Light interception and growth in agroforestry systems

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I hereby declare that this thesis is the result of
my own work except where stated otherwise.

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Abstract

Tree leaf area is a fundamental determinant of the productivity of both trees and pasture in agroforestry systems since it influences the amount of light intercepted by the trees and the amount that is transmitted to the understorey below. The distribution of leaf area density of different age classes of leaves within crowns of (*Picea sitchensis* [Bong.] Carr.) was measured in both vertical and horizontal dimensions in 36 trees. The maximum leaf area density was up to 13 times larger than the average within the whole crown and was located about a third of the way up from the base and one fifth of the way out from the trunk in unpruned, open-grown trees. The consequences of the measured non-uniformity of the distribution of leaf area density within tree crowns was profound: up to 50% less light was intercepted per tree and up to 40% more efficient use was made of the light that was intercepted for photosynthesis when compared with uniform crowns and there were significant differences in the spatial pattern of transmittance below the crowns in unpruned trees.

Intensive measurements were made of quantum flux density (QFD) above and below re-spaced tree stands of *P. sitchensis* and *Larix x eurolepis* Henry in conjunction with measurements of tree growth. QFD was also measured above and below pasture growing in simulated swards beneath the trees. The Monteith hypothesis that crop growth in unstressed conditions is linearly related to the amount of QFD intercepted by its canopy was found to hold for above ground growth of trees at agroforestry spacings within but not between sites. The dry matter:QFD quotient for unpruned, open-grown *Picea sitchensis* across a range of tree frequencies was estimated as 0.23 g mol^{-1} which is lower than typical values reported for agricultural crops and those previously reported for young container grown trees and closed-canopy *Picea sitchensis*. The dry matter:QFD quotient was unaffected by tree size and spacing in two adjacent stands, but was significantly lower for another stand in which the trees had been pruned.

The mean annual QFD transmitted to the understorey varied from 38.8% to 94.3% of that in the open across a range agroforestry treatments comprising trees of different size and spacing. The mean transmittance was similar but spatial variability of QFD was significantly higher in tree stands with crowns to ground level when compared with stands having similar crown dimensions but which had been pruned to approximately 1.3 m height. Almost 90% of the mean annual pasture growth was explained by a regression of grass growth on incident QFD. There was a linear relationship between intercepted QFD and grass growth for three pasture species with contrasting sward structure and productivity but whilst the relationship between incident QFD and grass growth varied between species the relationship between intercepted QFD and pasture growth did not. *Lolium perenne* was more productive than *Dactylus glomerata* and *Phleum pratense* in full sunlight and various levels of shade, which was principally associated with a higher tiller density, possibly resulting in a more even distribution of leaf area and hence more QFD being intercepted for a given leaf area index.

MAESTRO, an existing simulation model of radiative transfer for arrays of individual tree crowns, that incorporates two dimensional distribution of leaf area density within crowns, was validated for predicting QFD transmittance in agroforestry stands. The model was subsequently used to investigate the effects of varying tree spacing, arrangement and leaf area duration on the potential productivity of trees and pasture in a range of possible agroforestry scenarios.

Contents

1. Introduction

1.1. Objectives

While the light regimes of closed forest stands and open pasture have been quantitatively described and modelled, agroforestry involves greater complexity and spatial variability. This project has four principal aims.

(i) To test the hypothesis that the growth of trees and pasture is a linear function of intercepted radiation at a range of tree sizes and spacings appropriate to agroforestry.

(ii) To measure the two dimensional distribution of leaf area density within tree crowns and to investigate the effects of non-uniform distribution on radiative transfer within and below individual tree crowns.

(iii) To validate an existing simulation model of radiative transfer for individual trees and tree stands at agroforestry spacings, incorporating two dimensional distribution of leaf area density within crowns, and to develop this to investigate the implications for the understorey canopy, with appropriate treatment of spatial variability.

(iv) To investigate the effects of varying tree species, size, spacing and arrangement on the potential productivity of trees and pasture in a wide range of possible agroforestry scenarios by combining the empirical relationship in (i) with the mechanistic modelling approach in (iii).

1.2. Context

The purpose of this section is to explain the background to and the justification for the methodology of the present research, placing it within its national and global context. The scientific aspects of the relationship between light interception and growth and their modelling are discussed at the start of the respective chapters.

1.2.1. Definition and characterisation of agroforestry

Agroforestry has only become internationally recognised as a scientific subject area over the last decade although it has been a traditional practice for centuries (King, 1987). There has been some confusion about the scope of the term, as evidenced in the collection of definitions in the inaugural editorial of the journal Agroforestry Systems (Anon, 1982). Although the prevailing definition now in use does not distinguish between agroforestry as a general approach to land-use and as a set of integrated land-use practices (Lundgren, 1987), it is useful to do so.

> The approach is interdisciplinary and combines the study of woody perennials, herbaceous plants, livestock and people, and their interactions with one another in farming and forest systems. It embraces an ecosystem focus considering the stability, sustainability and equitability of land-use systems, in addition to their productivity (see Conway, 1985 & 1987; Marten, 1988). Consideration of social as well as ecological and economic aspects is implied.
>
> The set of land-use practices involve the deliberate combination of woody perennials and herbaceous crops and/or animals on the same land management unit in some form of spatial arrangement or temporal sequence such that there are significant ecological and economic interactions between woody and non-woody components. (Adapted from Lundgren, 1987).

Agroforestry practices have been classified according to the type of components involved and their arrangement, which governs the intensity of interaction between trees and agriculture (Huxley, 1983; Nair, 1990). The two broad categories important in the UK are:

1. silvoarable practices; that involve crop production in association with trees and/or shrubs, and,
2. silvopastoral practices; that involve grazing livestock in association with trees and/or shrubs.

Agroforestry practices are more complex and operate over a longer time period than agricultural practices. The fact that more than one species of plant and/or animal is involved, one of which is a woody perennial, creates greater ecological complexity than occurs in monocropping, in terms of both structure and function. The woody component tends to be large in structure and is persistent for a number of years. This leads to long production cycles governed by the component with the longest cycle, within which there may be many shorter agricultural production cycles and several different phases of intercropping. Examples of this include poplars planted on UK farms and intercropped with arable crops for the first seven years followed by grazed pasture (Miller, 1976; Beaton, 1987), and in

Asia it has been common to intercrop coconut with spices in years one to eight after establishment, and again after year 25, but not while the palms are nine to 24 years old (Nelliat *et al.*, 1974).

Agroforestry practices involve multiple objectives and a number of different outputs. These may not all be easily quantifiable products. The tree component may principally play a service role within the land-use system, being involved, for example, in maintaining soil fertility (Young, 1989), or, in wildlife conservation (Harding and Rose, 1986).

1.2.2. Reasons for the recent prominence of agroforestry

Agroforestry has become prominent because values and circumstances are changing. There is an increasing awareness that sustainability of agricultural systems in the long term is as important as their short term productivity. Land degradation and deforestation are perceived on a global scale to be occurring at alarming rates with uncertain consequences. Land degradation has recently been reviewed on a world basis (World Resources Institute, 1989), while the extent of the problem has not been reliably quantified for the world as a whole, it has been estimated that soil erosion may cause rain-fed crop productivity in developing countries to decline by 19 % to 29 % during the next 25 years (FAO, 1984). Estimates of the outright loss of agricultural land through soil erosion range from 6 to 20 million ha a^{-1} (Rozanov *et al.*, 1987, cited in World Resources Institute, 1989; Sfeir-Younis, 1986). An authoritative global assessment of soil degradation is currently in progress (Sombroek, 1989, cited in World Resources Institute 1989). The growing of woody perennials on such land is perceived as being able to reduce erosion by maintaining ground cover and soil organic matter content (Young, 1989). The apparent net change in global forest area, calculated from FAO Production Yearbooks, suggests that 5 million ha a^{-1} were converted to other forms of land-use during the 1980s, as compared to 4 million ha a^{-1} in the early 1970s and 10 million ha a^{-1} in the second half of that decade (Mather, 1990). The FAO figures need to be treated with caution and may well underestimate the net change in forest land. Felled areas designated for reforestation are classified as forest land, and net change is the difference between estimates of the amount of land deforested and reforested, which are both subject to error. It has been suggested that the FAO has not been able to verify nationally reported statistics which has led to understatement of areas deforested in some countries (Myers, 1980), and recent estimates from remote sensing appear to confirm this (Bowonder *et al.*, 1987). The overall pattern is that forest area is declining in tropical developing countries, where population is expanding, and increasing in higher latitudes. Mather (1990), shows an association between change in forest and arable land areas using the FAO national statistics, with the implication that agricultural expansion, caused by increasing population pressure, is a major factor in determining forest clearance.

It is becoming increasingly necessary for farmers to diversify production, particularly to include tree products. In less industrialised countries this is often because of shortages of fuelwood and construction timber beyond farm boundaries. In Europe, surplus food production and increasing interest in the way in which food is produced and the countryside is used for amenity and wildlife conservation, are changing both the incentives and the controls that govern farming practice (Whitby and Ollerenshaw, 1988; de Wit, 1990). Wildlife conservation is also becoming increasingly important in the tropics leading to the encouragement of agroforestry practices in buffer zones around reserved areas of tropical moist forest (Oldfield, 1988; WWF, 1990).

1.2.3. The consequences of the separate development of agriculture and forestry

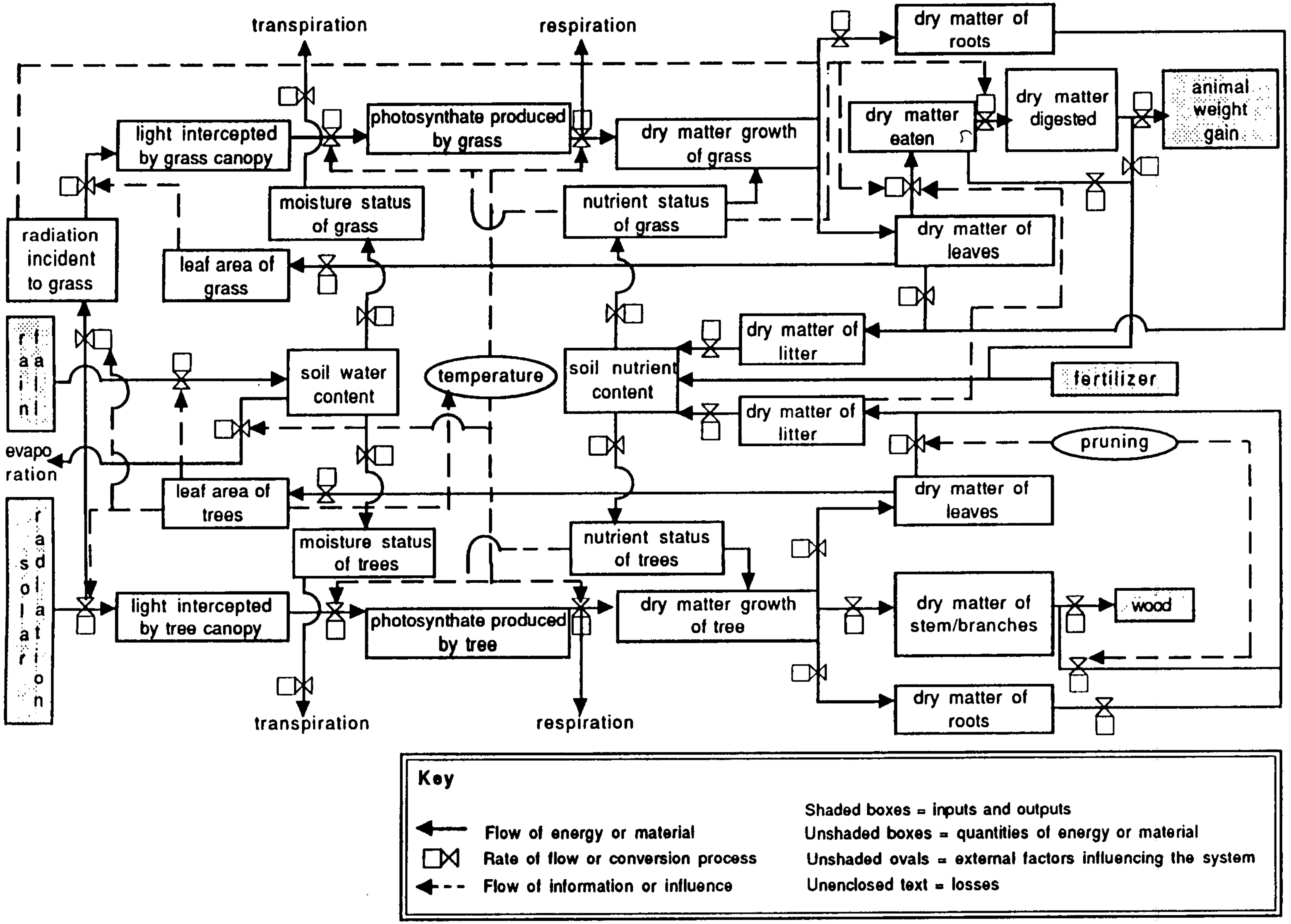
Forestry and agriculture have invariably had, throughout the world, quite separate administrations, research institutions, educational establisments and advisory services (Lundgren, 1987). The consequences of this have been that while a lot is known about how trees grow when they are close to and competing with other trees in forest stands, there is very little information available on open-grown trees or functional relationships that can be extrapolated to stands of widely-spaced trees. Spacing affects both the accumulation and the partitioning of dry matter. Crown structure is likely to be affected and, therefore, radiation transfer, photosynthesis and transpiration within crowns (Wang and Jarvis, 1990a). Competition from an agricultural understorey is likely to affect tree root growth and development. The partitioning of carbon within trees is not well understood (Cannell, 1985; Santantonio, 1989) but the intensity of both above- and below- ground competition is altered by increasing tree spacing. Similarly, most of the information available on the productivity of agricultural crops is relevant to crops grown in monocultures without overhead shade or competition from tree roots. There is a body of empirical research on mixed cropping of herbaceous species (reviewed by Willey, 1979a & b; Trenbath, 1986; see also compilations in Beets, 1982; Francis, 1986), but neither a comprehensive database of crop responses nor a well accepted theoretical framework have developed (Vandermeer, 1989; Snaydon, 1991).

1.2.4. Interactions

There is much less empirical data on intercropping herbaceous crops with perennials, for which greater complementarity has been proposed on the basis that structural and phenological diversity of canopy and root systems between components leads to greater separation of resource-use in space and time. Much of the well-cited literature on agroforestry either, postulates what might occur in herbaceous/perennial crop mixtures based on current knowledge of plant responses (e.g. Huxley, 1983); is largely descriptive of agroforestry practices (e.g. Nair, 1989); or concentrates on practicalities and socio-economic aspects (e.g. Reid and Wilson, 1985; Rocheleau, Weber and Field-Juma, 1988). More detailed empirical data have been published on a few specific agroforestry systems such as grass production and animal performance under *Pinus radiata* D. Don in New Zealand (Knowles, 1991) and under *Cocus nucifera* L. in South East Asia (Smith and Whiteman, 1983 and 1985), and, on alley cropping in the humid tropics (Kang and Wilson, 1987). Recently, the results of more fundamental work on the mechanism of some of the interactions in alley cropping systems in semi-arid environments have indicated that competition for limiting resources is much greater than had been expected from the humid tropics, highlighting the different behaviour that similar practices have in different environments (Ong *et al.*, 1991; Ong and Black, in press; Woomer *et al.*, in press). A methodology for examining biological interactions in agroforestry, based on intensive study of the interface between trees and crops, has been proposed (Huxley *et al.*, 1989). This does not take into account the cumulative microclimatic effect of larger expanses of agroforestry and, as yet, few data have been published. A recent review of research on ecological interactions in agroforestry (Anderson and Sinclair, 1993) revealed that few hard data on interactions in agroforestry systems were available despite nearly two decades of scientific interest, largely because of the predominance of adaptive research. There is evidence, however, of a shift in emphasis in current research towards developing an understanding of the underlying processes (Sanchez, 1995). This embraces research on nutrient dynamics (Palm, 1995), root competition (Schroth, 1995; Van Noordwijk and Purnomosidhi, 1995), individual tree growth (de Reffye *et al.*, 1995) and the coupling of tree and crop process-based models (Lawson *et al.*, 1995). Farmers with a tradition of practising agroforestry in the tropics have been found to hold a sophisticated understanding of ecological interactions and tree attributes that affect them (Thapa, Sinclair and Walker, 1995) and to select particular elements of agroforestry technology packages for integration into their farming systems rather than to adopt entire packages extended to them (Buck, 1990). This suggests that providing farmers with information on the likely consequences of various decisions regarding incorporation of trees into farming landscapes, based on the results of fundamental research, may be more effective than attempting to provide them with technology packages. Such a shift from the extension of prefabricated designs to the provision of decision-support, demands a more sophisticated extension service but is currently receiving serious consideration in the international development arena (Anderson, Muetzelfeldt and Sinclair, 1993).

One of the problems in understanding interactions in agroforestry, is the complexity that is involved. Figure 1.1 illustrates some of the major interactions in a temperate silvopastoral system, focusing on the accumulation of dry matter. While many other factors are involved in agroforestry systems, economic performance is dependent upon the amount and quality of production achieved for a given level of input. The accumulation of biomass by different plant components is, therefore, a fundamental aspect of any agroforestry system. It is more durable than the socio-economic factors related to prices or planting grants and subsidies. The present research is directed towards predicting the biomass accumulation of different components within an agroforestry system. (Section 1.2.10).

Figure 1.1. Flow diagram of a temperate silvopastoral system showing the major interactions affecting the accumulation of dry matter.



1.2.5. The history of agroforestry in the UK

Agroforestry has a long tradition in the UK, although not by that name, but has been declining since the middle ages. In his text on ancient woodlands, Rackham (1980) devotes a chapter to wood-pasture systems dating back to Anglo-Saxon times. He distinguishes between wood-pastures in forests (referring to the medieval legal designation of Crown land), as parkland, and on common land. Harding and Rose (1986), primarily concerned with the conservation of epiphytes and saproxylic invertebrates today, include winter-grazed woodland as a separate category. Wood-pasture systems were both deliberately managed and stable. They involved both the use of compartments, where animals were excluded from regenerating woodland until trees were capable of withstanding grazing, and tree management strategies to prevent grazing damage. These included pollarding and making use of the protection afforded to timber trees by thorny shrub species. The fifth edition of Evelyn's discourse on silviculture (1729), the first was published in 1664, abounds with references to the use of pollarding, and describes a method of tree protection involving the construction of an elaborate mound of turfs around newly planted trees with thorny shrubs planted on the mound. Grazing of permitted domestic animals (cattle, horses and sheep) within glades in medieval forests was regulated (James, 1981), while pigs were allowed into wooded land at particular times of the year (Wiseman, 1986). Dorward and Carruthers (1990), have recently reviewed the literature on the integration of pigs and poultry with trees revealing a tradition dating back to the middle ages.

1.2.6. Recent experience of agroforestry in the UK

Wood-pasture systems declined as timber production became the primary role of forested land and agricultural land was enclosed from the beginning of the 18th century. Modern forestry practice, based on plantations, has occurred on separate land from agriculture. Uncontrolled forest grazing in Europe, which has had deleterious effects on trees, and perceived competition for land resources, has lead to antipathy between forest and farm interests (Adams, 1975). There have been some exceptions. There is a long experience of shelterbelt planting in the UK (Caborn, 1957 & 1965) and some experience of integration of forest blocks and agriculture at the enterprise level (Mutch and Hutchinson, 1980). Successful combinations of widely spaced poplar (*Populus* spp.) and cereals, followed by grazing after tree establishment, have been practised in lowland Britain and were encouraged by Bryant and May in the 1960's (Miller, 1976; Beaton, 1987). Unfortunately little information on the yields obtained or the interactions between trees, crops and livestock has been retained or published. Adams (1976), found that short periods of intensive sheep grazing in a young plantation of Sitka spruce (*Picea sitchensis*[Bong.] Carr.) reduced tree growth but utilisable amounts of forage were provided until canopy closure. The reduction in growth was attributed to root damage by trampling since there was hardly any evidence of browsing. Better drained soils or less intensive grazing regimes, with trees at wider spacings, may not result in stock having the same impact on tree growth. Cattle have also been shown to reduce annual tree growth and cause browsing damage and soil compaction when overwintering in farm woodland in the uplands, but not to an extent that ruled out the use of young woodlands for this purpose (Cumming, 1981). Quantitative evaluation of the interactions involved in deliberate combinations of trees and agriculture in the U.K. is virtually non-existent.

1.2.7. The rationale for agroforestry in the UK

A resurgence of interest in agroforestry in the UK occurred in the mid 1980s as a result of the need to find alternatives to agricultural production in the face of mounting agricultural surpluses in the European Community (Carruthers, 1986a). Increased timber production was envisaged as a major line of diversification because of the need for the product. The UK was only 10% self sufficient in wood and wood products in 1986 and though wood production is forecast to increase in the future as existing plantations come into maturity, this may only keep pace with consumption, which is expected to double by 2025 (Carruthers, 1986b). The future availability of quality timber on the world market had also been estimated to decline with consequent increases in price. Interest in agroforestry was also associated with the increasing pressure for more attention to be paid to environmental issues. This involved a need to reduce pollution caused by extant levels of agricultural inputs, increase the diversity of wildlife in the countryside and maintain an agricultural landscape with a mosaic of fields, hedgerows and woodland (Jarvis and Sinclair, 1990). Agroforestry was particularly appealing because of its potential role in achieving these objectives and because of its apparent success in temperate climates in other parts of the world. It was also perceived as being less disruptive to the current rural structure than whole-scale afforestation and a less permanent, and more gradual change in land-use than the establishment of conventional farm woodland.

1.2.8. The relevance of Antipodean research to the UK

Justification for research into agroforestry in the UK has often drawn on the experience of successful agroforestry in other temperate regions (MacBrayne, 1982; Roche, 1986; Maxwell, 1986; Thomas, Penaloza and Kellas, 1990). Agroforestry research based on widely spaced and high-pruned *Pinus radiata* D. Don with sheep and cattle grazing around them has been conducted in New Zealand over the past 20 years (Reid and Wilson, 1985; Knowles, 1991). Similar systems have been established and studied in Chile (Penaloza, Herve and Sobarzo, 1985), and, based on *Pinus elliotii* Engelm. in the southeastern United States (Lewis and Pearson, 1987). The major thrust has been to develop empirical models to predict tree growth and subsequent animal performance from understorey pasture. Having one system of agroforestry made this approach appropriate. Field trials costing several million dollars were set up in New Zealand and tree and pasture growth measured, from which empirical equations relating total crown length ha^{-1} to pasture production were developed (Percival and Knowles, 1988). The situation in the UK was quite different. The Antipodean results could not be extrapolated directly to the UK because *Pinus radiata* D. Don is on the extreme edge of its environmental range and not an appropriate species for planting. Secondly, the opportunities for agroforestry in the UK are likely to be varied and tailored to particular farm requirements which will include satisfying multiple objectives of wood production (for farm use and profit), provision of shelter, maintenance of agricultural production while trees are established, provision of wildlife habitats, provision of cover for game, amenity value and landscape impact. These will occur in various mixes and with variable priorities, across a wide range of site types. There is an uncertain future in respect of the incentive structure governing farm forestry in terms of grants for planting trees, taking land out of agricultural production and conserving wildlife. It was impractical to attempt to produce purely empirical models for each possible scenario, therefore, a more fundamental understanding of interactions was required to be able to predict the consequences of using a wide range of different tree species, densities and arrangements.

1.2.9. Early simulation models

The first serious research activity in the UK was the construction of computer simulation models of silvopastoral systems, by two independent research groups. One was based on Douglas fir (*Pseudotsuga menzeisii* [Mirb.] Franco) in the uplands (Sibbald *et al.*, 1987), and the other on ash (*Fraxinus excelsior* L.) in the lowlands (Doyle, Evans and Rossiter, 1986). Both models relied on assumptions about interactions in the system rather than on experimentation and were not validated. Sibbald *et al.*, (1987), made estimates of agricultural revenue based on the reduction of net photosynthesis of grass caused by shading by tree crowns, calculated on the basis of projected crown area and beam fraction. The trees were assumed to be unaffected by the grass and no other interactions were taken into account. Doyle *et al.*, (1986), partitioned light between trees and grass by calculating attenuation of an empirically determined portion of incident light based on the crown area of the tree canopy. Direct beam radiation was not considered and homogeneity was assumed across the understorey, but competition for nutrients and water between trees and grass was considered. Both models suggested that silvopastoral systems in the UK would give similar financial returns to the purely agricultural systems that they might replace, over a 45-50 year production cycle at prevailing prices, costs and levels of support. The results were sensitive to the discount rate and timber price and predicted that grass production would be maintained as a high proportion of that on non-forested land for at least the first 15 years after planting at low tree stocking densities. These models indicated that agroforestry was worth investigating in the field. They also identified that in order to make confident predictions experimentation was required on: light, temperature and humidity regimes under widely spaced trees; tree growth and crown development at wide spacings; tree rooting patterns in competition with an understorey; and water and nutrient uptake. The need to validate these models against field experimentation has already been demonstrated. For example, measurements of grass growth under ash trees have indicated that grass production was underestimated in the lowland model because considerable grass growth occurs before leaf area develops on the trees in the spring (Newman *et al.*, 1990). Conversely in the uplands, measurements have indicated that overhead shelter provided by trees may extend the growing season for understorey pasture (Sibbald, Griffiths and Elston, 1991).

1.2.10. Research strategy

The intense interest in tree planting on farms from the agricultural and forest industries, concerned with the practicalities of establishment, evidenced by a plethora of conferences and meetings on the theme (CAS, 1986; SLF, 1986; RASE and ADAS, 1986; RASE, 1986), created the need for rapid results from experiments to provide better advice to farmers. But trees take a long time to grow, and many of the interactions in agroforestry are only expressed after several years of tree canopy development. Since mature trees were not available at agroforestry spacings in the UK two options were available. To identify existing open-grown trees in pasture or to thin existing closely spaced stands to different densities and establish pasture beneath them. Both approaches have been adopted in the UK and both have limitations (Sibbald and Sinclair, 1990). Experimentation with isolated trees was restricted by having to locate trees with a known history, and could not take into account the cumulative effect on microclimate of extensive areas of agroforestry. Thinned stands had to be based on commercially planted, closely-spaced trees. If they had not yet reached the stage of canopy closure then their canopies could be considered to be reasonably similar to those of open-grown trees. The soil had, however, been modified by the presence of the trees and was not representative of newly planted sites. This limitation was exacerbated by the fact that forest planting in the UK has tended to be confined to areas marginal for agricultural production. Where stumps and roots of the thinned trees were left in the ground the root development of understorey crops may have been affected, altering their ability to compete with live trees for water and nutrients. In one experiment the stumps and roots were physically removed by bulldozing, which modified the top soil structure and surface roots of the remaining trees (Davies and Taylor, 1987).

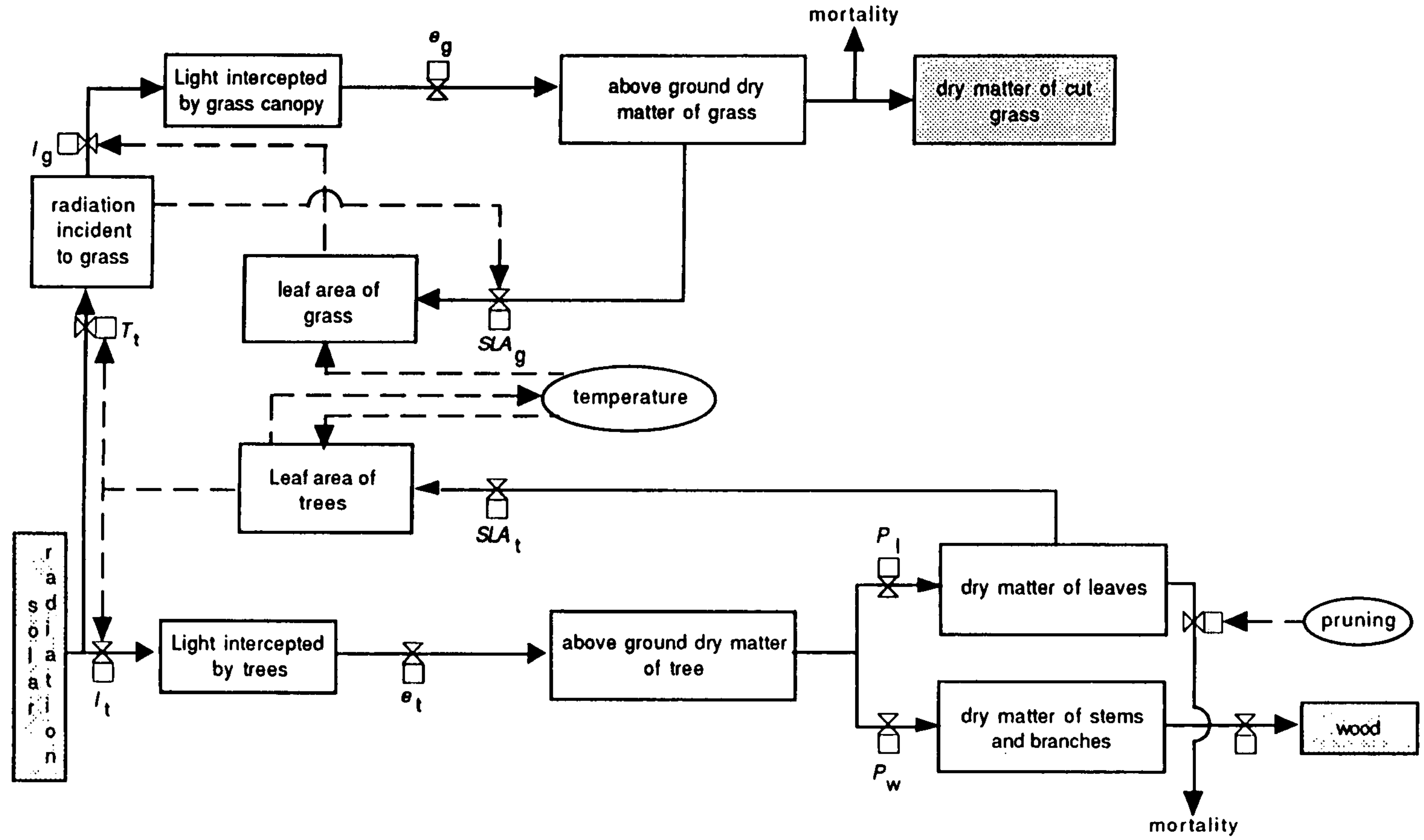
The approach adopted in the present research was to respace existing stands of trees and concentrate on the primary atmospheric interactions affecting growth. As explained above, this renders the below-ground conditions unrepresentative of those that would pertain if trees had been planted into grazed pasture on farm land, as is generally envisaged for establishing silvopastoral systems in the UK, and so the atmospheric interactions in the system were isolated for experimental purposes by eliminating below-ground competition. This was achieved by growing pasture in boxes and pots containing imported soil, thereby preventing competition for moisture and nutrients between trees and crops during the experiments and avoiding the influence of any soil changes caused by the presence of trees prior to respacing (Chapter 2). While this limited the scope of the research to quantifying the effects of atmospheric interactions, thereby considering only some of the interactive processes involved, it made the task of doing this easier by removing complications of below-ground competition. The system was further simplified by simulating grazing by frequent cutting and ensuring that nutrients were not limiting by the application of artificial fertilizer. It was considered unlikely that water would be limiting at the site. The reduced interactions in the simplified experimental system, are outlined in Figure 1.2, which can be compared with the whole system in Figure 1.1. The major assumptions involved in this approach are that moisture and nutrients are not limiting growth and that, in any case, the primary effect of temperature and the availability of nutrients and water is on the development and duration of leaf area (Section 4.1.1). The usefulness of this simplified approach can be justified in three counts:

- Experiments on simplified field models of complex agroforestry systems can provide an understanding of certain underlying processes, if these individual processes, such as light interception, are understood and mathematically modelled at a fundamental level, they can then be subsequently combined in more holistic simulation models that involve a larger number of processes, such as competition for nutrients and water, to explore system behaviour more thoroughly (Muetzelfeldt and Sinclair, 1993). The importance of different interactions will vary in relation to the availability of resources in different environments. On fertilized pasture in the wet temperate conditions of the UK, atmospheric interactions can be expected to predominate.

- Light is a primary driving variable in crop production and the amount of light available for plant growth determines potential productivity (Section 1.3 and 4.1.1). While reductions from this potential may occur as a result of other interactions in agroforestry systems, it is useful to know what agroforestry configurations have the potential to produce various amounts of tree and agricultural produce to narrow down the set of systems worthy of further investigation.

- Research in New Zealand has related pasture productivity in agroforestry to easily measured attributes of tree crowns (Section 1.2.8), but for tree and understorey species that are not directly appropriate in the UK. It is, therefore, reasonable to investigate the extent to which crown properties influence pasture productivity in UK conditions and hence to explore the extent to which such relationships derived elsewhere can be applied in the UK (Sibbald, Griffiths and Elston, 1994).

Figure 1.2. Flow diagram showing the major interactions affecting the accumulation of dry matter in the agroforestry stands.



Key

← Flow of energy or material
⊠ Rate of flow or conversion process
← - - Flow of information or influence

Shaded boxes = inputs and outputs
Unshaded boxes = quantities of energy or material
Unshaded ovals = external factors influencing the system
Unenclosed text = losses

I_t = fractional light interception by the tree
I_g = fractional light interception by the grass
P_l = proportional dry matter partitioned to leaf
P_w = proportional dry matter partitioned to wood
e_t = dry matter radiation quotient for trees

e_g = dry matter radiation quotient for grass
SLA_g = specific leaf area of grass
SLA_t = specific leaf area of trees

1.3. The methodology of the present study

Previous work on herbaceous crops (reviewed in Chapter 4) suggests that plant growth is a linear function of intercepted radiation, and that the efficiency of conversion of intercepted radiation to dry matter is conservative across species and environments (the Monteith hypothesis). This has yet to be established for tree crops.

The radiation intercepted by a foliage canopy depends upon the interaction of leaf area and its orientation and distribution, with the amount and distribution of incident radiation, which can be well represented in a mechanistic computer simulation model (Campbell and Norman, 1989; Norman, 1989). While the radiation intercepted by a horizontally homogeneous canopy is independent of the distribution of leaf area density (Saeki, 1963), the quantity of radiation intercepted by spaced tree crowns will be influenced by both the vertical and horizontal distribution of leaf area density within them. The light incident to the understorey grass sward will clearly be modified by the presence of the tree crowns above.

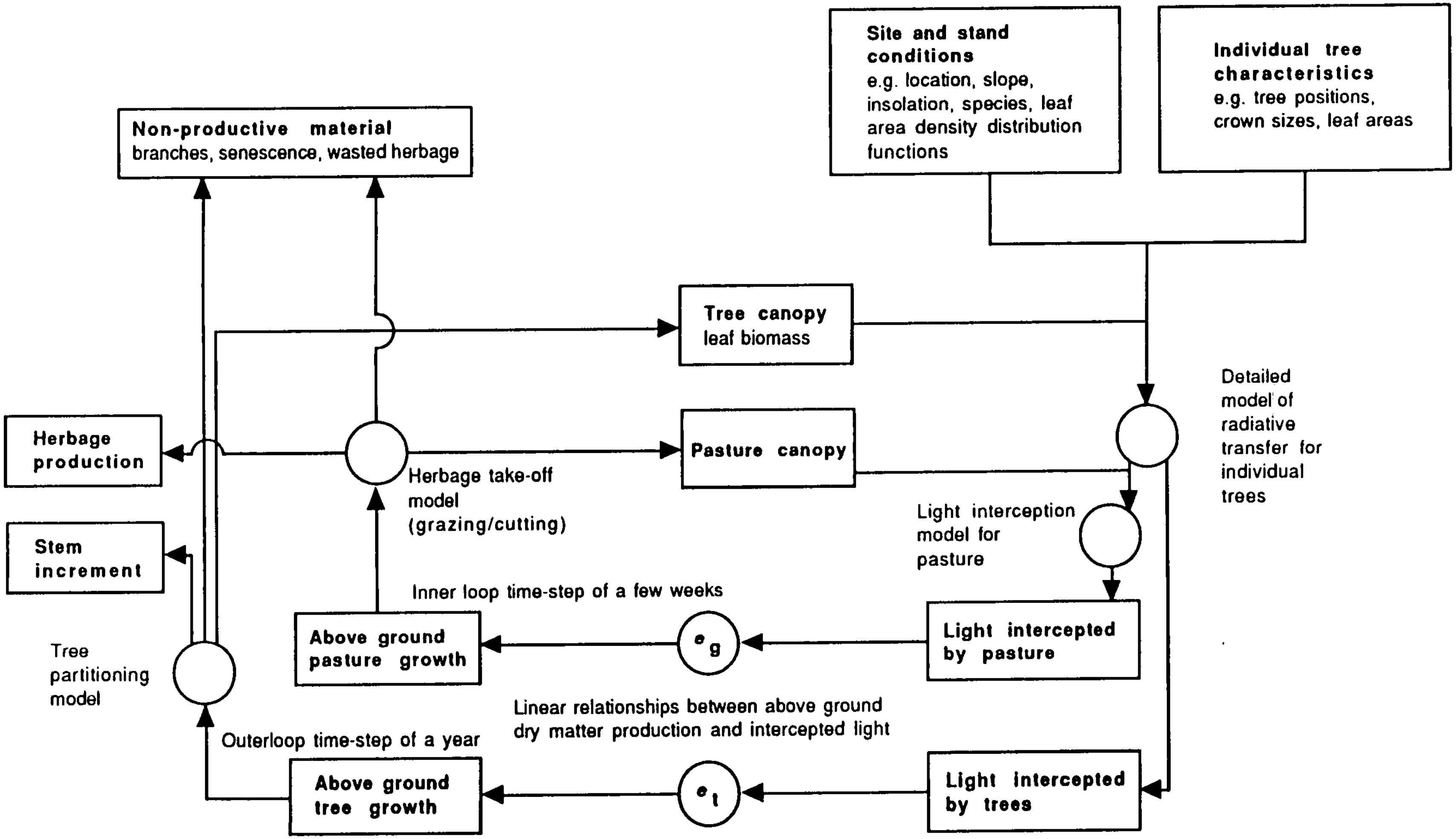
The overall aim of this research was to investigate the potential productivity of different configurations of trees and understorey pasture appropriate to agroforestry by combining mechanistic models of radiation interception by tree crowns with empirical models of above ground plant growth (Figure 1.3). This approach allows investigation of the potential productivity of trees and pasture within agroforestry stands of different tree sizes and spacing on a seasonal basis.

To achieve this overall aim:

1) the amount and two dimensional distribution of leaf area within tree crowns was measured and combined with measurements of tree locations and crown sizes to investigate and describe the vegetative structure in experimental agroforestry stands (Chapter 3);

2) the Monteith hypothesis, that there is an empirical linear relationship between intercepted light and above ground dry matter production, was tested for both trees and grass in agroforestry conditions (Chapters 4 and 5), and

Figure 1.3. Diagramatic representation of the modelling approach adopted in the present research. Arrows represent flows of information, circles represent modelling nodes (where either a mechanistic or an empirical model is used), boxes represent primary state variables in the modelling scheme.



3) a mechanistic model of radiation interception by tree crowns, incorporating explicit treatment of the two dimensional distribution of leaf area density in (1), MAESTRO (Wang and Jarvis, 1990b), was parameterised and validated for tree crowns at agroforestry spacings (Chapter 6) and used in conjunction with the empirical relationships between intercepted light and plant growth in (2) to investigate the potential productivity of different agroforestry scenarios (Chapter 7).

Measurements of quantum flux density (QFD) were made above and below trees and pasture in respaced stands of trees, with grass swards grown in boxes sunk to ground level (permananent sward phytometers). The QFD measurements were used:

1) to calculate the QFD intercepted by the tree (Q_t) and pasture (Q_g) canopies, which were then used in conjunction with measurements of the growth of the two components to test the Monteith hypothesis, and

2) to compare the measured QFD beneath tree crowns with predictions made by the mechanistic model, MAESTRO, to facilitate validation.

Vegetative structure was measured by destructive harvest of trees when stands were respaced to provide the detailed information utilised to parameterise the model, and as baseline data for developing allometric relationships of leaf area and above ground biomass with basal area. The data were also used to compare alternative non-destructive techniques for estimating leaf area of tree crowns based on mathematical inversion of gap fraction data collected using hemispherical photography, and two contrasting, prototype hand-held sensors that utilised diffuse and direct transmission respectively.

Measurement of QFD intercepted by grass growing in the permanent sward phytometers proved difficult because of patchy distribution of tillers and the low sensitivity of sensors with a small enough sensitive area to be used in the sward boxes. The growth and morphological development of three contrasting grass species grown in smaller temporary phytometers over short periods was, therefore, used to obtain relationships between intercepted QFD and grass growth (Chapter 5).

2. Field sites and general methods

Fieldwork was carried out at two sites where above-ground environments representative of agroforestry were created by respacing existing plantations (see Section 1.2.10 for discussion of this approach). The sites involved different tree species. The site at Cloich was more accessible from Edinburgh and involved respaced stands of Sitka spruce (*Picea sitchensis* [Bong.] Carr.). This species was chosen because of its availability, by virtue of ubiquitous planting in the UK, and not because it was considered likely to be important in agroforestry. This provided a suitable model of a conifer canopy for research taking a functional approach that involved relating differences in quantum flux density (QFD) and tree and understorey growth, to measured canopy parameters. Cloich was the larger site with a wider range of tree size and spacing treatments, and was more intensively instrumented and visited. The second site at Dunkeld comprising systematically respaced hybrid larch (*Larix x eurolepis* Henry), was set up to extend the test of the hypotheses and the modelling approach to a contrasting deciduous conifer canopy, with a much lower leaf area density.

2.1. Cloich

2.1.1. Site description and experimental layout

This site was set up in collaboration with the Macaulay Land Use Research Institute (MLURI), then the Hill Farming Research Organisation (HFRO), and the Forestry Commission (FC), during the winter of 1985/86 at Cloich in Glentress Forest, approximately 30 km south of Edinburgh, latitude 55° 42' N; longitude 03° 16' W. The mean annual rainfall was approximately 1100 mm. Nine distinct agroforestry environments were created by thinning Sitka spruce that had been commercially planted at 2 500 stems ha^{-1}. There were three stands of different tree height, and three spacing treatments were established within each stand. The mean tree heights were approximately 3 m (low), 5 m (intermediate) and 8 m (tall) in 1985. The low and intermediate stands were planted in 1972

(NW208473) on an even, south-east facing slope (20 %) ranging from 330 m to 400 m in altitude. The low stand was located on the lower part of the slope immediately below the intermediate trees. The tall stand was located 1 km to the south (NW208460) planted in 1970 on a gentler, south-east facing slope (6 %) ranging from 380 m to 405 m in altitude.

Within each stand three square spacing treatments with distances of 4 m (narrow), 6 m (medium) and 8 m (wide) between trees (corresponding to frequencies of 625, 278 and 156 trees ha^{-1}) were created by removing intervening trees. There were two control areas without any trees, one adjacent to the low and intermediate stands, and the other adjacent to the tall stand. There were also areas adjacent to the respaced areas where the plantation had not been respaced (2 500 trees ha^{-1}). The location of treatments and their labels are shown in Figure 2.1. The trees in the tall stand had branches removed up to 1.3 m height. Measurements were confined to plots in the centre of the respaced areas so that each experimental plot had a buffer area of the same tree size and spacing around it which extended to at least a distance (S_u) from the plot edge in all directions where:

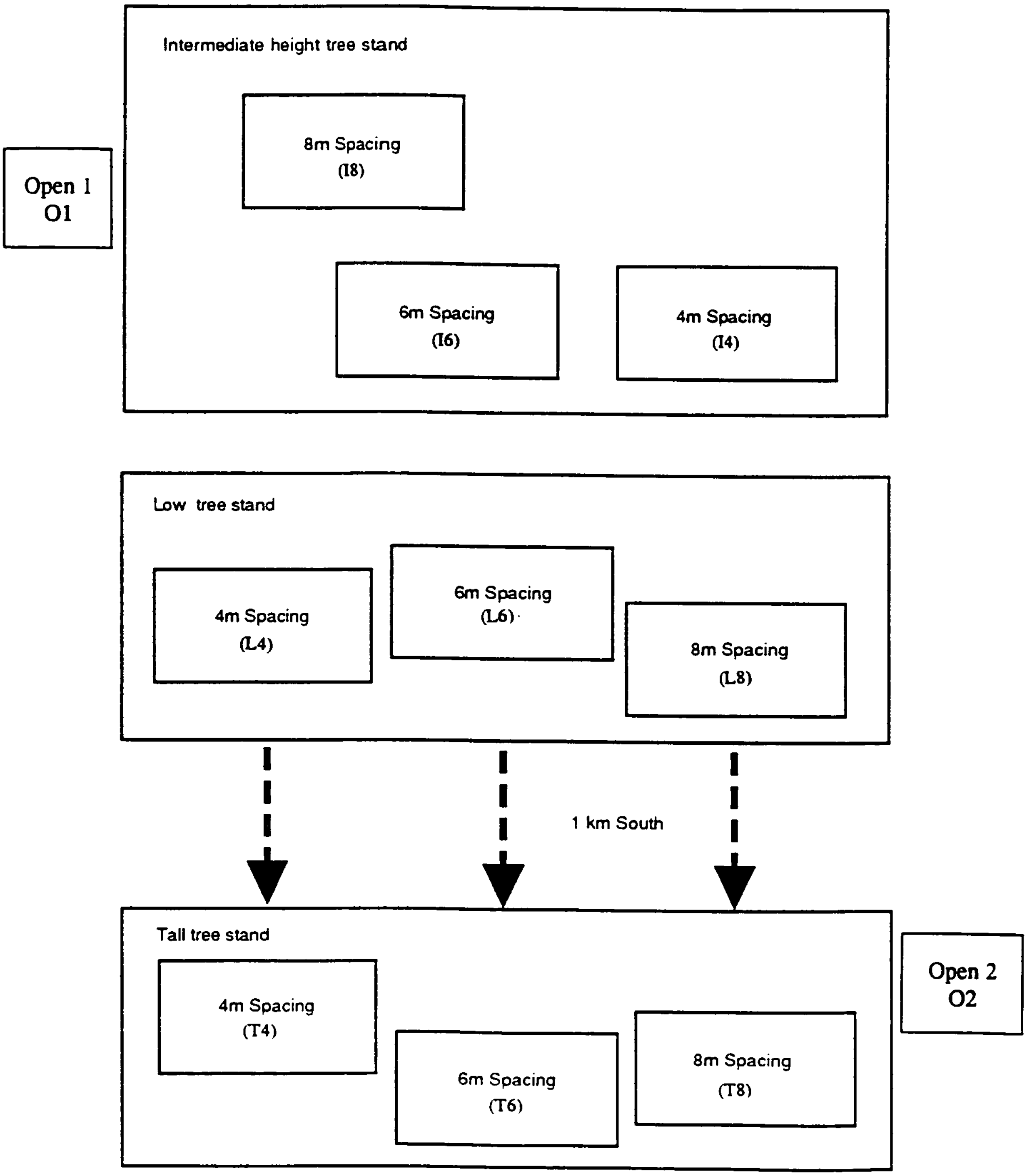
$$S_u = 2.5\,\underline{H_t} + S_t$$

where $\underline{H_t}$ = mean tree height, and, S_t = distance between trees.

The MLURI installed 324 wooden pasture boxes (0.6 m x 0.6 m x 0.3 m deep) sunk to present the box surface horizontal and at ground level in the first half of 1986. These contained imported loam soil with an established perennial ryegrass sward (*Lolium perenne* cv. Perma) and were used as permanent sward phytometers. The boxes were free draining but it was assumed that their sides prevented any effective competition between tree and grass roots. Nitrogen in the form of a slow release granular fertiliser was applied in two applications each year to the sward at the rate of 150 kg ha^{-1} a^{-1} (Sibbald, Griffiths and Elston, 1991).

Because experimental objectives involved assessing spatial variation under trees as well as means across the area, the square area bounded by any four trees (unit) was divided into a systematic grid of

Figure 2.1. Diagrammatic plan of location of tree height and spacing treatments at Cloich



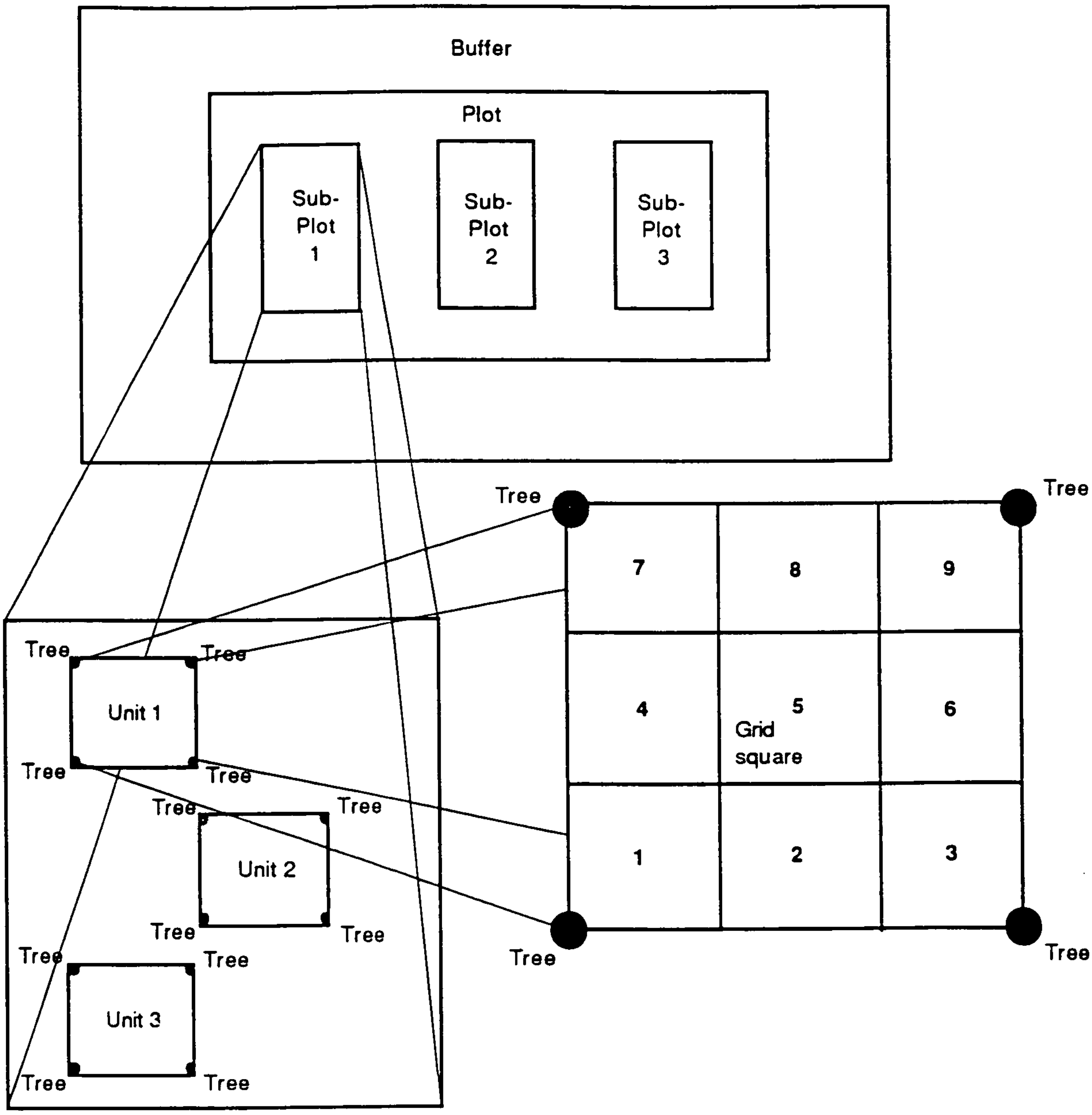
nine equal area squares (grid squares). This was the minimum number permitting differences in two dimensions to be assessed with equal precision. The grid square positions (used to refer to the location of a square within the grid rather than an actual grid square) were numbered one to nine from west to east and south to north (Fig 2.2). In order to allocate pasture boxes to treatments three sub-plots were identified in each plot, each containing three units. While efforts were made for selected units not to be contiguous this was not always possible and in some cases selected units within a sub-plot had one or two trees in common. One sward box was allocated to each grid square position in each sub-plot in a non-repeating random sequence with a stratification condition that each unit contained three boxes. The boxes were located randomly within the grid square to which they were allocated. This resulted in 27 boxes in each plot; nine in each of three sub-plots, one per grid square position arranged so that there were three boxes to each of three units.

2.1.2. Limitations of the experimental design

The reasons for using respaced trees, and the limitations imposed by this approach has been discussed previously (Section 1.2.10) as well as the choice of tree species (Section 2.) Within this general strategy the experimental design imposed the following further limitations.

Plots were not replicated, the replication at the sub-plot level allowed a measure of the variance within plots but not between them. Site and treatment effects were, therefore, confounded. This was a practical compromise arrived at because it was not possible to respace a large enough area to replicate plots with buffer areas surrounding them (an alternative compromise was employed at Dunkeld, Section 2.2). Given a limited area, inclusion of a range of canopy sizes and the reduction of edge effects was considered more important than plot replication. It was not possible to find a range of independent sites with existing trees of the same three heights and it was not feasible to have individual plots dispersed over a wide area. While this affected comparison of mean values between treatments the main thrust of the present research was the investigation of spatial variability in the understorey and the use of regression analysis of measured micrometeorological variables on growth.

Figure 2.2. Diagrammatic plan of the experimental layout for a single tree height and spacing treatment at Cloich



The whole experiment was located within a square km but there were indications that differences, other than those caused by the treatments, existed in growing conditions between the different stands. The low and intermediate stands were planted in the same year and, therefore, the smaller mean height of the low trees at the start of the experiment must have been the result of slower growth. This could be explained by their position on wetter ground, lower on the same slope. While the tall stand was further from the other sites, Sibbald *et al.*, (1991) detected no significant difference in mean annual dry matter production between the control sward boxes at the two locations. While this does indicate broadly similar atmospheric conditions, small annual differences that are not in themselves significant could be accumulated in tree stands. The major differential effects caused by historical differences in tree canopy development were largely eliminated in this research by measuring the light intercepted by trees and relating it to their growth (Chapter 4). The assumption is that the primary effect of variables affecting biomass accumulation is on the rate of development and duration of leaf area and hence the amount of light intercepted (Section 4.1.1). The tree canopy of each stand was, in any case, comprehensively measured at the beginning of the experimental programme by destructive harvest and is fully described (Section 3.2.1).

Grid squares in different treatments occupied the same proportion of a unit but were not of equal area, since the area occupied by a unit varied with tree spacing. This resulted in sampling intensity, when expressed per unit ground area, decreasing with increasing tree spacing. The grid was the minimum balanced stratification in two dimensions possible, but no attempt was made to increase the precision of the experiment by varying sampling intensity across the understorey in relation to variability. Given the appearance of variability at the outset of the experiment this was rational.

2.1.3. Measurements

The protocol of regular measurements made at the site is briefly outlined here. Where the same instrument or measurement has been used in the same way in different aspects of the research it is fully described here, otherwise specific details are given in the relevant chapters.

2.1.3.1. Tree positions

All trees in all stands were numbered and labelled. All stands were levelled using the rise and fall method (Perrott, 1970). The entire tall stand was surveyed after re-spacing by chain and compass survey (Perrott, 1970), with individual tree positions at the centre of the base of the stem, recorded to the nearest 0.2 m. Near-vertical stereo photographic coverage from the air was obtained for the whole site from a commercial company (Fountain Forestry, Perth). The photographs were taken using a camera with lens of focal length 50 mm loaded with 70 mm colour film, flown at a height above ground of approximately 460 m giving a scale of 1:2 500 on prints enlarged to 0.2 m x 0.2 m. The photographs were digitised, locating the centre of each tree crown using a digitising table (90 100 Galcomp, Anaheim). Comparison of tree positions mapped from the aerial photographs and the ground survey for the tall site agreed well and tree positions for the intermediate and low stands were also obtained from the photographs. Exact positions of all trees within units were measured on the ground using a cloth tape.

2.1.3.2. Tree biomass and canopy parameters

A stratified sample of 36 trees, 12 from each stand, were destructively harvested immediately prior to respacing. These were systematically dissected to provide baseline data on biomass and leaf area and its distribution over the sites (Chapter 3). Annual measurements of crown dimensions were made and leaf area was periodically assessed in the respaced stands using a variety of non-destructive techniques based on the inversion of gap fraction data (Chapter 3).

2.1.3.3. Tree growth

Annual measurements were made during the winter from 1985 to 1988 of: tree height (H_t); to the nearest 0.1 m; and diameter at breast height (D_r), to the nearest 1 mm, for all trees in all stands, by the FC.

2.1.3.4. Grass growth

Pasture boxes were harvested by the MLURI when the sward height reached between 80 to 100 mm in the fastest growing boxes, cutting to leave a stubble height of 25 mm using electric shears. A strip (80 mm wide) around the edge of each box was cut and discarded. The harvested material from the centre of the box was dried at 80°C for 24 hours and dry matter yield for each box, for each harvest recorded.

An additional 120 smaller pots containing three different grass species were installed at the tall site during 1988. The species grown were perennial ryegrass (*Lolium perenne* cv. Contender), cocksfoot (*Dactylis glomerata* cv.Jesper) and timothy (*Phleum pratense* cv. Erecta RvP). The details of pot preparation, sampling positions and harvests are given in Chapter 5 where results from them are reported.

2.1.3.5. Radiation

Measurements of quantum flux density (QFD) were made using laboratory built sensors of two sizes (Section 2.3), connected to automatic data loggers (delta logger, Delta-T devices Ltd, Cambridge). Unless stated otherwise sensors were scanned every 10 seconds and average hourly values for each sensor stored. The sensors were mounted above the tree canopy on a tower, and in arrays below the tree canopy, both above the grass canopy (array 1) and at ground level below the grass canopy (array 2). This allowed calculation of the light incident on and intercepted by the tree crowns and the grass canopy.

The sensors in array 1 were held by spring clips fastened to an aluminium strip (150 mm long, 35 mm wide and 2 mm thick) twisted with a 90° turn from the top and mounted at the base on a wooden pole (0.5 m long, 50 mm wide and 50 mm thick) with a sharpened point driven into the ground. Levelling was achieved by placing a ball level on the top of the sensor and bending the aluminium strip by hand, which was rigid enough to hold the position. The miniature sensors in array 2 were pushed into the soil and levelled with a ball leveller. They stayed in place held by the surrounding soil.

Different sampling strategies were used to position sensors for different purposes and they are discussed where results are reported. Over the research as a whole up to 175 light sensors were used at any one time, connected to up to six data loggers in different sites and plots. Data were collected from loggers at no more than fortnightly intervals and sensors were cleaned and levels checked at the same time.

In addition the MLURI maintained two reference weather stations on the open control plots. Each of these had two solarimeters (CM5, Kipp and Zonnen, Delft); one with a shade band, thereby measuring diffuse radiation only, and the other unobscured measuring global solar radiation.

2.2. Dunkeld

2.2.1. Site description and experimental layout

This was a site of hybrid larch (*Larix x eurolepis* Henry) on the Atholl Estates situated near to Dunkeld (NO033436), about 12 miles north west of Perth at latitude, 56° 34' N; longitude 03° 35' W; altitude, 160 m - 170 m. The site was on undulating terrain with an underlying southwest facing slope of 5%. A 1 ha area consisting of approximately 1200 trees (corresponding to an average spacing, assuming square arrangement, of 2.9 m between trees) with a mean stem diameter at breast height ($\underline{D}_r$) of 145 mm and mean height ($\underline{H}_t$) of approximately 12 m was respaced in autumn, 1986. The thinning was done to approximate a Nelder fan design (Nelder, 1962) comprising 16 concentric arcs of trees spaced in a geometric progression. This produced a continuous variation of tree frequency with a range of ground area per tree from 15 m^3 to 100 m^3 (which corresponds to frequencies ranging from 667 trees ha^{-1} to 100 trees ha^{-1} or to distances between trees, assuming square spacing, of 3.9 m to 10 m). The trees were high pruned to produce a clear stem length of approximately 5 m. The final tree positions (Figure 2.5) do not conform exactly to the geometric progression because initial positions of the trees available for respacing were fixed (Figure 2.3) and flexibility only existed with respect to which trees were removed. This was done by measuring the D_r and mapping the position of all trees prior to respacing (Figure 2.3), superimposing an ideal

Figure 2.3. Tree positions at Dunkeld prior to respacing. Only trees that were available for respacing are shown; they are surrounded on all sides by the original stand.

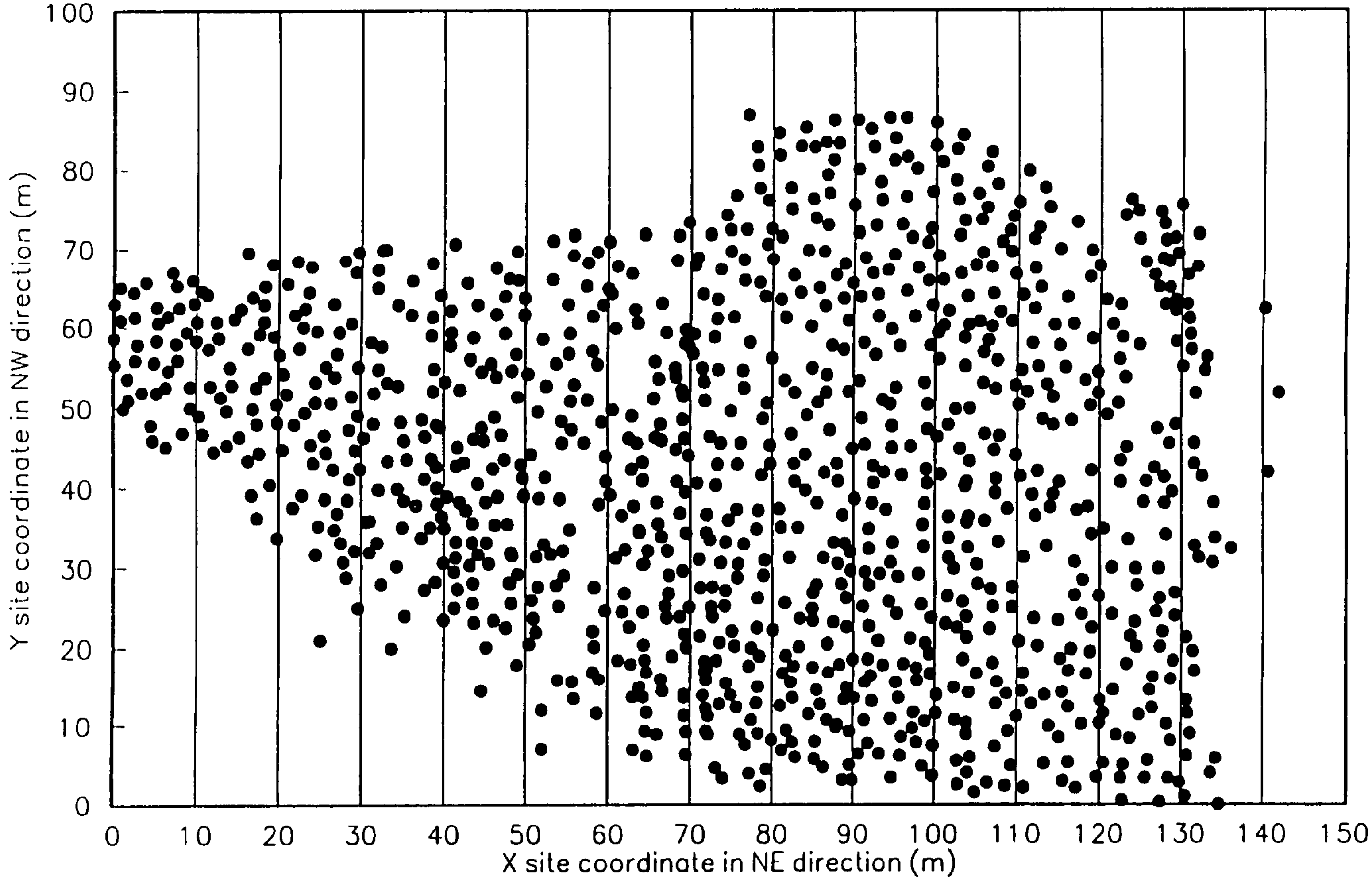


Figure 2.4. Ideal tree positions to conform to the geometric spacing pattern of a Nelder fan design at Dunkeld. The objectives of the design were to encompass a range of 16 to 100 m^2 of ground area tree^{-1} in 16 concentric arcs in a 1 ha site. The design comprises 16 arcs of trees with a minimum of 11 trees per arc.

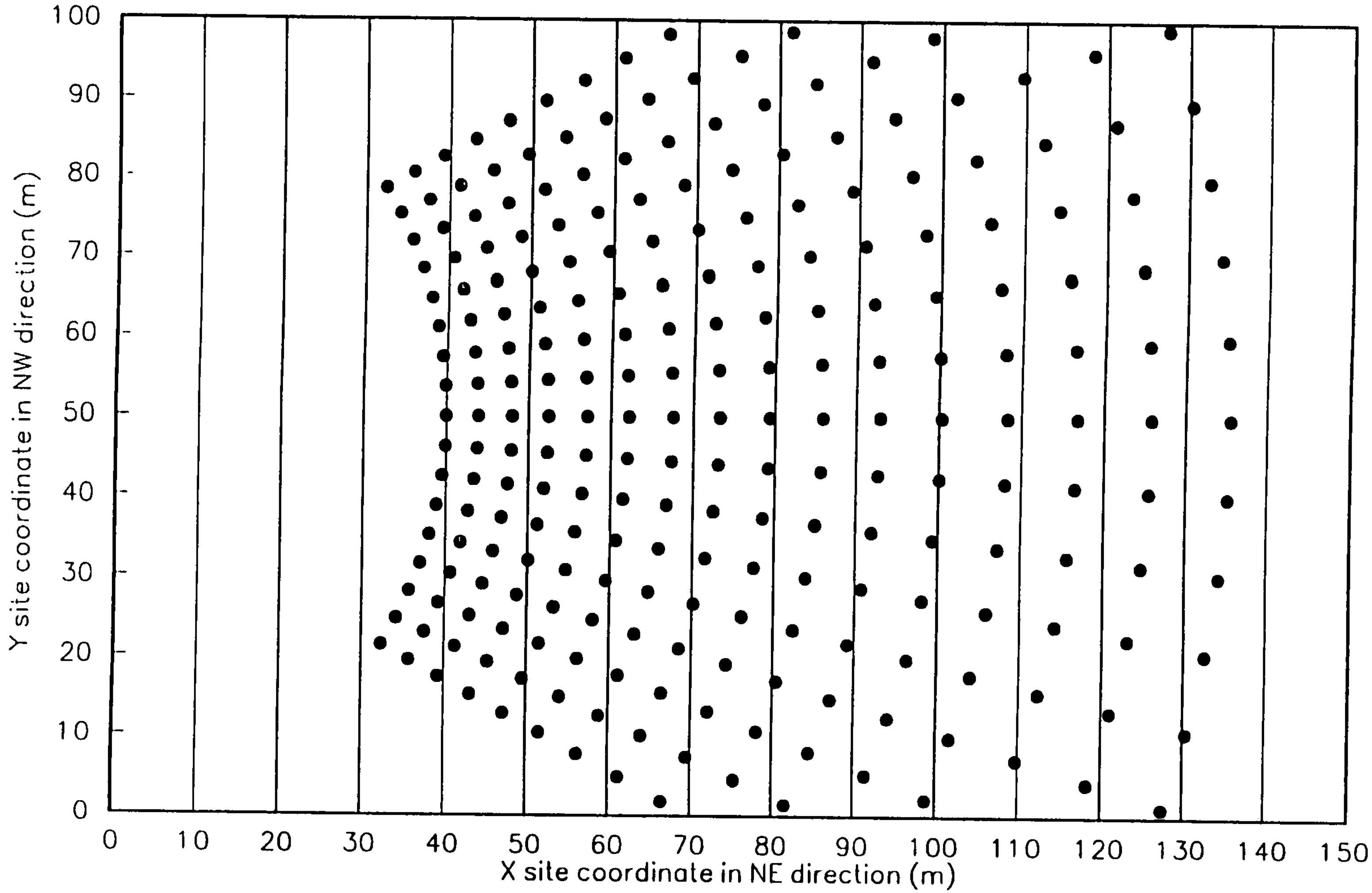
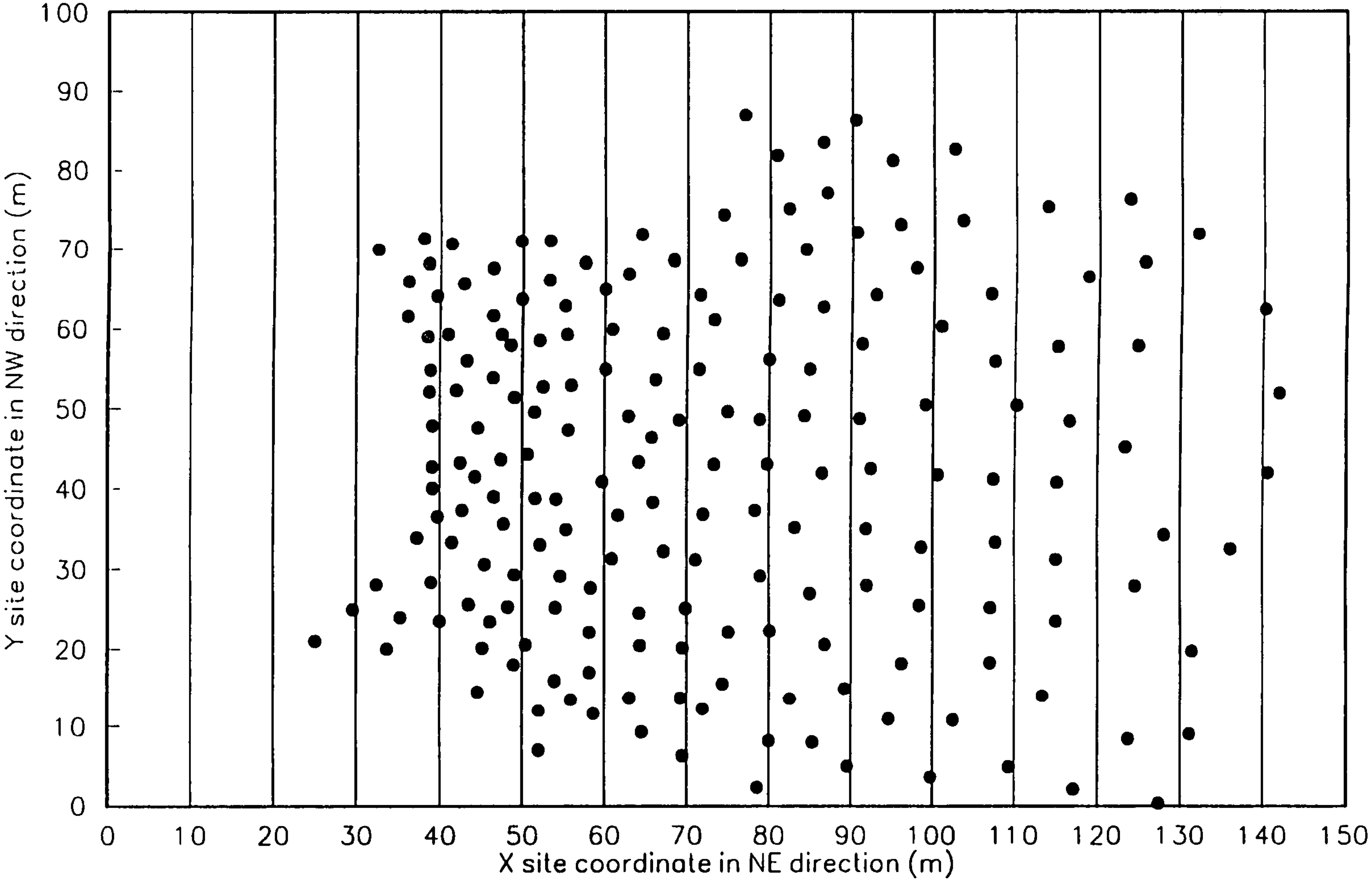


Figure 2.5. Tree positions at Dunkeld after respacing. Only trees within the Nelder fan design are shown; they are surrounded on all sides by the original stand.



geometric spacing pattern on top (Figure 2.4), and selecting trees to remain that were of a reasonable size and form and best placed in relation to the design. Compromise in respect of the D_r class of trees, their form and position had to be made. Figures 2.3, 2.4 and 2.5 show the original, ideal and final tree positions. The re-spaced trees were surrounded by the original stand on all sides.

The spacing gradient increased in a north-east direction across the site. Perennial ryegrass (*Lolium perenne* cv Perma) was sown into 12 hand cultivated observation units across the site in spring 1987 (Figure 2.6). The succession of vegetation on the rest of the site was spectacular with *Deschampsia flexiosa* [L.] Trin. dominating in the first year after respacing with *Digitalis pupurea* L. becoming widespread in the second.

The experimental design ensured that each treatment (or arc of the Nelder fan) was adjacent to similar treatments thus eliminating the need for a buffer area for each treatment. The trees in the outer two rows and two arcs in all directions were used as a buffer for the whole fan; referred to as guard rows, arcs and trees, respectively in Nelder's terminology (1962). As trees were not in exact geometrical progression the fan was divided into three plots roughly corresponding to the treatments at Cloich of 4 m (narrow), 6 m (medium) and 8 m (wide) between trees and frequencies of 625, 278 and 156 trees ha^{-1}). Within each of these plots three measurement units were randomly selected as in the sub-plots at Cloich (Section 2.1.3.1). The location of the measurement units and their treatment labels are shown in Figure 2.6. A previously cleared area nearby was used as a control area.

2.2.2. Limitations of experimental design

This design was used to fit a large treatment variation into the small area available for re-spacing. As the fan itself was not replicated analysis of variance was precluded and regression analysis used. Care was taken in setting out the design to avoid any systematic, non-treatment variation running in the same direction as the treatment gradient. There was no systematic trend in H_t or D_r (Figure 2.7) but the underlying slope of the land did follow the treatment gradient. Local topographical variability occurring randomly in the plot was likely to have been more significant than the overall trend in slope, which was, in any case, not very steep (5%). Measured growth increment was related

Figure 2.6. Location of measurement units and observation areas at Dunkeld.

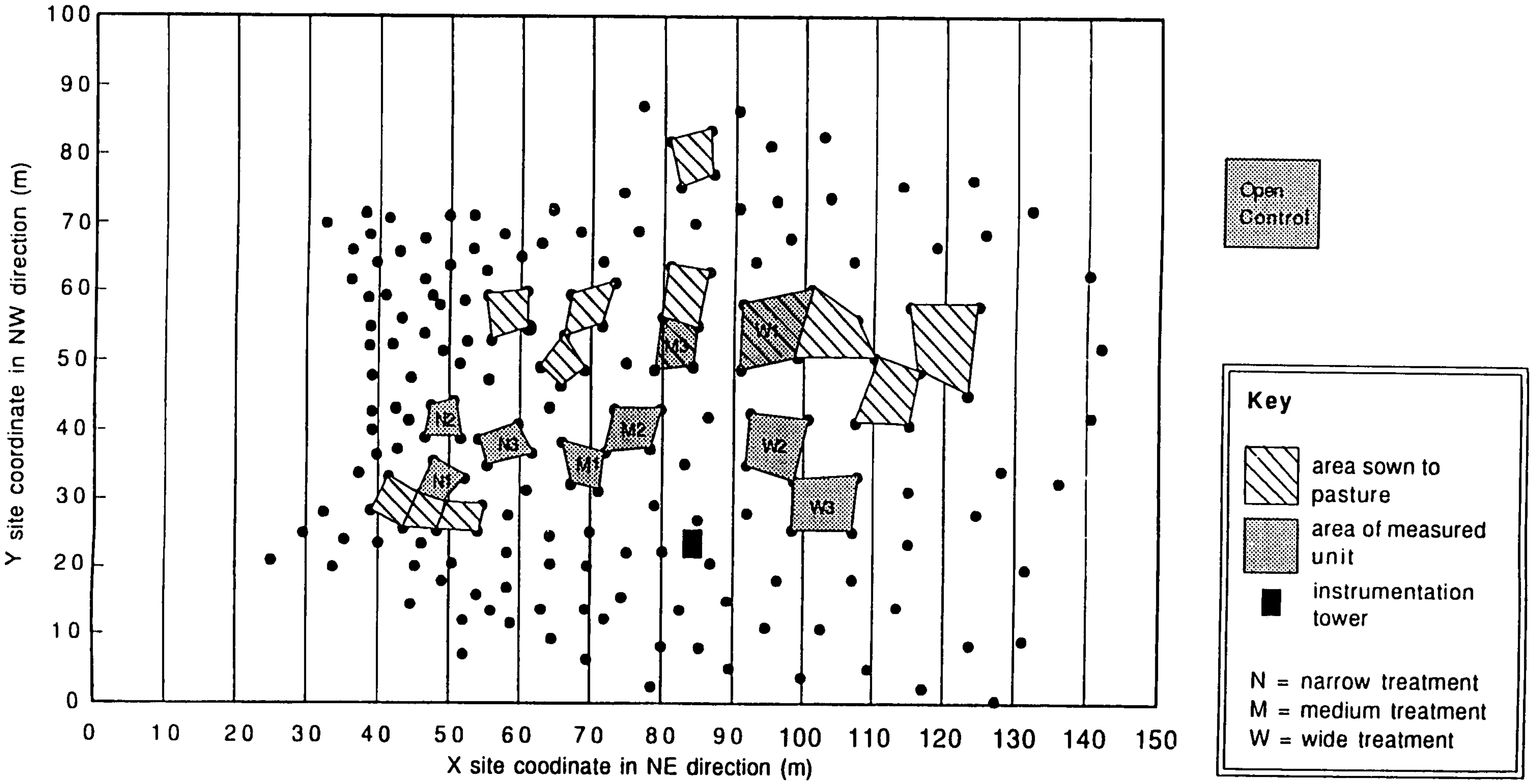
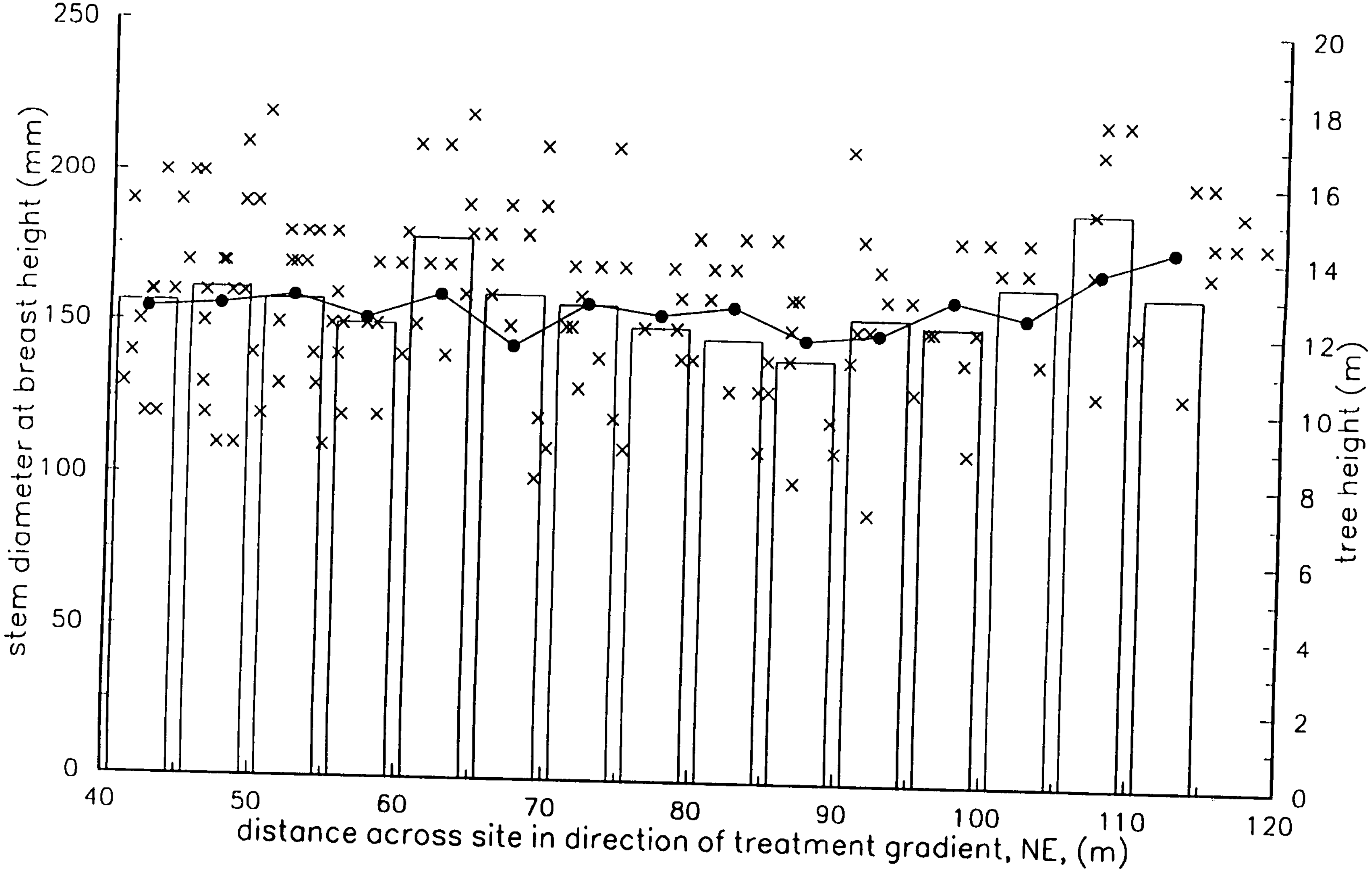


Figure 2.7. Variability of stem diameter at breast height (D_r) and tree height (H_t) in relation to the direction of the treatment gradient within the respaced Nelder fan at Dunkeld. Guard arcs and rows are excluded; these are, the arc of smallest and largest radius and the two outer radial rows. Crosses represent D_r of individual trees measured in 1986, and bars the mean ($\underline{D}_r$)for 15 equal divisions of the X-axis, the solid circles and line represent mean tree height ($\underline{H}_t$) for the same X-axis divisions.



to intercepted quantum flux density rather than tree spacing (or area per tree), so that non-treatment variation was largely eliminated from the analysis.

2.2.3. Measurements

2.2.3.1. Tree positions

All trees were numbered and labelled. The entire stand was surveyed after re-spacing by chain and compass survey (Perrott, 1970), with relative individual tree positions at the centre of the base of the stem, recorded to the nearest 0.2 m. Exact positions of all trees within measurement units were measured on the ground using a cloth tape.

2.2.3.2. Tree biomass and canopy parameters

Annual measurements of crown dimensions were made and leaf area was periodically assessed in the respaced stands using a variety of non-destructive techniques based on the inversion of gap fraction data (Chapter 3).

2.2.3.3. Tree growth

Annual measurements were made in 1986 to 1988 of tree height (to the nearest 0.1 m) and stem diameter at breast height (to the nearest 1 mm) for all trees during the winter.

2.2.3.4. Grass growth

Thirty-six small pots of grass, 12 each of three species (*Lolium perenne* cv. Contender, *Dactylis glomerata* cv. Erecta RvP and *Phleum pratense* cv. Jesper) were sunk to ground level in a randomly selected measurement unit in each spacing treatment and in the control area and were harvested periodically to assess grass growth in 1988 (Chapter 5). The details of pot preparation, sampling positions and harvests are given in Chapter 5 where results from them are reported.

2.2.3.5. Radiation

Instruments measuring total incoming solar radiation (CM5, Kipp and Zonnen, Delft, Holland) and quantum flux density (SD 101 Q, Macam Photometrics Ltd, Livingstone, UK), were mounted on a tower above the tree canopy, and an array of 27 laboratory built quantum sensors (Section 2.3), mounted as in array 1 at Cloich (Section 2.1.3.5) were used to measure the light intercepted by trees and transmitted to the understorey. Sensors were connected to a data logger (delta logger, Delta-T Devices, Cambridge, UK) and automatically scanned at 10 second intervals, with hourly average values being stored. Sampling strategies are described where data are reported.

2.3. Quantum sensors

Sensors were required to measure the quantum flux density (QFD) of photosynthetically active radiation in the waveband 400 nm to 700 nm, both above and below tree and grass canopies. As a large number of sensors were required, they were laboratory built at a tenth of the cost of commercially available alternatives. One hundred and seventy five quantum sensors, comprising a filtered silicon photodiode connected to a resistor to produce voltage output for use with automatic data loggers, and mounted in a waterproof cosine-corrected housing, were constructed (after Biggs *et al.*, 1971). These were made in two sizes and in three separate batches with slightly different characteristics (Table 2.1). Full details of their design, components and performance are given in Appendix 1. Their performance compared favourably with a secondary standard (LI 190 SA, Li-Cor Ltd, Nebraska, USA).:

> All sensor designs produced a linear response in daylight in comparison with the Li-Cor sensor over a range of 0 to 1000 μmols m^{-2} s^{-1} PAR.
>
> The spectral response of all sensor designs was reasonably flat over wavelengths 400 to 650 nm (Figure 2.8). The output of the large 1986 sensors, however, declined to 25% relative to the Li-Cor output across the 650 to 690 nm waveband and was only 50% at 670 nm. This was improved in the 1987 sensors (60% relative to Li-Cor at 700 nm) by changing the

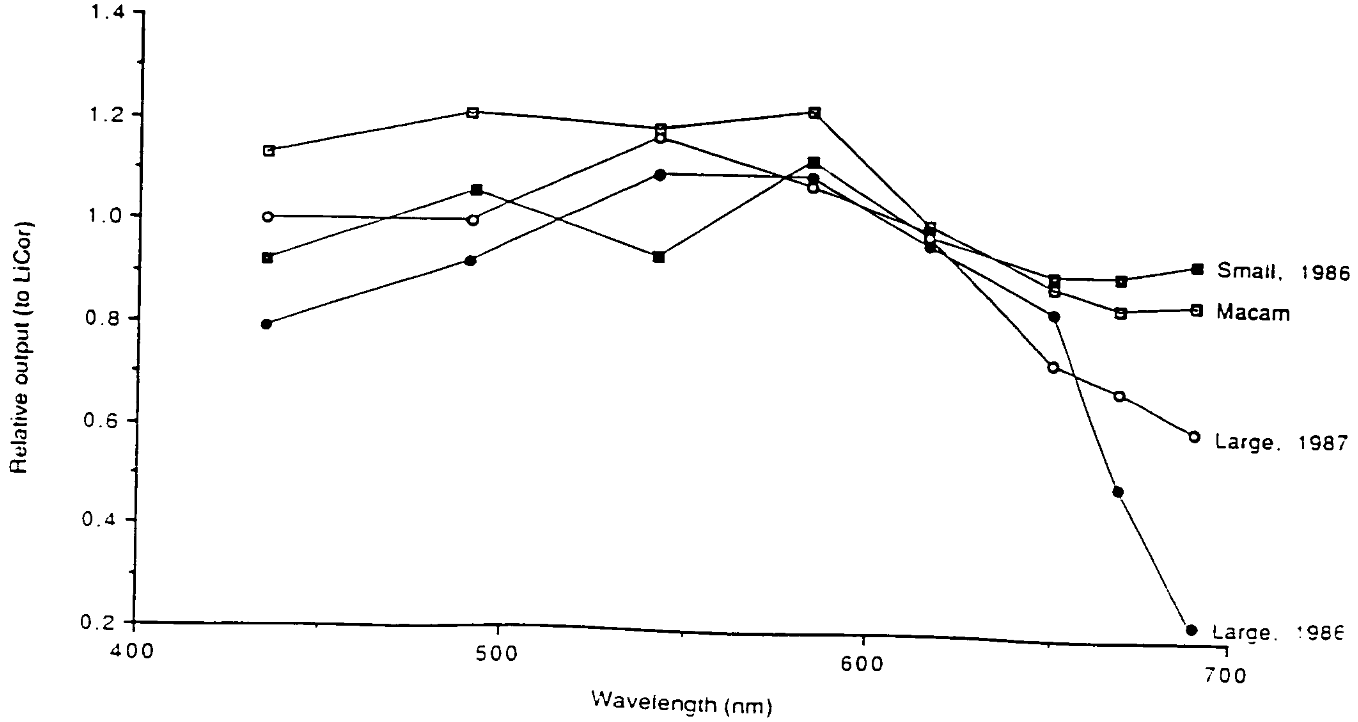
Table 2.1 Size and sensitivity of the different batches of quantum sensors.

batch	external dimensions (mm)		sensitivity (mV/mmol m^2 s^{-1})		change in sensitivity over two years (%)	
	height	diameter	mean (SD)	range	mean	range
large 1986	40	30	5.55 (skew)	3.76 - 6.34#	+3.1	-0.5 - +10*
small 1986	25	15	1.29 (0.17)	0.96 - 1.76	+1.3	-10 - +9.7
large 1987	40	30	5.81 (0.44)	4.63 - 6.86	+2.4	-0.6 - +7.8*

distribution positively skewed, with >80% of the sensors with sensitivity in the range 5.0 - 6.5; the few untypically low sensitivities may have been caused by potting compound leaking into the top of the sensor housing during construction. The effect of this would be to reduce the effective sensing area. As the compound sets hard the sensors could be expected to operate normally with reduced sensitivity.

* distribution negatively skewed, with >70% of the sensors showing changes in the range 0 - 5 %

Figure 2.8. Spectral response curves of the different quantum sensor batches. The curves were measured relative to a Li-Cor quantum sensor (LI 190 SA, Li-Cor, Nebraska) using a randomly selected sensor within each batch. Light in narrow wavebands was obtained using a set of interference filters (B-40, Balzer). Results are expressed relative to the output of the LiCor sensor, the Macam sensor (SD 101 Q, Macam Photometrics Ltd, Livingstone) is included for comparison.



specification of the interference filter used. The early cut-off in the large 1986 sensors could result in a slight underestimation of intercepted QFD, since the flux density of sunlight is generally higher at the larger wavelength end of the PAR spectrum and the proportion of radiation generally absorbed by leaves in the 650-700 nm band is higher than between 400-650 nm, being low between 500-600 nm (Smith, 1986). However, effects on the measurement were minimised by the calibration procedure and are likely to be small; an early cut-off is preferable to a late one, since 700 nm is a threshold for absorption of near infra red by water in leaves.

The cosine response of all sensor designs was reasonably flat to a Zenith angle of 80°.

The output of both batches of large sensors was in the range 0 to 16 mV over 0 to 2000 μmols m^{-2} s^{-1} PAR, well within the measurement range of commercially available automatic data loggers. The smaller sensing area of the small 1986 sensors resulted in a lower output in the range of 0 to 5 mV over the same PAR range. As these sensors were designed for measuring in heavy shade this low sensitivity was undesirable.

The sensitivity of individual sensors within each batch was variable (Table 2.1). Each sensor was calibrated annually in unobstructed sunlight against the secondary standard. The successive annual calibrations have shown slight ageing effects. The large sensors tended to increase in sensitivity with age (Table 2.1). Changes in sensitivity over time could be caused by an increase in transmissivity of the perspex diffuser, which could be expected to be associated with exposure to sunlight. The effects of ageing do not follow a clear trend in the small sensors; which were generally used in heavy shade.

3. Vegetation structure

3.1. Introduction

The amount of leaf area, its distribution, orientation and optical properties determine what proportion of incident QFD is absorbed by leaves (Norman and Jarvis, 1975). Because photosynthetic properties of leaves change with age, interaction of the radiation regime within a canopy with the distribution of leaves of different ages further influences the rate of photsynthesis (Jarvis and Sandford, 1986). The complexity of tree crown structure, and variability between trees, make complete description of the crowns of all trees in an agroforestry stand unmanageable. In simulation studies of conifer plantations, at both tree and canopy scales, changes in total leaf area and its spatial distribution had a much larger influence on QFD absorbtion than crown shape or leaf inclination (Wang and Jarvis, 1990a; Jarvis and Leverenz, 1983). While it has been demonstrated that in a horizontally homogeneous canopy the amount of PAR absorbed is independent of the distribution of leaf area density (Saeki, 1963), within spaced, individual tree crowns in agroforestry stands QFD absorption is influenced by both the vertical and horizontal distribution of leaf area density. The common assumptions of either uniform or random density distributions within tree crowns (e.g. Charles-Edwards and Thornley, 1973) lead to underestimates of the QFD within and below the tree crown (Norman and Jarvis, 1975; Oker-Blom and Kellomaki, 1983; Wang and Jarvis, 1990a). This would lead to errors in calculating biomass production by both trees and understorey in agroforestry systems, as tree crowns are manipulated as a result of management decisions. Therefore, the priorities in this study were to:

i) quantify the total leaf area of individual tree crowns;

ii) measure the position and size of individual crowns, defining the volume within which the leaf area was distributed, and;

iii) quantify the spatial distribution of this leaf area within crowns for each stand.

Destructive harvest of trees to measure leaf area and its spatial distribution is difficult and laborious, therefore, it was decided to sample trees at the start of the experiment within each stand to develop regression equations relating total tree leaf area to stem basal area (Section 3.1.2). These equations could then be applied to non-destructive measurements of stem basal area on individual trees. While the spatial distribution of leaf area has been shown to vary markedly amongst trees (Massman, 1982), there is little evidence that this is related to easily measured tree attributes (Kellomaki *et al.*, 1980; Wang, Jarvis and Benson, 1990). The variation in spatial distribution of leaf area between the different stands can be expected to be more significant, as well as more easily quantified, than that between trees within the stands. On the assumptions that a) the relationship between leaf area and stem dimensions; and, b) the relative spatial distribution of leaf area within the crown; did not change over the experimental period, equations derived from the initial harvest in 1986 were applied to stem and crown measurements of individual trees in 1987 and 1988.

3.1.1. Distribution of leaf area density within crowns

Vertical distribution of leaf area has been studied in various conifer species at a range of ages, but predominantly in pines and mature plantations; for example, *Pinus resinosa* Ait. (Stephens, 1969), *Pinus taeda* L. (Kinerson *et al.*, 1974), *Pinus contorta* Dougl. (Gary, 1976), *Pinus sylvestris* L. (Whitehead, 1978; Kellomaki *et al.*, 1980; Beadle, Talbot and Jarvis, 1982), *Pinus lambertiana* Dougl. (Massman, 1982), *Pseudotsuga menziesii* (Massman, 1982; Schmid and Morton, 1981), *Abies concolor* (Gord. and Glend.) Lindl. (Schmid and Morton, 1981), *Picea sitchensis* (Norman and Jarvis, 1974; Ford, 1982) and *Chamaecyparis obtusa* (Sieb. and Zucc.) Endl. (Hagihara and Hozumi, 1986). There have been a wide range of sampling intensities and methods employed, within and between trees and data have been presented in various forms from ratios of leaf area in different vertical crown slices (e.g. Schmid and Morton, 1981) to complex distribution functions of leaf area density (e.g. Gary, 1976). Leaf area density has been variously distributed along actual and normalised tree and crown heights. Earlier preferences for fitting a normal distribution to leaf area density data (e.g. Stephens, 1969) sometimes with a term to take account of significant skewness (Beadle *et al.*, 1982) have been replaced more recently by use of a more flexible beta function combined with normalisation in respect of crown dimensions and total tree leaf area (e.g. Kellomaki *et al.*, 1980). Massman (1982) compared five different distributions and found that the beta distribution, which has the flexibility of more complex functions, gave the best fit for the mature tree crowns in his study. Wang, Jarvis and Benson (1990) applied independent beta functions in the vertical and horizontal to describe the spatial variation of normalised leaf area density within normalised crowns of *Pinus radiata*. There are only a few other documented studies of two dimensional leaf area distributions in woody perennials, utilizing variable sampling strategies and measurement techniques, (Philip, 1965; Kurachi, Hagihara and Hozumi, 1986; Koike, 1986). Wang (1988) combined the vertical distribution from a previous study at one site (Norman and Jarvis, 1974) with a horizontal distribution calculated from a stratified sample of 18 branches from only three trees from a second site for *Picea sitchensis*.

3.1.2. Relationships between tree foliage and stem dimensions

Allometric relationships between foliage mass and D_r in a range of temperate conifer and broadleaved tree species have been demonstrated and used in conjunction with stand tables to estimate foliage mass and leaf area per unit land area (Kittredge, 1944). The same form of relationship has been found to hold for the mass of foliage on individual branches as a function of basal branch diameter throughout the crown of *Eucalyptus obliqua* L'Herit (Attiwill, 1962); while Loomis, Phares and Crosby (1966) found the diameter of the stem at the base of the live crown to be the best single estimator of foliage mass in *Pinus echinata* Mill., and that the relationship between the two variables was unaffected by stand density. As would be expected, similar relationships have been obtained relating the total leaf area within tree crowns (F_t) to D_r (Cable, 1958; Carbon, Bartle and Murray, 1979), and in comparing regressions of F_t on various combinations of D_r, H_t and D_r^2 for *Eucalyptus* spp., the best fit was obtained with D_r (Carbon *et al.*, 1979).

While these allometric relationships, measured empirically for individual species and sites, may be used to predict F_t from D_r within the range of D_r over which they were determined there is no physiological basis that permits extrapolation or generalisation across species, sites and stand conditions. In contrast, Shinozaki, Hozumi and Kira (1964a and 1964b) found linear proportionality between the mass of foliage and the mass of nonphotosynthetic tissue, from the base of the live canopy upwards, from analysis of various vascular plants. They concluded that a given unit amount of leaves was serviced by a continuum of conducting tissue of constant cross-sectional area, analagous to a system of pipes serving both as a vascular passage and a mechanical support. According to this 'pipe model theory' the sapwood xylem represent 'pipes' associated with living foliage and heartwood represents pipes that were associated with foliage on branches that have died. They demonstrated that below the base of the live crown there was no fixed ratio of total cross sectional area of stem to supported foliage.

Linear relationships between foliage biomass or leaf area with sapwood basal area (A_r) have subsequently been reported for a range of conifer species, including *Picea sitchensis*, at various sites (Grier and Waring, 1974; Whitehead, 1978; Kaufmann and Troendle, 1981; Waring, Schroeder and Oren, 1982; Whitehead, Edwards and Jarvis, 1984; McIntosh, 1984). Snell and Brown (1978), compared D_r and A_r as estimators of crown biomass in seven conifer species, while A_r was better in three cases, there was no significant difference in the other four. McIntosh (1984) also found little difference between D_r and A_r as estimators of leaf area for two polestage stands of *Picea sitchensis* in southern Scotland, probably because there was little or no heartwood development in the young trees. Waring *et al.* (1982), reported unpublished data of Thies, demonstrating that sapwood area tapered linearly from the base of the crown to a breast height of 1.37 m in more mature *Pseudotsuga menziesii*, and this is consistent with the existence of linear relationships between leaf area and A_r. Long, Smith and Scott (1981), working with the same species, found that cross-sectional area of sapwood was linearly related to foliage mass above the point of measurement for any height up the stem, consistent with the pipe model theory.

The ratio of leaf area to sapwood area has been found to vary five fold between conifer species, with values from 0.14 to 0.75 m^2 cm^{-2} (Waring *et al.*, 1982). The cause of this variation is not entirely clear. Different studies have employed different methods of measuring tree leaf area both in sampling foilar mass and in converting this to leaf area, and have measured sapwood area either at breast height (A_r) or the base of the live crown (A_c). In some cases regressions have included an intercept (e.g. McIntosh, 1984) while in others the regression has been forced through the origin (e.g. Whitehead *et al.*, 1984) and this makes it difficult to compare regression coefficients across studies. A positive relationship between site quality and foliage per unit sapwood area has been reported for conifer species (Brix and Mitchell, 1983; Bancalari, Perry and Marshall, 1987), and Waring (1983) has suggested that plants adapted to arid areas have lower ratios consistent with sapwood conducting tissue being related to transpirational demand rather than leaf area. Whitehead and Jarvis (1981) have shown algebraically that the slope of the regression must be a function of the average vapour pressure deficit of a site, since this is the primary variable driving transpiration in trees, and the drier the air, the more transpiration will occur for the same leaf area. Trees of the same species growing at wider spacings have also exhibited higher leaf area to sapwood area ratios than when at closer spacing (Whitehead, 1978; Granier, 1981), as have faster growing *Pseudotsuga menzeisii* (Bancalari *et al.*, 1987) and dominant as opposed to suppressed *Pinus contorta* (Thompson, 1989). These results are consistent with the high density wood resulting from slow growth having a low hydraulic conductivity (Edwards and Jarvis, 1982), and Whitehead *et al.* (1984), were able to reconcile differences in the slope of regressions of F_t on A_r for different tree species and fertilizer treatments (*Picea sitchensis* plus and minus fertilizer, and *Pinus contorta*) by developing a single linear relationship between leaf area and the product of sapwood basal area and permeability.

For the relatively young stands of *Picea sitchensis* in the present study (< 20 years old), little or no heartwood development was expected and, therefore, both D_r and the cross sectional area of the stem at the base of the live crown (M_c) could be expected to be good estimators of leaf area, the latter with a sound physiological basis for extrapolation. The more significant problem was the difficulty in non-destructive measurement of stem diameter at an appropriate height on the low and intermediate tree stands where the crowns reached ground level and breast height was 1.3 m above the crown base. McIntosh (1984), found that relationships between both D_r and A_r with F_t did not change significantly in stands of 23-year-old *Picea sitchensis* subjected to various thinning and fertilizer treatments over three growing seasons in southern Scotland. It was, therefore, considered appropriate to make one initial destructive harvest at the start of the experiment in 1986 to establish relationships between stem dimensions and leaf area and assume that these remained constant over the following three years.

3.2. Methods

Vegetation structure was intensively measured at the Cloich site. A destructive harvest of 36 sample trees at re-spacing in 1986 (Section 3.2.1) was followed by annual measurement of H_t and D_r for every tree during the experimental period (Section 2.1.3.3). In addition periodic and independent assessment of canopy dimensions (Section 3.2.2) and leaf area (Section 3.2.3) were made, the latter by analysis of gap fraction data collected using non-destructive sensors (Section 3.2.3).

3.2.1. Destructive harvest

The destructive harvest comprised two phases.

1) The selection and systematic dissection of sample trees in both vertical and horizontal planes and in relation to age of foliage, with measurement of fresh mass of various parts.

2) Subsequent subsampling of dissected parts, separation of leaf material and measurement of dry mass and projected leaf area of subsamples.

The first phase was accomplished jointly with the MLURI. The data from both phases were combined in a single database prior to the analysis.

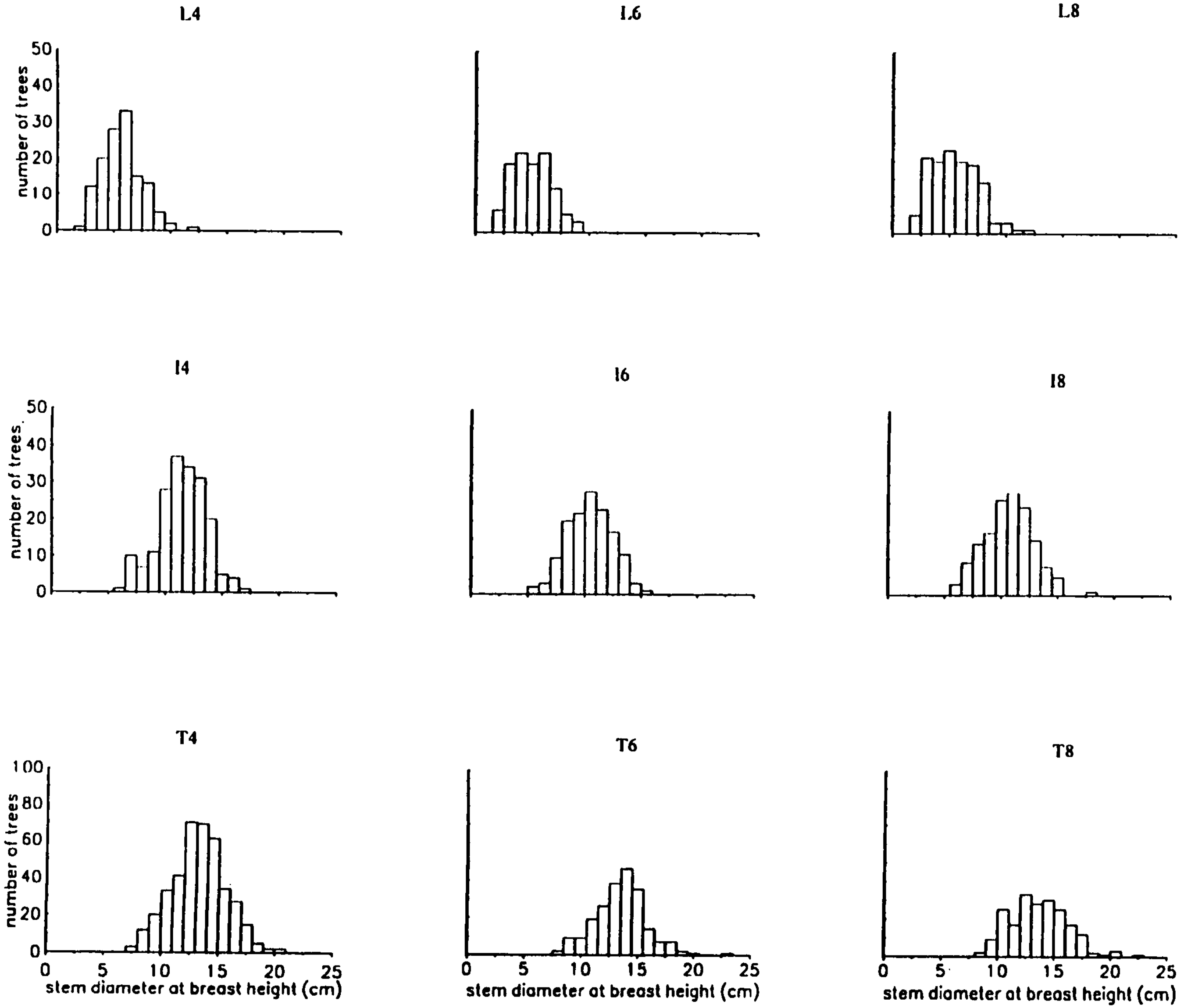
3.2.1.1. Selection of sample trees

The three tree stands of different tree mean height at Cloich were treated as separate identifiable populations prior to the allocation of treatments and respacing. Random samples of approximately one hundred trees from each stand were located and D_r and H_t measured. The frequency distributions of D_r for each stand were approximately normal and this is consistent with a randomly variable stand prior to canopy closure. Histograms of the D_r for all trees in each plot immediately after respacing are shown in Figure 3.1. D_r and H_t were positively correlated (Table 3.1), more strongly for the low tree stand ($r > 0.8$) than for the intermediate and tall tree stands ($0.70 > r > 0.50$). Because of the general functional relationship between stem cross-sectional area and leaf area (Section 3.1.2), the requirement to establish such relationships for extrapolation and the absence of reliable data on the variability of the key variables to be measured (leaf area and biomass), sampling was stratified across the range of D_r sizes. For each stand, the sample D_r data were divided into six equal classes based on frequency (each class contained an equal number of observations) and two trees from each class were randomly selected for harvest. This resulted in destructive sample of twelve trees from each stand.

Table 3.1 Correlation coefficient (r) of tree height (H_t) in m, and stem diameter at breast height (D_r), in cm, for trees at Cloich at the start of the experiment (n = the number of trees measured). Treatment labels as in Figure 2.1.

Treatment	**r**	**n**
L4	0.82	130
L6	0.84	107
L8	0.88	127
I4	0.51	188
I6	0.65	140
I8	0.69	150
T4	0.62	393
T6	0.54	214
T8	0.53	201

Figure 3.1. Distribution of stem diameter at breast height (D_r) for treatment plots at Cloich at the start of the experiment. Treatment labels as in Figure 2.1.



3.2.1.2. Systematic dissection and measurement

Each sample tree was felled as close to the base as possible and the stump height was recorded. The length of the leader was recorded, and then two randomly selected branch angles and branch lengths were measured on each whorl of branches. Branch angles were measured by placing a large protracter along the stem and recording the angle formed between the stem and the branch above the point of attachment. Each whorl of branches was then removed and the number of branches and their total fresh mass was measured using a spring balance. The length of stem between each whorl was measured (internode length) and if there were any branches on the internode two branch angles and branch lengths were measured at random and then all branches were removed, counted and the fresh mass of branches for each internode recorded. Stem sections (3 cm thick) were cut from the base of the tree and at 1.3 m from the base of the tree, and dried to constant mass at 80 °C. Working from the top of the tree, a sample branch was randomly selected from whorls 1,2,3 and then odd numbered whorls thereafter. The branch was laid out on a table marked with horizontal lines at 20 cm intervals across it and then divided into 20 cm distance classes starting from the base of the branch. Each distance class was further divided into three age classes representing the previous season's growth (A1), material between 1 and 2 years old (A2), and material over 2 years old (A3). The fresh mass of the shoots in each distance and age class were measured. The material was then put in plastic bags and stored in a cold room (4 °C).

3.2.1.3. Measurement of leaf area

The shoots in each distance and age class were later retrieved from the cold store, layed out on a bench and divided ocularly into, up to three, groups of shoots with similar leaf to wood ratio. The fresh mass of each group was measured using a digital balance (RE1614, Sauter, Greissensee, Switzerland). A subsample was then taken from each group containing, where possible, a minimum of 30 leaves. Each subsample was held with tongs and immersed in liquid nitrogen for a few seconds after which leaves were easily separated from twigs. Single-sided projected leaf area was then measured using a leaf area meter (LI-3100, LI-COR, inc., Lincoln, Nebraska) and the fresh mass of leaf and stem fractions were measured using the digital balance. Dry mass was then measured after oven drying to constant mass at 80 °C.

3.2.2. Non-destructive tree measurements

3.2.2.1. Height and basal area

The H_t and D_r of all trees were measured annually by the FC (Section 2.1.3.3)

3.2.2.2. Crown diameter

The mean crown diameter (D_c) of open grown trees at the base of the live crown, has been shown to be well correlated (r = >0.96) with D_r for a range of broadleaved and coniferous species (Krajicek, Brinkman and Gringrich, 1961) and *Picea sitchensis* in upland Britain in particular (r =0.93; Tabbush and White, 1988). However, it was not possible to develop a reliable equation for predicting D_c from measured D_r using data from the destructive harvest (Section 3.2.1.2), calculating D_c from measurements of branch lengths and angles. Although the positive correlation of the two variables (r =0.87) was highly significant, linear regression of D_c on D_r (Table 3.2) indicated that:

> 1) the precision of predicting D_c from stem diameters in the upper range of D_r sampled was not adequate (for D_r = 16.5 cm the 95% confidence limits for prediction of D_c were 4.60 m and 3.36 m and an error of over 0.6 m in estimating diameter of individual crowns is clearly unacceptable in the present context); and
>
> 2) the slope of the relationship was lower, and its standard error was higher, than in two previous studies with larger samples and range of tree sizes that have indicated that the slope may be conservative for the same species at different sites and for similar species (Table 3.2).

Table 3.2 Regression parameters for the relationship of crown diameter (D_c) and stem diameter at breast height (D_r). Bracketed figures are standard errors. Regression equation:
$D_c = a + b\ D_r$ where; D_c and D_r are measured in cm.

source	species	sample size	D_r range (cm)	regression parameters constant, *a*	slope, *b*
destructive harvest (Section 3.2.1)	*Picea sitchensis*	36	1.5 - 16.5	179 (11.5)	13.3 (1.15)
Tabbush and White (1988)	*Picea sitchensis*	72	7.0 - 80.0	188 (15.6)	15.3 (0.71)
Krajicek *et al.* (1961); standard errors estimated from their Fig. 3 by Tabbush and White (1988).	*Picea abies*	157	7.0 - 100	154 (15.3)	15.8 (0.35)

It was, therefore, necessary to measure crown diameter independently. The standard FC procedure for measuring D_c involves measuring the projection of the shortest (S_n) and the longest (S_x) branch with a horizontal graduated rod at 1.3 m height (Hummel *et al.*, 1958). Crown diameter (D_c) is then calculated as:

$$D_c = S_n + S_x + D_r \qquad \text{(Equation 3.1)}$$

and mean crown radius (R_c) as:

$$R_c = D_c / 2 \qquad \text{(Equation 3.2)}$$

Measurements of D_c considered adequate for analysis of stand competition processes have involved making from three (Tabbush and White, 1988) to six (Hamilton, 1969) radial measurements but no estimation of the error in the mean crown radius of individual trees associated with these measurements is available. Wang and Jarvis (1990b), showed variation in measured and simulated QFD on bright days which may be caused by errors in measuring inividual crown positions and sizes. Therefore, a variability study to calculate the number of random radial measurements required to obtain an accurate estimate of mean crown radius per tree was made in the tall stand. Twelve radial measurements were made at random compass bearings on 20 randomly selected trees from the tall stand. For each measurement a rigid pole with 1 cm graduations marked on it was extended horizontally from the tree trunk at the selected bearing and the furthest extent of the crown measured. The number of measurements (n) required to estimate the mean radius for each tree ($\underline{R}_C$) was calculated as suggested by Snedecor and Cochran (1980); their Equation 21.6.1 for 95% confidence limits:

$$n = 4\, s^2/L^2 \qquad \text{(Equation 3.3)}$$

Where L, is the allowable error and s, the standard deviation of the twelve radial measurements. These data while limited both in the number of trees and radii sampled indicated:

1) that crown radius was variable (the mean CV for 20 sample trees = 19.4%) and that extremely variable crowns occurred at a low frequency (15% with a CV of > 30%; Figure 3.2); and

2) that it was impractical to measure mean crown diameter of individual trees by taking a random sample of radii since the number of measurements required for a reasonable error of between 0.1 m and 0.2 m in the estimation of the mean would involve too much time if repeated for each tree and a practical number of measurements per tree of between three and five would produce an unacceptable error, not significantly improving on the regression of D_c on D_r (Figure 3.3)

This method did not take into account tree structure, whereas other methods have been based on measuring branch lengths (Tabbush and White, 1988), or their projection on the ground (Hamilton, 1969). These procedures might be expected to reduce the variability in the estimate, but to overestimate the mean crown radius, because the outline shape of branches is tapered, causing the radial extent of the canopy between branches to be less than that at the branch tips. Some data on the variability of branch lengths was available from a random sample of 14 whorls from the

Figure 3.2. Variability of crown radius within 20 tree crowns in the tall tree stand at Cloich. CV = the coefficient of variation (%). Details of measurements are in text (Section 3.2.2.2.).

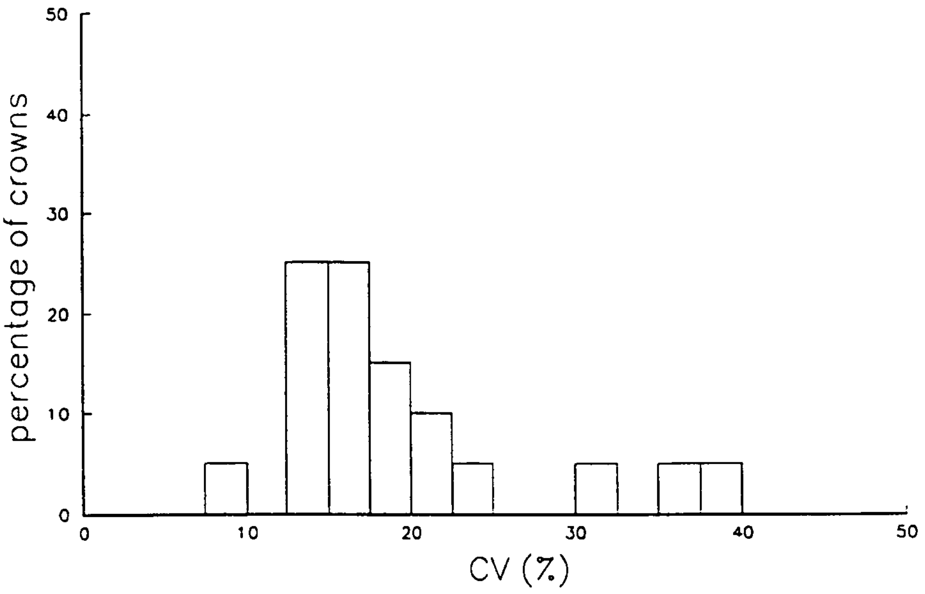
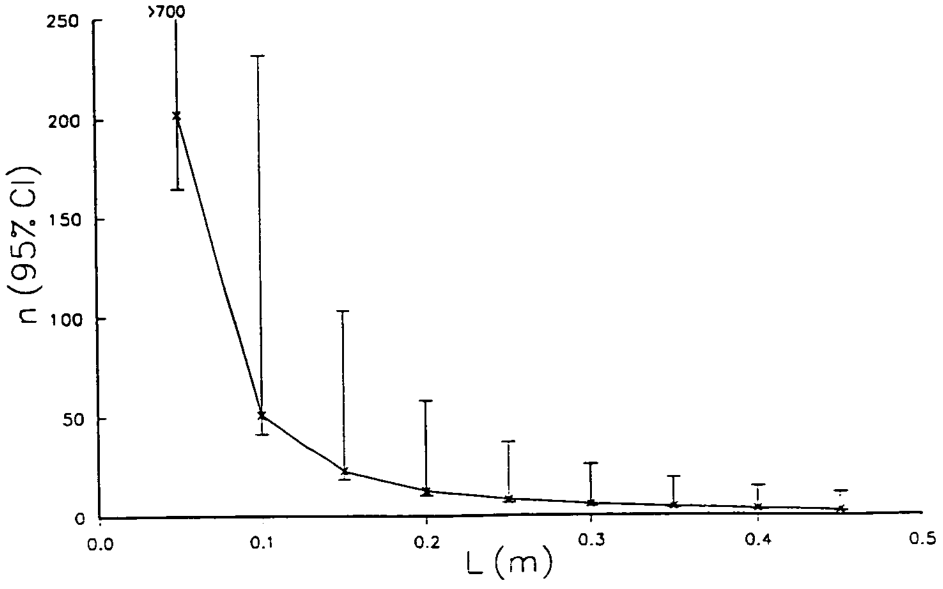


Figure 3.3. Number of samples (n) required to estimate the mean crown radius of trees for different allowable errors (*L*) calculated from Equation 3.3 using data from 20 trees in the tall tree stand at Cloich. Points are the mean value for all sampled tree crowns, the bars show the range for all sampled trees.



destructive harvest (Section 3.2.1.2) in which branch length was measured for all branches in the whorl. These data showed similar variability to random measurements of crown radii (range of CV was 7 to 41%). However, the difference between the true mean radius and that estimated by summing the lengths of the shortest and longest branches and dividing by two ranged from <0.01 m to 0.16 m and was typically below 0.1 m suggesting a tolerable error margin. Comparison of selecting three equidistant measurements per crown (Tabbush and White, 1988) with the mean value of the largest and shortest from the random sample of crown radii suggested that the latter method introduced less error (mean error = 0.08 m; range 0.00 - 0.20 m) than the former (mean error = 0.12; range 1.00 - 0.27 m). Based on this evidence and the compatibity of the method with many previous studies and with the destructive harvest, and feasibility of repetition on a reasonable number of trees, D_c was measured on all trees within plots annually during the winter by measuring the lengths of the longest and shortest branches (identified subjectively by eye), and then employing Equation 3.1

3.2.2.3. Crown length

The intermediate and low trees had branches down to ground level throughout the experiment so that crown length was assumed to be equal to H_t. In the tall stand, lower branches were removed to the base of the live crown at approximately breast height when the stand was respaced. The height of the base of the crown (C_t) of trees in the plots in the tall stand were measured in 1989. Crown length (S_c) was calculated as follows:

$$S_c = H_t - C_t \qquad \text{(Equation 3.4)}$$

3.2.3. Gap frequency data

Non-destructive estimates of leaf area index of plant stands have been obtained by mathematical inversion of gap frequencies obtained from the penetration of probes or of sunlight (Warren Wilson, 1959, Lang, Xiang Yueqin and Norman, 1985). The method requires an assumption that leaf area is distributed randomly unless the gap frequency is separately measured over small segments of transects, in which case large gaps in the canopy are effectively eliminated from the calculation, and the method is suitable for discontinuous canopies (Lang and Xiang Yueqin, 1986). Gap frequency data for a range of probe angles (θ) can be used to obtain a simplified estimate of leaf area index from the regression coefficient of θ against $K(\theta)$, where K is a log transformation of gap frequency (Lang, 1987). These methods have been successfully used in discontinuous canopies provided that gap frequency is separately determined over small segment lengths (Lang and Xiang Yueqin, 1986). Three methods of measuring gap frequencies at a range of probe angles by using transmission of sunlight were compared across the range of tree frequencies in the tall stand and resulting estimates of leaf area index were compared with estimates derived from the destructive harvest.

3.2.3.1. Direct beam transmission

This method involved traversing a light sensor focussed on the direct beam of the sun under the tree canopy at different times of the day. The beam sensor constructed after Lang *et al.*, 1985 was connected in voltage mode to a datalogger (CR21x, Campbell Scientific, Nottingham). Each measurement of gap frequency involved the following procedure.

> The sensor was focussed on the unobstructed sun outside the canopy and the reading stored. The operator then walked at an even pace along a randomly orientated transect under the tree canopy keeping the sensor held so that it was focused on the sun. During this transect the sensor was scanned at intervals of 0.03 s and the average transmission value for each segment, consisting of 10 scans, was calculated. The transmittance of each segment $[T(\theta)]$ was then found as the ratio between the stored unobstructed reading and the average transmittance value for the segment. The pace of the walk was adjusted so that the segment length (referring to the length of transect over which transmission was averaged) was approximately 10 S_l, where S_l is the mean leaf length. The contact number (K) for each segment was then calculated using Equation 3.5 and the mean value of K for the transect stored.

$K = -\cos\theta \ln T(\theta)$ (Equation 3.5)

The procedure was repeated three times in each plot for each zenith angle (θ). Zenith angles for each transect were calculated from standard equations based on the time of day and latitude of the site (Iqbal, 1983). As wide a range of θ were used on each measurement day as possible, but there were few suitable days when the sun was unobstructed for long enough periods to make a full range of measurements across plots. The range of θ used are presented with the results. Leaf area index (F) for each plot was calculated as:

$F = 2(a+b)$ (Equation 3.6)

Where a and b were the intercept and slope of the regression of θ against $K(\theta)$ (Lang, 1987).

3.2.3.2. Diffuse transmission

Prototype sensors with an integrated logger, now commercially available as canopy analysers (LI 2000, LI-COR, inc., Licolcn, Nebraska), were used in diffuse sky light conditions in 1988. The instrument contains a filtered photodiode with an arrangement of lenses and shadebands so that when horizontal the flux density of radiation in a narrow waveband was simultaneosly recorded for five annuli corresponding to zenith angles (θ) of 7°, 23°, 38°, 55°, and 70°. By comparing measurements above and below the canopy the gap frequencies at the five zenith angles are obtained using essentially the same underlying theory as for the beam sensor. Two cross calibrated sensors were used. One sensor was positioned above the tree canopy and stored reference values once a minute, the other made similar measurements below the canopy. For each estimation of F, nine points were located at random within a randomly selected unit (Section 2.1.1) and a below canopy reading was made at a recorded time at each location. This procedure was repeated three times for each plot. The automatic pairing of above and below canopy readings and pre-programmed calculation of F did not function correctly in the prototype instruments and so this was done as described for the beam sensor (Section 3.2.3.1) using the raw data from the two individual instruments. Because segmentation of the annuli was not possible, an assumption of completely random distribution of leaf area in the tree canopy must be made, and this does not take account of the non-random distribution of the foliage that is a feature of agroforestry canopies and of the treatments at Cloich in particular.

3.2.3.3. Hemispherical photographs

The third method of determining gap frequency was by image analysis of hemispherical photographs. A camera fitted with an equiangular hemispherical lens with a 178° field of view (Nikkon Fish eye 1:5.6, f=7.5, Nippon Kogaku KK, Tokyo) was positioned horizontally with the top of the camera pointing due north, 0.25 m above the ground and levelled using the arrangement described for light sensors (Section 2.1.3.5). The photographs were taken using medium speed (125 ASA) black and white 35 mm film (FP4, Ilford, Mobberley) in overcast sky conditions (Anderson, 1971). Nine photographs were taken in each plot, one in each grid square position (Section 2.1.1), located randomly within randomly selected grid squares. Negatives were scanned and processed using a digital image analysis system (Quantimet 970, Cambridge Instruments). The specification of the threshold grey level was varied until the captured image resembled a live projection of the negative. This subjective judgement was reasonably consistent because it was done by the same operator for all negatives, and in all cases after a series of changes in the threshold level that only altered the image slightly, an increment was reached that caused a much larger change which clearly excluded leaf area. After the grey level had been set, five annuli corresponding to the zenith angles used for the LI-COR canopy analyser (Section 3.2.3.2) were imposed on the image and the gap fraction calculated as the proportion of white to black pixels in each annulus. These data were then analysed identically to the transmission data from the LI-COR canopy analyser to obtain an estimate of F for each negative, mean values (n=9) were used as an estimate of F for each plot.

3.3. Results and discussion

3.3.1. Total leaf area within tree crowns

Total leaf areas of each destructively sampled tree (Section 3.2.1.) are presented in Table 3.3. They were calculated by summation of sampled leaf area and biomass according to equations 3.7, 3.8 and 3.9. Where F_s, F_b, F_w, F_t,are the leaf area of samples, branches, whorls and trees respectively; W_s,

Table 3.3. Total leaf area (F_t), crown and stem dimensions of 36 trees sampled from the low (L) intermediate (I) and tall (T) stands at Cloich. $\underline{R}_c$ = mean crown radius; S_c = crown length; D_r = stem diameter at breast height (1.3 m); D_b = stem diameter at base; $\underline{L}_{vh}$ = mean leaf area density in the crown.

stand	**tree number**	F_t m^2	$\underline{R}_c$ m	S_c m	D_r cm	D_b cm	$\underline{L}_{vh}$ $m^2\ m^{-3}$
L	1	5.92	1.02	2.31	2.2	6.5	2.35
L	2	8.36	1.09	2.90	3.0	8.5	2.32
L	3	9.21	1.06	2.98	4.0	7.0	2.63
L	4	5.32	0.88	2.23	2.6	5.5	2.94
L	5	15.36	1.25	2.78	5.0	11.0	3.38
L	6	19.15	1.29	4.50	7.0	12.0	2.44
L	7	8.41	1.23	2.44	2.9	7.0	2.18
L	8	12.75	1.07	3.49	6.0	10.0	3.05
L	9	3.15	0.95	1.99	1.5	5.5	1.68
L	10	15.02	1.30	3.21	4.0	10.5	2.64
L	11	14.76	1.28	4.60	5.4	11.2	1.87
L	12	12.33	1.19	3.21	5.0	10.5	2.59
I	1	52.45	1.81	6.28	12.5	18.0	2.43
I	2	51.29	1.81	5.21	13.0	18.0	2.87
I	3	30.41	1.70	5.68	10.5	17.0	1.77
I	4	29.66	1.40	4.34	8.5	14.0	3.33
I	5	49.42	1.48	5.06	10.0	14.5	4.26
I	6	36.10	1.40	5.15	10.5	15.5	3.41
I	7	51.08	1.89	5.35	14.5	19.0	2.55
I	8	36.13	1.57	5.28	10.0	17.0	2.65
I	9	27.45	1.56	3.88	8.0	13.0	2.78
I	10	15.80	1.39	4.26	8.5	11.5	1.83
I	11	30.48	1.59	3.91	12.0	14.0	2.94
I	12	24.97	1.62	4.07	7.0	12.0	2.23
T	1	35.64	1.69	6.25	12.5	16.5	1.91
T	2	42.32	1.90	5.04	13.0	20.0	2.22
T	3	38.43	1.98	6.38	16.5	20.0	1.47
T	4	53.84	1.80	7.39	16.0	21.0	2.15
T	5	32.68	1.40	5.39	11.0	16.0	2.95
T	6	40.07	1.37	5.74	13.0	18.0	3.55
T	7	31.23	1.45	5.81	12.5	15.5	2.44
T	8	21.30	1.18	5.59	9.5	12.0	2.61
T	9	28.39	1.60	5.90	11.0	14.0	1.80
T	10	38.23	1.89	5.35	14.0	19.0	1.91
T	11	34.63	1.76	7.64	14.5	19.0	1.40
T	12	18.18	1.39	5.58	10.0	13.0	1.61

W_g, W_b, W_w are the fresh mass of samples, groups, branches and whorls, respectively; and k, l, m, and n are the numbers of groups per age class, age classes per distance class, distance classes per branch, and whorls per tree respectively. The leaf area of each sampled branch (F_b) was calculated as:

$$F_b = \sum_1^m \sum_1^l \sum_1^k (F_s / W_s) W_g \ . \qquad \text{Equation 3.7}$$

The leaf area of each sampled whorl (F_w) was then calculated as:

$$F_w = W_w(F_b / W_b). \qquad \text{Equation 3.8}$$

For the alternate whorls that were not sub-sampled for leaf area, and interwhorls (all the branches between two whorls) the F_b/W_b ratio from the whorl immediately above was used with the mass of the whorl as in Equation 3.8. The leaf area of the whole tree (F_t) was then calculated as:

$$F_t = \sum_1^n F_w \qquad \text{Equation 3.9}$$

Mean tree leaf area and crown dimensions for the sampled trees from the three stands are presented in Table 3.4. which shows considerable variability of F_t within each stand. Much of this variability is associated with differences in tree size: L_{vh} is more conservative and there is a strong linear correlation between F_t and D_r (Section 3.3.1.2). Comparisons between stands are difficult since site, age and genetic effects are confounded but larger variability in F_t amongst the low as opposed to the intermediate trees (CV = 45% and 33%) is perhaps indicative of more heterogeneous site conditions and some resulting degree of imposed stress, which is consistent with slower growth. The tall trees, which have had lower branches removed, have as a result a lower and less variable F_t than the intermediate trees, despite larger D_r. The tall trees were approaching canopy closure and the extent to which leaf area was removed during brashing as opposed to natural shedding remains unclear, but the lower mean leaf area density suggests that leaf area may have been reduced proportionately more than crown volume in the operation. This is consistent with the trends in the vertical distribution of leaf area density (Section 3.3.2.4.).

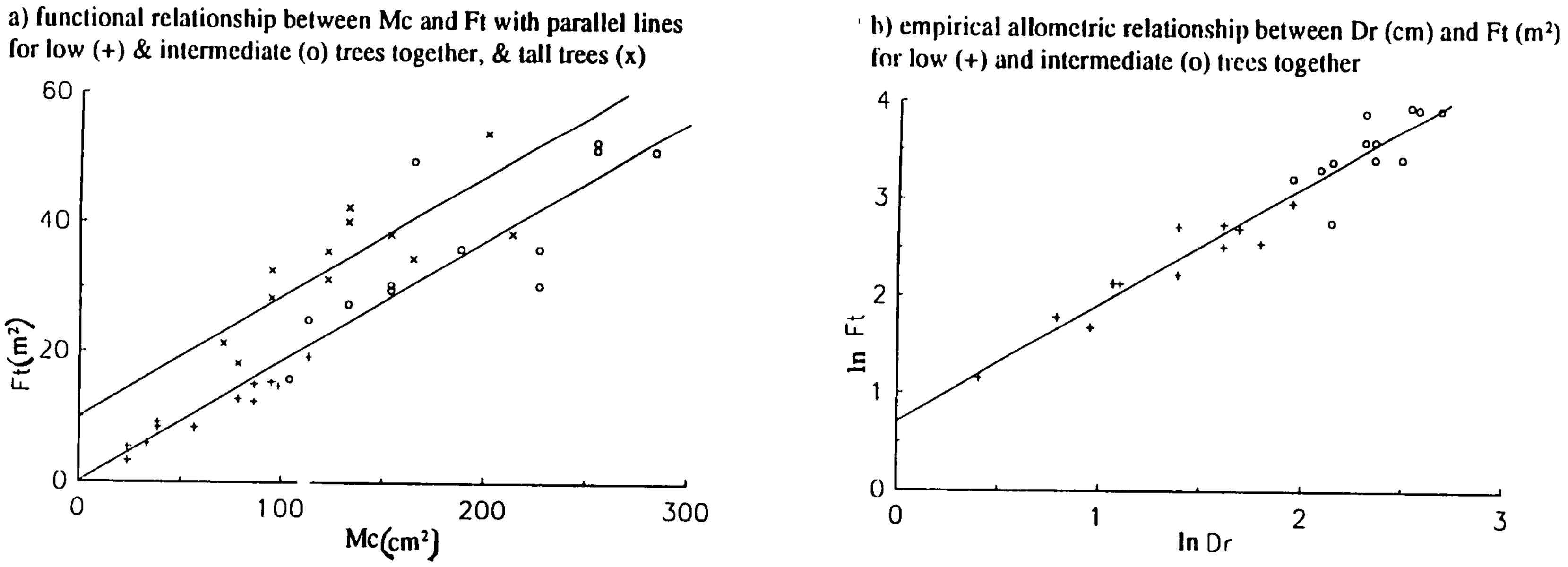
Table 3.4. Mean total leaf area ($\underline{F}_t$), crown and stem dimensions for sampled trees from the low (L) intermediate (I) and tall (T) stands at Cloich. 12 trees were sampled in each stand. Numbers in brackets are standard deviations. $\underline{R}_c$ = mean crown radius; $\underline{S}_c$ = crown length; $\underline{D}_r$ = stem diameter at breast height (1.3 m); $\underline{D}_b$ = stem diameter at base; $\underline{L}_{vh}$ = mean leaf area density in the crown.

stand	$\underline{F}_t$ (m^2)	$\underline{R}_c$ (m)	$\underline{S}_c$ (m)	$\underline{D}_r$ (cm)	$\underline{D}_b$ (cm)	$\underline{L}_{vh}$ m^2 m^3
L	10.81(4.83)	1.13(0.14)	3.05(0.83)	4.05(1.67)	8.77(2.37)	2.50(0.48)
I	36.27(12.12)	1.60(0.17)	4.87(0.77)	10.42(2.24)	15.29(2.50)	2.76(0.70)
T	34.58(9.48)	1.62(0.26)	6.01(0.80)	12.79(2.21)	17.00(2.96)	2.17(0.64)

3.3.1.1. Relationships between total leaf area and stem dimensions

The trees in all three stands were young (< 20 years old) and, therefore, it was reasonable to assume that a high proportion of stem cross-sectional area at the base of the live crown (M_c) was water conducting tissue (sapwood); and to expect that the sapwood cross-sectional area at the base of the live crown (A_c) would be linearly related to F_t (Section 3.1.2). In the low and intermediate tree stands the crown base was at ground level and M_c was taken to be the cross-sectional area of the stem at its base. In the tall stand trees had been pruned to a height approximately equal to breast height (1.3 m) and, therefore, M_c was taken to be the cross-sectional area of the stem at this height. There was a strong linear relationship between F_t and M_c for all stands. Analysis of variance of linear regressions for different combinations of tree stands revealed no significant difference between separate and joint regressions for the low and intermediate stands and non-significant intercepts. There was, however, a larger and statistically significant intercept for the tall tree stand, but the slope of the relationship was not significantly different for the tall stand than the other two stands (Table 3.5a). Two parallel regression lines, therefore, provided the best fit to the data and the parameters of these are presented in Table 3.5a. The low and intermediate stands were close to each other, younger than the tall trees and had not been pruned. The positive intercept for the tall stand may indicate that some leaf area was removed above breast height during brashing but could also occur if heartwood development had commenced and some proportion of M_c was not sapwood. The ratio of A_c/M_c was not independently measured at the tall site, but studies with older trees of the same species, in similar conditions, suggest that the proportion of sapwood could be expected to be high.

Figure 3.4. Relationships between stem dimensions and total leaf area of trees (Ft) from low, intermediate and tall tree stands at Cloich. Equations of the regression lines are presented in Table 3.5.



a) functional relationship between Mc and Ft with parallel lines for low (+) & intermediate (o) trees together, & tall trees (x)

b) empirical allometric relationship between Dr (cm) and Ft (m²) for low (+) and intermediate (o) trees together

Table 3.5. Regression analysis of relationships between total tree leaf area (F_t) in m^2, and two stem dimensions: stem cross-sectional area at the base of live crown M_c in cm^2 and stem diameter at breast height (D_r) in cm.

a) Parameters of the parallel fitted lines for linear regression of $F_t = a + b\,M_c$ which are shown graphically in Figure 3.4a.

stand (s)	***a*** **(se)**	***b*** **(se)**	**r^2**
L&I combined	0.08^{ns} (2.09)	0.1858 (0.0138)	86
T	9.97 (1.99)		

a1) Analysis of variance for joint regression of all trees versus separate regressions for each stand

Source	**DF**	**SS**	**MS**	**F**	
Overall regression	1	5888.93	5888.93	184.84	***
Intercepts	2	875.59	437.80	13.74	***
Slopes	2	3.57	1.79	0.06	
Residual	30	955.80	31.86		
Total		7723.90	220.68		

a2) Analysis of variance for joint regression of low (L) and intermediate (I) trees versus separate regressions for each stand

Source	**DF**	**SS**	**MS**	**F**	
Overall regression	1	5096.08	5096.08	173.01	***
Intercepts	1	72.75	72.75	2.47	
Slopes	1	2.69	2.69	0.09	
Residual	20	589.11	29.46		
Total	23	5760.62	250.46		

a3) Analysis of variance for joint regression of the L and I stands combined with the tall stand, versus separate regressions

Source	**DF**	**SS**	**MS**	**F**	
Overall regression	1	5888.93	5888.93	182.74	***
Intercepts	1	793.62	793.62	24.63	***
Slopes	1	10.11	10.11	0.31	
Residual	32	1031.23	32.23		
Total	35	7723.90	220.68		

b)Parameters for the linear regression $\ln F_t = \ln a + b \ln D_r$ which is shown graphically in Figure 3.4b.

stand (s)	***b*** **(se)**	***a*** **(se)**	**r^2**
L&I combined	1.2113 (0.0723)	0.701 (0.138)	92

The ratio of A_r/M_r in 27-year-old *Picea sitchensis* at Benmore was reported as 0.66 (McIntosh, 1984) and in 30 year-old-trees at Glentrool as 0.55 and 0.58 in control and fertilized plots respectively (Whitehead *et al.*, 1984). The mean ratio of F_t/A_c for low and intermediate trees at Cloich is best estimated by the slope of the regression of F_t on M_c (0.1858 $m^2\ cm^{-2}$), but was higher (0.27 $m^2\ cm^{-2}$) for the tall tree stand consistent with the positive intercept. While these estimates fall within but near the low end of the range of ratios of F_t/A_r (0.14 - 0.75 $m^2\ cm^{-2}$) reported for a range of conifer species (Waring, *et al.*, 1982), comparisons are of limited interest because these ratios relate to sapwood cross-sectional area measured at a fixed stem height irrespective of the height of the live crown base. Inspection of a regression line of F_t on A_r, forced through the origin for 30-year-old *Picea sitchensis* (Figure 3 in Whitehead *et al.*,1984), suggests a slope of approximately 0.37 $m^2\ cm^{-2}$ and McIntosh (1984), reports mean ratios of 0.29 and 0.26 in 23-year-old and 27-year-old trees of the same species. The similarity of the measured ratio in the tall stand to those reported by McIntosh (*op. cit.*) suggest that A_c was similar to M_c for the tall stand and that heartwood development was not significant, even in the oldest of the three tree stands at Cloich.

D_r was measured annually throughout the experiment, and M_c for tall trees can be calculated directly from it, the equation in Table 3.5, therefore, provides a suitable basis for estimating the leaf area of trees in the tall stand during the experiment. It has a sound physiological basis in relating the cross sectional area of what can be assumed to be largely water conducting tissue at the crown base to leaf area. The low and intermediate stands have the base of the live crown at ground level and accurate measurement of stem cross-sectional area at the stem base was not practical. There was, however, a strong linear relationship between F_t and D_r. Transformation of both D_r and F_t to their natural logarithms was a convenient way of both equalising the variance and employing linear regression to fit a biologically relevant power function appropriate for multiplicative growth processes (Causton, 1985) of the form when unlogged of:

$$F_t = a\, D_r^{\,b} \qquad \text{Equation 3.10}$$

The linear regression of *ln* F_t on *ln* D_r is shown in Figure 3.4b and Table 3.5. This explained more of the variation in the data ($r^2 = 92\%$) than simple linear regression of F_t on D_r ($r^2 = 86\%$) and improved the plot of residuals. Using M_r rather than D_r did not improve the fit.

While differences in the ratio of F_t to A_r have been found in response to thinning (Granier, 1981), possibly related to greater transpiration in more open stands (Whitehead, 1978; Waring, 1983), and, therefore, potentially significant in agroforestry, it is unlikely that differences in relationships would occur over short time periods of a few years. Despite fertilizer addition to some plots McIntosh (1984), found no significant differences in the ratio of F_t to either A_r or D_r over a two year period in 23-year-old and 27-year-old *Picea sitchensis*. It was, therefore, considered reasonable to estimate F_t by applying the regression equations presented in Table 3.5a for the tall stand and Table 3.5b for the low and intermediate stands with measurements of D_r made in 1987 and 1988.

3.3.1.2. Leaf area and crown dimensions after re-spacing

The leaf area of all trees in each plot at the beginning and end of the experiment were calculated from measurements of D_r by applying the regression equation in Table 3.5a for the tall stand and that in Table 3.5b for the low and intermediate stands. The mean F_t for each plot at the beginning of 1986 and 1989, the mean leaf area density within the tree crowns and the relative increase in F_t (R_f) over the experimental period are presented in Table 3.6. Formal statistical comparisons of these means are not appropriate because site and tree height are confounded and the treatment areas are not replicated. Therefore, differences between means cannot be unequivocally attributed to treatments. Variability of F_t within plots was high (CV ranged from 19% to 45%), but there were clear trends in plot means that merit comment. The within plot variability in F_t was higher in the low stand (CV ranges from 30% to 45 %) than in the other stands (CV ranges from 19% to 27%), and decreased over the three year period in the low stand (CV ranges from 39% to 45 % in 1986 and from 30% to 33% in 1989). The increase in F_t over three years was large in all plots. Trees in the low stand approximately doubled in leaf area while those in the intermediate and tall stands increased by about 60% and 45% respectively.

Table 3.6. Tree leaf area (F_t) calculated by applying the regression equation derived from the destructive harvest (Section 3.3.1.1) to measurements of D_r for each tree, and mean leaf area density within crowns ($\underline{L}_{vh}$), assuming a conical crown shape, with one standard deviation (SD), at the start and finish of the experimental period for agroforestry treatment plots at Cloich. R_f is the relative change in F_t over the experimental period $R_f = (F_t\ 1989 - F_t\ 1986) / F_t\ 1986$.

stand	spacing	1986		1989		
	(m)	F_t (m^2) mean (SD)	$\underline{L}_{vh}$ ($m^2\ m^{-3}$) mean (SD)	F_t (m^2) mean (SD)	$\underline{L}_{vh}$ ($m^2\ m^{-3}$) mean (SD)	R_f
L	4	16.00(6.25)	2.58(0.38)	34.01(10.09)	2.46(0.38)	1.126
L	6	13.40(5.84)	2.67(0.38)	28.95(9.44)	2.70(0.30)	1.187
L	8	15.49(7.02)	2.52(0.32)	29.99(10.04)	2.62(0.35)	0.936
I	4	38.31(8.52)	2.22(0.23)	59.59(11.51)	1.92(0.23)	0.555
I	6	33.68(7.96)	2.33(0.25)	55.05(11.40)	2.08(0.24)	0.634
I	8	34.94(8.81)	2.30(0.26)	57.95(11.22)	2.09(0.26)	0.658
T	4	35.63(9.20)	1.28(0.13)	51.19(13.53)	1.24(0.11)	0.437
T	6	36.67(9.17)	1.33(0.13)	54.47(13.36)	1.34(0.12)	0.485
T	8	37.24(10.15)	1.29(0.13)	52.87(13.76)	1.31(0.13)	0.420

Table 3.7. Leaf area index (F) of stands and mean leaf area per tree ($\underline{F_t}$) in October, 1988 estimated from gap fraction data collected using a beam sensor (Section 3.2.3.1.), prototype LI-COR canopy analysers (Section 3.2.3.2.) and hemispherical photographs (Section 3.2.3.3.), for agroforestry treatment plots and a closed canopy control area (2 m tree spacing) in the tall stand at Cloich. R_l is the estimate from the non-destructive method relative to that calculated by applying the regression equation derived from the destructive harvest to measurements of D_r for each tree (Table 3.6).

tree spacing	harvest		beam			LI-COR			photograph		
(m)	$\underline{F_t}$ (m^2)	F	$\underline{F_t}$ (m^2)	F	R_l	$\underline{F_t}$ (m^2)	F	R_l	$\underline{F_t}$ (m^2)	F	R_l
2	42.24	10.56	33.23	8.31	0.79	24.74	6.18	0.59	*	*	*
4	51.19	3.20	78.45	4.90	1.53	27.78	1.74	0.54	21.92	1.37	0.43
6	54.47	1.51	79.99	2.22	1.47	21.94	0.61	0.40	17.86	0.50	0.32
8	52.87	0.82	74.83	1.17	1.41	22.14	0.35	0.42	14.39	0.22	0.27

* hemispherical photographs of sufficient quality for image analysis were not obtained from the closed stand

Lower R_f in the tall stand than the intermediate stand despite similar F_t suggests that pruning the trees may have led to changes in biomass partitioning or crown structure that resulted in reduction of either QFD intercepted per unit of leaf area or light use efficiency within the crowns. These possibilities are investigated through simulation in Section 3.3.2.7. Within the intermediate stand R_f increased with decreasing tree frequency, consistent with larger QFD interception per tree in more open stands. In the low and tall stands R_f increased from the 4 m (625 stems ha^{-1}) to 6 m (278 trees ha^{-1}) tree spacing but was lowest at the 8 m (156 tree ha^{-1}) spacing. Observations at the site suggest that the lower R_f at wide spacings in the low and tall stands may be caused by effects of exposure. Several of the trees in the 8 m spaced plot at the tall stand were windblown during the experimental period and had to be pulled back to a vertical position and held in position with guy ropes.

3.3.1.3. Comparison of non-destructive methods of measuring leaf area

To compare the three methods of obtaining a non-destructive estimate of F_t described in Section 3.2.3., the leaf area index (F) of each plot at the tall site was assessed using each method over a two week period in October, 1988 and compared with the estimate derived by applying the regression equation from the destructive harvest to measurements of D_r for every tree (Table 3.6); additional measurements of D_r for trees in an unthinned part of the tall stand were made to obtain data for a closed forest canopy. Non-destructive estimates of F were converted to F_t by multiplying by the reciprocal of the tree frequency m^{-1} and are presented in Table 3.7. The non-destructive methods include the area index of non-photosynthetic structures within the crown as well as that of leaves, which have been estimated as 10% of the total for *Picea sitchensis* (Wang, Jarvis and Taylor, 1991; based on unpublished data associated with a major study of canopy structure in *Picea sitchensis* by Norman and Jarvis, 1974); and found by destructive harvest and planimetry to account for 14% of the total surface area index in 15 year old *Pinus radiata* growing at a tree frequency of 700 ha^{-1} in Australia (Lang, McMurtrie and Benson, 1991).

In comparison with the destructive harvest, the beam sensor underestimated F by 21% in the closed stand, which has both a high F and a continuous canopy but overestimated F by 40 - 50% in plots with discrete individual tree crowns with spaces between them. Estimates from the LI-COR canopy analysers are similar, but slightly higher, than those from hemispherical photographs. They underestimate F by 40 - 60 % when compared with the destructive harvest, the disagreement increasing with decreasing tree frequency.

Apart from any differences associated with sampling the plots themselves and the inclusion of the area index of non-photosynthetic structures, there are three principal variations in method which may explain different estimates;

- the number and range of solar zenith angles (θ) sampled;
- differences in detecting transmittance at the zenith angles used, and
- the method of averaging transmittance at each zenith angle.

The number and range of zenith angles are predetermined and identical for the LI-COR and hemispherical photographs but are restricted by the zenith angles at which the sun is unobstructed on the days of measurement for the beam sensor. The range of zenith angles was 37° to 62° for the measurements by the beam sensor reported in Table 3.6. A greater range of zenith angles could be expected to improve the accuracy of the estimation (Lang, 1987).

Potential problems in detection of non-interceptance vary according to the sensor used and the characteristics of the canopy. Measurements with the beam sensor under high F could be affected by the threshold level of the detector, and difficulty in maintaining the sensor focused on the solar beam when traversing parts of the transect with zero beam transmittance. Overestimation with the beam sensor under spaced trees is consistent with the sensor not remaining completely focused on the sun when traversing large gaps between trees. Lower estimates from the photographs compared with the LI-COR could be caused by some leaf area being excluded from the photographs either on the negative or when the grey level was set during image analysis.

Theoretically, since the logarithm of one is zero, gross discontinuity in the canopy should be eliminated by the logarithmic average of transmittance of small transect segments employed in the beam sensor method. Errors associated with non-randomness in the arrangement of leaf area should then be restricted to those occurring on the local scale of the segment length. F has been underestimated previously when transmittance is averaged linearly and randomness assumed, as done here with the LI-COR sensors and hemispherical photographs, (Baldocchi *et al.*, 1985; Neumann, Den Hartog and Shaw, 1989). The results obtained here for the closed stand follow the same pattern but involve slightly greater disagreement with direct leaf area measurements, than those obtained by Lang *et al.* (1991), who used a beam sensor to estimate total surface area indices of *Pinus radiata* stands with trees of similar size and leaf area to those at Cloich. In that study, logarithmic and linear averaging of transmittance resulted in estimates of surface area indices of leaves that were on average 86%, and 65% of those obtained by direct measurement. The slightly larger disagreement in the present study in the closed stand is well within what might be expected from differences in departure from non-randomness amongst different tree species and differences in methods of direct measurement of tree leaf areas. Wang *et al.* (1991), found much closer agreement (less than 6% difference) for beam sensor estimates with logarithmic averaging in pole stage *Picea sitchensis*, but a 10% correction factor for the surface area of woody structures was used, and the regression equation for F_t on D_r used for direct comparison was obtained from a different site (McIntosh, 1984). The closer agreement may, therefore, be fortuitous.

With widely spaced individual tree crowns, the concept of leaf area index is not appropriate, since leaf area is confined within discrete tree crowns; methods based on estimation of F do not appear to work well in these circumstances. More recently, the beam sensor has been used to measure leaf area of individual tree crowns by restricting the measurement area to the shadow area of the crown (Lang and McMurtrie, 1992). Estimates obtained in this way of the leaf area of small *Eucalyptus grandis* trees were 14% lower than direct measurements by planimeter. This method may be appropriate for very widely spaced trees in agroforestry stands, especially when they are small, but not where shadow areas of individual trees overlap. The use of hemispherical photographs with logarithmic, as opposed to linear averaging, may be worth further investigation, but some leaf area appears to be excluded from the analysed image and the restriction in the waveband of light measured by detectors used in the beam sensor and LI-COR canopy analyser, to those which are most fully absorbed by leaves, may result in more accurate measurement of gap fraction than is possible with photographic methods. None of the non-destructive methods employed in this study were found to yield estimates of tree leaf area of sufficient accuracy across the range of tree size and frequency required in present research on agroforestry.

3.3.2. Distribution of leaf area within tree crowns

3.3.2.1. Assumptions and definitions

The analysis follows that of Wang *et al.*, (1990) who have shown that; making the following assumptions:

- the distribution of leaf area density in the vertical which will be denoted, $L_v(h)$ is independent of that in the horizontal which will be denoted, $L_h(r)$
- L_h is the same at different heights within the tree crown
- L_h is independent of the azimuth angle

Normalising with respect to total tree leaf area, F_t, crown length, S_c, and crown radius, R_c, at any relative height, h', *i.e.* $R_c(h')$, so that they are all equal to one, then the leaf area density within the crown (L_{vh}) at height, h, and radial distance, r, is given by:

$$L_{vh}\,(h, r) = F_t\, S_c^{-1} R_c(h)^{-2} L'_v(h') L'_h(r') \qquad \text{Equation 3.11}$$

Primes indicate normalised, or relative, properties. $F_t\, S_c^{-1} R_c(h)^{-2}$ is a scaling factor and, $L'_v(h')$ is the relative leaf area density in the vertical; $L'_h(r')$ is the relative leaf area density in the horizontal and, when combined, $L'_v(h')L'_h(r') = L'_{vh}(h',r')$, which is the relative leaf area density within the crown. If both L'_v and L'_h are approximated with beta functions (Sections 3.1.1; 3.3.2.3; 3.3.2.4) then:

$L'_v(h') = B_1 h'^{B_2}(1-h')^{B_3}$, and Equation 3.12
$L'_h(r') = B_4 r'^{B_5}(1-r')^{B_6}$ Equation 3.13

It follows that, when treated independently, the relative height of maximum L'_v *i.e.* (V_x), and the skewness of L'_v *i.e.* (V_s); and the relative radial distance of maximum L'_h *i.e* (H_x) and the skewness of L'_h *i.e* (H_s) are as follows:

$V_x = B_2/(B_2 + B_3)$ Equation 3.14
$V_s = 2(B_2 - B_3)/(B_2 + B_3 + 4)$ Equation 3.15
$H_x = B_5/(B_5 + B_6)$ Equation 3.14
$H_s = 2(B_5 - B_6)/(B_5 + B_6 + 4)$ Equation 3.15

combining the relative vertical and horizontal distributions and, assuming a conical crown shape, the relative height (V'_x) and the relative radial distance at that height (H'_x) at which L'_{vh} is maximum are given by:

$V'_x = B_2/(B_2 + B_3 - 2)$ Equation 3.16
$H'_x = H_x$ (see Equation 3.14).

To describe the needle age structure within the crown, Wang *et al.*, (1990) used age transition functions that defined the relative proportions of leaf area in age class i to that in age class j (where j= i-1). If the vertical and horizontal distributions of leaf area density are $f'_1(h'), f''_1(r'); f'_2(h'), f''_2(r')$ and $f'_3(h'), f''_3(r')$ for leaves in age classes A1, A2 and A3 respectively (Section 3.2.1.2), each of which has different values for the parameters of the beta function describing its distribution, then the age transition functions in the vertical, with parameters labelled C_1, C_2 and C_3, are:

$f'_{21}(h') = f'_2(h') / f'_1(h')$ Equation 3.17
$f'_{32}(h') = f'_3(h') / f'_2(h')$ Equation 3.18

and those in the horizontal, also with parameters labelled C_1, C_2 and C_3, are:

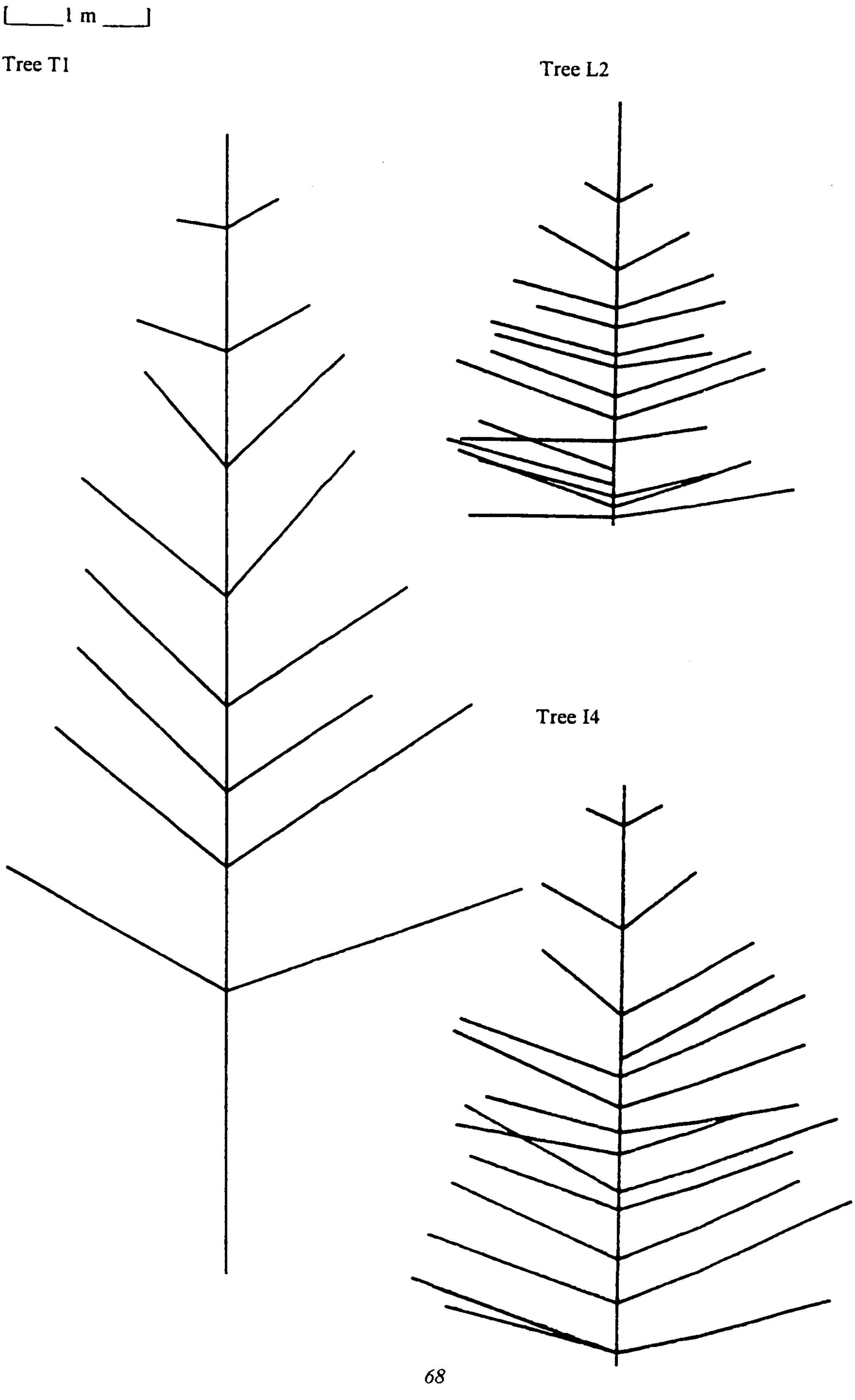
$f''_{21}(r') = f''_2(r') / f''_1(r')$ Equation 3.19
$f''_{32}(r') = f''_3(r') / f''_2(r')$ Equation 3.20

3.3.2.2. Data analysis

Vertical leaf area density distributions have often been calculated by summing leaf area for each whorl and dividing this by the crown volume or crown length occupied by the whorl, which was assumed to be defined by the length of the main stem internode above the point of attachment of the whorl. This was not appropriate for the trees at Cloich since there was significant overlap of branches resulting in parts of branches from different whorls occupying the same vertical position (Figure 3.5). Therefore, to calculate the amount of leaf area in any age class, occurring for any vertical slice of the crown, and within any vertical slice for any interval of radial distance the following procedure was adopted:

> Leaf area for each age class of leaves was summed for each distance class along the sampled branch, (F_{nd}); where n denotes the age class (for A1, n=1; A2, n=2 and A3, n=3), and d is the distance class and using symbols as defined in Section 3.3.1., as follows:
>
> $$F_{nd} = \sum_{1}^{k}(F_s / W_s)W_g. \qquad \text{Equation 3.21}$$
>
> The total leaf area for the whole whorl (calculated as in Equation 3.8) was then distributed in space in the same proportions as that on the sampled branch. This was achieved by scaling the size and number of distance classes on the sampled branch to the mean branch length for the whorl and then assigning to each a leaf area in each age class (F'_{nd}) calculated as follows:
>
> $$F'_{nd} = F_{nd}\, F_w/F_b. \qquad \text{Equation 3.22}$$
>
> The relative height within the crown (h') and the relative radial distance within the crown at that height (r') of the centre of each scaled distance class was then calculated from the measured internode lengths, the mean branch angle for the whorl, and the distance along the branch of each scaled distance class. For alternate whorls and interwhorls from which a branch sub-sample was not taken, the sampled branch from the whorl immediately above was

Figure 3.5. Primary branch structure of typical trees from the tall (T), intermediate (I) and low (L) tree stands at Cloich. Diagrams show two branches sampled at each whorl drawn from measurements made of their point of attachment, angle and length (Section 3.2.1.2). Scale = 1:40.



used. In this way all of the leaf area in the crown was appropriately assigned to points of h' and r'.

Calculation of relative leaf area density in the vertical (L'_v)

For each tree the leaf area was then summed for each of 20 equal divisions of h'. The relative vertical leaf area density (L'_v) assigned to the mid point of the h' interval, and normalised with respect to crown length and the total leaf area within the crown, was then:

$$L'_v = X/F_t\,(h'_2 - h'_1) \qquad \text{Equation 3.23}$$

where: X is the sum of the leaf area over the h' interval; and, h'_1, h'_2 are the relative heights at the beginning and the end of the h' interval, respectively.

Calculation of relative leaf area density in the horizontal (L'_h)

For each relative height interval the leaf area was summed within each of 15 equal divisions of r'. The relative horizontal leaf area density (L'_h) assigned to the mid point of the r' interval, and normalised with respect to crown area and the total leaf area within the vertical crown slice, was then:

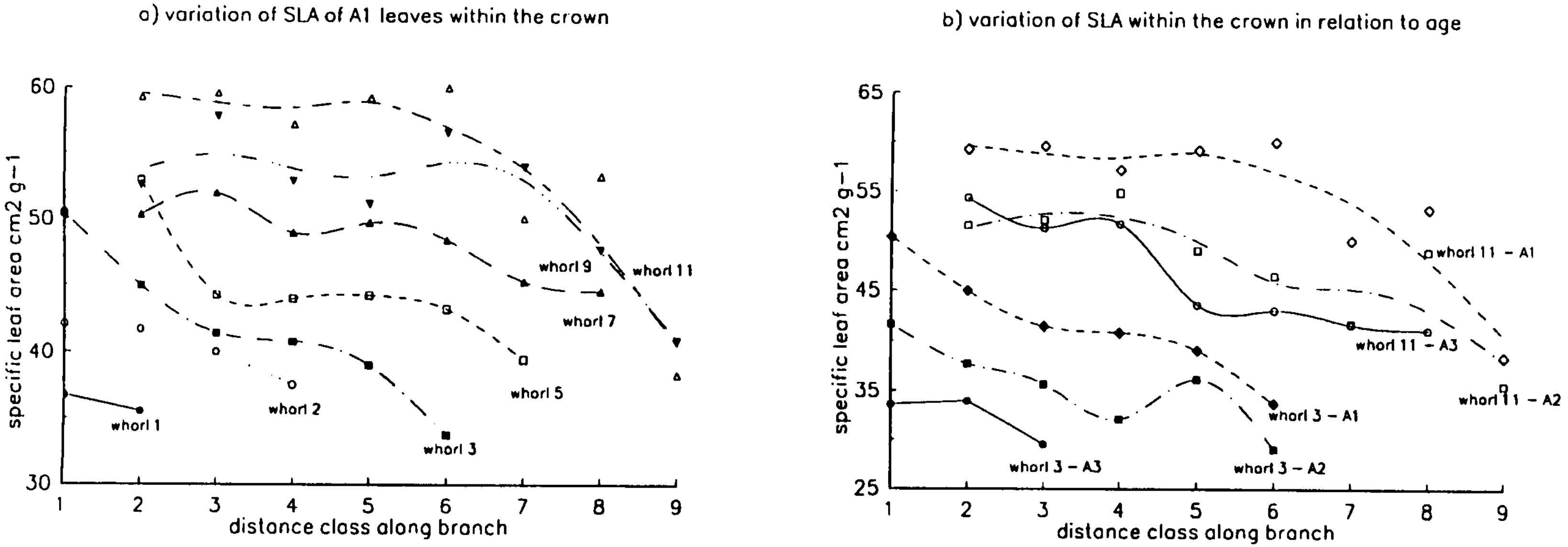
$$L'_h = Y/F_v\,(r'^2_2 - r'^2_1) \qquad \text{Equation 3.24}$$

where: Y is the sum of the leaf area over the r' interval; F_v is the sum of the leaf area in the vertical slice, and, r'_1, r'_2 are the relative radial distances at the beginning and the end of r' interval, respectively.

3.3.2.3. Variation of specific leaf area within crowns

The systematic dissection and measurement of leaf area (Sections 3.2.1.2 and 3.2.1.3) resulted in a direct measurement of leaf area and its dry mass for each age class of leaves in each distance class along a sampled branch in each sampled whorl. This provided a detailed profile of specific leaf area

Figure 3.6. Variation in specific leaf area (SLA) within intermediate tree crowns from the destructive harvest at Cloich. Points represent mean values of SLA at each distance by age category, for the 12 sampled trees from the stand and are connected by locally weighted regression lines. Whorls are numbered sequentially from the top of the crown downwards, age classes of leaves and the details of tree dissection are given in Section 3.2.1.



(SLA) in relation to the vertical and horizontal position of leaves, which showed similar trends in all trees. The variation of SLA in relation to the prevailing QFD conditions within the crown is most clearly illustrated in the current year's growth since this occurs throughout the crown. The mean SLA of leaves less than one year old (A1) in different whorls and horizontal distance classes within the crown are shown for the intermediate trees in Figure 3.6a. The SLA of A1 leaves varied from 35 to 60 $cm^2 g^{-1}$ within the crown, and although highly variable, increased with vertical depth in the canopy, and decreased along branches from the trunk outwards. This is consistent with leaves emerging in shaded parts of the canopy having a higher specific leaf area, which may be an acclimation to lower QFD (Lewandowska and Jarvis, 1977; Leverenz and Jarvis, 1979) or a response to lower QFD as a result of a lower starch content in shaded leaves. It is also apparent that the SLA was smaller in older leaves than younger leaves, in the same position within the crown (Figure 3.6b). While this would be consistent with older leaves having developed in less shaded conditions than those that prevailed when the younger leaves developed, it could also be a result of the accumulation of mass in older leaves as new phloem is laid down each year. If differences in the SLA are, to some extent, an acclimation to the prevailing QFD conditions when leaves emerge, then younger leaves developing within the crown are likely to be more acclimated to the prevailing QFD than older leaves that developed in different conditions. While some leaves in *Picea sitchensis* may be retained for up to seven years (Ford, 1982), more than a third of the total leaf population was less than one year old in all three stands at Cloich and only 20% to 36% of total leaf area was more 2 years old (Table 3.8).

Table 3.8. Proportions of leaf area of different age classes within tree crowns at Cloich. Numbers are means for 12 trees in each stand. A1 = leaves < 1 year old; A2 = leaves >1 and < 2 years old; and A3 = leaves > 2 years old.

stand	A1	A2	A3
L	0.46	0.34	0.20
I	0.38	0.34	0.28
T	0.34	0.30	0.36

The range of values for SLA at Cloich are similar to those reported for 20-year-old *P. sitchensis* at 4 000 trees ha^{-1} in north-east Scotland (Norman and Jarvis, 1974) and 16 to 18-year-old trees at a similar but slightly lower frequency in southern Scotland (Ford, 1982). While Norman and Jarvis (*op cit.*) found that SLA decreased towards the top of the canopy and with increasing age at each canopy height, Ford (*op cit.*) reported that 'needles on branches lost mass with increasing age' an observation which was supported by a table showing higher SLA for older branch segments at the same canopy height. This apparent conflict occurred because the age of Ford's branch segment refers to the age of the main branch stem internode rather than the leaves on it, which were of different ages. Ford's branch segments are analogous to the distance classes in the present study. It is not inconsistent for the SLA of leaves, of different ages, to be higher on older branch segments that are also closer to the trunk and, therefore, more heavily shaded: the SLA would, none-the-less, increase with age within each segment. One of the features of the *P. sitchensis* crowns in the present study, is that new leaf area developed throughout the crown volume, and this is consistent with maintaining a large leaf area per tree (Section 3.3.2.5).

3.3.2.4. Vertical distribution of leaf area density

The relative leaf area density in the vertical (L'_v) for 20 equal intervals of relative height (h') were calculated for each tree and the mean value of L'_v for the 12 trees in each stand was plotted against the h' of the mid point of the interval. The resulting distribution could be approximated by a beta function which was fitted for each stand separately for total leaf area and for each age class separately using the non-linear regression facilities in Genstat 5 (Genstat 5 Committee, 1989). The parameters of the fitted beta functions are given in Table 3.9. and are shown graphically in Figure 3.7.

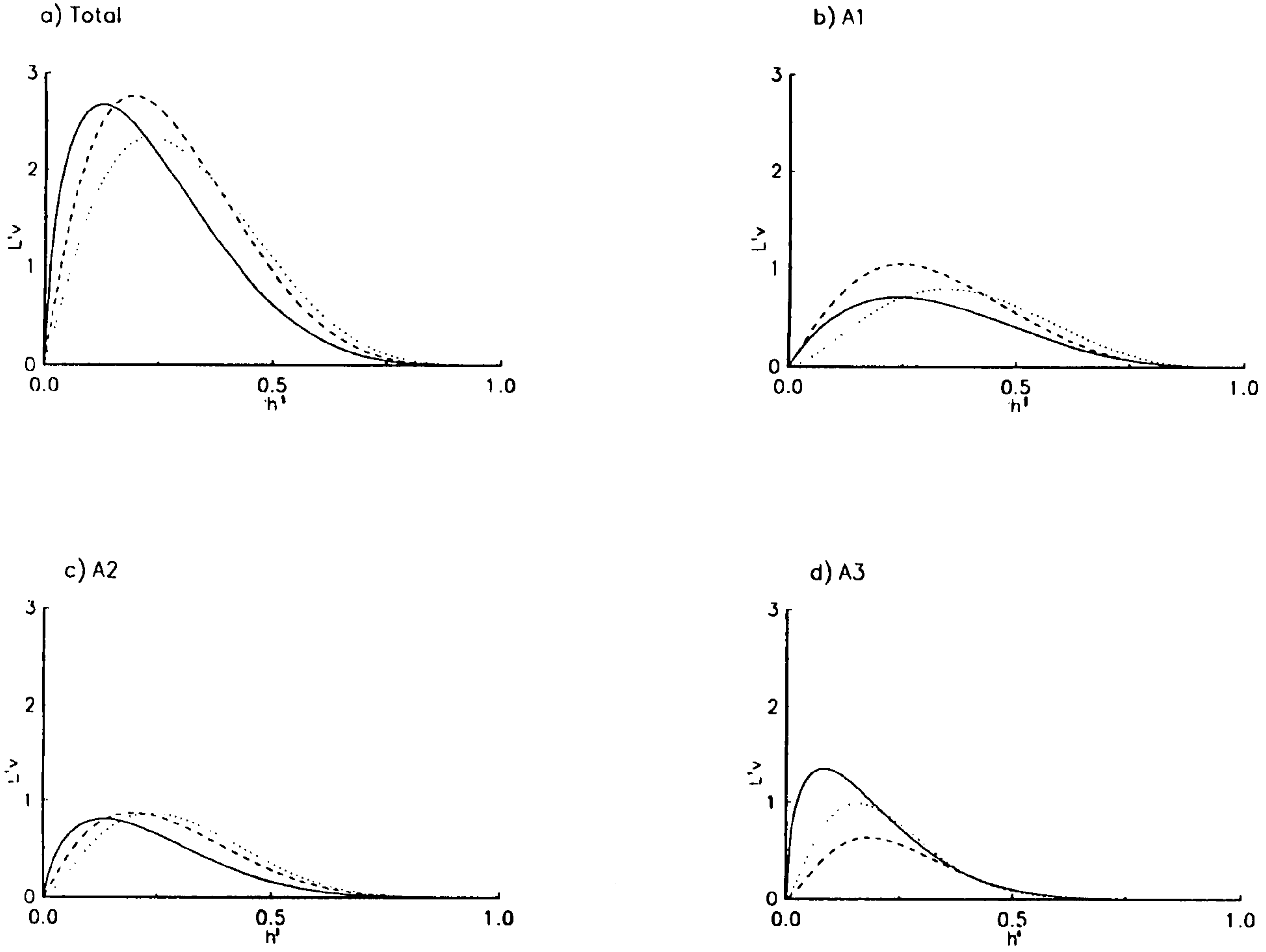
3.3.2.4.1. Variation in L'_v within and between trees

Previous research has shown considerable but non-systematic variability in the distribution of L'_v between trees and significant differences between stands of different density or subject to different

Table 3.9. Parameters of vertical (L'_v) and horizontal (L'_h) relative leaf area density distributions for leaves of different ages within tree crowns for three tree stands at Cloich. Beta functions were fitted to mean data from 12 trees for each stand. See text for details of procedures and definitions of treatments and symbols.

stand	dimension	age class	B_1	SE	B_2	SE	B_3	SE	r^2	V_x	V_s
L	V	T	37.20	15.60	1.10	0.17	4.30	0.55	84.90	0.20	-0.68
L	V	A1	14.82	5.44	1.17	0.16	3.61	0.42	93.90	0.24	-0.56
L	V	A2	15.34	6.91	1.14	0.18	4.64	0.61	93.30	0.20	-0.72
L	V	A3	34.60	34.00	1.54	0.38	6.95	1.48	85.40	0.18	-0.87
			B_4		B_5		B_6			H_x	H_s
L	H	T	12.00	21.80	0.62	0.81	1.86	1.87	24.30	0.25	-0.38
L	H	A1	5.15	8.29	0.89	0.88	1.46	1.30	24.20	0.38	-0.18
L	H	A2	6.50	16.10	0.75	1.09	2.35	2.72	14.80	0.24	-0.45
L	H	A3	7.10	16.20	0.71	0.85	3.80	3.36	49.90	0.16	-0.73
			B_1		B_2		B_3			V_x	V_s
I	V	T	36.40	11.90	1.17	0.14	3.93	0.40	95.70	0.23	-0.61
I	V	A1	22.10	10.40	1.77	0.25	3.40	0.44	92.60	0.34	-0.36
I	V	A2	29.70	12.10	1.54	0.18	4.88	0.49	96.00	0.24	-0.64
I	V	A3	65.40	35.10	1.51	0.20	8.18	0.90	95.80	0.16	-0.97
			B_4		B_5		B_6			H_x	H_s
I	H	T	5.45	0.40	0.28	0.03	1.57	0.08	64.46	0.15	-0.44
I	H	A1	1.72	0.71	0.86	0.27	0.85	0.26	62.90	0.50	0.00
I	H	A2	2.68	1.88	0.44	0.29	1.81	0.79	55.10	0.20	-0.44
I	H	A3	6.73	5.01	0.49	0.25	3.80	1.26	76.30	0.11	-0.80
			B_1		B_2		B_3			V_x	V_s
T	V	T	15.41	3.36	0.58	0.08	4.09	0.36	97.50	0.12	-0.81
T	V	A1	6.93	2.54	0.99	0.16	3.15	0.42	92.20	0.24	-0.53
T	V	A2	6.96	1.75	0.72	0.09	4.67	0.42	97.30	0.13	-0.84
T	V	A3	8.44	0.44	0.53	0.01	5.97	0.13	91.00	0.08	-0.99
			B_4		B_5		B_6			H_x	H_s
T	H	T	4.36	1.11	0.15	0.10	1.32	0.29	87.20	0.10	-0.43
T	H	A1	1.97	0.80	0.91	0.25	1.04	0.28	70.70	0.47	-0.04
T	H	A2	4.91	2.19	1.01	0.23	2.15	0.41	86.70	0.32	-0.32
T	H	A3	3.69	0.14	0.13	0.01	2.76	0.09	81.50	0.04	-0.76

Figure 3.7. Plots of beta functions describing the distribution of relative leaf area density in the vertical (L'_v) for the low (------), intermediate (······) and tall (——) stands at Cloich. The functions were fitted to mean L'_v of 12 trees for each of 20 equal divisions of relative tree height. Distributions are shown for a) L'_v for all leaves together (T) b) L'_v for leaves < 1 year old (A_1) c) L'_v for leaves 1< 2 years old (A_2) and d) L'_v for leaves > 2 years old (A_3) Parameters of the fitted functions are given in Table 3.9.



irrigation and fertilizer treatments (Kellomaki *et al.*, 1980; Wang *et al.*, 1990). The sampling strategy in the present research (Section 3.2.1.2.) was, therefore, designed to obtain a description of L'_v for each stand with replication of leaf area measurements on branches between rather than within trees. Consequently one branch was randomly sampled for leaf area measurement on alternate whorls in each tree. This provided a stratified, random sample of branches for each stand and made it possible to calculate a full vertical profile of leaf area distribution for each tree from measurements of the fresh mass of whorls and branch lengths and angles (Section 3.3.2.2). Figure 3.8 shows the vertical leaf area density for each relative height interval for all trees, the mean value for each interval in each stand and the beta function fitted to the mean data. The considerable scatter for each relative height interval is caused both by variations within and between trees. The data for individual trees (typical trees from each stand are shown in Figure 3.8) are jagged indicating some gaps in the vertical canopy profile, and this is consistent with photographs taken of each tree before dissection. Fitting a beta function to data from individual trees produces a smooth curve which can be used to make comparisons amongst trees. The parameters of beta functions for the leaf area density of all leaves together for individual trees are shown in Table 3.10. The r^2 values are an indication of the variability within the tree about the fitted function. While a few individual trees in the low stand have a low r^2 (< 50), in the vast majority of trees more than 60% of variation is explained by the fitted line and for about half of the trees $r^2 > 80\%$, indicating that the fitted functions are a reasonable approximation. The variability of individual parameters between trees is high. The relative magnitude of B_2 and B_3 control the location of the maximum leaf area density and the skewness of the distribution and are much less variable than B_1, which is a scaling factor that, excluding two extreme observations, varied by a factor of 10^3. Within each stand V_x and V_s varied considerably (CV 20% to 40%), more so in the low trees. Overall V_x varied from 0.08 to 0.40, and was typically around 0.2 in the low and intermediate trees and around 0.15 for the tall trees, so that the maximum leaf area density in the vertical was always in the lower half of the crown and generally in the lowest quarter. In order to explore the possibility of systematic variation in V_x and V_s with crown size, correlation coefficients with F_t, S_c and R_c were examined separately for the low and intermediate stands. This was not done for the tall stand because, lower branches had been

Figure 3.8. Plots in the top three graphs show measured L'_v (——) for selected individual trees for the low (a), intermediate (b), and tall (c) tree stands at Cloich, and the beta functions fitted to these data (------). Parameters of fitted functions are given in Table 3.10. Lower three graphs show measured L'_v (x) from all trees in each stand, the mean stand value of L'_v for each of 20 divisions of relative height (bar) and the beta function fitted to these data (——) for the low (d), intermediate (e) and tall (f) tree stands at Cloich. Parameters of the fitted functions are given in Table 3.9.

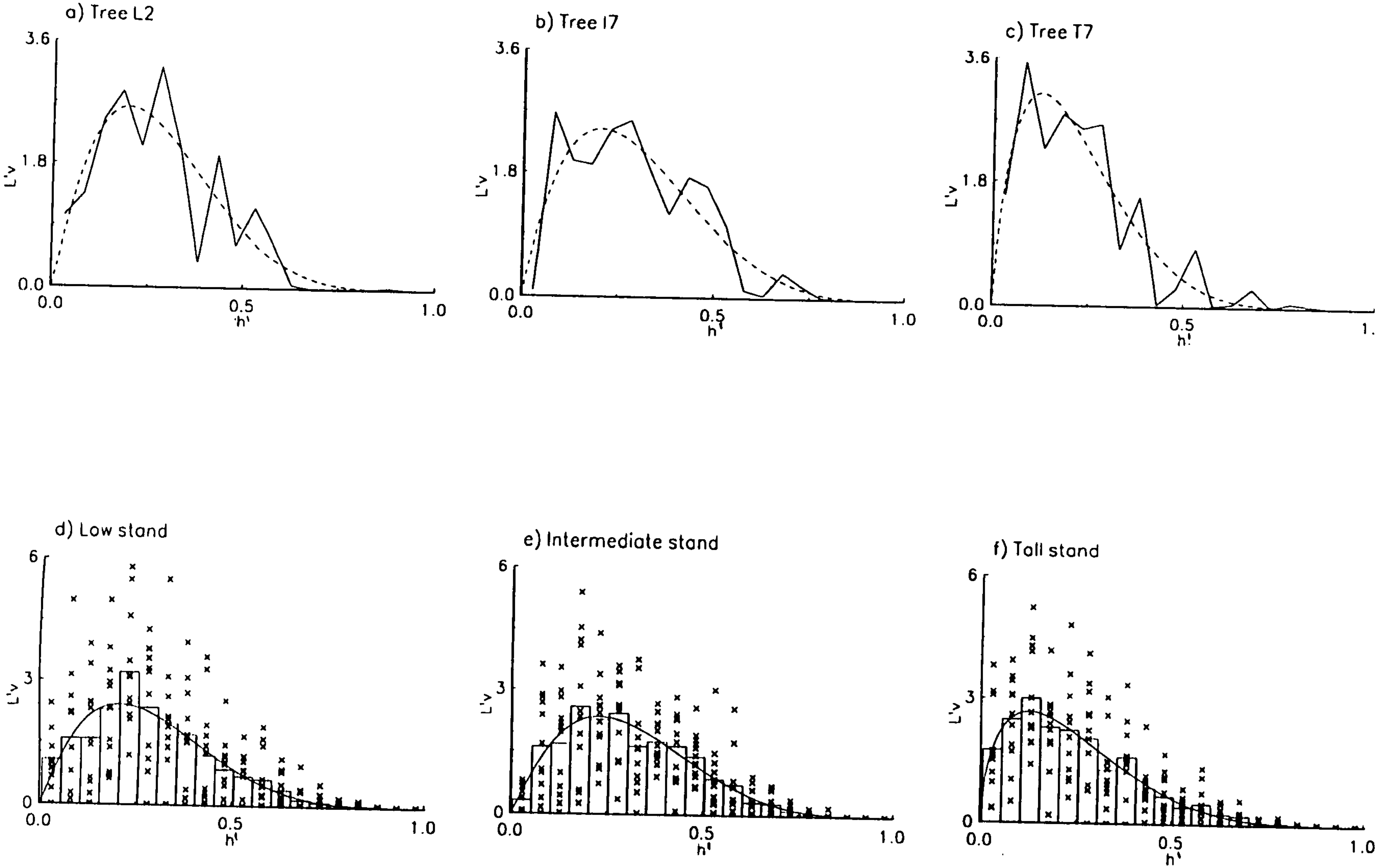


Table 3.10. Paramaters of beta functions fitted to the vertical distribution of relative leaf area denisty (L'_v) within individual tree crowns from the destructive harvest at Cloich.

stand	tree number	B_1	SE	B_2	SE	B_3	SE	r^2 (%)	V_x	V_s
L	1	$9.32\text{x}10^{10}$	$2.96\text{x}10^{11}$	11.80	3.61	26.64	4.08	95.0	0.31	-0.70
L	2	48.00	40.00	1.15	0.34	4.73	1.14	80.4	0.20	-0.72
L	3	35.80	56.90	1.04	0.64	4.30	2.15	52.4	0.20	-0.70
L	4	34.00	73.70	1.22	1.01	3.03	2.42	46.1	0.29	-0.44
L	5	$4.13\text{x}10^3$	$4.75\text{x}10^3$	2.61	0.44	12.40	1.86	94.9	0.17	-0.99
L	6	63.10	74.40	1.02	0.41	6.42	2.10	74.3	0.14	-0.94
L	7	59.00	112.00	0.95	0.64	6.93	3.65	45.9	0.12	-0.99
L	8	24.30	44.70	0.86	0.71	4.17	2.65	29.9	0.17	-0.73
L	9	670.00	$1.33\text{x}10^3$	2.66	0.96	6.48	2.17	73.2	0.29	-0.58
L	10	5.77	2.45	0.24	0.15	2.68	0.66	85.9	0.08	-0.71
L	11	$8.33\text{x}10^4$	$3.55\text{x}10^4$	6.01	2.47	9.16	3.72	60.5	0.40	-0.33
L	12	51.80	60.50	1.20	0.47	4.88	1.59	67.0	0.20	-0.73
I	1	175.00	254.00	1.35	0.51	8.40	2.64	71.6	0.14	-0.99
I	2	132.00	228.00	1.83	0.80	5.00	1.95	57.6	0.27	-0.59
I	3	$2.22\text{x}10^3$	$2.28\text{x}10^3$	2.48	0.41	10.85	1.58	96.1	0.19	-0.97
I	4	109.00	149.00	2.28	0.79	3.52	1.16	66.2	0.39	-0.25
I	5	31.30	39.10	1.04	0.52	3.95	1.61	63.3	0.21	-0.65
I	6	10.20	11.10	0.60	0.44	2.69	1.38	45.3	0.18	-0.57
I	7	28.40	18.60	0.99	0.27	3.87	0.85	83.0	0.20	-0.65
I	8	969.00	$2.91\text{x}10^3$	2.18	1.18	9.69	4.60	63.1	0.18	-0.95
I	9	108.40	92.50	1.48	0.35	5.71	1.16	85.8	0.21	-0.76
I	10	28.70	35.00	1.35	0.62	2.86	1.17	53.6	0.32	-0.37
I	11	$2.13\text{x}10^3$	$4.81\text{x}10^3$	3.63	1.21	6.77	2.16	83.0	0.35	-0.44
I	12	69.70	64.30	1.52	0.42	4.45	1.06	86.2	0.25	-0.59
T	1	9.27	5.85	0.37	0.21	3.64	1.11	82.3	0.09	-0.82
T	2	3.65	0.26	0.48	0.17	2.69	0.31	92.2	0.15	-0.61
T	3	57.10	75.00	1.40	0.59	4.27	1.54	61.7	0.25	-0.59
T	4	35.70	25.80	0.90	0.26	5.27	1.18	83.3	0.15	-0.86
T	5	272.00	106.00	1.61	0.14	8.25	0.66	98.6	0.16	-0.96
T	6	14.30	10.80	0.72	0.31	3.14	0.99	69.8	0.19	-0.62
T	7	33.00	21.80	0.78	0.23	5.61	1.19	86.5	0.12	-0.93
T	8	13.25	4.46	0.55	0.12	3.83	0.53	97.4	0.13	-0.78
T	9	3.54	0.50	0.81	0.46	2.40	0.57	73.5	0.25	-0.44
T	10	$3.82\text{x}10^3$	$8.17\text{x}10^3$	2.50	0.98	12.16	4.27	78.0	0.17	-0.99
T	11	4.03	0.89	0.32	0.12	3.08	1.10	54.0	0.09	-0.75
T	12	19.00	11.00	0.68	0.20	4.36	0.93	92.7	0.13	-0.82

removed during pruning, and there was, therefore, no reason to expect L'_v to be related to the remaining crown size. The correlation coefficients (Table 3.11) were generally negative, but only significant for S_c for intermediate trees. This suggests that within the intermediate tree stand, the maximum leaf area density of tall trees was at a lower relative height and the vertical distribution was more heavily skewed towards the base of the crown. This is consistent with trees with large internode extensions in the upper part of the crown on trees with a large leaf area on lower branches. Because of the small sample sizes, (there were 10 degrees of freedom for testing the significance of r within each stand), r was sensitive to individual pairs of data. Since r was negative, except for S_c in the low stand, a general trend of lower V_x and more pronounced skewness towards the crown base in larger trees may occur but further research would be required to confirm this. Clearly much of the variation in V_x and V_s can not be systematically associated with other crown variables and may be caused by random genetic differences amongst trees and microenvironmental variations within sites. The larger variability in V_x amongst trees in the low tree stand is consistent with greater heterogeneity of site conditions.

Table 3.11. Correlation coefficients (r) relating the location of maximum leaf area density in the vertical (V_x) and the skewness of the vertical leaf area density distribution (V_s) within crowns of trees in the low (L) and intermediate (I) stands at Cloich to their overall crown dimensions. F_t is the total leaf area within the crown; R_c the mean crown radius at the crown base and S_c the crown length. Significance levels $^{+}$=10%; *=5%; **=1%

	F_t		R_c		S_c	
	L	I	L	I	L	I
V_x	-0.098	-0.451	-0.147	-0.352	0.308	-0.763**
V_s	-0.302	-0.335	-0.426	-0.544	0.917	-0.749**

3.3.2.4.2. Variation in L'_v between stands

The distributions of vertical leaf area density for all leaves together and for each age class separately for the three stands at Cloich are shown graphically in Figure 3.7 and the parameters of the corresponding functions are given in Table 3.9. In all stands the location of the maximum leaf area density is lower for older leaves and located within the lowest quarter of the crown for all leaves together. The vertical distribution of leaf area density is heavily skewed towards the base of the crown in all stands, more so for older leaves, and there is very low density of leaf area in the top quarter of the crown. The intermediate trees have higher V_x and less skewed distribution than the low trees, mainly because of the preponderance of the younger leaves. This may reflect changes that occur in relation to stand growth, more mature stands that have been measured have had much less skewed vertical distributions and higher V_x (Norman and Jarvis, 1974; Wang, 1988). Lower V_x and more pronounced skewness towards the crown base can be expected where leaf area has been more frequently measured rather than inferred from distributions of leaf biomass (e.g. Kellomaki *et al.*, 1980) because specific leaf area can vary by a factor of two from the top to the bottom of the crown (Section 3.3.2.3). The tall trees in the present study were pruned and as a result V_x is lower and the distribution more heavily skewed to the crown base than in the other stands, as would be expected. The trees in the present study, in contrast to previous results from stands where canopy closure has occurred and lower branches are in the process of being shed, all had live crowns right down to the base. This is consistent with V_x being lower and V_s more negatively skewed. Since in agroforestry trees are characteristically grown in open conditions, and pruned for silvicultural reasons, this trend can be expected to occur more generally.

3.3.2.5. Horizontal distribution of leaf area density

The relative leaf area density in the horizontal (L'_h) for 15 equal intervals of relative radial distance (r') were calculated for each tree and the mean value of L'_h for the 12 trees in each stand was plotted against the mid point of the relative radial distance interval. The resulting distribution, although not as regular as in the vertical was also approximated by a beta function which was fitted for each stand separately for total leaf area and for each leaf age class separately, as for the vertical distribution. The parameters of the fitted functions are given in Table 3.9. and the functions are shown graphically in Figure 3.9.

Figure 3.9. Plots of beta functions describing the distribution of relative leaf area density in the horizontal (L'_h) for the low (------), intermedicate (·······) and tall (——) stands at Cloich. The functions were fitted to mean L'_h of 12 trees for each of 15 equal divisions of relative tree height. Distributions are shown for a) L'_h for all leaves together (T) b) L'_h for leaves < 1 year old (A_1) c) L'_h for leaves 1< 2 years old (A_2) and d) L'_h for leaves > 2 years old (A_3). Parameters of the fitted functions are given in Table 3.9.

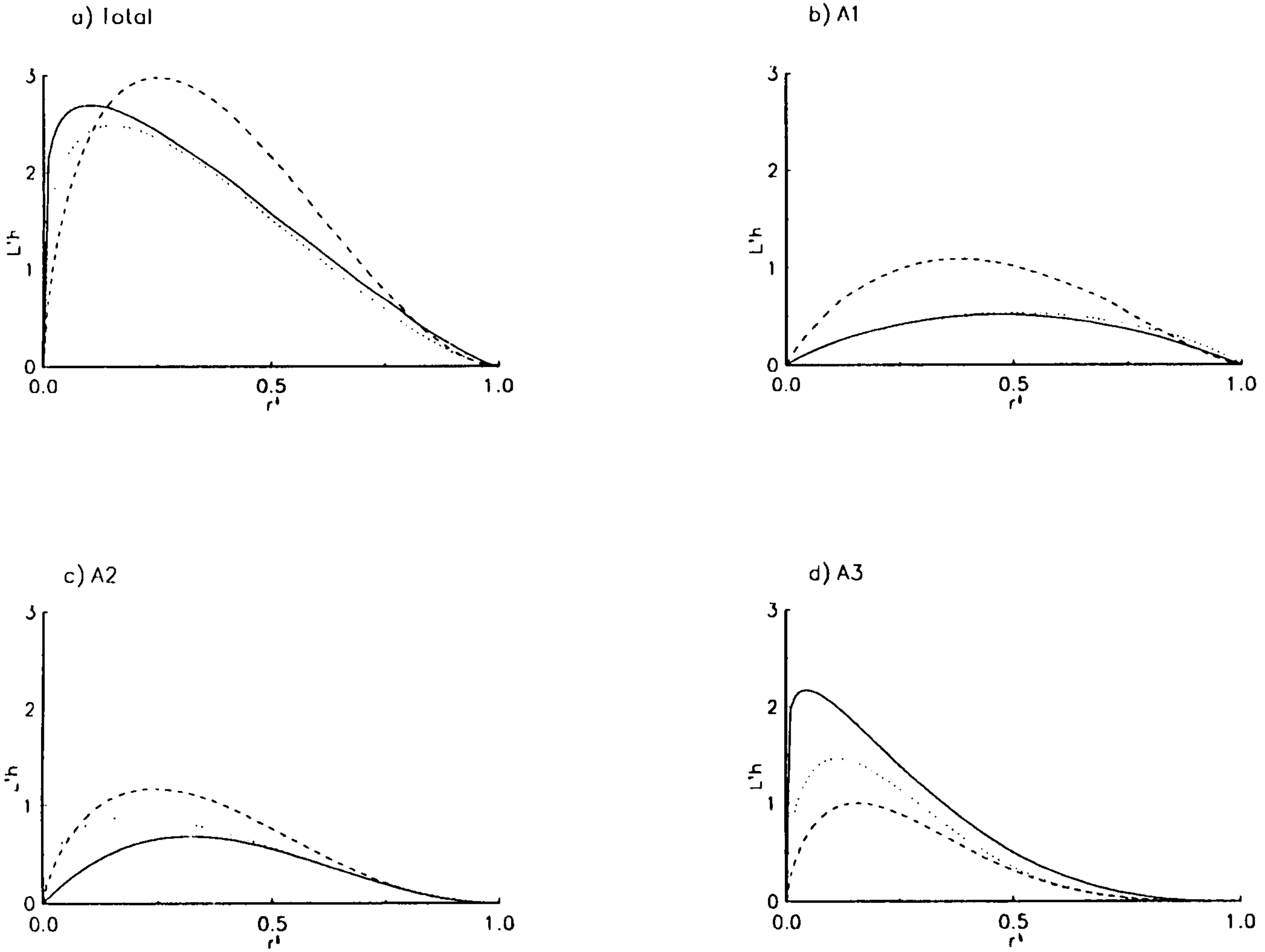


Table 3.12. Paramaters of beta functions fitted to the horizontal distribution of relative leaf area denisty (L'_h) within individual tree crowns from the destructive harvest at Cloich. Where B_5 is negative the function is exponential and H_x does not exist.

stand	tree number	B_4	SE	B_5	SE	B_6	SE	r^2 (%)	H_x	H_s
L	1	2.49	0.31	-0.35	0.05	1.23	0.14	90.9	*	-0.65
L	2	8.20	10.50	0.44	0.52	1.88	0.00	55.3	0.19	-0.46
L	3	5.05	7.38	0.24	0.58	1.42	1.64	69.0	0.14	-0.42
L	4	4.86	7.40	0.34	0.65	1.33	1.55	14.0	0.20	-0.35
L	5	8.72	7.17	0.59	0.38	1.60	0.80	54.0	0.27	-0.33
L	6	3.62	3.19	0.38	0.43	0.89	0.73	11.0	0.30	-0.19
L	7	14.00	20.10	0.69	0.67	1.83	1.42	28.0	0.28	-0.35
L	8	10.80	14.10	0.41	0.51	2.08	1.58	36.8	0.16	-0.52
L	9	1.41	1.74	-0.49	0.51	0.66	1.15	79.4	*	-0.55
L	10	3.52	2.29	-0.02	0.26	0.88	0.65	57.9	*	-0.37
L	11	5.44	5.18	0.45	0.44	1.29	0.89	23.8	0.26	-0.29
L	12	12.20	17.60	0.58	0.62	1.97	1.56	27.7	0.23	-0.42
I	1	2.57	0.86	-0.12	0.13	0.90	0.36	88.0	*	-0.42
I	2	12.60	11.50	1.07	0.51	1.73	0.74	51.9	0.38	-0.19
I	3	4.00	2.31	0.18	0.23	1.15	0.61	48.7	0.13	-0.36
I	4	4.45	5.00	0.30	0.48	1.24	1.13	11.2	0.19	-0.34
I	5	3.61	3.85	0.31	0.49	0.97	0.95	5.0	0.24	-0.25
I	6	10.90	19.20	0.45	0.66	2.57	2.39	12.4	0.15	-0.60
I	7	14.20	16.90	0.95	0.61	1.97	1.08	39.5	0.33	-0.30
I	8	1.99	1.44	-0.23	0.28	0.46	0.63	40.0	*	-0.32
I	9	4.09	0.65	-0.17	0.05	1.49	0.22	98.9	*	-0.62
I	10	11.10	13.20	0.63	0.53	1.92	1.24	41.4	0.25	-0.39
I	11	2.82	1.27	0.14	0.18	0.95	0.44	52.9	0.13	-0.32
I	12	13.44	9.08	0.46	0.25	2.82	0.96	69.7	0.14	-0.65
T	1	6.49	2.61	0.44	0.18	1.50	0.41	75.8	0.23	-0.36
T	2	5.32	2.20	0.21	0.16	1.55	0.49	75.7	0.12	-0.46
T	3	5.72	0.98	0.11	0.20	2.04	0.16	66.2	0.05	-0.63
T	4	4.68	2.78	0.24	0.24	1.34	0.65	52.2	0.15	-0.39
T	5	13.40	25.30	0.99	1.08	1.79	1.52	24.9	0.36	-0.24
T	6	3.37	2.92	0.25	0.38	0.92	0.78	14.0	0.21	-0.26
T	7	6.29	6.28	0.50	0.46	1.42	0.96	24.7	0.26	-0.31
T	8	8.50	10.30	0.53	0.52	1.87	1.32	25.2	0.22	-0.42
T	9	5.22	1.59	-0.08	0.11	1.82	0.40	98.7	*	-0.66
T	10	3.15	1.89	0.06	0.23	0.98	0.63	44.0	0.06	-0.37
T	11	20.40	27.30	0.95	0.63	2.52	1.38	40.4	0.27	-0.42
T	12	14.10	24.50	0.62	0.71	2.57	2.13	16.7	0.20	-0.54

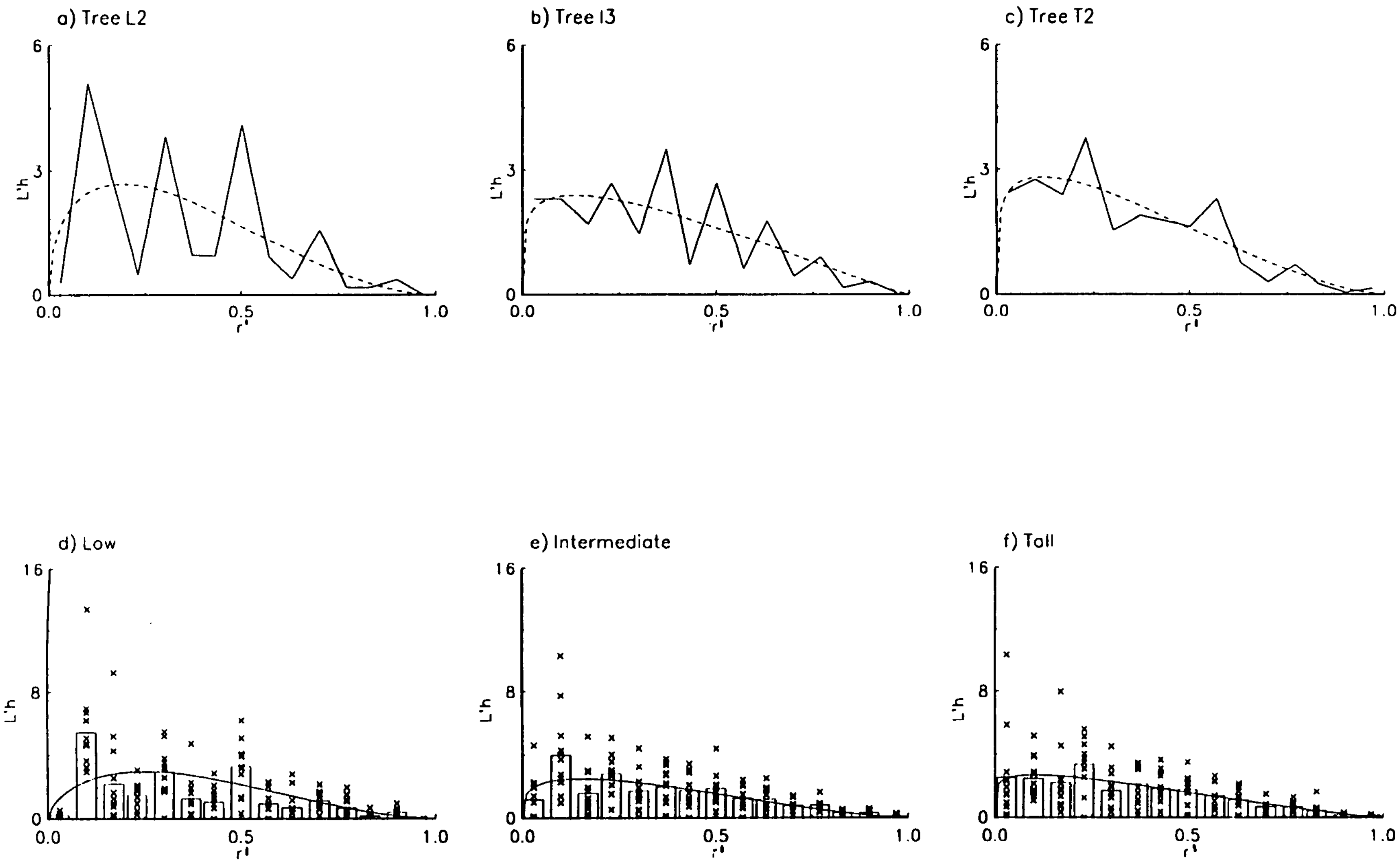
3.3.2.5.1. Variability in L'_h within and between trees

The beta functions fitted less well for the horizontal distribution of total leaf area density than for the vertical: less than 50% of the variation in the data was explained by the fitted curve in about half of the trees, and in several trees the fitted value of B_5 was negative so that the curve had an exponential form (Table 3.12). The lower r^2 values were associated with trees which had high leaf area density both close to the trunk and about half way along the crown radius (distributions in typical trees and mean values of L'_h in each relative radial distance interval for each stand are shown in Figure 3.10). Because area increases with the square of the radial distance, high values of leaf area density close to the tree trunk would be expected. Photographs of the individual sampled branches, however, generally show the largest number of shoots towards the centre of the branch in the middle of the crown, and somewhat further out in branches from the lower part of the crown. Since the distance class length was fixed, trees with a large crown radius have a correspondingly large number of sample points. Similarly, lower branches have more sample points than upper branches. This results in greater confidence in the horizontal distributions from larger trees than from smaller trees. For the intermediate and tall trees H_x and H_s are more variable than corresponding parameters in the vertical distribution and correlation coefficients for both H_x and H_s with respect to crown dimensions in the low and intermediate stands are positive although only significantly so (5% level) for F_t with H_x in the intermediate stand and R_c with H_x in the low stand (Table 3.13). However, positive correlations for H_x and H_s with F_t were significant at the 10% level in both stands providing some evidence that trees with a large leaf area may have a more symmetrical horizontal distribution of leaf area density than trees with a small leaf area.

Table 3.13. Correlation coefficients (r) relating the location of maximum leaf area density in the horizontal (H_x) and the skewness of the horizontal leaf area density distribution (H_s) within crowns of trees in the low (L) and intermediate (I) stands at Cloich to their overall crown dimensions. F_t is the total leaf area within the crown; R_c the mean crown radius at the crown base and S_c the crown length. Significance levels $^{+}$=10%; *=5%; **=1%

	F_t		R_c		S_c	
	L	I	L	I	L	I
H_x	0.554^{+}	0.629^{*}	0.757^{**}	0.489	0.321	0.348
H_s	0.525^{+}	0.541^{+}	0.527^{+}	0.361	0.442	0.292

Figure 3.10. Plots in the top three graphs show measured L'_h (——) for selected individual trees for the low (a), intermediate (b), and tall (c) tree stands at Cloich, and the beta functions fitted to these data (------). Parameters of fitted functions are given in Table 3.12. Lower three graphs show measured L'_h (x) from all trees in each stand, the mean stand value of L'_h for each of 15 divisions of relative height (bar) and the beta function fitted to these data (——) for the low (d), intermediate (e) and tall (f) tree stands at Cloich. Parameters of the fitted functions are given in Table 3.9.



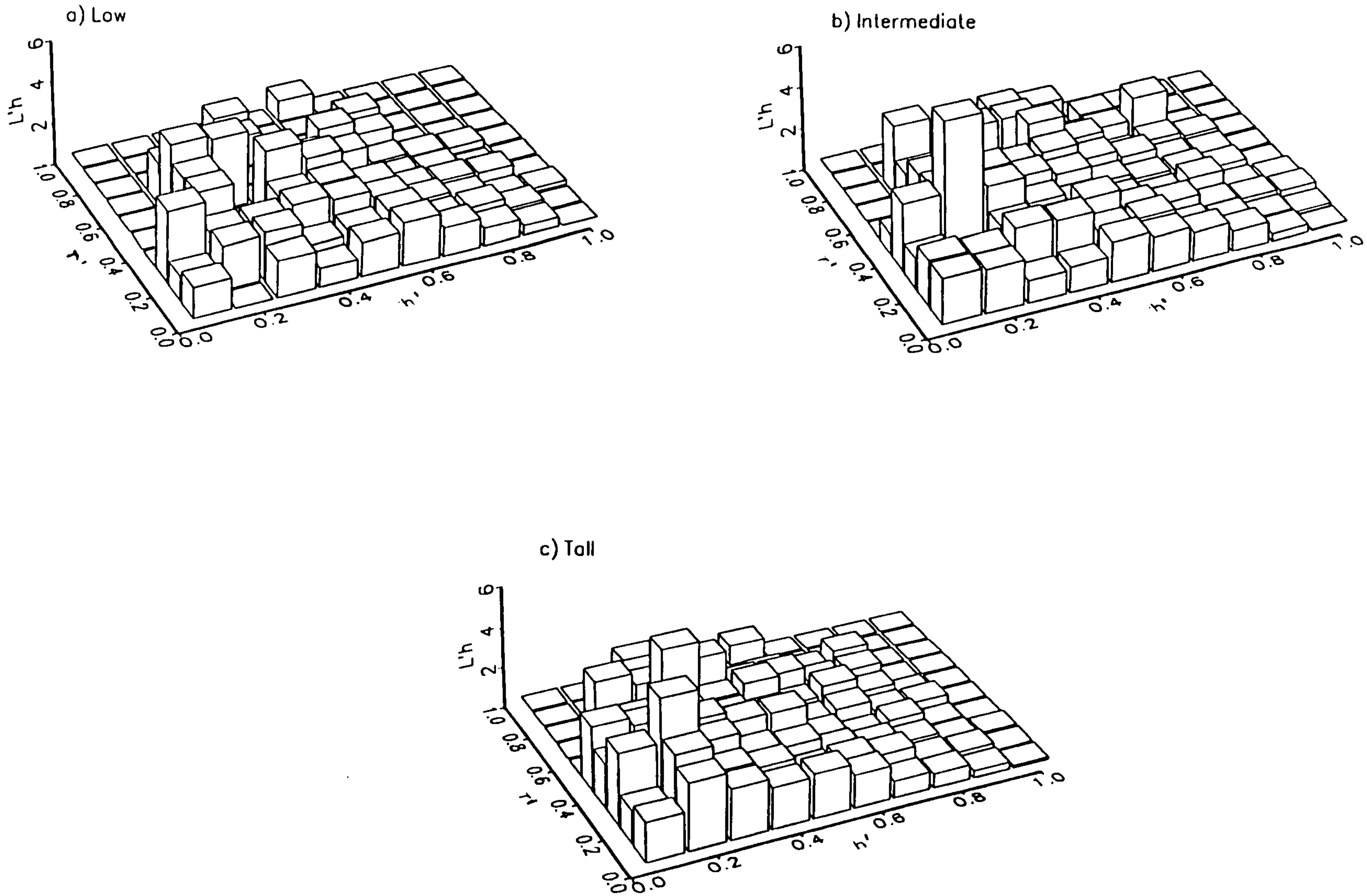
The analysis of the two dimensional distribution of leaf area density in the crown was greatly simplified by assuming that the horizontal distribution was the same at different heights. To examine the validity of this assumption the horizontal distribution of total leaf area density was calculated for ten different vertical crown slices (Figure 3.11.). While there is some evidence in all three stands that the peak of the distribution shifts outwards as h' increases for most of the crown length, there is also considerable irregularity in the distribution at each h' interval. The irregularity may be caused by the fixed horizontal distance class length, resulting in a restricted range of the crown radius in which sampled points fall as h' increases. It was considered reasonable for present purposes to use the same horizontal distribution for each age class of leaf area for the whole crown length for the following reasons:

- L'_h is less important than the L'_v in respect of radiation absorption by tree crowns (Wang, 1988);
- adequate description of the horizontal distribution in the upper part of the crown would require sampling with very small horizontal distance classes; and
- the variation in L'_h of total leaf area at different relative heights is less than between different age classes of leaf area averaged over the crown height.

3.3.2.5.2. Variation in L'_h between stands

The location of maximum leaf area density for all leaves together is close to the trunk in all stands, but varies markedly for leaves in different age classes. For current leaves the maximum is close to the centre of the crown radius and is uniformly distributed about the centre but as leaf age increases the location of maximum L'_h occurs at a lower r' and the distribution becomes increasingly skewed towards the trunk. The functions do not fit well for the low tree stand (less than 30% of the variation in the mean data was explained by the fitted curves), and this is probably because of the restricted number of horizontal distance classes within crowns of small radius, as discussed above. The trends in L'_h for different leaf age classes are, however, similar in all stands and, because of the preponderence of younger leaves within the low tree crowns (Table 3.8), the H_x for total leaf area (0.25) is further out from the tree trunk, and the skewness of the distribution less pronounced than in the other stands. There are few comparable studies with which to compare these results. Wang *et al.*, (1990), found a more symmetrical horizontal distribution of leaf area density in *Pinus radiata*, with H_x close to the centre of the crown radius and broadly similar distributions for different aged

Figure 3.11. Horizontal distribution of relative leaf area density (L'_h) in ten vertical crown slices. Bars represent the mean value of L'_h for 12 trees in each stand, for each of ten radial distance increments, for each vertical slice.



leaves. Wang (1988), presents data for 20-year-old *Picea sitchensis* from a small sample of 18 branches taken from three trees; H_x and H_s for total leaf area, calculated as 0.27 and - 0.41 respectively from his Table 1.4.5.1., are similar to the results of the present study. These results are consistent with leaves being retained for longer, deep in the crown in *Picea sitchensis* than *Pinus radiata,* and new leaf area developing throughout the crown volume. This is consistent with the maintenance of a high leaf area index in closed stands (Cannell, 1987), and a high leaf area per tree in agroforestry stands.

3.3.2.6. Age distribution of leaf area density within crowns

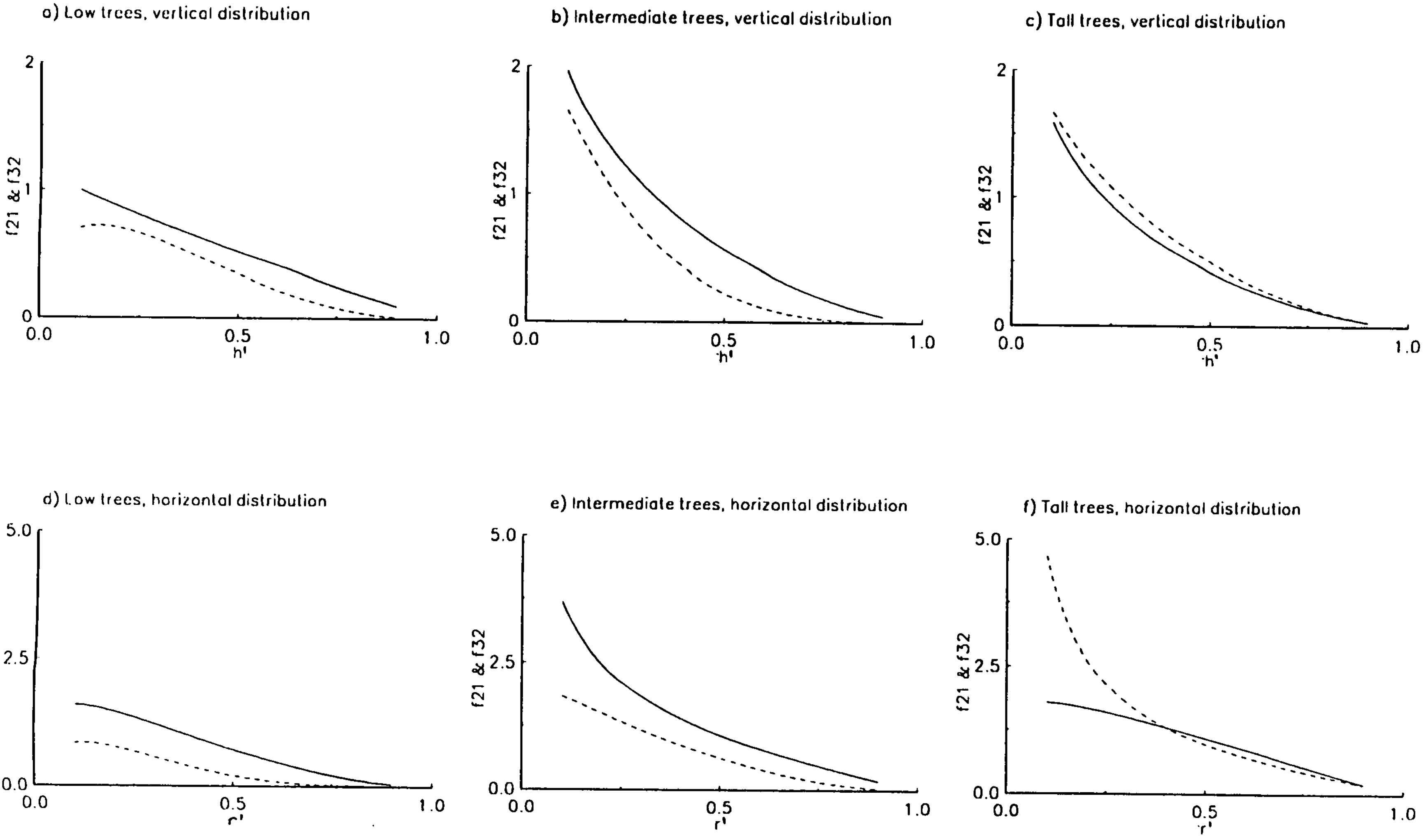
Photosynthetic properties of leaves change with age and, therefore, the age structure of leaves within the crown influences tree productivity (Ludlow and Jarvis, 1971). It is clear from Sections 3.3.2.4. and 3.3.2.2. that the location of maximum leaf area density was higher up the tree crown and further out from its centre for younger leaves. Similarly, the distribution of leaf area density was more skewed to the base of the tree and to the centre of the crown for older leaves. The proportions of leaf area in one age class relative to another are described by age transition functions which were calculated for both the vertical and horizontal dimensions for each stand according to Equations 3.17 to 3.20 and are given in Table 3.14 and shown graphically in Figure 3.12.

In the vertical dimension C_2 was generally negative, indicating an exponential decline in the proportion of older leaf area with increasing crown height. The only exception was the proportion of leaf area in age class A3 relative to A2 in the low tree stand, for which C_2, although positive, was very small (0.04). The age transition functions in the vertical were similar for the intermediate and tall stands, but, because of a much higher proportion of younger leaves in the crowns of the low trees (Table 3.8), the proportion of older leaf area was lower and its rate of decline with relative height less steep. Age transition functions in the horizontal were more variable than in the vertical (Figure 3.12). While for most of the crown radius in all stands the relative proportion of older leaves declined with increasing relative radial distance, there was no similarity within or between stands in the form of this decline.

Table 3.14. Parameters of age transition functions in the vertical (f'_{ij}) and horizontal (f''_{ij}) for tree stands at Cloich, describing how the proportion of leaf area in age class j to that in age class i changes with relative height and radial distance respectively. They are calculated as described in the text (Equations 3.17 - 3.20, Section 3.3.2.1) from the beta functions for different age classes of leaf area for each stand given in Table 3.9.

stand	**dimension**	**function**	C_1	C_2	C_3
L	V	f'_{21}	1.04	-0.03	1.03
L	V	f'_{32}	2.25	0.40	2.31
L	H	f''_{21}	1.26	-0.14	0.89
L	H	f''_{32}	0.80	0.04	1.45
I	V	f'_{21}	1.35	-0.23	1.48
I	V	f'_{32}	2.20	-0.03	3.30
I	H	f''_{21}	1.55	-0.42	0.96
I	H	f''_{32}	2.51	0.05	1.99
T	V	f'_{21}	1.00	-0.27	1.52
T	V	f'_{32}	1.21	-0.19	1.30
T	H	f''_{21}	2.50	0.10	1.11
T	H	f''_{32}	0.75	-0.88	0.66

Figure 3.12. Age transition functions for vertical (a, b, c) and horizontal (d, e, f) leaf area density distributions for low (a, d); intermediate (b, e) and tall (c,f) tree stands at Cloich. The parameters of the functions f_{21} (solid line) and f_{32} (broken line) are calculated from those in Table 3.9. as described in the text, and are given in Table 3.14.



The presence of a larger proportion of younger leaves towards the upper and outer parts of the crown is a self evident consequence of the growth habit. Because current leaves have a higher maximum photosynthetic rate than older leaves (Ludlow and Jarvis, 1971), they can utilize the high QFD there more efficiently, while the lower QFD in the inner and lower parts of the crown is as efficiently used by older leaves (Wang and Jarvis, 1990a), however, it is clear that in the stands at Cloich, new leaf area developed throughout the crown volume. The amount and spectral quality of radiation are the primary environmental variables that condition the photosynthetic properties of leaves (Jarvis *et al.*, 1976) and leaves developing in lower QFD acclimate by having lower maximum rates of photosynthesis and higher specific leaf areas (Leverenz and Jarvis, 1979). In general, the younger leaves are better adapted to whatever crown position they occupy than older foliage because they have developed in the prevailing radiation regime whereas older leaves become increasingly less well acclimated as the crown develops around them, although this is mitigated to some extent by a reduction in photosynthetic capacity as the leaves age (Ludlow and Jarvis, 1971). While leaves may be retained for up to seven years in *P. sitchensis* (Ford, 1982), most of the leaf area within the crowns at Cloich was less than three years old (> 70% was no more than two years old in the unpruned stands). The development of new leaf area throughout the crown volume requires considerable amounts of carbon, and nutrition and water stress have been found to shift the location of the maximum leaf area density of younger leaves upwards and outwards in crowns of *Pinus radiata*, and to cause a reduction in the proportion of new leaf area developed and the retention of older leaves (Wang *et al.*, 1990).

3.3.2.7. Two dimensional leaf area density within the tree crown

The vertical and horizontal distributions of leaf area density (Table 3.9) were combined (Equation 3.11), to produce two dimensional maps of relative leaf area density (L'_{vh}) within crowns (Figure 3.13). Relative leaf area density can be converted to actual values of leaf area density (L_{vh}) for trees of particular dimensions by multiplying by a scaling factor (Equation 3.11; Figure 3.14). The variation of L'_{vh} within the crown, depends upon the assumed crown shape. The crowns of the

Figure 3.13. Two dimensional relative leaf area density (L'_{vh}) within tree crowns combining independent vertical (Fig. 3.7; Table 3.9) and horizontal (Fig. 3.9; Table 3.9) distributions, for leaf area density in all leaves in the a) low, b) intermediate and c) tall tree stands at Cloich. To obtain actual leaf area density at any point in the crown for a tree of particular dimensions $L_{vh} = L'_{vh} F_t/Sc\, R^2_c(h)$; where: F_t = total leaf area within the crown (m^2); S_c = crown length (m); and R_c(h) = mean crown radius at relative height (h). Figure 3.14 shows the actual distribution of L_{vh} for typical trees in each stand.

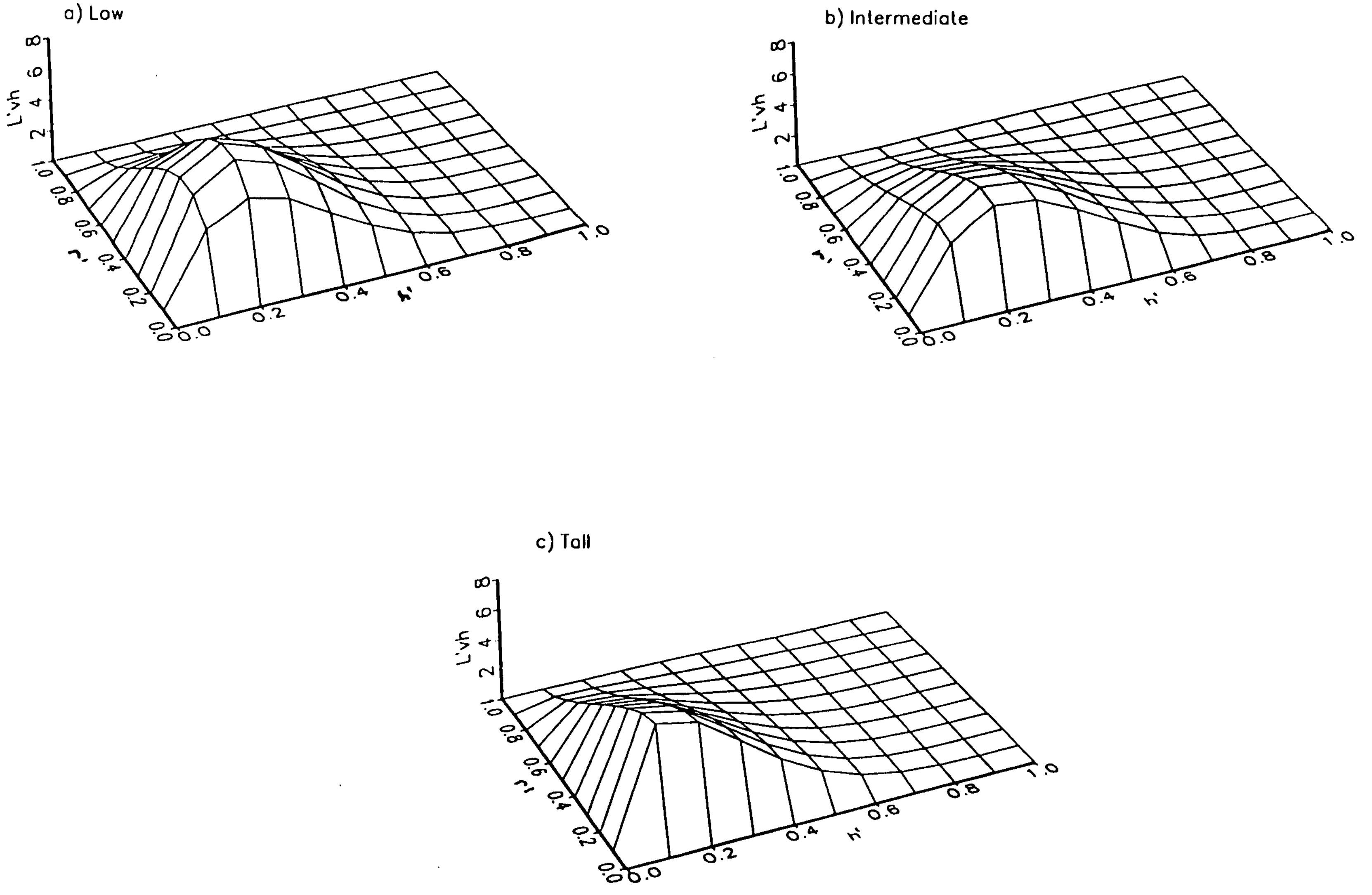
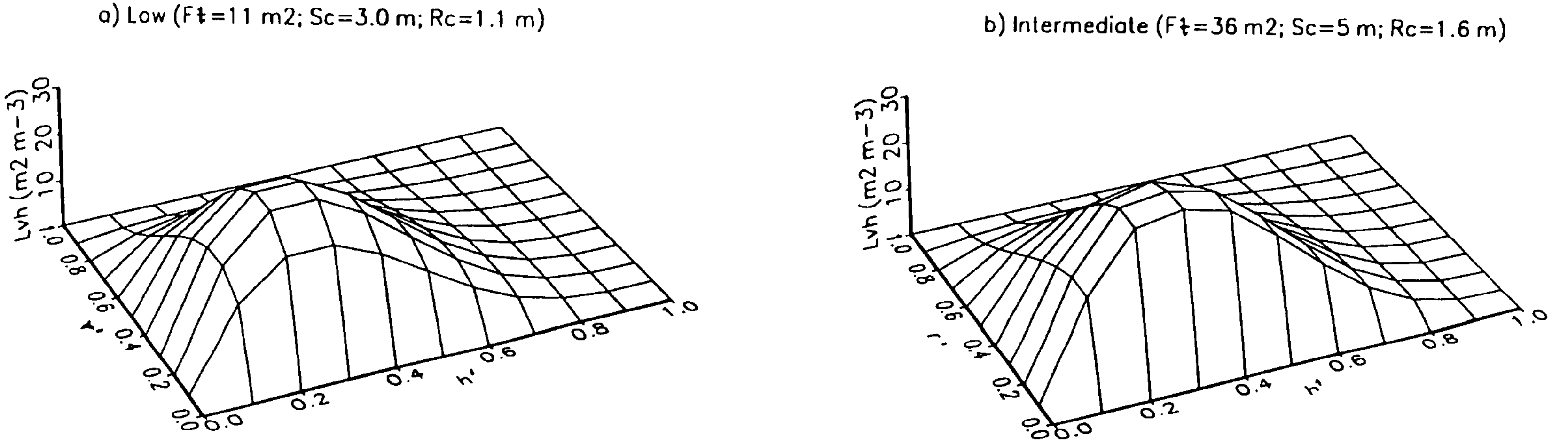
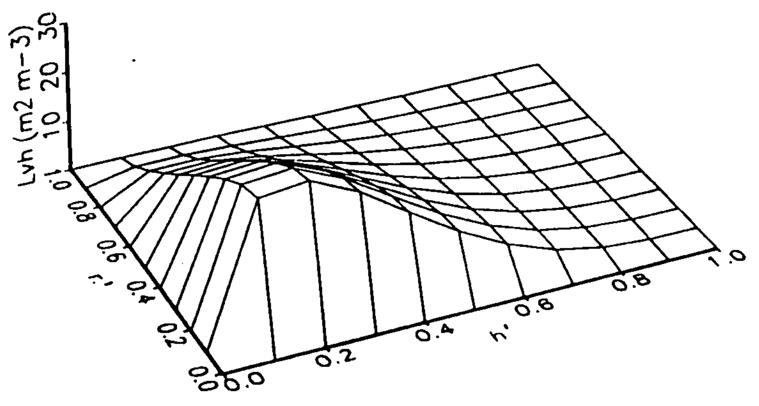


Figure 3.14. Two dimensional distribution of total leaf area density (L_{vh}) of typical trees in a) low, b) intermediate and c) tall tree stands at Cloich. F_t = total tree leaf area (m^2); S_c = crown length (m) and R_c = mean crown radius at base of crown. Tree crowns are assumed to be conical. Distributions are calculated as described in Figure 3.13 with the tree dimensions given for each case.


a) Low (Ft=11 m2; Sc=3.0 m; Rc=1.1 m)

b) Intermediate (Ft=36 m2; Sc=5 m; Rc=1.6 m)


c) Tall (Ft=35 m2; Sc=6 m; Rc=1.7 m)

relatively open grown trees in the present study were well approximated by a cone. The maximum L_{vh} within the crowns for each stand (39, 33 and 21 m^2 m^{-3} for low, intermediate and tall stands respectively) were 10 to 13 times greater than the average L_{vh} within the whole crown. The location of the maximum L'_{vh} within the crown (Equations 3.14 and 3.16) for the low, intermediate and tall stands occurred at h' of 0.32, 0.38 and 0.22 and r' of 0.25, 0.15 and 0.10, respectively. Comparison of the low and intermediate stands indicates a shift upwards and towards the trunk as the open grown crowns developed, although gradation in site conditions rather than the stage of crown development may contribute to this variation. The variability of L_{vh} within the crown, calculated as the maximum divided by the average for the whole crown, was of the same order of magnitude as that reported for 20-year-old *Picea sitchensis* by Wang, (1988), who, when assuming a conical shape, calculated a maximum L_{vh} of 24 m^2 m^{-3} and an average of 2.0 m^2 m^{-3}. Wang *et al.* (1990) concluded that there was greater variability when a conical crown shape was assumed as opposed to half ellipsoidal or paraboloidal models, but the conical model did not fit their data presented for *Pinus radiata* and the ratio of maximum to average L'_{vh} of 12.0:1, 12.6:1 and 13.1:1 calculated from Wang (1988), for conical, half ellipsoidal and paraboloidal crown shapes for *Picea sitchensis* indicate similar variability for all three shapes and lowest for the conical shape. In marked contrast to the present results, Wang (1988), found the location of the maximum L'_{vh} to occur in the upper third of the crown in closed canopy, 20-year-old *Picea sitchensis*. This may reflect differences associated with crown development after canopy closure. Wang (1988) combined vertical and horizontal distributions from different stands: the vertical distribution, calculated from data of Norman and Jarvis (1974), was from trees in a dense stand (over 4 000 trees ha^{-1}) with no leaf area below 4 m height. An upward shift in the location of maximum L'_{vh} as crowns increase in size is consistent with lower branches becoming more heavily shaded for more of their length as the crown above them develops. Where crowns are closer together, mutual shading could be expected to increase this effect dramatically since lower branches are shaded along their entire length.

3.3.2.8. Effects of non-uniform leaf area density within crowns on QFD intercepted and photosynthesis

The significance of non-uniform distribution of leaf area density within tree crowns for the productivity of agroforestry practices depends upon:

- the amount of QFD intercepted by tree crowns and hence transmitted to the understorey; and,
- the efficiency with which the QFD that is intercepted by the trees is used in photosynthesis.

To investigate these effects the derived distributions of leaf area density at Cloich were used to parameterize the simulation model MAESTRO (Wang and Jarvis, 1990b - see Table 3.16) which was used to make predictions for idealised stands based on the tall and intermediate tree stands at Cloich. The model is described and validated for transmittance in agroforestry stands in Chapter 6. Details of the simulations for a sunny day in June at Cloich, which are reported here, are given in Table 3.16, Table 3.17 and the weather data and parameters used are given in Appendix 2.

3.3.2.8.1. QFD absorbed by tree crowns and photosynthesis

Simulations of the QFD absorbed by tree crowns (Q_t) with uniform and non-uniform leaf area density and their daily net photosynthesis (P_t) are given in Table 3.16. In the tall, closed stand (2 m spacing, 2 500 trees ha^{-1}) predictions of Q_t assuming a uniform L_{vh} were 23% higher than with a non-uniform distribution. The difference was twice as large for identical tree crowns at wider spacings; predictions were 48% higher for a uniform distribution at a tree frequency of 625 trees ha^{-1} (4 m spacing) and 50% and 51% higher at tree frequencies of 278 and 156 trees ha^{-1} (6 and 8 m spacing respectively). Differences in P_t were smaller and did not vary with tree frequency; predictions of P_t with uniform leaf area density were within 3% of those with non-uniform L_{vh} for the intermediate trees and around 20% higher in the tall trees. Q_t is mainly affected by the distribution of leaf area density but because physiological parameters of leaves change more with age and position in the crown than their absorptance, P_t is also affected by the age structure of leaves within the crown. The tall trees had more open crowns (a lower mean leaf area density) and their non-uniform leaf area density

Table 3.16. Simulated daily QFD absorption (Q_t) and daily net photosynthesis (P_t) in tree crowns with uniform and non uniform distributions of leaf area density (L_{vh}). Results were obtained by running the simulation model MAESTRO (Wang and Jarvis, 1990b - described and validated for QFD interception at agroforestry tree spacings in Chapter 6) for a sunny day in June, 1987 at the Cloich fieldsite. Meteorological and tree structural data were obtained from Cloich, the trees are all assumed to be identical with dimensions based on the mean data for the tree stands obtained from the destructive harvest and given in Table 3.4 and Figure 3.14. Trees are assumed to be regularly spaced on a square grid formation at the frequencies shown, which correspond to the treatments at Cloich described in Section 2.1.1. The parameters for non-uniform L'_{vh} distributions in two dimensions for each stand are those measured in the destructive harvest and given in Table 3.9. Physiological parameters of leaves of *Picea sitchensis* are from the literature and are given in Appendix 2 together with the hourly meteorological input data.

stand	tree spacing (m)	tree frequency (stems ha^{-1})	L_{vh} distribution	Q_t mol tree^{-1}day^{-1}	P_t mol tree^{-1}day^{-1}	P_t/Q_t (x 10^{-3})
I	2	2 500	non-uniform	107.85	1.35	12.52
I	2	2 500	uniform	119.15	1.31	10.99
I	4	625	non-uniform	151.08	2.14	14.16
I	4	625	uniform	215.85	2.18	10.10
I	6	278	non-uniform	157.92	2.17	13.74
I	6	278	uniform	229.29	2.20	9.59
I	8	156	non-uniform	159.50	2.12	13.29
I	8	156	uniform	232.83	2.15	9.23
T	2	2 500	non-uniform	97.84	1.14	11.65
T	2	2 500	uniform	120.54	1.36	11.28
T	4	625	non-uniform	153.81	1.78	11.57
T	4	625	uniform	227.75	2.15	9.44
T	6	278	non-uniform	162.62	1.87	11.50
T	6	278	uniform	244.66	2.23	9.11
T	8	156	non-uniform	164.94	1.85	11.22
T	8	156	uniform	249.96	2.21	8.87

distribution within the crown was more heavily skewed to the base in the vertical and to the trunk in the horizontal, and this would explain larger differences in daily net photsynthesis than for the intermediate trees. At low tree frequencies in both stands, there were smaller differences in P_t than Q_t and an increase of up to 40% in photosynthetic efficiency of crowns with non-uniform leaf area density. This is consistent with a more uniform distribution of QFD within crowns that have a non-uniform leaf area density, so that more leaves are illuminated at lower QFD (Wang and Jarvis, 1990a). In previous simulation studies of coniferous forest stands the combined effect of non-uniform leaf area density and leaf age structure enhanced crown photosynthesis in *Picea sitchensis* by up to 30% (Wang and Jarvis, 1990a) and permitted a larger leaf area index because higher QFD penetrated to leaves deeper in the canopy and, therefore, they were able to operate with a positive carbon balance (Wang *et al.*, 1990). A larger influence of non-uniform leaf area density in the horizontal can be expected when trees are widely spaced, as occurred here, because crowns are less shaded along their length and a higher incident QFD is received from a larger range of zenith angles, over more of the crown surface.

3.3.2.8.2. QFD transmitted to the understorey

Understorey crops or pasture often provide more immediate and higher returns to the farmer than the tree crop in agroforestry and, therefore, the amount and pattern of transmittance of QFD, which determines the potential productivity in the understorey, may be more important than effects on tree productivity. The results of simulating transmittance across the understorey for stands at Cloich are presented in Table 3.17 and Figures 3.15 and 3.16. The major difference between the two stands is that the tall trees have been pruned, resulting in crowns of similar dimensions to the intermediate trees but with their base more than a metre from the ground. The mean residual transmittance (the difference between assuming non-uniform and uniform leaf area density, $\underline{T}_r$) varied from 2% to 10% of incident QFD for the stands that were simulated (Table 3.17). For the agroforestry stands $\underline{T}_r$ decreased with decreasing tree frequency, but was lowest for the closed stand. The point to point variability of residual transmittance in the understorey increased with decreasing tree frequency and was much greater in the intermediate tree stand where the crown base reached ground level

Table 3.17. Summary of simulated QFD transmittance (T) in tree stands with uniform and non uniform distributions of leaf area density within tree crowns (L_{vh}). Results were obtained by running the simulation model MAESTRO as described in Table 3.16. For each simulation, transmittance was calculated for 81 points located 25 cm above ground level in a nine by nine systematic grid centred in what corresponds to an experimental unit at Cloich (Section 2.1.1.). Residual transmittance (T_r) for any point is calculated as: $T_r = T_n - T_u$; where T_n and T_u are the transmittance assuming non-uniform and uniform leaf area density, respectively. $\underline{T}_r$ is the mean residual transmittance, MINT_r the minimum, MAXT_r the maximum, and RMST_r the root mean square; r is the correlation coefficient for T_n with T_u and is significant at the 5% level if its absolute magnitude is greater than 0.217.

stand	**tree spacing** (m)	**tree frequency** (trees ha^{-1})	L_{vh} **distribution**	$\underline{T}$	**r**	$\underline{T}_r$	**MIN**T_r	**MAX**T_r	**RMS**T_r
I	2	2 500	non-uniform	0.09	-0.595	0.04	-0.04	0.14	0.06
I	2	2 500	uniform	0.05					
I	4	625	non-uniform	0.64	0.921	0.09	-0.05	0.28	0.13
I	4	625	uniform	0.55					
I	6	278	non-uniform	0.82	0.951	0.05	-0.01	0.27	0.09
I	6	278	uniform	0.77					
I	8	156	non-uniform	0.91	0.947	0.04	-0.01	0.26	0.08
I	8	156	uniform	0.87					
T	2	2 500	non-uniform	0.05	0.205	0.02	0.00	0.05	0.02
T	2	2 500	uniform	0.03					
T	4	625	non-uniform	0.58	0.902	0.10	0.03	0.16	0.11
T	4	625	uniform	0.48					
T	6	278	non-uniform	0.79	0.973	0.06	0.01	0.14	0.06
T	6	278	uniform	0.74					
T	8	156	non-uniform	0.88	0.980	0.03	0.00	0.14	0.05
T	8	156	uniform	0.84					

Figure 3.15. Residual transmittance for a grid of 81 points at 25 cm height in the understorey, simulated using MAESTRO (see legend to Tables 3.16 and 3.17) for tree stands based on treatment plots in the tall and intermediate stands at Cloich. The systematic grid of points are numbered in nine rows (ascending from south to north) of nine points (ascending from west to east within the row).

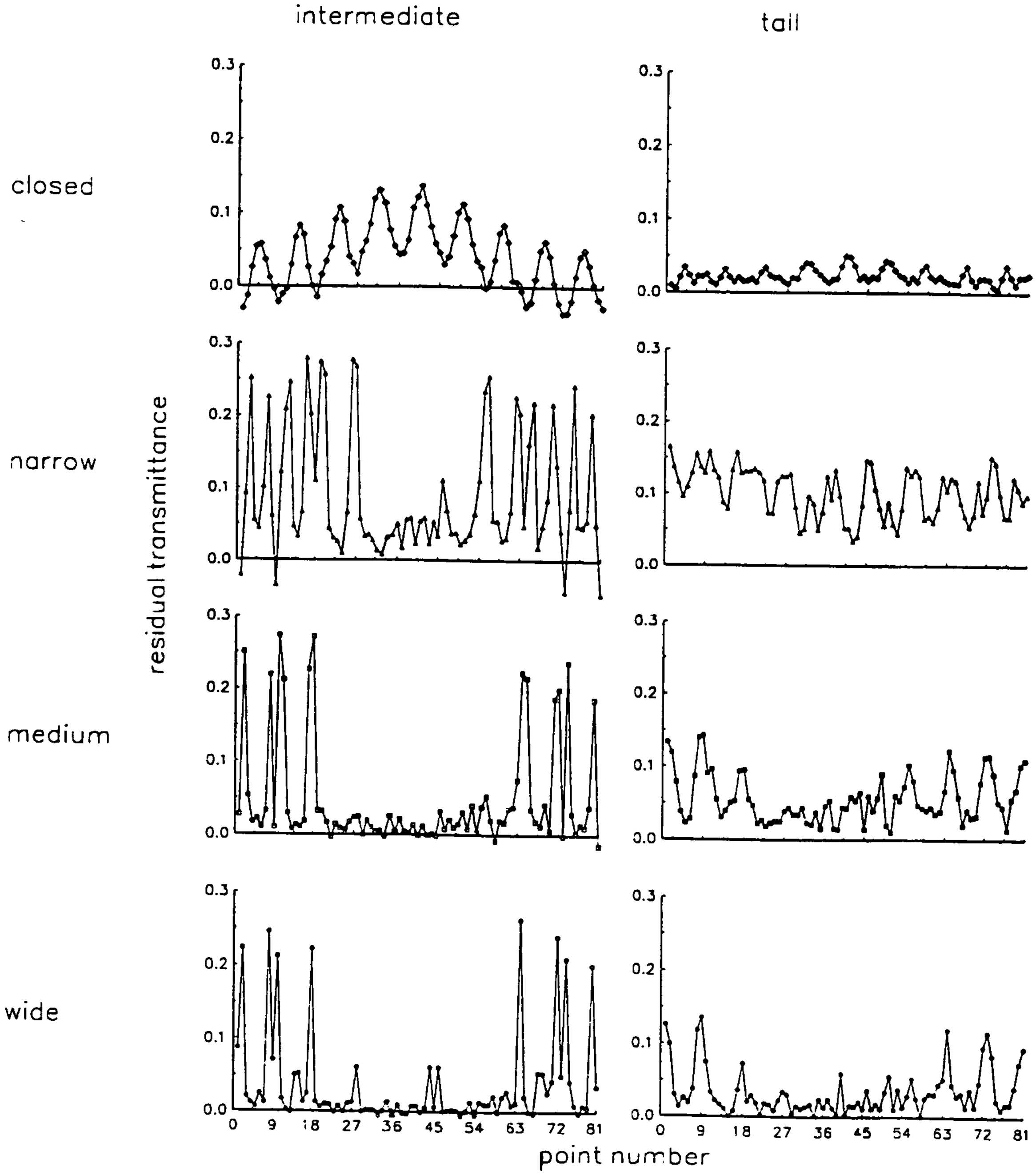
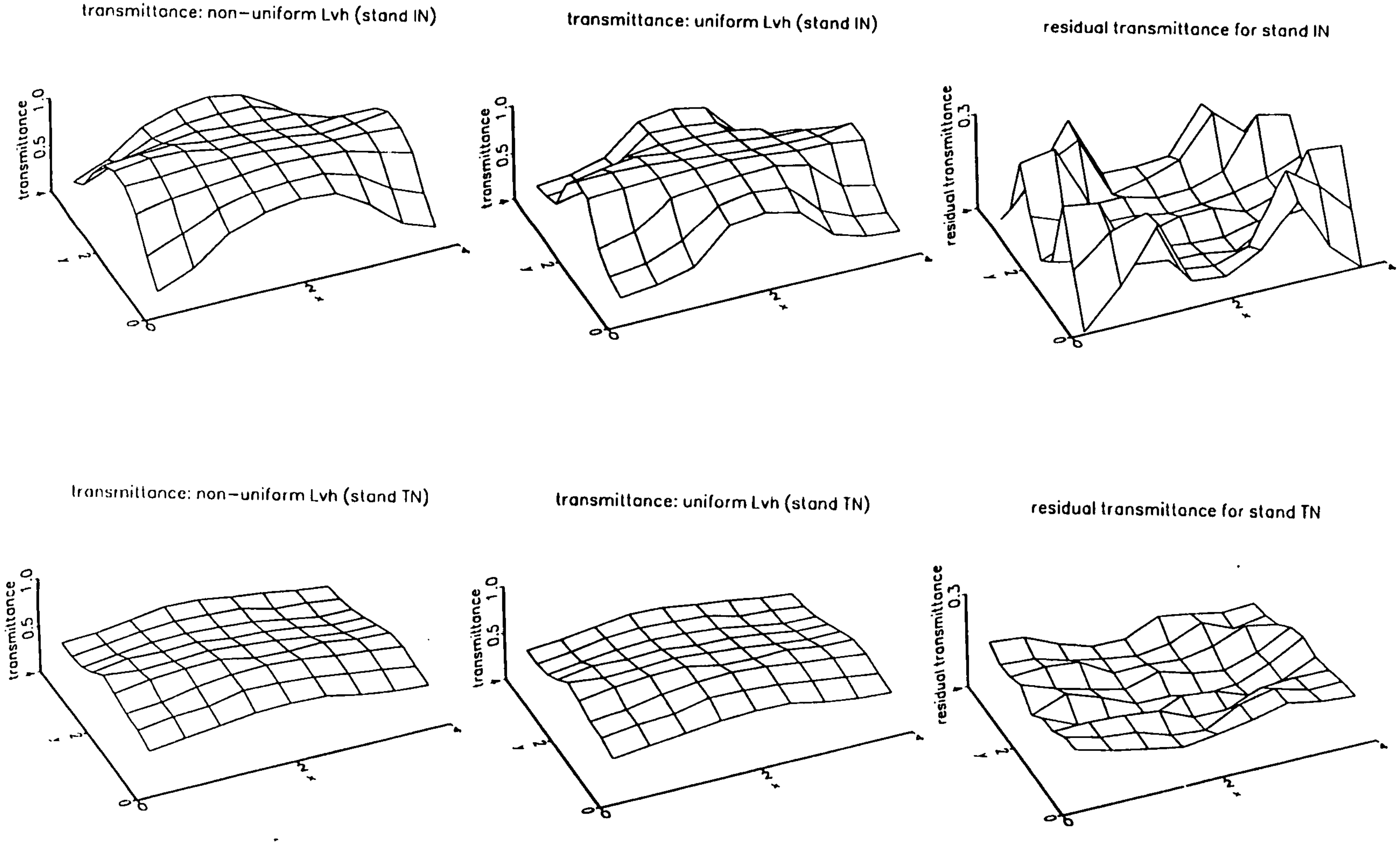


Figure 3.16. Simulated spatial variation of transmittance under tree crowns, with dimensions based on the trees in treatment plots at Cloich, with uniform and non-uniform leaf area density distributions, and the residual transmittance. Details of the simulation are given in the legends to Tables 3.16 and 3.17. The x and y co-ordinates refer to the distance (m) from a tree in the south west corner of a square with a tree at each corner corresponding to an experimental unit at Cloich (Section 2.11) in a northerly direction (y) and to the east (x).



transmittance: non-uniform Lvh (stand IN)

transmittance: uniform Lvh (stand IN)

residual transmittance for stand IN

transmittance: non-uniform Lvh (stand TN)

transmittance: uniform Lvh (stand TN)

residual transmittance for stand TN

(Figure 3.15). For individual points in the understorey, non-uniform leaf area density resulted in up to 28% more of the incident QFD being transmitted than uniform leaf area density. While the mean residual transmittance was similar for the tall and intermediate stands (Table 3.17), the spatial variability of residual transmittance (Figure 3.15) was larger in the intermediate than the tall stand as a consequence of the crown base being elevated through pruning in the tall stand. The spatial pattern of transmittance (Figure 3.16), shows that, for the intermediate stand, there was little difference in the predicted transmittance beneath the central part of crowns when the different leaf area density distributions were used, but more QFD was transmitted beneath the outer parts of crowns with non-uniform leaf area density than those with uniform leaf area density, which is an expected consequence of the pronounced skewness of the horizontal distribution of leaf area density towards the crown centre.

3.4. Summary of Conclusions

The distribution of vertical and horizontal leaf area density within open-grown *Picea sitchensis* crowns were approximated by independent beta functions in each dimension. The parameters of these distributions were variable amongst trees within the stands measured, and poorly related to overall crown dimensions, although there was some evidence that the distributions were more heavily skewed to the crown base in the vertical and more symmetrical in the horizontal in trees with larger leaf area. The vertical distribution of total leaf area was skewed towards the base of the crown and the horizontal distribution skewed towards the trunk. When the vertical and horizontal distributions were combined within the confines of a conical crown shape the maximum leaf area density was up to 13 times larger than the average and located, in unpruned trees, about a third of the way up from the base of the crown and about a fifth of the way out from the trunk along the horizontal radius at this height. This is lower in the crown and closer to the trunk than reported for conifers in more mature and closed canopy stands.

New leaves developed throughout the crown volume with a larger specific leaf area in more shaded positions lower in the crown and closer to the trunk. The location of maximum leaf area density was higher up from the base, further out from the trunk and more symmetrical for younger leaves. Along most of the crown length up from the base and along most of the crown radius out from the trunk, the proportion of older leaf area decreased so that younger leaves were more numerous in the upper and outer parts of the crown.

The measured non-uniform leaf area density distributions within crowns, in two dimensions, for three age classes of leaf area, were compared through simulation with a uniform distribution of leaf area density. Differences in the daily amount of QFD intercepted per tree were much larger for discrete tree crowns, at lower frequencies, than for identical crowns in a closed canopy and up to 51% more QFD was intercepted by uniform crowns. Daily net photosynthesis of crowns varied less (3-20%) because the smaller amount of QFD that was intercepted by non-uniform crowns was more efficiently utilised. The overall photosynthetic efficiency of crowns with non-uniform leaf area density distribution, in widely spaced stands, was up to 40% higher than with uniform leaf area density. Averaged over the understorey, up to 10% more of the incident QFD was transmitted in agroforestry stands with non-uniform leaf area density, but the spatial pattern of transmittance resulted in localised differences of up to 28% more QFD transmitted under the outer parts of unpruned tree crowns. Transmittance under pruned crowns was more even and, because differences between uniform and non-uniform crowns were effectively spread over a larger area of the understorey, the differences were smaller and unlikely to have significant effects on understorey productivity.

The consequences for agroforestry productivity of non-uniform leaf area density within tree crowns are likely to vary with differences in crown dimensions, frequency and arrangement, and with the amount and beam fraction of incident QFD. The results of using measured distributions of leaf area density to simulate QFD absorption and photosynthesis for a range of tree sizes and frequencies existing in the agroforestry experiment at Cloich, suggest that effects of non-uniform leaf area density distribution on QFD absorption per tree and overall photosynthetic effiency of tree crowns would be significant. While there are also notable effects of non-uniform leaf area density distribution on the spatial distribution of QFD transmitted to the understorey beneath unpruned tree crowns, these are much less pronounced in pruned crowns at frequencies being considered for agroforestry in the uplands of the UK (Sibbald *et al.*, 1991) and are, therefore, less likely to be significant for understorey productivity which is investigated in Chapter 5.

4. Tree growth in relation to light interception

4.1. Introduction

The major objective of the research described in this Chapter was to test the hypothesis that a linear relationship exists between intercepted QFD and tree growth across a range of tree sizes and spacings typical of agroforestry and to compare experimentally determined values of the dry matter:radiation quotient e_t for tree stands with that of agricultural crops.

4.1.1. Relationships between plant growth and absorbed radiation

The concept of potential productivity has been useful in comparing possible production from different plant stands (Monteith, 1981; Jarvis and Leverenz, 1983; Rook, *et al.*, 1985). This assumes that dry matter production of a crop is linearly related to the light intercepted by its foliage canopy, and that reductions from a potential maximum defined by incident radiation and foliage characteristics occur when other factors (such as water status or nutrient availability) limit the development of foliage area, or if prolonged, the efficiency with which intercepted radiation is utilised.

The examination of a first order effect, such as the distribution of intercepted light within the system, defines potential productivity of different combinations of trees and pasture, and formed the basis for their comparison in terms of the productivity of individual components and the system as a whole (Chapter 7). The methodology can be subsequently expanded to incorporate the effects of secondary factors, such as temperature, and, water and nutrient supply.

Monteith (1977) proposed the central hypothesis that in unstressed conditions plant growth is linearly related to intercepted light. This provides a useful framework for analysis of productivity in which biomass (G) is considered as the time integrated product of incident light (Q), the fraction of incident light intercepted by the canopy (i), and the dry matter:radiation quotient (e) Equation 4.1).

$$G = e.i.Q\,dt \qquad \text{(Equation 4.1)}$$

Monteith (1977), suggested that *e* was conservative quoting a figure of 2.8 g MJ^{-1} PAR for above ground dry matter for a range C3 crops in the UK from cereals to apples and estimated 3.0 to 4.0 g MJ^{-1} PAR for total dry matter. He later demonstrated that this was consistent with a maximum leaf photosynthetic rate of 2 g m^{-2} h^{-1} and extinction coefficients typical of field crops (Monteith, 1981). The linear relationship between light interception and growth has been established for a variety of agricultural crops across different climatic conditions (Biscoe and Gallagher, 1977; Gallagher and Biscoe, 1978; Legg *et al.*, 1979; Allen and Scott, 1980; Hipps *et al.*, 1983). There are difficulties in comparing measured values for *e* because different studies have measured radiation in different ways, failed to distinguish between intercepted and absorbed radiation and not always measured growth of the whole plant (Russell, Jarvis and Monteith, 1989). Where necessary for comparative purposes values for *e* have been converted to similar units using the following assumptions set out and justified by Russell *et al.* (1989): that 1 MJ of PAR is equivalent to 4.6 mol quanta and 1 MJ of total solar radiation to 2.3 mol quanta and, assuming a typical value for the energy content of plant dry matter as 20 kJ g^{-1}, that *e* expressed in g mol^{-1} (PAR) is equivalent to a dimensionless energy conversion efficiency (%). Recent compilations of values for *e* in crops adequately supplied with water and nutrients (Cannell *et al.*, 1987; Gosse *et al.*,1986; Russell *et al.*, 1989) have shown a range of values for *e* based on above ground dry matter of 1.6 to 4.2 g MJ^{-1} PAR, with most values falling between 1.6 and 2.6 g MJ^{-1} PAR. For total biomass, reported values of *e* fall between 2.2 and 3.6 g MJ^{-1} PAR. There are few data available for trees but Linder (1985) presents a linear relationship between measured above ground biomass production and estimates of QFD intercepted by trees (Q_t), calculated from leaf area estimates for several temperate forest stands. He estimated e_t at 0.9 g MJ^{-1} PAR for a stand of *E. globulus* over its first ten years of growth and 1.7 g MJ^{-1} PAR for a range of evergreen stands in Europe and the Antipodes up to 55 years of age. He includes estimates for one stand of pole stage *Picea sitchensis* (Ford, 1982) that is well above the regression line. These estimates suggest more variable and lower values of *e* for trees than agricultural crops. This would be consistent with the respiration requirement for maintenance of woody parts. Much higher values of e_t have been reported for young fast growing trees in containers (Cannell, 1985, Cannell *et al.*, 1987; Cannell, 1989). These studies quote a value of around 3 g MJ^{-1} PAR for total biomass in *Salix viminalis* and *Populus trichocarpa* grown over one season from cuttings and a more variable range of 2.0 to 2.8 g

MJ^{-1} PAR for above ground biomass, attributed to different partitioning of dry matter to root and shoot between seasons and species. These values were obtained as the regression coefficient of accumulated radiation on accumulated biomass for a sequence of measurements through the season. This is not a statistically justifiable procedure because the successive measurements are not independent (Russell *et al.*, 1989). Wang, Jarvis and Taylor (1991) measured QFD over four years above, below and reflected from crowns of pole-stage *Picea sitchensis* in six plantation forest plots with a range of thinning and fertilizer treatments. They found that above ground biomass production, predicted using an appropriate regression equation on basal area for the species, was proportional to the QFD absorbed, irrespective of treatments. Using estimates of QFD absorbed in a larger number of treatment plots at the same site they calculated e_t as 0.43 g mol^{-1} (1.98 g MJ^{-1} PAR) for nitrogen-fertilized plots and 0.33 g mol^{-1} (1.52 g MJ^{-1}PAR) for other plots, phosphorus fertilization and thinning had no significant effect on e_t.

The agroforestry treatments in the present experimentation involved tree spacings far beyond the range of forest thinning treatments in previously measured plantation stands, nevertheless, the expectation from the Monteith hypothesis is that e_t will not be altered by re-spacing the trees unless this in turn alters the availability of resources limiting tree growth. The primary aim of the research reported in this chapter was, therefore, to use the agroforestry treatments at Cloich to provide a fundamental test of the hypothesis that the annual dry matter production of trees is linearly related to the QFD absorbed by their crowns.

4.2. Methods

4.2.1. Tree growth

Individual measurements of D_r were made annually from 1985 to 1988 for every tree within the plots at Cloich by the FC (Section 2.1.3.3). Regression equations relating above ground dry-matter per tree (G_{at}) to basal area per tree M_r were calculated for the stands at Cloich using data from the initial destructive harvest of trees (Section 3.2.1). The dry-mass (biomass) of branches and foliage was summed for each harvested tree as described previously for leaf area (Section 3.3.1). The biomass of the tree stems was calculated by measuring the specific mass (dry mass/volume) of two stem disks per tree and multiplying this by the volume of the stem calculated from measurements of stem lengths and diameters (Section 3.2.1.2). The regression equations derived for each stand were then used to calculate the biomass of each plot tree in each year. Biomass increments in each year were then obtained by difference and expressed per unit of land area for comparison with measurements of the QFD intercepted by the tree crowns. An assumption was made that the relationships between above ground biomass per tree and basal area per tree did not change over the three years of the experiment.

4.2.2. Interception of QFD

Quantum flux density above and below the tree crowns in all nine agroforestry treatments at Cloich were measured for complete years in 1987 and 1988 (Section 2.1.3.5). The light intercepted by the tree crowns was calculated from the difference between these measurements. The sampling strategy used was based on analysis of intensive measurements made in the 6 m spaced plot in the intermediate tree height stand in autumn, 1986. Initially 25 sensors were randomly distributed within each of three units (areas bounded by four trees, see Figure 2.2), from which it was calculated using Equation 3.3, that for weekly integration periods a random sample of 519 points was required to estimate the mean QFD for a unit with an allowable error of 10% and 95% confidence limits. However, the shading effect of the trees is not random, and, therefore, it was reasonable to expect greater precision in estimating the mean by adopting spatial stratification of the sampling pattern. This was empirically tested by laying out a centred systematic grid of 81 sensors within a unit and then allocating a further nine roving sensors to random locations, one within each of the nine grid square positions (a 3 x 3 grid of squares of equal area imposed on the unit, see Figure 2.2). The locations of the nine roving sensors were re-randomised within their grid squares at weekly intervals and the systematic grid was moved at two weekly intervals so that three units were sampled. For weekly integration periods the mean of the nine roving sensors was within 5% of the mean of the 81 sensors in the systematic grid and there was never more than a 10% difference between daily means of the two sets of sensors.

During 1987 and 1988 nine sensors per treatment plot were allocated to random locations within each of the nine grid square positions. Sampled grid square positions were allocated at random to three sampling units (an area bounded by four trees) within the plot with a non-repeating stratification condition that three grid square positions per unit were sampled (Figure 2.2). During 1988 the whole sampling pattern was re-randomised every two weeks from April to September and every month in the winter, to permit spatial analysis of light transmittance within the unit (Section 5.3.3).

For some time periods additional sensors were mounted facing downwards at the tall site, both at 50 cm height and on a tower above the tree crowns, therefore measuring reflected QFD from the understorey and the vegetation as a whole. The total reflected QFD measured above the tree crowns, integrated over two week measuring periods was never greater than 5% of incident QFD, but was consistently higher in the 8 m spaced plot (4.8%) in July and August, 1988 than in the 4 m spaced plot (3.2%). This was not associated with a high reflectance for the experimental grass swards (2-4%) and was, therefore, probably caused by reflection from the natural understorey vegetation that was not separately measured. It was not possible to sample reflectance across a representative area of the spatially variable mixture of tree and understorey canopies in plots with widely spaced trees because it was necessary to mount sensors on a tower for each point measured and, therefore, accurate calculation of total reflectance and its partition between the tree crowns, the experimental understorey and the natural understorey vegetation was not attempted. Intercepted rather than absorbed QFD was calculated from sensor measurements and used in subsequent analyses.

4.3. Results

4.3.1. Relationships between basal area and above ground dry-matter

There was a strong linear relationship between above ground dry mass (G_{at}) and basal area (M_r) of trees from the destructive harvest (Figure 4.1). There was a slightly larger intercept (p=0.05) and a substantially lower slope (p=0.01) for the tall stand than the low and intermediate tree height stands, that were not significantly different from each other (Table 4.1). This is consistent with the tall stand having been pruned prior to sampling. The tall stand was also located 1 km away from the other two stands and site differences may also have influenced the relationship. The two separate regression lines

Figure 4.1. Relationship between above ground biomass (G_{at}) in kg and stem cross-sectional area at 1.3 m (M_r) in cm^2 for low (+) and intermediate (o) stands together (short dashes) and the tall (x) stand (long dashes) at Cloich. The regression equations and accumulated analysis of variance are given in Table 4.1 and the measurement procedure is described in Section 4.2.1.

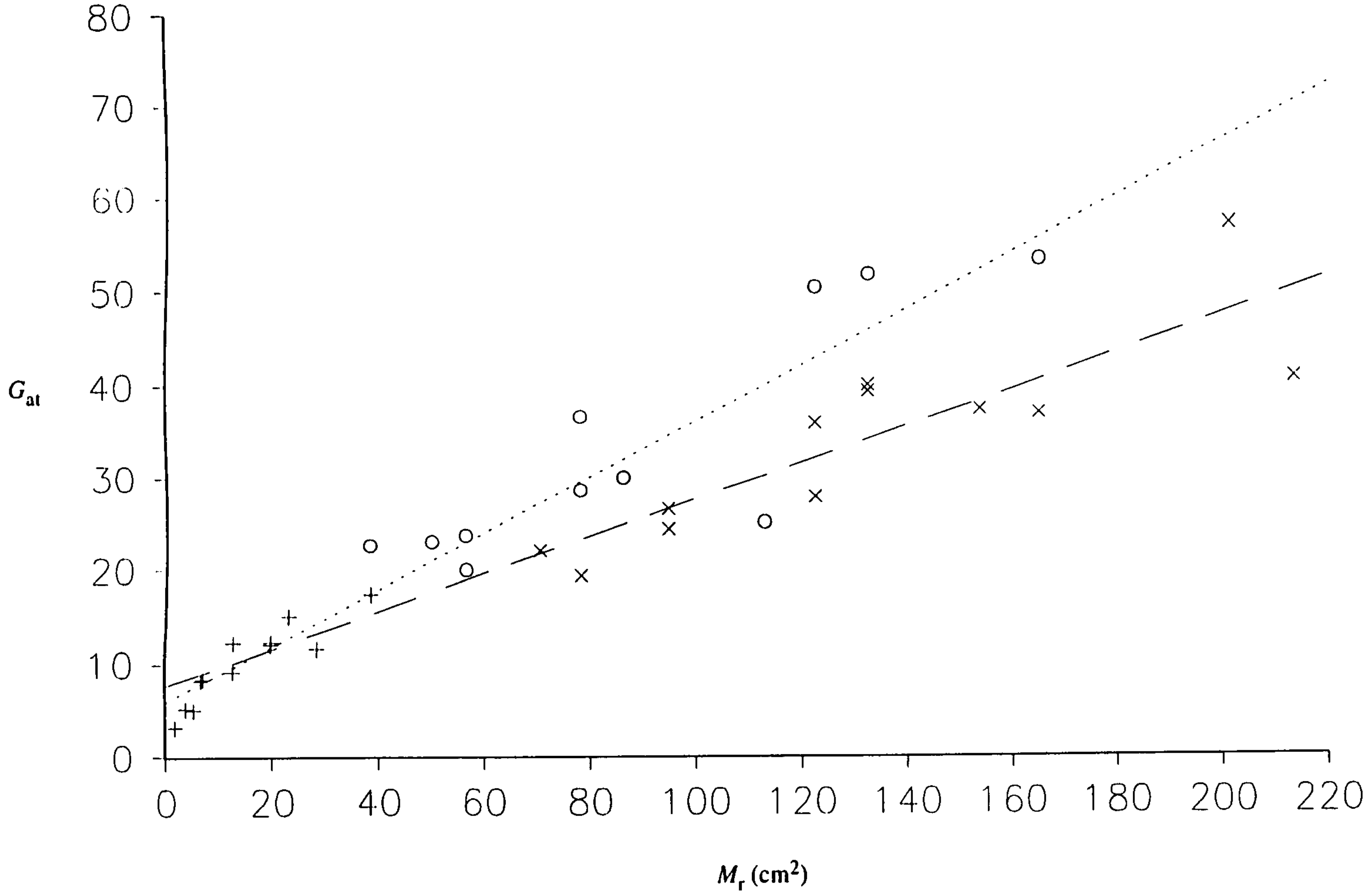


Table 4.1 Regression analysis of relationship between the above ground biomass (G_{at}) in kg and stem cross-sectional area at 1.3 m (M_r) in cm^2 for tree stands and sites at Cloich.

a) Parameters of the fitted linear regression $G_a = bM_r + a$ shown graphically in Figure 4.1.

stand (s)	***a*** **(se)**	***b*** **(se)**	r^2
L and I combined	5.76 (1.51)	0.3022 (0.0219)	89
T	7.58 (4.53)	0.2001 (0.0326)	

a1) Analysis of variance for joint regression of all trees versus separate regressions for each stand

Source	**DF**	**SS**	**MS**	**F**	
Overall regression	1	6181.26	6181.26	245.83	***
Intercepts	2	488.62	244.31	9.72	***
Slopes	2	76.15	38.07	1.51	ns
Residual	30	754.35	25.14		
Total	35	7500.37	214.30		

a2) Analysis of variance for joint regression of low (L) and intermediate (I) trees versus separate regressions for each stand

Source	**DF**	**SS**	**MS**	**F**	
Overall regression	1	4567.07	4567.07	205.35	***
Intercepts	1	7.55	7.55	0.34	ns
Slopes	1	5.55	5.55	0.25	ns
Residual	20	444.81	22.24		
Total	23	5024.98	218.48		

a3) Analysis of variance for joint regression of the L and I stands combined with the tall stand, versus separate regressions.

Source	**DF**	**SS**	**MS**	**F**	
Overall regression	1	6181.26	6181.26	257.74	***
Intercepts	1	389.66	389.66	16.25	***
Slopes	1	162.01	162.01	6.76	**
Residual	32	767.44	23.98		
Total	35	7500.37	214.30		

**	significant at p = 0.05
***	significant at p = 0.01
ns	not significant

explain 89% of the variability in the data and although there appeared to be some heterogeneity of variance for trees in the tall stand, neither the plot of residuals nor the amount of variation explained were improved by logarithmic transformation and the equations in Table 4.1 were subsequently used to calculate biomass of trees in the respective stands (Section 4.3.2).

4.3.2 Above ground dry-matter of trees

Initial distributions of stem diameter at breast height at the beginning of the experiment in the plots at Cloich were presented in Figure 3.1. Mean values for above ground dry matter per tree for each plot calculated from applying the regression equations in Table 4.1 to basal area of each tree measured annually are presented in Table 4.2. and frequency distributions for each plot are presented in Figure 4.2. Over the life of the experiment trees in the low stand almost doubled their above ground biomass with annual relative growth rates (RGR) in the order of 0.35 kg $kg^{-1}a^{-1}$ and in the low stand the widely spaced trees (8 m) had a lower relative growth rate (0.32 kg $kg^{-1}a^{-1}$) than more closely spaced trees that may reflect variability in site conditions rather than a treatment effect as spacing treatments were not replicated within stands. There was no identifiable trend in RGR with tree spacing in the intermediate and tall stands that had lower relative growth rates of about 0.3 kg $kg^{-1}a^{-1}$ in the intermediate stand and 0.2 kg $kg^{-1}a^{-1}$ in the tall stand. RGR of stands did not differ appreciably between years despite a higher annual incident QFD in 1988 (Figure 4.3). There were no discernible trends in the variability amongst trees in plots (Table 4.2) nor the shape of the frequency distributions of above ground biomass within plots (Figure 4.2) with either tree spacing or time. Frequency distributions of tree biomass were approximately normal in the intermediate plots but there was a negatively skewed pattern in the low and tall tree stands. While above ground biomass per tree remained comparable for spacing treatments within stands during the experiment, G_{at} per unit land area varied four fold in proportion to tree frequency (Table 4.3). Above ground dry matter production (ΔG_{at}) varied with tree size and spacing from 0.79 Mg ha^{-1} to 9.51 Mg ha^{-1} (Table 4.3).

Figure 4.2 Distribution of above ground dry matter of trees (G_{at}) for treatment plots at Cloich in 1986, 1987 and 1988. Treatment labels as in Figure 2.1.

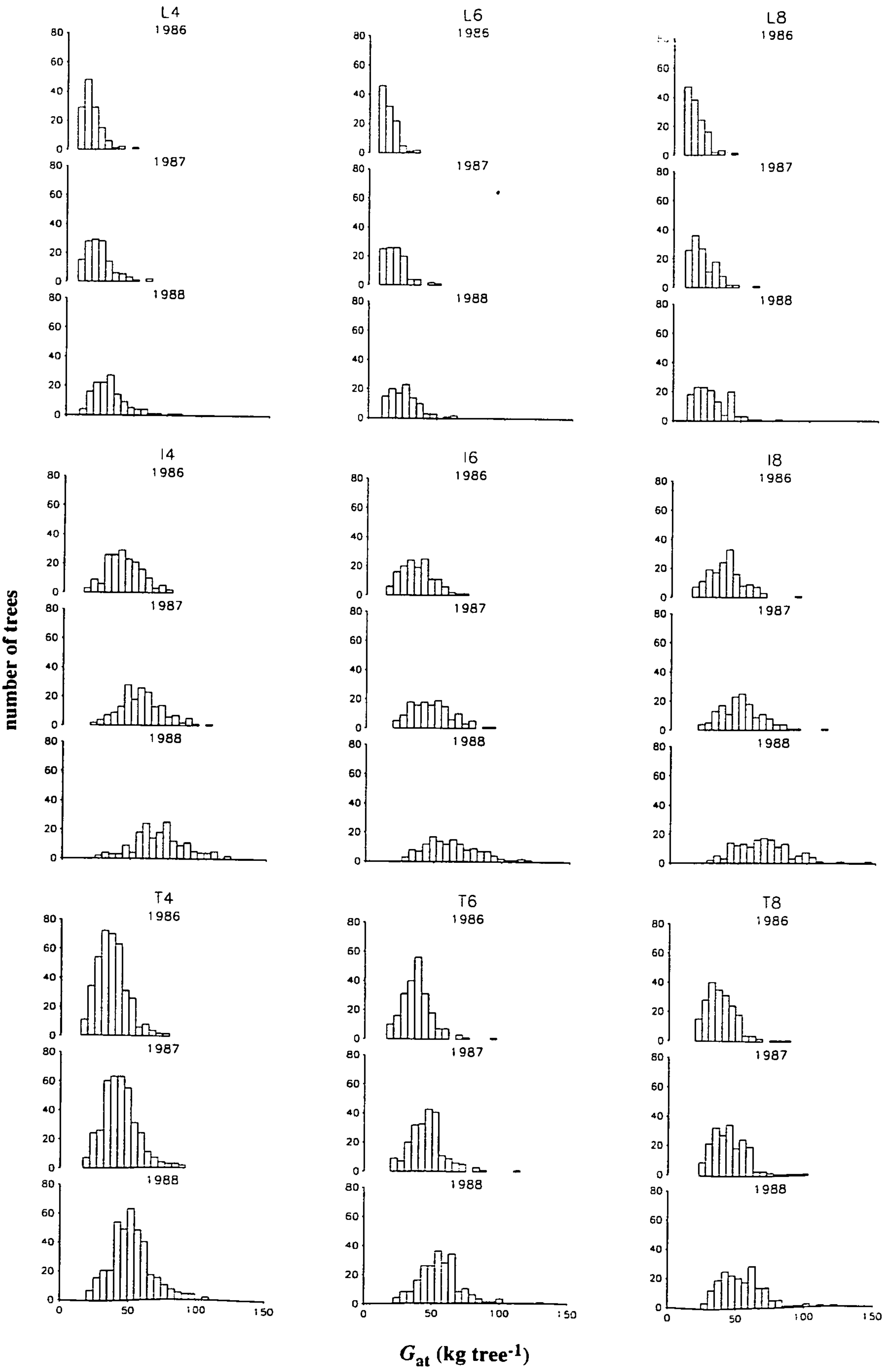


Figure 4.3 Monthly incident QFD to the Cloich site measured above the tree canopy.

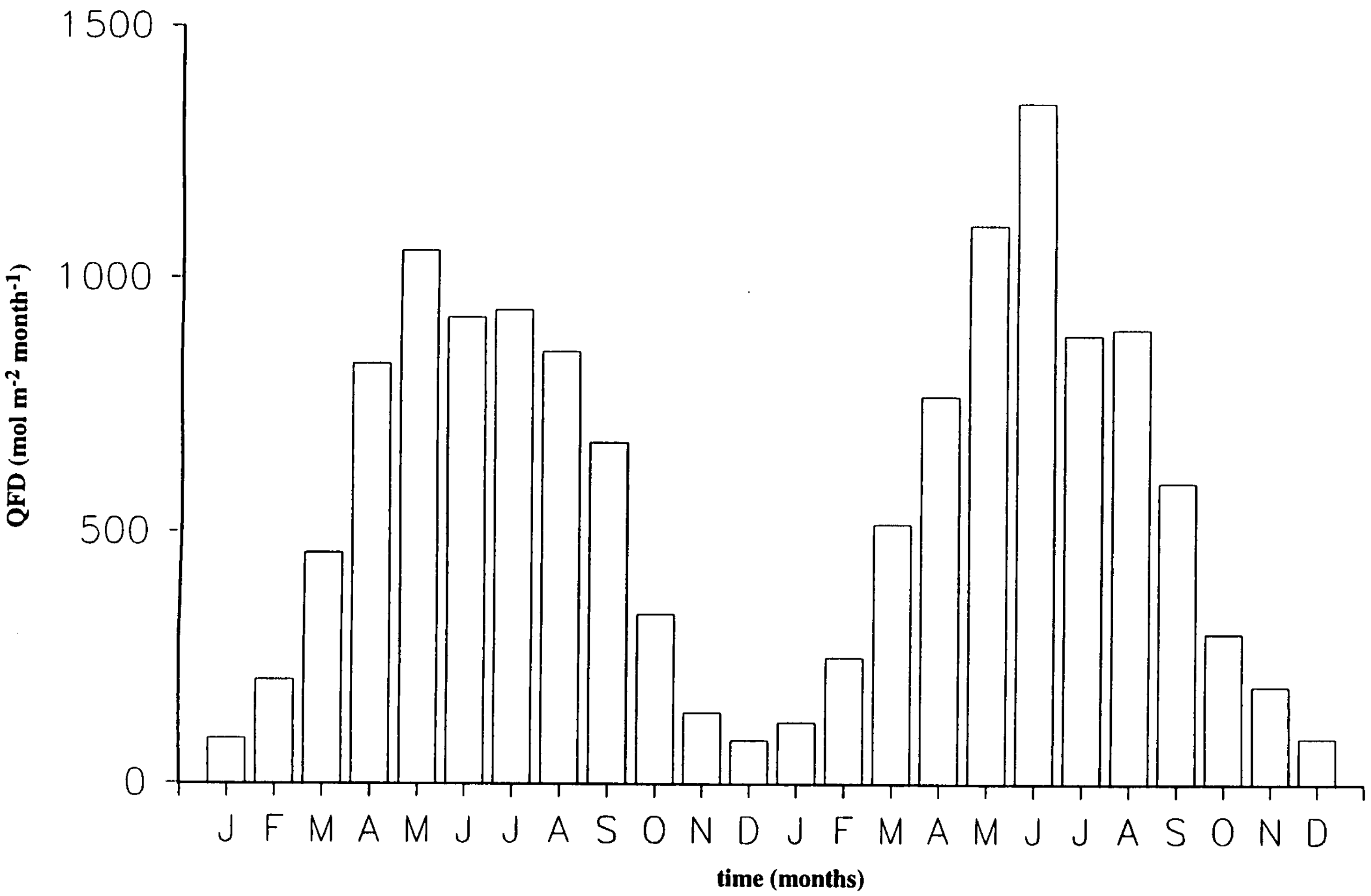


Table 4.2 Above ground dry mass of trees in treatment plots at Cloich. D_r of all trees was measured and biomass calculated from equations in Table 4.1. The standard deviations (sd), therefore, refer to the population rather than a sample. Frequency distributions are given in Figure 4.2.

stand	tree spacing (m)	above ground biomass G_{at} (kg tree $^{-1}$) 1986		1987		1988	
		mean	**sd**	**mean**	**sd**	**mean**	**sd**
L	4	17.41	6.96	23.84	9.49	32.14	12.94
L	6	14.19	5.49	19.36	7.88	26.18	10.80
L	8	16.01	6.65	21.08	8.95	27.85	12.24
I	4	43.74	12.62	57.02	15.80	71.97	20.11
I	6	36.36	11.53	47.57	14.67	62.85	19.36
I	8	39.54	12.48	51.43	15.28	67.95	19.66
T	4	37.09	10.89	43.72	12.65	52.29	15.23
T	6	38.23	10.56	46.24	12.55	55.79	15.12
T	8	38.00	11.16	45.30	13.07	54.19	16.16

Table 4.3 Above ground dry matter of trees in treatment plots at Cloich in 1986, 1987 and 1988 expressed per unit land area, see Table 4.2 for biomass values per tree and within plot variability, and the biomass increment, ΔG_{at}, which was calculated for each tree and then expressed per unit area.

stand	tree spacing (m)	1986	1987		1988	
		G_{at} (Mg ha^{-1})	G_{at} (Mg ha^{-1})	ΔG_{at} (Mg ha^{-1})	G_{at} (Mg ha^{-1})	ΔG_{at} (Mg ha^{-1})
L	4	10.88	14.90	4.01	20.09	5.19
L	6	3.94	5.38	1.43	7.28	1.89
L	8	2.50	3.29	0.79	4.34	1.06
I	4	27.34	35.64	8.30	44.98	9.51
I	6	10.11	13.22	3.11	17.47	4.25
I	8	6.15	8.02	1.86	10.60	2.58
T	4	23.18	27.32	4.14	32.68	5.35
T	6	10.63	12.85	2.22	15.50	2.63
T	8	5.92	7.07	1.14	8.45	1.38

4.3.3 Intercepted quantum flux density

Cumulative monthly totals of QFD incident to the site, measured above the tree crowns are presented for 1987 and 1988 in Figure 4.3. There was a higher total QFD receipt in 1988 (7.1 k mol m^{-2} a^{-1}) than in 1987 (6.6 k mol m^{-2} a^{-1}), largely because of a particularly high QFD receipt in June, 1988. While the monthly pattern of incident QFD varied between years, about 80% of the annual QFD receipt was received between April and September in both years. The fraction of incident QFD intercepted by tree crowns, i_t, varied on an annual basis from 0.04 in the low tree height, 8 m spaced plot in 1987 to 0.61 in the intermediate tree height, 4 m spaced plot in 1988 (Table 4.4). In general, i_t was higher in the winter months when incident QFD was low than in the summer months when incident QFD was high (Figure 4.4) and was higher in 1988 than 1987. Since a larger proportion of solar radiation was diffuse in the winter months, the overall seasonal pattern of i_t was consistent with a lower fractional interceptance of beam radiation than diffuse radiation and the increase in 1988 over 1987 with increasing leaf area as tree crowns developed (Section 3.3.1.2). The actual variation in i_t from month to month that was observed (Figure 4.4) may well have been further complicated by negative correlation of mean hourly transmittances through the tree crowns with the zenith angle of the sun (Wang and Jarvis, 1990a). Solar zenith angles are smallest in mid-summer and, therefore, a reduction in i_t in summer months would be expected. Conversely, leaf expansion and shoot elongation of *Picea sitchensis* in Scotland generally occurs over a six week period in June and July (Cannell, 1987), which would be expected to result in an increase in i_t from June onwards. The net result of these competing influences is the jagged pattern of i_t (Figure 4.4), reasonably consistent across tree size and spacing treatments but variable in relation to weather conditions.

The total QFD intercepted by trees, on a plot basis, was similar in the tall tree and intermediate tree stands but less than half as much in the low tree stand (Table 4.4). Within each stand the total QFD intercepted decreased with increasing tree spacing, as would be expected. In the tall tree stand, in which mean tree size was similar in all spacings (Table 4.2), there was a regular pattern of decrease in Q_t with decreasing tree frequency, with approximately half as much QFD intercepted at 6 m tree spacing than at 4 m spacing and a third as much at 8 m spacing (Table 4.4). However, Q_t expressed per tree in the tall stand, in which tree crowns were just touching at 4 m spacing, increased with decreasing

Figure 4.4 a Monthly totals of QFD intercepted by tree crowns, Q_t (bars), and the fraction of incident QFD intercepted, i_t (line), for the 4 m spaced plots in the three stands at Cloich. Stand labels as in Figure 2.1. Error bars show the standard deviation calculated from the cumulated mean QFD intercepted over a month in each grid square (n=9), that is, the lowest level of sampling stratification.

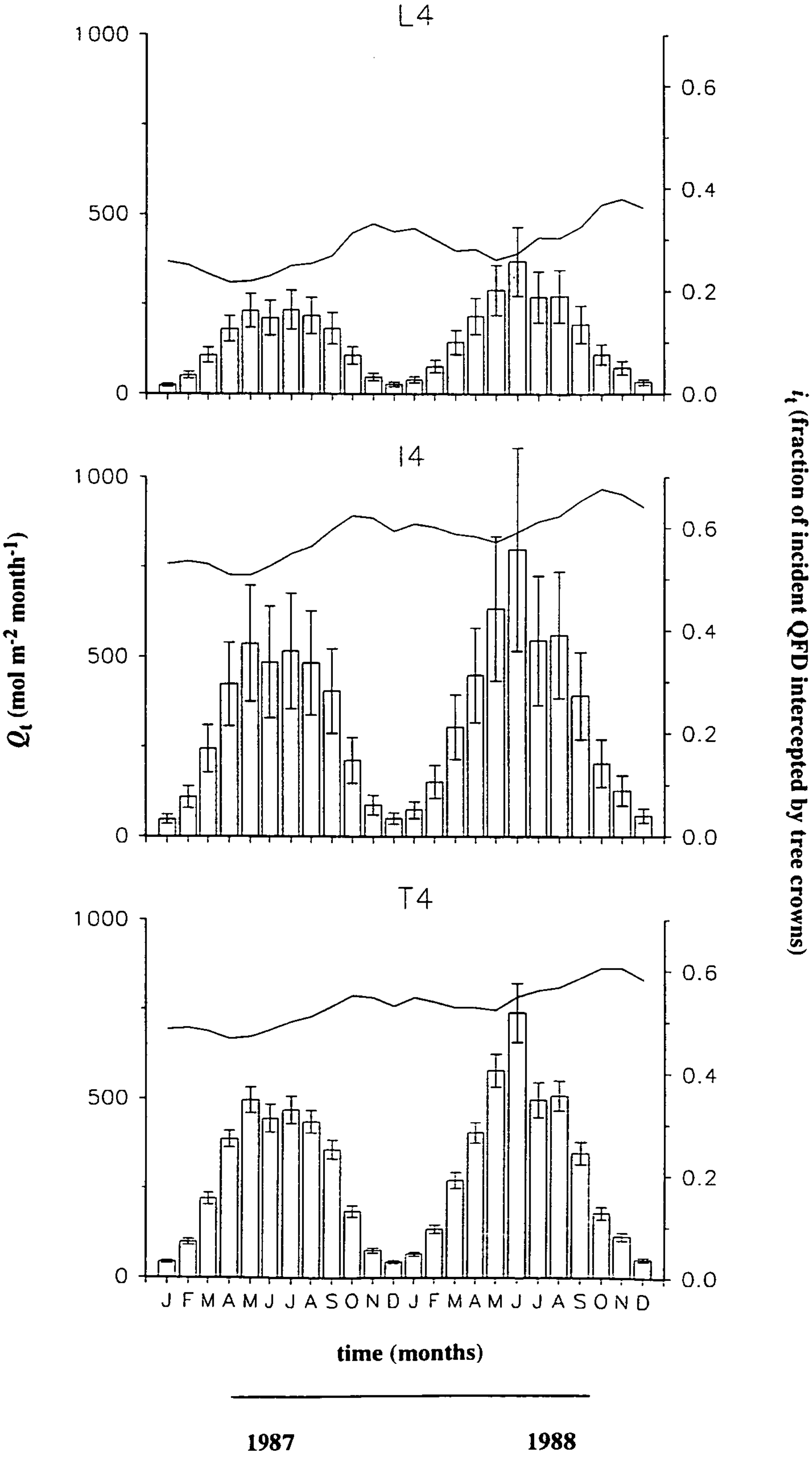


Figure 4.4 b Monthly totals of QFD intercepted by tree crowns, Q_t (bars), and the fraction of incident QFD intercepted, i_t (line), for the 6 m spaced plots in the three stands at Cloich. Stand labels as in Figure 2.1. Error bars show the standard deviation calculated from the cumulated mean QFD intercepted over a month in each grid square (n=9), that is, the lowest level of sampling stratification.

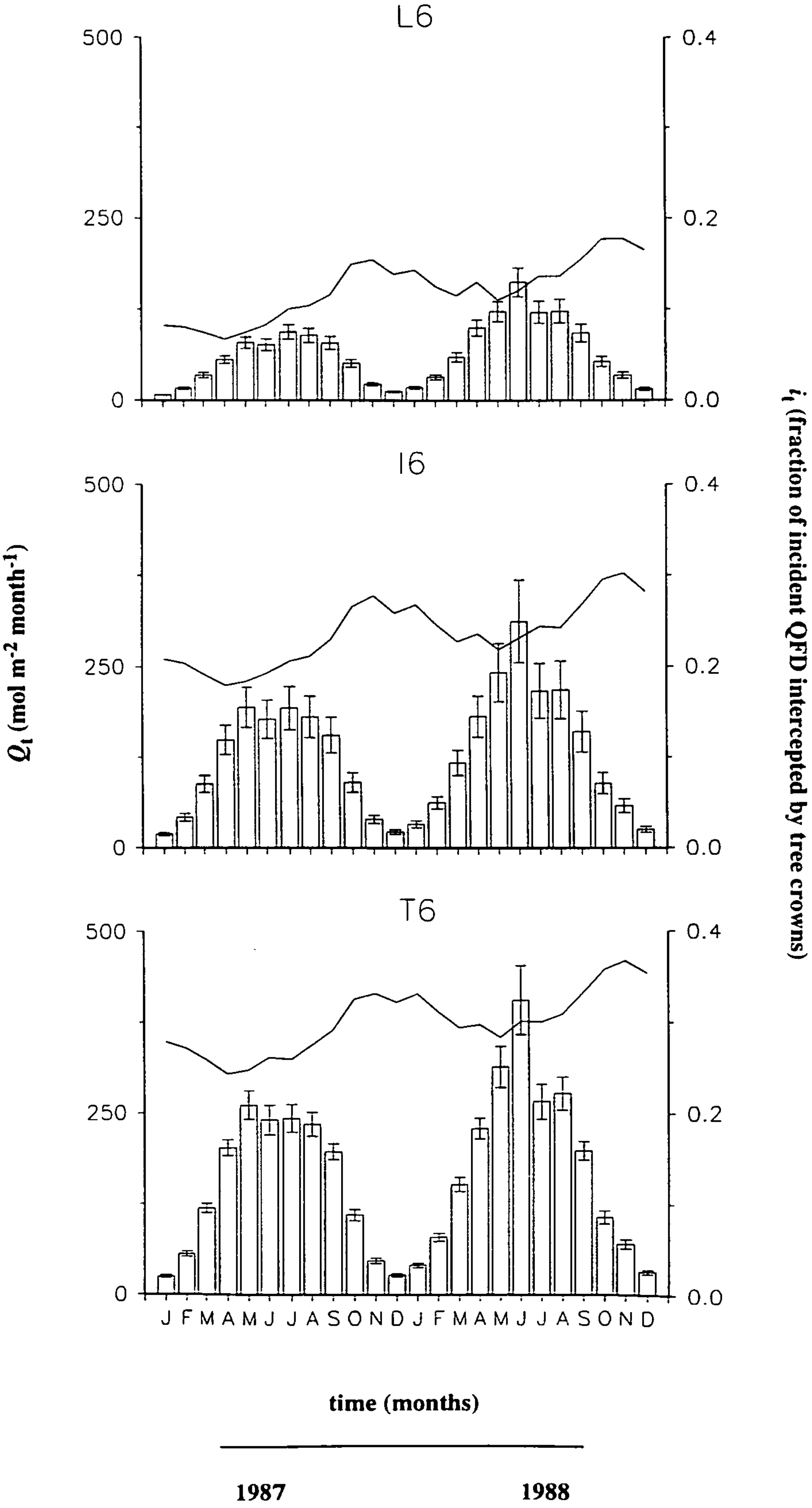


Figure 4.4 c Monthly totals of QFD intercepted by tree crowns, Q_t (bars), and the fraction of incident QFD intercepted, i_t (line), for the 8 m spaced plots in the three stands at Cloich. Stand labels as in Figure 2.1. Error bars show the standard deviation calculated from the cumulated mean QFD intercepted over a month in each grid square (n=9), that is, the lowest level of sampling stratification.

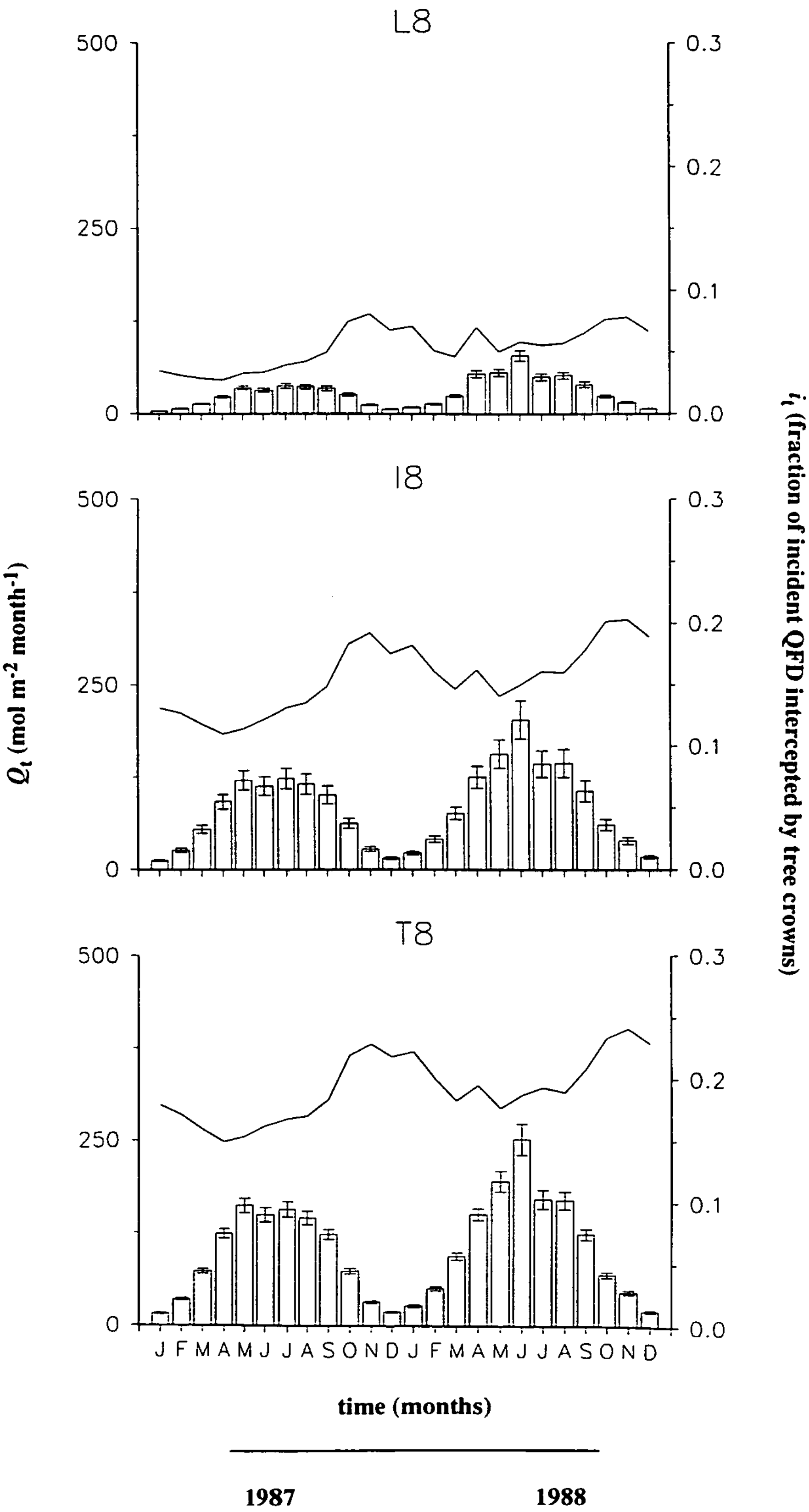


Table 4.4 The quantum flux density intercepted by tree crowns (Q_t) in treatment plots at Cloich in 1987 and 1988 expressed per unit land area.

stand	tree spacing (m)	1987 Q_t (kmol m^{-2} a^{-1}) mean	1987 Q_t sd	1987 i_t	1988 Q_t (kmol m^{-2} a^{-1}) mean	1988 Q_t sd	1988 i_t
L	4	1. 617	0.357	0.15	2.088	0.528	0.30
L	6	0.608	0.064	0.09	0.926	0.112	0.13
L	8	0.259	0.021	0.04	0.417	0.038	0.06
I	4	3.584	1.073	0.54	4.282	1.382	0.61
I	6	1.344	0.199	0.20	1.708	0.290	0.24
I	8	0.856	0.096	0.13	1.126	0.142	0.16
T	4	3.251	0.248	0.49	3.899	0.352	0.55
T	6	1.754	0.123	0.27	2.168	0.187	0.31
T	8	1.104	0.063	0.17	1.364	0.092	0.19

Table 4.5 The quantum flux density intercepted by individual tree crowns (Q_t) in treatment plots at Cloich in 1987 and 1988.

stand	tree spacing (m)	Q_t (mol tree^{-1} a^{-1}) 1987 mean	1987 sd	1988 mean	1988 sd
L	4	25.88	5.70	33.41	8.44
L	6	21.90	2.31	33.32	4.03
L	8	16.57	1.36	26.67	2.43
I	4	57.34	17.18	68.51	22.11
I	6	48.38	7.15	61.48	10.42
I	8	54.77	6.15	72.05	9.067
T	4	52.02	3.96	62.39	5.63
T	6	63.14	4.42	78.06	6.72
T	8	70.63	4.04	87.30	5.88

tree frequency, consistent with lower self shading amongst tree crowns as tree spacing increased (Table 4.5). While the same general trends in Q_t expressed per unit land area occurred in the other two stands, differences in tree sizes between different spacing treatments within stands resulted in a less regular pattern of decline in Q_t per unit land area with increasing tree spacing and obscured trends of increasing Q_t per tree with decreasing tree frequency.

4.3.4. The dry-matter:radiation quotient

Nine values for the quotient, e_t, of above ground dry matter produced and QFD intercepted were calculated from independent measurements of ΔG_{at} (Section 4.3.2) and Q_t (Section 4.3.3) made across the range of tree sizes and spacings at Cloich in each of two years (Table 4.6). While varying from 0.10 g mol^{-1} to 0.31 g mol^{-1}, e_t was similar across spacings, years and tree sizes in the low and intermediate stands, but consistently lower in the tall stand, which was 1 km from the other two stands and had been pruned prior to the experiment. There was a strong linear relationship between QFD intercepted and above ground dry matter produced (Figure 4.5), but significant differences between the slope and intercept of the relationship for the tall stand and that for the other two stands combined, with the two regression equations explaining 99.3% of the variation in the data (Table 4.7).

The intercept for the intermediate and low tree stands combined was not significant ($p = 0.05$) and, therefore, the relationship was assumed to pass through the origin, consistent with an absolute linear proportionality between intercepted QFD and above ground dry-matter production. The slope of the relationship yields a value for e_t for the low and intermediate tree stands of 0.23 g mol^{-1}. Interpretation of the relationship for the tall tree stand is less straightforward, there is a significant negative intercept and the slope of the relationship yields a significantly smaller value of e_t than in the intermediate and low stands of 0.15 g mol^{-1}. Negative intercepts in regressions of above ground dry matter production on intercepted radiation have previously been explained as accounting for the below ground biomass component or severe winter periods when radiation was intercepted but no photosynthesis occurred (Linder, 1985). *Picea sitchensis* can be expected to continue photosynthesis through most of the winter in Scotland (Cannell, 1987) but partitioning of a larger fraction of carbon

Figure 4.5 Relationship between QFD intercepted by tree crowns (Q_t) and above ground dry matter production of trees (G_{at}) measured for low and intermediate (circles) and tall tree (triangles) plots at the Cloich fieldsite in 1987 (solid symbols) and 1988 (open symbols). Treatment plots as in Figure 2.1.

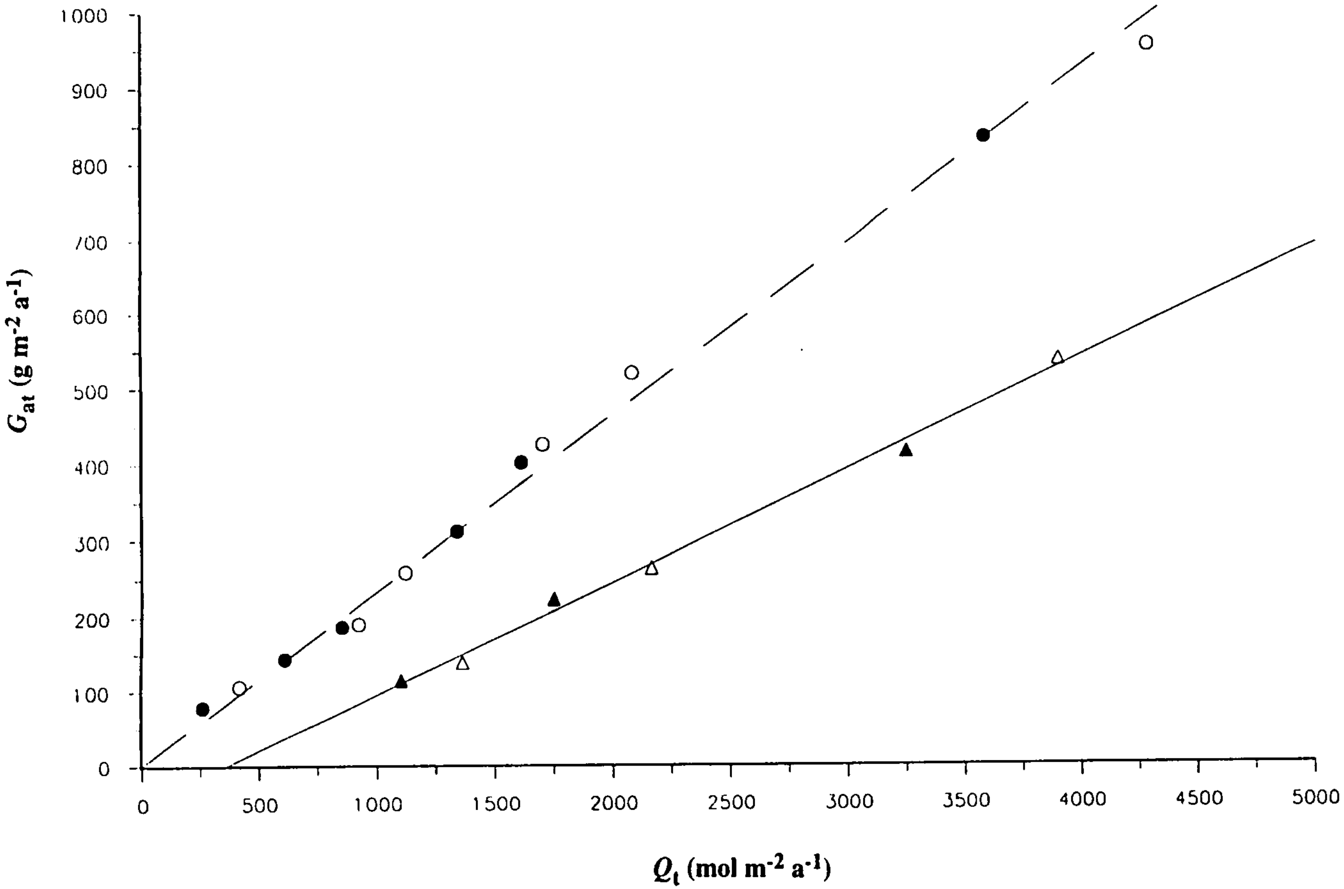


Table 4.6 The dry-matter : radiation quotient, e_t, for above ground dry matter production of trees in treatment plots at Cloich in 1987 and 1988. See Section 4.3.4 for methods of calculation and Figure 2.1 for treatment labels.

		e_t (g mol^{-1})	
stand	**tree spacing (m)**	**1987**	**1988**
L	4	0.25	0.25
L	6	0.24	0.20
L	8	0.31	0.25
I	4	0.23	0.22
I	6	0.23	0.25
I	8	0.22	0.23
T	4	0.13	0.14
T	6	0.13	0.12
T	8	0.10	0.10

Table 4.7 Regression analysis of relationship between the above ground biomass increment (ΔG_{at}) and the QFD intercepted (Q_t) by trees at Cloich in 1987 and 1988.

a) Parameters of the fitted linear regression $\Delta G_{at} = bQ_t + a$ shown graphically in Figure 4.5 where ΔG_{at} is in g m^{-2} a^{-1} and Q_t is in mol m^{-2} a^{-1}

stand (s)	***a* (se)**	***b* (se)**	**r^2**
L and I combined	12.71 (9.71)^{ns}	0.22571 (0.00494)	99.3
T	-53.79 (22.5)	0.14847 (0.00960)	

a1) Analysis of variance for joint regression of all trees versus separate regressions for each stand

Source	**DF**	**SS**	**MS**	**F**	
Overall regression	1	804616.5	804616.5	1956.16	***
Intercepts	1	189906.7	189906.7	461.70	***
Slopes	1	26635.6	26635.6	64.76	***
Residual	14	5758.5	411.3		
Total	17	1026917.4	60406.9		

b) Regression coefficients calculated by Bartlett's (1949) method for fitting a straight line when both variables are subject to error:

$$b = (\underline{y}_3 - \underline{y}_1)/(\underline{x}_3 - \underline{x}_1)$$

where:

$\underline{y}_1$ = mean of the lowest third of the y observations
$\underline{y}_3$ = mean of the highest third of the y observations
$\underline{x}_1$ = mean of the lowest third of the x observations
$\underline{x}_3$ = mean of the highest third of the x observations

stand(s)	**b**
L and I combined	0.2321
T	0.1489

***	significant at p = 0.01
ns	not significant

below ground after thinning at the tall site, in response, for example, to increased stem movement with increasing wind speeds and turbulence around trees (Green, 1990), if it did occur, would be expected to decrease the slope rather than the intercept.

There are three distinguishing features of the tall stand that may have caused differences in e_t. Firstly, the tall stand was located 1 km from the low and intermediate stands and, therefore, there may have been site differences in terms of soil conditions and exposure. Differences in availability of nutrients amongst sites, for example, may affect the efficiency of solar energy conversion into dry matter. Application of nitrogen fertilizer to *Picea sitchensis* with a yield class of 20 in Scotland increased e_t by 30% (Wang *et al.*, 1991). Secondly, the tall stand was pruned prior to the experiment and this may have both complicated the interpretation of the biomass values calculated from basal area measurements in 1987 and 1988 and led to different tree responses to re-spacing, since tree crowns of a similar size to those in the intermediate stand occurred at an elevated height in the tall stand. Thirdly, the tall stand, prior to pruning, comprised older, larger trees (Section 2.1.1) than in the other tree stands, and e_t for woody biomass can be expected to decrease with increasing tree size because of a larger respiration requirement (Jarvis and Leverenz, 1983).

As pruning occurred before the destructive harvest, the biomass of prunings was not measured, and this may have affected the estimation of the slope of the relationship between basal area and above ground tree biomass. Pruning was to a fixed tree height, and if this resulted in removal of a fixed amount of above ground biomass per tree then it would have led to a change in the intercept of the relationship between basal area and above ground dry matter rather than the slope. Conversely, removal of a fixed proportion of the crowns, would have caused a change in the slope rather than the intercept and, therefore, underestimation of the biomass when the regression equation was applied to basal areas measured in subsequent years. The low value for e_t for the tall stand could, therefore, reflect either site conditions limiting the efficiency with which intercepted QFD was utilised (for example low availability of nutrients or effects of waterlogging) or an underestimation of the biomass increment in 1987 and 1988.

There are several considerations in using regression analysis to establish the linearity of the relationship between ΔG_{at} and Q_t and in estimating e_t that merit comment. Firstly, both variables are similarly subject to error in their measurement which can lead to a biased estimate of the regression coefficient (Sprent, 1969). Woodward (1972), recommends a simple means of testing this by calculating the regression coefficient following a method suggested by Bartlett (1949). Application of this method resulted in similar estimates of the slope of the lines to that produced from the conventional linear regression model in Genstat (Table 4.7b). The estimates from the two methods agreed to the first two decimal places, considered appropriate for quoting e_t from the present research, although those produced by Bartlett's method were slightly larger than those from the conventional model. Secondly, pairs of points from the same plots in two consecutive years were used in the analysis. While these are not strictly independent, since the above ground biomass at the end of 1987 is also the initial biomass used in calculating the increment in 1988, there was different incident QFD in each year and the fraction of this intercepted by trees of different size and leaf area was independently measured in each year. Thirdly, the treatment combinations resulted in an uneven distribution of points, with the widely spaced tree plots (8 m spacing) in the intermediate tree stand having a high leverage. Given the remarkable linearity of the plotted points (Figure 4.5) and the high r^2 value for the regression (Table 4.7), any disproportionate influence of the 8 m plots in the intermediate stand can be safely assumed to be negligible.

4.4. Discussion and conclusions

In comparison with closed-canopy forest, the above ground dry matter productivities per unit land area in the widely spaced tree plots at Cloich was low (0.79 to 9.51 Mg ha^{-1} a^{-1}). They can be compared with pole-stage stands of *Picea sitchensis* in Scotland of similar age where a very high productivity of 27 Mg ha^{-1} a^{-1} has been reported from a high density (3 817 trees ha^{-1}) 17-year-old stand in Greskine Forest (Ford, 1982) and a range of 7.71 to 17.75 Mg ha^{-1} a^{-1} over four years in a fertilzer and thinning trial (2 500 and 1 250 trees ha^{-1}) in a 16 to 20-year-old stand (Wang *et al.*, 1991). Given that the stand density of the plots with highest tree frequency at Cloich (625 trees ha^{-1}) was half that of the lowest density stands measured by Wang *et al.* (*op. cit.*) in Tummel Forest, the productivity of the intermediate stand at Cloich was comparable with the thinned, unfertilized stands at Tummel. The productivity of the tall stand at Cloich was, in comparison, very low. Annual grass productivity of 8.08 to 9.29 Mg ha^{-1} in open plots (with no tree cover) at the Cloich site measured in 1987 and 1988 (Sibbald, Griffiths and Elston, 1994) are comparable with the 4 m spaced intermediate tree plot. Clearly the low productivity per unit land area of widely spaced trees is to be expected and would be compensated for in an agroforestry situation by the productivity of the understorey.

Above ground dry matter production was proportional to the amount of QFD intercepted within tree stands at Cloich, irrespective of tree spacing, confirming the Monteith hypothesis. The dry-matter:radiation quotient of 0.23 g mol^{-1} (1.06 %) in the low and intermediate stands at Cloich was lower than that reported for closed canopy *Picea sitchensis*, in fertilized (0.43 g mol^{-1} or 2.0%) and unfertilized (0.33 g mol^{-1} or 1.5%) plots at Tummel (Wang *et al.*, *op. cit.*) and high density plots (1.6%) at Greskine (e_t estimated by Linder, 1985 from productivity and leaf area data of Ford, 1982). However, it is similar to that reported for young *Eucalyptus globulus* in Australia and falls well within the range (0.48 to 2.13 %) estimated for 17 forest ecosystems globally (coarse root biomass included) by Jordan (1971) but well below a typical value for agricultural crops of 2.8 % (Monteith, 1977).

While gross differences in tree size and spacing did not significantly affect e_t within the low and intermediate stands at Cloich, the tall tree stand had a significantly lower quotient. This may have been caused by site differences, the effects of pruning on the efficiency of utilization of intercepted QFD and/or underestimation of biomass production in 1987 and 1988 (Section 4.3.4).

Different values of e_t, even for the same tree species, have been reported from different sites in the literature (discussed above). It is reasonable to assume that site factors, such as nutrient availability, are limiting e_t at the Cloich site generally. Even the higher value of e_t for the low and intermediate tree stands is only about a third of the potential maximum of 0.6 g mol^{-1} suggested by Wang *et al*, 1991. They set out the maximum efficiency of solar conversion for *Picea sitchensis* in Scotland as defined by the quantum efficiency of photosynthesis (constraining e_t to 5%), the efficiency of utilization of beam radiation within the tree crown (further constraining e_t to 4%) and the requirements of respiration (further constraining e_t to 2.8%) and demonstrated a 30% increase in e_t from 1.5 % to almost 2.0 % in response to nitrogen fertilization. Increasing nitrogen availability may have increased the photosynthetic rate of the existing leaf area and/or reduced the proportion of carbon allocated to roots. Sibbald *et al.*, (1994) report unshaded annual grass productivity as more than 10% higher adjacent to the tall stand than adjacent to the low and intermediate stands at Cloich. Since the pasture was grown in boxes containing imported soil, this indicates possible differences in the atmospheric conditions at the two sites, which could have been aggravated for trees at the tall site by removal of the lower part of the crown leading to increases in wind speed and turbulence within the stand (Green, 1990).

Thinning (Madgwick, Jackson and Knight, 1977) and pruning (Forrest and Ovington, 1970) were found to increase the apparent solar conversion efficiency of tree stands at sites where water may have limited photosynthesis. Pruning in such circumstances would remove some of the transpiring leaf surface, which would explain why the remainder was able to utilise intercepted QFD more effectively. Water availability is not expected to limit growth at Cloich. Linder (1985), has suggested that pruning of lower branches may result in a smaller change in productivity than would be expected from the amount of foliage removed and the reduction in QFD intercepted, since the lower branches are less productive than those higher in the crown. However, the crown structure of *Picea sitchensis* (Section 3.3.2.8.1) ensures penetration of light to lower branches, and at the tree spacings in the present agroforestry research, it is unlikely that lower branches would have received inadequate illumination for efficient photosynthesis. It may be expected that pruning, would lead to a lower maintenance requirement and, therefore, an increase in e_t, rather than the apparent decrease observed at Cloich. The lack of any effect of the very different tree stocking densities within stands on e_t at Cloich, suggests that changes in the tree leaf area *per se* are unlikely to have caused changes in e_t.

In conclusion, the strong linear relationship between intercepted QFD and above ground tree productivity irrespective of tree spacing confirms the Monteith hypothesis and the suitability of using empirical relationships between intercepted QFD and tree productivity to investigate the effects on tree productivity of changing tree stocking density and arrangement on a particular site. Comparison of the values of e_t obtained at Cloich with those in the literature suggest that e_t may often be limited by site factors, particularly fertility, on forest soils in the uplands of the UK. Since agroforestry may well involve combination of trees with fertilized pasture or crops e_t may not remain conservative with respect to agroforestry treatments when below-ground as well as above-ground interactions are taken into account and the uptake of nutrients by trees may depend on inter and intra species competition mediated by plant spacing and arrangement.

5. Understorey grass growth in relation to transmitted and intercepted light

5.1. Introduction

In agroforestry the QFD available for growth of the understorey is influenced by the tree crowns above. The amount, distribution and spectral composition of QFD will thus be modified. The aim of the research reported in this chapter was to analyse the effects of tree crowns on the spatial variability of QFD incident on the understorey and to relate this to pasture productivity. Following on from the establishment of a linear relationship between interception of QFD and growth of trees regardless of spacing on a particular site, the consistencey of the radiation : dry matter quotient for grass (e_g) of various species subject to various degrees of shade was investigated.

5.2. Methods

5.2.1 Measurement of QFD transmitted to the understorey

An array of 81 quantum sensors (Section 2.1.3.5) re-randomised in a stratified sampling pattern every two weeks (Section 4.2.2) was used throughout 1988 across the tree height and spacing treatments at Cloich to measure transmitted radiation incident to the understorey.

5.2.2 Measurement of spectral composition of light transmitted to the understorey

Measurements of the red : far-red ratio (R:FR) were made at the tall tree site at Cloich on 81 days in the period May to September 1988, simultaneously above and below the tree crowns, using a pair of ratio sensors each comprising two photodiodes filtered so that one photodiode sensed a narrow waveband centred at 660 nm and the other a narrow waveband centred at 730 nm (SKR 110, Skye Instruments, Llandrindod Wells). The sensors were connected to a datalogger (Delta logger, Delta T Devices, Cambridge) and scanned every 10 seconds with hourly means recorded. The sensor located below the tree crowns was repositioned each day using a non-repeating stratified random sampling pattern such that the sensor was located for one day randomly within each grid square of each sampling unit of every sub plot (Figure 2.2) at the tall tree site at Cloich. Interpretation of results was made difficult by irregularities in the cross calibration of the two sensors. Subsequently independent commercial calibration showed this to be caused by different responses in the 730 nm band in the two sensors and problems in the cut-off of the response in both wavebands. Subsequently both sensors were modified by the manufacturer and recalibrated. Thus while the modification of the R:FR ratio by tree crowns could not be reliably determined from these data, the readings from the sensor located below the tree crowns provided some indication of the mean R:FR for each tree spacing treatment at the tall site at Cloich.

5.2.3 Permanent sward phytometers (MLURI sward boxes)

5.2.3.1 Layout and sampling

The positioning of the MLURI sward boxes was fully described previously (section 2.1.1) and remained constant throughout the experimental period.

5.2.3.2 QFD incident to and intercepted by the sward

Mean values of quantum sensors for each grid square for each grass growing period were used to estimate QFD incident on grass boxes in each treatment. In addition, during 1987, 49 miniature quantum sensors (Section 2.3) were placed randomly beneath the grass canopy throughout grass boxes in the tall narrow treatment for one grass growth period and subsequently in a systematic grid in one different, randomly chosen, box for each of three growing periods. Analyses of these data as previously for sensors in array 1 (Section 4.2.2) indicated that measurement of mean light intercepted per box across treatments was impractical with the number of sensors available because of the patchiness of grass growth in shaded conditions resulting in large variability of grass cover and hence transmitted QFD.

5.2.3.3 Growth

The harvest procedure for MLURI grass boxes was previously described in full (Section 2.1.3.4).

5.2.4 Temporary grass phytometers (grass pots)

As it was impractical to measure intercepted QFD in large permanent sward boxes (Section 5.2.3.2), smaller pots of grass were put out in the field for short time periods in the tall stand at Cloich as temporary grass phytometers. These were used to investigate responses of young grass of different species to shaded conditions in the field in midsummer and autumn, rather than seasonal sward productivity for which the permanent phytometers were more appropriate. This permitted calculation of e_g for different grass species under different levels of shade occurring in the field under agroforestry conditions.

5.2.4.1 Pot preparation and layout

Plastic plant pots, diameter 18 cm at top, 15 cm at bottom, height 16 cm were filled to 1 cm from the top with a potting compost with slow release N; no fertilizer was subsequently applied. The composition of the compost was 25 % sand, 75 % peat. To every 100 litres of this was added; 15 g potassium nitrate, 15 g potassium sulphate, 120 g superphosphate, 295 g magnesium limestone, 235 g calcium carbonate, 35 g fritted trace elements and 75 g slow release N fertilizer (Gold N, SAI, Newbridge). Thirty six pots were each sown with 100 seeds of one grass variety (all supplied by SAI, Newbridge) *Lolium perenne* (cv. Contender), *Phleum pratense* (cv. Erecta RvP) and *Dactylus glomerata* (cv. Jesper) on 29/6/88. The pots were maintained well watered, and in natural light in an unheated greenhouse until 28/7/88 when the swards were cut to pot surface height, thinned to 50 tillers per pot and transferred to the field. Pots were allocated in a stratified random arrangement, one to the centre of each grid square throughout the 4, 6 and 8 m spacing treatments in the tall stand at Cloich such that each species appeared once in each grid square position. This layout was used to obtain a range of shade representative of the treatments for regression of growth on incident and intercepted light, rather than to provide comparative data on overall productivity from the treatments, for which the permanent phytometers (Section 5.2.3) were more appropriate.

5.2.4.2 Light incident to and intercepted by sward

QFD sensors from array 1 and array 2 (Section 2.1.3.5) were located centrally at pots in grid positions 1, 3 and 8 for each grass species in each treatment. Intercepted light was calculated as the difference between the two sensors.

5.2.4.3 Harvest and sward structural measurements

Grass in each pot was harvested by cutting to the rim of the pot on the 27/7/88 (on transfer to the field), then at fortnightly intervals on the 10/8/88, 24/8/88, 7/9/88, subsequently at the end of the growing season on the 9/10/88 and finally near the beginning of the next season on 17/4/89. The cut samples were oven dried at 80 °C to constant weight and dry matter recorded. Prior to the first harvest three tillers per pot from 10 pots per species were destructively sampled. The length and the width of each leaf, at the mid point, was measured using vernier callipers and then projected leaf area was measured using an optical planimeter (LI-600, LiCor, Nebraska). Linear regressions of leaf area on leaf length x leaf width were used to obtain relationships (Section 5.3.1) which were subsequently used for predicting leaf area from length and width measurements in the field. Immediately prior to all harvests, sward height was measured at 10 random positions per pot, and prior to harvests 1 (10/8/88) and 2 (24/8/88), pots in grid positions 1,3,and 8 were sampled in more detail for sward structure. This involved a count of the number of tillers per pot, a count of the number of each class of leaves per tiller (emerging, fully emerged, senescent) on 10 randomly selected tillers per pot and the length and width of five randomly selected leaves for each leaf class per pot. This enabled estimates of leaf area per pot to be made and hence calculation of specific leaf area by dividing leaf area per pot by dry mass per pot.

5.3. Results and discussion

5.3.1 Relationship between leaf dimensions and leaf area for grass species

Single sided leaf area increased linearly with the product of leaf length and leaf width at the mid point of the leaf (Figure 5.1a). Linear regression analysis revealed that there were significant differences in the slope of the relationship for different species (Table 5.1a1) commensurate with leaves of different species exhibiting different leaf shape and characteristic taper. There was no significant difference between leaves grown in full sunlight prior to being transferred to the agroforestry plots and those sampled later having experienced various degrees of shade.

The 95 % confidence limits for the intercepts for all species included zero and they were therefore omitted. Fitting separate slopes for each species (Table 5.1a and Figure 5.1b-d) forced through zero explained 85.2 % of the variability in the data and were subsequently used to estimate leaf area from measurements of leaf length and width made in the field (Section 5.3.2).

5.3.2 Grass growth and canopy structure

The above ground dry matter production (G_{ag}) of the ryegrass on the temporary phytometers was substantially longer after 15 days in the field at harvest 1 than for cocksfoot or timothy, which were not significantly different from eachother (Figure 5.2a). G_{ag} varied from less than 4 g m^{-2} day^{-1} to over 10 g m^{-2} day^{-1} across the various grass species and tree spacing treatments and compares with remarkably constant summer growth rates of sown perennial ryegrass cultivars in small plots of 7 g m^{-2} day^{-1} in full sunlight reported by Sheehy and Peacock (1977). The tree spacing treatments of 4 m, 6 m and 8 m resulted in mean annual QFD transmittances of 0.44, 0.68 and 0.80 respectively (Table 5.4).

The ranking of the species in terms of productivity, ryegrass > cocksfoot > timothy, remained the same irrespective of tree spacing treatment. As would be expected, within each species there was a clear trend of decreasing yield with decreasing tree spacing. The presence of trees at 4 m spacing with crowns touching, reduced grass productivity to less than half of that in the open control for all species (Table 5.2), whereas yields of ryegrass and cocksfoot with trees at 8 m spacing were more than 90 % of that achieved in the open. Sward height, however, was remarkably constant across the species and shading treatments (Figure 5.2b) so that the height/dry matter ratio was lower for ryegrass than the other two species and substantially increased with decreasing tree spacing within each species (Figure 5.2c).

Figure 5.1 Linear relationships between leaf dimensions and leaf area for *Dactylis glomerata* denoted by c, *Lolium perenne* denoted by r, and *Phleum pratense* denoted by t, grown in pots and measured before (open symbols) and after (shaded symbols) the pots were placed in various degrees of shade at the Cloich and Dunkeld agroforestry field experiments in July 1988.

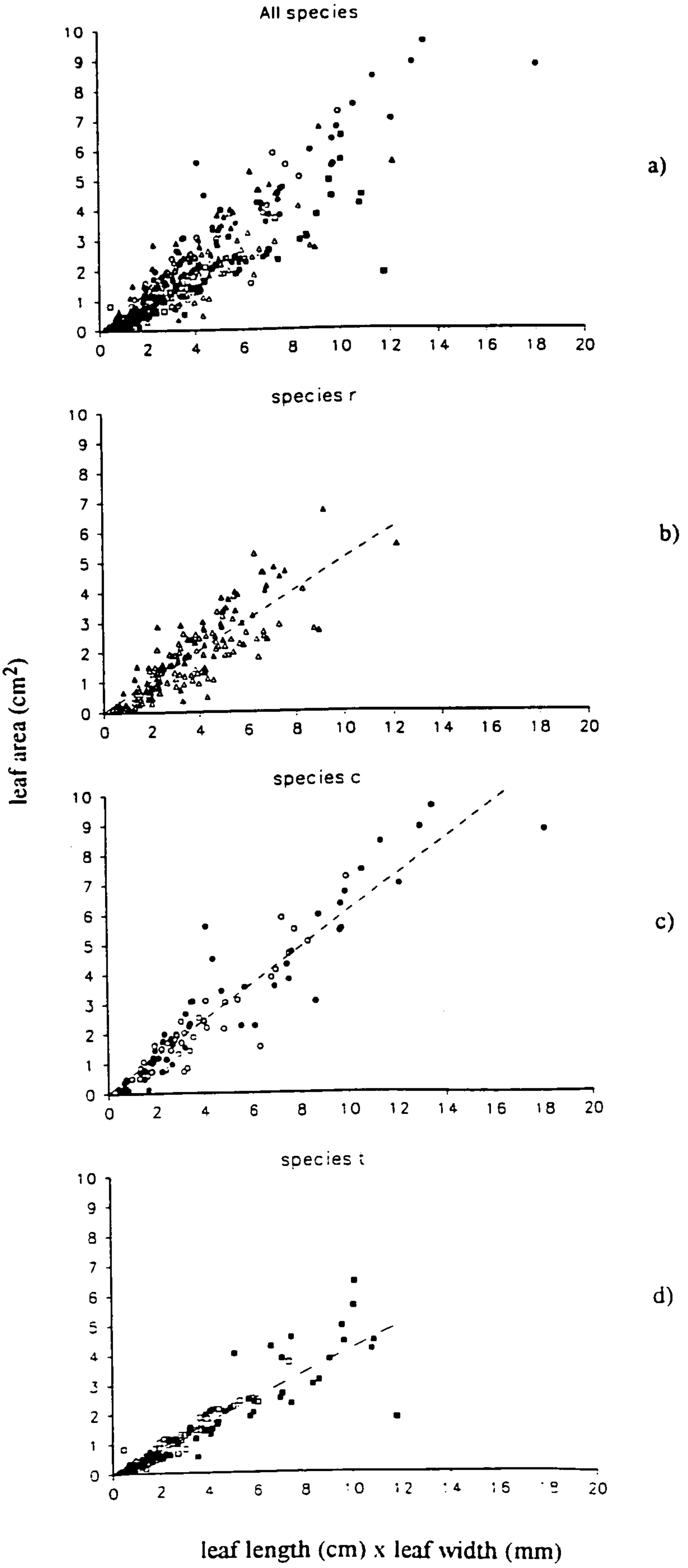


Table 5.1 Regression analysis of relationship betwen leaf dimensions and leaf area for three grass species grown in pots. See Figure 5.1 for details of species labels and text for sampling strategy. F_g = leaf area (cm^2), F_{lw} = leaf length (cm) x leaf width (mm).

a) Parameters of the fitted linear regression $F_g = bF_{lw}$ shown graphically in Figure 5.1 .

species	***b*** **(se)**	**r^2**
C	0.6195 (0.0183)	
R	0.5356 (0.0297)	85.2
T	0.4450 (0.0269)	

a1) Analysis of variance for joint regression of all species versus separate regressions for each species, the estimated intercepts were not significant in a t test.

Source	**DF**	**SS**	**MS**	**F**	
Overall regression	1	927.6121	927.6121	2357.83	***
Intercepts	2	25.7325	12.8662	32.70	***
Slopes	2	16.6978	8.3489	21.22	***
Residual	423	166.4160	0.3934		
Total	428	1136.4583	2.6553		

a2) Analysis of variance for joint regression versus separate regressions for each species with the intercept term omitted.

Source	**DF**	**SS**	**MS**	**F**	
Omission of intercept term	-1	-1243.3042	1243.3042	3139.94	***
Overall regression	1	2164.2637	2164.2637	5465.80	***
Slopes	2	46.8178	23.4089	59.12	***
Residual	426	168.6809	0.3960		
Total	428	1136.4583	2.6553		

**	significant at p = 0.05
***	significant at p = 0.01
ns	not significant

This indicates that the bulk density of swards in the temporary phytometers was reduced by increasing shade, which could be expected to have consequences for the utilization of swards by grazing animals if occurring on a field scale. Individual performance of grazing animals is determined by the quantity and quality of herbage they ingest, with the rate of intake being determined primarily by sward canopy characteristics (Maxwell, 1990). The depth of the leafy layer in the canopy and the bulk density within this are significant determinants of bite size in sheep grazing sown ryegrass swards (Hodgson, 1982) and, therefore, the lower bulk densities of shaded swards may result in lower intake by animals. While sheep may respond to reduced bite size by taking more bites per minute and grazing for longer, such compensatory measures cannot generally counter reduced intake per bite so that the net effect of smaller bite size is a decrease in daily intake rate (Hodgson and Grant, 1985; Penning, 1986).

The reduction in G_{ag} with increasing shading for all species contrasts with previous experimentation with ryegrass sown in pots, where reduction of ambient illumination by 50 % for periods of 24 days during August and September had little effect on herbage yield (mainly leaf blade) although root and stubble growth were reduced (Thomas and Davies, 1978). However, neutral density shade was used in the experiment which would have reduced the amount of QFD but would not have modified the spectral composition of transmitted radiation. The tree crowns in the present agroforestry experiment clearly lowered the R:FR ratio experienced by the understorey (Table 5.3). While there may be instantaneous fluctuations in the R:FR ratio of normal sunlight, long term, mean values are remarkably constant at about 1.10 (Holmes and Smith, 1977). R:FR ratios of from 0.15 to 0.76 have been reported under coniferous woodland (Morgan and Smith, 1981) and the reduction in the ratio to be log-linearly related to leaf area index (Smith, 1986). It has also been established that shade avoiding plants respond morphologically to low R:FR independently of the QFD (Smith, 1986). The natural vegetational shade under the tree crowns at Cloich thus comprises two confounded environmental factors, QFD and the R:FR ratio that can be expected to have independent physiological effects - the former affecting photosynthetic rate and the latter the pattern of growth and development.

The more detailed sward structure measurements (Figure 5.3) were made on a small number of replicate pots (n = 3, Section 5.2.4.3) resulting in large standard errors for most of the variables

Figure 5.2 Pasture production in relation to shading in temporary grass phytometers in agroforestry treatments at Cloich at the first harvest: a) above ground dry matter production b) sward height and c) sward height/dry matter, for *Lolium perenne* (clear bars), *Dactylis glomerata* (dotted bars), *Phleum pratense* (striped bars) with their standard errors. C on the x axis denotes the control with no trees.

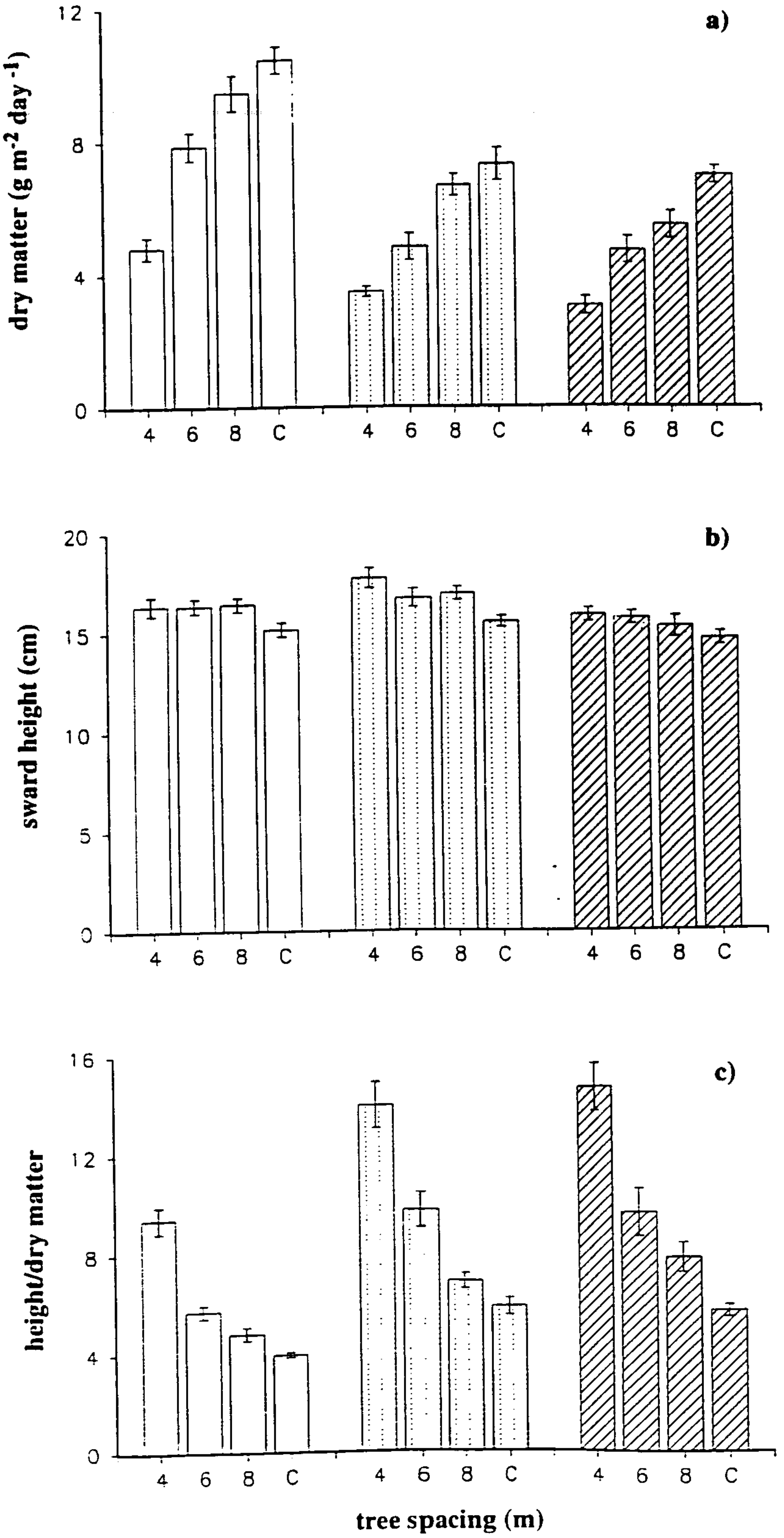


Table 5.2 Relative pasture productivity in relation to shading for temporary grass phytometers in agroforestry treatments at Cloich at the first harvest. Productivity is expressed as a percentage of the control with no trees (see Figure 5.2a for biomass measurements and their variability). Grass species labels as in Figure 5.1

Grass species	Tree spacing (m)	Relative productivity
C	4	0.47
	6	0.66
	8	0.91
R	4	0.46
	6	0.75
	8	0.91
T	4	0.43
	6	0.67
	8	0.78

Table 5.3 Mean daily values of the red : far red ratio (R:FR) of transmitted light in agroforestry treatments measured in summer 1988 at the tall tree stand at Cloich with their standard errors in brackets (n = 27). See Section 5.2.2 for details of the measurements and sampling.

Tree spacing (m)	R:FR
4	1.080 (0.1954)
6	0.980 (0.1959)
8	0.733 (0.1415)

measured. However, a number of trends are discernable. For all species, tiller density decreased and specific leaf area increased in shaded conditions as has been found previously (Thomas and Davies, 1977; Thomas and Norris, 1981). Leaf area index was generally depressed in the 4 m tree spacing treatment whereas the number of leaves per tiller remained constant. Leaf shape, described as the ratio of length to width (Figure 5.3f) was influenced by shade in cocksfoot and timothy (longer and thinner leaves in shade) but not in ryegrass.

A higher tiller density and lower specific leaf area were the principal differences between the ryegrass sward structure and that of the less productive cocksfoot and timothy. The higher tiller density may have led to a more even distribution of leaf area in ryegrass so that an even distribution of smaller tillers with thicker leaves may have resulted in more light being intercepted and hence higher productivity (Section 5.3.5).

5.3.3. Spatial distribution of QFD incident to the sward

The mean annual QFD transmitted to the understorey in the agroforestry plots at Cloich during 1988 varied from 39 % to 94 % of that in the open (Table 5.4). Comparison of the standard errors in Table 5.4 indicates that, overall, point to point spatial variability increased with decreasing tree spacing within each stand and was lower in the tall stand, where the trees had been basal pruned to 1.3 m than in the other two stands where the tree crowns extended to the ground level. This is commensurate with a more even spatial distribution of transmitted QFD as the height of the base of the overstorey canopy increases. Within each treatment plot the spatial variability was larger in the corner grid square positions (numbers 1, 3, 7 and 9 in Figure 2.1) most heavily affected by the presence of the tree crowns which was also reflected in lower QFD transmittances in these grid square positions (Figure 5.4). These effects were most pronounced in the low and intermediate tree height stands with crowns down to ground level and at closer tree spacings.

There were significant differences between row (north-south) and column (east-west) means in the 4 m tree spacing treatments for all three stands except for rows in the T4 treatment ($p = 0.05$, ANOVA in Genstat treating annual grid square means as observations and so testing the variance ratio for rows and columns with 2 and 4 degrees of freedom). Neither east-west nor north-south

Figure 5.3 Sward structure in relation to shading in agroforestry treatments for temporary grass phytometers at Cloich for the first harvest: *Lolium perenne* (clear bars), *Dactylis glomerata* (dotted bars), *Phleum pratense* (striped bars) with their standard errors.

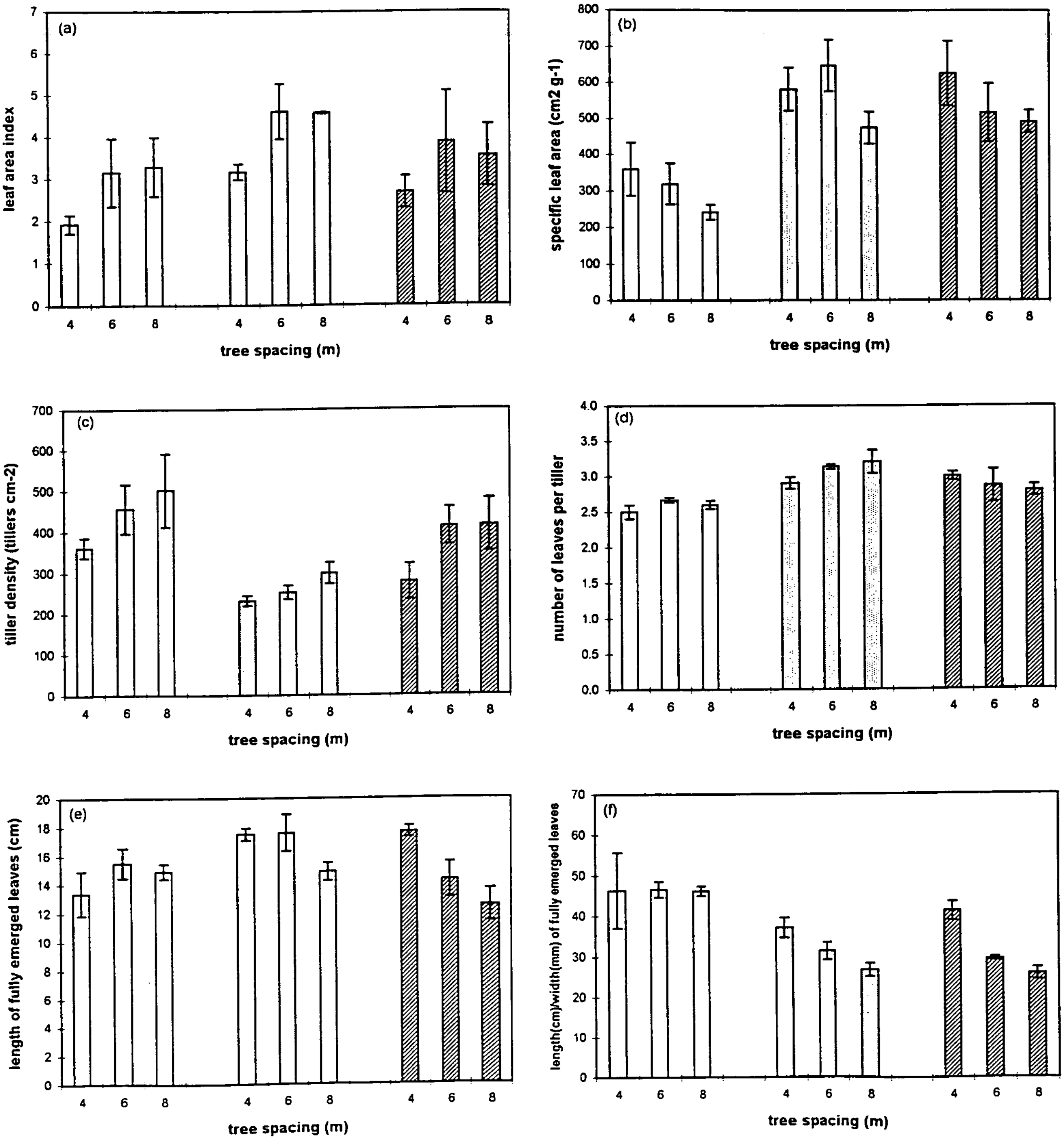


Figure 5.4 Mean annual QFD transmittance for grid square positions in each tree height and spacing treatment at Cloich (see Figure 2.1 for details of the experimental layout and treatment labels and Section 5.2.1 for details of the spatial sampling pattern). Numerical values and their variability are shown in Table 5.4.

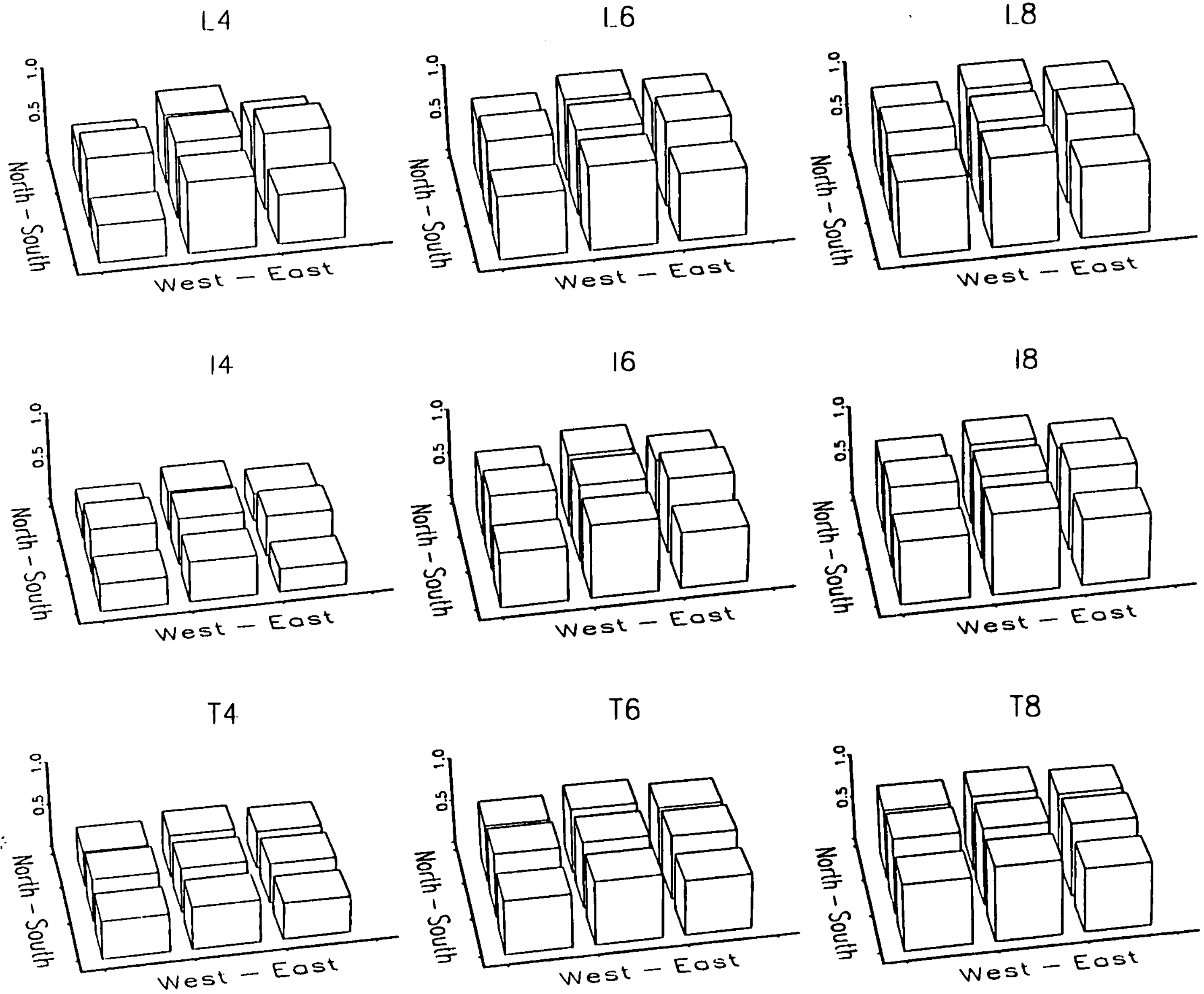


Table 5.4 Mean annual OFD transmittance with standard error in brackets for grid square positions in each tree height and spacing treatment at Cloich (labelling as on Figure 5.4). Transmittances of larger than unity in the L8 stand are as measured and are attributed to measurement error (<3%).

L4

	West		*East*	All
North	0.492 (0.2286)	0.793 (0.0424)	0.569 (0.2877)	0.618 (0.1671)
	0.782 (0.0497)	0.861 (0.0295)	0.864 (0.0267)	0.836 (0.0348)
South	0.427 (0.2396)	0.804 (0.0287)	0.563 (0.2457)	0.598 (0.1470)
All	0.567 (0.1491)	0.819 (0.0334)	0.665 (0.1628)	0.684 (0.1074)

L6

	West		*East*	All
North	0.765 (0.2442)	0.937 (0.0246)	0.802 (0.2431)	0.835 (0.1616)
	0.938 (0.0174)	0.966 (0.0173)	0.964 (0.0161)	0.956 (0.0169)
South	0.707 (0.2565)	0.951 (0.0291)	0.770 (0.2581)	0.809 (0.1679)
All	0.803 (0.1595)	0.952 (0.0236)	0.845 (0.1614)	0.867 (0.1104)

L8

	West		*East*	All
North	0.854 (0.2404)	1.022 (0.0114)	0.911 (0.2202)	0.929 (0.1498)
	1.000 (0.0200)	1.023 (0.0132)	1.012 (0.0189)	1.011 (0.0173)
South	0.841 (0.2561)	1.010 (0.0153)	0.813 (0.2643)	0.888 (0.1672)
All	0.898 (0.1635)	1.018 (0.0133)	0.912 (0.1588)	0.943 (0.1079)

I4

	West		*East*	All
North	0.283 (0.1001)	0.442 (0.0500)	0.317 (0.0928)	0.347 (0.0766)
	0.498 (0.0256)	0.517 (0.0218)	0.446 (0.0414)	0.487 (0.0291)
South	0.296 (0.0949)	0.436 (0.0338)	0.253 (0.0739)	0.328 (0.0625)
All	0.359 (0.0643)	0.465 (0.0345)	0.339 (0.0655)	0.388 (0.0527)

I6

	West		*East*	All
North	0.667 (0.1851)	0.818 (0.0323)	0.662 (0.1744)	0.716 (0.1236)
	0.838 (0.0184)	0.863 (0.0168)	0.842 (0.0158)	0.847 (0.0170)
South	0.605 (0.1820)	0.806 (0.0338)	0.622 (0.1734)	0.677 (0.1206)
All	0.703 (0.1180)	0.829 (0.0274)	0.709 (0.1113)	0.747 (0.0824)

I8

	West		*East*	All
North	0.763 (0.1812)	0.898 (0.0179)	0.770 (0.1775)	0.811 (0.1197)
	0.904 (0.0233)	0.925 (0.0230)	0.913 (0.0200)	0.914 (0.0221)
South	0.695 (0.1824)	0.895 (0.0236)	0.735 (0.1907)	0.775 (0.1239)
All	0.787 (0.1211)	0.906 (0.0215)	0.806 (0.1220)	0.833 (0.0853)

T4

	West		*East*	All
North	0.392 (0.0344)	0.478 (0.0177)	0.424 (0.0355)	0.431 (0.0286)
	0.474 (0.0244)	0.492 (0.0160)	0.439 (0.0171)	0.469 (0.0192)
South	0.414 (0.0358)	0.464 (0.0171)	0.399 (0.0258)	0.426 (0.0259)
All	0.427 (0.0312)	0.478 (0.0169)	0.421 (0.0260)	0.442 (0.0244)

T6

	West		*East*	All
North	0.641 (0.0804)	0.733 (0.0194)	0.654 (0.0578)	0.676 (0.0511)
	0.707 (0.0300)	0.739 (0.0170)	0.712 (0.0295)	0.720 (0.0254)
South	0.591 (0.0634)	0.700 (0.0162)	0.606 (0.0650)	0.633 (0.0465)
All	0.647 (0.0568)	0.724 (0.0176)	0.658 (0.0498)	0.676 (0.0405)

T8

	West		*East*	All
North	0.782 (0.0685)	0.845 (0.0178)	0.780 (0.0662)	0.802 (0.0499)
	0.839 (0.0255)	0.857 (0.0170)	0.818 (0.0315)	0.838 (0.0245)
South	0.733 (0.0617)	0.829 (0.0169)	0.707 (0.0719)	0.756 (0.0485)
All	0.785 (0.0511)	0.844 (0.0172)	0.768 (0.0556)	0.799 (0.0406)

effects were significant in the low tree height stand at 6 m and 8 m tree spacing, which is attributable to the trees being small, whereas the north-south effect, but not the east-west effect, was significant in the intermediate tree height stand at both 6 m and 8 m tree spacings.

Where orientation effects were significant, transmittance was highest in the central area of the plots and higher in the north of the plots than the south confirming earlier modelling results (Anderson, 1991). There was no consistent east-west effect. Clearly the impact of the solar track on spatial distribution of transmitted QFD depends on tree dimensions and will also be influenced by the extent and orientation of slope at the site and there is some confounding of these factors in the tree stands at Cloich (Section 2.1.1).

5.3.4. Relationships between QFD incident to sward and productivity

The QFD transmitted to any part of the understorey determines the ceiling of productivity for the pasture located there and may, therefore, be expected to explain a large proportion of the variance in the pasture growth rate of the temporary phytometers in the period up to the first harvest where water and nutrients are not expected to limit growth. While the QFD incident (Q) to the phytometers was strongly positively correlated with G_{ag} (Figure 5.5) there were significant differences in the slope and intercept of the regression of G_{ag} on Q for the perennial ryegrass when compared with the other two grass species (Table 5.5) and only 75 % of the variation in the data was explained by the regression. The significant positive intercept for ryegrass implies that some growth would be achieved without any photosynthesis occurring, which is commensurate with stored carbohydrate being mobilised from stubble and/or the root system in order to re-establish leaf area after defoliation. Leafe (1972) measured net CO_2 uptake and found that a perennial ryegrass sward cut in early July had a negative carbon balance for several days after cutting. Thomas and Davies (1978) explained similar foliage productivity in pot-grown perennial ryegrass subject to different levels of shade by herbage production after defoliation initially being maintained from mobilization of stubble resources and later, once the plants began to increase in mass, by a lower proportion of photosynthate being transferred to shoot bases and the root system in shaded as opposed to non-shaded plants. This highlights the dangers of relating herbage yield to current QFD and photosynthesis. An ability in perennial ryegrass to utilize

Figure 5.5 Linear relationships between dry matter production and incident QFD for *Dactylis glomerata* denoted by c (shaded circles), *Lolium perenne* by r (open triangles), and *Phleum pratense* denoted by t (open boxes), grown in pots at the Cloich and Dunkeld agroforestry field experiments in July-August 1988.

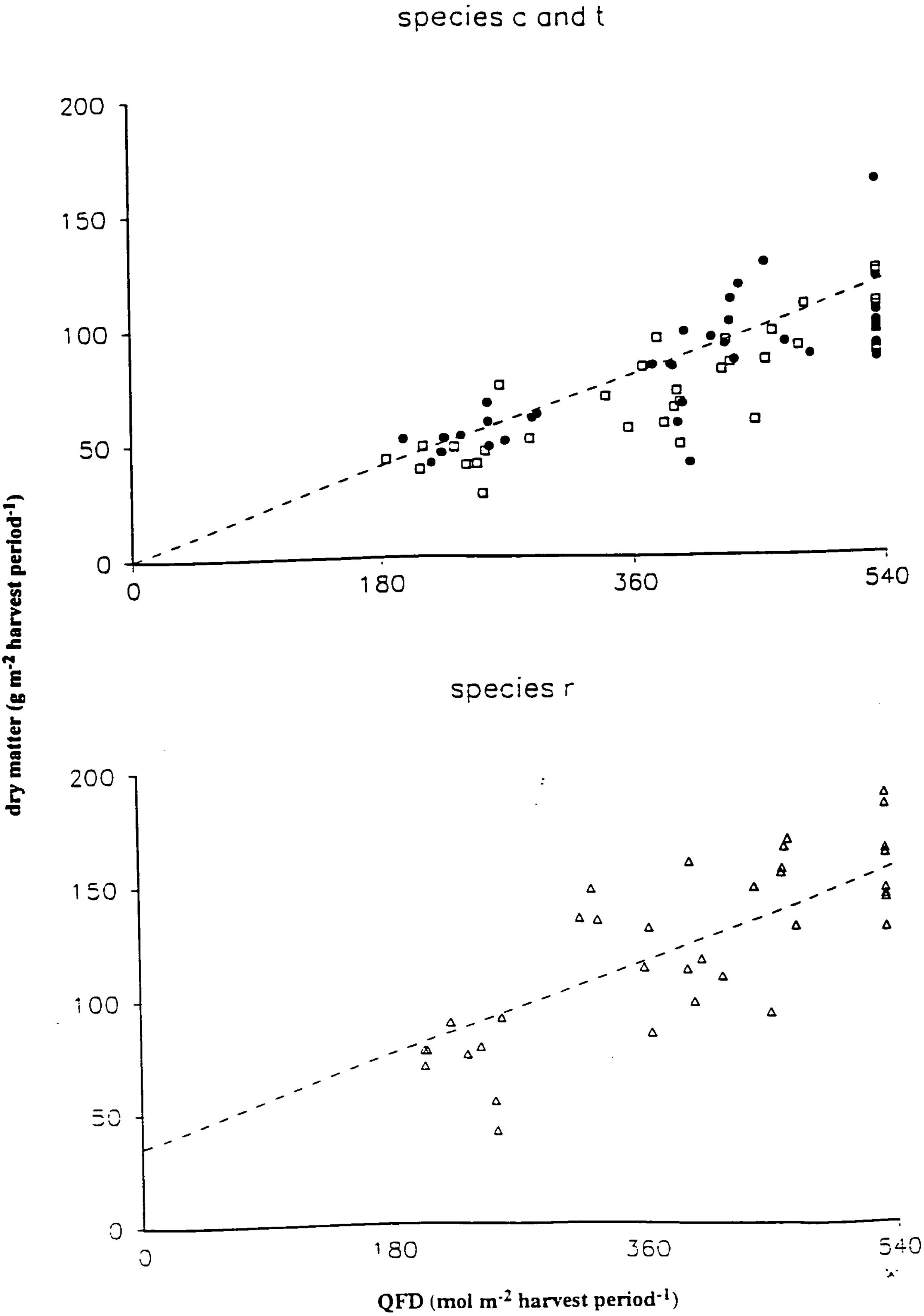


Table 5.5 Regression analysis of relationship between the above ground biomass (G_{ag}) of grass in g m^{-2} and incident QFD in mol m^{-2}.for three grass species grown in pots for 15 days in a range of agroforestry treatments at the Cloich fieldsite in July/August 1988. See Figure 5.5 for grass species labels and Section 5.2.4.1 for details of the pot layout.

a) Parameters of the fitted linear regression $G_{ag} = bQ + a$ shown graphically in Figure 5.5.

species	*a* (se)	*b* (se)	r^2
C and T combined	$-7.66(6.59)^{ns}$	0.2212(0.0158)	75.1
R	35.47(3.79)		

a1) Accumulated analysis of variance for regressions of all all three species.

Source	DF	SS	MS	F	
Overall regression	1	67188.9	67188.9	202.47	***
Intercepts	2	45663.6	22831.8	68.80	***
Slopes	2	1331.5	665.8	2.01	ns
Residual	102	33848.8	331.9		
Total	107	148032.9	1383.5		

a2) Accumulated analysis of variance for separate regressions for C and T combined and R.

Source	DF	SS	MS	F	
Overall regression	1	67188.9	67188.9	200.32	***
Intercepts	1	44638.3	44638.3	133.08	***
Slopes	1	1322.7	1322.7	3.94	ns
Residual	104	34883.0	335.4		
Total	107	148032.9	13883.5		

a3) Accumulated analysis of variance for regressions for separate regressions for C and T combined and R. fitting separate constant terms only with the same slope.

Source	DF	SS	MS	F	
Overall regression	1	67188.9	67188.9	194.85	***
Intercepts	1	44638.3	44638.3	129.46	***
Residual	105	36205.6	344.8		
Total	107	148032.9	1383.5		

**	significant at p = 0.05
***	significant at p = 0.01
ns	not significant

stubble resources more effectively to refoliate after cutting may at least partly explain the higher productivity of the perennial ryegrass over the other two species.

Over longer time periods with established grass swards, annual productivity may be further influenced by light and temperature conditions during the winter, influencing spring tiller densities (Thomas and Norris, 1981; Munro and Davies, 1973). There are likely, however, to be empirical correlations between QFD and temperature and between QFD transmittance in summer and winter months under evergreen trees, so that the mean annual QFD for agroforestry treatments at Cloich might be expected to be well correlated with mean annual pasture production. Regression of mean annual dry matter production of grass in the permanent MLURI sward boxes on mean annual QFD incident to the understorey in the agroforestry treatments at Cloich for 1987 and 1988 (n=18) explained almost 90 % of the variation in the data (Figure 5.6). The negative intercept implies a threshold level of QFD below which swards collapse, which is commensurate with low QFD leading to a reduction in the number of new tillers emerging. At very low tiller densities in spring, swards may be unable to establish sufficient leaf area to intercept the QFD that is available in mid season.

Interestingly, Sibbald, Griffiths and Elston, 1994, were able to explain 94 % of the variation in the same grass production data using a regression on the horizontal projection of the tree crown area, improving on the use of the green crown length ha^{-1} ($r^2 = 92.5$ %) that has been successfully used to predict pasture production under *Pinus radiata* in New Zealand (Percival and Knowles, 1988). However, whereas the regressions on easily measured attributes of the tree canopy are likely to be species specific, regressions on QFD are potentially more versatile, provided that the QFD is known or can be estimated, for example by exploring alternative crown structures using an appropriate simulation model, such as MAESTRO, to calculate the light intercepted by tree crowns (Sections 6.2.1, 3.3.2.8.2 and 7.3).

5.3.5. Relationships between QFD intercepted by sward and productivity

The QFD intercepted by grass (Q_g) growing in 36 of the temporary phytometers at Cloich was measured in 1988 (Section 5.2.4.2). There was a strong linear relationship ($r^2 = 99.3$) between above

Figure 5.6 Regression of mean annual pasture production (G_{ag}) on mean annual OFD incident to the understorey (Q) for treatment plots at Cloich in 1987 and 1988. The regression equation $G_{ag} = bQ + a$ is shown on the graph where $b = 0.2061 \pm 0.0172$ and $a = -4.939 \pm 0.895$ with an r^2 value of 89.3.

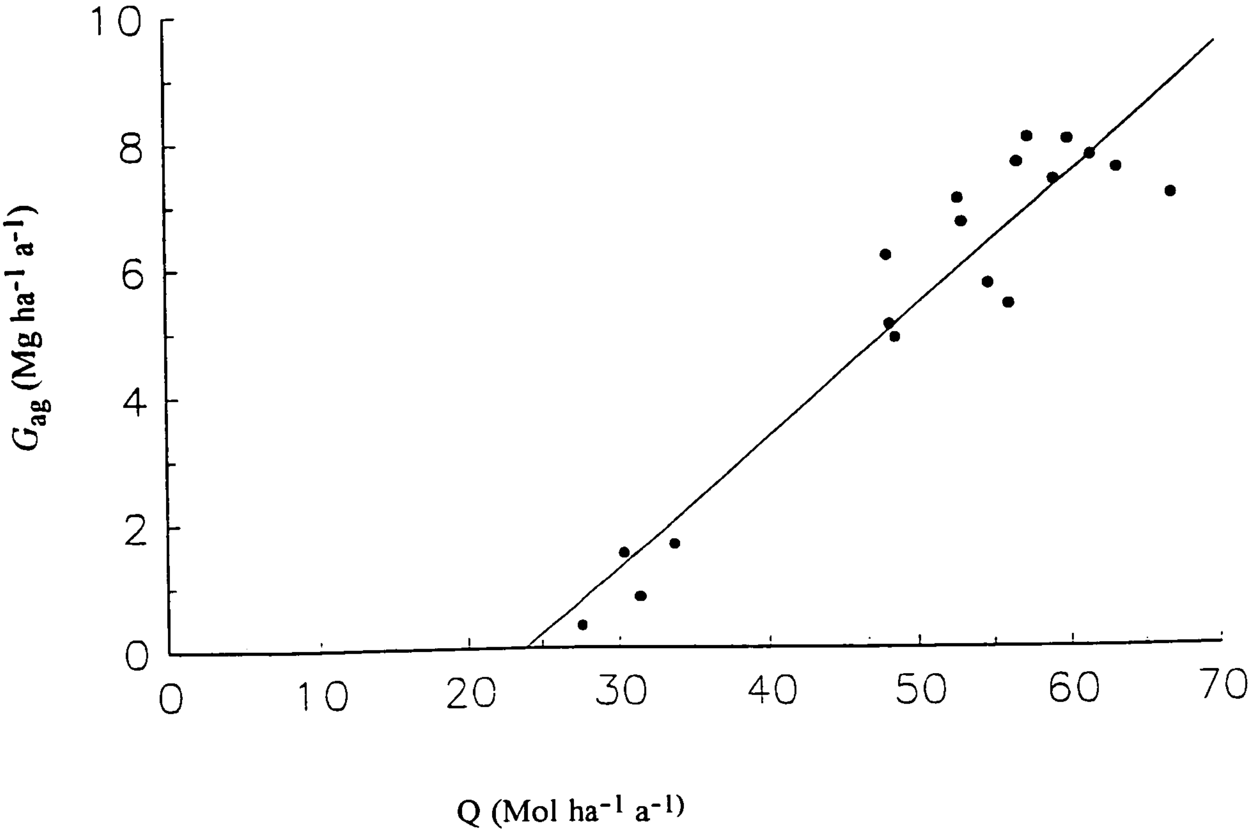
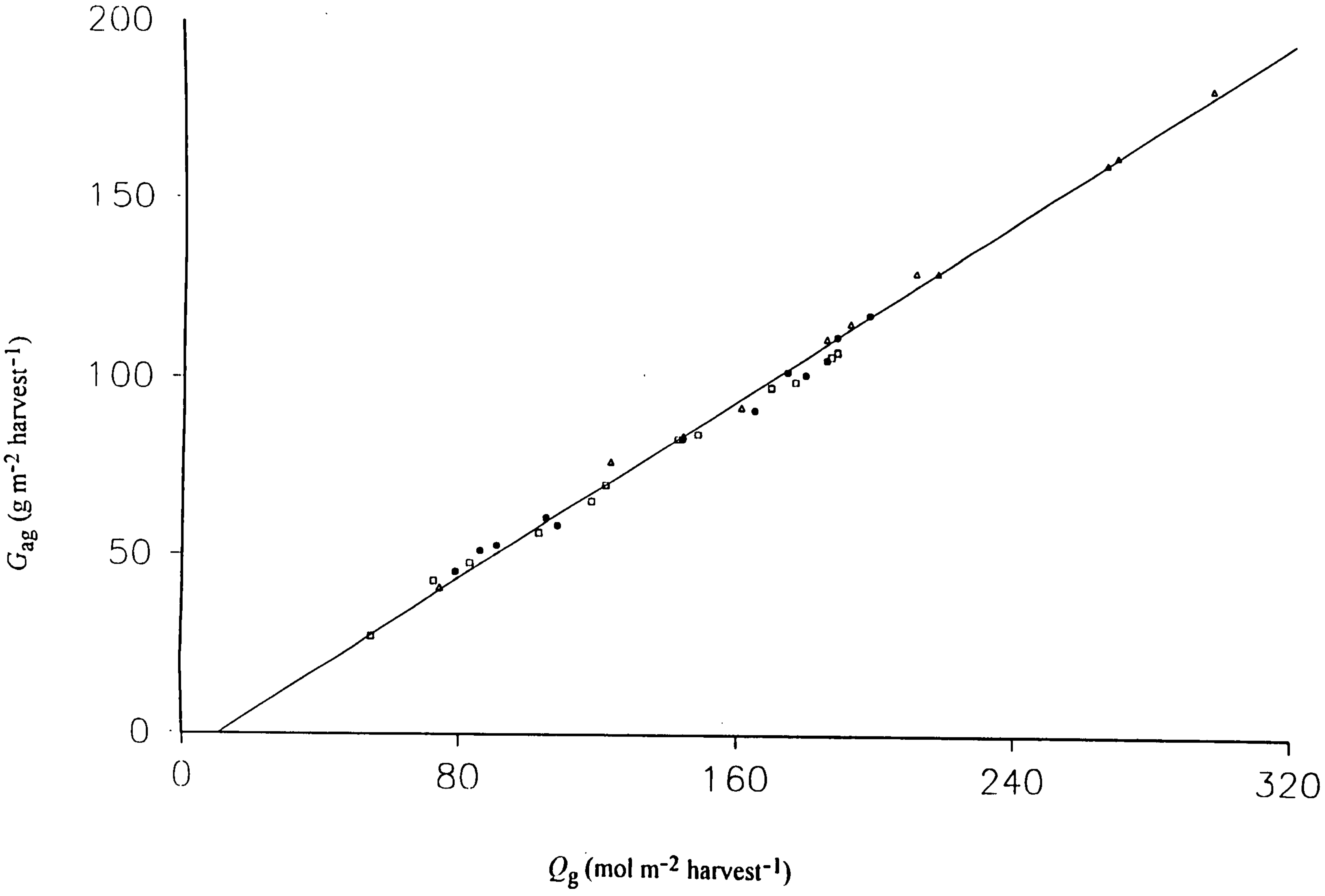


Figure 5.7 Relationship between above ground grass production,a G_{ag} and intercepted QFD, Q_g, for temporary grass phytometers in the first growing period at the Cloich field site. *Dactylis glomerata* is denoted by shaded circles, *Lolium perenne* by open triangles and *Phleum pratense* by open boxes. The line of the graph represents the regression equation $G_{ag} = b\,Q_g + a$ where $b = 0.62942 \pm 0.00524$, $a = -6.852 \pm 0.893$ with an r^2 value of 99.3.



ground grass growth (G_{ag}) and Q_g (Figure 5.7), with the dry matter : radiation quotient for grass, e_g, estimated by the slope of the regression line as 0.63 g mol $^{-1}$ (2.9%). This is almost three times larger than the value of the quotient for trees (e_t) measured previously (section 4.3.4) and close to a typical value for agricultural crops of 2.8 % (Monteith and Elston, 1983). Sheehy and Cooper (1973) reported higher values ranging from 3.9 % to 7.8 % in six contrasting grass species including timothy and cocksfoot grown in high light with water and nutrients non-limiting, whereas Brougham (1960) quoted a figure of 3 - 4 % for ryegrass pasture. Varietal differences in e_g have encouraged plant breeders to obtain increases in crop growth rate by selecting genetic material with erect leaves and a low extinction coefficient for QFD (Rhodes, 1971).

There were, however, no significant differences between the grass species or amongst tree spacing treatments despite differences in productivity and sward structure in the present experiment. There is conflicting evidence in the literature about the extent to which e varies both in relation to shade and amongst genotypes of the same or similar species (Russell, Jarvis and Monteith, 1989). Kasim and Dennett (1986) found that field beans (*Vicia faba*) exhibited higher values of e when grown in shade than when grown in full sunlight, while Hughes *et al.* (1987) have shown differences in e between erect-leaved and prostrate-leaved types of chickpea (*Cicer arietinum*) and Bonhomme *et al.* (1982) found differences in e between three maize genotypes. In contrast Heath and Hebblethwaite (1985) only found differences in e between three pea (*Pisum sativum*) varieties with contrasting leaf habit under conditions of water shortage. As the perennial ryegrass in the present experiment achieved a higher growth rate than the other grass species without a commensurately higher leaf area index (Figures 5.2 and 5.3) it might have been expected that it would have had a lower maintenance requirement per unit of photosynthesis achieved and hence a higher e_g. However, the relative size of the root system was not measured, and as has been noted earlier, foliage production may have been significantly due to mobilization of photosynthate from stubble rather than reflecting current interception of QFD. Whereas an empirical linear relationship between annual above ground tree growth and Q_t was clearly useful for estimating tree productivity, since the canopy structure of the tree endures over considerable time periods, the short time scale of the grass growth cycle and the fact that leaf expansion after defoliation may be substantially based on stored carbohydrate, renders this approach less useful for estimating grass productivity in the present context. The use of physiologically based simulation models of grass growth incorporating leaf area expansion and senescence (Johnson and Thornley, 1983; Sheehy, Cobby and Ryle, 1979 and 1980) may be more appropriate.

6. Validation of a mechanistic model of light interception by trees

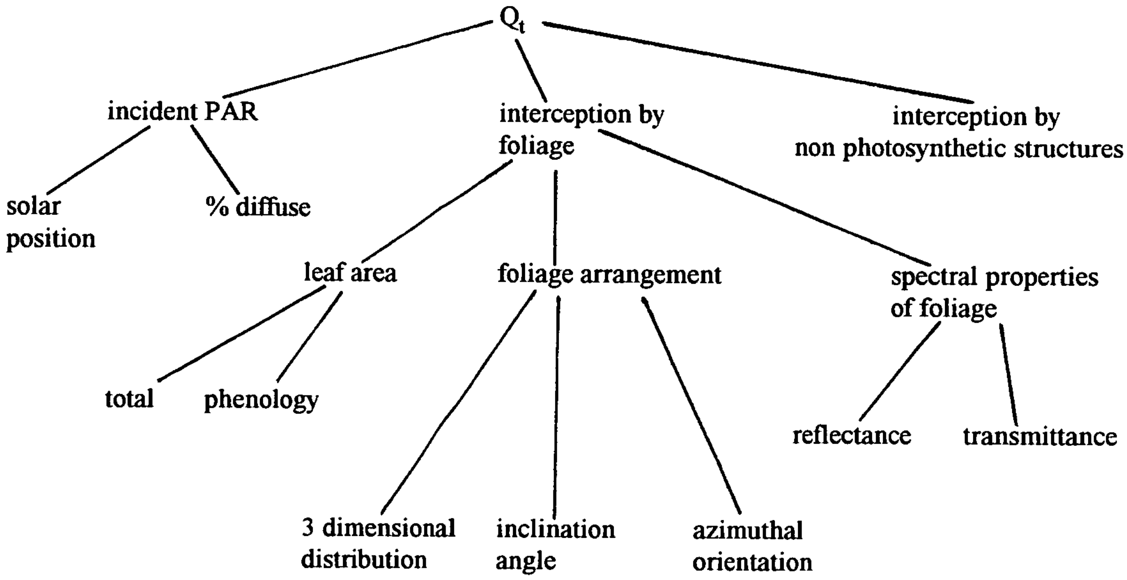
6.1 Introduction

The aim of the research reported in this chapter was to explore the use of an existing explanatory model of radiative transfer in individual tree crowns, MAESTRO (Wang and Jarvis, 1990b) described in Section 6.2.1, for tree sizes and spacings representative of agroforestry. Detailed measurements of foliage amount (Section 3.3.1) and its distribution within tree crowns (Section 3.3.2) were combined with measurements of incident QFD (Section 4.3.3) to parameterize MAESTRO for the Cloich site. Model predictions were then compared with measured QFD fluxes below the tree canopy.

6.1.1. Factors affecting light interception

Factors affecting light interception by a tree crown (Q_t) are listed diagramatically in Figure 6.1.

Figure 6.1 Factors affecting light interception by a tree canopy.



6.1.2. Approaches to modelling light interception

Despite the continuous development of elaborate radiative transfer models that involve explicit treatment of many of the variables outlined in Figure 6.1, Monsi and Saeki's (1953) approach to light attenuation, sometimes with treatment of leaf transmission (Kasanga and Monsi, 1954) is still generally used in agronomic models (Monteith, 1981; Johnson and Thornley, 1983; France and Thornley, 1984; Nygren and Jimenez, 1993). At its most basic this treats the canopy as a homogeneous collection of infinitely thin, black, opaque leaves all with the same inclination angle and random azimuthal orientation. As a result, many of the variables influencing Q_t remain lumped together in an empirically determined extinction coefficient (E). This approach is not adequate for a general treatment of individual tree crowns. Models have been developed that incorporate an explicit treatment of beam and diffuse penetration, solar position, spectral composition, scattering and leaf inclination angle (de Wit, 1965; Cowan, 1968; Ross and Nielson, in Anderson, 1969) and some include non-random, vertical and horizontal distributions of foliage, at various levels of detail within canopies (Acock *et al.*, 1970; Nilson, 1971; Norman and Jarvis, 1974; Oker-Blom and Kellomaki, 1983).

Discontinuity has been considered with various degrees of complexity. The Monsi and Saeki (1953) approach has been applied to attenuation of an empirically determined fraction of incident radiation that is taken to be affected by an overstorey canopy, with the assumption that the remaining fraction misses that canopy layer altogether (Jackson and Palmer, 1979). While this approach has been suggested for agroforestry (Jackson, 1983; Jackson and Palmer, 1989), it does not explicitly treat the spatial arrangement of tree crowns, and averages transmittance over the area below the canopy. Several models have confined foliage within geometric shapes to examine crowns arranged in rows. Charles-Edwards and Thorpe (1976) considered diffuse and beam penetration for a series of elongated ellipsoids representing closed canopies along the rows, with the foliage distributed randomly within that volume and this approach has been more recently applied to alleycropping (Nygren and Jimenez, 1993). Allen (1974) considered the direct beam only for cubic row geometry with uniform leaf area density along the row but with variation in the vertical and across the rows, while Arkin *et al.* (1978) represented individual plants as cubic foliage envelopes and proposed a simplified consideration of crown overlap including both within and between row shading. Mann *et al.* (1980) incorporated individual ellipsoid crown shapes with row structure and considered leaf area density and leaf orientation with respect to the direct beam in a general model. Three-dimensional models of isolated plants have also considered both random (Charles-Edwards and Thornley, 1973) and non-random foliage distribution (Mann, Curry and Sharpe, 1979) and more recently ray tracing techniques have been combined with complex architectural models of trees to simulate radiative transfer through individual oil palm (*Elaeis guineensis*) crowns (Dauzat, 1994).

MAESTRO is an elaborate and general radiative transfer model based on arrays of specified crown shapes within which leaf area density and foliage angle are statistically distributed. Both direct and diffuse radiation, multiple scattering in visible and near infra-red wavelengths and emission of thermal wavelengths are considered (Norman and Welles, 1983). The crowns can be spaced in any manner desired so that MAESTRO is suitable for simulating agroforestry designs (Wang and Jarvis, 1990b). This was, therefore, a relevant model to use as the basis for investigating the present agroforestry combinations because crown sizes and arrangement can be manipulated, transmittance for any point beneath the canopy and its hourly variation predicted, and foliage density and its distribution in the crown specified at different levels of detail.

6.2. Methods

6.2.1. Model structure and assumptions

The overall structure of MAESTRO has been fully described, and validated for hourly and daily integrals of point predictions of QFD fluxes below continuous canopies of *Picea sitchensis* and *Pinus radiata* (Wang and Jarvis, 1990b). A major feature of the model is its capacity to treat the individual tree within the stand. The present research extends the validation of the model to widely spaced tree stands with discrete tree crowns and seasonal integration periods and incorporates analysis of spatial variation of predictive accuracy of transmittance to an understorey crop. A spatial analysis of model performance is made.

MAESTRO is a model of an array of tree crowns in a stand. The position of each crown is specified in three dimensional space, together with its size and total leaf area. The leaf area density for subvolumes within crowns is calculated by applying independent beta functions in vertical and horizontal dimensions to the specified leaf areas (Wang, Jarvis and Benson, 1990; Section 3.3.2.7). The model operates on an hourly time step and a spatial scale of a point. The model deals with both the physical processes of radiation transfer within tree crowns and the physiological processes of transpiration and photosynthesis, employing seven independent and substitutable submodels (Wang and Jarvis, 1990b) . As the present research is concerned with the light intercepted by trees, validation was restricted to submodels dealing with sun position, partitioning of radiation, crown structure and radiation absorption; the physiological submodels were not utilised. The relevant submodels used are described below (after Wang and Jarvis, 1990b).

6.2.1.1 Description of submodels

Submodel 1 : sun position

This submodel calculates the hourly position of the sun in the sky during the day and the daylength for specific days. The inputs are the day of the year, latitude and longitude of the site. The outputs are the hourly zenith and azimuthal angles of the sun during the day and the daylength (see Barkstrom, 1981).

Submodel 2: radiation partitioning

This submodel partitions the incident radiation into beam and diffuse in the PAR and NIR wavebands using a model presented by Weiss and Norman (1985). The inputs of this submodel are the zenith angle of the sun and the incident radiation flux densities above the canopy. The outputs are the beam fractions of PAR and of NIR, cloudiness of the sky and hourly fractions of sunshine duration. Some parts of this submodel are optional, and were not used because the beam fraction was available as a measured input.

Submodel 3 : crown structure

This submodel calculates the mean leaf area density and the area fractions of the leaves in different inclination angle classes at each grid point. The leaf area density may be treated as either uniform or variable within the tree crown. Variations of leaf area density are taken into account using a complete beta function with three parameters in both the vertical and the horizontal dimensions for each leaf category.

The leaves within the tree crown are classified into three age classes and three ecological types within each age class. The leaves in different age classes may have different spatial distributions within the tree crown. The spatial leaf area density distributions of leaves in different age classes strongly affect how much PAR is absorbed and how efficiently the absorbed PAR is used, since leaves in the different age classes may have different photosynthetic light responses. This is very important for estimating the contributions of the leaves in different parts of the tree crown to the daily total carbon gain.

If actual leaf inclination angle frequencies are not provided as inputs, an ellipsoidal leaf inclination angle distribution with a single parameter is used to calculate the area fractions of leaves within different inclination angle classes (Campbell, 1986). Alternatively, the average leaf inclination angle can be utilised if required (Wang and Jarvis, 1988). The leaf orientation angle distribution is assumed to be uniform.

The inputs to this submodel are parameters to define the leaf area density distribution and area of leaves of each age class within the tree crown, the parameter of the ellipsoidal leaf inclination angle distribution and crown dimensions. The outputs are positions of all grid points, mean leaf area density and subvolume of each grid point, and diffuse radiation extinction coefficients through the tree crown.

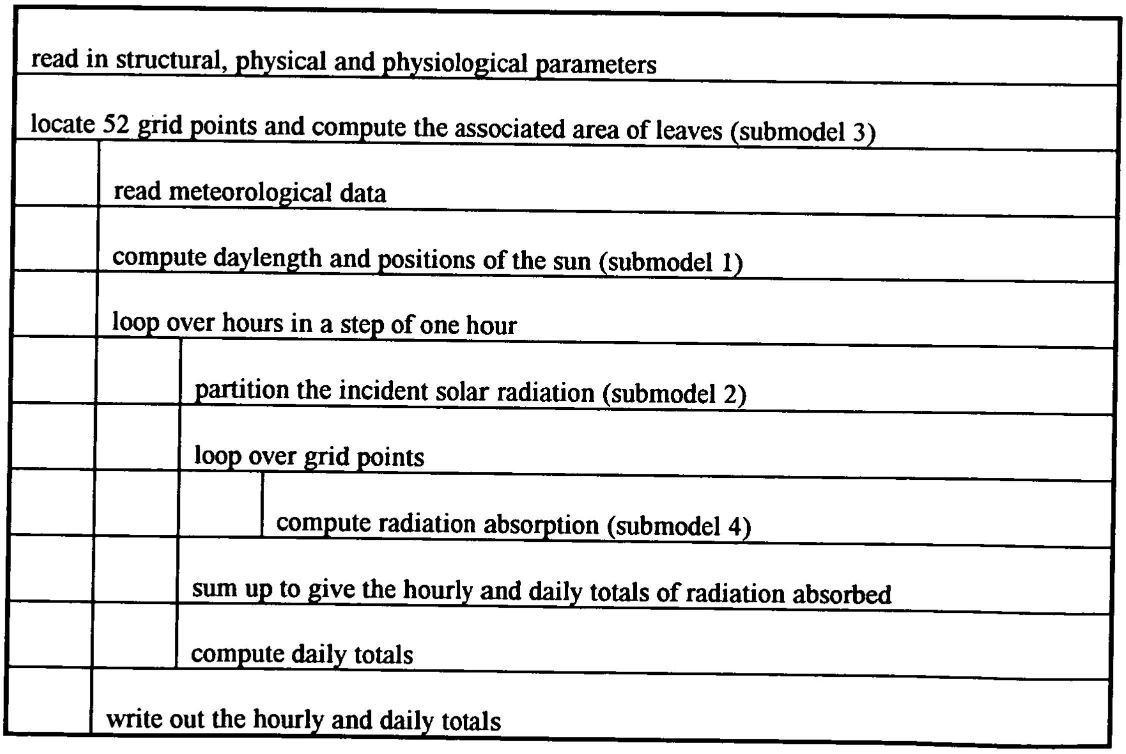
Submodel 4 : radiation absorption

This submodel calculates the flux densities of PAR, NIR and thermal radiation absorbed by the leaves within the tree crown. This submodel is based on the theory of Norman (1979), and has previously been used by Jarvis *et al*, (1985) with some simplifications.

The inputs are beam fractions of both PAR and NIR, incident flux densities of PAR, NIR and thermal radiation on the horizontal plane, identity of target tree and crown structural properties of all trees in the stand. The outputs are the hourly and daily amounts of PAR, NIR and thermal radiation absorbed by the target tree.

The following additional assumptions are made: (1) the radiance distribution of scattered radiation within the tree crown is isotropic; (2) leaf and air temperatures are everywhere equal to the air temperature at the reference height (Jarvis *et al*, 1976); (3) penumbral effects can be ignored. Penumbra may have a considerable effect on photosynthesis on a clear day (Oker-Blom, 1985) but have little influence on radiation absorption.

Figure 6.2 Diagram to show assembly of submodels (Source: after Wang and Jarvis, 1990b).



```
read in structural, physical and physiological parameters
locate 52 grid points and compute the associated area of leaves (submodel 3)
    read meteorological data
    compute daylength and positions of the sun (submodel 1)
    loop over hours in a step of one hour
        partition the incident solar radiation (submodel 2)
        loop over grid points
            compute radiation absorption (submodel 4)
        sum up to give the hourly and daily totals of radiation absorbed
        compute daily totals
    write out the hourly and daily totals
```

6.2.1.2 Inputs

The inputs to the model were as follows:

- for each site; latitude, longitude, slope and bearing, plot dimensions and number of trees, hourly incident flux density of global radiation and beam fraction, hourly incident flux density of QFD, start and end of period for the model to run;
- for each tree; x, y, and z coodinates for the mid point of the crown base, crown length, crown radius, and total leaf area within the crown;
- for the trees in general; transmittances and reflectances of QFD, NIR, and thermal radiation for three age classes of leaves specified separately for upper, middle and lower parts of the crown (Section 3.3.2.6), leaf inclination angle distribution (Section 6.2.1.4), and parameters of beta functions describing the distribution of leaf area vertically and horizontally within the tree crown for each of three leaf age classes (Section 3.3.2.7);
- for each prediction point; x, y and z coordinates.

6.2.1.3 Outputs

The outputs obtained were the hourly, and daily flux densities of QFD for each prediction point.

6.2.1.4 Assumptions

The use of the model, therefore, involved the following general assumptions being made:

- the tree stands consisted of conical tree crowns, symmetrical around the tree trunk with no azimuthal distortion;

- leaf area was continuously distributed within tree crowns and could be described by two independent beta functions in the vertical and horizontal each with three parameters (Section 3.3.2);

- leaf inclination angle was assumed to have an ellipsoidal distribution (Campbell, 1986), and the leaf orientation angle to have a uniform distribution;

- leaf area was classified as being up to one year old, more than one year old but less than two years old or older than two years old and as being in the upper, middle or lower part of the crown (Section 3.3.2.6);

- physical properties of the leaves were specified for each age by position category but were assumed to be uniform within each category;

- woody parts of the tree were ignored for the purposes of calculating radiation absorption.

6.2.2. Measurements

Details of the site layout are described earlier (Section 2.1.1) Tree leaf areas were calculated by application of the regression equations of D_r on total tree leaf area from the destructive harvest (Table 3.5), to measured *Dr* for each tree in 1988. Measurements of D_r were made at the beginning and the end of the season and leaf area assumed to increase linearly during June and July (Cannell, 1987). Other model parameters were set as described in Section 6.2.1.

Incident global solar radiation and beam fraction were continuously measured by the MLURI (Section 2.1.3.5), and QFD was obtained from reference sensors above the canopy (Section 2.1.3.5). The data used for validation were collected from an array of 81 light sensors below the trees (array 1, Section 2.1.3.5) during 1988. There were nine sensors per plot, each allocated, for two-week periods, to a grid square position. The nine grid squares were distributed between three measurement areas and their position re-randomised every two weeks. The position of the sensors within grid squares was completely randomised on a 5 x 5 grid of equidistant points. Sensors were scanned every 10 seconds and hourly averages stored. This sampling strategy ensured an adequate sample for hourly and daily comparisons spatially across the understorey as well as mean monthly and seasonal values for the whole plot.

The position of each sensor was determined by measuring the distance from the sensor to the two corner trees in the southern edge of the sampling unit (See Figure 2.2) with a cloth tape enabling the x and y co-ordinates of the sensor in the plot to be calculated from knowledge of the tree positions (Section 2.1.3.1). The height of each sensor from the ground was measured with a ruler. Model predictions were, therefore, obtained for each sensor position defined by its x, y and z co-ordinates in the plot.

6.3. Results and discussion

A large body of data was available to compare model predictions with measured QFD. Wang and Jarvis (1990b) have previously validated MAESTRO in closed stands of *Picea sitchensis* and *Pinus radiata* in Scotland and Australia comparing hourly model predictions with measurements from shaded and well lit sensors on both bright and overcast days. They present data for 11 sensors on six days and found that although mean residuals of hourly transmittances were as large as 37.8 %, differences between the predicted and measured mean daily transmittances were less than 10 % QFD transmittance, and that the occurrence of sunflecks was reasonably well predicted when the model was run with non-uniform leaf area density distributions within the tree crown as in the present study (Section 3.3.2.7). The present concern is with longer intergration periods appropriate for simulating seasonal productivity of agroforesty combinations and with situations where trees are widely spaced. Therefore, data collected in 1988 from the 6 m and 4 m spaced plots in the intermediate tree stand are presented here. The trees have crowns extending to the ground and whereas there was crown overlap in the 4 m spaced plots, tree crowns remained discrete at 6 m tree spacing. This enables comparison of model performance with respect to discrete crowns and a continuous canopy, and in relation to differential tree cover. The trees intercepted 25 % and 61 % of incident OFD in the 6 m and 4 m plots respectively (Table 5.4).

Residual transmittance (T_r) for any point is calculated as: $T_r = T_m - T_p$; where T_m and T_p are the measured and predicted transmittance respectively. $\underline{T}_r$ is the mean residual transmittance and is equivalent to the mean bias error (Iqbal, 1983), it provides an indication of the average deviation of the predicted values from the measured values. MINT_r is the minimum residual transmittance, MAXT_r the maximum, and RMST_r the root mean square, which is equivalent to the measure used by Wang and Jarvis, (1990b) and the root mean square error (Iqbal, 1983), it provides a measure of the variation of predicted values around the measured values and r is the correlation coefficient for T_m with T_p., providing an indication of the linearity of the relationship between measured and predicted values.

6.3.1 Daily transmittance in relation to tree spacing

Summary statistics comparing model predictions with measurements for the 4 m and 6 m spaced plots throughout 1988 in the intermediate tree height stand are shown in Table 6.1. For each treatment plot nine sensors were available and their locations were re-randomised every fortnight, data for one day in each fortnight, chosen randomly were used to compile the table so that 234 mean daily transmittance values were used in calculating each statistic.

Table 6.1 Comparison of measured and simulated QFD transmittance (%) for 4 m and 6 m tree spacing in the intermediate stand at Cloich (see text for explanation of the statistics quoted).

Tree spacing (m)	T	r	$\underline{T}_r$	MINT_r	MAXT_r	RMST_r
4	38.8	0.794	-1.59	-8.1	4.6	2.97
6	74.7	0.864	-2.98	-13.20	8.4	5.85

It is evident from Table 6.1 that :

- the model has a small negative bias, underpredicting measured transmittances by between 1.5 to 3 % transmittance,
- individual mean daily transmittance values predicted by the model were different from the measured values by up to 13.2 % transmittance but the mean discrepancy lay between 3 and 6 % transmittance,
- differences between model predictions and measured values were about two times larger for the plot with discrete tree crowns and a higher overall transmittance than with the continuous canopy.

These results confirm Wang and Jarvis' (1990b) earlier findings that the model predicts mean daily transmittances within 10 % transmittance of measured values in a continuous canopy and extends the validation to stands of discrete trees for which, while errors are higher, the model predictions are still remarkably close to measured values when averaged over space and time which are further examined below.

6.3.2 Spatial variation of model performance

Summary statistics comparing model predictions with measurements for each grid square position in the intermediate tree height, 6 m spaced plot are shown in Table 6.2. The plot with discrete tree crowns was chosen to further examine model performance, since this is representative of an agroforestry situation and appears to be a more severe test than a continuous canopy. There was one sensor randomly located in each grid square position for each of 26 fortnightly integration periods. The mean fortnightly transmittance values for 26 sensor positions per grid square were, therefore, compared with model predictions over the whole year.

Table 6.2 Spatial variation of model predictions of transmittance (%) in relation to grid square position (Figure 2.2) at the intermediate tree height, 6 m tree spacing stand at Cloich for 26 fortnightly integration periods during 1988. One sensor was located randomly in each grid square position in each integration period (Section 6.2.2), see text for explanation of the summary statistics.

		West		East
North	$\underline{T}$	66.7	81.8	66.2
	r	0.466	0.67	0.110
	$\underline{Tr}$	-1.00	-2.87	-3.40
	RMSTr	3.86	7.51	4.17
	$\underline{T}$	83.8	86.3	84.2
	r	0.865	0.999	0.975
	$\underline{Tr}$	-3.27	-1.77	-2.8
	RMSTr	5.21	4.49	4.38
	$\underline{T}$	60.5	80.6	62.2
	r	0.337	0.968	0.297
	$\underline{Tr}$	-2.02	1.98	-1.54
South	RMSTr	2.12	2.09	1.70

It is evident from Table 6.2 that model predictions are less well correlated with measured values in the more shaded corner grid squares than the central areas of the plot that enjoy a higher mean QFD transmittance, although mean errors are higher (up to 7.51 % transmittance) in the central areas than under the tree crowns. Clearly the precise positions of sensors in relation to branches and stems may be more important closer to trees, so that the lower correlation coefficients in the corner grid squares may reflect errors determining the relative position of sensors.

6.3.3 Seasonal variation of model performance

Summary statistics comparing model predictions with measurements on a monthly basis throughout 1988 in the intermediate tree height, 6 m tree spacing plot are shown in Table 6.3. There were nine sensors re-randomised once during each month, so that mean fortnightly transmittances for 18 points per month contributed to each statistic in the table.

Table 6.3 Seasonal variation of model predictions of transmittance (%) at the intermediate tree height, 6 m tree spacing stand at Cloich. Each monthly statistic is calculated from 18 fortnightly mean transmittance values from nine sensors whose positions were re-randomised during the month.

Month	$\underline{T}$	r	$\underline{Tr}$	RMSTr
January	66.6	0.775	-1.34	2.12
February	68.3	0.762	-3.32	4.612
March	69.9	0.813	-0.92	2.96
April	71.8	0.922	-3.10	4.87
May	71.5	0.936	-1.03	1.94
June	70.2	0.991	-10.20	10.45
July	70.0	0.988	-10.17	10.42
August	68.7	0.948	-3.87	3.97
September	65.6	0.887	-0.90	1.75
October	62.4	0.846	-1.04	2.22
November	62.3	0.839	-1.32	2.15
December	63.7	0.772	-6.80	7.12

It is evident from Table 6.3 that model predictions and measurements were less well correlated in the winter months that experience lower QFD and transmittance than summer months, although mean errors were higher (up to about 10 % transmittance) in the summer months. This is significant since the model is performing less well when a greater proportion of the annual radiation receipt is received.

6.3.4 Conclusion

The validation, while suggesting that the model has a small negative bias in predicting mean daily transmittance, which may be larger under discrete tree crowns as opposed to a closed canopy, clearly shows that the model is appropriate for calculating QFD transmittance from detailed information on the vegetative structure of an agroforestry stand and the incident radiation. Comparing point measurements with model predictions is a stringent test of the model, and differences between model predictions and measured values may be partially caused by errors in measurement as well as in model performance. The validation suggests that model predictions integrated across spatial scales of a plot and seasonal timescales are likely to be within 10 % transmittance of measured values.

7. Simulation of effects of varying tree type, spacing and arrangement

7.1. Introduction

Previous approaches to modelling the effects of light distribution amongst components in agroforestry systems have involved a lumped parameter approach in which a series of assumptions about leaf area and its distribution between and within tree crowns are accomodated in the form of empirical extinction coefficients *E* (eg. Jackson, 1983, 1989; Reifsnyder, 1989, Nygren and Jimenez, 1993). For many possible agroforestry scenarios, however, it is impossible to determine *E* empirically because trees of a sufficient size are not available at the appropriate spacings or arrangements. It will be some time before trees planted at agroforestry spacings in the UK displaying canopy structures representative of agroforestry systems will be available so that such measurements can be made..

Whilst it is more desirable and confers greater flexibility in approach to take explicit information about canopy structure and then to model QFD transmittance through the overstorey, detailed measurements of leaf area, distribution and orientation are not yet available for typical agroforestry systems. This chapter reports research that used the simulation model MAESTRO, (validated and described in Chapter 6), in conjuction with empirical models of tree growth (Chapter 4) and pasture growth (Chapter 5), to model annual transmittance of QFD and seasonal productivity and its distribution amongst components in silvopastoral systems, in relation to structural characteristics of tree crowns that can be manipulated by management.

7.2 Tree types and manipulation of tree crowns by management decisions.

Farmers managing a silvopastoral system are able to manipulate the productivity of the system and the relative proportion of tree and pasture production by manipulating the tree crowns both in terms of what species are planted in the first place, the arrangement and density of planting and the subsequent management of crown development through pruning. In terms of species choice a number of tree attributes are of relevance which will be subject to genotype x environment interactions and so vary with location. These include the leaf area density within the crown, leaf phenology, crown size and shape and tree height, all of which vary markedly amongst species (Cannell, 1982). Clearly there are possibilities for selecting species that have ecological combining ability with agricultural crops. For example, ash (*Fraxinus excelsior*) comes into leaf in southern England at the end of May whereas pasture productivity peaks before then. There are many options for pruning trees to encourage different crown development (Cannell, 1983) and different strategies may be appropriate for combination with crops with different light responses (Jackson, 1989)

7.3. Methods

Simulations throughout this chapter use MAESTRO (as fully described in section 6.2.1), as parameterised for the Cloich field site and weather in 1988 (Sections 3.3.2.8.1 and 6.2.1), except where alternative parameters which are the subject of exploration are explicitly mentioned. MAESTRO was used to calculate the QFD transmitted to the understorey and then, where appropriate, empirical relations between the amount of QFD intercepted by the tree crowns and the growth (Table 4.7) and the amount of QFD incident to the understorey and annual pasture production (Figure 5.6) were used to calculate productivity.

7.4 Simulations

7.4.1 The importance of tree variability within stands

The position, crown dimensions and leaf area of trees are individually specified in the input data for MAESTRO, and actual tree crowns, even in even-aged commercial foresty plantations, vary considerably from tree to tree (Section 3.3.1). In order to investigate the significance of incorporating the actual variability of tree sizes and crown attributes typical of field situations, MAESTRO was run with tree input data as measured at the site and compared with a simulation in which a mean tree was specified. Tree positions remained as measured at Cloich. This was done for the tall tree stand at 4 m and 8 m spacings and the effect of basal crown pruning was also investigated by including a non-

Figure 7.1a. Investigation of the effects of measured tree variability on the pattern of transmittance and productivity in agroforestry plots at Cloich. Comparison of using actual tree measurements (R) and mean trees(A) for pruned (P) and not pruned (NP) tree crowns in the tall 4 m spaced stand at Cloich. MAESTRO was run for a year 16 times for each simulation with a grid of 81 points on each of sixteen units based on data from Cloich. Transmitted QFD is plotted across the area beneath 25 trees.

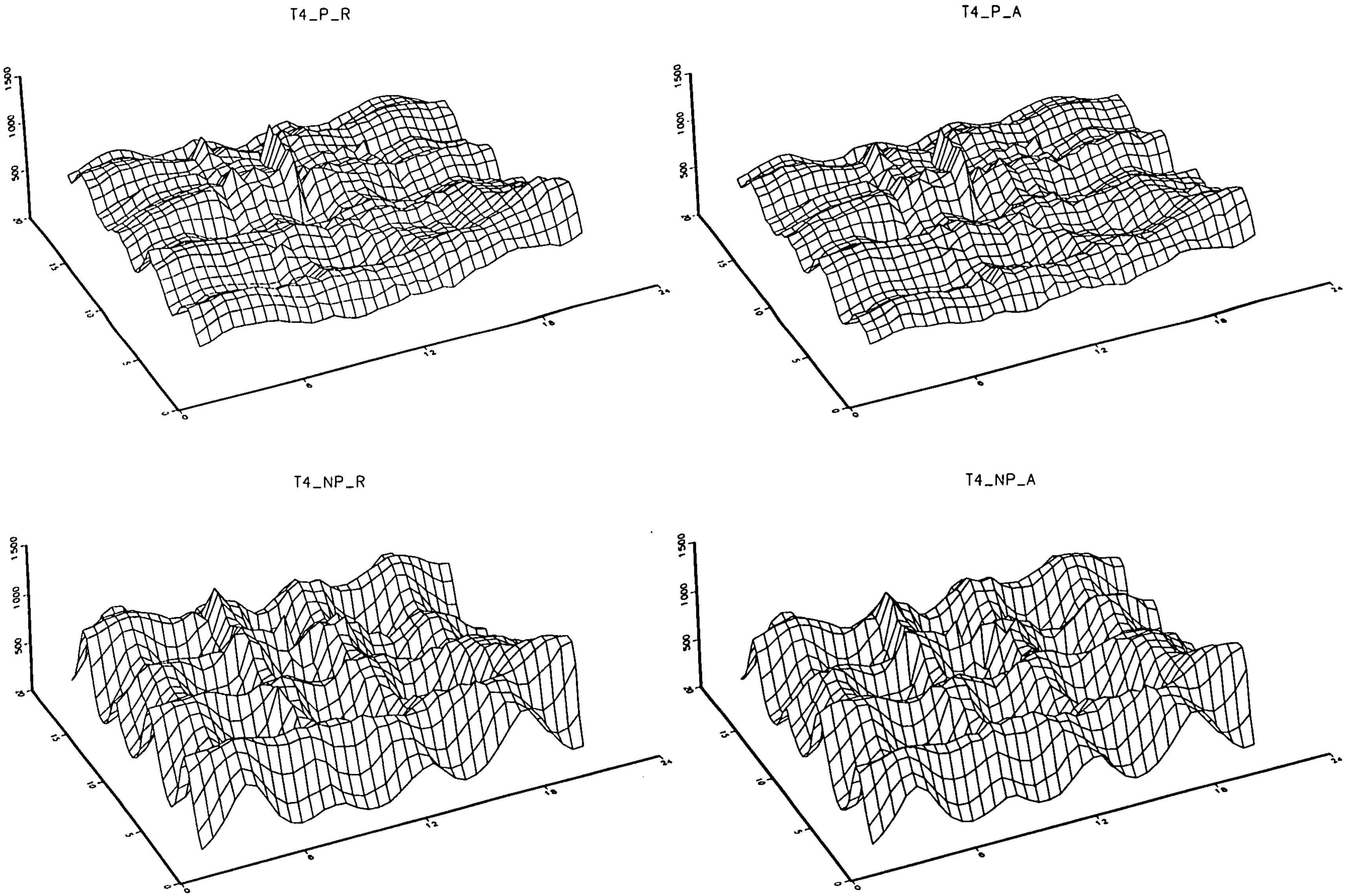
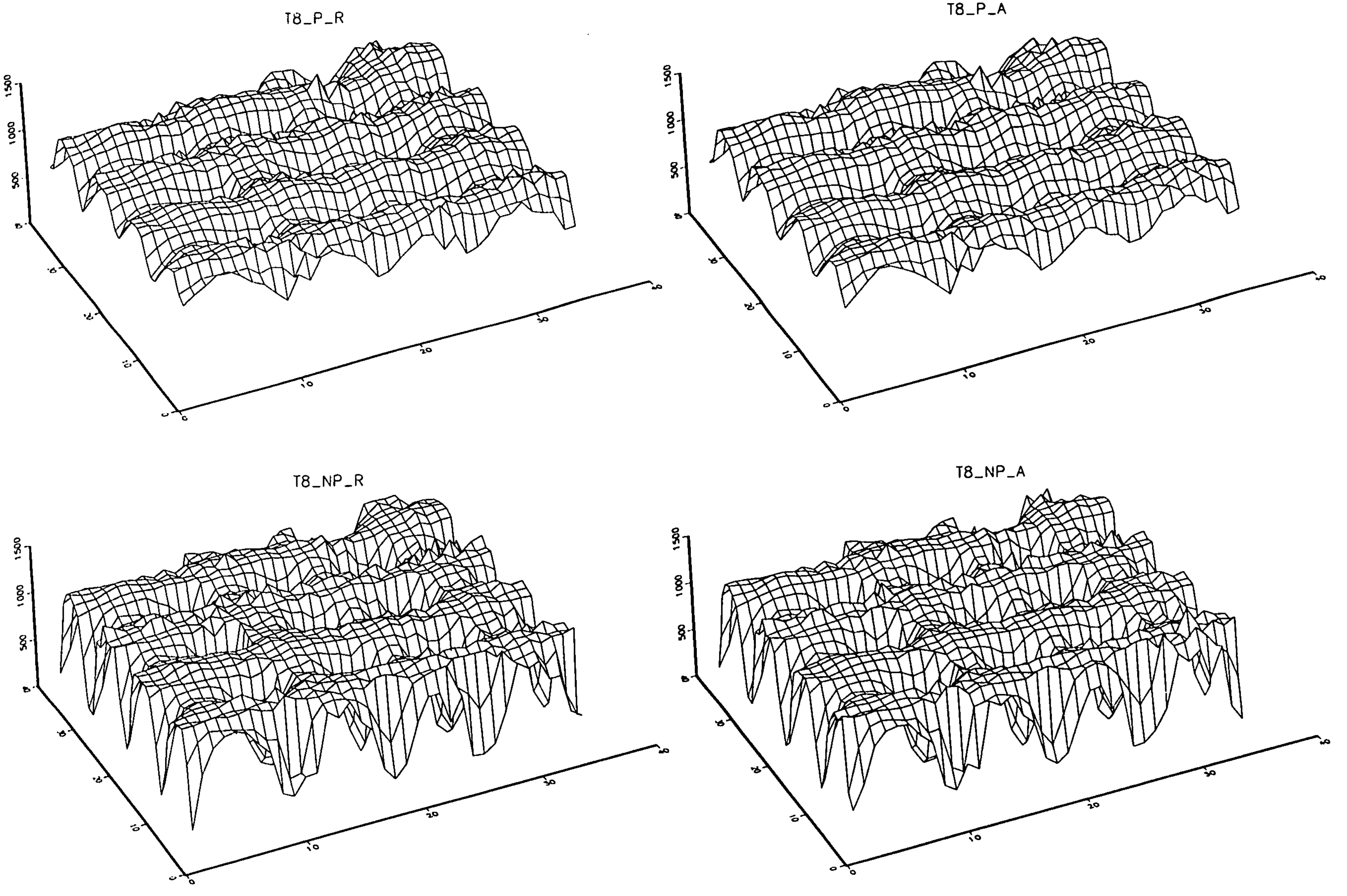


Figure 7.1b Investigation of the effects of measured tree variability on the pattern of transmittance and productivity in agroforestry plots at Cloich. Comparison of using actual tree measurements (R) and mean trees(A) for pruned (P) and not pruned (NP) tree crowns in the tall 8 spaced stand at Cloich. MAESTRO was run for a year 16 times for each simulation with a grid of 81 points on each of sixteen units based on data from Cloich. Transmitted QFD is plotted across the area beneath 25 trees.



pruned comparison, by simply setting the base of the live crown to zero (the trees at the tall site at Cloich were basal pruned to 1.3 m). The results indicate that the distribution of transmitted light is more even when trees are pruned than when an identical set of crowns begin at ground level (Figure 7.1a and Figure 7.1b) but that the actual variability in crown attributes makes little difference to the distribution of transmitted QFD which was more affected in the present example by irregularities in tree positions. Neither the use of the mean tree as opposed to real tree measurements nor the different heights to the base of the crown significantly affected the mean QFD transmitted to the understorey.

7.4.2. Leaf area density and tree frequency

Differences in the amount of leaf area and its distribution in the overstorey canopy as defined by its enclosure in tree crowns was investigated by simulating light transmittance for four tree stocking densities of 100, 200, 400 and 800 stems ha^{-1} each with tree leaf area indices for the plot as a whole of 0.4, 0.8, 1.6, and 3.2 confined within crowns of a constant 2 m radius (Figure 7.2). This resulted in increasingly variable distribution of QFD across the understorey as the leaf area index was increased (Figure 7.2). Both increases in tree stocking density for a given tree leaf area index and increases in tree leaf area index for a given stocking density resulted in higher QFD interception by the tree component and consequently a higher proportion of tree production also associated with a higher total productivity of the silvopastoral mixture (Table 7.3).

7.4.3. Leaf area duration

As discussed in section 7.2 leaf phenology can have a profound impact on the ecological combining ability of trees and agricultural crops. The Faidherbia albida parklands of the Sahel region of Africa are testament to this, as the reverse phenology of the tree species, which loses its leaves in the rainy season when crops develop their leaf area, facilitates resource sharing (Sanchez, 1995). In the UK deciduous species such as larch are likely to present different opportunities for intercropping than evergreen trees. Amongst broadleaved trees times of bud break and leaf fall also vary markedly, compare, for example, ash and sycamore. Effects of leaf area duration may well be confounded with leaf area density when choosing species. To investigate the importance of varying leaf area duration

Figure 7.2 Plan of tree crowns for four tree frequency scenarios each simulated for four leaf area indices. Results are presented in Figure 7.3 and table 7.3

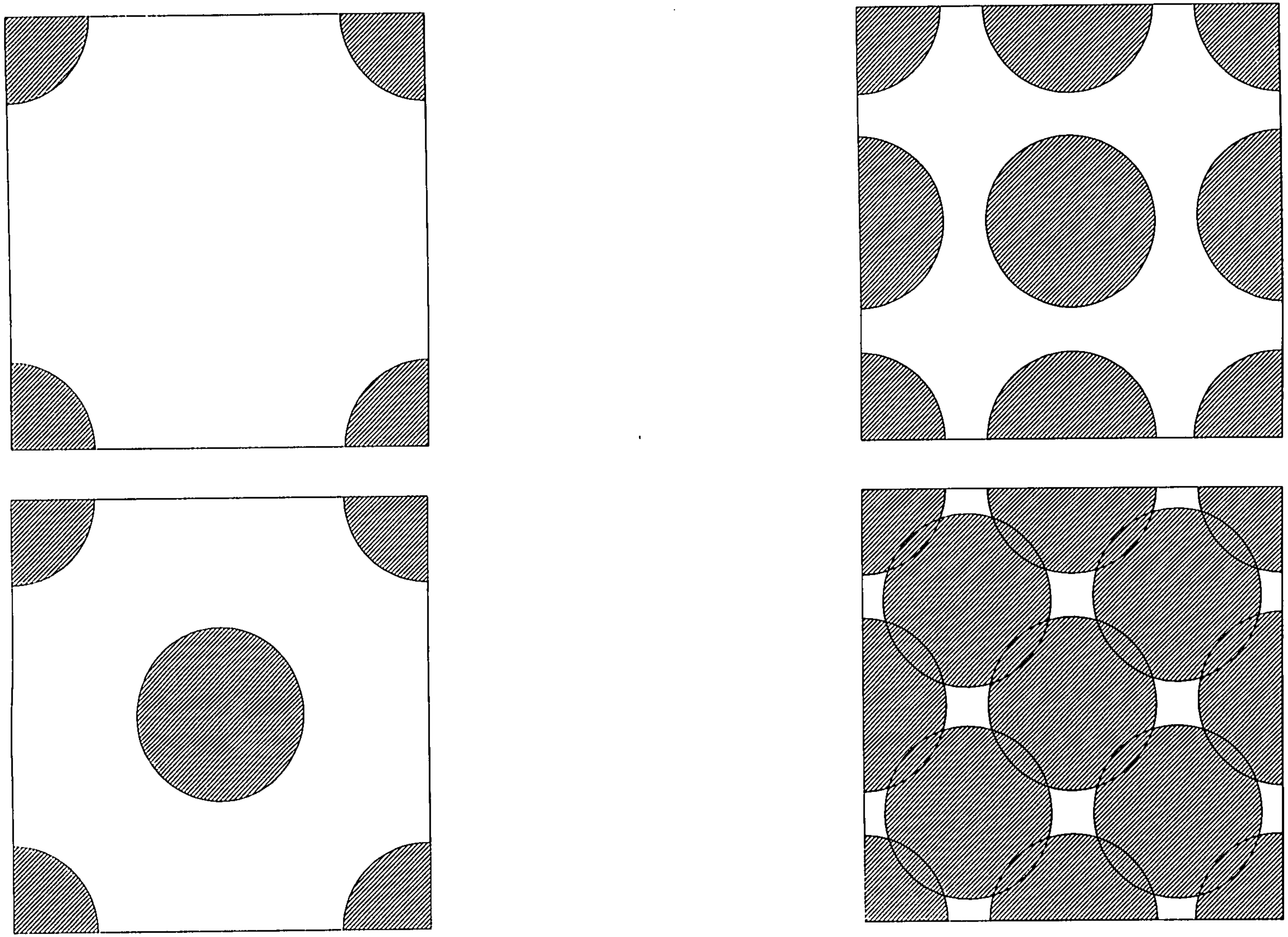


Figure 7.3 Simulated QFD under various agroforestry scenarios on which tree frequency and leaf area were varied as depicted in Figure 7.2 and tabulated in Table 7.3

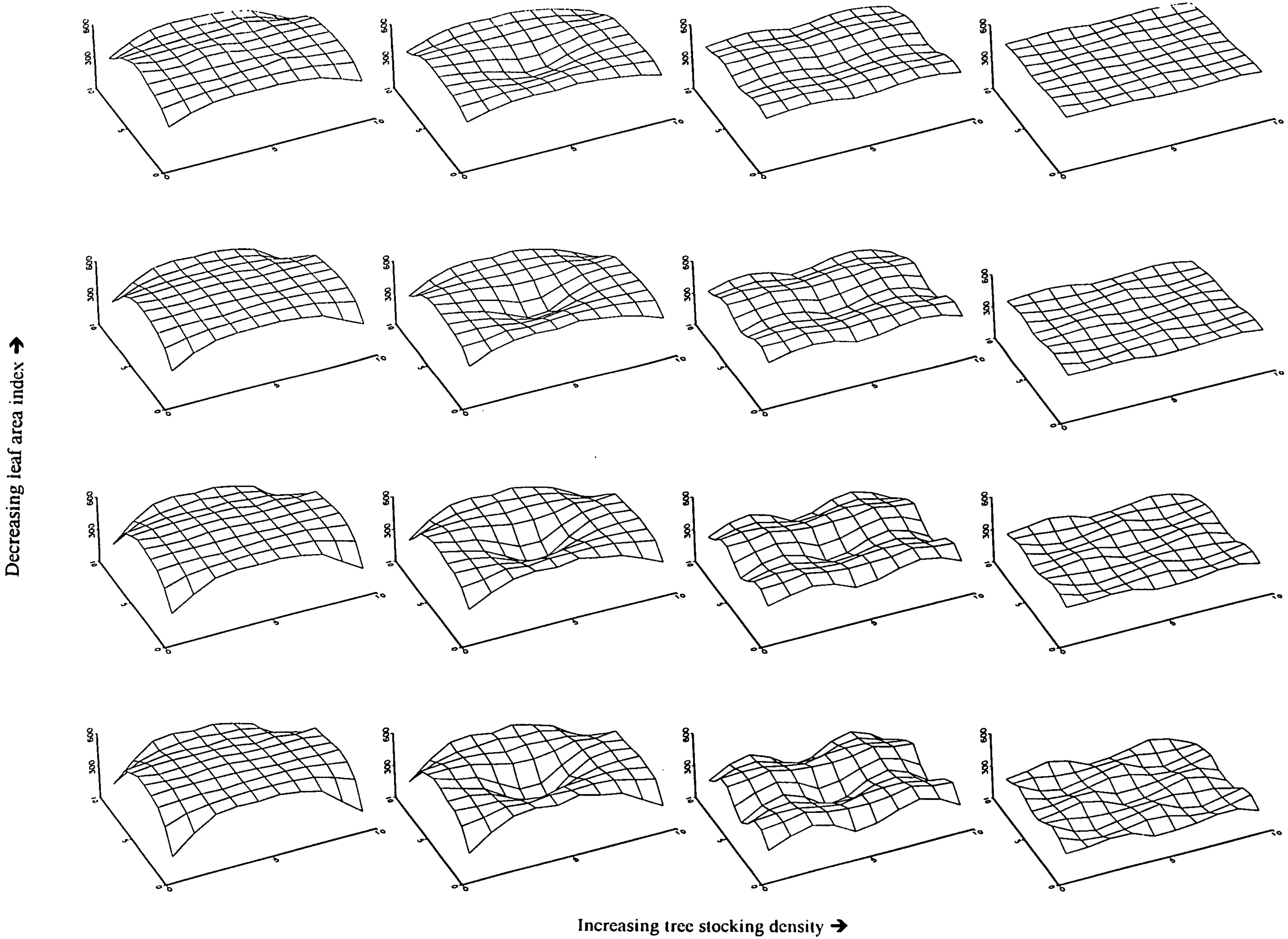


Table 7.3 Simulated QFD transmittance and estimated tree and pasture productivity for a series of agroforesty configurations where total leaf area and its distribution in space have been varied. Plans of the arrangements of tree crowns for each tree density are presented in Figure 7.2 and the pattern of trnsmittance is shown in Figure 7.3. The simulation was run for a year with predictions of QFD made for a grid of 81 points systematically distributed at ground level. The 1988 weather data measured at the Cloich fieldsite were used as input data.

G_{at} above ground dry matter of trees
G_{ag} above ground dry matter of grass
G_{tot} total annual production from trees and pasture

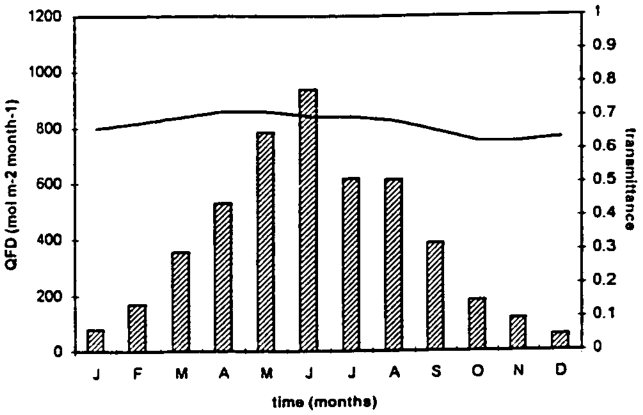
Tree Density (trees ha^{-1})	Leaf Area Index F	Transmittance T	G_{at} (Mg ha^{-1}a^{-1})	G_{ag} (Mg ha^{-1}a^{-1})	G_{tot} (Mg ha^{-1}a^{-1})
100	0.4	0.940	0.980	8.816	9.796
100	0.8	0.875	2.041	7.865	9.906
100	1.6	0.855	2.368	7.572	9.940
100	3.2	0.840	2.613	7.353	9.966
200	0.4	0.864	2.221	7.704	9.925
200	0.8	0.810	3.103	6.914	10.017
200	1.6	0.763	3.870	6.226	10.096
200	3.2	0.725	4.491	5.670	10.161
400	0.4	0.831	2.760	7.221	9.981
400	0.8	0.737	4.295	5.846	10.141
400	1.6	0.640	5.879	4.426	10.305
400	3.2	0.559	7.202	3.241	10.443
800	0.4	0.820	2.939	7.060	9.999
800	0.8	0.693	5.013	5.202	10.215
800	1.6	0.535	7.593	2.890	10.483
800	3.2	0.383	10.076	0.665	10.741

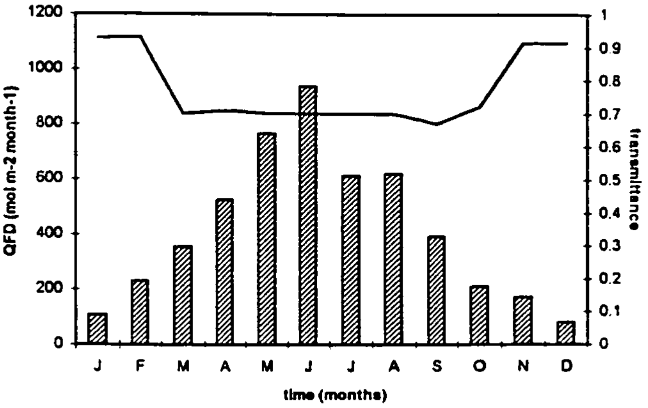
alone, the tall tree stand at 6 m spacing at Cloich was used. Leaf area durations of seven (March to October and April to November), six (March to September, April to October and May to November) five (April to September, May to October and June to November) and four (May to September and June to October) months were simulated by reducing the leaf per tree to 10 % of its normal value (to represent non-photosynthetic structures) in months without leaves. Leaf area was assumed to increase linearly over two months from bud break and to decrease linearly for two months at leaf fall. Results of these different leaf area duration scenarios (Figure 7.4) show marked differences in mean transmittance amongst similar leaf area durations with different bud break and leaf fall dates, as a result of their interaction with the 1988 weather pattern at Cloich, as well as the expected higher mean annual trasmittances for shorter tree leaf area duration. Effects on the understorey could be disproportionate to the mean annual transmittance where crop phenology enables the leafless period of the trees to be exploited as for the ash/pasture mixture in southern England, discussed in Section 7.2.

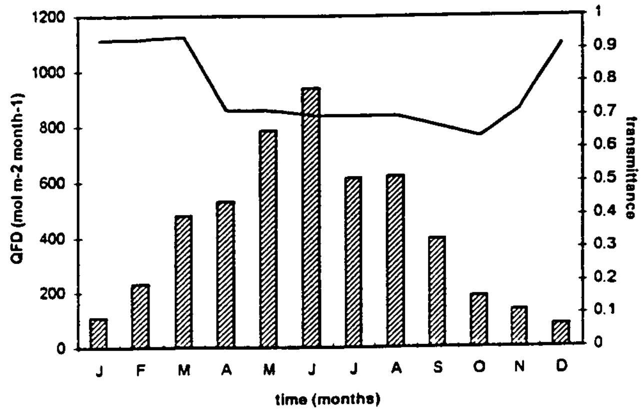
7.5 Conclusions

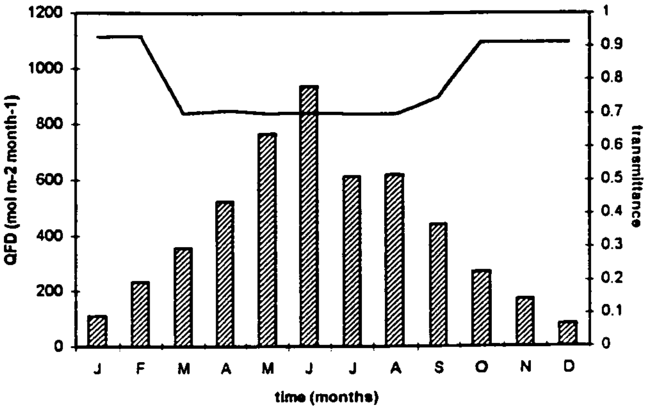
The present research has shown that a detailed model of radiative transfer in tree crowns coupled with the specification of the vegetative structure of agroforestry tree stands and empirical relationships between intercepted light and plant growth can be used to explore the potential productivity of alternative tree configurations at a particular site. The simulation model MAESTRO, while computationally demanding, produces remarkably accurate predictions of QFD intercepted by tree crowns and transmitted to the understorey. While estimating annual tree productivity using empirical relationships with intercepted QFD was appropriate, such relationships were not so useful understanding productivity of frequently defoliated grass swards growing beneath trees for which a more physiologically based approach that captures the interactions between microclimate modification and grass growth processes would be appropriate. Clearly, the absence of below-ground interactions in the present study limited the extent to which interactive processes in agroforestry could be understood. A priority area of future research in agroforestry is the relationship between shoot and root processes since in general farmers can manipulate the shoot system more readily than they can the roots. Tree leaf area is a fundamental property of agroforestry systems, affecting tree and understorey productivity. One of the strengths of the present approach was to measure and represent tree leaf area and its distribution in agroforestry situations allowing various alternative structures to be investigated. This approach can now be extended to include the coupling of tree and crop process-based models and root competition which is already in progress (Lawson et al, 1995).

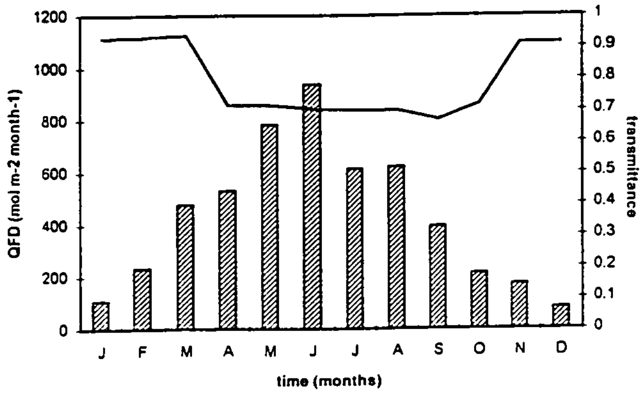
figure 7.4a A simulated seasonal and mean annual transmittance T for a range of leaf area duration scenarios in the tall 6 m tree stand at Cloich for 1988 as discussed in the text.


(a) Leaf area duration - January to December
T=0.693


(b) Leaf area duration - March to October
T=0.726


(c) Leaf area duration - April to November
T=0.741


(d) Leaf area duration - March to September
T=0.742


(e) Leaf area duration - April to October
T=0.751

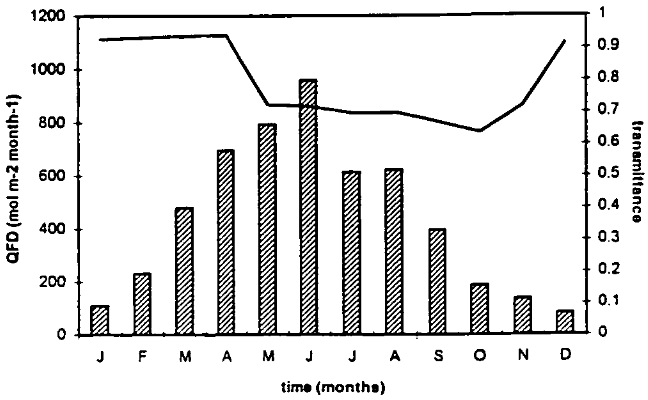
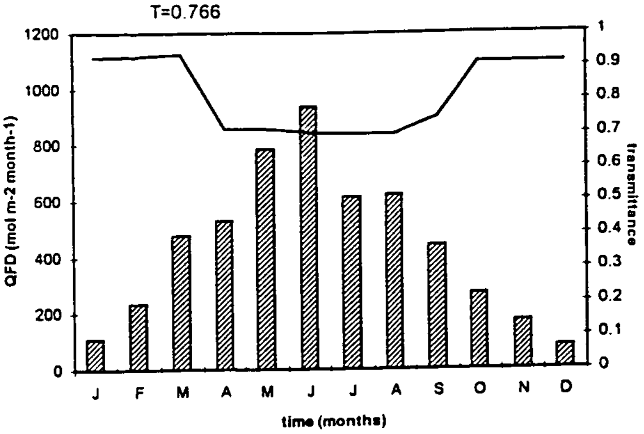
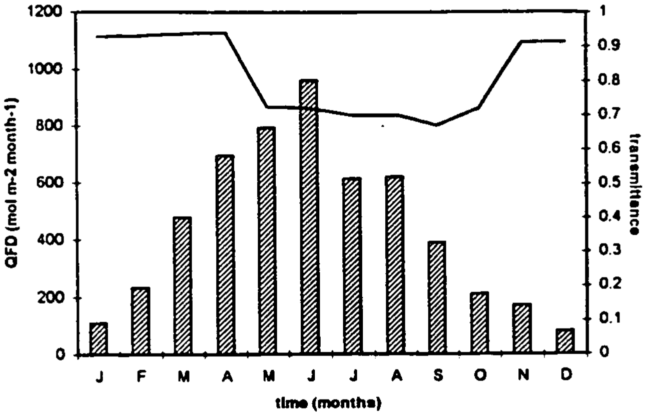

(f) Leaf area duration - May to November
T=0.774

figure 7.4a cont.

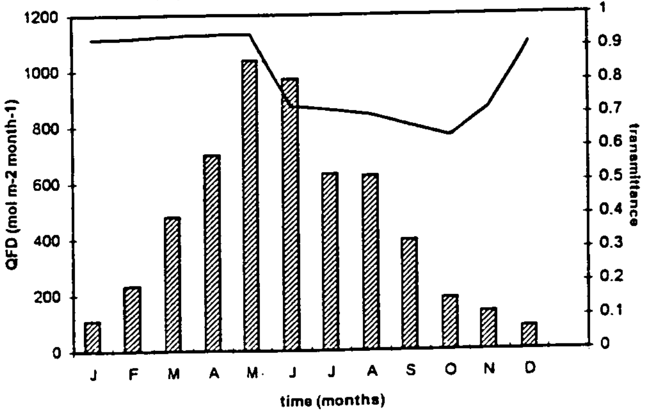
(g) Leaf area duration - April to September
T=0.766



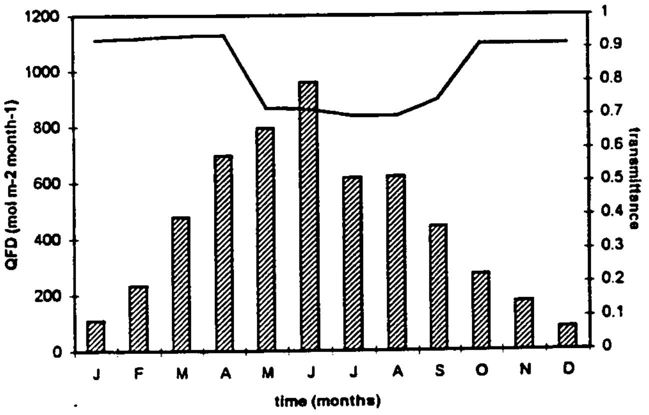
(h) Leaf area duration - January to December
T=0.783



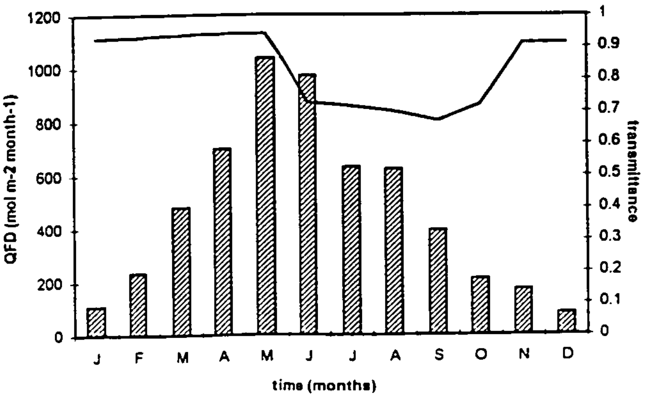
(i) Leaf area duration - June to November
T=0.816



(j) Leaf area duration - May to September
T=0.797



(k) Leaf area duration - June to October
T=0.823



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Appendix 1

These notes describe components and basic performance of the quantum sensors built at the Department of Forestry and Natural Resources, University of Edinburgh in 1986 and 1987 and complement the details given in Section 2.3. Paul Jarvis and Andrew Sandford supervised their design and David Mackenzie precision drilled the Acetal rod.

Components

Detectors

1986	large units	SD-172-12-12-021, Rofin-Sinar Laser UK Ltd
	small units	SD-076-12-12-011, Rofin-Sinar Laser UK Ltd
1987	large units	United Detector Technology, PIN-5DP SB, Melles Griot (UK) Ltd

Filters

1986	large units	Omega Optical 700 SP 12 mm, Glen Creston Insts Ltd
	small units	Omega Optical 700 SP 8 mm, Glen Creston Insts Ltd
1987	large units	Omega Optical 710 SP 12 mm, Glen Creston Insts Ltd

Diffuser

3 mm White Translucent Medium Opal 050 Perspex sheet

Case

Precision ground, black Acetal rod, Polypenco Ltd

Resistors

1 kΩ, 0.125 W metal film 1%, RS Components Ltd
(± 50 ppm/^{0}C) 144-245

Cable

1986	Miniature, low noise braided screen 367-280	RS Components Ltd
1987	RG174A/U 388-502	

Potting glue

Black epoxy 557-944 RS Components Ltd

Design and Assembly

Workshop drawings are attached for the large and the small sensors built in 1986 (Figures A1.1 and A1.2, respectively).

The dimensions of the rim and lip around the diffuser, together with the thickness of the diffuser are crucial for the cosine response. The light striking the filters should be parallel. A jig was made up to assist in drilling the parallel holes in the large units. The sleeve for the detectors has to be a good fit, otherwise the detector is not held rigidly and the glue that is used to pot the rear of the unit may squeeze round onto the filter. Greater sensitivity of all units can be achieved by increasing the size of the resistor to say 10 kΩ without loss of linearity but with some increase in noise. Greater sensitivity of the small unit would be achieved by placing the dector and filter closer to the diffuser. Greater sensitivity of the large unit, and ease of construction, was achieved in 1987 by replacing the seven small holes with a simple 4 mm diameter hole, just 5 mm deep, with no detriment to the spectral response. The space in the back of the small unit is small and assembly is fiddly. Miniature resistors help but it is still a problem getting the base plate fixed in position. A glue that adheres well to acetal has not been found and there is little room for screws.

Specification

The performance of the sensors was assessed by comparison with a secondary standard in the form of a Li-Cor quantum sensor (LI 190 SA, Li- Cor, Nebraska). For linearity actual outputs were compared. The relative output shown in the Figure 4 is relative to the secondary standard.

Sensitivity: summarized in Table 2.1 (Chapter 2)
Spectral response curve: summarized in Figure 2.8 (Chapter 2)
Linearity:see Figure A1.3, attached
Cosine responses:see Figure A1.4, attached

Linearity is good. The cosine response is tolerable and is as good as for the LiCor and Macam sensors that were measured at the same time.

Figure A1.1. Design of large 1986 sensor.

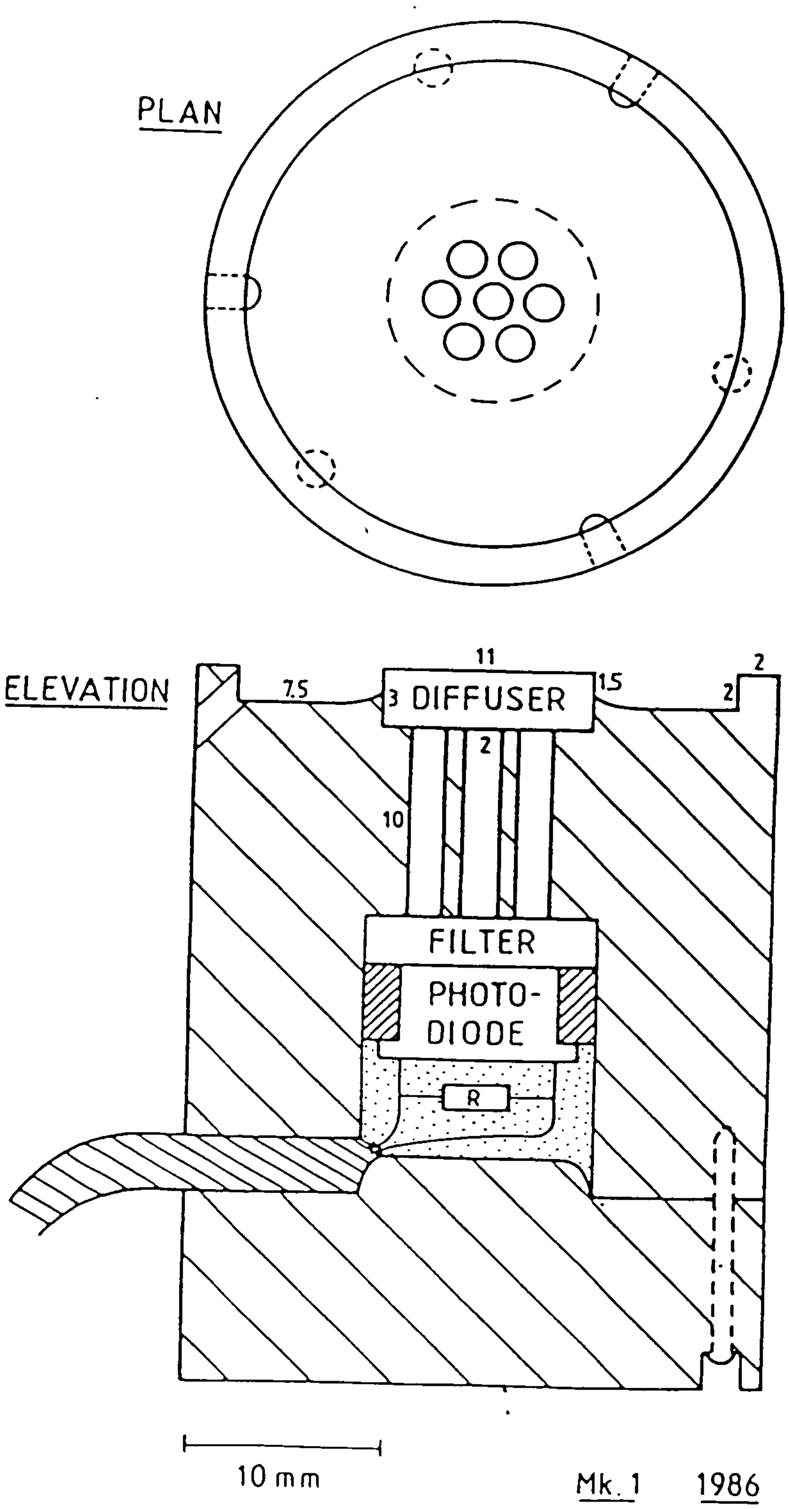


Figure A1.2. Design of small 1986 sensor.

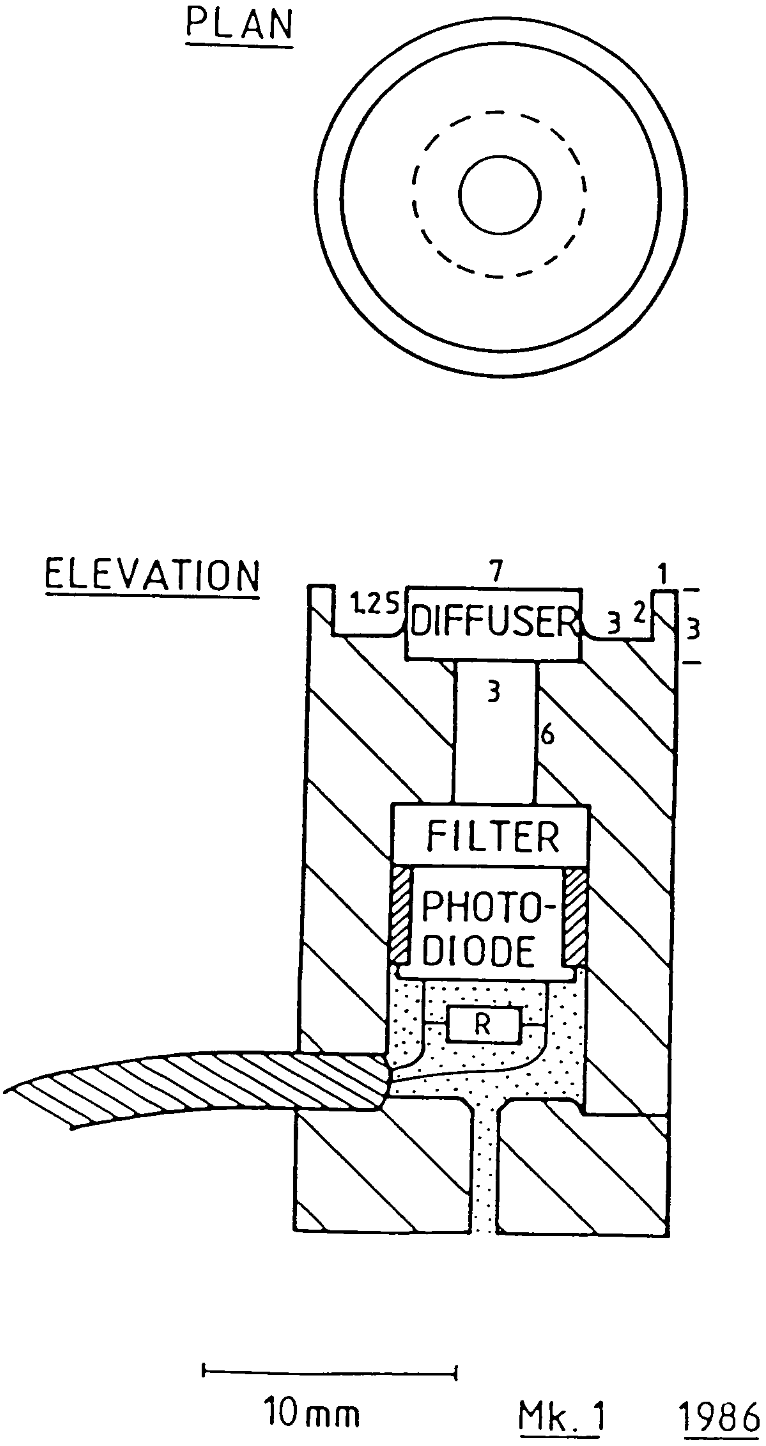


Figure A1.3. Linearity

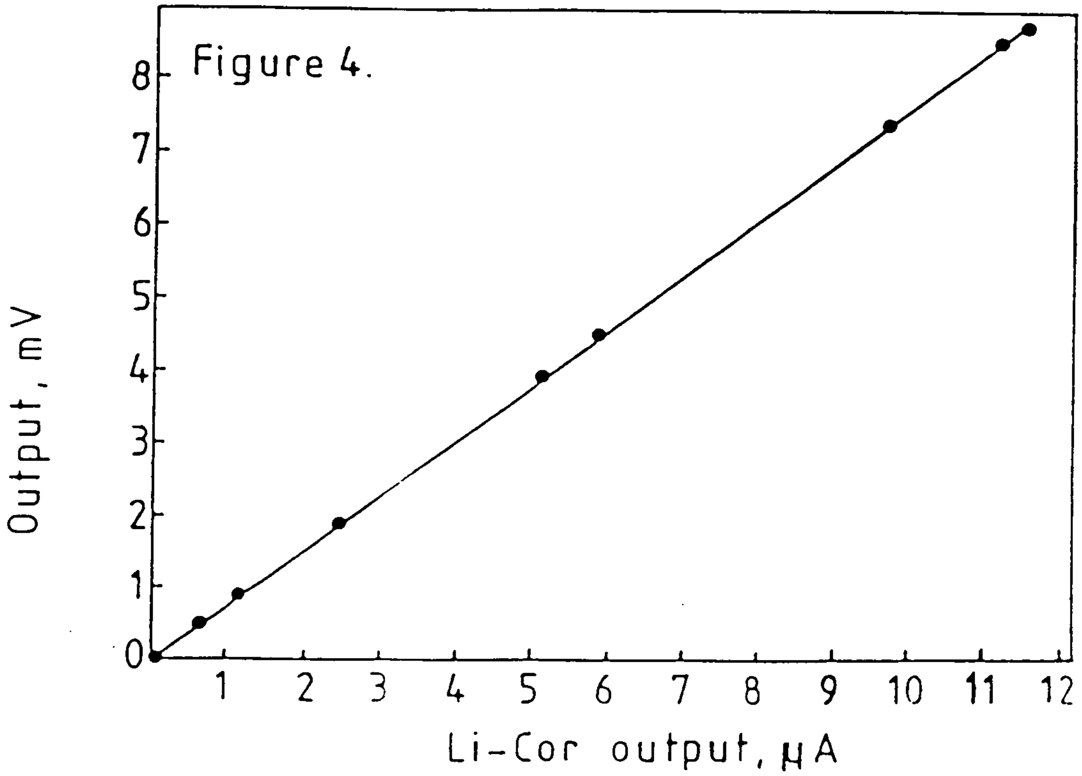
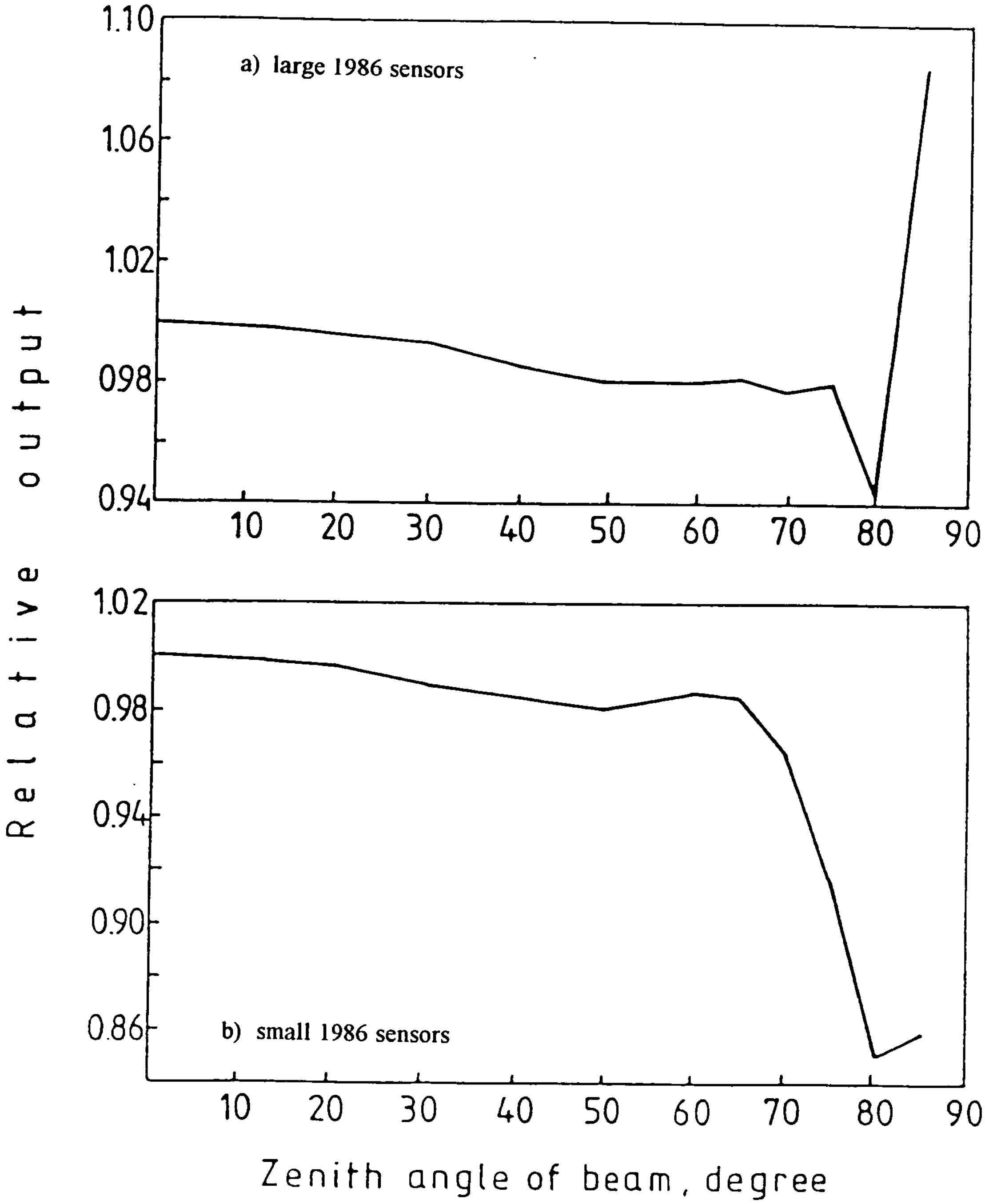


Figure A1.4. Cosine response



Appendix 2. Physiological parameters of leaves of *Picea sitchensis* used to parameterise MAESTRO in Section 3.3.2.8

Table A2.1. The physiological parameters of leaves of *Picea sitchensis*. Definitions of all parameters are given in Table A2.3; taken from Wang and Jarvis, 1990a.

parameter	value	units	source
C_R	0.082	$^{\circ}C^{-1}$	Jarvis and Leverenz (1983)
C_O	-0.07	$\mu mol\ m^{-2}s^{-1}$	Miranda (1982)
T_{ls}	-5.0	°C	Jarvis (1976)
T_{os}	21.5	°C	Neilson et al. (1972)
T_{hs}	40.0	°C	Jarvis (1976)
T_{lm}	-5.0	°C	Neilson et al. (1972)
T_{om}	15.0	°C	Neilson et al. (1972)
T_{hm}	40.0	°C	Neilson et al. (1972)
α_g	0.0204	$mol\ \mu mol^{-1}$	Jarvis (1976)
α_v	0.4037	$mol\ m^{-2}s^{-1}kPa^{-1}$	Sandford (1984)
g_{so}	0.059	$mol\ m^{-2}s^{-1}$	Jarvis (1976)
α_n	0.55	dimensionless	Leverenz and Jarvis (1979)
R_{no}	0.1347	$\mu mol\ m^{-2}s^{-1}$	Leverenz and Jarvis (1979)

Table A2.2. The physiological parameters of leaves in different age classes. A1, A2 and A3 designate current, one-year-old and older needles, respectively and g_{smax} and g_{mmax} are the maximum values of stomatal and mesophyll conductances (mol $m^{-2}s^{-1}$), respectively

Crown level	leaf age class	θ_n	g_{smax}	g_{mmax}
Upper	A1	0.86	0.40	0.10
	A2	0.82	0.27	0.06
	A3	0.78	0.18	0.04
Middle	A1	0.88	0.31	0.06
	A2	0.84	0.21	0.04
	A3	0.79	0.14	0.03
Lower	A1	0.91	0.16	0.03
	A2	0.85	0.11	0.02
	A3	0.81	0.07	0.01

Table A2.3. Symbols used in Tables A2.1 and A2.2, including abbreviations, and their definitions and units

symbol	**definition**	**units**
C_R	Temperature coefficient of dark respiration	$^oC^{-1}$
C_O	PAR coefficient of dark respiration	
T_{is}	Low temperature for zero leaf stomatal conductance	^oC
T_{os}	Optimal temperature of the leaf stomatal conductance	^oC
T_{hs}	High temperature for zero leaf stomatal conductance	^oC
T_{lm}	Low temperature for zero leaf stomatal conductance	^oC
T_{om}	Optimal temperature for the leaf mesophyll conductance	^oC
T_{hm}	High temperature for zero leaf meosphyll conductance	^oC
α_g	Initial slope of the quantum response of the stomatal conductance	mol μmol^{-1}
α_v	Initial slope of the VPD response to the stomatal conductance	mol $m^{-2}s^{-1}kPa^{-1}$
g_{so}	Stomatal conductance in the dark	mol $m^{-2}s^{-1}$
α_n	Quantum efficiency of the needles (dimensionless)	
R_{no}	Dark respiratory rate at a temperature of 0.0^oC	$\mu mol\ m^{-2}s^{-1}$