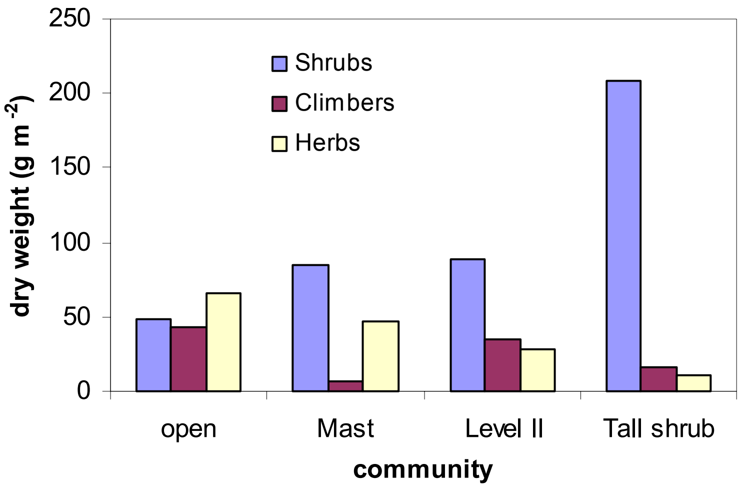


Fig. 10. Incremental growth for 1999-2000 of the three main plant groups in each of the four communities.

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

3.4.3 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 more 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 herbaceaous species was almost equal to that of grass species in the Open community in May (20 – 23 g m^{-2}). In the Mast community, the importance of the herbaceous species was maintained through both July and October, with species such as stitchwort, herb robert, violet and wild strawberry, which are prevalent in spring, being superseded in summer by goosegrass, bugloss, *Stachys sylvatica* and nettle. In autumn the contribution of *Veronica* sp and *Galium* sp to understorey biomass became evident.

The biomass of the remaining categories of non-woody plants is small in all treatments. 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. In contrast, despite the whole site being uniformly on clay soils, the occurrence of rush is limited to the Open and Mast sites, where it grows vigorously in July (0-18 g m^{-2}) and persists in moribund form throughout the winter. Its presence is insignificant in the Level II community, and is entirely absent in the Tall shrub community, possibly reflecting a higher light requirement than sedge. The biomass of the ferns, which occur in all communities is even lower, reaching a peak of 3.5 g m^{-2} in July, and 2.5 g m^{-2} in October in the Mast and Tall shrub communities respectively. However, ferns also persist semi-moribund throughout the winter months in the Straits with biomass totalling 1.0 g m^{-2} on average in February. The contribution from each of the plant groups represented in the herbaceous ground vegetation is given in Fig. 11, with a summary of total incremental growth given in Table 13, including the proportion made up by foliage, compared to the production of woody biomass..

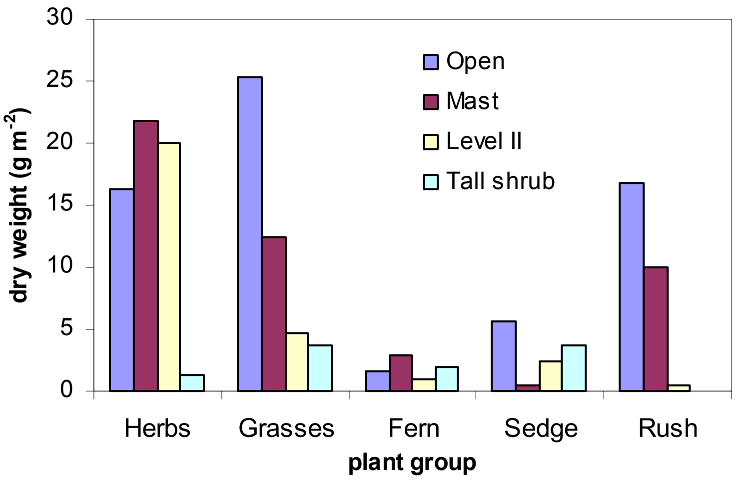


Fig. 11. Incremental growth for 1999-2000 of herbaceous ground vegetation in each of the four communities.

	biomass production (g m^{-2})			
	Open	**Mast**	**Level II**	**Tall shrub**
woody species	93.5	94.5	136.5	225.3
herbaceous species	65.7	47.6	28.3	10.7
total	**159.2**	**142.1**	**164.8**	**236.0**
proportion as foliage (%)	68.3	56.6	61.7	53.6

Table 14. Summary of 1999-2000 incremental growth for each the four communities.

4. Conclusions

The work reported here has provided essential background data for many of the research projects that are carried out in the Straits Enclosure. In addition, methodologies have been developed enabling some of those projects to be carried forward. The analysis of both biomass and leaf area by vegetation community has also indicated 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 heterogenous nature of the stand. The measurements of understorey leaf area index (rising to between 2.3 and 3.6 depending on vegetation community), standing biomass (2.0 to 8.3 t ha^{-1}) foliage turnover (0.8 to 1.3 t ha^{-1}) and incremental woody growth (0.5 to 1.1 t ha^{-1}) indicate the importance of the understorey in stand carbon balance, particularly relating to flux modelling and NPP studies. To place these in context, overstorey LAI has been measured as 5.0 in the Mast community and 6.3 (1999) in the Level II community, whilst NEF was 3.7 t C ha^{-1} in 1999 (~7.4 t dry matter ha^{-1}). However, none of these studies deal with any long term sequestration of carbon in the soil through litter build up, or year to year variation in rates of litter decomposition or soil respiration.

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.

APPENDIX 1: Summary of Straits ecological survey for each sampling point

May 1999

TREATMENT					OPEN									MAST										LEVEL II									TALL SHRUB							
Location	1				2			3			1				2			3			1				2			3			1				2			3		
Quadrat no.	A	B	C	D	A	B	C	A	B	C	A	B	C	D	A	B	C	A	B	C	A	B	C	D	A	B	C	A	B	C	A	B	C	D	A	B	C	A	B	C
Woody shrubs & saplings																																								
Betula pendula					r	r																																		
Corylus avellana						o			r											o	r				fr										ab					
Crataegus monogyna		r					o					fr				fr										ab	o		fr		o	o			o		r			o
Fagus sysvatica																																								
Fraxinus excelsior					r	r	r			r		o	fr		o						o	fr	o																	
Ilex aquifolium																																								
Prunus spinosa																																								
Quercus robur					r											r																								
Rosa arvensis		o		r	o			fr						r	o	o					o		o															o		
Sorbus aucuparia											o		o																											
Viburnum opulus																																				r				
Climbers																																								
Hedera helix					o	o				o								r		o								o		o		o	o				r	o		
Lonicera periclymenum	o	o		o		r		o	o	o	o		r		r	o									r	o	o	fr	o	fr			o	o	r	o	r		r	
Rubus fruticosus	r		o	o	o			fr		r	o	o	fr	r	fr	r	o		fr	fr	o	fr	o	o	o	fr	ab	fr	o	o				r			o	o		
Solanum dulcamara																			o																					
Herbs																																								
Ajuga reptans														o																										
Arum maculatum																												r												
Betonica officinalis																																								
Circaea lutetiana			o	r		r																																		
Cardamine prat./Epipactis sp													r/														r/					/r								
Euphorbia amygdaloides		r		r															r																			r		
Fragaria vesca																					o		r				fr										r			
Galium aparine						r					fr	fr	fr		r		r	o	o	fr	ab					o	o	fr	o		o	o	fr	o						
Geranium robertium						r	o							ab								r																		
Geum urbanum/Galeobdolon												r/										/r		r						/o										
Glechoma hederaceae																													r											
Hypericum pulchrum															r																									
Hypericum maculatum																																								
Lysimachia nemorum																				r																				
Mercurielis perenne													r																											
Oxalis acetosella			r	r									r		r		r			r																				
Primula vulgaris																									r															
Ranunculus repens																																								
Stachys sylvatica											r		o	o	r			r		o	r		o							o										
Stellaria holostea					o									fr		o					o	ab		ab	fr															
Urtica dioca											r	o																												
Veronica hederifolia											r			r									r						r											
Veronica montana															o						r																			
Viola riviniana			r	r		o	o	o								r																								
Grasses																																								
Deschampsia caespitosa	r		r	o		fr	r		o		r	r			o	fr	o							o	r						r		r	r		r		o		
Holcus lanatus																										r				o										
Holcus mollis																o									o				r											
Millium effusum						r	o	r	o	o	r				o		r		fr				o			r	r			r		o								
Sedge, Rush & Ferns																																								
Carex sylvatica						r							r			r											r		o								r			
Juncus inflexus															o	r											r													
Dryopteris dilatata				o					r																								o	r					o	
D. felix-mas											r	o					o		r					r					r	r						r				
Mosses																																								
Polytrichum commune																																								
Rhytidiadelphus sp																																								
all mosses % cover					10			10			10			15							10		5		15	30		15		30		20		30	25				15	10
Bare ground %	70	60	80	50					40	50		10						40	30									50	20	20	50	40	75	70		40	25		95	
Tall shrub overhang %	60	10					30				10						75	25	30		25	10			10		10	80		10	IOO	IOO	IOO	IOO	IOO	IOO	IOO	75	IOO	IOO
Secondary canopy species	H	H					C				H						H	H	C		H	I			C		C	C		C	C			H	H	C	H	H	H	H
KEY: ab=abundant; fr=frequent; o=occasional; r=rare; H=hazel; C=hawthorn; R=rosa; I=holly																																								

July 1999

TREATMENT					OPEN									MAST										LEVEL II									TALL SHRUB							
Location	1				2			3			1				2				3		1				2			3			1				2			3		
Quadrat no.	A	B	C	A	B	C	A	B	C	D	A	B	C	A	B	C	A	B	C	D	A	B	C	A	B	C	A	B	C	D	A	B	C	A	B	C	A	B	C	D
Woody shrubs & saplings																																								
Betula pendula				o																																			r	
Corylus avellana																			fr	o					fr										fr					
Crataegus monogyna					o		r			r			o							fr					r	r					o		o			fr			fr	o
Fagus sysvatica											o																		r											
Fraxinus excelsior		r					r	o	o	r		o	r	r	r					r			o						o	o			r			r				
Ilex aquifolium																																								
Prunus spinosa					r	o					o																													
Quercus robur								r																							r								r	
Rosa arvensis	o		r		fr	fr			fr			ab																									r			
Sorbus aucuparia																																								
Viburnum opulus																																								
Climbers																																								
Hedera helix				fr	r											r			o	r		r			r							r					r			r
Lonicera periclymenum			o	o	fr	o				r					o						fr			o	o	o	o	fr	o	o	o	r	o	o		o	o	r	fr	o
Rubus fruticosus	r	fr		o		o	o	o	o		fr	fr	o	o	o	r	r	fr	o		fr	r	fr	fr	o	o	o	o	o	fr			fr			o	o	r	o	o
Solanum dulcamara																				o																				
Herbs																																								
Ajuga reptans																	o																							
Arum maculatum																								r																
Betonica officinalis																																								
Circaea lutetiana		fr					o		r	r	o	o	o	o		r	r			o	o		r			r	r	r												
Epipactis sp																r																								
Euphorbia amygdaloides			r																																					
Fragaria vesca												r							o			r																		
Galium aparine											r		r		fr			o	fr					o	o		o	r	o											
Geranium robertium	r	fr				o		fr	fr	o					r	fr	r				o																			
Geum urbanum													o	r																										
Glechoma hederaceae																																								
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Lysimachia nemorum																																								
Mercurielis perenne																																								
Oxalis acetosella															r	o	r			o																				
Primula vulgaris																																								
Ranunculus repens																		o																						
Stachys sylvatica							r	ab					r	o				o	o																					
Stellaria holostea/media																						fr	r					o		o										
Urtica dioca													r	fr			r																							
Veronica hederifolia																																								
Veronica montana																					o	r	o						o		r									
Viola riviniana									ab																															
Grasses																																								
Deschampsia caespitosa	o	o	r	o										o	fr	r						o	o	r	o								o				o	o	o	r
Holcus lanatus				r																																				
Holcus mollis							fr	fr	o			o															r	r	o	o		r								
Millium effusum				r		fr				o		o			fr		o									r					r		o		r				r	
Sedge and Rush																																								
Carex sylvatica										o		o					r						o	r												r		r	r	
Juncus inflexus							ab											fr		o																				
Dryopteris dilatata		o										r																												
D. felix-mas		o		o			r						o				o											o	o		o	r	r	o						
Mosses																																								
Polytrichum commune													15				5																							
Rhytidiadelphus sp																																								
all mosses % cover	5	10		20	10						15			5						5		5			30	75		15			20				5		10			
Bare ground %	60	10				15				10	25							15		50		10					30				60	90	IOO	90	50		40	80		15
Tall shrub overhang %			60													30	75	20	80			60	10	60			25	50	30		75	90	30	30	IOO		IOC	40	10	
Secondary canopy species			H/C													H	H	H	H/C			H	H	H			C	H	H		H	H	R	H	H		H	H	H	
KEY: ab=abundant; fr=frequent; o=occasional; r=rare; H=hazel; C=hawthorn; R=rosa; I=holly																																								

October 1999

TREATMENT					OPEN										MAST										LEVEL II										TALL SHRUB							
Location	1			3			2				1			2			3				1				2			3			1			2			3			
Quadrat no.	A	B	C	A	B	C	A	B	C	D	A	B	C	A	B	C	A	B	C	D	A	B	C	D	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	D
Woody shrubs & saplings																																								
Betula pendula					r																																			
Corylus avellana			fr	fr						o					o	r						o					fr				fr									
Crataegus monogyna		fr					fr					o						o	r		r	o					o	fr		o							fr	o	r	
Fagus sysvatica																																								
Fraxinus excelsior					r	o		r	r	r	o	r	o		o		r		r	r	o	r	fr	o				o	r	o								r		
Ilex aquifolium																o						r		o												r				
Prunus spinosa							o					fr													r															
Quercus robur		r			r			r		r									r																	r				
Rosa arvensis	fr	o	o			o	fr	r		o	r				o	fr						o				o														
Sorbus aucuparia/Salix sp				r				o								/r	r																							
Viburnum opulus																																								
Climbers																																								
Hedera helix				r		r	r	r		fr							o				o				o				r	r	r			r					r	r
Lonicera periclymenum	o	o	o	o	r		r	r	o		o				r		r							o	o	fr		r	fr	o	o		r	r	r	r	o	fr	ab	r
Rubus fruticosus	o		o	r	o	r	o	o	o	fr	o	o	fr	o			o	r	fr	o	o	r	o	o	o	o	o	o	o	o		r		r	r	o	o	r	o	o
Solanum dulcamara																		fr																						
Herbs																																								
Ajuga reptans																																								r
Arum maculatum																																								
Betonica officinalis																									o															
Circaea lutetiana	o															r			o		r																			
Epipactis sp / Epilobium sp										/r																														
Euphorbia amygdaloides	r		r																																			r		
Fragaria vesca																		r	o															r						
Galium aparine																																								
Geranium robertium	o	fr			r		o			fr				r	r	o					r																			
Geum urbanum													r			r	o								r															
Glechoma hederaceae																																								
Hypericum pulchrum																																								
Hypericum maculatum																																								
Lysimachia nemorum																	ab	r	r								r													
Mercurielis perenne											r																													
Oxalis acetosella												r			o		r			r	r				r		r								r	r				
Primula vulgaris																																								
Ranunculus repens																																								
Stachys sylvatica					fr								o					o	o	o		r			r															
Stellaria holostea													r	o	fr						o																			
Urtica dioca											o	r					o																							
V. hederifolia/Verbascum sp			o																						/r		/r													
Veronica. montana																					o/fr	o	fr	o			o	fr	o	o										
Viola riviniana				r											o	o					r									r							r	r		
Grasses																																								
Deschampsia caespitosa		o	r		r	ab	r	ab	fr	r	o		fr	ab	fr						r			r			o		o								o	o		r
Holcus lanatus							fr								o				o		r													r			r			r
Holcus mollis					o	r																																		
Millium effusum	r			r	fr	r		r		o	r					fr									r		r		r			r	r							
Sedge and Rush																																								
Carex sylvatica				r	o						r			o	o	r	r	o		r							r		r							o				r
Juncus inflexus				r		r						r	r					r				r					o													
Dryopteris dilatata															o		o	o														o								
D. felix-mas				o							o									r									r	o	o		o	o			o			o
Mosses																																								
Polytrichum commune																																								
Rhytidiadelphus sp																																								
all mosses % cover			10							10	15														40	30	15	10	15	15					25	10			10	
Bare ground %		25	15				15													25											50	75		60		50		20		
Tall shrub overhang %		30									10			25								25		30	10	10	IOO			20			75	75	80	90	80	75	90	50
Secondary canopy species		C												H/C								H		H/I	C	H	H			H			H	H	H	H	H	H	H	C
KEY: ab=abundant; fr=frequent; o=occasional; r=rare; H=hazel; C=hawthorn; R=rosa; I=holly																																								

TREATMENT					OPEN					MAST						LEVEL II						TALL SHRUB			
Location	3				1	2	2				1	3	1				2	3	2				1	3
Quadrat no.	A	B	C	D	A	A	A	B	C	D	A	A	A	B	C	D	A	A	A	B	C	D	A	A
Woody shrubs & saplings																								
Betula pendula																								
Corylus avellana	o		o					o		r									r					
Crataegus monogyna					r											r			o		r			
Fagus sysvatica														r	o			r						
Fraxinus excelsior	o	r			o		r							r		o		r						
Ilex aquifolium																								
Prunus spinosa																								
Quercus robur													r											
Rosa arvensis						o	o		o	o				r	o									
Sorbus aucuparia/Salix sp											o	fr												
Viburnum opulus																								
Climbers																								
Hedera helix							o		o			r	r			o		r	r		r		r	
Lonicera periclymenum	o		o		r	o	o		fr		o		o	o	r	o		fr	fr	r	o	o	o	r
Rubus fruticosus	r	o		o	o	o	fr		o	r	fr	fr	o	r	o		o	o	o	o	o	o	o	r
Solanum dulcamara																								
Herbs																								
Ajuga reptans																								
Arum maculatum																r								
Betonica officinalis																								
Circaea lutetiana																								
Epipactis sp / Epilobium sp																								
Euphorbia amygdaloides					r							o												
Fragaria vesca	r						r					o	o				o							r
Galium aparine										r	r	o	r	r		r								
Geranium robertium	o				o		o	o	o	o														
Geum urbanum	o																				r			
Glechoma hederaceae																								
Hypericum pulchrum																								
Hypericum maculatum																								
Lysimachia nemorum																								
Mercurielis perenne																								
Oxalis acetosella							o																	
Primula vulgaris																								
Ranunculus repens																								
Stachys sylvatica																								
Stellaria holostea		r	fr					r	r						r									
Urtica dioca																		r						
V. hederifolia/Verbascum sp					/r																			
Veronica. montana													o	o	o	o		r						
Viola riviniana		r				r		r													r			
Grasses																								
Deschampsia caespitosa		ab	o	o	o	fr	o	o	r	o	fr		r				fr	r		r	o	r	r	
Holcus lanatus																								
Holcus mollis	o																							
Millium effusum				o		r			o				r	r	r		o		r					
Sedge and Rush																								
Carex sylvatica	fr	r	o						o	r	o	fr					r				o	o		r
Juncus inflexus	ab			o																				
Dryopteris dilatata		r						r/o		o							r	o				o	o	
D. felix-mas																								
Mosses																								
Polytrichum commune																								
Rhytidiadelphus sp																								
all mosses % cover	10	10				10							20											
Bare ground %				25										70	70				80	80			50	
Tall shrub overhang %								25						75	50	50		50	IOC	80	30	50		90
Secondary canopy species								H						H/I	H	I		H	H/C	H/C		H		H
KEY: ab=abundant; fr=frequent; o=occasional; r=rare; H=hazel; C=hawthorn; R=rosa; I=holly																								

February 2000

APPENDIX 2: Raw leaf area analysis data

MAY 1999

		ground vegetation leaf area ($cm^2\ m^{-2}$)								Leaf area index	
Open		Climbers	Herbs	Grasses	Fern	Sedge	Rush	shrubs	Total	hazel	total
	1	585	0	218	0	0	0	60	862		
		751	96	1236	0	0	0	56	2139		
		308	163	195	0	0	0	24	690		
		1435	389	636	186	98	0	71	2814		
	2	3895	103	510	0	0	0	1813	6321		
		1237	41	3703	68	0	0	2561	7609		
		693	50	3866	0	0	0	76	4684		
	3	446	198	4318	0	0	670	178	5810		
		188	3414	4069	0	3351	0	956	11978		
		337	2587	681	0	663	243	355	4864		
Mean		**987**	**704**	**1943**	**25**	**411**	**91**	**615**	**4781**	**0.18**	**0.66**
SD		1097	1231	1790	60	1053	217	891	3430		
Mast											
	1	1821	2819	1855	68	0	0	770	7333		
		2408	5949	1756	524	647	44	4712	16041		
		4092	3437	518	13	163	0	2252	10474		
		355	7440	235	0	0	0	254	8284		
	2	883	987	3358	66	860	1046	2056	9256		
		694	456	2990	100	267	206	223	4936		
		379	91	3723	173	175	85	7061	11687		
	3	386	3152	138	0	0	0	74	3749		
		3251	2001	5568	96	0	0	1619	12534		
		3582	2305	0	0	68	732	0	6686		
Mean		**1785**	**2864**	**2014**	**104**	**218**	**211**	**1902**	**9098**	**0.40**	**1.31**
SD		1456	2332	1867	158	301	370	2322	3714		
Level II											
	1	2304	12860	389	0	250	0	2418	18221		
		9828	7969	151	0	0	0	4680	22627		
		1640	6179	243	0	0	0	1142	9203		
		3111	2873	309	179	0	0	231	6703		
	2	2311	3047	572	0	0	0	18539	24469		
		16116	922	1285	0	0	0	5916	24240		
		4749	2106	594	255	450	0	1531	9685		
	3	7878	1438	4185	0	0	0	0	13500		
		1580	873	62	751	2852	0	1114	7233		
		8882	1883	3097	259	0	0	0	14121		
Mean		**5840**	**4015**	**1089**	**145**	**355**	**0**	**3557**	**15000**	**0.81**	**2.31**
SD		4764	3874	1411	240	891	0	5626	6973		
Tall shrub											
	1	198	159	11	0	0	0	10	378		
		221	31	1346	0	0	0	385	1983		
		140	193	136	152	0	0	0	622		
		653	232	483	104	0	0	0	1471		
	2	2606	0	0	0	0	0	680	3286		
		817	0	774	80	0	0	2609	4279		
		797	202	1148	0	253	0	0	2399		
	3	1839	30	880	107	0	0	193	3050		
		2518	0	0	142	0	0	176	2836		
		0	0	0	0	0	0	2048	2048		
Mean		**979**	**85**	**478**	**58**	**25**	**0**	**610**	**2235**	**2.12**	**2.34**
SD		987	98	524	65	80	0	940	1205		

July 1999

		ground vegetation leaf area ($cm^2\ m^{-2}$)								Leaf area index	
Open		Climbers	Herbs	Grasses	Fern	Sedge	Rush	shrubs	Total	hazel	total
	1	1017	409	2938	0	0	0	1176	5540		
		4621	8376	56	3718	2640	0	546	19956		
		2468	92	1275	0	0	0	89	3924		
	2	4567	229	4957	356	0	0	2336	12446		
		27673	66	627	0	0	0	8685	37051		
		4645	206	3661	0	0	0	5085	13597		
	3	4090	5217	12608	1029	0	11526	1379	35849		
		661	9781	13793	0	0	228	3391	27854		
		5588	22508	6143	0	7679	0	4960	46878		
		306	11101	6303	0	6225	0	2214	26149		
Mean		**5564**	**5798**	**5236**	**510**	**1654**	**1175**	**2986**	**22924**	**0.29**	**2.58**
SD		8253	7547	4998	1230	2601	3833	2773	15134		
Mast											
	1	11810	14254	0	1656	0	245	9052	37016		
		8065	468	7577	2329	552	67	6245	25303		
		2587	1411	1726	3029	763	560	522	10598		
		8302	7574	2640	0	1409	0	0	19925		
	2	1065	2040	10109	643	236	77	30	14200		
		1159	7191	4478	0	0	0	355	13183		
		1494	1498	1542	3636	170	0	0	8340		
	3	1259	8624	279	0	598	2333	0	13091		
		2467	7525	0	0	32	3309	24195	37528		
		1442	2964	0	0	0	606	7033	12045		
Mean		**3965**	**5355**	**2835**	**1129**	**376**	**720**	**4743**	**19123**	**0.36**	**2.27**
SD		3907	4396	3523	1423	460	1153	7683	14225		
Level II											
	1	8782	9337	63	0	0	0	5382	23563		
		1815	4213	4587	0	0	0	163	10778		
		1641	2514	4523	0	595	262	2078	11614		
	2	11301	956	1291	0	345	97	0	13990		
		15262	221	1337	0	0	0	235	17055		
		11436	89	1483	0	0	0	2568	15576		
	3	2999	1380	2320	0	0	0	56	6755		
		4459	2601	205	1419	0	0	0	8683		
		2263	10538	303	683	0	0	1969	15755		
		12806	1403	1497	706	0	0	530	16942		
Mean		**7276**	**3325**	**1761**	**281**	**94**	**36**	**1298**	**14071**	**0.88**	**2.29**
SD		5197	3702	1630	493	207	85	1741	5544		
Tall shrub											
	1	1381	0	563	518	0	0	4961	7423		
		173	53	937	0	0	0	0	1163		
		7535	49	1300	858	0	0	117	9859		
		531	0	0	452	0	0	348	1331		
	3	1150	0	535	0	0	0	0	1685		
		6640	0	0	0	173	0	29530	36343		
		1587	0	841	0	0	0	249	2677		
	2	555	0	1464	0	80	0	148	2246		
		2109	0	2639	0	82	0	4438	9268		
		5048	2051	0	0	0	0	10230	17329		
Mean		**2671**	**215**	**828**	**183**	**33**	**0**	**5002**	**8932**	**2.69**	**3.58**
SD		2704	645	825	312	59	0	9256	12276		

October 1999

		ground vegetation leaf area (cm^2 m^{-2})								Leaf area index	
Open		**Climbers**	**Herbs**	**Grasses**	**Fern**	**Sedge**	**Rush**	**shrubs**	**Total**	**hazel**	**total**
	1	2984	1255	117	0	0	0	2119	6475		
		1070	697	3102	0	0	0	15946	20815		
		4596	3655	257	0	0	0	4459	12967		
	2	2792	499	6719	0	0	0	1072	11082		
		3367	213	16207	0	0	0	9041	28828		
		1801	85	17759	0	0	0	262	19907		
		4424	3350	9371	0	0	0	5522	22667		
		2393	407	4806	2766	198	439	368	10938		
		5082	11745	13481	0	593	0	377	31278		
		480	125	25225	0	0	0	2178	28009		
Mean		**2899**	**2203**	**9704**	**277**	**79**	**44**	**4134**	**19296**	**0**	**2.31**
SD		1523	3599	8301	875	191	139	5013	13967		
Mast											
	1	3232	1947	2153	293	0	156	8444	16068		
		3699	430	0	0	0	338	14358	18487		
		3834	1972	3816	0	269	162	3750	13641		
		690	341	4177	0	222	0	0	5430		
		96	2224	11426	1676	332	0	2174	17928		
		1199	1600	7221	0	285	0	1816	12121		
		703	26421	0	2022	506	149	100	29751		
		1722	3821	0	505	949	45	2708	9706		
		2870	6251	1087	0	0	0	122	10330		
		3566	902	5788	0	0	0	0	10256		
										or	
Mean		**2161**	**4591**	**3567**	**450**	**256**	**85**	**3347**	**14372**	**0.51**	**1.96**
SD		1432	7869	3754	761	301	114	4653	11949		
Level II											
	1	2052	2883	1808	0	0	0	2774	9518		
		521	1683	1730	0	256	7	4726	8917		
		3242	2675	79	0	0	0	1041	7036		
		4653	1655	368	0	0	0	5521	12197		
		2709	847	948	0	0	0	1221	5726		
		1794	505	2719	0	0	68	129	5147		
		4105	333	86	0	0	0	850	5373		
		3434	2024	324	0	0	0	10473	16255		
		1567	924	1747	1709	505	0	123	6574		
		811	241	0	623	283	0	1719	3677		
Mean		**2489**	**1377**	**981**	**233**	**104**	**8**	**2858**	**8042**	**0.80**	**1.61**
SD		1375	953	957	554	180	21	3246	4721		
Tall shrub											
		435	0	0	888	0		0	1323		
		165	0	232	1317	0		0	1713		
		33	0	0	178	0		0	212		
		244	0	22	2010	0		10	2286		
		728	0	0	0	0		32	760		
		707	72	378	0	397		44	1201		
		1318	115	1525	306	32		4186	7450		
		100	312	3292	0	0		63	3767		
		1366	0	0	0	0		0	1366		
		483	151	971	1099	142		4797	7501		
Mean		**558**	**65**	**642**	**580**	**57**		**913**	**2758**	**2.80**	**3.08**
SD		476	103	1064	710	128		1891	3012		

February 2000

		ground vegetation leaf area (cm^2 m^{-2})								Leaf area index	
Open		**Climbers**	**Herbs**	**Grasses**	**Fern**	**Sedge**	**Rush**	**shrubs**	**Total**	**hazel**	**total**
	1	611	390	1559	0	0		0	2560		
	2	249	212	818	0	2392		48	3718		
	3	406	18	7794	1500	783		0	10502		
	4	108	1087	2677	0	1468		0	5340		
	5	638	226	3295	0	0		0	4160		
	6	593	0	5180	0	0		0	5772		
Mean		**434**	**322**	**3554**	**250**	**774**		**8**	**5342**	**0.03**	**0.61**
SD		200	367	2342	559	904		18	2536		
Mast											
	1	3264	1227	0	0	0		0	4491		
	2	3318	168	951	0	156		0	4593		
	3	0	331	886	1125	0		0	2341		
	4	267	162	2005	0	1362		0	3796		
	5	595	973	613	183	61		0	2425		
	6	1615	0	965	0	0		0	2580		
Mean		**1510**	**477**	**903**	**218**	**263**		**0**	**3371**	**0.00**	**0.39**
SD		1485	500	651	450	542		0	1050		
Level II											
	1	476	681	27	0	0		0	1184		
	2	239	966	1701	0	0		0	2907		
	3	873	640	0	257	0		0	1770		
	4	795	448	474	0	0		0	1716		
	5	38	679	234	0	0		0	951		
	6	199	737	0	0	0		9346	10282		
Mean		**437**	**692**	**406**	**43**	**0**		**1558**	**3135**	**0.00**	**0.32**
SD		339	167	661	105	0		3815	3566		
Tall shrub											
	1	195	0	27	0	0		0	223		
	2	304	0	24	0	0		0	328		
	3	512	163	678	0	1960		0	3313		
	4	639	0	30	1032	2023		0	3724		
	5	357	18	0	0	288		0	663		
	6	417	0	0	677	0		0	1094		
Mean		**404**	**30**	**127**	**285**	**712**		**0**	**1557**	**0.00**	**0.16**
SD		157	65	271	455	998		0	1555		

APPENDIX 3: Raw biomass analysis data

May 1999

	Shrubs	Climbers	Herbs	Grasses	Ferns	Sedge	Rush	Total
OPEN								
	2.5	8.7	0.0	1.9	0.0	0.0	0.0	13.1
	0.9	10.7	1.0	10.8	0.0	0.0	0.0	23.4
	0.8	3.9	2.0	1.7	0.0	0.0	0.0	8.3
	6.8	15.8	5.6	5.6	2.8	0.7	0.0	37.3
	75.9	81.8	0.6	4.2	0.0	0.0	4.1	166.6
	65.8	23.5	0.0	32.3	0.3	0.0	0.0	122.0
	3.8	11.1	0.5	33.8	0.0	0.0	0.0	49.2
	6.3	10.0	1.8	37.7	0.0	0.0	3.4	59.2
	39.3	2.3	50.8	39.4	0.0	25.3	0.0	157.2
	6.4	5.2	13.3	6.9	0.0	7.1	5.5	44.4
mean	**20.8**	**17.3**	**7.6**	**17.4**	**0.3**	**3.3**	**1.3**	**68.1**
SD	28.8	23.5	15.7	16.1	0.9	8.0	2.2	58.8
MAST								
	10.7	18.9	10.9	15.0	0.3	0.0	0.0	55.9
	268.7	31.2	31.5	15.3	2.3	4.9	0.9	354.7
	40.4	58.1	20.8	6.3	0.1	0.0	3.3	128.9
	7.9	5.1	69.0	2.9	0.0	0.0	0.0	85.0
	34.8	9.6	7.0	29.3	0.3	7.6	20.9	109.6
	14.8	5.9	4.3	25.0	0.3	2.0	4.1	56.3
	82.8	5.8	0.5	44.0	0.8	1.3	1.5	136.7
	0.7	5.6	20.6	0.7	0.0	0.0	0.0	27.7
	32.3	44.9	24.0	24.8	0.5	0.0	0.0	126.5
	0.0	50.3	14.9	0.0	0.0	0.5	14.6	80.3
mean	**49.3**	**23.5**	**20.4**	**16.3**	**0.4**	**1.6**	**4.5**	**116.2**
SD	81.0	20.9	19.6	14.5	0.7	2.6	7.3	91.3
LEVEL II								
	46.1	28.9	61.1	4.5	0.0	1.9	0.0	142.5
	34.7	119.6	42.2	1.0	0.0	0.0	0.0	197.6
	20.7	19.9	45.8	2.1	0.0	0.0	0.0	88.3
	2.9	35.8	23.7	1.6	0.8	0.0	0.0	64.8
	297.2	110.0	23.3	5.4	0.0	0.0	0.0	436.0
	250.1	176.3	5.7	8.2	0.0	0.0	0.0	440.3
	0.0	65.2	13.8	4.1	1.2	0.0	0.0	84.3
	0.0	70.4	8.4	36.6	0.0	0.0	0.0	115.3
	109.2	17.7	5.4	0.0	3.7	21.6	0.0	157.5
	0.0	87.3	8.0	16.6	1.3	0.0	0.0	113.1
mean	**76.1**	**73.1**	**23.7**	**8.0**	**0.7**	**2.3**	**0.0**	**184.0**
SD	109.9	51.3	19.6	11.1	1.2	6.8	0.0	139.4
TALL SHRUB								
	65.4	5.0	1.0	0.1	0.0	0.0	0.0	71.5
	10.1	6.5	3.0	9.2	0.0	0.0	0.0	28.7
	0.0	3.9	3.8	1.2	2.5	0.0	0.0	11.3
	0.0	13.6	2.1	7.7	1.6	0.0	0.0	25.0
	37.3	47.0	0.0	0.0	0.0	0.0	0.0	84.2
	71.0	12.8	0.0	9.4	0.4	0.0	0.0	93.6
	0.0	9.5	1.2	13.9	0.0	1.9	0.0	26.5
	23.2	23.1	1.5	9.5	0.5	0.0	0.0	57.8
	9.7	29.4	0.0	0.0	0.6	0.0	0.0	39.7
	107.3	0.0	0.0	0.0	0.0	0.0	0.0	107.3
mean	**32.4**	**15.1**	**1.3**	**5.1**	**0.6**	**0.2**	**0.0**	**54.5**
SD	37.2	14.3	1.4	5.3	0.8	0.6	0.0	33.2

July 1999

	Shrubs	Climbers	Herbs	Grasses	Ferns	Sedge	Rush	Total
OPEN								
	44.9	5.7	1.5	12.9	0.0	0.0	0.0	65.0
	31.7	20.4	24.3	11.6	15.3	0.0	0.0	103.2
	2.7	26.9	1.7	6.4	0.0	0.6	0.0	38.3
	23.7	42.5	0.8	21.8	1.1	0.0	0.0	89.8
	168.7	312.6	0.2	2.3	0.0	0.0	0.0	483.7
	104.9	31.4	0.7	13.7	0.0	0.0	0.0	150.6
	20.7	37.6	25.0	41.2	3.1	0.1	177.6	305.2
	18.7	5.5	41.5	49.4	0.0	0.0	3.5	118.6
	53.9	40.4	60.4	19.7	0.0	33.8	0.0	208.2
	30.7	2.1	31.3	28.5	0.0	27.4	0.0	120.0
mean	**50.1**	**52.5**	**18.7**	**20.7**	**1.9**	**6.2**	**18.1**	**168.3**
SD	50.1	92.6	21.2	15.1	4.8	13.0	56.0	134.5
MAST								
	202.6	80.0	10.1	0.6	5.0	0.0	3.7	302.0
	49.3	109.8	3.8	28.8	7.1	2.4	1.0	202.2
	114.1	18.6	6.2	6.1	9.2	3.4	8.6	166.2
	0.0	56.2	37.2	9.5	0.0	6.2	0.0	109.1
	0.4	27.6	9.8	49.5	2.0	1.0	1.2	91.5
	2.5	7.0	22.5	19.2	0.0	0.0	0.0	51.1
	0.0	10.9	5.7	5.5	11.0	0.8	0.0	33.9
	0.0	10.8	37.3	1.1	0.0	2.6	35.9	87.7
	423.1	25.3	40.7	0.0	0.0	0.1	51.0	540.2
	81.4	10.6	12.3	0.0	0.0		9.3	113.6
mean	**87.3**	**35.7**	**18.5**	**12.0**	**3.4**	**1.8**	**11.1**	**169.7**
SD	135.7	35.0	14.6	16.2	4.3	2.1	17.8	152.0
LEVEL II								
	196.2	265.1	23.6	0.2	0.0	0.0	0.0	485.2
	270.7	14.9	21.1	23.1	0.0	0.0	0.0	329.7
	20.7	35.8	5.0	22.7	0.0	2.6	4.0	90.9
	0.0	105.6	6.7	4.1	0.0	1.5	1.5	119.3
	4.3	112.2	1.4	6.7	0.0	0.0	0.0	124.7
	157.5	84.5	0.4	5.3	0.0	0.0	0.0	247.7
	0.8	17.5	5.3	7.4	0.0	0.0	0.0	31.0
	0.0	35.8	8.5	0.8	4.3	0.0	0.0	49.4
	27.8	16.3	21.2	1.2	2.1	0.0	0.0	68.4
	6.5	115.9	8.5	4.8	2.1	0.0	0.0	137.8
mean	**68.4**	**80.4**	**10.1**	**7.6**	**0.9**	**0.4**	**0.6**	**168.4**
SD	100.6	77.0	8.6	8.4	1.5	0.9	1.3	144.1
TALL SHRUB								
	129.7	34.2	0.0	2.0	2.3	0.0	0.0	168.2
	0.0	4.4	0.3	3.4	0.0	0.0	0.0	8.1
	3.1	57.2	0.3	5.6	2.6	0.0	0.0	68.8
	0.0	14.2	0.0	0.0	1.4	0.0	0.0	15.6
	0.0	3.9	0.0	1.9	0.0	0.0	0.0	5.8
	1469.8	61.7	0.0	0.0	0.0	0.8	0.0	1532.3
	4.0	6.8	0.0	4.2	0.0	0.0	0.0	15.0
	1.6	4.6	0.0	7.4	0.0	0.4	0.0	13.9
	133.9	22.6	0.0	13.3	0.0	0.4	0.0	170.2
	574.5	51.1	0.0	0.0	0.0	0.0	0.0	625.6
mean	**231.7**	**26.1**	**0.1**	**3.8**	**0.6**	**0.1**	**0.0**	**262.3**
SD	470.0	23.3	0.1	4.2	1.1	0.3	0.0	484.6

October 1999

	Shrubs	Climbers	Herbs	Grasses	Fern	Sedge	Rush	Total
OPEN								
	49.5	38.5	13.4	1.3	0.0	0.0	0.0	102.7
	215.0	8.7	2.5	15.1	0.0	0.0	0.0	241.4
	33.3	22.3	6.4	0.4	0.0	0.0	0.0	62.3
	70.7	27.2	1.8	27.8	0.0	0.0	0.0	127.5
	68.2	16.5	0.7	75.9	0.0	0.0	0.0	161.2
	4.5	20.8	0.3	86.4	0.0	0.0	0.0	112.0
	61.4	53.4	17.2	34.1	0.0	0.0	0.0	166.1
	6.5	30.6	1.3	17.2	10.5	1.3	6.8	72.8
	6.7	46.3	45.6	49.4	0.0	3.8	0.0	151.7
	85.0	4.6	0.4	119.3	0.0	0.0	5.9	215.2
mean	**60.1**	**26.9**	**9.0**	**42.7**	**1.0**	**0.5**	**1.3**	**141.3**
SD	61.9	15.7	14.2	39.6	3.3	1.2	2.7	57.8
MAST								
	219.7	33.8	12.2	7.7	1.1	0.0	2.4	276.9
	286.2	41.2	3.0	0.0	0.0	0.0	5.2	335.6
	45.9	35.1	8.4	18.5	0.0	1.7	2.5	112.1
	0.0	3.6	2.1	21.0	0.0	1.4	0.0	28.0
	26.3	2.1	9.5	51.6	7.8	2.1	0.0	99.4
	31.3	10.5	18.2	25.9	0.0	1.8	0.0	87.7
	1.7	11.3	96.7	0.0	7.6	3.2	0.0	120.5
	117.8	57.8	24.3	0.0	1.9	6.0	0.7	208.5
	5.2	25.0	44.4	3.9	0.0	0.0	0.0	77.5
	0.0	33.9	4.9	18.9	0.0	0.0	0.0	27.7
mean	**73.4**	**25.4**	**22.4**	**14.8**	**1.8**	**1.6**	**1.1**	**137.4**
SD	102.2	18.2	29.0	16.2	3.2	1.9	1.8	103.4
LEVEL II								
	51.9	27.1	12.4	5.8	0.0	0.0	0.0	97.4
	81.4	4.8	12.0	0.9	0.0	1.6	0.0	100.8
	20.0	37.8	18.9	0.4	0.0	0.0	0.0	77.0
	298.4	86.3	10.2	1.8	0.0	0.0	0.0	396.5
	50.2	38.7	4.9	3.4	0.0	0.0	0.0	97.2
	6.0	34.2	1.7	11.6	0.0	0.0	1.1	54.6
	57.5	66.6	2.1	0.3	0.0	0.0	0.0	126.5
	127.6	46.7	14.3	1.0	0.0	0.0	0.0	189.6
	2.2	37.8	6.5	8.6	8.0	0.0	0.0	66.2
	110.4	7.9	0.8	0.0	2.9	1.8	0.0	123.8
mean	**80.5**	**38.8**	**8.4**	**3.4**	**1.1**	**0.3**	**0.1**	**133.0**
SD	87.1	24.4	6.1	4.0	2.6	0.7	0.3	100.1
TALL SHRUB								
	0.0	5.0	0.0	0.0	3.3	0.0	0.0	8.4
	0.0	0.9	0.0	0.7	6.1	0.0	0.0	7.7
	0.0	27.1	0.0	0.0	0.8	0.0	0.0	27.9
	0.1	3.4	0.0	0.1	9.2	0.0	0.0	12.8
	0.1	32.5	0.0	0.0	0.0	0.0	0.0	32.6
	0.3	8.5	0.3	1.9	0.0	2.5	0.0	13.5
	310.0	31.7	0.3	7.1	1.2	0.2	0.0	350.4
	18.8	18.6	1.3	16.6	0.0	0.0	0.0	55.2
	0.0	37.6	0.0	0.0	0.0	0.0	0.0	37.6
	312.3	5.8	0.5	4.5	4.1	4.1	0.0	328.1
mean	**64.2**	**17.1**	**0.2**	**3.1**	**2.5**	**0.7**	**0.0**	**87.4**
SD	130.3	14.0	0.4	5.3	3.2	1.4	0.0	133.7

May 1999 summary

	Shrubs	Climbers	Herbs	Grasses	Fern	Sedge	Rush	Total
Open	20.8	17.3	7.6	17.4	0.3	3.3	1.3	65.8
Mast	49.3	23.5	20.4	16.3	0.4	1.6	4.5	116.2
Level II	76.1	73.1	23.7	8.0	0.7	2.3	0.0	184.0
Tall shrub	32.4	15.1	1.3	5.1	0.6	0.2	0.0	54.5

July 1999 summary

	Shrubs	Climbers	Herbs	Grasses	Fern	Sedge	Rush	Total
Open	50.1	52.5	18.7	20.7	1.9	6.2	18.1	168.3
Mast	87.3	35.7	18.5	12.0	3.4	1.8	11.1	169.7
Level II	68.4	80.4	10.1	7.6	0.9	0.4	0.6	168.4
Tall shrub	231.7	26.1	0.1	3.8	0.6	0.1	0.0	262.3

October 1999 summary

	Shrubs	Climbers	herbs	Grasses	Fern	Sedge	Rush	
Open	60.1	26.9	9.0	42.7	1.0	0.5	1.3	141.3
Mast	73.4	25.4	22.4	14.8	1.8	1.6	1.1	137.4
Level II	80.5	38.8	8.4	3.4	1.1	0.3	0.1	133.0
Tall shrub	64.2	17.1	0.2	3.1	2.5	0.7	0.0	87.4

APPENDIX 4: Derivation of allometric relationships for Coryllus avellana

A4.1 Rationale
Understorey shrubs, dominated by hazel comprise a large proportion of the understorey in the Straits Enclosure, particularly in those areas which have not been subjected to management intervention in recent years. As a result of the considerable growth that has occurred during the period of up to 8 years since the last scrub clearance operation, direct measurement was not a feasible method of biomass or leaf area determination, within the time constraints of the project. Allometric relationships based on measured stem diameter were therefore developed for the estimation of woody biomass (both stem and twig) and leaf area.

A4.2 Methodology
Thirty stems of a variety of sizes were cut at ground level from the Tall shrub and Level II communities, close to, but not inside the vegetation assessment quadrats. The first fifteen were sampled at random in late July, when it was assumed that the majority of twig and leaf extension was complete. After initial processing of data, small differences in the biomass of new twig growth were observed between the two communities analysed, and the later samples (in September and February) included additional samples from the Mast community.

Stem diameters were averaged from two measurements at right angles at ground level. 'Twig end' sections were cut at the level of the annual growth ring representing the start of the two previous years extension growth, which in all cases, subtended the majority of the current foliage. Dead side twigs were excluded from this analysis.

A4.3 Results
Allometric relationships were developed between leaf biomass, twig biomass, stem biomass and stem diameter. These relationships are described in the following sections, and summarised in Table A1.

A4.3.1 Observed allometric relationships

Fig. A4.1 summarises the ratio between twig dry weight and leaf dry weight in July 1999.
This relationship was used to estimate leaf weight from cut twig ends avoiding the necessity to individually strip all twigs collected from every stem. Specific leaf area was measured throughout the summer as part of the ecological sampling, with values of 264 and 292 $cm^2\ g^{-1}$ assumed for July and September, indicating continuing leaf expansion during mid- and late summer.

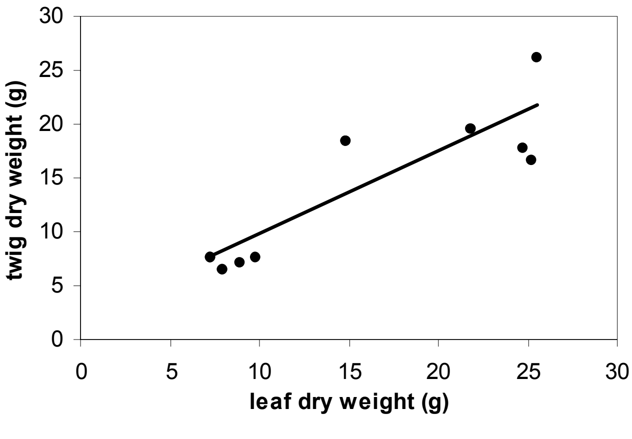

Fig. A4.1. Relationship between leaf and twig biomass for hazel in at the point of maximum canopy development in July.

The relationships between stem diameter and both twig/leaf weight and stem total dry weight were developed, enabling the estimation of hazel biomass from the non-destructive measurement of stem diameter.

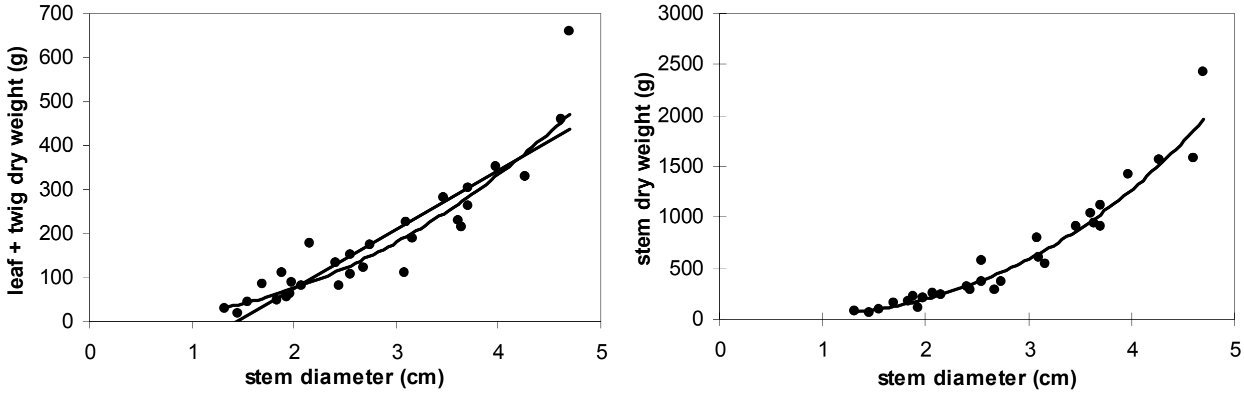

Fig. A4.2. (a) Relationship between leaf and twig weight combined and stem diameter. Linear and power relationships were fitted by least sum of squares. ($y=113.8x-145.6$; $r^2=0.87$, $y=18.0x^{2.08}$; $r^2=0.86$). (b) Relationship between stem dry weight and stem diameter ($y=31.2x^{2.67}$; $r^2=0.96$).

A4.3.2 Derived allometric relationships

Using the observed linear relationships between stem diameter and combined leaf/twig weight (Fig. A4.2a), and twig to leaf weight above (Fig. A4.1), the relationship between leaf area and measured stem diameter was derived, as shown in Fig. A4.3.

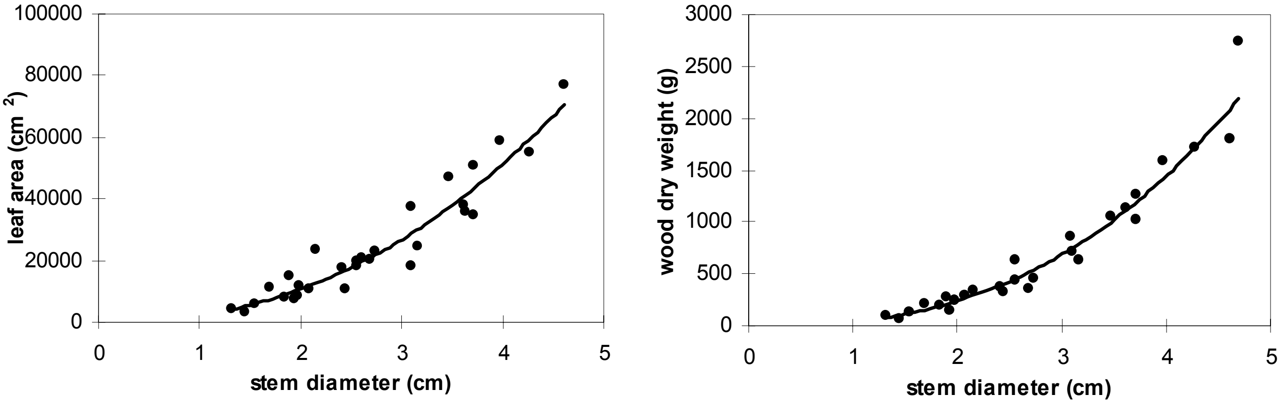

Fig. A4.3 Derived relationships between (a) leaf area and stem diameter ($y=2238x^{2.26}$; $r^2=0.90$) and (b) total wood biomass and stem diameter ($y=39.4x^{2.60}$; $r^2=0.96$), respectively.

A4.3.3 Inter-community variation in allometric relationships

An additional 15 stems cut in February 2000 were added to the September analysis to increase the data-set on the biomass of twig extension growth during the previous growing season. This addition brought an improvement to the relationship, enabling a more robust estimate of 1999 growth to be made. This analysis excluded the mid-season data from July, when extension growth may have not been complete. The data-set was broken down by community, and a subtle difference emerged in the relationship between twig biomass and stem diameter, presumably reflecting differences in the age structure of the secondary canopy in the two communities, or differences in the light regimes leading to effects on extension growth of woody material.

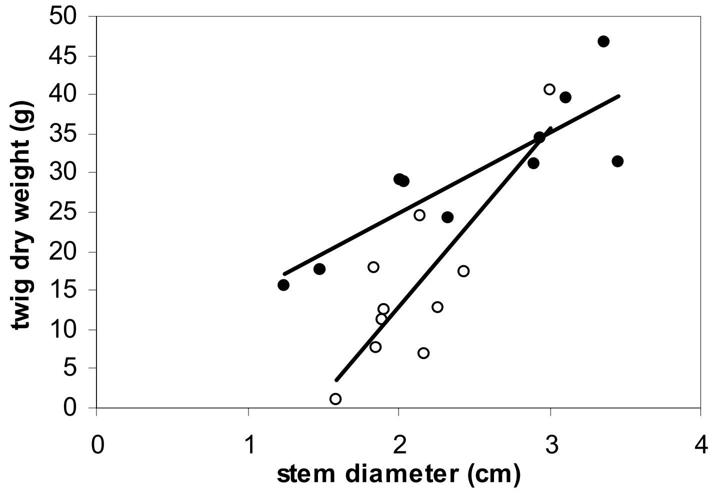

Fig. A.4.4. Relationships between twig dry weight and stem diameter for the Tall shrub (open circles: y=22.8x-32.9; r^2=0.68) and Mast and Level II communities (closed circles: y=10.3x+4.1; r^2=0.75).

As an example, a stem of 2.5 cm diameter would result in estimates of incremental growth of 29.9 g in the Mast and Open communities, and 24.1 g in the Tall shrub community. This difference in calculated twig incremental growth would thus have an impact on estimated leaf area for the different communities. Therefore the relationship between leaf area and twig biomass was modified for the Tall shrub community to take into account the effect of exposure on twig extension growth, and thus improve the robustness of the analysis.

A4.3.4. Summary of allometric relationships for hazel

Open, Mast and Level II communities:	
Leaf area (cm2) subtended from stem diameter (cm)	$\mathbf{y=2208x^{2.28}}$
Standing woody biomass (g) from stem diameter (cm)	$\mathbf{y = 40.6x^{2.60}}$
Twig biomass (g) from stem diameter (cm)	**y = 10.3x+4.1**
Tall shrub community:	
Leaf area (cm2) subtended from stem diameter (cm)	$\mathbf{y= 1447x^{2.57}}$
Standing woody biomass (g) from stem diameter (cm)	$\mathbf{y = 41.1x^{2.58}}$
Twig biomass (g) from stem diameter (cm)	**y = 22.8x-32.9**

A4.3.5. Derivation of Hazel leaf area

Field measurements of stem diameter and number were made to enable biomass and leaf area determinations to be carried out using the relationships summarised in section A4.3.4. These measurements were made in five quadrats in each of the four communitites. As this is a non-destructive process, measurements could be made within the ecological, the ECN and the Level II plots. Stem numbers varied between 20 and 250 per 10 m x 10 m square. The data for the open community include a small number of very large shrubs, which had not been removed during the last scrub clearance operation as a result of their proximity to large oak trees. These had a disproportionately large effect on calculated standing biomass and leaf area, and those quadrats in which they were present (in O2B and O1A) were excluded from the analysis.

The leaf area and biomass estimates given in Table A4.2 demonstrate a level of variation that would be expected for woodland of this type, reflecting the different management activities that had been undertaken in recent years in the four vegetation communities that have been identified. The high value of leaf area index in the Tall shrub community (3.02 m^2 m^{-2}) was confirmed by the collection and analysis of leaf litter from the forest floor (see section A4.3.6 and Table A4.3). If the data from quadrat T4 are excluded on the grounds that this area of the Tall shrub community is particularly sparse and on the edge of the woodland block, mean hazel leaf area becomes 2.76 m^2 m^{-2} , which may be a more representative value. This could be an important adjustment to total understorey leaf area, as the Tall shrub treatment also covers the largest portion of the Straits enclosure (35%).

	No of stems	**stem diameter (cm)**	**SD**	**leaf area (m^2 m^{-2})**	**leaf weight (g m^{-2})**
Open					
O2A	42	1.545	0.82	0.364	
O2B	76	1.358	1.05	1.358	
O1A	66	1.548	1.33	1.548	
O3A	20	1.236	0.47	0.086	
O3B	59	1.228	0.83	0.352	
O81	42	1.422	0.89	0.322	
				0.28	**9.7**
Mast					
M2	93	1.27	0.56	0.454	
M3A	38	1.238	0.62	0.185	
M3B	59	1.537	0.56	0.419	
M1/ECN	69	1.494	0.61	0.48	
M62	57	1.577	0.69	0.461	
				0.45	**15.5**
Level II					
L1A	85	1.623	1.01	0.783	
L1B	84	1.586	0.87	0.779	
L2	74	1.658	0.72	0.909	
L3	140	1.441	0.77	0.528	
L3ECN	193	0.989	0.52	1.021	
				0.80	**27.7**
TallShrub					
TS1	160	2.031	0.89	2.288	
TS2	253	1.936	1.04	3.727	
TS3	174	2.037	0.89	2.616	
TS16	129	2.204	1.12	2.391	
(T4	219	2.367	0.84	4.088)	
				2.76 (3.02)	**104.1**

Table A4.2. Estimates of hazel leaf area and weight for the four communities based upon measurements of stem diameter and the application of the allometric relationships given in section A3.4.5.

A4.3.6. Estimates of hazel leaf area from analysis of ground litter: 1999 and 2000

In order to check the data for leaf area derived from allometric relations, ground quadrats were cleared of fallen litter in late autumn of 1999 under the Level II and Tall Shrub treatments, and again in year 2000 under both Tall Shrub and Mast areas. Hazel leaves are very thin at the point of abscission (SLA 300+), and are therefore likely to decay quickly once on the ground. Thus, in the year 2000 repeat collection were made by clearing 0.25m^2 quadrats from the six replicates sites, then re- clearing these plots at three intervals during the autumn leaf fall, and totalling the weights. Specific leaf areas were calculated separately in 1999 and 2000 from newly dropped leaves in both mast and TS sites.

	ground litter analysis leaf weight (g m^{-2})	sd	leaf area (m^2 m^{-2})	derived analysis leaf area (m^2 m^{-2})
1999				
Level II	15.1	7.6	0.46	0.80
Tall shrub 1	48.3	14.1	1.49	2.29
Tall shrub 2	73.7	11.1	2.01	3.73
Tall shrub 4	85.3	9.6	2.63	4.09
Tallshrub 16	61.2	18.8	1.88	2.39
2000				
Mast	10.3	-	0.31	-
Tall shrub 1	61.6	-	1.95	-
Tall shrub 4	80.6	-	2.55	-

Table A4.3. Comparison of hazel leaf area index from ground litter analysis and a derived analysis based on measured stem diameter and the allometric relationships described in sections A4.3.3 to A4.3.6.

There was remarkable uniformity within the replication samples at one site considering the simplicity of the technique. However, compared to Table A1 estimates of leaf area, these mean values are lower in both the Mast and Tall shrub areas by approximately 25 %.This difference is possibly due to a combination of factors, including the rate at which the hazel leaves may be lost on the ground by decay between harvests, and slight overestimation of growth by the allometric models, for which more extensive field data sets should be obtained. Thus realistic leaf areas probably lie between the two estimates - but the litterpick data is useful confirmation that the allometric estimates are within the right order of magnitude. The allometric measures are those used in the ecological leaf area tables and diagrams.

A4.3.7 Annual increase in hazel biomass: 1999-2000

Relationships between stem height and diameter, weight and age of hazel were derived in order to estimate biomass change during the 1999-2000 growing season. According to the Forest Enterprise Management plan of 1990-1995, work on understorey clearance in specific blocks was due to commence in 1991. However, significant windthrow in the western block during winter 1990, led to a delay in the schedule and thus some doubt as to the actual dates of completion. However, within the blocks designated as the ‘Tall shrub community’ clearance and thinning may well have been undertaken in 1991, and preparatory work for the Level II network was definitely completed in 1994. The block in which the flux mast was established was thinned in 1996.

Data for a range of stems where annual rings could be easily identified results in the relationship for all communities between stem diameter and age shown and shown in Fig. A4.4a. The mean stem diameter for the Level II and Tall shrub communities of 1.6 cm and 2.2 cm respectively correspond well with 4/5 and 7/8 years growth that is expected for these communities as described above.

Hazel stem heights were also recorded for a limited number of stools from both Tall shrub, Level II and Mast communities to characterise the population in each treatment, resulting in the tight relationship between stem height and diameter shown in Fig. A4.4b Tall shrub stems commonly reached lengths of 4-5 m.

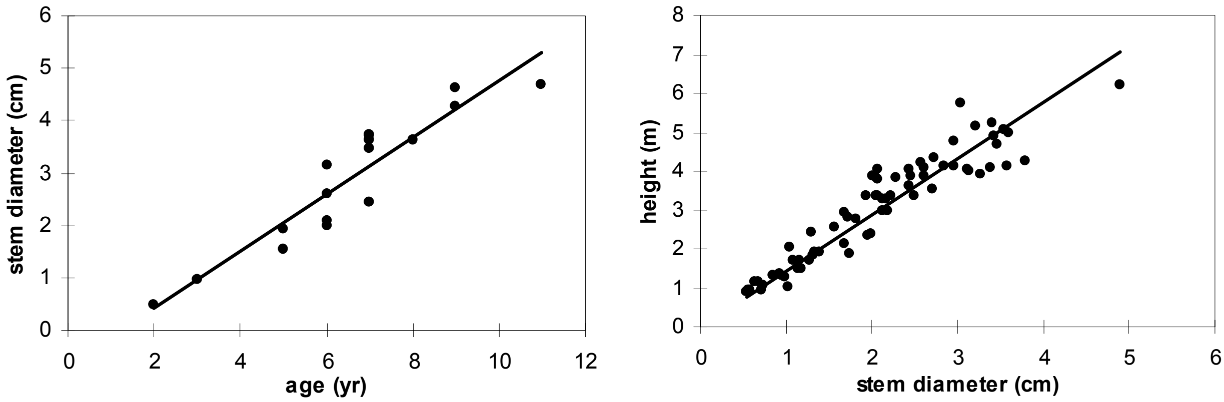

Fig. A4.5. Relationships between (a) stem diameter and age for the Tall shrub community ($y=0.54x-0.65$; $r^2=0.87$) and (b) height and stem diameter for a combined data set from the Mast, Level II and Tall shrub communities ($y=1.44x$; $r^2=0.88$).

Furthermore, through incorporation of the relationships between stem diameter and age (Fig. A4.5a), twig biomass and stem diameter (community specific – Tall shrub or Open, Mast, Level II: Fig. A4.4) or stem biomass and stem diameter (Fig. A4.2b), it is possible to make an estimate of the incremental growth of both the stem (woody parts over one year old) and twig biomass (Table A4.5) for each community. As a result of the age difference between the four communities, this then allows a preliminary relationship between incremental rate and age for these two components to be developed, as shown in Fig. A4.6.

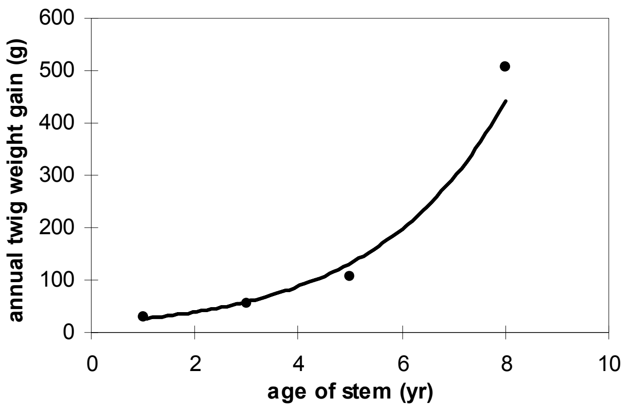

Fig. A4.6. Relationship between annual twig weight increment and age of stem ($y=17.4\exp^{(0.40x)}$; $r^2=0.98$).

A similar relationship can also be developed between age and stem increment alone (Fig. A4.7) by subtracting the total twig increment over the life of the growing stems from the measured standing biomass recorded in each of the four treatments (Table A4.4).

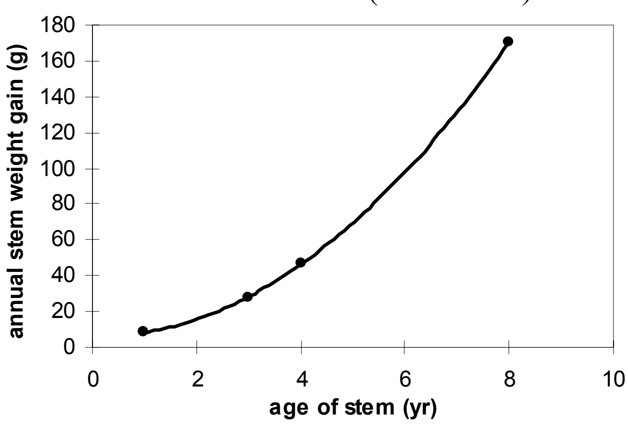

Fig. A4.7. Derived relationship between annual hazel stem weight gain and age of stem ($y=2.6x^2-0.29x+5.8$)

	biomass (kg ha-1)	
	standing biomass (09/1999)	**annual increment (1999)**
Open	373	82
Mast	703	245
Level II	1235	368
Tall shrub	4605	805

Table A4.4. Estimates of woody increment of hazel for each of the four communities in 1999.

There is a potential problem with data from the Open community, as the data-set includes stems left standing after scrub clearance, in addition to new (one year) re-growth, such that the reported incremental growth is likely to be an overestimate. There is however, a steady increase through the other treatments of both stem and twig increment with age. The relative slowing down of the rate of stem increment in the Tall shrub community is to be expected however, with increasing competition for light from the overstorey leading to reduced growth and dieback of the lower branches.

community	**estimated age**	**September 1999 standing biomass ($g\ m^{-2}$)** twig	stem	total	**1999 increment ($g\ m^{-2}$)** twig	stem	**May 1999 standing biomass**
Open							
				52.9			
				14.1			
				40.9			
				42.6			
	1	**8.2**	**29.4**	**37.6**	**8.2**	**29.4**	**0**
Mast				70.4			
				73.3			
				79.7			
				57.9			
	3	**28.0**	**42.3**	**70.3**	**10.4**	**14.1**	**45.8**
Level II				121.7			
				113.3			
				112.0			
				147.1			
	4	**46.6**	**76.9**	**123.5**	**17.6**	**19.2**	**86.7**
Tall shrub				410.3			
				572.9			
				449.7			
				409.2			
	8	**170.1**	**290.4**	**460.5**	**44.2**	**36.3**	**380.0**

Table A4.5. Calculation of annual twig and stem biomass increment for 1999. Total woody biomass was calculated as a function of stem diameter, using separate relationships for the Open, Mast, Level II and Tall shrub communities ($y=40.6x^{2.60}$; $y=41.1x^{2.58}$, respectively). Twig biomass increment was calculated using a similar approach ($y=12.3x-2.3$; $y=22.8x-32.9$).

A preliminary corroboration of this approach was made in November 2000 in the Mast community, with three randomly chosen complete stems broken down into twig and stem components, based on observed, marked extension growth during the 2000 growing season. The three stems ranged in diameter from 1.3 to 2.5 cm corresponding to 4.6 to 11.6 g of twig biomass (average of 8.6 g per stem). Estimated biomass for these same stems based on the allometric relationships described above yielded a value of 10.4 g per stem. Although this analysis is limited, it does indicate that the estimates of twig increment derived here are of the correct order of magnitude.