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**THE ARCHITECTURE AND  
RADIATION REGIME OF  
A KIWIFRUIT STAND**

A thesis presented in partial fulfilment  
of the requirements for the degree of

MASTER OF SCIENCE

in

PLANT SCIENCE

at

MASSEY UNIVERSITY

EDMOND ROBERT MORGAN

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## Abstract

The theory of the interrelations between plant canopy structure and light penetration is reviewed using principles developed for point quadrat analysis. Estimates of leaf area index and leaf orientation can in principle be obtained from measurements of the average transmission of direct sunlight through vegetation using an indirect measurement procedure. The architecture of a kiwifruit (*Actinidia deliciosa* (A. Chev) C.F. Liang et A.R. Ferguson c.v. Hayward) canopy was measured using direct methods and the indirect measurement procedure. The methods gave good agreement for estimates of the mean leaf angle and the G-function. However the indirect procedure produced values for the leaf area index that were about 1.7 times greater than those obtained from direct methods. This was consistent over a range of leaf area indices (measured directly) from 1.7 to 3.5. The evidence provided suggests that this discrepancy is most likely due to the leaves in the canopy having a regular distribution rather than being randomly arranged.

The Poisson law and the positive and negative binomial models provided the basis for further analysis of light penetration into plant stands. The results were compared with observed values of light transmission through the canopy. It was suggested that the measured values of light transmission could be used in conjunction with expected values of light transmission calculated from the direct measurements of canopy architecture to estimate leaf distribution in the canopy. The distribution of leaves in a stand could be determined at two levels, one is a local level within each plant and the other level is associated with growth of the plants in the stand. At the level of the plant, light in the stand was attenuated about 1.7 times faster than expected for a random leaf distribution. At a higher level, which corresponded to the entire stand, light was attenuated about 1.4 times faster than expected for a random stand. The difference is attributed to the non-uniform (discontinuous) structure of the stand which results from localized variations in leaf area index.

The measurements of the distribution of leaf area in the stand are used in conjunction with the direct measurements of canopy architecture to construct a computer model that can be used to simulate the stand. The model is used to simulate the light environment in the canopy so that the daily integral of photosynthetically active

radiation penetrating into the canopy can be determined as a function of the leaf area index. The available information on the effects of light intensity on kiwifruit growth was used to determine the leaf area index at which low light levels could begin to affect fruit growth and yields. For an orchard with a pergola trellis, the maximum leaf area index that could be allowed without affecting fruit growth was calculated to be about 1.6.

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## Introduction

In recent years the kiwifruit industry has expanded rapidly with the development of new markets. This has led to increased research into ways to improve the yield and quality of the crop. A factor which has been identified as influencing yield and quality is the radiation regime within the canopy (Grant and Ryugo, 1984; Morgan *et al.*, 1985; Laing, 1985). These workers have shown that light intensity influences both the yield and the quality of kiwifruit through effects on flowering, leaf photosynthetic rates, fruit growth, and through influencing water use and temperature of plant organs.

Light intensity influences the number of flowers produced on the vine (Grant and Ryugo 1984; Morgan *et al.* 1985). Each year flowers are initiated for the following season's crop, probably about nine months before petal opening and pollination (Warrington, 1986). If the vines are shaded during the initiation period the number of flower buds is reduced and the following season's potential yield decreases. It is reported that replacement canes exposed to full sunlight were three times more fruitful than those trained in a shaded position (Grant and Ryugo, 1984). Studies in controlled environments confirm field results that low light levels (one third or less of full sunlight reaching the shoot) result in reduced bud break, fewer fruiting shoots, fewer flowering nodes per shoot and fewer good flowers per node (Morgan *et al.* 1985).

It is well known that photosynthesis decreases with decreasing irradiance, falling to negligible rates as light levels fall to below one-third of the intensity of full sunlight (Laing 1985). The shaded leaves produce less carbohydrate resulting in reduced potential for plant and fruit growth. A continuous leaf layer on a vine will absorb more than 90% of the incoming photosynthetic irradiance (Smart, 1984) so the effects of shading are major.

Shading of vines is also known to have an effect on fruit development and quality, but detailed information is sparse because it has been difficult to set up well controlled experiments. Shading reduces pollination through reduced bee activity at flowering. The size of a fruit depends on the number of fertilized ovules so reduced pollination leads to smaller fruit sizes. At this stage, however, it is not known whether the reduced bee activity is due to temperature or visible light levels at the flowers. A second problem associated with shading is that fruit are found to have a lower concentration of

soluble solids than fruit from sunlit positions, resulting in later maturity and therefore later harvest (Grant and Ryugo, 1984).

The effects of shading listed here for kiwifruit have been reported for a wide range of crop species. For this reason the effect of stand architecture on the penetration of light into plant canopies has received considerable attention. The basis of the relationship between stand architecture and light penetration will be introduced here. This discussion will first examine penetration of light into a plant stand and will be followed by brief discussions on describing and measuring stand architecture. This will be followed by brief discussion on the problems of measuring the radiation regime within a plant stand.

### **Light penetration**

A number of models have been developed which attempt to formalize the relationships between stand architecture and light penetration (e.g. de Wit, 1965; Duncan *et al.*, 1967; Idso and de Wit, 1970; Lemeur and Blad, 1974; Allen, 1974; McPherson and Torssell, 1970, 1977; Mann *et al.*, 1980). These models have been used to investigate factors affecting penetration of light into plant stands and provide a logical basis for planning crop management procedures and for planning further experimentation.

The model of McPherson and Torssell (1970) was used in the early stages of this work to develop an understanding of the various factors affecting radiation within the canopy. The radiation field within a plant stand is determined by the angular distribution and wavebands of the incident radiation, the architecture of the stand, and the spectral properties of the leaves, stems, flowers (or fruits) and the soil which comprise the stand. If attention is confined to the photosynthetically active radiation (PAR), then the importance of the architectural factors is greater than that of the spectral properties by an order of magnitude (e.g. Ross, 1971). For example, for PAR the scattering coefficient of the leaves and soil is about 10 or 20%, so that multiple scattering of radiation can be neglected in this case (Ross, 1971). To a first approximation, the distribution of radiation in crops is an architectural problem and not an optical one.

PAR in plant stands may be divided into three components according to its immediate source. These are direct solar radiation, diffuse sky radiation and reflected radiation scattered from plant organs within the canopy and the soil beneath. Direct solar radiation is the most important of these components so a correct treatment of the sunflecks in crops is a central problem in describe the radiation regime within a plant

stand. Various analyses (Nilson, 1971; Ross, 1975; Mann, *et al.*, 1977; Ross, 1981; Lang *et al.*, 1985; Lang and Xiang, 1986) indicate that the treatment of sunflecks beneath a canopy is a purely geometrical problem albeit a difficult one to solve. If the geometrical arrangement of the foliage is known then penetration of direct sunlight into the canopy can be predicted. The penetration of diffuse radiation from the sky into the canopy can be described using the same procedures if the angular distribution of the sky light is known.

### **Describing stand architecture**

Measuring and describing the architecture of a kiwifruit stand is an important first step in simulating the canopy radiation regime. Stand architecture can be thought of as a set of features delineating the shape, size, geometry and external structure of a plant or in the instance of a plant stand, a set of plants. A detailed description of stand architecture would include details of the size, shape, orientation, and positions of all the plant organs in the stand. It is usually impracticable to obtain such information for each organ so statistical characteristics of the plant stand are usually obtained instead.

The amount of material present in the canopy may be represented by the leaf area index,  $L$ . This is the ratio of the total leaf area (upper surface only) to the total ground area beneath. Similar indices can be constructed for the surface area of stems and fruit and flowers. A foliage area index can be constructed for the entire canopy by combining area indices for the leaves, branches and reproductive organs.

The orientation of leaves in a canopy is described by the distribution of leaf angles. Leaf angle distributions describe the fraction of the total leaf area in a canopy oriented at various angles to the vertical (leaf inclination angle,  $\theta_L$ ) and to the points of the compass (leaf azimuth angle,  $\phi_L$ ).

The simplest descriptions of stand architecture and light penetration treat canopies as a "horizontally homogeneous turbid layer" (*e.g.* Ross, 1981). These models usually assume that plant organs are randomly distributed in space. However, descriptions are available for regular and clumped distributions of organs (Acock, *et al.*, 1970; Nilson, 1971; reviews by Ross, 1975, 1981). These treatments use empirical coefficients to correct for deviations from randomness found in discontinuous canopies.

Stand structure refers to the collective arrangement of the foliage of the individual plants that make up the stand. A stand is said to be discontinuous if there are large gaps between plants, *e.g.* a row crop before canopy closure (such a stand is treated as having a clumped canopy by the simple models listed above).

More sophisticated treatments have been developed to account for the effects of canopy structure on light penetration in discontinuous canopies (e.g., Allen, 1974; Mann *et al.*, 1980; Lang and Xiang, 1986). Discontinuous canopies include large or irregular areas in which there is no foliage, e.g. in many crops before canopy closure, or breaks in forest canopies caused by the fall of large trees.

The treatments given by Allen (1974), Mann *et al.* (1980) and Lang and Xiang (1986) treat the canopy as being comprised of zones that contain different amounts of foliage (i.e. a non-uniform canopy). This seems to provide a more appropriate treatment for light penetration into plant stands than treating the canopy as a continuous layer. For example Lang and Xiang (1986) found for their remote sensing procedure that treating the canopy as being comprised of different zones gave more accurate estimates of leaf area index than regarding the canopy as a uniform layer of foliage. A uniform canopy has equal amounts of foliage in all of its zones.

#### **Measuring stand architecture**

The most obvious method for obtaining information on stand architecture is to measure the area, shape, angle and position of each plant organ by hand. Unfortunately these procedures tend to be very time consuming and therefore expensive. They also tend to disturb the canopy and, at least in the case of measurements of leaf angles, such disturbance can compromise the quality of the data. These limitations have led to interest in the development of indirect methods for measuring canopy architecture.

One group of indirect methods is based on the probability of probes, either mechanical or notional, penetrating the canopy. The technique of point quadrat analysis was introduced as a tool for measuring canopy architecture by Warren Wilson (1959, 1965). One of the procedures he discussed involved recording only the first contact made with foliage by the probe. Repeated measurements give the mean number of first contacts per hundred quadrats (Warren Wilson, 1965). The proportion of the quadrats that make no contact with the foliage is equal to the proportion of the incoming sunlight that penetrates the canopy without interception. If some assumption is made about the distribution of the foliage then theoretical analyses of the effects of leaf area index and leaf orientation on light interception are possible.

Lang (Lang *et al.*, 1985; Lang and Xiang, 1986; Lang, 1986; Lang, 1988) used the principles of point quadrat analysis developed by Warren Wilson (1959) to develop a technique for remote sensing of canopy architecture. He measured the penetration of

direct sunlight through the canopy for a range of sun angles; this information was used (successfully) to infer details of canopy architecture in plant stands where the leaves are randomly distributed.

### **Measurement of the canopy radiation environment**

The problem of obtaining accurate measurements of the solar radiation beneath plant stands is complicated by the highly irregular distribution of radiation in both space and time. Reifsnyder *et al.* (1971) analysed the problem of obtaining accurate measurements of the light environment beneath two forest canopies. Only one or a few sensors were needed to obtain a statistically adequate estimate of a daily average for radiation penetration, but many were required to obtain satisfactory instantaneous measurements. A further problem is that the sensors suitable for measuring short-wave radiation or PAR are expensive and may require elaborate recording systems. This has meant that a lot of measurements have been made with only one, or a few, radiometers.

The difficulties of measuring radiation within and beneath canopies encourage the use of models from which canopy light levels can be calculated. Much theory is available to describe the transmission of radiation through canopies. However the complexity of canopy architecture and the variability of the above crop radiation environment means that the mathematic methods are complex and the calculations can be tedious. Hence this theory is often used in simulation models which are solved using computers.

### **Scope of this thesis**

At the outset of this work the primary objective was to evaluate a remote sensing procedure for measuring canopy architecture in a kiwifruit orchard. The architectural information obtained from these measurements was used to model the penetration of light into a kiwifruit canopy growing on a pergola type trellis.

This thesis has four further chapters which are largely self contained. Each chapter deals with a different aspect of this work. The second chapter deals with the direct measurement of the architecture of the stand used for this work. The third chapter is concerned with the remote sensing procedure to measure stand architecture and the results are compared with results from the second chapter. In the fourth chapter theoretical expressions used for describing the effects of leaf distribution on light penetration are analysed. The fifth chapter describes a model that was used to simulate the radiation regime within the stand.

Measurements were made of the leaf area index,  $L$ , the mean leaf angle,  $\theta_L$ , and the projected leaf area,  $G(\theta_L)$  using both direct and indirect procedures. There was a large

disagreement between the two estimates of  $L$ , but agreement was good for other parameters of stand architecture inferred from measurements made using the remote sensing procedure.

The cause of this disparity is most likely due to the regular, rather than random arrangement of leaves in the kiwifruit canopy. This means that the leaves intercept more light than they would if the leaves were distributed at random in the canopy. The effects of non random leaf distributions were analysed theoretically to show the effects of leaf distribution on light interception.

The information on the architecture of the kiwifruit stand obtained from the direct and indirect measurements was incorporated into a simulation model to predict light penetration into the canopy. This model was used to calculate the radiation regime in the kiwifruit canopy used for this study. It is estimated that light is depleted about 40% faster than in a uniform stand that has similar architectural properties, e.g. leaf area, leaf angle distribution, but with randomly distributed leaves. If the stand is treated as a uniform canopy, then light is depleted 70% faster than in uniform stand with randomly distributed leaves.

The information on canopy architecture used in the model to describe the canopy was obtained from measurements described in chapters two, three and four. The results from the model suggest that modifying stand architecture through orchard management decisions such as choice of trellis design, or pruning practices have considerable effect on the canopy radiation regime. Such modifications to canopy architecture may help to increase yields of high quality fruit through changes to the canopy radiation regime.



## 2

## Canopy Architecture in a Kiwifruit Orchard

### Introduction

In the course of a growing season the canopy of a kiwifruit orchard progresses from an array of leafless branches located about a trellis to a complete verdant canopy. The distribution and extent of plants, the distribution and density of foliage within the canopy volume, and the orientation of leaves all play significant roles in the interaction of the crop with the incident radiation.

This chapter describes direct measurements of the architecture of a kiwifruit canopy growing on a pergola. The architecture of a plant is a set of features that defines the size, shape, geometry and external structure of the plant. The results obtained provide a reference against which to compare the results from the remote sensing procedure that is described in the next chapter.

The foliage area of the canopy was measured and the contribution of leaves, wood and reproductive organs to the total foliage area was estimated. The orientation of the foliage was investigated and analysed in terms of three dimensional distribution functions. These distribution functions provide a statistical description of the angular distribution of the leaf area inside the canopy volume.

Several definitions are needed to describe the concepts used to describe L and leaf orientation. These definitions are then used throughout this work.

### **Leaf area index**

The leaf area index, L, is the ratio of the total leaf plan area of a canopy to the area of the ground beneath. The leaf area index is a dimensionless quantity expressed as m<sup>2</sup> of leaf area per m<sup>2</sup> of ground area. The leaf area index at a point, P, in the canopy is given by

$$L(P) = \int_0^z \mu(P) dz \quad (2.1)$$

where  $\mu(P,z)$  is the leaf area density and  $z$  is height above the ground. The leaf area density is the leaf plan area per unit canopy volume, expressed as m<sup>2</sup> per m<sup>3</sup> (m<sup>-1</sup>). With the assumption that the canopy is comprised of randomly distributed leaves, L is

given by

$$L = \int_0^z \mu dz \quad (2.2)$$

(Lang *et al.*, 1985) and would then be the same throughout the canopy.

### Leaf orientation

The orientation of leaves in a stand is characterized by the distribution of leaf area with inclination,  $\theta_L$ , and azimuth,  $\phi_L$ . In most plants the upper surfaces of the leaves face the upper hemisphere so that  $\theta_L$  varies between  $0^\circ$  and  $90^\circ$ , while  $\phi_L$  varies between  $0^\circ$  and  $360^\circ$ . The orientation of a leaf is characterized by the orientation of the leaf normal. The geometry of leaf orientation is shown in figure 2.1 and is described in full later. The distribution function of foliage area orientation  $g(P, \theta_L, \phi_L)$  defines the fraction of the leaf area oriented with the inclination  $\theta_L$  and the azimuth  $\phi_L$  (Ross and Nilson, 1967) and expresses the probability that a leaf has an inclination within  $(\theta_L, \theta_L + d\theta_L)$  and an azimuth within  $(\phi_L, \phi_L + d\phi_L)$ . When the values of  $\theta_L$  and  $\phi_L$  are mutually independent, the two variables can be separated and  $g(P, \theta_L, \phi_L)$  can be written as

$$g(P, \theta_L, \phi_L) = g'(P, \theta_L) \cdot g''(P, \phi_L) = 1 \quad (2.3)$$

where  $g'(P, \theta_L)$  is a leaf inclination density function and  $g''(P, \phi_L)$  is an azimuthal density function.

If it assumed that leaf orientation is the same throughout the canopy then the distribution function of foliage area orientation is given by

$$g(\theta_L, \phi_L) = g'(\theta_L) \cdot g''(\phi_L) = 1 \quad (2.4)$$

(Lemur, 1973).

## Methods

### Site description

All measurements were made in a commercial orchard of kiwifruit (*Actinidia deliciosa* (A. Chev) C.F. Liang *et al.* A.R. Ferguson c.v. Hayward) sited near Wanganui in the North Island of New Zealand ( $175^\circ 5'E$  long.,  $39^\circ 30'S$  lat.). The vines were planted, in 1981, with a row by vine spacing of 4.5m by 5m. The rows are oriented approximately north to south. The orchard was first trained on a tee-bar trellis but in the 1985 season, the training system was changed to a pergola. The orchard is divided into blocks of seventy plants. Each block is surrounded by a shelter belt that is about 8m in height. The orchard is located on flat to rolling terrain. This work was carried out in a block of the orchard where the terrain was level.

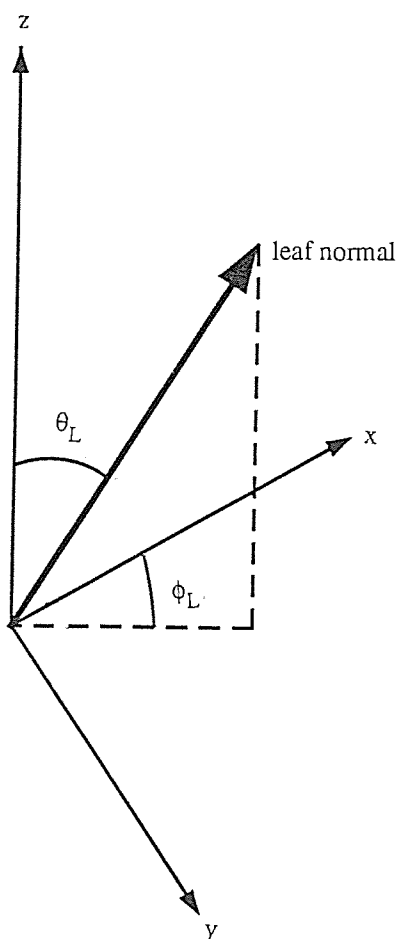


Figure 2.1. Diagrammatic representation of the orientation of a leaf normal in the crop frame of reference. Full details are given in the text (page 12).

### Sampling techniques

Canopy measurements were made in December 1986 and in February 1987. In December the plants were flowering while in February fruit had replaced the flowers.

In December the measurements were made across a large area which contained 70 plants. In February the measurements were confined to three small blocks each containing five plants. These small blocks differed in their canopy structure; blocks #1 and #2 appeared to have uniform distributions of leaf area, while block #3 was chosen because it had large gaps in its canopy where the male plants had been heavily pruned after flowering. The third block also appeared to be under some form of stress but the cause of this was unknown. The leaves on several of the plants in block #3 were wilting.

The measurements of canopy architecture were made on canopy elements (leaves, stems, flowers, fruit) that fell within vertical cylindrical sample volumes with basal areas of  $196\text{cm}^2$  extending from the ground to the top of the canopy. The bases of these cylinders were randomly located on the ground in the sample areas. The measurements were made in one hundred sample volumes on each occasion; one hundred for the whole block in December, and one hundred in each of the three small blocks in February. The outer edge of the outside rows was not included in any of the measurements of light transmission or canopy architecture.

The sample volumes were defined with the aid of a frame mounted upon a camera tripod. This apparatus could be quickly and easily moved between sample locations. The density of the canopy was such that it was necessary to position the frame beneath the canopy to avoid disturbing the geometrical and spatial characteristics of the canopy. The boundary of the sample volume within the canopy was defined by moving a meter long rod around the inside of the frame. Measurements were then made on the elements within the sample volume, starting with those at the bottom. Once the necessary measurements had been made the element could be moved aside as needed so that elements higher in the canopy could be measured more easily.

A leaf was included if the junction of the lamina and the petiole was within the sample volume. The coordinates associated with this point were then measured. The length, width, orientation and height of the leaf above the ground was measured (the measurement procedure is discussed later). The cross section area and height of branches, and flowers and fruit was recorded. The height of the trellis near the sample

volume was also measured, and this height is used as a reference in presenting the data in later sections. The trellis height is used as a reference because the vines are tied down to it.

Additional measurements of orchard leaf area index were made on leaves picked after the fruit had been harvested at the end of the 1985/86 and 1986/87 seasons. These leaves were also used to develop a regression equation for estimating individual leaf areas from measurements of leaf dimensions.

#### Measurement of foliage area

I measured the maximum length and width of every leaf within the sample volumes. Leaf area was then determined using a regression relationship between leaf area and leaf dimensions. This relationship had been determined earlier using a sample of 980 leaves picked in the orchard following the 1986 harvest. This procedure was repeated with a smaller sample (140 leaves) following the 1987 harvest and the regression equation obtained was found to be not significantly different. The equation was

$$L_a = -1.81 + 0.55 L_w L_l + 0.306 L_w^2$$

where  $L_a$  is leaf area in  $\text{cm}^2$ ,  $L_w$  is lamina width in cm,  $L_l$  is lamina length in cm,  $r^2=0.96$  and standard error of estimate  $\approx 0.5\text{cm}^2$ .

The leaf area index of the canopy was also determined by leaf harvest. The procedure here was to determine the leaf area found within  $1\text{m}^2$  quadrats that were located at random through the study areas. The leaves were dried for three days at  $95\text{C}$  and then weighed to obtain the leaf-sample dry weights. The leaf sample dry weights were multiplied by a conversion factor to obtain the leaf area in each of the quadrats.

The conversion factor for oven-dry leaf weight to leaf area was obtained from sub-samples that were selected at random from the harvested material. These included leaves collected through the full depth of the canopy. The area of these leaves was measured with a leaf area meter (LI-3100, LiCor Inc., Lincoln, Nebraska, U.S.A.) and the leaves were then dried as above. A conversion factor for oven-dry weight per unit leaf area was calculated and found to be  $0.77\text{m}^2$  of leaf area per kilogram of dry weight.

For branches, the length within the sample volume and the width and the height at which it passed into and out of the sample volumes was measured. The dimensions of the branches were measured. The branches were assumed to be cylinders and the silhouette area was obtained by multiplying length by diameter. The orientation of the

branches was not studied. This technique for measuring the woody elements is not very accurate ( $\pm 20\%$ ) but is justified by the small area of the wood relative to the total foliage area and because more accurate measurements had proved to be very time consuming.

The heights of the flowers and fruit were noted. Flowers with petals were assigned an area of  $16\text{cm}^2$  and flowers without petals were assigned an area of  $1.2\text{cm}^2$ . The lengths of the fruit were measured, they were assumed to be spherical and fruit lengths were taken to equal their diameters. This technique for measuring the silhouette areas of the reproductive organs is not very accurate ( $\pm 15\%$ ) but their small contribution to the total foliage area justifies its use.

### Measurement of foliage orientation

Measurements of the inclination ( $\theta_L$ ) and azimuth ( $\phi_L$ ) angles of the leaves are needed to describe the orientation of leaf normals. Inclination was defined as the angle between the leaf normal and the vector  $0,z$  (figure 2.1). Leaf inclination was divided into six  $15^\circ$  angle classes to cover the range  $0 \leq \theta_L \leq 90^\circ$ . These classes were centred on  $\theta_L = 7.5, 22.5, \dots, 82.5^\circ$ . Azimuth was defined as the angle between the projection of the normal on the plane  $xOy$  and north ( $x=0$ ). Azimuth was taken as positive in a clockwise direction about  $0$  (figure 2.1). Azimuth spans the range  $0 < \phi_L \leq 360^\circ$ . For analysis, azimuth was subdivided into eight classes centred on  $\phi_L = 0, 45, \dots, 315^\circ$ . The proportions of leaf area in each of the 48 possible combinations of elevation and azimuth defined the distribution of leaf orientation.

The leaf orientation data were obtained using an instrument made from a compass and a protractor as described by Norman and Campbell (1986) (see plate 2.1). Leaf orientation was found by placing the disc parallel to the leaf surface so that the rod approximated the normal to the leaf surface; the orientation data was then read from the protractor and compass scales. Kiwifruit leaves are rarely completely flat so for these measurements the disk was aligned with the section of the lamina which represented the biggest flat section on the leaf. Only the side of the leaf oriented upward was considered. The number of inverted leaves was noted and was found to be less than 1%.

Some care was required not to disturb the leaves before measurement as this would compromise the quality of the data. For this reason the elevation of the leaves was measured first, then the orientation and last the leaf dimensions. The first two operations did not require that the leaves be touched. The protractor-compass was

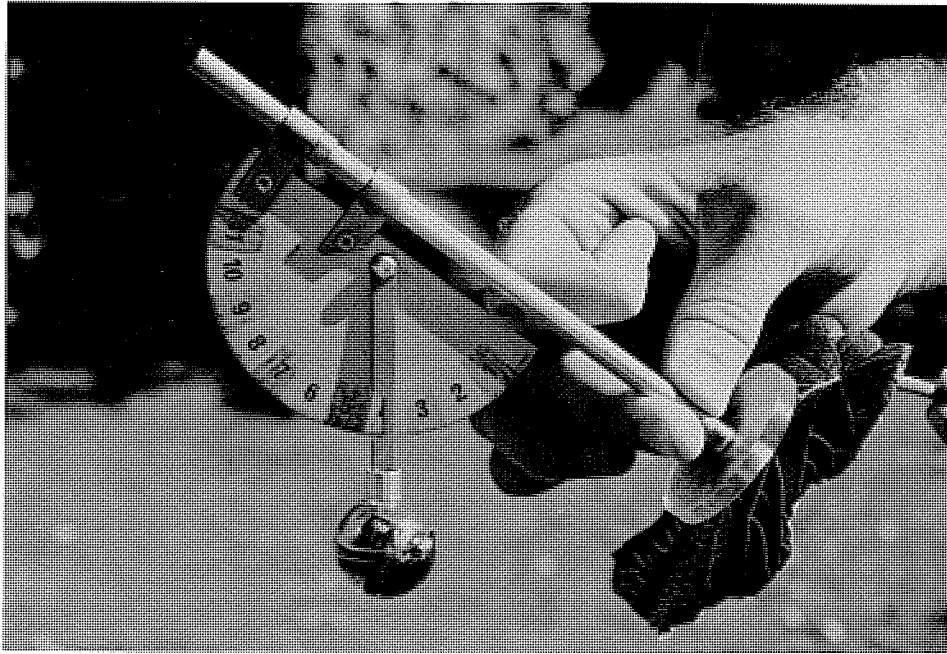


Plate 2.1. The instrument used to measure the zenith and azimuth angle of the normal to the leaf lamina. The rod approximates the leaf normal, and the perspex disc the leaf lamina. This instrument is the same as one described by Norman and Campbell (1987).

found to be difficult to use in places where the leaves were close together because of the proximity of neighbouring leaves; care was required to ensure that the leaves weren't disturbed.

The orientation data were used to determine the probability density functions for leaf inclination,  $g'(\theta_L)$ , and leaf azimuth  $g''(\phi_L)$  (Lemur, 1973). It was assumed that  $g(\theta_L, \phi_L) = g'(\theta_L) \cdot g''(\phi_L)$  which requires that the quantities  $\theta_L$  and  $\phi_L$  are independent. This assumption seems reasonable because examination of the leaf orientation data (given later in table 2.2) reveals no apparent dependence between leaf inclination and leaf azimuth (leaf orientation is uniform with azimuth). Consequently to derive the distribution function for leaf inclination, the leaf area of all azimuth classes was pooled. The increments of the cumulative distribution function,  $\Delta G'(\theta_L)$ , were obtained by dividing the leaf area in each inclination class by the total leaf area in all azimuth classes. Division by  $\pi/12$  gave the value of the leaf inclination density function corresponding to the midpoint of that inclination interval. A similar procedure was followed to obtain  $\Delta G''(\phi_L)$ . These values are divided by  $\pi/4$  to calculate the azimuthal density function,  $g''(\phi_L)$ .

### **Sun-tracking leaf movements**

It had been anticipated that heliotropic leaf movements might occur in kiwifruit. Possible leaf movements were measured in three ways. In the first tests the orientation of labelled spots on one hundred and twenty leaves was measured in the morning and again in the afternoon (4-5 hours later) using the instrument in plate 2.1. The measurements were made on a calm day. No heliotropic leaf movements were detected but this may have been due to the insensitivity of the instrument used to measure changes in leaf orientation.

Another experiment was devised to confirm the lack of heliotropic movements in kiwifruit leaves. For this several plants were moved into a room with black painted walls where they were exposed to directional light supplied by incandescent spotlights. The orientation of labelled regions on their leaves was measured when they were placed in the room and these measurements were repeated at intervals over several days.

As a final test a plant was placed in a darkened room where it received light from one direction only. A camera was mounted on a tripod and photographs were taken of the position of several leaves relative to a datum placed behind the leaves. The first photographs were taken immediately the plant was placed in the room. More photographs were taken at intervals over the next 72 hours.



## Results

### **Foliage area**

When the first measurements were made in December, the crop had approximately three-quarters of its final total foliage area and the plants had overlapped within and between the rows to give a closed canopy. When the measurements of canopy structure were made in February, the canopy had finished growing for the season. In February there were large gaps present in the canopy of block 3 because the male plants had been heavily pruned after flowering. Blocks 1 and 2 appeared to have a uniform distribution of leaf area in their canopies.

The contribution of leaves, wood and fruits to the area of the kiwifruit canopy determined by the 'sample volume' measurements is shown in table 2.1. The foliage area index (FAI) for the areas of the leaves, branches and reproductive organs at the time of the December measurements was 1.9 and the FAI in February for the three areas sampled was 3.5, 2.2 and 2.0 for blocks one, two and three respectively; in June the FAI was measured at 2.3 and 1.7 for blocks one and two respectively. In December the foliage was composed of leaves, branches and flowers; in February fruit had replaced the flowers. The wood component of the canopy was not measured in June but was assumed not to have changed since February. The values given for the wood in February are also used in the June results.

In December and February the leaves are contributing about 92% of the total foliage, the wood contributed 5%, and the fruit and flowers about 3%. By June many leaves had fallen but leaves still comprised over 90% of the total foliage area.

### **Vertical distribution of foliage area**

The vertical distribution of the foliage area measured in February is shown in figure 2.2. These are the averaged results from blocks #1, #2 and #3. The results for the three blocks were similar. The maximum height of the foliage was 0.87m above the trellis and the minimum height was 1.14m below the trellis. The maximum leaf area density is located in the first 0.2m above the trellis, and most of the leaf area (about 80%) is located in the first 0.6m above the trellis. The branches are mainly located in a layer from 0.2m below the trellis to 0.2m above the trellis, although branches are present through the full depth of the canopy. Most of the fruit are found in the layer from 0.2m below the trellis to 0.2m above the trellis. The trellis was used as the reference for these comparisons because the branches are tied down to the trellis and the height of the trellis changes across each block.

<u>Sample</u>		<u>Leaf</u>	<u>Wood</u>	<u>Fruit/Flower</u>	<u>Total</u>
Dec 1986		$1.72 \pm 0.14^*$	$0.09 \pm 0.02$	$0.09 \pm 0.01$	$1.90 \pm 0.15$
Mar 1987	#1	$3.28 \pm 0.22$	$0.13 \pm 0.01$	$0.09 \pm 0.01$	$3.50 \pm 0.22$
	#2	$2.02 \pm 0.14$	$0.11 \pm 0.01$	$0.06 \pm 0.01$	$2.19 \pm 0.14$
	#3	$1.85 \pm 0.17$	$0.09 \pm 0.01$	$0.05 \pm 0.01$	$1.99 \pm 0.18$
Jun 1987	#1	$2.2 \pm 0.1$	$0.13 \pm 0.01$	a	$2.3 \pm 0.1$
	#2	$1.6 \pm 0.2$	$0.11 \pm 0.01$	a	$1.7 \pm 0.1$

\* standard error

a the estimates of wood area are assumed to be the same as those measured earlier in the season.

Table 2.1. The contribution of the components of the canopy to the total foliage area measured in December 1986, February 1987, and June 1987. The result for each component is given in terms of its area (upper surface only) per unit ground area.

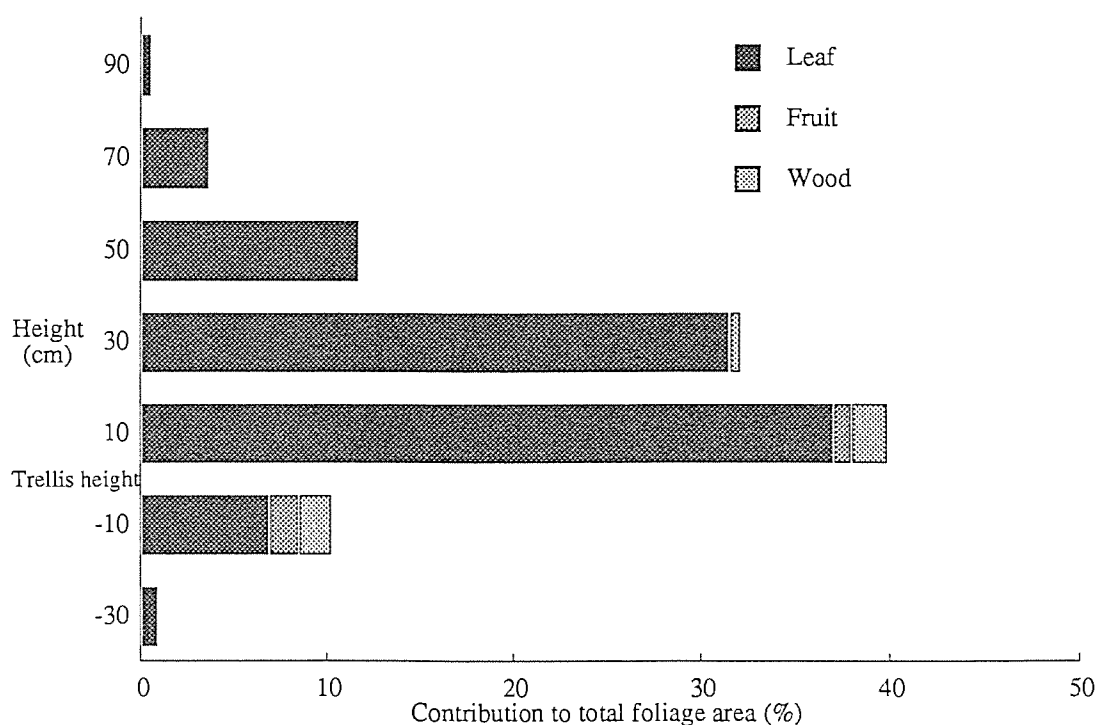


Figure 2.2. The vertical distribution of the foliage in the canopy. The figure shows the distribution of the leaves, wood and reproductive organs that comprise the total foliage area and provides a visual representation of the results given in table 2.1. The height of the foliage elements is relative to the height of the trellis (height = 0) on which the crop is growing.

The canopy was divided into horizontal layers on the basis of cumulative leaf area index (each layer had a cumulative leaf area index of about 1) to see whether the average leaf size changed with depth in the canopy. The number of layers varied from four in block 1, to three in block 2, and there were two in block 3 and for the December results. This analysis was carried out separately for the measurements made in December and for each of the three blocks measured in February. The average area of individual leaves was found to be greater at the top of the canopy than at the bottom. This increase in leaf size is most marked in block #1 where the mean leaf size in the lowest layer was 124cm<sup>2</sup> and in the top layer it was 180cm<sup>2</sup>. In blocks #2 and #3 the increase in leaf size between the two layers was from about 120cm<sup>2</sup> to about 140cm<sup>2</sup>. In December the mean size was 97cm<sup>2</sup> at the bottom of the canopy and 133cm<sup>2</sup> at the top.

### **Foliage orientation**

The measurements of leaf orientation made in December and in the three blocks in February were tested for differences between them. For this analysis the leaf angle distributions with inclination and azimuth were considered. The results for leaf inclination and azimuth were compared between the four sets of measurements using the chi-square test. (A 5% level of significance was used for all statistical analyses.) No significant difference was found between the observed frequencies of leaf inclination angles ( $\chi^2=21.18$ , 15d.f.) or leaf azimuth angles ( $\chi^2=13.49$ , 21d.f.) so the results were pooled for further study. The pooled results for the leaf orientation data are given in table 2.2. Figure 2.3 provides a visual representation of the results given in table 2.2.

Almost all (90%) of the foliage was found to have an inclination in the range  $0 < \theta_L < 60^\circ$ , with most of the foliage (59%) in the range  $15 < \theta_L < 45^\circ$ . Relatively small proportions of foliage were found in the classes centred on 62.5 and 82.5°. The mean leaf inclination for the pooled measurements was 33°. The leaf angle distribution function for the pooled result is shown in figure 2.4. The vertical bars in figure 2.4 show that there is little variation attributable to azimuth in the proportion of foliage in any one class of leaf inclination.

The azimuthal distribution of leaf area for the whole canopy can be seen in figure 2.3, for the eight classes of  $\phi_L$ . The azimuthal distribution of the leaves is not different from uniform ( $\chi^2=4.55$ , 7d.f.); the slight trend for the leaves to orient toward the north is not significant.

Leaf orientation at different depths was also analysed. To do this the canopy was divided into horizontal layers on the basis of cumulative leaf area (as was described

$\phi_L$	$\theta_L$ ( $^\circ$ )						n
	7.5	22.5	37.5	52.5	67.5	82.5	
0	33	59	36	30	6	8	172
45	26	60	40	14	12	5	157
90	35	49	37	29	15	3	168
135	23	58	33	24	9	7	154
180	20	61	35	21	8	6	151
225	23	50	36	30	15	2	156
270	25	55	34	32	12	4	162
315	22	74	46	26	10	3	181
n	207	466	297	206	87	38	1301

Table 2.2. Pooled results for leaf orientation data. These are the pooled results from measurements of leaf orientation made in December 1986 and February 1987. The results are shown as the observed number of leaves seen in each of the inclination and azimuth classes. The inclination and azimuth angles shown are the midpoints of the respective angle classes.

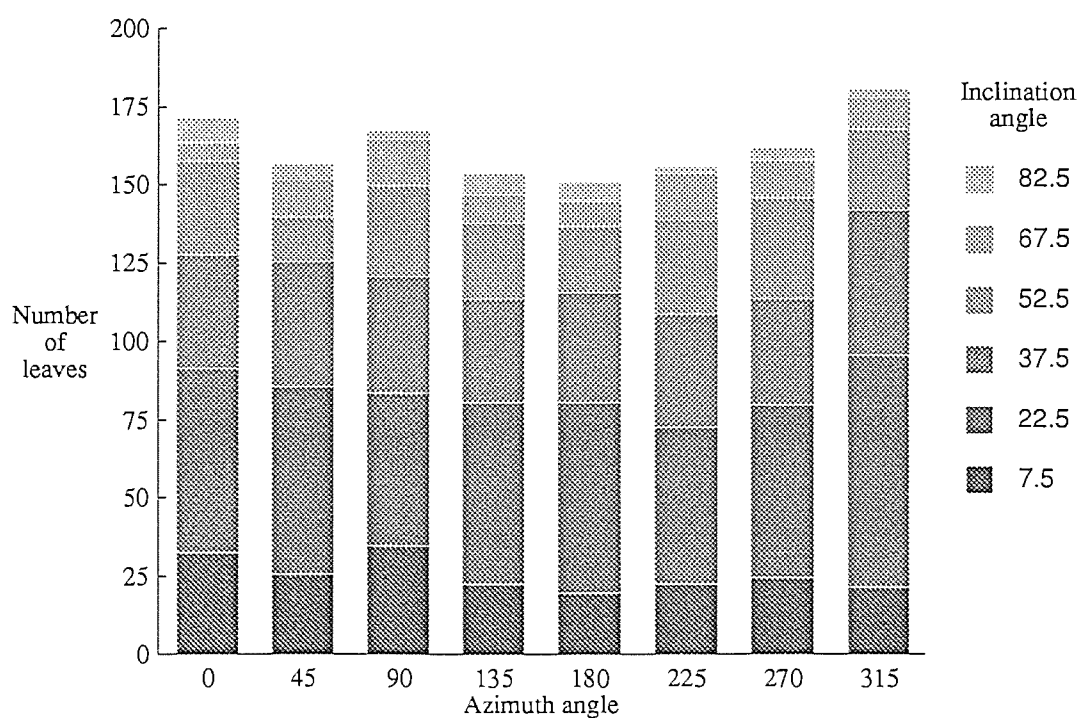


Figure 2.3. Orientation of leaf area in the kiwifruit canopy. These are the data from table 2.2. The columns represent the azimuthal classes of leaf orientation and are divided into six classes of leaf inclination.

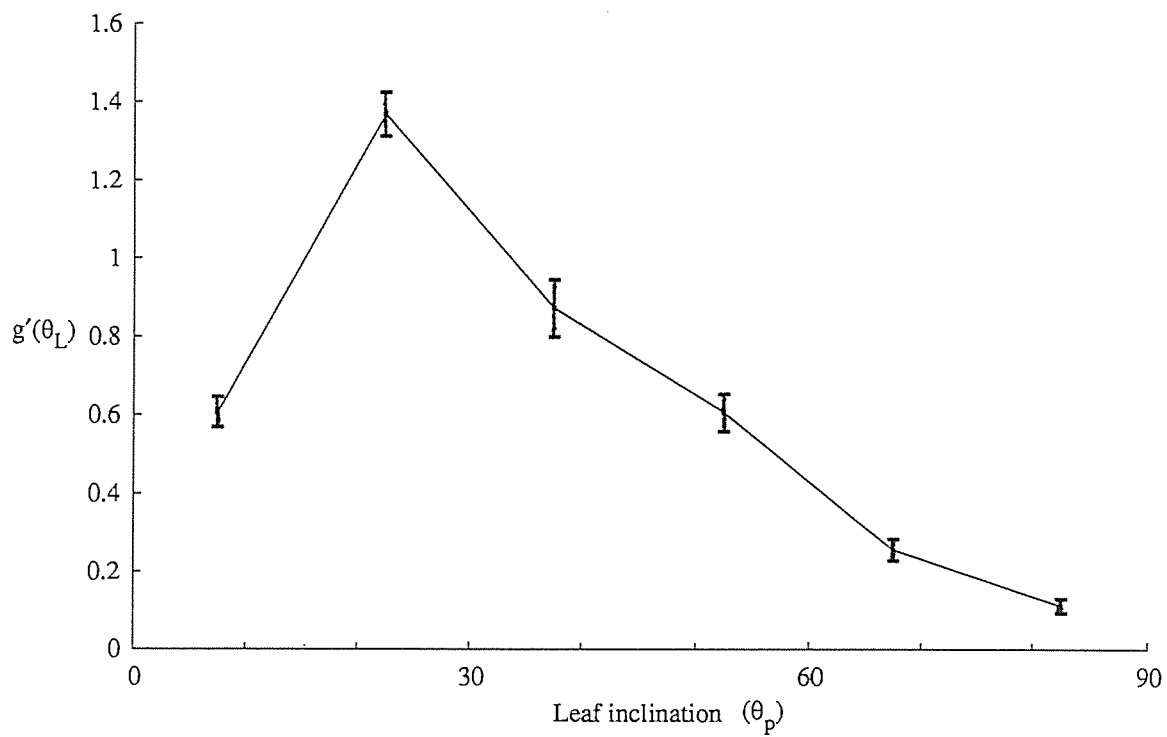


Figure 2.4. The leaf angle distribution function calculated for kiwifruit from the leaf orientation data given in table 2.2. The error bars show that there is little variation attributable to azimuth in  $g'(\theta_L)$ .

earlier). No significant statistical differences were found in the leaf inclination distribution function,  $g'(\theta_L)$ , between the different layers. Slight differences in the mean leaf inclination angle at the bottom and the top of the canopy were observed for all of the sets of leaf angle measurements. This difference was greatest in block #1 where the mean leaf angle varied from  $29^\circ$  in the top layer, to  $32^\circ$  in the bottom layer of the canopy.

The data was analysed to see if leaves of different sizes had different leaf elevations. For this analysis the pooled data for the leaves was divided into four size classes:  $0-75\text{cm}^2$ ,  $75-125\text{cm}^2$ ,  $125-175\text{cm}^2$  and over  $175\text{cm}^2$ . The leaf inclination distribution functions were not significantly different between the different size classes ( $\chi^2=22.61$ , d.f.=15). The same result was found from an analysis of leaves from the separate blocks.

In conclusion, the orientation of leaves in this kiwifruit canopy was characterized by an absence of significant azimuthal variation and a mean inclination of  $33^\circ$ .

#### **Heliotropic leaf movements**

The results of experiments to test for heliotropism in the leaves of kiwifruit failed to show any evidence for its occurrence in mature kiwifruit leaves. The results of the first experiment suggested that leaf movements did not occur, but were judged to be inconclusive because of the insensitivity of the instrument used to measure the leaf movements. The results of the second experiment provided no evidence to suggest that the leaves were reorienting themselves to the light even after several days of exposure to directional light. The result of the third experiment supported the findings of the first two experiments. Examination of the photographs taken over the course of the experiment showed no evidence of any movements by the leaves to reorient themselves to the light. The conclusion here is that kiwifruit leaves are not heliotropic.

#### Discussion

The maximum leaf area density was found in the lower to middle layers of the canopy, and was slightly above the point where fruits and branches are concentrated. It is not surprising that the area of the branches is at a maximum at trellis height since the main branches (the leaders and the fruiting arms) of the vines are tied to the trellis, although branches are present through the full depth of the canopy. The leaves have long petioles (8-10cm) and large laminae (average dimensions of 11cm long and 13cm wide). Observation of leaves and branches in the canopy suggests that the lamina is able to grow into a position where it can improve its exposure to light through bending

and orientation of the lamina and petiole (see plates 2.2 and 2.3). The extent to which the leaves can grow and reorient themselves relative to the branches from which they originate is apparent when it is realised that kiwifruit has a  $1/3$  spiral phyllotaxis.

The leaf angles are closer to the horizontal (more planophilic) than would be found for a uniform leaf angle distribution. The mean leaf angle of  $33^\circ$  for kiwifruit is comparable to values that have been reported for horse beans ( $30^\circ$ , Ross and Nilson 1967), cucumber (about  $32^\circ$ , Shell *et al.*, 1974), sunflower ( $29^\circ$ , Lemeur, 1973;  $35^\circ$ , Shell *et al.*, 1974; Shell and Lang, 1975), lupin ( $27-37^\circ$ , Scott and Wells, 1969) and lucerne ( $31-35^\circ$ , Scott and Wells, 1969). It is less than values reported for tobacco ( $40^\circ$ , Whitfield and Connor, 1980), barley ( $44-53^\circ$ , Scott and Wells, 1969) and is much less than values reported for pepper ( $47^\circ$ , Shell *et al.*, 1974) and sorghum ( $c.54^\circ$ , Lang *et al.*, 1985).

The azimuthal distribution of leaf area was not significantly different from uniform. The structural data were collected throughout the course of the day and any heliotropism was assumed to be negligible. Norman (1978) claimed that it is rare to find canopies in which significant azimuthal asymmetry exists. Data available in the literature support this claim. For example, an absence of significant azimuthal asymmetry has been reported for horse beans (Ross and Nilson, 1967), cucumber and young pepper plants (Shell *et al.*, 1974), Jerusalem artichoke (Lemeur, 1973) and soybeans (Lemeur, 1973). An exception to this rule is sunflower in which the azimuthal distribution is asymmetric and the leaves are heliotropic (Lemeur, 1973; Ross, 1981; Lang, *et al.*, 1985). It has been found that kiwifruit grown on tee bar trellises have an asymmetrical azimuthal distribution of leaf area, with leaves being oriented to the inter-row gaps (Dr. R.E. Smart, personal comm., 1987). With the apparent ability of kiwifruit leaves to orient themselves to improve light reception by phototropic leaf growth this is perhaps to be expected as the leaves will orient themselves to the outside of the canopy and in a tee-bar a large proportion of the canopy surface area will be facing the inter-row gaps. That is, the finding here, that leaves of kiwifruit plants trained on a pergola trellis have no preferred azimuthal orientation is specific to this type of training system; other training systems may lead to some asymmetry.

The leaf angle distribution is not different between the top and the bottom of the canopy despite the leaves at the top being younger and larger than those found lower down. Scott and Wells (1969) found that in barley the mean leaf angle varied from  $44^\circ$

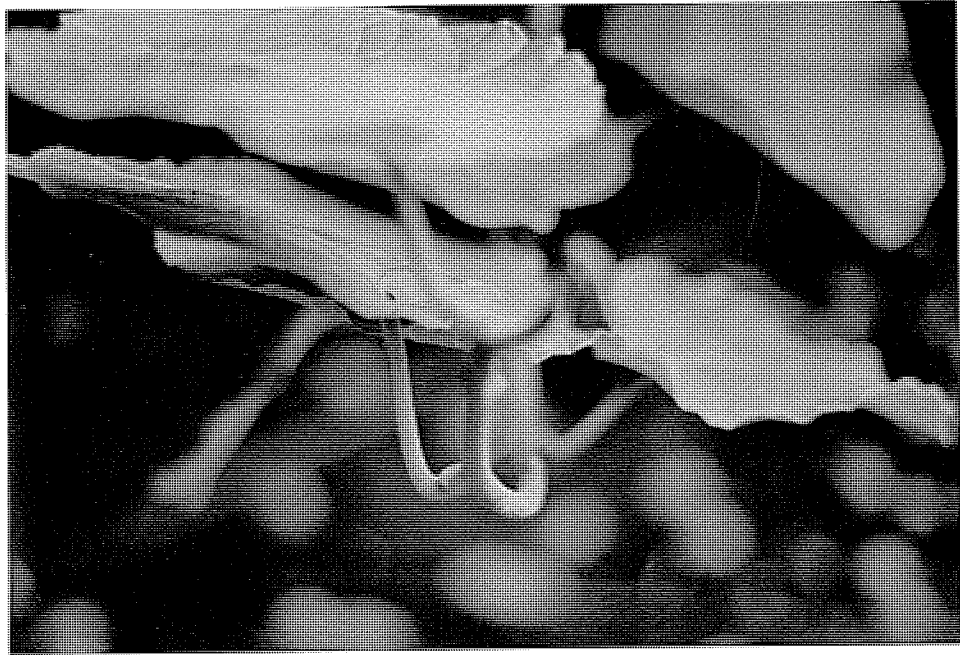


Plate 2.2. Growth of leaves relative to the branch from which they have arisen. This shows the extent to which the leaves can be orientated relative to the branches.



Plate 2.3. Effects of petiole growth on the positions of the leaves in the canopy. This is another view of the leaves in plate 2.2.



near the top of the stand to  $53^\circ$  near ground level. For lupin the corresponding values were  $27-37^\circ$  and for lucerne were  $35-31^\circ$ . Lemeur (1973) reported that in sunflower the older leaves tended to be inclined at some angle between  $20$  and  $30^\circ$ , but the upper part of the canopy was extremely planophile, so that the younger leaves are more horizontal. Hutchison *et al.* (1986) reported that in a deciduous forest canopy the mean leaf angle for the overstorey above the zone of closure was  $38^\circ$ , in the overstorey below crown closure it was  $20^\circ$ , and in the sub-canopy it was  $10^\circ$ .

Heliotropism has been studied in other species and the findings from these studies should be considered with regard to the experimental procedures used and the absence of leaf movements found in kiwifruit. Rates of leaf movement reported for Lupinus succulentus reached about  $15^\circ.\text{hr}^{-1}$  (Vogelmann and Bjorn, 1983) and for Lavatera cretica reached more than  $90^\circ.\text{hr}^{-1}$  (Koller, 1981; cited by Smith, 1984). Vogelmann and Bjorn (1983) reported that leaf movements began within 30-60 minutes of the start of light stimulation. Vogelmann (1984) used white light  $95.5\mu\text{mol}.\text{s}^{-1}$ , 350-800nm) to stimulate leaf movements in Lupinus succulentus. It is thought that the experiments described here to detect the occurrence of heliotropism in kiwifruit would certainly have produced heliotropic responses in Lupinus succulentus as described by Vogelmann and Bjorn (1983). If it is assumed that the stimuli causing heliotropic leaf movements and the responses to such stimuli are similar in all plant species, then it can be concluded from the results given here that significant heliotropic leaf movements don't occur in kiwifruit.

### Summary

This chapter has reported the results of measurements of architecture of a kiwifruit canopy made using direct methods. Aspects of canopy architecture that influence the canopy radiation regime have been examined. The important findings were that the mean leaf inclination angle was  $33^\circ$ , the orientation of the leaves showed azimuthal symmetry, and there is no evidence of heliotropism. In the next chapter these results are compared with estimates of canopy structure obtained using a remote sensing procedure for measuring plant canopies.

### 3

## Remote Sensing of Plant Canopy Architecture

### Introduction

Estimates of leaf area index (L) and leaf orientation are useful for following canopy development and for predicting both light interception and productivity of crops. Direct methods for measuring these properties of crop structure are time consuming and laborious and therefore expensive. Attention has thus been given to the development of indirect methods, which will return the required measurements with satisfactory statistical reliability e.g. Norman *et al.* (1979), Ross (1981), Lang *et al.* (1985).

One group of indirect methods is based on the average number of contacts that a probe makes as it passes through foliage. This "contact frequency" depends upon the direction of the probe, the leaf area index, the angular dispositions of the leaves and the distribution of the leaves with respect to one another. The use of probes to investigate the architecture of plant canopies was first tried by Warren Wilson (1959) who called the technique point quadrat analysis. In principle the use of suitable probes can provide estimates of the geometrical properties of a canopy.

One variant of this approach is based on the probability of a probe not striking any foliage as it is pushed through the canopy. This gives the gap frequency of a canopy (gap frequency may also be recorded using hemispherical (fisheye) photographs (Anderson, 1970; Bonhomme and Chartier, 1972), or by measuring the transmission of direct sunlight through the canopy (Adams and Arkin, 1977; Norman *et al.*, 1979; Lang *et al.*, 1985)).

The procedures for estimating L and the average leaf angle from measurements of contact frequencies or gap frequencies are similar and have been developed by Warren Wilson and Reeve (1959), Miller (1967), Philip (1965), Norman *et al.*, (1979), and Lang (Lang *et al.*, 1985; Lang, 1986; Lang and Xiang, 1986; Lang, 1988).

The work of Lang has produced a method for estimating leaf area index, L, the mean angle of inclination of the leaves,  $\theta_L$ , and the projected leaf area of the canopy,  $G(\theta_p)$ , from measurements of the transmission of direct sunlight. The attraction of Lang's

method is that it offers a rapid, convenient and non-destructive way to estimate canopy architecture. It is especially attractive for use in forests where it is difficult to measure  $L$  and leaf angles using direct methods. Lang's work was first directed towards obtaining estimates of  $L$  and leaf angle distributions,  $g'(\theta_L)$ , but this proved to be impractical. However it was possible to obtain leaf area index,  $L$ , the mean leaf angle,  $\theta_L$ , and  $G(\theta_p)$ , the leaf area projected in the direction of the sunlight.

The purpose of this chapter is, firstly, to review theory that can be used to describe the architecture of a plant canopy. Then it is shown that measurements of the transmission of direct sunlight through a canopy can be used to provide accurate measurements of the gap frequency and that canopy gap frequencies can be used to estimate  $L$ ,  $\theta_L$  and  $G(\theta_p)$ . The procedure for measuring transmission of direct sunlight and for inferring details of canopy architecture from these measurements are reviewed. The results are compared to those obtained from direct measurements of the canopy which are given in chapter 2.

### Theory

In this section theoretical procedures used to describe canopy architecture and light penetration are reviewed. Then the procedures used to recover geometrical information from gap frequencies in plant canopies are examined. The probes used to measure gap frequencies can be either mechanical (e.g. a point quadrat) or notional (e.g. a ray of sunlight). The sun is treated as a probe and the transmission of sunlight through the canopy is related to the gap frequency. This treatment follows that developed by Lang (Lang *et al.*, 1985; Lang and Xiang, 1986; Lang 1986; Lang, 1988) as far as possible. Where other workers are cited, the reference is given.

### **Canopy structure and light penetration**

Consider a canopy consisting of horizontal leaves distributed on a horizontal surface. Suppose that  $n$  identical leaves, each of area  $A_L$ , are randomly distributed on a surface of area  $A_s$ . The probability of a probe passing through a gap between the leaves (the gap frequency,  $P_0$ ) is given exactly by the binomial expression

$$P_0 = (1 - (A_L/A_s))^n \quad (3.1)$$

(Monsi and Saeki, 1953). For this canopy  $L$  is given by

$$L = n(A_L/A_s) \quad (3.2).$$

Substitution of eq. 3.2 into eq. 3.1 gives

$$P_0 = (1 - (L/n))^n \quad (3.3).$$

If the quantities  $L$  and  $A_L$  are fixed, eq. 3.3 shows that increasing the sampling area,  $A_s$ , increases  $n$ . Taking the limit, as  $n \rightarrow \infty$ , eq. 3.3 becomes

$$P_0 = e^{-L} \quad (3.4).$$

Equation 3.4 is the Poisson law. It follows that

$$L = -\ln P_0 \quad (3.5).$$

This result is well known (e.g. Monsi and Saeki, 1953).

The geometry of the leaves in a canopy is defined by the foliage area density function,  $\mu(P)$ , and the distribution function of foliage area orientation,  $g(P, \theta_L, \phi_L)$ . The foliage area density function describes the leaf area per unit volume about the point  $P$  in the canopy and has units of  $m^2/m^3$  or  $m^{-1}$ . The distribution function of foliage area orientation describes the fraction of the leaf area oriented with the inclination  $\theta_L$  and the azimuth  $\phi_L$  (Ross and Nilson, 1967).

The contact frequency  $v(P, \theta_p, \phi_p)$ , is the probable number of contacts per unit length that a probe, penetrating in the direction  $(\theta_p, \phi_p)$ , will make with plant elements in a domain about  $P$ . The contact frequency measures the obstruction caused by the foliage to the penetration of the probe and depends upon the density of the foliage and the inclination of the leaves relative to the orientation of the probe. It is given by

$$v(P, \theta_p, \phi_p) = \mu(P)G(P, \theta_p, \phi_p) \quad (3.6)$$

where  $G(P, \theta_p, \phi_p)$  is the mean projection of unit area of leaf in the direction  $(\theta_p, \phi_p)$  on the plane normal to the direction of the probe (Ross, 1981). The quantity  $G(P, \theta_p, \phi_p)$  is given by

$$G(P, \theta_p, \phi_p) = \int_0^{\pi/2} \int_0^{2\pi} g'(P, \theta_L) g''(P, \phi_L) |\cos \psi| \sin \theta_L d\theta_L d\phi_L \quad (3.7)$$

(Lemur, 1973), where  $\psi$  is the angle between the direction of the probe,  $(\theta_p, \phi_p)$ , and the normal to the leaf surface  $(\theta_L, \phi_L)$ .

In this analysis it is assumed that the leaves are randomly distributed in the canopy, that the leaf area is uniformly distributed with azimuth and that the leaves are opaque. These assumptions greatly simplify the theoretical analysis needed here. The assumption of a random distribution of leaves in the canopy means that leaf area does not change with location in the canopy, so the term  $P$  is no longer needed for this treatment. With the assumption that the leaf area is uniformly distributed with azimuth, the projected areas of the leaves no longer depend on the azimuthal orientation of the sun, but on the zenith angle only. The assumption of opaque leaves in the canopy means that the penetration of sunlight into the canopy is now only a geometrical problem (this will be discussed again later).

If it is assumed that the probability distribution function for leaf normals is uniform with the azimuth angle,  $\phi_L$ , then  $g''(\phi_L)=1$  for all  $\phi_L$  so that eq. 3.7 simplifies to

$$G(\theta_p) = 1/2\pi \int_0^{2\pi} |\cos\psi| g'(\theta_L) \sin\theta_L d\theta_L \quad (3.8).$$

With the assumptions that the leaves are randomly distributed on a plane normal to the direction of the probe, and that a Poisson distribution is acceptable, the gap frequency for the path 0 to  $\epsilon$  along the probe is given by

$$P_0(\theta_p) = \exp\left(-\int_0^\epsilon \mu G(\theta_p) d\epsilon\right) \quad (3.9).$$

For  $G(\theta_p)$  constant along the path 0 to  $\epsilon$  and recalling eq. 2.2 in the previous chapter i.e.

$$L = \int_0^z \mu dz \quad (2.2)$$

in which  $L$  is the leaf area index, and  $z$  is the vertical axis with origin at the ground, it follows that

$$-\ln P_0(\theta_p, \phi_p) = (\epsilon/z) LG(\theta_p, \phi_p) = LG(\theta_p, \phi_p)/\cos\theta_p \quad (3.10)$$

(Nilson, 1971). When the distribution of leaf angles is uniform with azimuth,

$$\ln P_0(\theta_p) = LG(\theta_p)/\cos\theta_p \quad (3.11).$$

The gap frequency ( $P_0(\theta_p)$ ) is obtained from measurements of the transmission of direct sunlight through the canopy. The mean transmission of direct sunlight on the horizontal is the same irrespective of the presence or absence of penumbral effects (Miller and Norman, 1971). It follows that the mean transmission of direct sunlight through the canopy,  $T(\theta_p, \phi_p)$  is equal to the gap frequency,  $P_0(\theta_p, \phi_p)$  provided that the leaves are opaque. Thus

$$-\cos\theta_p \ln T(\theta_p, \phi_p) = LG(\theta_p, \phi_p) \quad (3.12)$$

and when the distribution of leaf angles is uniform with azimuth

$$-\cos\theta_p \ln T(\theta_p) = LG(\theta_p) \quad (3.13).$$

When eqs. 3.6, 2.1 and 3.13 are compared it is seen that, provided the Poisson distribution is appropriate for the canopy,  $-\cos\theta_p \ln T(\theta_p, \phi_p)$  or  $-\cos\theta_p \ln T(\theta_p)$  is the integral of the gap frequency along the path 0 to  $\epsilon$ . Lang et al. (1985) called  $-\cos\theta_p \ln T(\theta_p)$  the "contact number" and assigned it the symbol  $k$ . The contact number is equivalent to the contact frequency (Warren Wilson, 1959) integrated along the path 0 to  $\epsilon$  (Lang et al., 1985).

Lang et al. (1985) used eq. 3.12 to provide useful measures of  $L$  for crops with uniform canopy cover and random leaf distributions by a complicated mathematical procedure. In later papers Lang extended his analysis to non-uniform canopies (Lang and Xiang,

(1986), and simpler methods for obtaining estimates of canopy architecture were developed (Lang, 1986; Lang, 1988). Lang's analysis is outlined below.

### Canopy structure and gap frequency in discontinuous canopies

In the previous section it was shown that, in principle,  $L$  for crops can be determined using the sun's beam as a probe. Lang *et al.* (1985) has demonstrated that this theory can be successfully applied in uniform (continuous) canopies of crops such as sorghum. Where the canopy was not uniform, *e.g.* in a row crop before canopy closure,  $L$  was underestimated. The purpose of this section is to outline theory which shows that  $L$  can be measured in canopies with large gaps by using a procedure that involves suitable averaging of the transmission measurements.

A non-uniform distribution of foliage can be represented by a canopy which has zones with different leaf areas. Consider a canopy containing  $m$  zones of area  $a_i$ . Each of these zones has a local leaf area index of  $L_i$ . For this canopy,  $L$  is the mean of the leaf areas contained within all of the zones that comprise the canopy. It is given by

$$\bar{L} = \frac{\sum_{i=1}^m a_i L_i}{\sum_{i=1}^m a_i} \quad (3.14)$$

where  $\bar{L}$  is the mean leaf area index for the  $m$  zones in the canopy. It is assumed that the leaves within each zone are located randomly, which is less restrictive than the assumption that the whole foliage is random. From eq. 3.5

$$\bar{L} = \frac{\sum_{i=1}^m a_i (-\ln P_{0i})}{\sum_{i=1}^m a_i} \quad (3.15)$$

where  $P_{0i}$  is the local gap frequency for the region  $a_i$ . When the zones are of equal area, eq. 3.15 simplifies to

$$\bar{L} = 1 / m \sum_{i=1}^m -\ln P_{0i} \quad (3.16)$$

The last two equations, eq. 3.15 and eq. 3.16, provide correct values of  $\bar{L}$  in the presence of gaps or clumps provided that the Poisson law applies locally. This result can be used to show that the Poisson law is a special case of a more general law which can be used to describe light penetration in canopies (*e.g.* Mann *et al.*, 1977).

### Sampling area

A non-uniform distribution of leaf area affects the pattern of transmission of sunlight through the canopy. To successfully account for the local gap frequencies in different regions in the canopy, measured values of the local transmission must discriminate between zones with different  $L$ . This can be done by averaging the transmission measurements over as short a distance as possible, which discriminates between zones with different  $L$ , and in particular between foliage and large gaps in the canopy. The

analysis in this section will provide a practical sampling scheme that can be used to exploit eq. 3.16.

In selecting the minimum sampling area,  $a_i$  for averaging transmission measurements Lang and Xiang (1986) considered two factors. If  $a_i$  was too large, it would not discriminate between different zones in the canopy, for example, between vegetation and gaps, or between regions with different  $L$ . If  $a_i$  was too small, measured values of  $P_0$  would often be zero and the logarithm of zero is not defined. The best choice of averaging area for  $P_0$  is the smallest of the areas which satisfied the two criteria, that the Poisson law (eq. 3.5) is an acceptable approximation to the binomial (eq. 3.3), and, that the probability of an experimental measurement of  $P_0$  being zero was negligible.

If  $P_0$  is estimated using the binomial distribution (eq. 3.3) but  $\hat{L}$  is estimated using the Poisson law (eq. 3.5), then from eqs. 3.2, 3.3, and 3.5 and with

$$R = A_s/A_L \quad (3.17)$$

it follows that

$$\hat{L} = -\ln(1-(1/R))^{LR} \quad (3.18)$$

The ratio  $\hat{L}/L$  is then given by

$$\hat{L}/L = -R \ln(1-(1/R)) = F(R) \quad (3.19)$$

and the accuracy of the estimate,  $\hat{L}$ , depends only upon the ratio of the area of the leaves to the sampling area. The relationship between  $F(R)$  and  $R$  is shown in figure 3.1. For example, when  $R=10.6$ ,  $F(R)=1.05$ , which is a 5% over-estimation of the contact number. (This is the same result as Monsi and Saeki, 1954, p.36.).

When the sampling area is long in one dimension and very much narrower than a leaf in the other, as is the case with a small sensor traversing a canopy,  $l/d$  may be substituted for  $R$  ( $l$  is the distance over which the gap frequency is averaged and  $d$  is the mean length of secants through a leaf). (A secant is the length of a straight line cut by the outline of a leaf.) This conclusion is based on the result of an analysis of the sun-fleck area beneath a canopy carried out by Mann *et al.* (1977). The path length for acceptability of the Poisson law can be obtained from eq. 3.19 or figure 3.1. The procedure for calculating  $I_i$  will be discussed later.

#### **Path length so that gap frequency is greater than zero**

Lang and Xiang (1986) calculated the theoretical probability that the measured gap frequency is greater than zero for various values of  $L$  (Lang and Xiang, 1986). They found for low values of  $L$  that a moderate path length gives a high probability of encountering a gap. However for high values of  $L$  the probability of encountering a

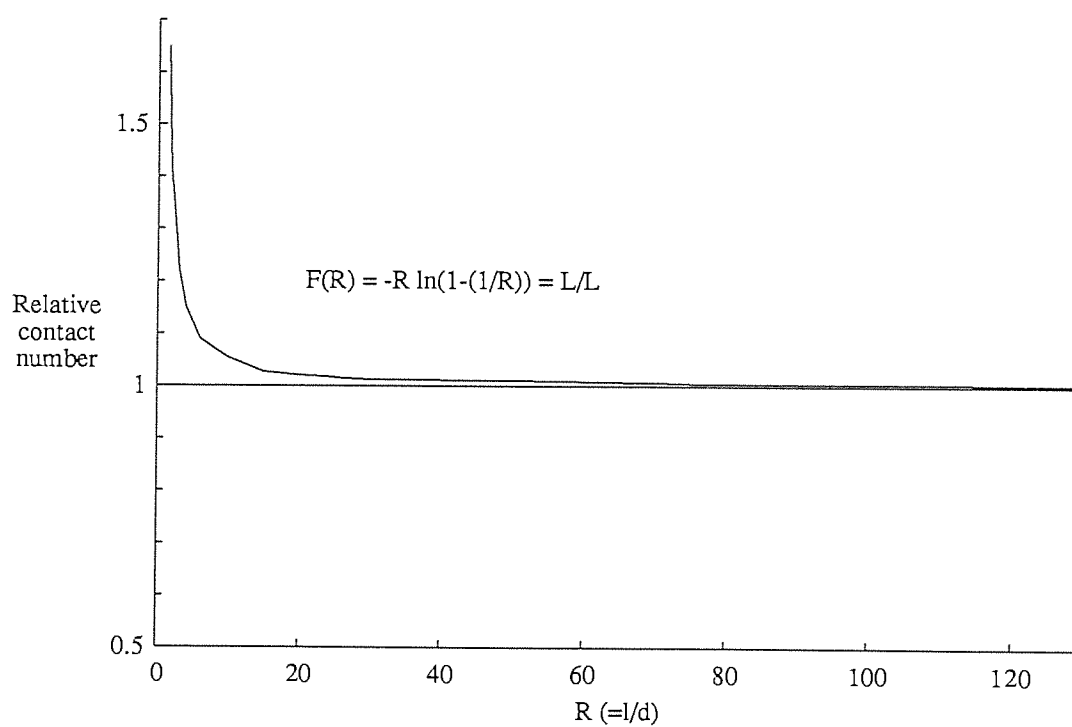


Figure 3.1. Variation in contact numbers estimated from the Poisson law (eq. 3.4) as a function of changes in the relative sample size ( $R=l/d$ ).  $F(R)$  is the ratio of the Poisson law to the binomial equation.



this procedure. This is probably due to the sensor always receiving a small amount of the light that is transmitted and reflected by the canopy (Lang and Xiang, 1986). Since this problem is unimportant in practice it will be neglected in further discussion.

When eq. 3.13 and eq. 3.16 are combined,  $L$  is given by

$$\begin{aligned} L_i G_i(\theta_p) &= -\cos\theta_p \ln P_{0i}(\theta_p) \\ &= k_i(\theta_p) \end{aligned} \quad (3.20).$$

If it is assumed that leaf orientation is the same in all the sub areas of the canopy, then  $G_i(\theta_p)$  is constant for all zones and averages can be taken over all of the zones in the canopy:

$$G(\theta_p) \sum_{i=1}^m a_i L_i = \sum_{i=1}^m a_i \cos\theta_p \ln P_{0i}(\theta_p) \quad (3.21).$$

Letting

$$k(\theta_p) = \sum_{i=1}^m a_i \cos\theta_p \ln P_{0i}(\theta_p) \quad (3.22)$$

eq. 3.21 can be expressed as

$$\bar{L} = \bar{k}(\theta_p)/G(\theta_p) \quad (3.23)$$

which is of the same form as eq. 3.13. Lang and Xiang (1986) found that even when there are large gaps in the canopy, eq. 3.22 gave good estimates of  $L$ ,  $\theta_L$  and  $G(\theta_p)$ .

In the practical application of eq. 3.23 in the field, the contact number was determined for a range of different probe angles and an equation was used to relate the contact numbers to  $L$  and the mean leaf angle (Lang *et al.*, 1985). A set of such equations was inverted by computer to provide estimates for  $L$  and the angular distribution of leaves. A simpler graphical procedure for obtaining geometrical information from the contact numbers was provided by Lang (1986). Recently Lang (1988) has simplified the procedure still further. This new procedure is derived from the work of Miller (1967). It provides a technique which is as accurate, but simpler to use than previous methods for estimating  $L$  from measured contact numbers. In the next section the procedures of Lang (1986) and Lang (1988) are reviewed.

#### Estimation of leaf area index from transmission measurements

The mathematical inversion of the equations which link  $k(\theta_p)$  with the leaf area index and the leaf angle distribution is known to be unstable (Lang *et al.*, 1985). This instability led Lang *et al.* (1985) to argue that only two variables could be recovered from the inversion,  $L$  and  $\theta_p$ . The graphical procedure (Lang, 1986) will be discussed first and then the more recent procedure reported by Lang (Lang, 1988).

Study of eq. 3.23 shows that  $k(\theta_p)$  is a scaled form of  $G(\theta_p)$ , the scaling factor being  $L$ . The form of  $G(\theta_p)$  as a function of probe angle for some model leaf angle distributions is shown in figure 3.2. The distributions chosen represent actual plant canopies (de Wit, 1965; Ross, 1981). (These leaf angle distributions will be described later.) Lang (1986) approximated the curves of  $k(\theta_p)$  as straight lines. This seems reasonable because the curves of  $G(\theta_p)$  are reasonably linear and the scatter of measurements of  $k(\theta_p)$  as a function of  $\theta_p$  (figure 3.7) is large compared with the differences between the curves of  $G(\theta_p)$  and the matching straight lines (Lang, 1988). The graphical procedure of Lang (1986) matches the linearized form of  $G(\theta_p)$  with lines of best fit to the experimentally measured contact numbers.

In figure 3.3 straight lines have been fitted to the curves of  $G(\theta_p)$  for intervals of  $\theta_p$  which are symmetrical about  $\theta_p=45^\circ$ . Figure 3.3 shows the lines fitted to  $G(\theta_p)$  for the interval  $25 < \theta_p < 65^\circ$ . The slopes of these lines are monotonically related to the mean inclination of the leaves,  $\theta_L$  as shown in figure 3.4. Lang (1986) obtained  $\theta_L$  as functions of  $\Delta G/\Delta \theta_L$  by empirically fitting polynomials of degree 5 to figure 3.4. (The coefficients are given in table 3.1.) The mean leaf angle can be calculated either from figure 3.4 or the coefficients in table 3.1 when the slope of  $\Delta G/\Delta \theta_p$  on a known interval of  $\theta_p$  is available.

Inspection of figure 3.3 shows that the spread of  $G(\theta_p)$  for different leaf angle distributions is least at  $\theta_p=55^\circ$  (Warren Wilson, 1959). This is the key to the procedure for obtaining  $L$  and  $\theta_L$  from the contact numbers. Figure 3.5 shows the value of  $G(\theta_p)$  interpolated at  $\theta_p=55^\circ$  along the straight lines as a function of leaf angle for different ranges of  $G(\theta_p)$ . This is all the information needed to estimate  $L$  and  $\theta_p$  using the graphical procedure (Lang, 1986).

The procedure developed by Lang (1986) is as follows:

- (1) Plot  $k(\theta_p)$  versus  $\theta_p$  and fit a regression line with intercept  $A$  and slope  $B$ .
- (2) Interpolate  $k_{55} = A + 55B$ .
- (3) Use  $G_{55} = 0.5$  as a first approximation of  $G$  at  $\theta_p=55^\circ$ .
- (4) Approximate leaf area index as  $L = k_{55}/G_{55}$ .
- (5) Estimate the slope of  $\Delta G/\Delta \theta_p$  as  $B/L$ .
- (6) Estimate  $\theta_L$  using the coefficients given in table 3.1.
- (7) Obtain an improved estimate of  $G_{55}$  from figure 3.5 using the leaf angle from step (6) over the appropriate range of  $\theta_p$ .
- (8) Repeat from step (4) until solutions for  $L$  and  $\theta_L$  are sufficiently precise.

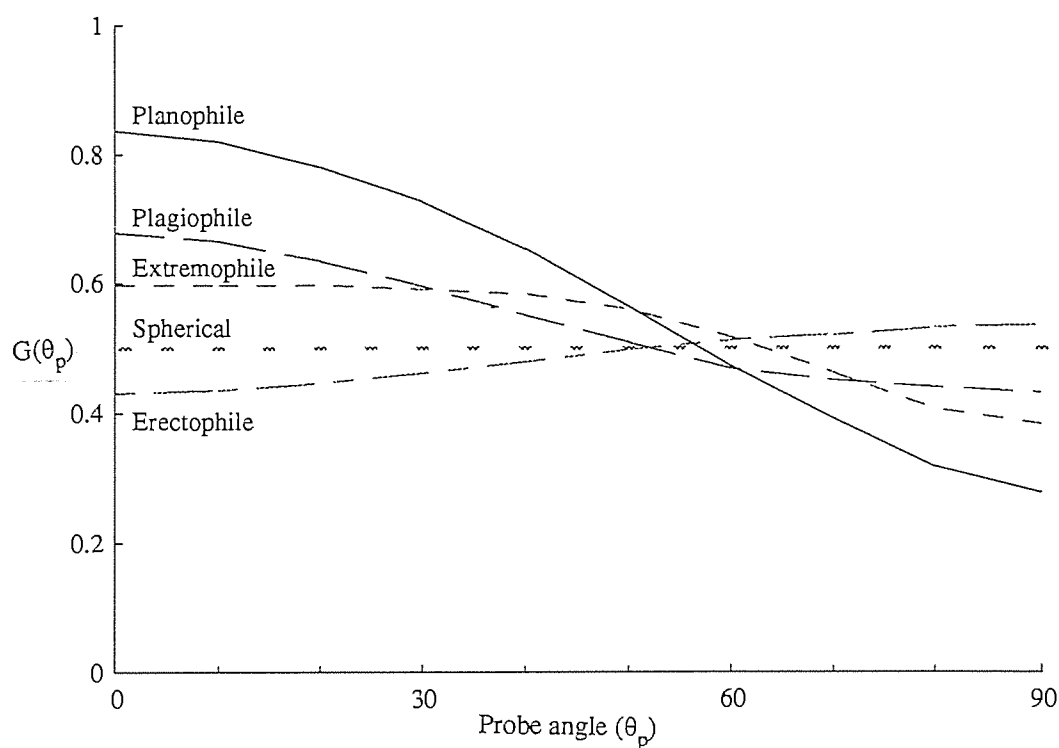


Figure 3.2. The mean projections,  $G(\theta_p)$ , for model leaf angle distributions as a function of the probe angle ( $\theta_p$ ). These model leaf angle distributions represent real canopies (e.g. de Wit, 1965; Ross, 1981).

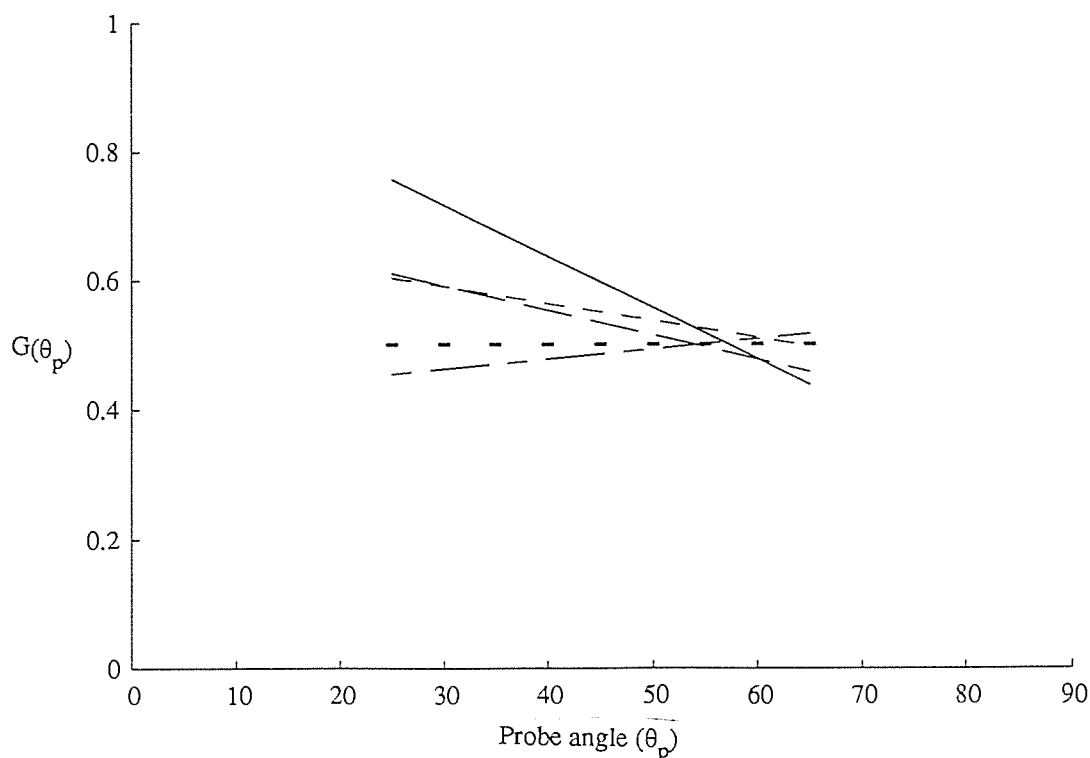


Figure 3.3. Lines of best fit for  $G$  as a function of  $\theta_p$  for the interval  $25 < \theta_p < 65^\circ$  for the  $G$ -functions given in figure 3.2.

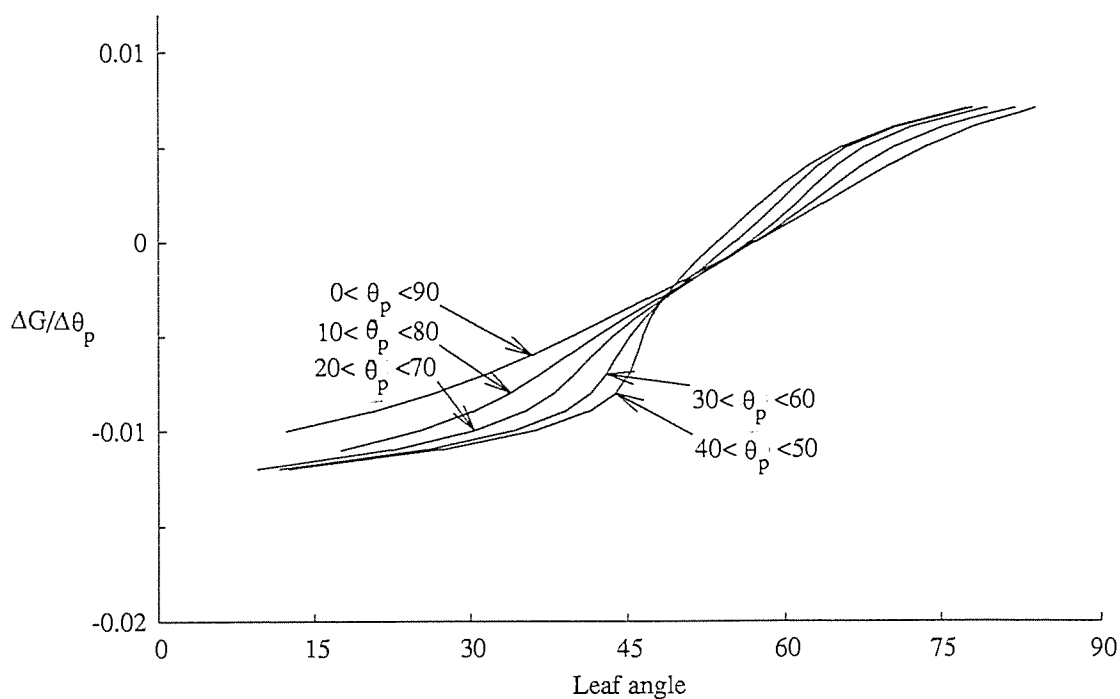


Figure 3.4. The slope of the line of best fit to  $G$  as a function of  $\theta_p$  for several  $G$ -functions calculated for constant leaf angles. The five curves represent five different intervals of  $\theta_p$  (from Lang, 1986).

$\theta_p$	$C_0$	$C_1$	$C_2$	$C_3$	$C_4$	$C_5$
0 - 90	57.21	3.2962E3	-47.101E3	-0.6945E6	1.8112E9	197.86E9
10 - 80	57.14	2.8629E3	-10.871E4	-8.2603E6	3.1464E9	323.35E9
20 - 70	56.63	2.5224E3	-14.147E3	-1.5588E7	4.1820E9	442.38E9
30 - 60	55.23	2.1974E3	-76.526E3	-1.5692E7	3.7776E9	448.98E9
40 - 50	53.51	1.9574E3	33.987E3	-1.1501E7	2.6032E9	386.84E9

Table 3.1. The coefficients in  $Y = C_0 + C_1x + C_2x^2 + C_3x^3 + C_4x^4 + C_5x^5$  where  $Y = \theta_L$  and  $x = \Delta G / \Delta \theta_p$ . Leaf angle and  $\theta_p$  are in degrees (Lang, 1986). These are the coefficients for the curves in figure 3.4.

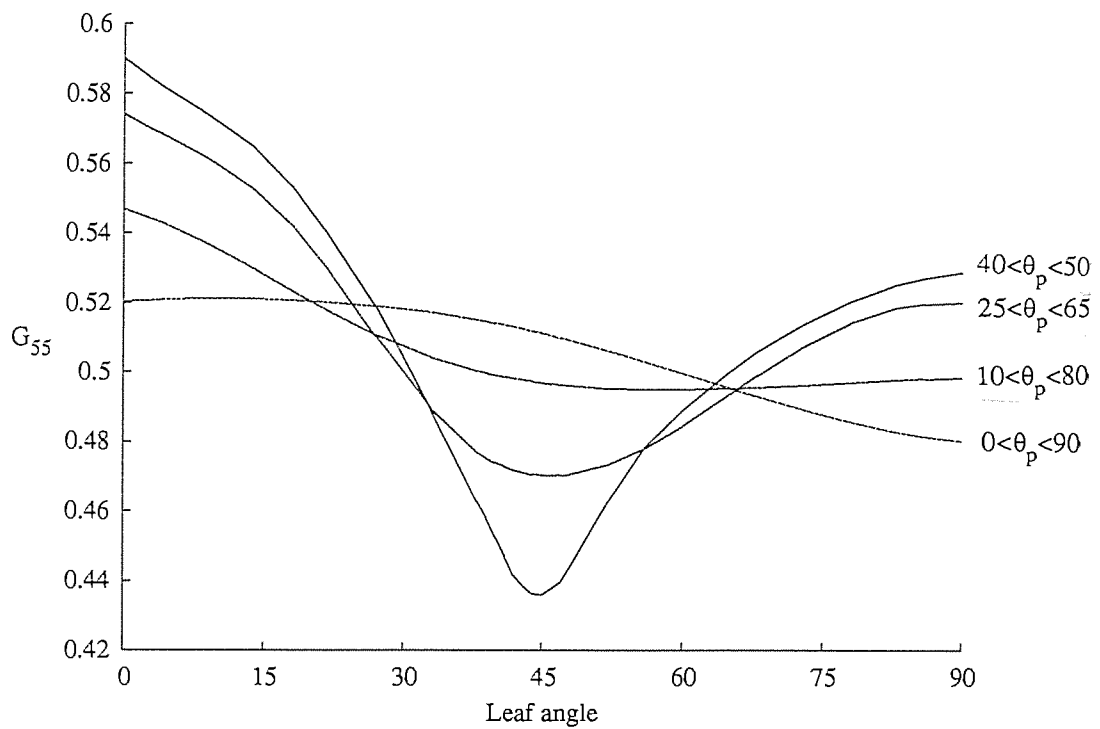


Figure 3.5. The value of  $G$  at  $\theta_p = 55^\circ$  interpolated from lines of best fit for the  $G$ -function (in fig. 3.3) for various leaf angles for several ranges of the probe angle. (From Lang, 1986.)

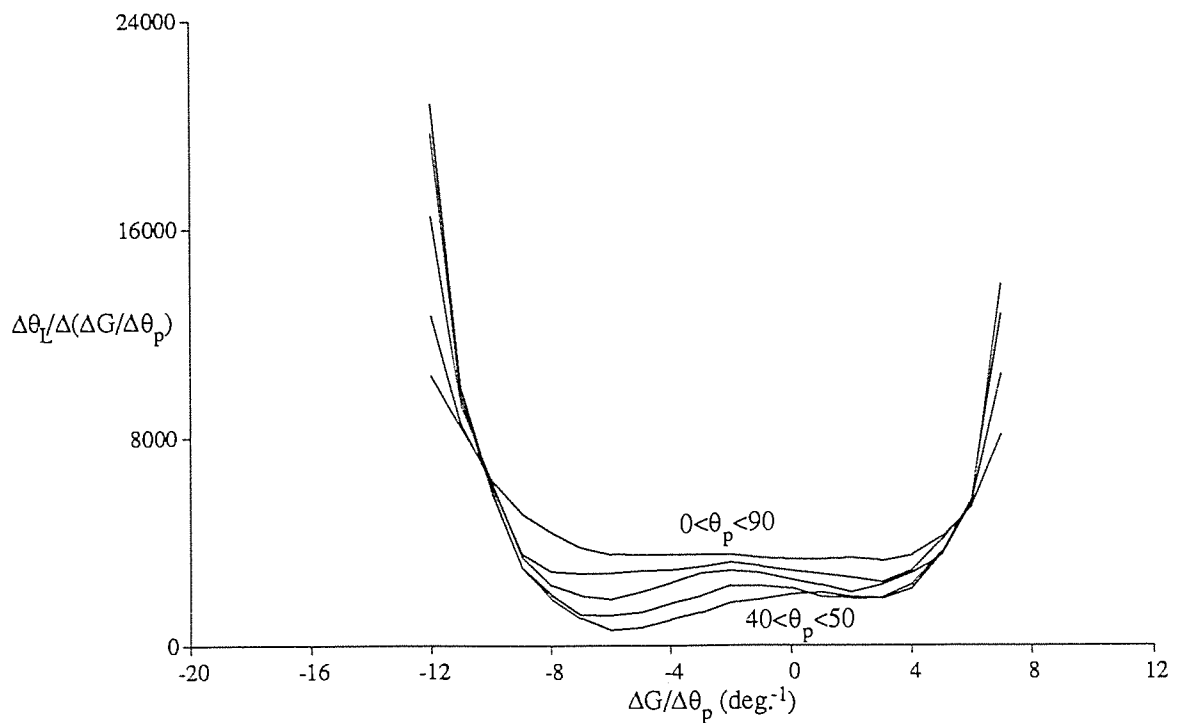


Figure 3.6. The sensitivity of estimation of the mean leaf angle upon the slope,  $\Delta G / \Delta\theta_p$ , and the range of probe angles,  $\theta_p$ . The ranges of probe angles are 0-90, 10-80, 20-70, 30-60 and 40-50°. (From Lang, 1986.)

Study of figure 3.4 shows that when  $\theta_L$  is either large or small, small errors in the slope of the line fitted to the contact numbers will cause relatively large errors in the estimate of  $\theta_L$  (Lang, 1986). Figure 3.6 shows the ratio of the error in  $\theta_L$  to the error in the slope  $\Delta G/\Delta\theta_p$  expressed as a function of the slope. Lang (1986) used figure 3.6 to set limits on  $\theta_L$  based on the known errors in the slope (this is discussed later).

Recently Lang (1988) has published details of an even simpler procedure for determining  $L$  from the contact numbers. Lang (1988) approximated a linear fit to the measured contact numbers as a function of the probe angle. Thus

$$k(\theta_p) = A + B\theta_p \quad (3.24)$$

where  $A$  and  $B$  are empirical constants (Lang, 1988). Using this procedure  $A$  is related to  $L$  and  $B$  to the mean leaf angle.

The relationship between  $L$  and  $k(\theta_p)$ , when observations are available for a range of probe angles from 0 to 90 degrees, was provided by Miller (1967). Lang (1988) rewrote Miller's eq. 4 to obtain eq. 3.25

$$L = 2 \int_0^{\pi/2} \sin\theta_p k(\theta_p) d\theta_p \quad (3.25)$$

When eq. 3.24 is substituted into eq. 3.25 and the result integrated, a very simple result is obtained. It is given by

$$L = 2(A + B) \quad (3.26)$$

where  $B$  is in  $\text{rad}^{-1}$  (Lang, 1988).

Use of eq. 3.26 is equivalent to interpolating a value of  $k(\theta_p)$  at a probe angle of  $57.3^\circ$  (1 radian) and taking  $G(\theta_p)$  at this point to be 0.5. The probe angle of  $57.3^\circ$  is the angle where the curves of  $G(\theta_p)$  come together (figure 3.2).

### Error Analysis

These two procedures for converting contact numbers to estimates of  $L$  and  $\theta_p$  were tested using data generated from computer models of plant canopies. These tests were done using model canopies with leaf angle distributions for which the  $G$ -functions were shown in figure 3.2. These distributions are described here. The erectophile canopy has most leaves erect. The extremophile has its leaves at extreme inclinations, both erect and horizontal. The plagiophile has most leaves at medium inclination angles. The planophile canopy has most of its leaves horizontal. The spherical canopy has its leaves oriented equally to all directions.

Lang (1986) and Lang (1988) reported that both methods provide satisfactory estimates of  $L$  from results of tests based on model "canopies" that have  $L=1$ . The accuracy of these procedures depends on both the type of leaf angle distribution and the range of probe angles used. The maximum error for the graphical procedure was a 13% over-estimate of  $L$  for an extremophile canopy with contact numbers for a narrow ( $10^\circ$ ) range of probe angles (Lang, 1986). For the simple procedure the maximum error was a 6% over-estimate of  $L$  which was found in an extremophile canopy and with a narrow ( $10^\circ$ ) range of probe angles (Lang, 1988). The error in  $L$  increases as the range of  $\theta_p$  diminishes and it depends upon the leaf angle distribution (Lang, 1986). This analysis shows that the error in the estimated values of  $L$  is small enough for practical purposes.

The accuracy of estimates of  $\theta_L$  depends on the range of probe angles used. The best approximations to  $\theta_L$  are obtained with the greatest range of  $\theta_p$ . As the range of  $\theta_p$  decreases, estimates of  $\theta_L$  will converge to a band of  $\theta_L$  between  $44$  and  $57^\circ$  (Lang, 1986).

In the next section the results of this theoretical analysis are used to measure some parameters of canopy architecture in a kiwifruit canopy. The contact numbers are estimated using eq. 3.22. Equation 3.26 is used to convert the contact numbers to estimates of  $L$ . The length of transect over which the transmission measurements are averaged is determined using eq. 3.19. These procedures will be used to estimate  $L$ ,  $\theta_L$ , and  $G(\theta_p)$ . These results will be compared to the results listed in the previous chapter. The  $G$ -function for kiwifruit will be calculated from the results in the previous chapter using eq. 3.7 and compared to that obtained from transmission measurements.

## Methods

### **Plants**

The measurements of light transmission were made on the same plants in the same orchard as described in the previous chapter. The measurements of light transmission were made in February and June 1987.

### **Remote sensing procedures**

The transmission of direct sunlight through the foliage was measured using a sensor designed by Lang *et al.* (1985). The sensor consisted of a small photoelectric detector which is filtered to a wave band centred on about 430nm (Lang *et al.*, 1985). The detector is collimated so that light acceptance is limited to a solid angle of  $0.302\text{sr}$

which eliminates diffuse light from 95% of the upper hemisphere (Lang *et al.*, 1985). Voltages from the detector were recorded at about 30Hz for 30 seconds with a Campbell CR21X micrologger as described by Green and Nicholson (1986), but with the instrumentation amplifier replaced by a resistor (S.R. Green, personal comm., 1987). With this modification, the response of the sensor to light intensity is linear. Details of the calibration are given in appendix 1.

The logger was programmed to measure the transmission of sunlight through the canopy and to calculate the sun angle ( $\theta_p$ ) from geographical position and time of day (details of the calculation of sun zenith angle are given in appendix 2). The logger program converts the measured transmission values and sun (probe) angles to contact numbers ( $k(\theta_p)$ ). The measured contact numbers are multiplied by 0.95 to correct for the 5% over-estimate in the contact number which arises from using the binomial law to estimate the contact number and the Poisson law to estimate L (the theoretical relative contact number =1.054 at  $l/d=10$ , see figure 3.1). The contact numbers and associated sun angles were converted to estimates of leaf area index using a FORTRAN77 program (Green and Nicholson, 1986) which implements the graphical procedure described by Lang (1986) and the newer procedure developed by Lang (1988) (S.R. Green, personal comm., 1987). The program iterates Lang's (1986) procedure using table 3.1 and figure 3.5 as look-up tables.

Measurements of light transmission required clear days, or at least periods when the sun was not obscured by clouds. At times this proved a major limitation to using this technique. The procedure for measuring light transmission was simple. A "dark" reading (0% transmission) is taken with the sensor shaded. A "full sun" reading (100% transmission) is taken with the sensor pointed at the sun. These two readings define the signal range so that the logger can convert voltages into transmission values. The sensor is kept pointed at the sun using the shadow sight (see plates 3.1 and 3.2).

The transmission measurements are averaged once per second by the logger and the logarithm of each of each of these averages is calculated and stored in memory. At the end of the transect the logger calculates the average of the logarithms of the one second averages to provide the average logarithm of light transmission for the transect. This value is multiplied by the cosine of the sun zenith angle to give the contact number for the transect. The sun angle, the contact number and the average logarithm for the transmission measurements are recorded manually for each transect. At least 20 transects were measured for each set of plants. This procedure provided the contact numbers that were used to estimate L.



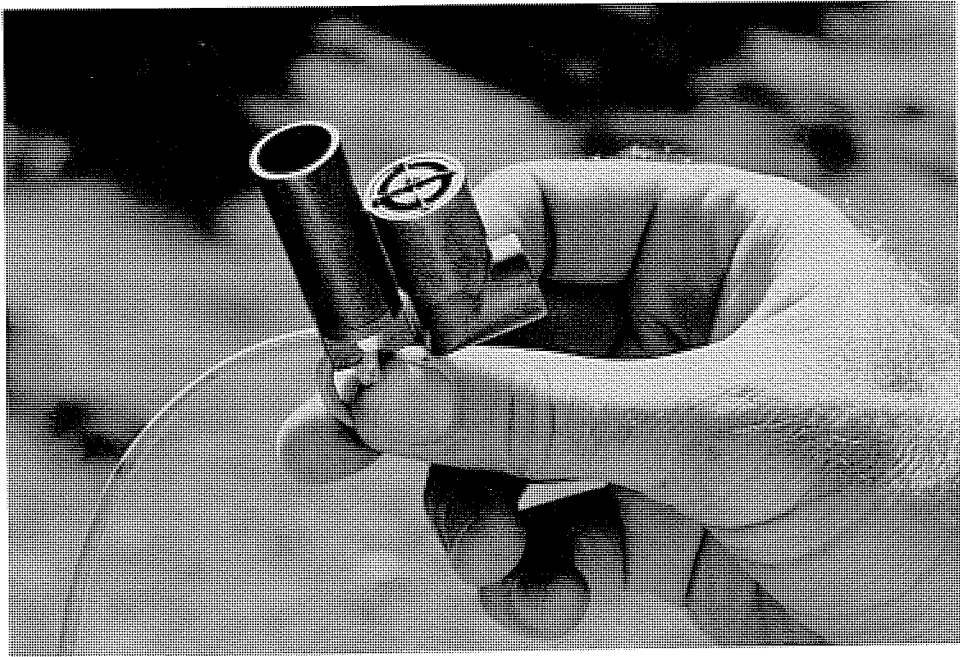


Plate 3.1.

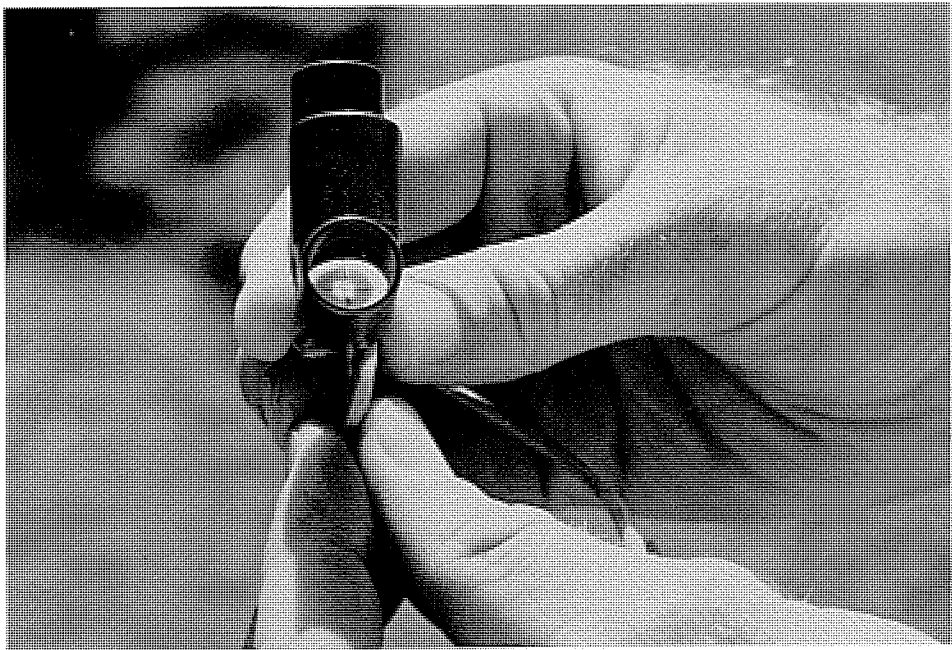


Plate 3.2.

Plates 3.1 and 3.2. Photographs of the sensor used to measure the direct beam of the sun. The sensor is built to the design of Lang *et al.* (1985).

The range of sun angles that could be used on a given day was limited by the declination of the sun and by the height of the shelter belts around the orchard. The range of sun angles that could be used in February was  $25^{\circ}$ - $60^{\circ}$ . In June the range of sun angles was from  $60^{\circ}$ - $70^{\circ}$ . The transects were measured at right angles to the rows. The lengths of the transects were measured and recorded. A typical transect was about 18m long. This was equal to the length of the small blocks used for study.

#### **Effect of averaging length on contact numbers**

In the theory section the effect of the distance over which the transmission values were averaged was discussed. The effect of using inappropriate averaging distances on the contact numbers can be analysed. On several occasions the individual transmission values for entire runs were recorded using the logger and stored on magnetic tape. These were transferred to computer to determine the effects of various sampling lengths on measurements of contact number. For each transect there were 900 measurements of transmission. The transmissions were averaged over segment lengths,  $l$ , such that  $l/d=2,5,10,20,30,40,80$  or 120. (In the field the contact numbers used to estimate  $L$  were taken at  $l/d=10$  only.) The logarithms of these averages were then averaged over the length of the transect to give a single value for each length of segment. These values for each segment length were converted to a contact number using eq. 3.22. The results for each transect were divided by the contact number at  $l/d=10$  and all results were then pooled. This analysis shows the effect of averaging distance on the measured values of the contact numbers.

#### **Calculation of mean secant length**

The procedure used here to calculate the mean secant length through a leaf,  $d$ , is slightly different to that used by Lang and Xiang (1986). To calculate  $d$  it was assumed that the leaves were oval in shape (see plates 2.2 and 2.3) and could be accurately represented by circles. Two circles were used to describe the leaves, one represented the average width of the leaves and the other, the average length. The projected diameter for each of these circles was calculated using the G-function for a spherical canopy (Lang and Xiang, 1986). The mean for the two sets of projected leaf diameters was calculated and this value was used for  $d$ .

Measurements of leaf size in the previous chapter gave mean leaf lengths and widths of 0.11m and 0.13m respectively. These results give a mean secant length of 0.06m.

#### **The G-function**

The G-function was estimated from the contact numbers and calculated using the results from the direct measurements of canopy architecture given in the previous

chapter are used to calculate  $G(\theta_p)$ . The results from the two procedures for estimating the form of the G-function are compared.

The form of  $G(\theta_p)$  can be estimated from the contact numbers and estimates of L obtained using the remote procedure by rearranging eq. 3.23. This is compared to the G-function calculated from architectural data obtained by direct measurements of the canopy.

The G-function for kiwifruit was calculated using the probability distribution functions for leaf orientation and the algorithm developed by Lemeur (1973). The G-function is determined from the following relationship

$$G(\theta_p) = \sum_{i=1}^{16} \sum_{j=1}^{12} g''(\phi_i) \cdot [A\phi_L + B\sin\phi_L] \frac{[G'(\theta_L)]^{\frac{\pi/24j}{\pi/24(j-1)}}}{\phi_i + \pi/16 - \phi_i - \pi/16}$$

where  $A = \cos\theta_j \cdot \sin\theta_p$  and  $B = \sin\theta_j \cdot \cos\theta_p$  (Lemeur, 1973). In this relationship  $\phi_i$  = the midpoint of the  $i$ th azimuthal class or  $\pi/8i$ ;  $g''(\phi_L)$  = the azimuthal density function;  $G'(\theta_L)$  = cumulative leaf inclination distribution function;  $\theta_j$  = the midpoint of the  $j$ th leaf inclination class or  $\pi/24(j-1) + \pi/48$ ; and  $\theta_p$  = solar elevation. To calculate the G-function, 12 values from the cumulative leaf inclination distribution function and 16 values from the azimuthal density function are needed; these values can be extrapolated from graphs of  $G'(\theta_L)$  and  $g''(\phi_L)$  which can be calculated from the leaf orientation data given in table 2.2.

Calculations of  $G(\theta_p)$  were made twice for each canopy because there are directions of maximum and minimum azimuthal density. Calculating  $G(\theta_p)$  separately for these two directions gives the maximum and minimum values of  $G(\theta_p)$  and provides an estimate of the effect of changes in the sun's azimuthal position on direct light penetration into the canopy. To find the maximum values of  $G(\theta_p)$  the calculation was done using an input vector with the first value equal to the value of the density function in the direction of maximum azimuthal density. The other values were substituted in sequence from the azimuthal density function in clockwise order. This gave a series of maximum values for the G-function as the solar azimuth is parallel with the direction of maximum azimuthal density. The minimum values of  $G(\theta_p)$  are found using a similar procedure, but starting from the direction of minimum azimuthal density. In this case the solar azimuth coincides with the direction of minimum azimuthal density, and the corresponding minimum values of the G-function are obtained. This procedure means that the real canopy geometry is taken into account in dealing with the radiation regime of the canopy.

## Results

The measured values of the logarithm of the transmission for each transect were converted to contact numbers using eq. 3.9. The contact numbers were associated with the sun zenith angle,  $\theta_p$ , at the time of measurement. The contact numbers measured in blocks 1, 2 and 3 on one day are shown in figure 3.7. The contact numbers were processed using the algorithm of Green and Nicholson (1986) and the procedure of Lang (1988) to give  $L$  and the mean leaf angle. These two procedures for estimating  $L$  gave identical results, being within 4% of each other.

Values of  $L$  and the mean leaf angle from the previous chapter and estimates from the remote sensing procedures are presented for comparison in table 3.2. Lang (1986) assessed the reliability of the indirect estimates of  $L$  and  $\theta_L$  using a procedure which incorporates the statistics for the coefficients of the straight line that is fitted to the contact numbers. The standard deviation of the estimates of  $L$  is given by:

$$S_L = S_{k_{55}}/G_{55},$$

where  $S_{k_{55}}$  is the sample standard deviation for the interpolated value of  $k(\theta_L)$  at  $\theta_p=55^\circ$  (Snedecor 1956, p.137). The standard deviation of the estimate of  $\theta_L$  is given by:

$$S_{\theta_p} = S_b G_{55} \Delta\theta_L / \Delta^2 G / \Delta\theta_p$$

where  $S_b$  is the sample standard deviation of the slope of the straight line fitted to  $\Delta G / \Delta\theta_p$  versus  $\theta_p$  (Snedecor 1956, p.135). Lang (1986) obtained the derivative in  $S_{\theta_p}$  using the equation and coefficients given in table 3.1. The relationship between the estimates of  $L$  obtained from the direct and indirect methods is shown in figure 3.8.

The estimates of  $L$  from the indirect measurements exceed those from the direct methods by a factor of about 1.7. This was consistent for all of the sets of measurements of  $L$  and was the same in all of the blocks measured. This is a major difference to what had been expected from the theoretical analysis and the results of Lang (Lang *et al.*, 1985; Lang and Xiang, 1986; and Lang, 1988). This problem will be analysed further in the rest of this chapter and possible reasons for this discrepancy considered.

### **Averaging length for transmission measurements**

The effect on  $k(\theta_p)$  of averaging transmission measurements over different lengths is shown in figure 3.9 where the results are compared to the theoretical curve given in figure 3.1 (calculated using eq. 3.19). It is apparent that the contact numbers are quite sensitive to the averaging distance used for measuring light transmission. This sensitivity to the averaging distance is most apparent for shorter averaging distances,

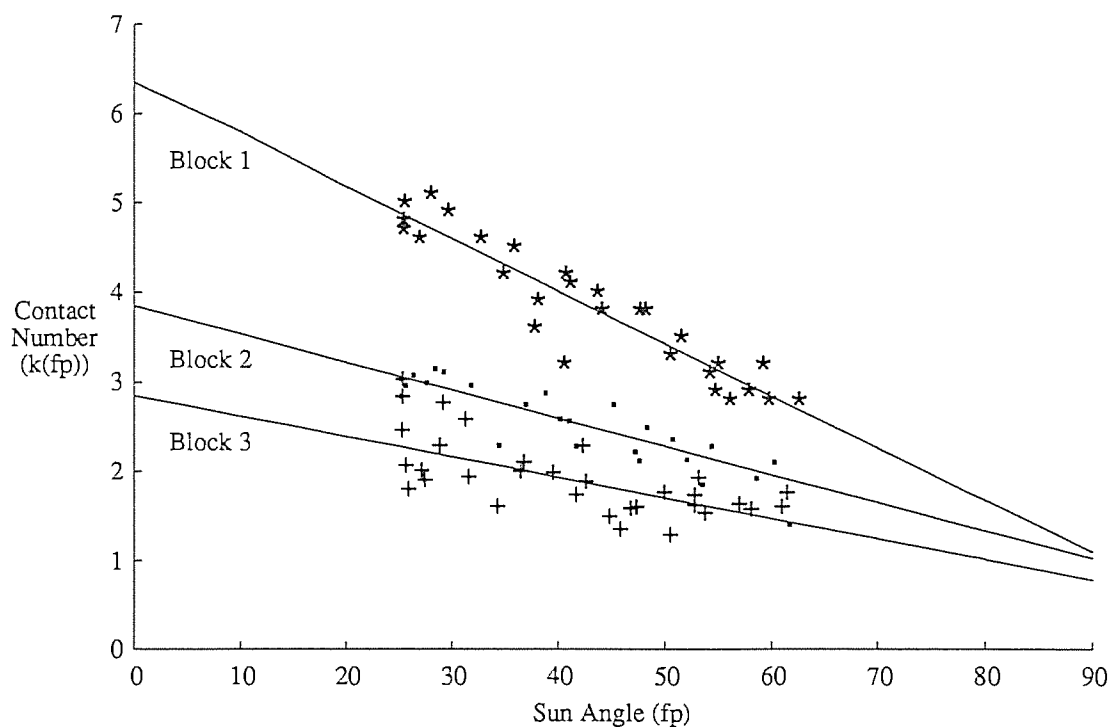


Figure 3.7. Contact numbers ( $k(\theta_p)$ ) as a function of the probe angle, measured in a kiwifruit orchard. The sample standard deviations of the measurements of  $k(\theta_p)$  at  $\theta_p = 57.3^\circ$  (1 radian) (equivalent to  $S_y$  in Snedecor, 1956, p.137), are 0.006, 0.004 and 0.011 for blocks 1, 2 and 3 respectively.

<u>Leaf area index</u>			<u>Mean leaf angle</u>	
<u>Direct method</u>	<u>Indirect method</u>	<u>LSD</u>	<u>Direct method</u>	<u>Transmission method</u>
$3.5 \pm 0.2^a$	$6.3 \pm 0.5$	0.74	$30 \pm 1^\circ$	$34 \pm 9^\circ$
$2.2 \pm 0.2$	$4.2 \pm 0.6$	0.89	$34 \pm 1^\circ$	$34 \pm 3^\circ$
$2.0 \pm 0.2$	$3.2 \pm 0.6$	0.89	$38 \pm 1^\circ$	$34 \pm 4^\circ$
$2.3 \pm 0.1$	$3.9 \pm 0.2$	0.41	<b>b</b>	
$1.7 \pm 0.2$	$2.8 \pm 0.5$	0.74		

**a** Limits are standard errors of means (se).

**b** Direct measurements of leaf orientation were not taken in June.

Table 3.2. Leaf area indices and mean leaf angles obtained by direct measurements of a kiwifruit canopy (described in chapter 2) and transmission of direct sunlight using procedures described in this chapter. The least significant difference (LSD) is the root mean square value of  $t(se)\sqrt{2}$  for each standard error (Snedecor, 1957, p.251). For the transmittance results,  $t=2.09$ , and for the direct measurements,  $t=1.98$  for the February results and 2.12 for the June results. (A 5% level of significance was used.)

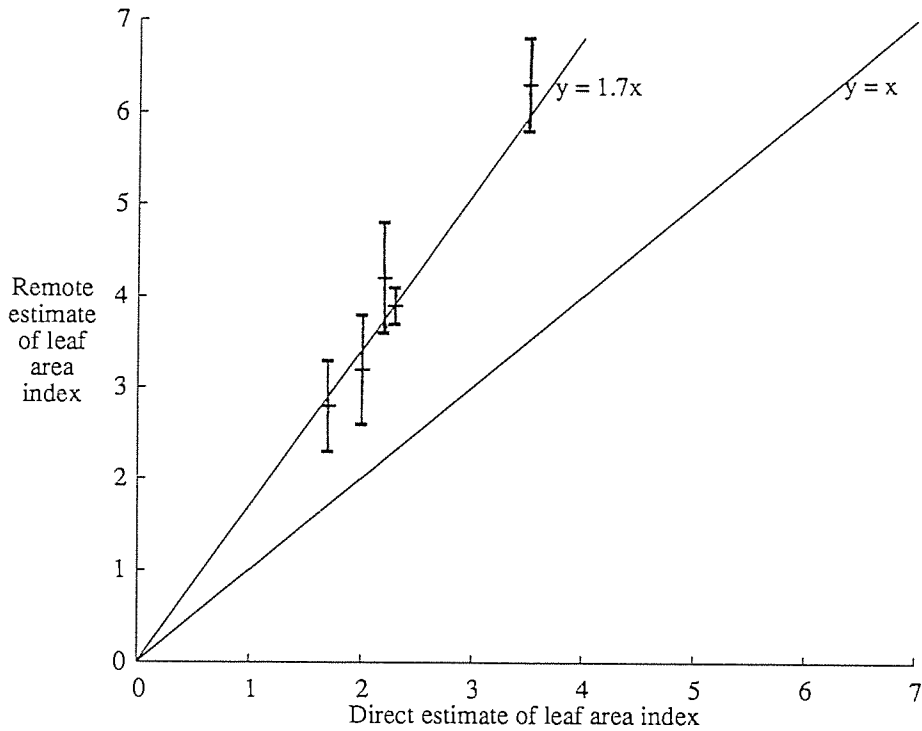


Figure 3.8. The relationship between the estimates of  $L$  obtained using direct and indirect measurement techniques. The standard errors are those given in table 3.1 for the transmission results.

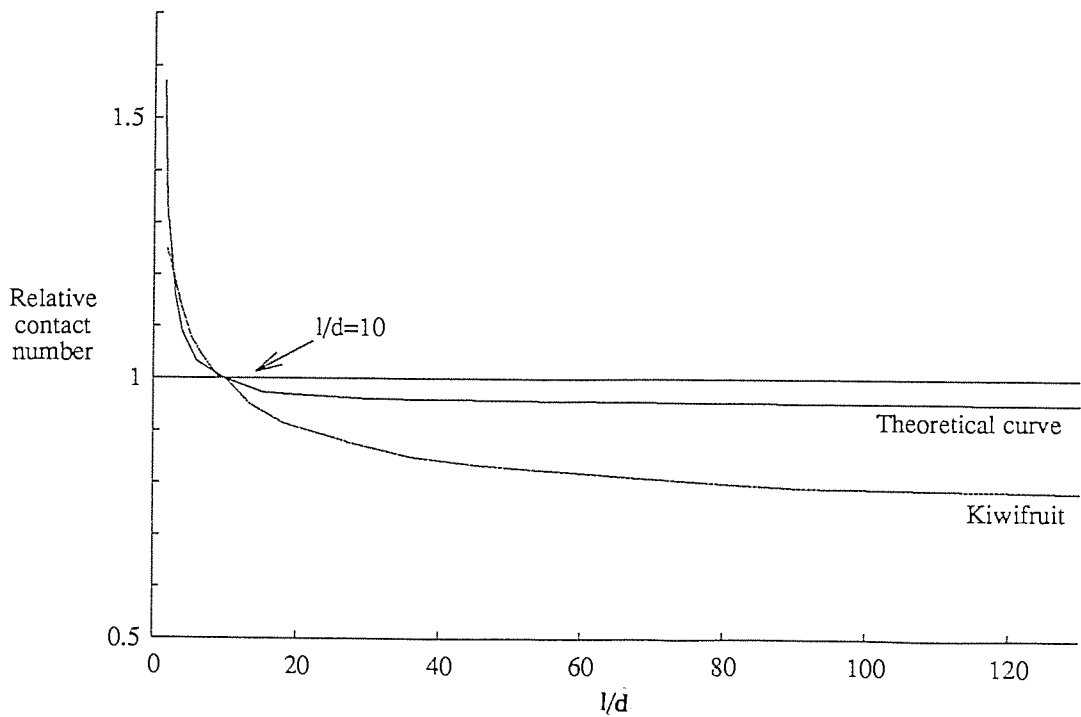


Figure 3.9. Experimental relative contact numbers from averages over various lengths. The contact numbers from each transect were divided by the value at  $l/d=10$ . The normalized values were averaged to produce the graph. The theoretical curve is from eq. 3.19, but with  $l/d$  substituted for  $R$ . The standard error for the kiwifruit results was less than 0.019.

but the curve eventually approaches a limiting value. In the theoretical curve the relative contact number approaches a limiting value slightly less than 1. For kiwifruit, the limiting value is about 0.8. The likely cause of the difference between the limiting values in the two curves will be discussed later.

### **G-function**

The results in table 2.2 in the previous chapter were used to calculate  $G(\theta_p)$  for kiwifruit. The calculated G-function is shown in figure 3.10.  $G(\theta_p)$  varies from 0.86 for small zenith angles, to 0.26 at large zenith angles. The upper and lower limits of  $G(\theta_p)$  for kiwifruit were calculated to determine the variability in  $G(\theta_p)$  that could arise through the slight asymmetry in the azimuthal distribution of leaf area. The maximum error introduced by assuming azimuthal symmetry is a negligible  $\pm 4\%$ .

The G-function can be estimated from the contact numbers,  $L$  and eq. 3.24. The form of  $G(\theta_p)$  estimated from the remote procedure can be compared to that from the direct methods. To estimate the G-function from transmission measurements, the contact number is divided by the value of  $L$  obtained from the remote procedure. These results are presented in figure 3.10 and show that the shape of  $G(\theta_p)$  obtained from the indirect procedure is the same as that from the direct procedure. When the contact numbers are divided by values of  $L$  obtained from direct measurements, the magnitude of  $G(\theta_p)$  is considerably higher than expected (by a factor of 1.7).

In conclusion, the remote sensing procedure used here over-estimates measurements of  $L$  obtained using direct methods by a factor of about 1.7. However the mean leaf angle,  $\theta_p$ , and the G-function estimated from the remote procedure are similar to those obtained from direct measurements.

### Discussion

There is a significant difference between the results obtained from the two procedures for estimating  $L$  in a kiwifruit canopy. When the disagreement between the two methods became apparent all equipment and procedures were carefully checked and compared to the procedures used by Lang (Lang *et al.*, 1985; Lang and Xiang, 1986). In 1986 Dr. Lang visited New Zealand to demonstrate his method. During this visit measurements were made in the same orchard and a similar disagreement was found. It is thought unlikely that the discrepancy was due to an error in the measurement technique or calculations.

The cause of the difference between the estimates of  $L$  for the two procedures was attributed to a regular distribution of leaves in the canopy. This means that the

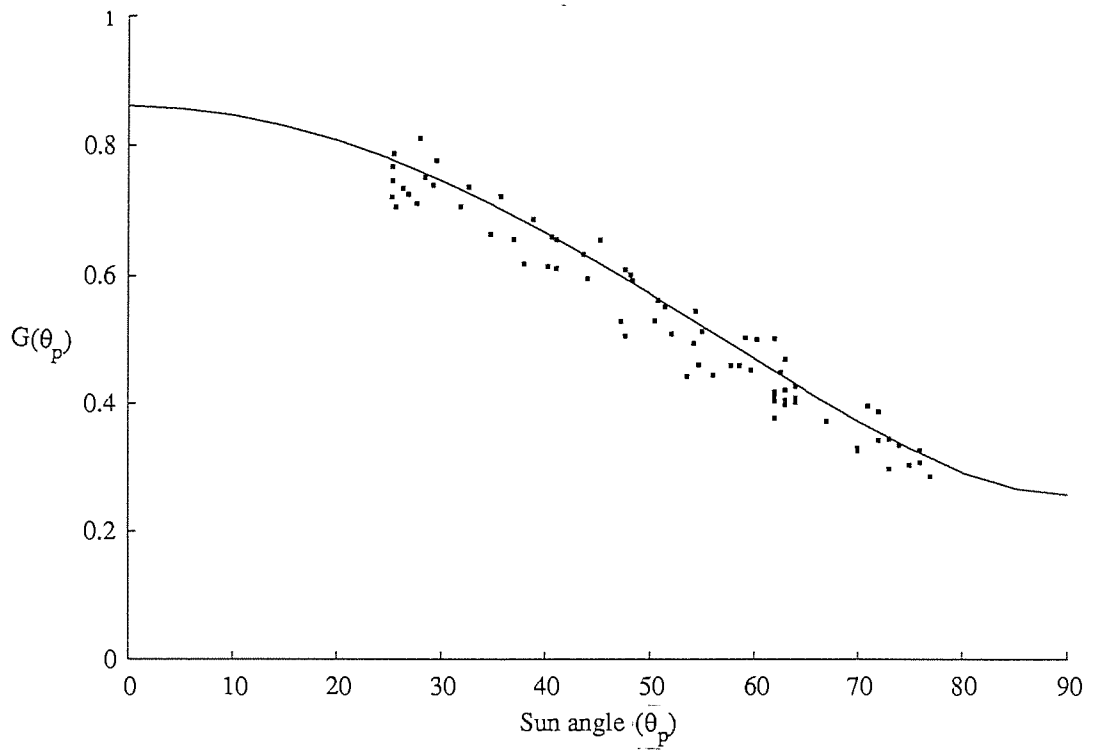


Figure 3.10.  $G(\theta_p)$  for kiwifruit. These results are obtained from the direct measurements given in chapter 2 (—) and from the measurements of light transmission (.).



assumption of a random distribution of leaves (and the Poisson distribution) is violated. In the first publication of the series of papers that describe the use of measurements of light transmission to measure  $L$ , Lang *et al.* (1985) reported that  $L$  was over-estimated in sunflower canopies but was under-estimated in discontinuous canopies of crops such as sorghum when light transmissions were averaged over the length of the entire transect (equivalent to  $l/d=120$ ). The disagreement between the estimates of  $L$  for sunflower was attributed to a regular distribution of leaves in the canopy. This means that the leaves intercept more light on average than if they were distributed randomly in the canopy. In contrast, discontinuous canopies can be treated in two ways; they can be regarded as having a clumped distribution of vegetation (*i.e.* not random but the opposite case to a regular leaf distribution), or else they can be treated as being comprised of a number of zones with different leaf areas. The second approach was used by Lang and Xiang (1986) to develop a procedure which successfully accounts for the presence of large gaps in the canopy. Lang and Xiang (1986) showed that this procedure (which was used here) gives correct estimates of  $L$  in discontinuous canopies in which the leaves are distributed at random in the zones that comprise the canopy. The problem of non-random leaf distributions in plant canopies is of considerable interest and will be analysed further in chapters four and five.

The regular distribution of leaves in the canopy is a serious difficulty in using transmission to determine absolute estimates of  $L$  in a kiwifruit canopy. The trends in the magnitude of  $L$  between different blocks were accurately followed (figure 3.8), however it is not clear whether this will persist with estimates of  $L$  beyond the range of orchard leaf area indices used here. Given the constancy of the discrepancy between the two methods for determining  $L$ , it seems fair to divide estimates of  $L$  from the remote procedure by 1.7 to give a value close to the actual leaf area index, at least for remote estimates of  $L$  in the range  $2.5 < L < 6.5$ . However it is not clear whether this will be appropriate to all kiwifruit orchards because it has been suggested that azimuthal leaf orientation may be affected by trellis type (see chapter 2) which results in a further violation of the assumptions about canopy architecture introduced in the theory.

The accuracy of the estimates of  $L$  from the transmission measurements depends on the ratio of the area of the leaves to the sampling area (Lang and Xiang, 1986). The effect of the ratio of the leaf area to the sampling area on the contact numbers is shown in figure 3.9. The difference between the theoretical and measured curves is attributed to the non-uniform distribution of leaf area in the canopy (and is discussed further in

the next chapter). The selection of  $l/d=10$  as the averaging length for the transmission measurements was to ensure that the error between the binomial and Poisson laws would be no more than 5% (A.R.G. Lang, personal comm., 1987). The larger the value of  $l$  the smaller the error for an extensive random sample. The smaller the value of  $l$  the better the discrimination between zones of different foliage denseness. The agreement between estimates of  $L$  obtained from direct and transmission measurements reported by Lang and Xiang (1986) supports their choice of an averaging length based upon the mean secants through projected leaves. This empirical evidence gives confidence in the procedure that was recommended by Lang and Xiang (1986) and used here.

The G-function is widely used to describe and compare the radiation regime between plant stands e.g. Lemeur (1973), Ross (1981) and Cohen and Fuchs (1987). The use of  $G(\theta_p)$  seems to be accepted as the best way to relate light interception to the geometry of the leaves in a canopy (e.g., Ross, 1981, p. 116; Lang *et al.*, 1985). The shape of  $G(\theta_p)$  for kiwifruit (figure 3.10) is similar to that reported for white clover (results of De Wit, 1965; calculated in Ross, 1981, p. 117), and tobacco (Whitfield, 1980), although the range of  $G(\theta_p)$  is greater for kiwifruit than for these other species. The greater range in  $G(\theta_p)$  reflects the more planophile leaf angle distribution found in kiwifruit than in the other species. The good agreement between the G-function calculated from the direct measurements (chapter 2) and the transmission measurements (listed here) supports the use of measurement of direct light transmission through canopies as a tool for estimating this property of plant canopy architecture.

### Summary

In this chapter a procedure for remote sensing of the architecture of plant canopies has been described and used to measure a kiwifruit canopy. Comparisons were made between three components of canopy architecture,  $L$ ,  $\theta_L$  and the G-function. Agreement was poor for estimates of  $L$ , but was good for  $\theta_L$  and the G-function. The estimates of  $L$  from the remote procedure exceeded those from direct measurements by a factor of 1.7. The difference between the two procedures was consistent for a range of  $L$  (1.7-3.5) and for canopies that were uniform as well as discontinuous. The difference between the two estimates is attributed to the regular rather than random distribution of leaves in the canopy. The effects of leaf distribution on canopy gap frequency are discussed further in chapter four.

## 4

## A Theoretical Analysis of Models of Canopy Structure

### Introduction

A comparison of measured and calculated values of gap frequencies for a range of crops has shown that measured values often differ to values calculated on the assumption of a random leaf distribution (Ross 1975, 1981). Recently Lang *et al.* (1985) reported similar results for several plant stands when they found that the leaf area index ( $L$ ) was under-estimated for stands of sorghum but over-estimated for stands of sunflower by the remote sensing technique. A result similar to that for sunflower has been reported in chapter 3 for measurements in a kiwifruit canopy. A possible explanation for such discrepancies is that for some crops the assumption of a random spatial distribution of leaves is not valid.

Point quadrat measurements reported by Warren Wilson (1959, 1961, 1965) show that leaves can be either more clumped or more regularly distributed than expected for a random leaf distribution. Warren Wilson (1961) also found that the degree of randomness in canopies varied with probe angle. Ross (1975, 1981) reported similar results from measurements in a range of agricultural crops. The effect of variation from a random leaf distribution is to change the average amount of light intercepted by the leaves. For example, a regular distribution means that the leaves in the canopy intercept more light on average than they would if they were randomly distributed. By contrast, a clumped distribution of leaves means that the leaves intercept less light on average than they would if they were randomly distributed. The effects of leaf distribution on gap frequency are obvious.

In the previous chapter, the principles of point quadrat analysis provided the basis of a technique for estimating some parameters of canopy architecture from measurements of light transmission through the crop stand. The contact number was determined and used to estimate  $L$ , the  $G$ -function ( $G(\theta_p)$ ) and the mean leaf angle ( $\theta_L$ ). The estimates of  $L$  obtained from the remote technique (chapter 3) were 70% higher than estimates obtained from direct measurement (chapter 2). This discrepancy would be explained if the leaves in a kiwifruit canopy are distributed regularly, rather than randomly, as the theory of chapter 3 assumes.

It is necessary at this point to define several terms that relate to leaf distribution in a plant canopy. The terms uniform and non-uniform (or discontinuous) will be used to describe canopy structure and its effects on light penetration. For example, a row crop in which there are distinct gaps between the rows has a non-uniform distribution of leaves. The distribution of leaves relative to one another (e.g. the arrangement leaves on an individual plant which is due to the form or habit of the plant species) will be described using the terms random, clumped and regular (after Nilson, 1971). A uniform canopy with randomly distributed leaves has no apparent row structure and the leaves are located independently of one another. This terminology will be used throughout the remainder of this work.

Almost all work on the problem of sunlight penetration through a canopy has been based on the assumption that the foliage is uniform and with the leaves located randomly e.g. Monsi and Saeki (1953), Warren Wilson (1960, 1963, 1965, 1967), Anderson (1966, 1966b), de Wit (1965), Philip (1965), Nilson (1971) and Lang *et al.* (1985). In nature this assumption can be violated. The distribution of foliage can depend strongly on solar elevation and hence change throughout the day (Ross, 1975, 1981).

Nilson (1971) discussed several models that can be used empirically to describe penetration of sunlight into canopies that were described as random, clumped or regular. He assumed that plant stands had uniform leaf distributions. Therefore his definition of a clumped canopy would include stands that are described here as discontinuous and with a random leaf distribution. The treatments of Allen (1974) and Mann *et al.* (1980) incorporated non-uniform distributions of foliage into models of sunlight penetration in row crops. Mann *et al.* (1977) developed a general law for direct light penetration which is applicable to arbitrary foliage area distributions. Lang and Xiang (1986) adopted the model of Mann *et al.* (1977) for remote sensing measurements to account for the occurrence of gaps in the stand. This gave reliable estimates of  $L$  in canopies which had discontinuous canopies but in which the leaves were located randomly with regard to one another.

In this chapter models for foliage penetration of sunlight through plant canopies are analysed. The model developed by Mann *et al.* (1977) is used to analyse light penetration through plant canopies. The principles of this model have been used in chapter 3 to account for the effects of discontinuous canopies on sunlight penetration. It is suggested that the limiting results for sunlight penetration obtained from the model

of Mann *et al.* (1977) and the procedure of Lang and Xiang (1986) can be analysed to provide a simple procedure for comparing light interception in stands which have different structures. The Poisson law and the positive and negative binomial laws are used to relate the results obtained from the analysis provided by Mann *et al.* (1977) and Lang and Xiang (1986) to the distribution of leaves in the canopy. This analysis shows that light penetration is affected by the form and habit of the plant and by the arrangement of the plants in the stand. It is also suggested that simultaneous measurements of  $L$  and sunlight penetration through the canopy can be used to separate the effects of canopy structure and leaf distribution on light penetration in the canopy.

### Theory

The general law developed by Mann *et al.* (1977) shows that light penetration is strongly influenced by canopy structure. This theory has already been used in a modified form in the previous chapter to obtain correct estimates of the leaf area index for a plant canopy from measurements of light transmission through the canopy. In this section the effect of different leaf distributions on sunlight penetration will be emphasized. The terminology of Mann *et al.* (1977) is used to discuss their general law for penetration of sunlight.

#### **A general law for penetration of sunlight**

Consider a transect of length  $D$  which is arbitrarily located within or beneath a plant or crop canopy. The part of the canopy located between the sun and the transect is assumed to be projected onto the transect along lines which are parallel to the sun's rays. The sun's rays are assumed to be parallel. For simplicity the foliage is assumed to consist only of leaves. The objective of this analysis is to determine what fraction of the transect is expected to be sunlit when there are  $N$  leaf projections on the transect. A limiting result will be derived for large  $N$ . The width of the projection of each leaf in the canopy is given by the mean secant length ( $d$ ) through the leaves (as described in chapter 3).

It is assumed that a coordinate system is imposed such that the transect is described by the interval  $(0, D)$ . The locations of leaf projections along the transect are given by the position of their midpoints. Their locations are assumed to be identically and independently distributed random variables with continuous distribution function  $F$  and associated density  $f$ . Methods for determining  $F$ ,  $N$ , and  $d$  will not be considered here, but it is assumed that all the necessary information is available.

The probability that the point  $x$  on the transect is sunlit, or not covered by any of the  $N$  leaf projections is given by

$$P(x | N) = [F(x-d/2)+1-F(x+d/2)]^N \quad (4.1)$$

where  $F(x-d/2) \equiv 0$  for  $x < d/2$  and  $F(x+d/2) \equiv 1$  for  $x > D-d/2$  (Mann *et al.*, 1977). The expected gap frequency for the transect is given by the sum of the probabilities of the individual points along the transect being sunlit (giving the fraction of the transect which is sunlit) divided by the transect length  $D$ . When the resulting integral is separated into segments to allow for the endpoint definitions, the average fraction of the sunlit length given  $N$  and  $d$  is

$$\begin{aligned} E\{\text{sun} | N, d\} = & 1/D \int_0^{d/2} [1-F(x+d/2)]^N dx \\ & + 1/D \int_{d/2}^{D-d/2} [F(x-d/2)+1-F(x+d/2)]^N dx \\ & + 1/D \int_{D-d/2}^D [F(x-d/2)]^N dx \end{aligned} \quad (4.2)$$

(Mann *et al.*, 1977). The solution of eq. 4.2 for a uniform distribution of leaf projections over  $(0, D)$  is of interest. For a uniform canopy,  $f(x) = x/D$  or  $0 \leq x \leq D$ . The result after integrating and collecting terms is the average gap frequency of the transect  $(0, D)$  for fixed  $N$  and  $d$  ( $d \leq D$ ), which is given by

$$P_{\text{av. sun}}(N, d | \text{uniform}) = (N-1)/(N+1) (1-d/D)^{N+1} + 2/(N+1) (1-d/2D)^{N+1} \quad (4.3)$$

(Mann *et al.*, 1977). In general the average gap frequency for the transect  $(0, D)$  is a function of the number of leaf projections on the transect ( $N$ ), the size of the projections ( $d$ ) and their locations along the transect. Results from eq. 4.3 for various values of  $N$  and  $d$  are presented in figure 4.1. These results show that if the total shadow length ( $c = N \cdot d$ ) is held constant while  $N$  is allowed to increase, the average sunlit fraction increases very rapidly.

It has been shown that light penetration onto a transect beneath a canopy can be described by a general law which can be used for any canopy. In the next section limiting results for sunlight penetration will be determined for several leaf distribution functions and it will be shown that the Poisson law is a special case of this general law.

### Limiting results

In the previous section, results from numerical studies indicated that if the total length  $Nd$  of the leaf projections is held constant ( $Nd = c$ ), the expected value of the sunlit fraction of  $(0, D)$  converges as the number of leaf projections ( $N$ ) increases (see figure

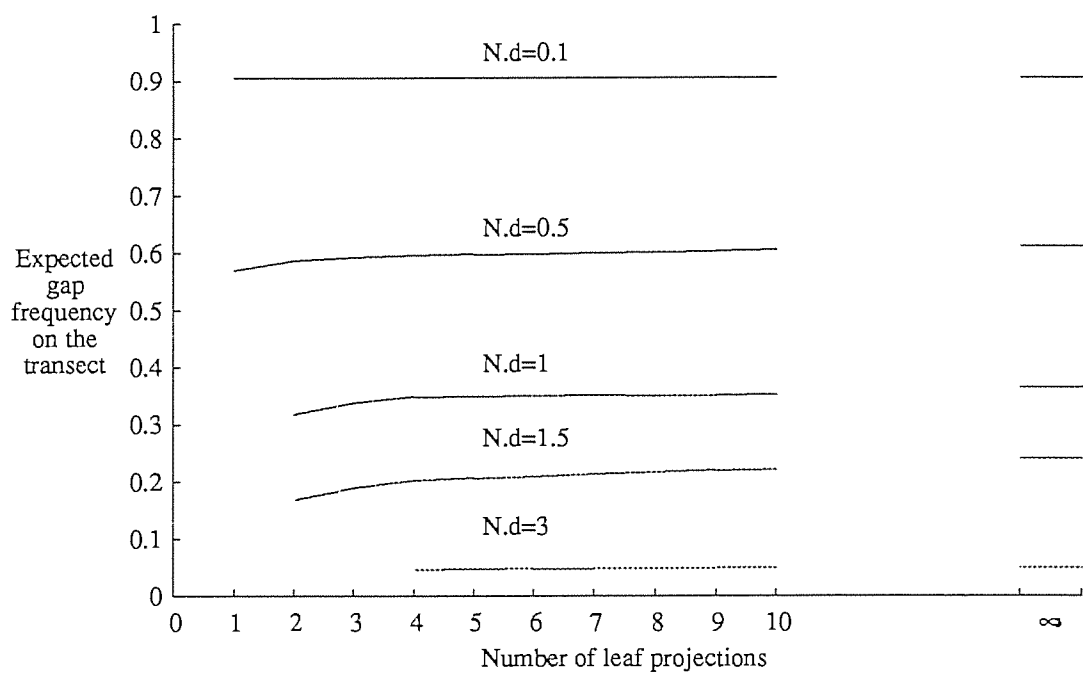


Figure 4.1. The expected gap frequency for a transect beneath a canopy for various values of the total length ( $Nd$ ) as a function of the number of leaf projections  $N$  (for  $L=1$ ).

4.1). For a uniform distribution of leaves, the convergence is very rapid and the limiting values of the sunlit fraction is given by  $e^{-c/D}$ . This is the standard Poisson result which can be verified by inserting  $d=c/N$  into eq. 4.3 ( $D=1$ ) and considering the mathematical limit as  $N$  increases beyond all bounds :

$$E(\text{sun}) = \lim E(\text{sun} | N, d) = e^{-c/D} \quad (4.4).$$

The limiting result for a general leaf-projection location distribution,  $f$ , as opposed to the uniform distribution used in eq. 4.4 is found by considering the limit of eq. 4.2, for  $Nd=c$ , as  $N$  increases beyond all bounds.

$$E(\text{sun}) = \lim E(\text{sun} | N, d) = 1/D \int_0^D e^{-cf(x)} dx \quad (4.5)$$

In equation 4.5, the density function  $f$  is assumed to be continuous over  $(0, D)$ . Equation 4.5 implies that the total foliage projected onto the transect should be apportioned to each point  $x$ , in proportion to the foliage density at that point. The leaf-projection location density ( $f$ ) is a function of the spatial foliage location distribution projected onto a plane containing the transect. It is therefore a function of sun and leaf orientation (these factors will be included into the theoretical analysis later).

Solving equation 4.5 for several leaf distribution functions illustrates the effect of the density functions on canopy gap frequency. Several limiting results are shown in figure 4.2. These results show that various distribution functions yield solutions for eq. 4.5 which are significantly different from the uniform limit.

#### Leaf projection length, $d$

The validity of the assumption of a constant leaf projection length  $d$  is of interest if the results of this analysis are to be regarded with confidence. This problem has been analysed and it can be shown (for the uniform distribution at least) that the mean leaf projection length,  $d$ , leads to a sufficiently accurate estimate of the gap frequency (Mann et al., 1977). I have accepted this conclusion.

This analysis has shown that light penetration through canopies is sensitive to the location of foliage in the canopy. It also shows that the limiting values of the relative contact numbers shown in figure 4.6 for several crops are related to the structure of the crop stand. In the next section models of stand structure are analysed to determine the effects of leaf distribution on sunlight penetration. The results of this analysis will be used in conjunction with the results from eq. 4.5 to quantify the effects of leaf distribution on light penetration. It will be shown that light penetration is determined at two levels, that of the plant and that of the whole stand. This idea will be discussed later.



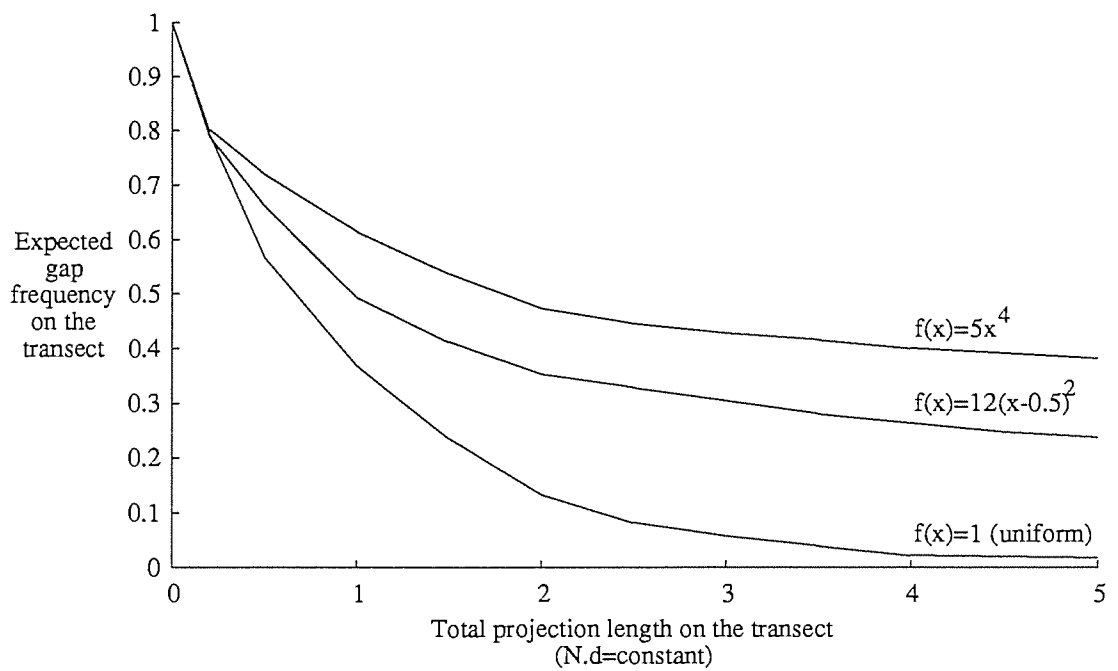


Figure 4.2. The expected gap frequency for a transect beneath a canopy. These are the limiting results for three arbitrarily chosen leaf location distributions (after Mann *et al.*, 1977).

The principles of point quadrat analysis (Warren Wilson, 1963) provide a convenient foundation for the theoretical treatment needed here. This discussion will be developed from the work in the previous chapters. The plant canopy will be assumed to consist of leaves arranged in space and unsupported by branches to simplify the theoretical treatment. Azimuthal symmetry of leaf orientation is assumed. The terminology and treatment provided by Nilson (1971) and Ross (1981) is similar and will be followed here.

### **Distribution of foliage**

The distribution of foliage in a canopy is most easily characterized by the relative variance ( $V'$ ) of the number of contacts with foliage (Warren Wilson, 1961; Nilson, 1971). Both the mean and variance are determined. The relative variance is the variance divided by the mean. In a canopy with randomly distributed leaves it is equal to 1; it exceeds 1 when the leaves are clumped and is less than 1 when the leaves are distributed regularly. The more pronounced the degree of clumping or regularity in the stand, the further  $V'$  deviates from unity (Warren Wilson, 1961). The distribution of leaves in canopies is described using  $V'$  by Warren Wilson (1961), Acock *et al.* (1970), Nilson (1971) and Ross (1981).

In the next section several models which have been used to describe canopy structure and penetration of direct sunlight will be introduced. The models used are the Poisson and the positive and negative binomial distributions. The corresponding formulae for the gap frequencies are presented. The application of these models is discussed.

### **Models of light penetration through plant canopies**

The application of the Poisson and binomial formulae to the problem of gap frequencies in plant stands has been analysed by Acock *et al.* (1970), Nilson (1971) and Ross (1981). The positive binomial formula was first used for modelling plant canopies by Monsi and Saeki (1953) and the negative binomial formula by Mototani (1968) (cited by Acock, 1970; Ross, 1981).

#### **The Poisson model**

The use of the Poisson law to model gap frequencies in plant stands requires that several assumptions are made about the structure of the stand. These are:

- (1) The stand consists of an infinitely large number ( $n$ ) of (statistically) independent horizontal layers, each of which has a thickness of  $\Delta L=L/n$ .
- (2) The probability of observing more than one contact within a thin layer  $\Delta L$  is infinitely small compared with the probability of one contact.
- (3) The probability of observing a contact within a thin layer  $\Delta L$  is equal to the mean number of contacts per layer, *i.e.*  $G\theta_p\Delta L/\cos\theta_p$  where  $G(\theta_p)$  is the fraction of the leaf

area projected onto a plane perpendicular to the probe direction  $\theta_p$  and  $P_0(\theta_p)$  is the gap frequency measured at the probe angle  $\theta_p$ . The probability of no contacts ( $P_0(\theta_p)$ ) is then given by  $1-G\theta_p\Delta L/\cos\theta_p$ .

On the assumption that  $n \rightarrow \infty$ , the probability,  $P_0(\theta_p)$ , that a probe passing through the canopy makes no contacts with the foliage is given by

$$P_0(\theta_p) = \exp(-LG\theta_p/\cos\theta_p) \quad (4.6)$$

(Nilson, 1971). The quantity  $P_0(\theta_p)$  is the gap frequency for the canopy at the probe angle  $\theta_p$ . Equation 4.6 is equivalent to

$$L = -\ln P_0 \quad (3.5)$$

which was used in chapter three to describe the gap frequency in a thin layer of randomly distributed flat leaves.

The Poisson model depends on the assumption that the positions of the elements are independent of each other and it describes a canopy with randomly distributed leaves. The mean and variance of the Poisson distribution are equal, so the relative variance is 1. When this condition is not met there is a deviation from the Poisson model and an alternative must be adopted.

### Binomial models

Positive and negative binomial models have been used to describe the probability that a probe will penetrate a canopy (Acock *et al.*, 1970; Nilson, 1971; Ross, 1981).

A number of assumptions are required for the **positive binomial** model.

- (1) The stand consists of a finite number,  $n=L/\Delta L$ , of equal and statistically independent horizontal layers.
- (2) Only zero or one contact within a layer,  $\Delta L$ , is possible.
- (3) The gap frequency of a layer in the canopy is given by  $1-G(\theta_p)\Delta L/\cos\theta_p$ .

On these assumptions the gap frequency of the canopy of  $n$  layers is given by

$$P_0(\theta_p) = (1-G(\theta_p)\Delta L/\cos\theta_p)^{L/\Delta L} \quad (4.7)$$

(Nilson 1971). The relative variance of the canopy is given by

$$V' = (1-G(\theta_p)\Delta L/\cos\theta_p) < 1 \quad (4.8)$$

(Nilson, 1971; Ross, 1981).

The positive binomial model describes the case of a regular distribution of foliage. The quantity  $\Delta L$ , the thickness of an individual layer, is an index of regularity; the more regular the distribution of the foliage, the less the gap frequency and the greater  $\Delta L$ . This will be discussed later.

The **negative binomial** model describes a clumped distribution of leaves. The assumptions for a negative binomial model are:

- (1) The stand consists of a finite number,  $n=L/\Delta L$  of equal and statistically independent layers.
- (2) More than one contact within a layer is possible.
- (3) The gap frequency for the canopy is given by

$$P_0(\theta_p) = (1+G(\theta_p)\Delta L/\cos\theta_p)^{-L/\Delta L} \quad (4.9)$$

(Nilson, 1971). The relative variance of the canopy is given by

$$V' = (1+G(\theta_p)\Delta L/\cos\theta_p) > 1 \quad (4.10)$$

(Nilson, 1971).

In the negative binomial model the quantity  $\Delta L$  is an index of the clumpiness of the canopy. The smaller  $\Delta L$ , the greater the clumpiness of the canopy and the greater the canopy gap frequency.

The positive and negative binomial distributions both tend to the Poisson distribution if the thickness of an independent layer  $\Delta L \rightarrow 0$ . The positive binomial formula estimates higher light penetration than the exponential formula and the negative binomial formula estimates smaller ones (see figure 4.3). The results in figure 4.3 were calculated from equations 4.6, 4.7 and 4.9. They show the gap frequencies when  $G(\theta_p)\Delta L/\cos\theta_p=1$  and  $\Delta L=0.9$  and  $0.5$  for the positive binomial model;  $\Delta L \rightarrow 0$  giving the Poisson model; and  $\Delta L=0.5, 4$  and  $10$  for the negative binomial model. From these results the differences between the three models are negligible when  $\Delta L \leq 0.2$ .

The Poisson model for a plant canopy assumes that the canopy is composed of an infinitely large number,  $n=L/\Delta L$ , of very thin layers. The probability of observing more than one contact within a layer,  $\Delta L$ , is infinitely small compared with the probability of one contact. For the binomial models the canopy is assumed to be composed of a finite number,  $n=L/\Delta L$ , of equal layers. For the positive binomial model only zero or one contact within a layer is possible. However for the negative binomial model, more than one contact within a layer is possible.

The magnitude of  $\Delta L$  provides an index of the distribution of leaves in the canopy for the two binomial formulae. The greater  $\Delta L$  the more the leaf distribution differs from the random case. This principle is most easily illustrated using the positive binomial model as an example. For this model it is assumed that only zero or one contact within

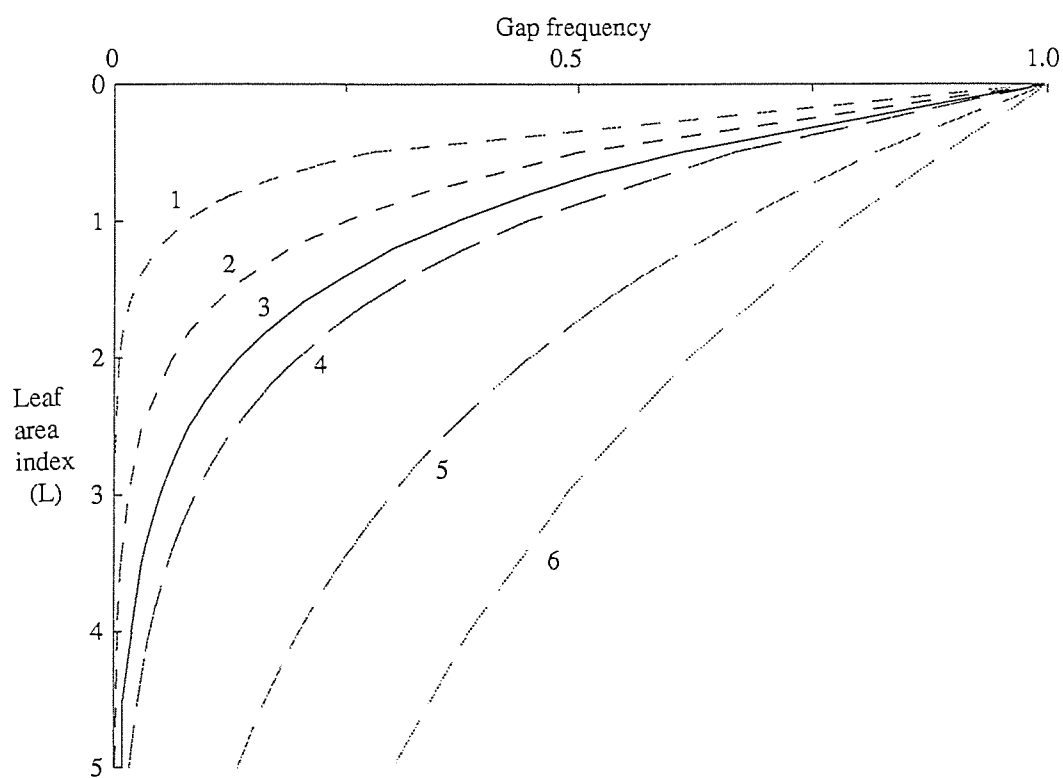


Figure 4.3. Predicted values of gap frequencies obtained using the Poisson and the positive and negative binomial models. The graph shows the rapid fall in the gap frequency with increasing leaf area index. Curves 1 and 2 are calculated from the positive binomial model using  $\Delta L=0.9$  and  $0.5$  respectively. Curve 3 is calculated using the Poisson model and represents the case of a random canopy. Curves 4, 5 and 6 were calculated using the negative binomial model using  $\Delta L=0.5, 4$  and  $10$  respectively. (After Nilson, 1971).

a layer  $\Delta L$  is possible. In a regular canopy,  $\Delta L=1$  will give a maximum of one contact, because if the canopy is completely regular there can be no shading of leaves by other leaves. However if the canopy is somewhere between regular and random, i.e. the canopy is semi-regular there will be more than one layer, but the actual number of layers will depend on the requirement that there is only zero or one leaf contact per layer. Similar principles apply to the negative binomial model, but there are different requirements for the number of contacts that may occur within a layer.

In the next section the relative variance and the phytoelement distribution coefficient are compared. These quantities are both used to describe the distribution of leaves in plant canopies but are measured in different ways. The relative variance is determined directly from measurements made with point quadrats. In contrast  $(C_s)$  is determined empirically from measurements of canopy gap frequency and parallel measurements of canopy architecture.

#### **Relative variance and the phytoelement distribution coefficient**

Gap frequencies measured in crop stands are often reported to differ from calculated values and the differences are usually attributed to the distribution of the foliage in the canopy. Ross (1975; 1981, p.227) included a phytoelement distribution coefficient,  $(C_s)$ , in relationships based on the Poisson law, e.g.

$$\ln P_0(\theta_p) \cos \theta_p = L G(\theta_p) C_s \quad (4.11)$$

(Ross, 1981). The phytoelement distribution coefficient  $(C_s)$  is an empirical index for the distribution of the projections of the leaves and describes the difference between the measured gap frequency and the gap frequency calculated for the same canopy on the assumption of a random leaf distribution. The phytoelement distribution coefficient can be calculated using

$$C_s = \ln P_0(\theta_p) \cos \theta_p / L G(\theta_p) \quad (4.12)$$

(Ross, 1981) where the gap frequency,  $L$  and  $G(\theta_p)$  are all measured in the canopy and  $\ln P_0(\theta_p) \cos \theta_p$  is the contact number.

The dependence of  $-\ln P_0$  on downward cumulative leaf area  $L(z)$  is often approximated by a straight line. When  $G(\theta_p)$  is constant with increasing  $L(z)$ , the theoretical formulae, both exponential and binomial, can be represented by straight lines which have different gradients in the graph of  $-\ln P_0$  against  $L$ . In the case of the exponential formula the gradient is equal to  $G(\theta_p)/\cos \theta_p$  and, for the binomial formulae to  $C_s G(\theta_p)/\cos \theta_p$ .

The phytoelement distribution coefficient has been defined in terms of relative variance. Ross (1981) reported that

$$C_s = \ln V' / 1 - V' \quad (4.13)$$

where  $V'$  is the relative variance (Ross, 1981 p.227).  $V'=C_s=1$  corresponds to a random distribution and the Poisson formula;  $V'<1$  and  $C_s>1$  corresponds to a semi-regular distribution and the positive binomial formula; and  $V'>1$  and  $C_s<1$  corresponds to a clumped distribution and the negative binomial formula.

In the next section the effect of leaf distribution on canopy gap frequency is examined. The binomial models introduced earlier are used to calculate gap frequencies for plant canopies with different values of  $V'$ .

### Relative variance and canopy gap frequency

The effects of a non-random leaf distributions on the gap frequencies of canopies can be estimated using theoretical models. Binomial models can be used to predict the gap frequency of a canopy if information on the geometry of the leaves is known (e.g. Nilson, 1971). I calculated canopy gap frequencies for relative variances in the range from 0 to 2 (previously reported measurements of relative variance have ranged from 0.5 to 2 (e.g. Warren Wilson, 1961)). For this analysis it is assumed that the canopy is a thin layer of flat leaves ( $L=1$ ) and that  $\theta_p=0$  which means that  $G(\theta_p)/\cos\theta_p=1$  and greatly simplifies calculations. Details of the calculations are given in appendix 3. The results of these calculations will be used in conjunction with the principles derived by Mann *et al.* (1977) and Lang and Xiang (1986) to compare the effects of plant form and stand structure on sunlight penetration.

In this analysis, canopy gap frequencies are predicted using the exponential model and the positive and negative binomial models. The case of the random canopy is given by the Poisson law (eq. 4.6); a canopy with a regular leaf distribution is given by the negative binomial model (eq. 4.7); and a canopy with a clumped leaf distribution is described by the positive binomial model (eq. 4.9). The gap frequencies were determined for a range of relative variances to determine the effects of the quantities  $V'$ ,  $C_s$  and  $\Delta L$  on the gap frequency of a canopy. This was done for  $V'$  from 0 to 2 using derivatives of equations 4.7 and 4.8 when  $V'$  is less than 1, equation 4.6 when  $V'=1$  and equations 4.9 and 4.10 when  $V'$  is greater than 1.

The results of this analysis are presented in table 4.1 and shown in figure 4.4. The result in figure 4.4 is compared to the result obtained by Warren Wilson (1961) from studies with model canopies. This result agrees well with that of Warren Wilson

	<u>Leaf distribution in the canopy</u>										
	Regular		Random							Clumped	
$P_0$	0.08	0.18	0.25	0.31	0.35	0.37	0.39	0.42	0.44	0.47	0.49
$V'$	0.10	0.30	0.50	0.70	0.90	1.00	1.10	1.30	1.50	1.70	1.90
$C_s$	2.56	1.72	1.39	1.19	1.05	1.00	0.95	0.88	0.81	0.76	0.71
$\Delta L$	0.9	0.7	0.5	0.3	0.1	0.0	0.1	0.3	0.5	0.7	0.9

Table 4.1. Comparison of values for  $V'$ ,  $C_s$ , and  $\Delta L$  on theoretical values of  $P_0$ . These values were calculated using equations 4.6, 4.7 and 4.9 as described in the text in this chapter and in appendix 3.

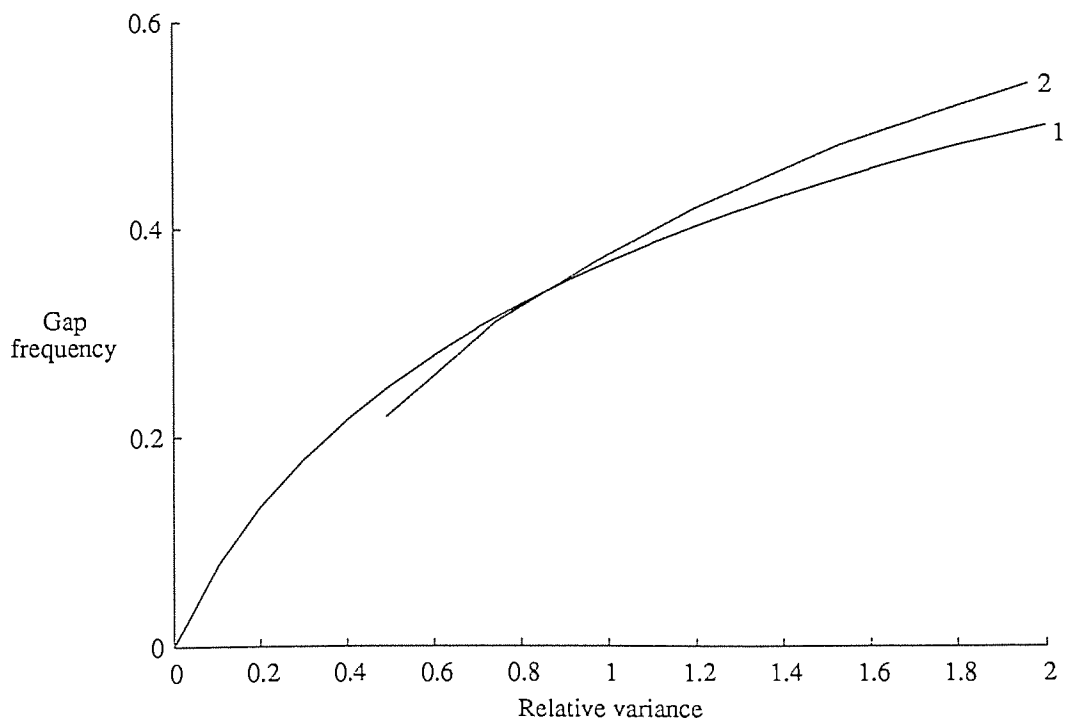


Figure 4.4. Estimates of the effect of relative variance on gap frequencies in plant canopies. Curve 1 was calculated using the binomial models discussed in this chapter and appendix 3. Curve 2 was determined by Warren Wilson (1961) from experiments with model canopies.



(1961) (fig. 4a, page 278). The agreement between the two sets of results is pleasing as it shows that the theory used here to describe leaf distributions in plant canopies fits Warren Wilson's (1961) concept of relative variance and it provides a method for checking the results of the calculations described in appendix 3. It is apparent from figure 4.4 that as the relative variance approaches zero, the gap frequency approaches a limit of zero. As the relative variance of the canopy increases above 1, the gap frequency increases and can approach a theoretical limit of 1 (e.g., Acock *et al.*, 1970).

The theoretical procedures outlined in this chapter will be tested using measurements of light transmission and canopy structure that are available for kiwifruit (chapters 2 and 3) and a range of field crops (Lang and Xiang, 1986). The transmission measurements, expressed as contact numbers ( $-\cos\theta_p \ln P_0(\theta_p) = k(\theta_p)$ ) to simplify calculations, will be analysed to show that light penetration depends on both plant habit and stand structure. The result for the kiwifruit stand will be compared to the results for crops measured by Lang (Lang *et al.*, 1985; Lang and Xiang, 1986).

### Methods

The structures of the stands for the various crops considered here are different. The Gabo wheat was grown as a uniform stand (Lang and Xiang, 1986). The kiwifruit stand was grown on a pergola trellis and appeared to be uniform from a visual assessment of canopy structure. There were two stands of sorghum used; one had a row spacing of 0.76m and the other had a row spacing of 1.52m (Lang and Xiang, 1986). The English wheat cultivar was grown in a stand comprising bands 1.2m wide with a leaf area index of about 8, and with clear spaces of about 0.6m between bands; the clear spaces were included in the transmission measurements.

The transmission of direct sunlight through the foliage was measured using the procedure described in chapter 3. This is the procedure of Lang *et al.* (1985). The transmission data were averaged over different segment lengths in order to investigate the effects of averaging length on measured values of gap frequency using the method of Lang and Xiang (1986). This procedure was described in the previous chapter for the measurements made in the kiwifruit orchard. The averages of the transmission measurements for different segment lengths were converted to relative contact numbers (relative to the contact number at  $l/d=10$  which has a theoretical value of 1.054) and are shown in figure 4.5. The result for kiwifruit in figure 4.5 is the same as that in figure 3.9.

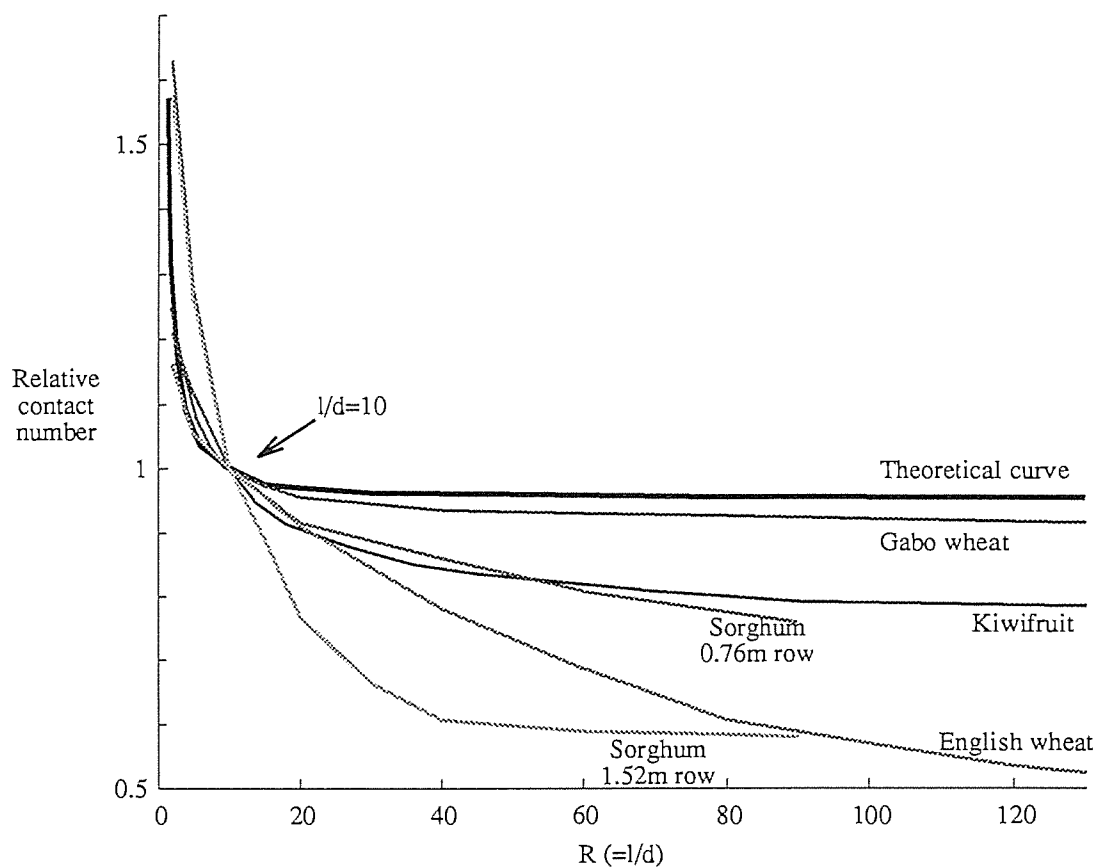


Figure 4.5. The relative contact numbers  $(\ln P_0(\theta_p)) \cos \theta_p$  calculated for a number of plant canopies. The theoretical curve is the expected result for a uniform canopy. The differences between the six curves are attributed to the different leaf distributions occurring in the five plant canopies. For example the Gabo wheat was grown as a uniform canopy whereas the English wheat had large gaps between blocks which contained the plants. The trends shown in these results were predicted and described earlier (see figure 4.2).

The transmission data for the field crop stands are taken from Lang and Xiang (1986). These results were obtained in the same way as the measurements for the kiwifruit stand. The results expressed in terms of relative contact numbers are shown in figure 4.5 with the results for kiwifruit.

The values of  $C_s$  for the kiwifruit stand is calculated by solving eq. 4.12 using estimates of  $L$  and  $G(\theta_p)$  obtained from direct measurement (given in chapters 2 and 3) and contact numbers measured at  $l/d=10$  and  $l/d=120$ .

$$C_s = \ln P_0(\theta_p) \cos \theta_p / L G(\theta_p) \quad (4.12)$$

The results for kiwifruit at  $l/d=10$  and  $l/d=120$  are shown in figure 4.6.

Results like those obtained using eq. 4.12 can be obtained more simply by using the estimates of  $L$  from the direct and indirect procedures and figure 4.5. The value of  $C_s$  at  $l/d=10$  can be obtained by dividing the indirect estimate of  $L$  by the direct estimate. The value of  $C_s$  at  $l/d=120$  can be obtained by dividing the indirect estimate of  $L$  taken at  $l/d=120$  by the direct estimate. This is equivalent to multiplying the value of  $C_s$  taken at  $l/d=10$  by the value of  $k(\theta_p)$  taken at  $l/d=120$ . The phytoelement distribution coefficients can be converted to values of  $V'$  or  $\Delta L$  using the values in table 4.1. The results for this analysis for the different crop stands are given in table 4.2.

### Results

The values of  $C_s$  calculated for the kiwifruit canopy from transmission measurements averaged at  $l/d=10$  and at  $l/d=120$  are plotted in figure 4.6. These results show that  $C_s$  has a constant value of about 1.7 for the range of  $(\theta_p)$  used in the analysis. This is the value by which  $L$  from the remote measurements exceeded  $L$  from the direct measurements. The results from  $l/d=120$  give  $C_s$  as about 1.4. This result can be obtained by multiplying the estimate of  $L$  from the remote measurements by 0.8 (the limiting value of the relative contact number for kiwifruit in figure 4.5).

The result for kiwifruit give a relative variance of about 0.3 at  $l/d=10$  and at  $l/d=120$  the relative variance is about 0.5. The results of the transmission measurements of Lang and Xiang (1986) at  $l/d=10$  gave estimates of  $L$  that were in good agreement with direct measurements of  $L$ . The corresponding values of  $C_s$  or  $V'$  are close to 1 which is the value expected for a random canopy. At  $l/d=120$  the values of  $C_s$  and  $V'$  are almost all different from what is expected for a random canopy and in all cases where differences occur, the deviation is towards the result expected for a clumped canopy. The exception is Gabo wheat which was grown as a continuous stand, and has the

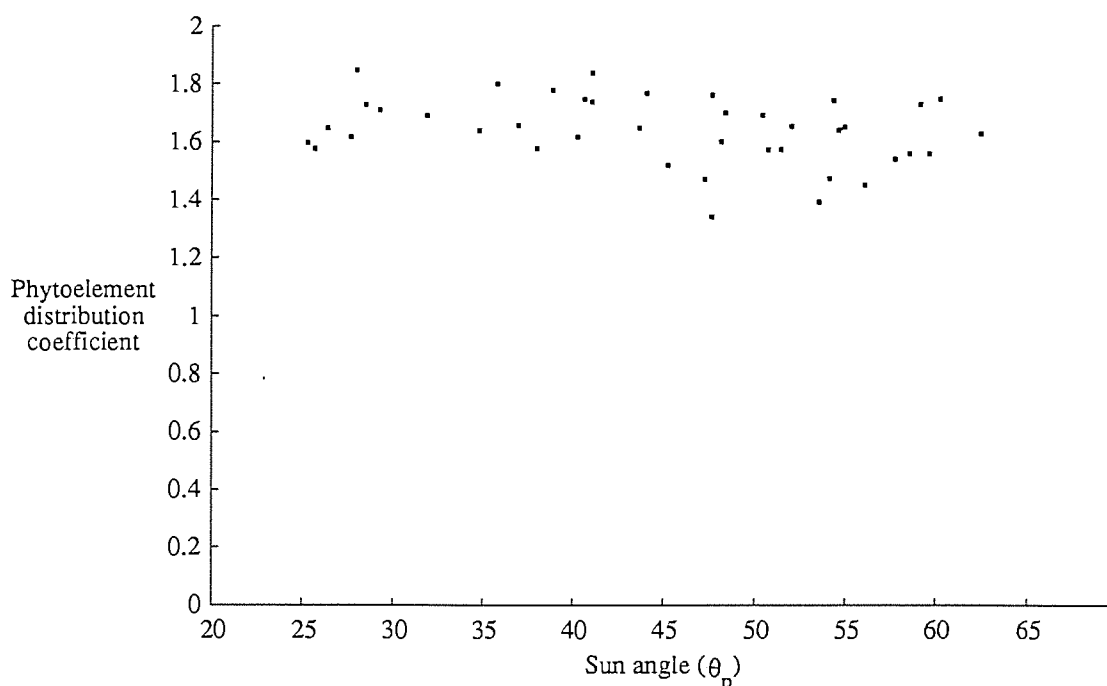


Figure 4.5. The phytoelement distribution coefficient ( $C_s$ ) calculated from measurements of light transmission made in a kiwifruit canopy.

Crop	Leaf area index		Leaf distribution ( $C_s$ and $V'$ )			
	Direct measurement	Light transmission	$l/d=10$		$l/d=120$	
			$C_s$	$V'$	$C_s$	$V'$
Kiwifruit						
	$3.5 \pm 0.2^a$	$6.3 \pm 0.5^c$	1.8	0.3	1.4	0.5
	$2.2 \pm 0.2$	$4.2 \pm 0.6^c$	1.9	0.3	1.5	0.4
	$2.0 \pm 0.2$	$3.2 \pm 0.6^c$	1.6	0.4	1.3	0.6
	$2.3 \pm 0.1$	$3.9 \pm 0.2^c$	1.7	0.3	1.3	0.6
	$1.7 \pm 0.2$	$2.8 \pm 0.5^c$	1.6	0.4	1.3	0.6
Sorghum						
0.76m row	$1.09 \pm 0.07$	$1.23 \pm 0.18$	1.1	0.9	1.0	1.0
1.52m row	$0.63 \pm 0.05$	$0.79 \pm 0.05$	1.3	0.6	0.7	1.9
Wheat						
Gabo						
day 319		$1.19 \pm 0.03$	0.9	1.3	0.9	1.3
day 326		$1.12 \pm 0.03$	0.8	1.5	0.8	1.5
day 328	$1.32 \pm 0.06$					
English						
day 316		$6.29 \pm 0.28$	1.0	1.0	0.5	2.0
day 320	$6.49 \pm 0.06$					
day 321	$6.45^*$	$6.80 \pm 0.14$	1.1	0.9	0.5	2.0
day 327	$6.24 \pm 0.06$					

<sup>a</sup> limits are standard errors of means

<sup>c</sup> values which exceeded the "least significance difference" from direct results

\* interpolated value

Table 4.2. Comparisons of estimates of leaf area indices for several crop stands obtained using direct and indirect measurement procedures. The phytoelement distribution coefficients ( $C_s$ ) and the relative variances ( $V'$ ) of the stands are shown for  $l/d=10$  and  $l/d=120$ .

same relative variance at  $l/d=10$  as at  $l/d=120$ . The results of this analysis for all of the crop stands used are presented in table 4.2.

### Discussion

The experimental results support the findings of the theoretical analysis of light penetration into plant stands reported by Mann *et al.* (1977). In all of the stands considered, measured values of light transmission tended towards some limit. The actual value of the limit depended on the structure of the stand; the more uniform the stand the higher the limiting result for light transmission (see figure 4.5).

The distribution of leaves in a plant canopy seems to be determined at two levels, one is set by the form of the plant and the other by the arrangement of the plants in the stand. The effect of plant form on light penetration is estimated at  $l/d=10$  in figure 4.5 and the effect of stand structure on light penetration is estimated at  $l/d=120$ . These two determinants of leaf distribution will be considered separately. This is the idea that leaf distribution can be considered at two levels, the level of the plant and the level of the stand, which was referred to earlier.

Plants often have some ability to influence leaf distribution through features such as internode length, the ability of the leaves to grow into gaps and the form of the plant *e.g.* whether the plant is a climber, a tree, or a herb. In chapter two the apparent ability of kiwifruit leaves to grow into gaps and to orient towards the sun by tropic growth mechanisms was discussed. This accounts for estimated values of  $V'$  being less than 1 (the average value measured was 0.3), which is equivalent to a regular leaf distribution. The other plants included in the analysis all give estimates of  $V'$  which are not significantly different from what is expected for a random canopy when light transmission measurements are analyzed at  $l/d=10$  (table 4.2).

The transmission measurements are analyzed at  $l/d=10$  to determine the effects of plant form and growth patterns on light penetration through the canopy. Light transmission at  $l/d=10$  is used because Lang and Xiang (1986) found that contact numbers estimated from transmission measurements averaged at  $l/d=10$  (which is the ratio of segment length to mean leaf secant) gave reliable estimates of  $L$  in canopies comprising randomly distributed leaves. These estimates were independent of the structure of the stand.

As plant canopies are rarely completely uniform the distribution of leaves in the canopy is strongly influenced by the arrangement of the plants in the canopy and

especially by the presence of large gaps in the stand. This is demonstrated in figure 4.5 where the crop stands which have large gaps in them have the lowest limiting values for the relative contact numbers e.g. English wheat and sorghum with a 1.52m row spacing. By contrast, the stand which has the most uniform canopy (Gabo wheat) is very close to the theoretical curve calculated for a uniform canopy. The trends apparent in these results agree well with results from the theoretical analysis of Mann *et al.* (1977) (e.g. figure 4.2) and give confidence in the results.

Transmission measurements are analyzed at  $I/d=120$  to estimate the effects of stand structure on light penetration. This value is used because at  $I/d=120$  all of the curves in figure 4.5 are at or close to the limiting value for light transmission in the respective stands.

The estimated values of  $C_s$  or  $V'$  for kiwifruit did not change with sun angle as has been reported to occur for some crop stands by Ross (1975, 1981) and Warren Wilson (1961, 1965). The measurements of Warren Wilson were made with point quadrats and Ross measured light transmission. The results in figure 4.6 are thought not to change with sun angle because the averaging procedures used on the transmission measurements.

Individual plants in crop stands have been modelled as spheroids (e.g. Whitfield, 1980) or in the case of a row crop, a row can be modelled as a cylinder or a box filled with leaves (e.g. Cohen and Fuchs, 1987). It is clear that in both of these cases the penetration of sunlight through the canopy and the distribution of the leaves is going to depend on the sun's orientation. For example, consider the case of a row crop with a north to south row direction. At low sun angles the canopy will appear uniform to the sun rising in the east. As the zenith angle decreases (the sun gets higher), the gaps between the rows will begin to influence the penetration of light through the canopy. In such a crop the distribution of leaves might be random within the volume occupied by an individual plant, but when viewed over the canopy, the presence of the gaps will give rise to a clumped leaf distribution at high sun angles. Results like this have been reported for a range of crops by Ross (1975; 1981, p.229-238).

The result reported in the previous paragraph, that leaf distribution changes with probe angle, is not apparent in the measurements of leaf distribution reported here. The reason for this is that the results given in figure 4.6 are the average of transmission measurements taken over several sun angles. It is thought that if the transmission

measurements taken at each sun angle were analysed separately, calculated values of the relative variance would change with sun angle. The averaging procedure used on the transmission measurements means that some aspects of canopy structure are excluded from the contact numbers.

In the next chapter the information from the last three chapters is used in a simple geometrical model to calculate light penetration into a canopy. This model is used to assess the effects of L on light penetration into the canopy. This information is then used in conjunction with information on the effects of light on the reproductive physiology of kiwifruit (Morgan *et al.*, 1985) to estimate the leaf area index when light may have a limiting effect on potential yield of the crop.

### Summary

In this chapter theoretical models of canopy structure have been used to examine the effects of leaf distribution on gap frequency. The relative variance used by Warren Wilson (1961) in point quadrat measurements was compared to the phytoelement distribution coefficient used by Ross (1975, 1981). The measured values of the phytoelement distribution coefficient obtained for kiwifruit were compared to the results obtained for several other crops. Kiwifruit was found to have a regular distribution of leaves in the canopy. This was attributed to the apparent ability of young leaves to grow into gaps in the canopy.

## 5

# A Model for Light in a Kiwifruit Canopy

### Introduction

The training systems and trellis structures developed for kiwifruit have been adapted from systems used for other fruit crops such as grapes. But while the methods for grapes have evolved from long-term experience these systems cannot be assumed to be suitable to all locations and all plant species. For example, experience with grape vines in New Zealand has shown that existing training systems need to be modified, or new systems developed because the plant grows more vigorously in New Zealand than in the traditional growing areas overseas.

For kiwifruit there is no long-term experience. New trellis and training systems are being designed and evaluated for kiwifruit in New Zealand but at present there is little indication of which system is superior and even within one region of New Zealand several types of trellis system are used.

One approach to evaluating trellis structures is through the use of computer models to simulate the light environment within the canopy. The light environment in a kiwifruit canopy grown on a pergola trellis is investigated by simulation using the information on canopy architecture from the three previous chapters. In particular the radiation regime within the canopy is calculated for conditions that occur in late February and early March at Wanganui, in the North Island of New Zealand.

The reason for choosing conditions appropriate to this period is that this appears to be a critical time in the annual cycle of a kiwifruit orchard. Low light levels within the canopy at this time may have several effects on crop productivity in both the current and the following season. For example, it is thought that flowers for the current seasons crop are initiated about nine months before petal opening and pollination (Warrington, 1986). Grant and Ryugo (1984) have reported that replacement canes grown in shaded positions are three times less fruitful than ones growing in sunny positions. Morgan *et al.* (1985) reported that studies in controlled environments confirm field results that low light (one third of full sunlight or less) results in reduced bud break, fewer flowering shoots, fewer flowering nodes per shoot and fewer good flowers per node. Low light levels in the canopy can also influence the current seasons



crop. Grant and Ryugo (1984) reported that fruit grown in shaded positions have a lower concentration of soluble solids than fruit from sunlit positions, resulting in later maturity and therefore later harvest. Laing (1985) has shown that leaf photosynthetic rates fall to negligible values as light intensity falls below one third of full sunlight.

A number of computer models have been developed to simulate penetration and absorption of radiation within plant canopies (e.g. de Wit, 1965; Duncan *et al.*, 1967; Idso and de Wit, 1970; McPherson and Torrsell, 1970; Lemeur and Blad, 1974; Allen, 1974; Mann *et al.*, 1980). The model developed by McPherson and Torrsell (1970) was modified for this simulation. There were several reasons for using this model. McPherson and Torrsell (1970) developed their model from the well tested model of Duncan *et al.* (1967). The model of McPherson and Torrsell (1970) itself has been well tested and shown to simulate accurately radiation penetration in plant canopies with randomly distributed leaves e.g. Torrsell and McPherson (1977) and Dauzat *et al.* (1984). A listing of the program code (McPherson and Torrsell, 1970) was readily available from the authors.

This chapter provides a description of the model and then compares the calculated radiation fluxes among several canopies with different leaf distributions. Three canopies were used in the simulations. One had a random leaf distribution and the other two had varying degrees of regularity. The description of the model given here follows that of McPherson and Torrsell (1970) and Torrsell and McPherson (1977) except that the terminology used here is the same as that used in previous chapters.

#### Theory and description of the model

##### **Description of the canopy**

The 'canopy' is made up of a number of horizontal layers for which several properties are specified. The leaf area within a layer is given by the difference between the leaf area index (L) at the upper and lower bounds of that layer. Leaf angles are specified separately for each layer and are assumed to be uniform within a layer. Heterogeneity of leaf angles within the canopy can be allowed by increasing the number of layers in the model. By specifying a number of layers with different leaf angles and containing different amounts of leaf area, the actual leaf angle distribution for a canopy can be simulated. The azimuthal orientation of the leaves in the canopy is assumed to be uniform.

##### **Calculation of light penetration**

In the model radiation is specified as flux densities measured through a horizontal plane. The model calculates mean values for the horizontal flux densities. The

incoming radiation is separated into direct sunlight and diffuse skylight. Direct sunlight is assumed to consist of parallel rays.

The interception of direct radiation in the canopy is taken to be an exponential function of the effective leaf area. It is given by

$$I = I_0 \exp[LG(\theta_p)C_s/\cos\theta_p] \quad (5.1)$$

where  $I_0$  is the light incident on the canopy from above and  $I$  is the flux density below the leaf area  $L$ . The  $G$ -function gives the projection of the leaf area in the direction  $\theta_p$  and  $C_s$  is an empirical coefficient that adjusts for the effects of non-random leaf distribution on light penetration into the canopy. The factor  $\cos\theta_p$  adjusts  $L$  for the changing optical path length through the canopy as the sun angle changes. Azimuth effects of sun orientation can be ignored as the azimuthal orientation of leaves is assumed to be uniform. In the model, light penetration is calculated separately for each layer using equation 5.1 but with appropriate values of  $I_0$ ,  $L$  and  $G(\theta_p)$  specified for the various layers.

Diffuse sky light is treated in a similar way to direct sunlight. The sky is assumed to be uniformly bright because the distribution of radiation under hazy conditions and under partly cloudy conditions is so variable that more complex assumptions are not useful. For calculation, the sky is divided into six concentric zones that subtend equal solid angles at a point on the ground. The radiation from a given skyzone is assumed to have  $\theta_p$  equal to the elevation of the midpoint of the zone above the horizon.

### **Intercepted radiation**

The amount of sunlight or skylight intercepted by a layer of leaves in the canopy can be calculated using eq. 5.1. The amount of light intercepted is taken as the difference between the  $I$  values above and below the layer in question. This intercepted radiation may be absorbed, reflected or transmitted depending on the orientation and the optical properties of the intercepting leaves; this is discussed in detail later.

The quantity of intercepted radiation that is reflected and transmitted is governed by the optical properties of the leaves. The reflection and transmission coefficients for the leaves determine the quantity of light leaving the leaf. These vary with wavelength, and the values used in the model are appropriate to the waveband 400-700nm. The reflection and transmission coefficients of the leaves are given later.

### **Treatment of reflected and transmitted radiation**

For each layer the model calculates the proportion of the light that is absorbed, reflected and transmitted and, for the reflected and transmitted light it calculates the

amount propagated in each direction. This is calculated on the assumption that scattering is random (Lambertian). The fraction of the illuminated leaf surface in a layer that is facing upward or downward is calculated using the leaf angle and the elevation of the radiation source and, relating these for each of the six leaf azimuth positions in turn. Together with the assumption of Lambertian scattering, this permits calculation of the proportion of radiation reflected at angles above and below the horizontal. Complementary calculations are used for transmitted radiation. The direction of propagation is specified by grouping the reflected and transmitted radiation in each of the upward or downward hemispheres into six elevation angle classes which are the same as those used for skylight.

The reflected and transmitted components of the radiation are calculated in a similar way. The principles used are considered here for the case of the reflected radiation. When  $\theta_p$  (the sun angle) is less than  $\theta_L$  (the leaf angle), the surface reflecting the radiation is always facing upwards. When  $\theta_p$  is less than  $\theta_L$  the reflecting surface may be facing either upwards or downwards depending, on the azimuthal direction of the leaf. To distinguish between these two cases the direction cosine of the normal to the leaf surface is calculated using

$$B = \sin\theta_L \cos\theta_p - \cos\theta_L \sin\theta_p \cos\phi_L \quad (5.2)$$

(adapted from Reeve in appendix to Warren Wilson, 1960 by McPherson and Torssell, 1970). In this formula when B is greater than zero the reflecting surface faces upwards, and downwards when B is less than zero.

Two cases suffice to illustrate all possible cases in relation to the directions of reflection and transmission of radiation. These are summarized in figure 5.1. In figure 5.1a the upper surface of the leaf is illuminated and in figure 5.1b the lower surface of the leaf is illuminated. As the radiation (represented by solid arrows) reflected from the point O, on the leaf COF, is assumed to be completely and uniformly scattered, the flux distribution can be represented by a hemisphere. The flux travelling within any solid angle is proportional to the magnitude of that solid angle. The total reflected radiation is first separated into that travelling above or below the horizontal and added for all azimuth positions (RUP1 + RUP2 and RDN1 + RDN2 respectively). For example the proportion of reflected radiation propagated below the horizontal, in case (a) or above the horizontal in case (b) is  $\theta/\pi$ . This radiation is further subdivided into that travelling at angles greater than or less than the leaf angle.

A similar but separate procedure is followed for transmitted radiation to allow for situations where the reflection and transmission coefficients are unequal. Finally, the

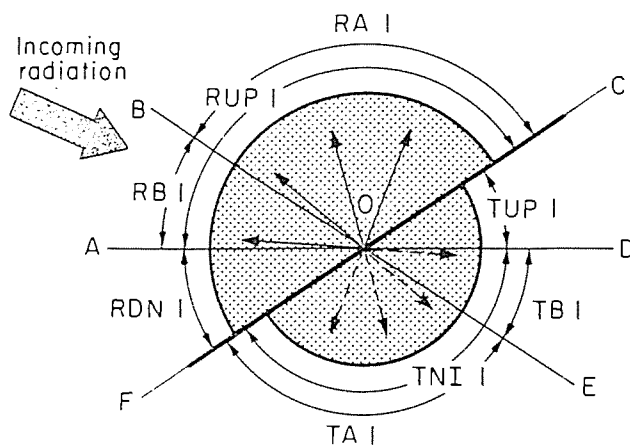


Figure 5.1a

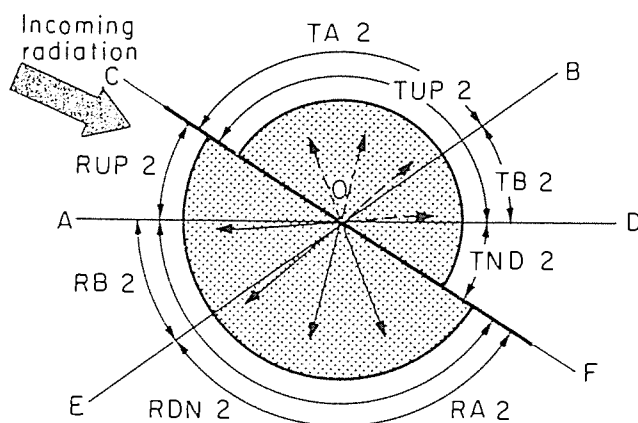


Figure 5.1b

Figure 5.1. The directions in which radiation is reflected and transmitted from point O on a leaf COF. Two azimuth positions, which are representative of all those possible, are shown: (a) radiation is intercepted by the upper surface of the leaf and (b) by the lower surface of the leaf. The radiation is divided into that which is travelling at angles greater than or less than the leaf angle (e.g. RUP1 is divided into RA1 and RB1 respectively). The proportion of the reflected radiation propagated at angles greater than the leaf angle is given by  $(1 - \cos\theta_L / 1 - (\theta_L / \pi))$ . A similar but separate procedure is followed for transmitted radiation (the broken arrows) to allow for situations where the reflection and transmission coefficients are unequal. The amount of radiation travelling upwards in each of the sectors AOB, BOC, COD (fig. 5.1a), AOC, COB, BOD (fig. 5.1b) and downwards in the sectors AOF, FOE, EOD (fig. 5.1a), AOE, EOF, FOD is determined and is divided equally among the number of propagation angle categories used which have mid-angles falling within each particular sector. (From Torssell and McPherson, 1977).

total amount of radiation travelling upwards and downwards in each of the sectors is determined and is divided equally among the number of propagation angle categories which have their mid-angles falling within each particular sector.

### **Tracing intercepted and reflected radiation**

The problem of accounting for the number of quantities and directions of radiation, which increases with each reflection or transmission, is simplified by grouping all reflected or transmitted radiation according to its direction of travel. Twelve angle categories are used in the same way as for skylight; six account for radiation travelling in directions below the horizontal and six account for those above. The need to allow for the effect of azimuth angle is precluded by the assumption of random azimuthal orientation of leaf area.

The procedure used to identify the direction of propagation of radiation leaving each layer in the model is quite simple. The radiation is identified according to its angle of travel regardless of whether its source is direct penetration through the layer, reflection, or transmission. This means that the number of radiation categories remains constant and these are adequate to specify the radiation input to the next layer.

### **Absorption**

As the penetration of radiation from all sources is followed from layer to layer, a count is kept of the flux passing upward or downward through each layer interface. This cumulative quantity gives the flux density at each interface and is an output from the model. The radiation absorbed is calculated as the difference between the net flux density above and below each particular layer.

### **Numerical solution of the model**

The sequence of operations followed in the calculation of the penetration of sunlight and sky light, and the subsequent propagation of transmitted and reflected radiation in the canopy is described by McPherson and Torssell (1970). The procedure is repeated to take into account successively high-order reflections and transmissions. The section of the computer program controlling this procedure takes the form of an iterative loop which repeats the calculations until a negligible proportion of the incoming radiation remains unaccounted for by absorption by leaves or the ground or by loss from the upper surface of the canopy.

## Methods

### **Validation of the model**

Complete validation of the model by measuring the light transmission in and below the canopy was not possible for logistical reasons. However, a partial validation was achieved using the results of the transmission measurements described in chapter 3.

The model was tested against the measured contact numbers (given in figure 3.7) by simulating the conditions under which light transmission was measured in the canopy. The reflection and transmission coefficients of the leaves were set to zero and diffuse light from the sky was ignored. The simulated values of light transmission through the canopy were converted to contact numbers which could be compared to values measured in the orchard. When a phytoelement distribution coefficient ( $C_s$ ) of 1.7 was inserted into eq. 5.1, the simulated contact numbers were within 5% of the contact numbers measured in the orchard (the results are presented in table 5.1). These results give confidence in the suitability of the model as a tool to simulate and predict the radiation regime within this kiwifruit canopy.

### **Incident light**

The dependence of the amounts of direct and diffuse light on the height of the sun has been measured and is available from a variety of sources. de Wit (1965) compiled this information for modelling photosynthesis in crop canopies. His graph shows the amounts of incident direct and diffuse sky-light as a function of sun angle. That graph is reproduced here in figure 5.2. This result is used to estimate the intensity of light from different sources impinging on the crop.

The relative intensities of light incident on the canopy at the latitude of Wanganui, New Zealand, for the 28th February are shown in figure 5.3. These were calculated from the results of de Wit (1965) and take into account the effect of the shelter belt on direct sunlight, and the range of sun angles appropriate to the latitude of Wanganui (39.5°S) in late February and early March. The shelter belt around the orchard is about 8m high so direct sunlight does not reach the canopy until the sun's zenith angle has reached about 60°. The declination of the sun is such that the maximum height of the sun is about 25° from the zenith. The shelter belt was assumed to have no effect on penetration of skylight into the canopy. The calculated effects of these factors on the light incident on the canopy are shown in figure 5.3.

### **Reflection and transmission coefficients**

This analysis was made for light in the wave band 400-700nm (photosynthetically active radiation (PAR)). Facilities were not available for measurement of all the appropriate leaf optical properties. However some measurements of leaf transmission were made with a quantum sensor. The average transmission of PAR through the leaves was about 5%. It was necessary to assume reflection values typical of this type of plant material. For ease of calculation the leaves are assumed to have equal optical characteristics on both sides with reflection =0.09 (Ross, 1981, p.186).

<u>Sun angle</u>	<u>Leaf area index</u>	<u>Measured contact numbers</u>	<u>Simulated contact numbers</u>
30°	2.0	2.39	2.53
	2.2	2.93	2.82
	3.5	4.74	4.48
40°	2.0	2.10	2.26
	2.2	2.61	2.49
	3.5	3.91	3.97
50°	2.0	1.73	1.94
	2.2	2.28	2.14
	3.5	3.37	3.40
60°	2.0	1.63	1.60
	2.2	1.81	1.76
	3.5	2.90	2.80

Table 5.1. Comparison of contact numbers measured in the orchard and values calculated from output from the computer model described in this chapter. The measured values are averages for 10° intervals with the midpoint at the sun angle given. The calculated results are determined for the given sun angle.

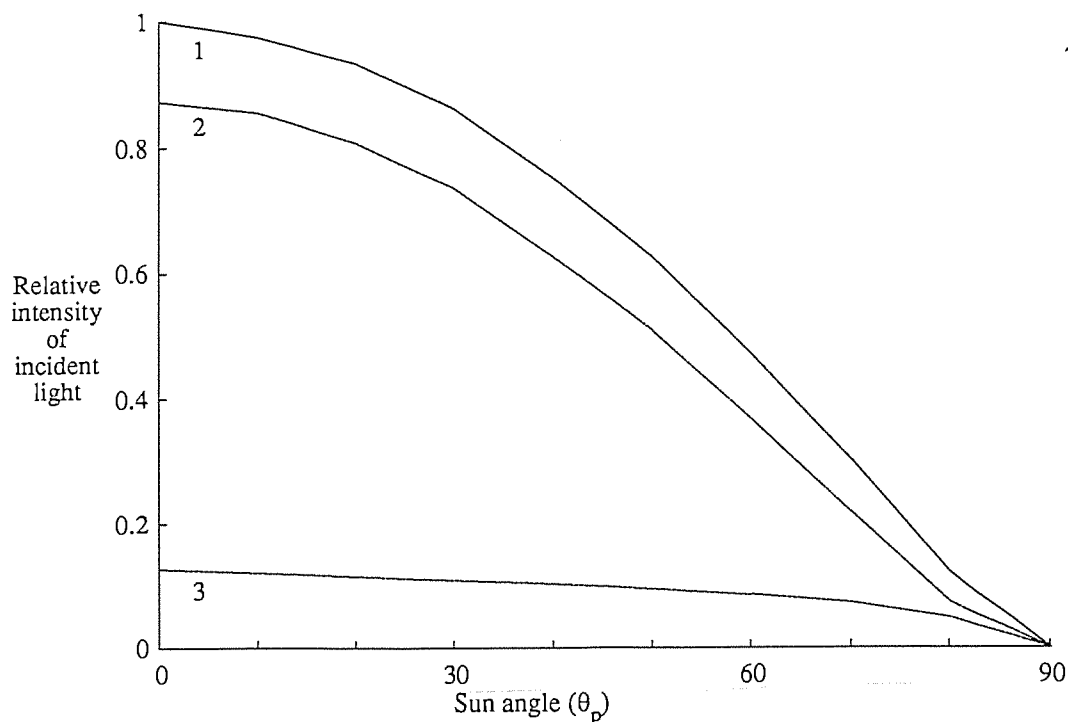


Figure 5.2 The relationship between sun angle and light intensities from various sources (from de Wit, 1965). Curve 1 represents the total incident light at a given sun angle and curves 2 and 3 represent the contribution of direct sunlight and diffuse skylight to the total in curve 1. The relative light intensity of 1 represents the light intensity if the sun were directly overhead. These results represent the situation for a clear day.

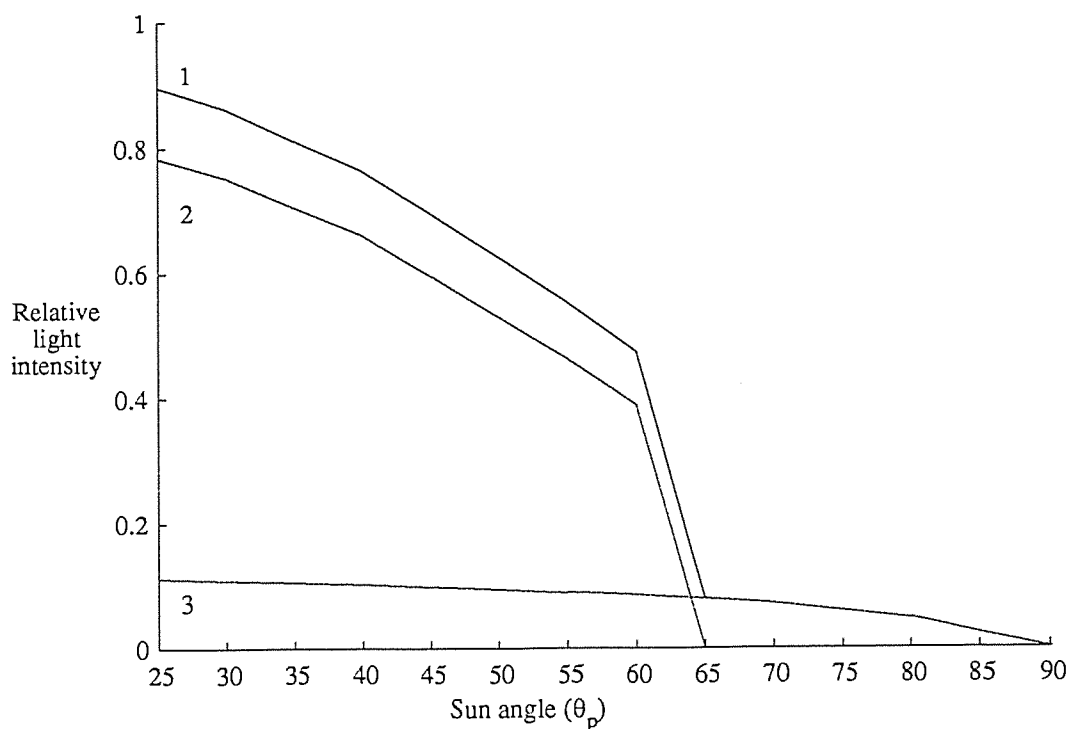


Figure 5.3 The intensities of light from different sources incident on a kiwifruit canopy at Wanganui New Zealand on or about February 28. These curves represent the situation for a clear day. Curve 1 is the total light incident on the canopy. Curve 2 is the intensity of sunlight and curve 3 is for diffuse light from the sky. The effects of the shelter belt on direct sunlight and the effects of the declination of the sun at this latitude and date are included. These curves are extrapolated from the results in figure 5.2.



The ground surface beneath the canopy consists of strips of short grass and bare soil, each of which occupy equal proportions of the ground area. The reflection coefficient of the soil and the grass strip was taken to be equal to 0.1. This value is comparable to values given by Ross (1981) and used by Torrsell and McPherson (1977). These values of leaf and soil reflection and leaf transmission are used in all further calculations.

The situation considered in the model is that for a clear sunny day. The data on canopy architecture given in the previous chapters (tables 2.1, 2.2 and 3.2 and figures 2.2, 2.3, 2.4) were used as inputs to the model. The simulation was used to calculate light penetration for a canopy with randomly distributed leaves ( $C_s=1$ ), a uniform kiwifruit canopy ( $C_s=1.7$ ) and a canopy with the leaf distribution that was inferred from measurements of gap frequencies made in the orchard ( $C_s=1.4$ ). The calculated results of light transmission for the three canopies are presented in figures 5.4 and 5.5.

### Results

The amount of light penetrating into the canopy at different sun angles is shown as a function of leaf area index in figure 5.4a for the random canopy and figure 5.4b for the uniform canopy. The canopy with a phytoelement distribution coefficient ( $C_s$ ) of 1.7 represents the extreme case of a uniform canopy in which the leaf distribution is not affected by the presence of empty spaces. In the random canopy the maximum light intensity falls below one third of full sunlight when the leaf area index reaches two. For the regular canopy, the maximum light intensity falls below a third of full sunlight when the leaf area index reaches about 1. The results for the model which represents the orchard in which the work was carried out (figure 5.4c) shows that the maximum light intensity beneath the canopy falls below one third of full sunlight at a leaf area index of 1.6.

The daily integrals of light are more easily understood. The daily integrals of the radiation penetrating into the three model canopies as a function of  $L$  is shown in figure 5.5. These curves show the total amount of light penetrating into the canopy as a function of  $L$ . The line represents one third of the daily integral of radiation which Morgan *et al.* (1985) thought significant in the physiology and growth of kiwifruit. For a random canopy, the daily light integral falls below one third of the daily total when  $L$  is about 2 (figure 5.5a). For the uniform canopy, the daily integral falls below one third of the daily total when  $L$  is about 1 (figure 5.5b). For the orchard canopy, the

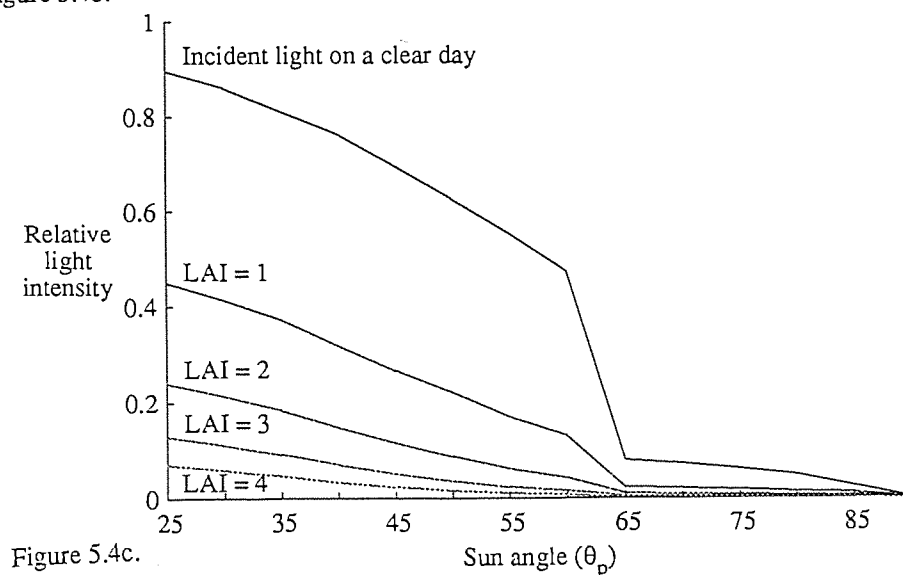
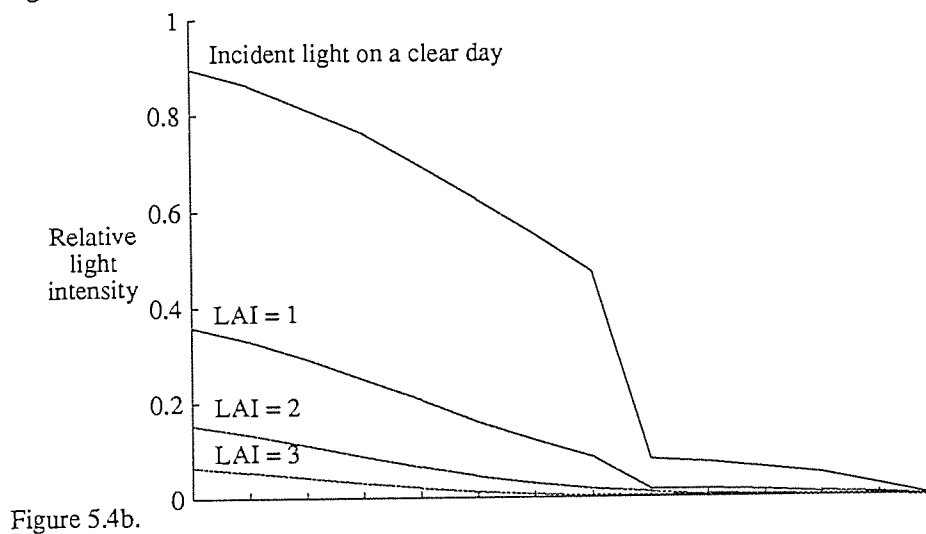
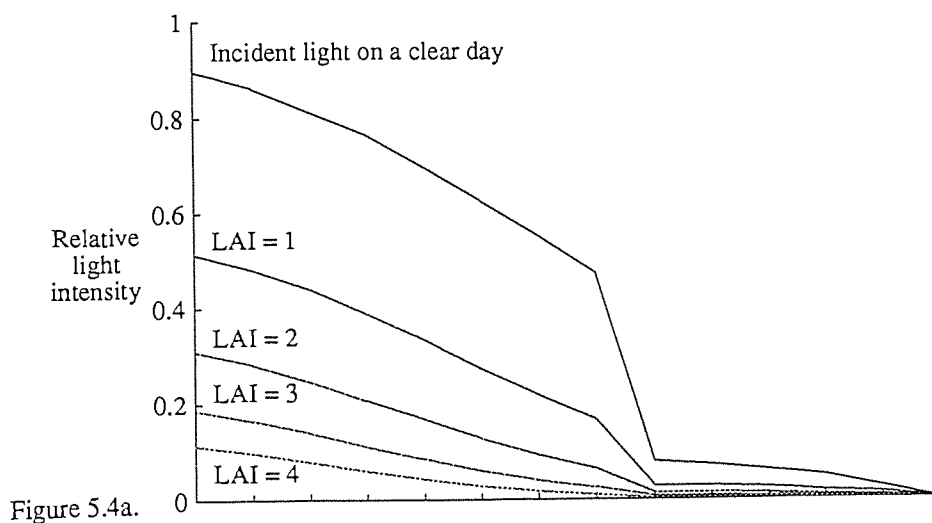


Figure 5.4. Light penetration into three plant canopies at different sun angles. Figure 5.4a is the result for a random canopy, figure 5.4b is the result for a uniform kiwifruit canopy and figure 5.4c is the result calculated for the orchard canopy. The different curves on each graph represent several leaf area indices (lai) for each canopy.

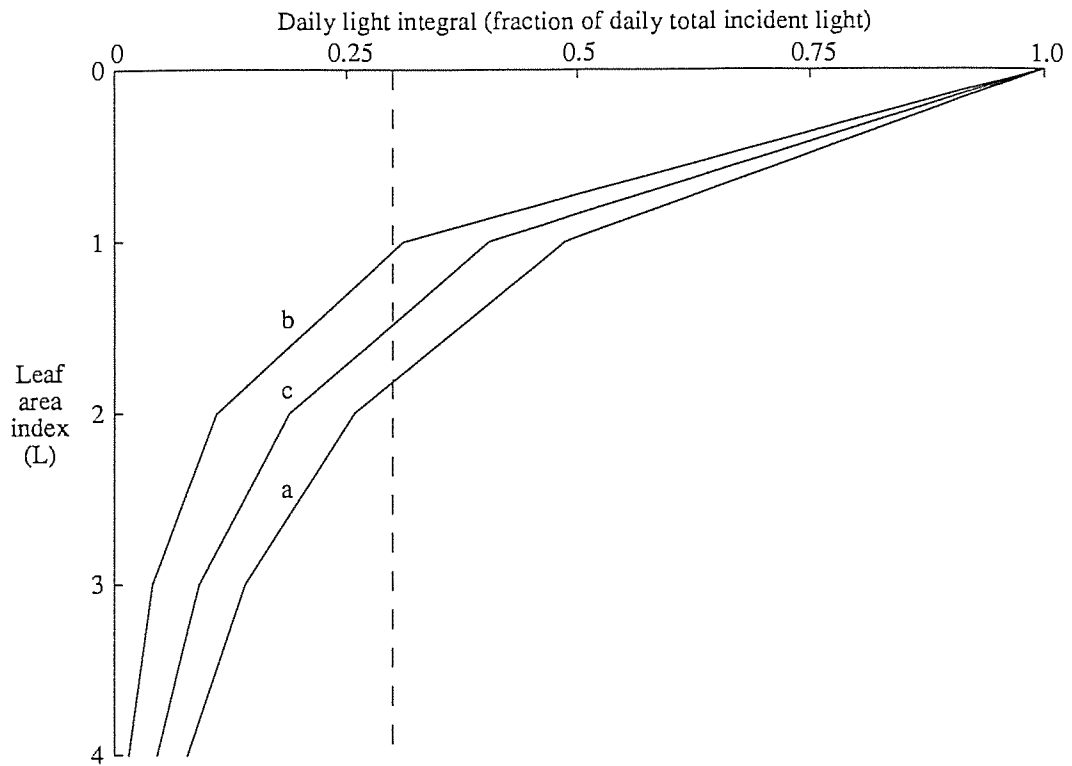


Figure 5.5. The daily integrals of radiation predicted as a function of leaf area index for several plant stands using a simulation model for plant canopies. Curve a is the expected result for a random canopy. Curve b is the expected result for a uniform kiwifruit canopy. Curve c is the result for the orchard canopy. The dashed line represents one third of the daily integral of the incident radiation.

daily light integral falls below one third of the daily total when L is about 1.6 (figure 5.5c).

### Discussion

It is known from chapter 3 that penetration of light into a kiwifruit canopy is much lower than expected for a random canopy. This is because the regular distribution of leaves increases light interception by the plant. Since more light is being intercepted by the leaves, it doesn't penetrate so deeply into the canopy as would be expected for a random canopy.

The results for the phytoelement distribution coefficient represent two possible cases for light interception in the kiwifruit canopy. The extreme case describes a uniform canopy in which the leaves are distributed according to the habit of the plant. In a real canopy the effects of leaf distribution within a plant are modified by the structure of the canopy. The second curve represents the situation actually found in the orchard. The distribution of the leaves in relation to one another in the zones in the canopy is the same as in the uniform canopy, but the effects of leaf distribution on light penetration are modified by the occurrence of gaps in the canopy. The net effect of large gaps in the canopy is to reduce the efficiency of light interception in the canopy. The result for the random canopy is calculated purely for comparative purposes.

The simulation was carried out using the waveband 400-700nm because controlled environment experiments have shown that the photosynthetically active radiation (PAR) affects fruitfulness in kiwifruit (Morgan *et al.* 1985).

These results are of interest with regard to designing trellises to maximize kiwifruit yields. Warren Wilson (1961) suggested that local variation in L leads to inefficient light utilisation, since it results in heavy shading of some foliage while elsewhere sunlight falls on the ground. The more uniform and regular the distribution of foliage, the greater is the crop growth rate at any L and the higher is the optimal L (Warren Wilson, 1961). Denholm and Connor (1982) simulated potential photosynthesis in a range of trellised canopies with different fork angles to investigate claims about the usefulness of the Tatura trellis. They reported that, at any L, the potential seasonal photosynthesis of a continuous flat canopy was greater than that of all the other canopies they considered. These results suggest that the best choice of canopy is one growing on a pergola.

To prevent excessive shading within the canopy, the vines must be pruned so that the leaf area doesn't get too large. The results from figure 5.5, the simulation of the daily light integral in the canopy and the results of Grant and Ryugo (1984b), Morgan *et al.* (1985) and Laing (1985) are used to estimate the value of  $L$  which can be expected to give the best potential yield. Assume that the vertical distribution of the foliage about the trellis is the same as that given in figure 2.2. This means that the fruit are all at, or close to, the bottom of the canopy and there is a negligible proportion of the leaf area beneath them. It is known that low light levels slow fruit growth (Grant and Ryugo, 1984) and reduce photosynthesis to negligible rates (Grant and Ryugo, 1984b; Laing, 1985). Therefore it seems reasonable to take a daily integral of one third full sunlight as the lower limit for light intensity at the bottom of the canopy. This means that light intensities in the canopy are not limiting yields from the current or the following year. The value of  $L$  needed to ensure that the daily light integral doesn't fall below one third of full sunlight can be interpolated from figure 5.5. The uniform canopy should not have  $L$  much greater than 1. However, it is expected to be very difficult to prune a kiwifruit orchard so that it is uniform.

The orchard in which the field work was carried out appeared to have a uniform structure even though the measurements of light transmission that it wasn't uniform. This level of uniformity is probably as good as can be achieved in an orchard through vine management procedures. The result from the orchard with a phytoelement distribution coefficient of 1.4 is used to estimate the leaf area index that is expected to ensure that light levels in the canopy do not fall to excessively low levels. The result interpolated from figure 5.5 suggests that the leaf area index in a kiwifruit orchard with a pergola trellis should be about 1.6.

### Summary

Simulation of the canopy radiation regime using a computer model shows that light in a kiwifruit canopy is attenuated more rapidly than in a canopy with randomly distributed leaves. If it is assumed that the model is dealing with a uniform kiwifruit canopy, then light is attenuated 1.7 times more rapidly than in a random canopy. If it is assumed that the canopy has the same structure as the one in the orchard used for study, then light is attenuated about 1.3 times faster than in a random canopy. If the critical light level in the canopy is taken to be a third of the daily integral of the incident light, then in the uniform canopy low light intensities in the bottom of the canopy can be expected to limit crop yields when  $L$  is greater than 1. For the orchard canopy in which this work was carried out, light levels are expected to begin to limit

yield when  $L$  is greater than 1.6. These results emphasise the importance of summer pruning in order to maintain high yields and the need for further work on the problem of trellis design to improve penetration of light into kiwifruit canopies.

## References

- Acock, B., Thornley, J.H.M., and Warren Wilson, J. (1970) Spatial variation of light in the canopy. In Plant Photosynthetic Production. Manual of methods. Edited by Sestak, Z., Catsky, J. and Jarvis, P.G.. W. Junk, The Hague. pp. 91-102.
- Adams, J.E. and Arkin, G.F. (1977) A light interception method for measuring row crop ground cover. Soil Science Society of America 41 : 789-792.
- Allen, L.H. (1974) Model of light penetration into a wide row crop. Agronomy Journal 66 : 41-47.
- Anderson, M.C. (1966) Some problems of simple characterisation of the light climate in plant communities. In Light as an Ecological Factor. Edited by Brainbridge, R., Evans, G.C., and Rackham, O. Oxford. Blackwell.
- Anderson, M.C. (1966b) Stand structure and light penetration. II. A theoretical analysis. Journal of Applied Ecology 3 : 41-54.
- Anderson, M.C. (1970) Radiation and crop structure. In Plant Photosynthetic Production. Manual of Methods. Edited by Sestak, Z., Catsky, J. and Jarvis, P.G.. W Junk, The Hague. p.412-466.
- Bonhomme, R. and Chartier, P. (1972) The interpretation and automatic measurement of hemispherical photographs to obtain sunlit foliage area and gap frequency. Israel Journal of Agricultural Research 22(2) : 53-61.
- Cohen, S. and Fuchs, M. (1987) The distribution of leaf area, radiation, photosynthesis and transpiration in a Shamouti orange hedgerow orchard. Part 1. Leaf area and radiation. Agricultural and Forest Meteorology 40 : 123-144.
- Dauzat, J., Methy, M. and Salager, J.L. (1984) A method for simulating radiative transfers within canopies, subsequent absorptance and directional reflectance. Oecologia Plantarum 5 (19) : 403-413.
- Duncan, W.G., Loomis, R.S., Williams, W.A., and Hanau, R. (1967) A model for simulating photosynthesis in plant communities. Hilgardia 38 : 181-205.
- Grant, J.A. and Ryugo (1984) Influence of within-canopy shading on fruit size, shoot growth, and return bloom in kiwifruit. Hortscience 19(6) : 834-836.
- Grant, J.A. and Ryugo (1984b) Influence of within-canopy shading on net photosynthetic rate, stomatal conductance, and chlorophyll content of kiwifruit leaves. Hortscience 19(6) : 834-836.
- Green, S.R. and Nicholson, H.F. (1986) Use of a Campbell CR21X logger to measure leaf area index using light transmission. D.S.I.R. (Plant Physiology Division) Technical Report No. 26.
- Hutchison, B.A., Matt, D.R., McMillen, R.T., Gross, L.J., Tajchman, S.J., and Norman, J.M. (1986) The architecture of a deciduous forest canopy in eastern Tennessee, U.S.A.. Journal of Ecology 74 : 635-646.

- Idso, S.B. and de Wit, C.T. (1970) Light relations in plant canopies. Applied Optics 9(1) : 177-184.
- Laing, W.A. (1985) Temperature and light response curves for photosynthesis in kiwifruit (Actinidia chinensis) cv. Hayward. New Zealand Journal of Agricultural Research 28 : 117-124.
- Lang, A.R.G. (1986) Leaf area and average leaf angle from transmission of direct sunlight. Australian Journal of Botany 34 : 349-355.
- Lang, A.R.G. (1988) Simplified estimate of leaf area index from transmission of the sun's beam. Agricultural and Forest Meteorology 41 : 179-186.
- Lang, A.R.G., Xiang Yueqin and Norman, J.M. (1985) Crop structure and penetration of direct sunlight. Agricultural and Forest Meteorology 35 : 83-101.
- Lang, A.R.G. and Xiang Yueqin (1986) Estimation of leaf area indices from transmission of direct sunlight in discontinuous canopies. Agricultural and Forest Meteorology 37 : 229-243.
- Lemur, R. (1973) A method for simulating the direct solar radiation regime in sunflower, Jerusalem artichoke, corn and soybean canopies using actual stand structure data. Agricultural Meteorology 12 : 229-247.
- Lemur, R. and Blad, B.L. (1974) A critical review of light models for estimating the shortwave radiation regime of plant canopies. Agricultural Meteorology 14 : 255-286
- Mann, J.E., Curry, G.L., Hartfiel, D.J., and DeMichele, D.W. (1977) A general law for direct sunlight penetration. Mathematical Biosciences 34 : 63-78.
- Mann, J.E., Curry, G.L., DeMichele, D.W., Baker, D.N. (1980) Light penetration in a row-crop with random plant spacing. Agronomy Journal 72 : 131-142.
- McPherson, H.G. and Torrsell, B.W.R. (1970) A computer program for the numerical solution of a model of the penetration, propagation and absorption of radiation within plant canopies. CSIRO (Division of Land Research) Technical Bulletin 70/8.
- Miller, E.E. and Norman, J.M. (1971) A sunfleck theory for plant canopies.II. Penumbra effect: intensity distributions along sunfleck segments. Agronomy Journal 63 : 739-743.
- Miller, J.B. (1967) A formula for average foliage density. Australian Journal of Botany 15 : 141-144.
- Monsi, M. and Saeki, T. (1953) Uber den lichtfaktor in den pflanzengesellschaften und seine bedeutung für die stoffproduktion. Japanese Journal of Botany 14 : 22-52. The light factor in plant associations and its importance in dry matter production. Translated by M. Slade. C.S.I.R.O. Translation No. 4201.
- Morgan, D.C., Stanley, C.J., and Warrington, I.J. (1985) The effects of simulated daylight and shade-light on vegetative and reproductive growth in kiwifruit and grapevine. Journal of Horticultural Science 60 : 473-484.
- Nilson, T. (1971) A theoretical analysis of the frequency of gaps in plant stands. Agricultural Meteorology 8 : 25-38.



- Norman, J.M. (1978) Modelling the complete crop canopy. In Modification of the Aerial Environment of Plants. Edited by Barfield, B.J. and Gerber, J.F.. American Society of Agricultural Engineers, St. Joseph, Michigan. pp. 249-277.
- Norman, J.M., Perry, S.G., Fraser, A.B., and Mach, W. (1979) Remote sensing of canopy structure. pp.184-185. American Meteorological Society. Proceedings of the 14th Conference on Agricultural and Forest Meteorology and 4th Conference on Biometeorology. April 2-6, 1979, Minneapolis, Minnesota. (American Meteorological Society: Boston). pp. 184-185.
- Norman, J.M. and Campbell, G.S. (1986) Canopy structure. In Field Methods and Instrumentation. Edited by Ehleringer, J.E., Mooney, H.A., Pearcy, R.W. and Rundel, P. Chapman and Hall. (in press).
- Philip, J.R. (1965) The distribution of foliage density with foliage angle estimated from inclined point quadrat observations. Australian Journal of Botany 13 : 357-366.
- Reifsnyder, W.E., Furnival, G.M. and Horowitz, J.L. (1971) Spatial and temporal distribution of solar radiation beneath forest canopies. Agricultural Meteorology 9 : 21-27.
- Ross, J. (1971) Mathematical models of photosynthesis in a plant stand. In Prediction and Measurement of Photosynthetic Productivity. Edited by Setlik, I.. Pudoc, Wageningen. pp. 29-45.
- Ross, J. (1975) Radiative transfer in plant communities. pp. 13-55. In Vegetation and the Atmosphere. Edited by J.L. Monteith. Volume 1. Academic Press, London.
- Ross, J. (1981) The Radiation Regime and Architecture of Plant Stands. W. Junk, The Hague. 391 pp.
- Ross, J. and Nilson, T. (1967) Prostranstvennaya orientatsiya list'ev v posevakh i methodika yeyo opredeleniya. In: Fotosinteziruyushchie Sistemy vysokoy Produktivnosti. Moskva, pp.109-125. Edited by A.A. Nichiporovich. The spatial orientation of leaves in crop stands and its determination. In: Photosynthesis of Productive Systems. Edited by A.A. Nichiporovich. Translated by N. Kraner, Israel Program of Scientific Translations. Jerusalem, pp.86-99.
- Scott, D. and Wells, J.S., (1969) Leaf orientation in barley, lupin, and lucerne stands. New Zealand Journal of Botany 7 : 372-388.
- Shell, G.S.G. and Lang, A.R.G. (1975) Description of leaf orientation and heliotropic response of sunflower using directional statistics. Agricultural Meteorology 15 : 33-48.
- Shell, G.S.G., Lang, A.R.G., and Sale, P.J.M. (1974) Quantitative measures of leaf orientation and heliotropic response in sunflower, bean, pepper and cucumber. Agricultural Meteorology 13 : 25-37.
- Smart, R.E. (1984) Canopy microclimates and effects on wine quality. p.113-132. In Advances in Viticulture and Oenology for Economic Gain. Edited by Lee, T.H. and Somers, T.C.. The Australian Wine Research Institute, Urrbrae, South Australia.

- Smith, H. (1984) Plants that track the sun. Nature 308 : 774.
- Snedecor, G.W. and Cochran, W.G. (1956) Statistical Methods. Iowa State College Press: Ames. 534 pp.
- Torrsell, B.W.R. and McPherson, H.G. (1977) An improved model for simulating the penetration, propagation and absorption of radiation within plant canopies. Australian Journal of Ecology 2 : 245-256.
- Vogelmann, T.C. (1984) Site of light perception and motor cells in a sun-tracking lupine (Lupinus succulentus). Physiologia Plantarum 62 : 335-340.
- Vogelmann, T.C. and Bjorn, L.O. (1983) Response to directional light by leaves of a sun-tracking lupine (Lupinus succulentus). Physiologia Plantarum 59 ; 533-538.
- Warren Wilson, J. (1959) Analysis of the spatial distribution of foliage by two-dimensional point quadrats. New Phytologist 58 : 92-101.
- Warren Wilson, J. (1960) Inclined point quadrats. New Phytologist 59 : 1-8.
- Warren Wilson, J. (1961) Influence of spatial arrangement of foliage area on light interception and pasture growth. Proceedings of the 8th International Grassland Congress. pp. 275-279.
- Warren Wilson, J. (1963) Estimation of foliage denseness and foliage angle by inclined point quadrats. Australian Journal of Botany 11(1) : 95-105.
- Warren Wilson, J. (1965) Stand structure and light penetration. I. Analysis by point quadrats. Journal of Applied Ecology 2(2) : 383-390.
- Warren Wilson, J. (1967) Stand structure and light penetration. III. Sunlit foliage area. Journal of Applied Ecology 4 : 159-165.
- Warrington, I.J. (1986) Some effects of light and temperature on performance of kiwifruit. In Proceedings of Kiwifruit Seminar, Te Puke Horticultural Field-day Seminars. M.A.F. Tauranga, 6-7 November, 1985. pp 18-40.
- Whitfield, D.M. and Connor, D.J. (1980) Architecture of individual plants in a field-grown tobacco crop. Australian Journal of Plant Physiology 7 : 415-433.
- Whitfield, D.M. (1980) Interaction of single tobacco plants with direct-beam light. Australian Journal of Plant Physiology 7 :435-447.
- de Wit, C.T. (1965) Photosynthesis of leaf canopies. Agricultural Research Reports No. 663. Centre for Agricultural Publications and Documentation, Wageningen, The Netherlands. 57p.

## Appendix 1: Calibration of the Light Sensor

The system used for the measurement of the gap frequency in the canopy was based on the method of Green and Nicholson (1986). The instrumentation amplifier described by Green and Nicholson was found to be unnecessary and was removed from the system. To ensure that the output of the detector is linear with light intensity the system was calibrated against an Eppley radiometer. This appendix describes the procedure used for the calibration and the response of the sensor to light intensity.

For this calibration the Eppley was fitted with a collimator so that diffuse light from the sky was excluded from measurements. The collimator fitted in such a way that the Eppley was a large scale version of the detector actually used for measuring gap frequencies. This meant that the two sensors could be pointed at the sun and the calibration between the two sensors was made using comparable light.

The calibration was carried out with several different resistors. In the circuit the resistor is connected in parallel with the detector. There were two criteria for the selection of the resistor. The response of the detector had to be linear with increasing light intensity. The largest possible range of output voltages from the detector was sought.

The response obtained using a 3k8 resistor was found to fit these criteria best. The response of the sensor to light intensity is shown in figure A.1.

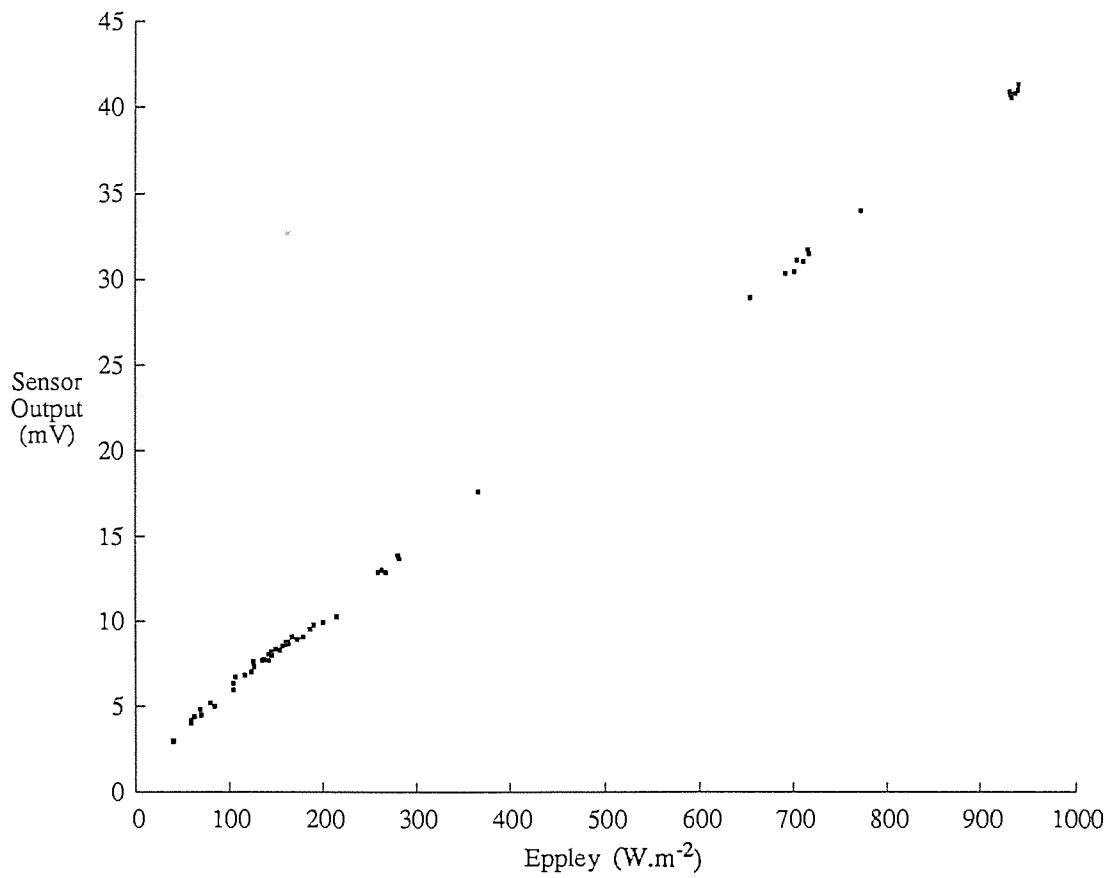


Figure A.1. The response of the detector used to measure light transmission in plant canopies. The calibration procedure is described in the text.

## Appendix 2: Sun Zenith Angle

The remote sensing procedure requires accurate estimates of the sun's zenith angle,  $\theta_p$ . A method for determining  $\theta_p$ , for any given geographical location, time of year and time of day is available in Spencer (1971) (cited by Green and Nicholson, 1986). This appendix gives the procedure used to calculate  $\theta_p$  for the remote sensing measurements (from Green and Nicholson, 1986).

The cosine of the sun's zenith angle is given by

$$\cos\theta_p = \sin(\text{dec}) \sin(\text{lat}) + \cos(\text{dec}) \cos(\text{lat}) \cos(\text{Th}) \quad (1)$$

where lat is the geographical latitude, dec is the sun's declination and Th is the sun's hour angle.

The sun's declination is given by

$$\begin{aligned} \text{dec} = & 0.006918 - 0.399912.\cos(\delta) + 0.070257.\sin(\delta) \\ & - 0.006758.\cos(2\delta) + 0.000907.\sin(2\delta) \end{aligned} \quad (2)$$

where dec is in radians. This estimates dec to within 0.005 radians. The angle  $\delta$  is defined in terms of the day number for the year, Dn (=0 for January 1), by  $\delta = (2\pi Dn)/365$ .

The sun's hour angle, Th, counts from solar noon. Th is symmetrical about the solar noon. The sun's hour angle is given by

$$\begin{aligned} \text{Th} = & \text{local apparent time} - 12 \text{ hours} \\ = & \text{clock time} + \text{long. corr.} + \text{Eq} - 12 \text{ hours} \end{aligned} \quad (3).$$

The longitudinal correction (long. corr.) amounts to 4 degrees for every degree of longitude east of the standard meridian (and then subtract any daylight saving time).

The equation of time (Eq) accounts for a difference between mean solar time and true solar time. The 'equation of time' (in radians) is given by:

$$\begin{aligned} \text{Eq} = & 0.000075 + 0.001868.\cos(\delta) - 0.032077.\sin(\delta) \\ & - 0.014615.\cos(2\delta) - 0.040849.\sin(2\delta) \end{aligned} \quad (4).$$

These equations are solved in the data logger to give  $\cos\theta_p$ .

### Appendix 3: Models of Canopy Gap Frequency

The effects of a non-random distribution of foliage on the gap frequency of a plant canopy can be estimated using theoretical canopy models. Binomial models can be used to predict the gap frequency of a canopy if information on the geometry of the leaves is known (e.g. Nilson, 1971).

In this analysis, canopy gap frequencies are predicted using the exponential and positive and negative binomial models. The case of the random canopy is given by (equation (4.6), page 57), a canopy with regular leaf dispersion is described by the positive binomial model (equation (4.7), page 57), and a canopy with a clumped leaf dispersion is described by the positive binomial model (equation (4.9), page 58). These gap frequencies are compared to those obtained by Warren Wilson (1971) who estimated the effect of leaf distribution on gap frequency using models in which the canopies were represented by disks arranged in different ways on a surface of known area.

The gap frequency for a random canopy is given by

$$\ln P_0 = -LG/\cos\theta_p \quad (1)$$

which is the exponential formula and where  $V'=1$ . For a canopy with a regular dispersion of leaves the gap frequency is given by

$$\ln P_0 = [1+\Delta L G/\cos\theta_p]^{-L/\Delta L} \quad (2)$$

which is the positive binomial formula and where  $V'<1$ . When the dispersion of leaves is clumped, the gap frequency is given by

$$\ln P_0 = [1-\Delta L G/\cos\theta_p]^{L/\Delta L} \quad (3)$$

which is the negative binomial formula and where  $V'>1$ .

An empirical coefficient can be incorporated into the exponential formula to account for the effects that non-random leaf dispersion can have on canopy gap frequency. This is the phytoelement distribution coefficient (Ross, 1981). The exponential formula then becomes

$$\ln P_0 = -LC_s G/\cos\theta_p \quad (4)$$

(Ross, 1981). The phytoelement distribution coefficient ( $C_s$ ) is related to the relative variance of the leaf dispersion in the canopy by the formula

$$-C_s = \ln V'/1-V' \quad (5)$$

(Ross, 1981).

If attention is confined to a canopy composed of flat leaves arranged on a horizontal surface, then the quantities  $G$  and  $\cos\theta_p$  both equal 1 and can be ignored. Thus the gap frequency in a random canopy is given by

$$P_0 = e^{-L} \quad (6)$$

where  $V'=1$ . Where the arrangement of the leaves is not random, then the gap frequency will change and can be described by the relationship

$$P_0 = e^{-L C_s} \quad (7).$$

For the simple canopy that we are considering here, the relative variance is related to the factor  $\Delta L$  in the binomial model by

$$V' = 1 + \Delta L \quad (8)$$

for the negative binomial model and by

$$V' = 1 - \Delta L \quad (9)$$

for the positive binomial model.

The gap frequency for a canopy with a regular dispersion of leaves is given by

$$P_0 = (1-\Delta L)^{L/\Delta L} \quad (10)$$

and for a canopy with a clumped leaf dispersion the gap frequency is given by

$$P_0 = (1+\Delta L)^{-L/\Delta L} \quad (11).$$

These relationships can be used to describe the inter-relationships between and the effects of the quantities  $V'$ ,  $C_s$  and  $\Delta L$  on the gap frequency of a canopy. The results of these calculations are given in table 4.1 and figure 4.4.