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Abstract This paper describes measurements of the architecture of a kiwifruit canopy grown on a pergola. The orientation of the leaves was analysed in terms of their inclination and azimuth angles. The mean leaf inclination was 33° from the horizontal and there was no significant relationship between leaf inclination and depth in the canopy. The azimuthal distribution of leaf area was not significantly different from that of a uniform distribution and there was no significant relationship between leaf azimuth and depth in the canopy. The contribution of leaves, wood, and reproductive organs to the total canopy area was estimated.

Keywords leaf area index; kiwifruit; *Actinidia deliciosa*; leaf angle

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INTRODUCTION

The architecture of a plant is that set of features which defines the size, shape, and geometry of the plant. In the course of a growing season a kiwifruit canopy progresses progresses from an array of leafless branches tied to a trellis, to a complete verdant canopy. The position and size of plants and their component parts, and the orientation of leaves all play significant roles in the interaction of the crop with the incident radiation.

The radiation regime within the canopy influences kiwifruit yield and quality. Grant & Ryugo (1984), Morgan et al. (1985), and Laing (1985) have shown that it affects flowering, leaf photosynthetic rates, fruit growth, water use, and temperature of plant organs.

This work describes measurements of the architecture of a kiwifruit canopy growing on a pergola. The contribution of leaves, wood, and flowers and fruit to the total canopy area was estimated. The orientation of the leaves was investigated and analysed. These results provide a statistical description of the angular distribution of the leaf area within the canopy volume. This information is essential for studies on radiation penetration into kiwifruit canopies.

Several experiments were performed to see if kiwifruit leaves track the sun. No evidence of significant heliotropic leaf movement was revealed. Experiments in dark rooms with directional light provided no evidence of leaves orienting in response to the light even after several days of exposure to light from various directions (Morgan 1988). For the work described in this paper, the effects of heliotropic movements on leaf orientation were assumed to be negligible.

DEFINITIONS

The leaf area index, L, is the ratio of the total plan area of leaves in a canopy to the area of the ground beneath. The downward cumulative leaf area index at a point, P, in the canopy is given by:

$$L(P) = \int_0^z \mu(P,z)dz \qquad (1)$$

where $\mu(P, z)$ is the leaf area density and z is height above the ground (z = 0 at ground level). The leaf area density is the leaf plan area (m^2) per unit canopy volume (m^3) with units of m^{-1}. If the leaves are distributed randomly over the horizontal plane, L is given by:

$$L = \int_0^z \mu(z)\, dz \qquad (2)$$

(Lang et al. 1985) and is the same for any profile through the canopy. A canopy area index can be determined and used for all canopy elements in the same way that the leaf area index is used for leaves.

The orientation of a leaf in a stand can be characterised by a vector with inclination, θ_L, and azimuth ϕ_L placed normal to the upper (adaxial) surface of the leaf as shown in Fig. 2. In most plants the adaxial surfaces of the leaves face the upper hemisphere so that θ_L varies between 0° and 90°, whereas ϕ_L varies between 0 and 360°. A two-dimensional probability function $g(\theta_L, \phi_L)d\theta_L, d\phi_L$, can be used to describe the fraction of the leaf area oriented with the inclination θ_L and the azimuth ϕ_L (Lemeur 1973). This function expresses the probability that a leaf has an inclination within (θ_L, $\theta_L + d\theta_L$) and an azimuth within ($\phi_L, \phi_L + d\phi_L$).

When the values of θ_L and ϕ_L are mutually independent, the two variables can be separated and $g(\theta_L, \phi_L)$ can be written as:

$$g(\theta_L, \phi_L) = g'(\theta_L).g''(\phi_L) \qquad (3)$$

where $g'(\theta_L)$ is a leaf inclination density function and $g''(\phi_L)$ is an azimuthal density function. Corresponding cumulative distribution functions can be obtained by integration giving:

$$G'(\theta_L) = \int_0^{\pi/2} g'(\theta_L')d\theta_L' \qquad (4)$$

$$G'(\phi_L) = \int_0^{2\pi} g''(\phi_L'')d\theta_L''$$

Proper selection of $g'(\theta_L)$ and $g''(\phi_L)$ will yield $G'(\pi/2) = G''(2\pi) = 1$ (Lemeur 1973).

The most obvious procedure for obtaining the distribution function of leaf area orientation is to measure the area, shape, angle, and position of every leaf by hand. It is usually impractical to obtain such information for each leaf so statistical sampling procedures are generally used instead.

METHODS

Site description

All measurements were made in a commercial orchard of kiwifruit (*Actinidia deliciosa* (A. Chev) C. F. Lang et A.R. Ferguson cv. Hayward) sited near Wanganui in the North Island of New Zealand (175°5 E long., 39°30'S lat.). The vines were planted, in 1981, with a row by vine spacing of 4.5 × 5 m. The rows are oriented approximately north to south. The orchard was first trained on a T-bar trellis, but in 1985 the training system was changed to a pergola. The leaf cover in different parts of the orchard was quite variable ranging in places from complete cover to areas with large gaps in the canopy. The orchard is divided into blocks of 70 plants. Each block is surrounded by a shelter belt that is c. 8 m in height. This work was carried out in a block of the orchard where the terrain was level.

When the first measurements were made in December 1986, the crop had about three-quarters of the final leaf area for the season and the plants had overlapped within and between the rows to form a closed canopy. When the measurements of canopy structure were made in the following 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. The canopies on Blocks 1 and 2 appeared to have a uniform distribution of leaf area in their canopies.

Sampling techniques

The aim of the programme was to obtain a statistical description of the architecture of a kiwifruit canopy. Canopy measurements were made in December 1986 and in February 1987. In December the plants were flowering whereas in February fruit had replaced the flowers and the male plants had been extensively pruned.

In December, 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.

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 cm^2 (internal cylinder diameter was 16 cm) extending from the ground to the top of the canopy. The bases of these cylinders were located at random on the ground in the sample areas. The measurements were made in 100 sample volumes on each occasion; 100 for the whole block in December, and 100 in each of the three small blocks in February.

The sample volumes were defined with the aid of a frame mounted on a camera tripod. This apparatus could be quickly and easily moved between sample locations. The frame was positioned beneath the canopy. Measurements could then be 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 in the sample if the junction of its lamina and 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, as described later. The cross-section area and height of branches, and flowers and fruit was recorded. A flower or fruit was included if the junction of the flower or fruit and its associated stalk was within the sample volume. 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.

Additional measurements of orchard leaf area index were made by removing leaves 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 lengths and widths.

Measurement of canopy area

The maximum length and width of every leaf within the sample volumes was measured. 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:

$$L_a = -8.6 + 0.99.L_w.L_l$$

where (L_a) is leaf area in cm^2, (L_w) is lamina width in cm, (L_l) is lamina length in cm, and $r^2 = 0.94$ (standard error of intercept = 1.46 and slope = 0.01).

The leaf area index of the canopy was also determined by leaf harvest. The leaves located within 16 randomly positioned 1 m^2 quadrats were picked for measurement. The leaves were dried for 3 days at 95°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 subsamples of harvested material that were selected at random from 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, United States). The leaves were then dried, as above. The conversion factor was 0.77 m^2 of leaf area/kg dry weight.

The lengths of branches within the sample volumes were measured along with width and the height above ground at which each passed into and out of the sample volume. The branches were assumed to be cylinders and the areas were obtained by multiplying length by diameter. The orientations of the branches were not measured. This technique for measuring the woody elements was fast but not very accurate (±20%). It was considered adequate because the area of the wood was small relative to the total foliage area.

The heights of the flowers and fruit were noted. Flowers with petals were assigned an area of 16 cm^2 and flowers without petals were assigned an area of 1.2 cm^2. The lengths of the fruit were measured. For simplicity they were assumed to be spherical with lengths equal to their diameters. This technique for measuring the silhouette areas of the reproductive organs is not very accurate (±15%) but the small contribution of the reproductive organs to the total canopy area justifies its use for our purposes.

The data on individual leaves were grouped according to their position in the canopy to see whether the average leaf size changed with depth in the canopy. Canopy "depth" was measured by downward cumulative leaf area index; each layer had a cumulative leaf area index of c. 1. The number of layers in February was four in Block 1, three in Block 2, two in Block 3; and in December there were two layers. This analysis was carried out separately for the measurements made in December and for each of the three blocks measured in February.

Measurement of leaf orientation

The leaf orientation data were obtained using an instrument made from a compass and a protractor as described by Norman & Campbell (1989) (see Fig. 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 were then read from the protractor and compass scales. Kiwifruit leaves are rarely completely flat so for these measurements the disk was aligned with the

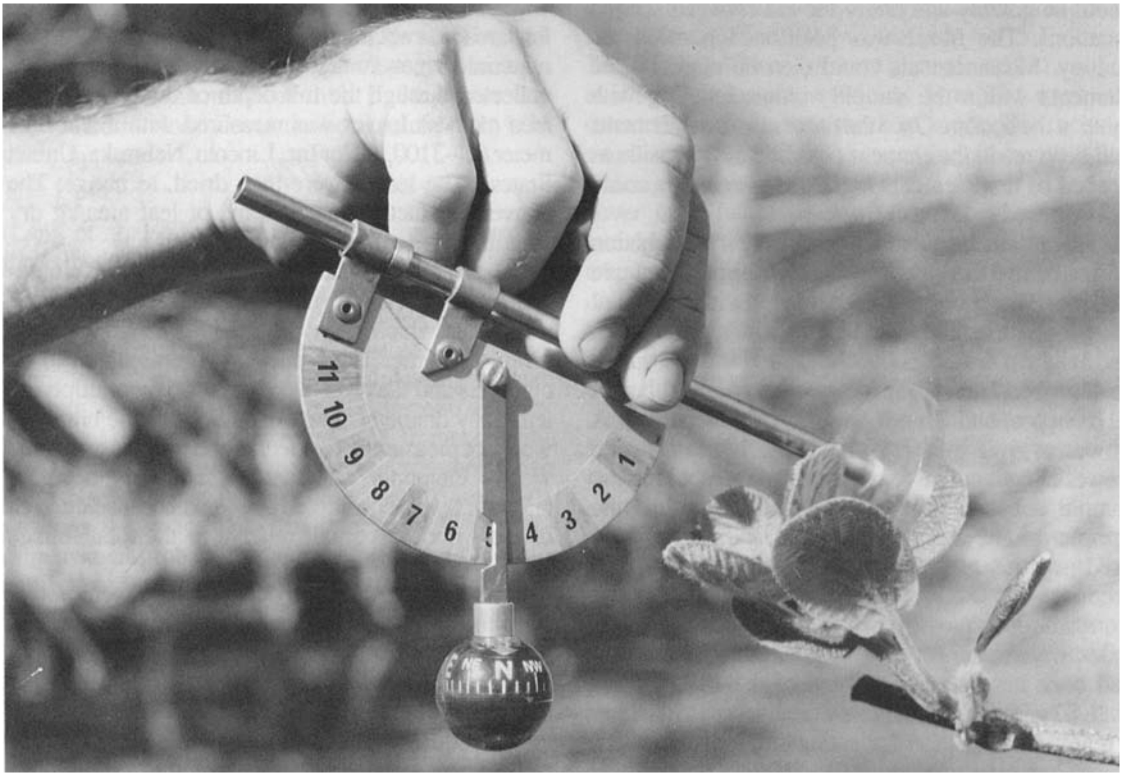

Fig. 1 Instrument used to measure the inclination and azimuth angle of the normal to the leaf surface. The rod approximates the normal to the leaf surface, and the perspex disc the leaf lamina. The inclination angle is read from the protractor and the azimuth angle from the ball compass. This instrument is similar to one described by Norman & Campbell (1989).

section of the lamina which represented the biggest flat section on the leaf. 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 orientation, and last the leaf dimensions. The leaves were not touched during the first two operations. The protractor-compass was found to be difficult to use in places where the leaves were close together. It was important to measure more accessible leaves before moving them aside to expose less accessible leaves.

Inclination was defined as the angle between the leaf normal and the vertical vector 0, z (Fig. 2); it was read from the protractor in Fig. 1. Leaf inclination was divided into six equal size angle classes of 15° each to cover the range $0 \leq \theta_L \leq 90°$. These classes were centred on $\theta_L = 7.5, 22.5, \ldots, 82.5°$. Azimuth was defined as the angle between the projection of the normal on the plane xOy and north (x = 0); it was measured using the compass on the instrument shown in Fig. 1. Azimuth was taken as positive in a clockwise direction about 0 (Fig. 2). For analysis, azimuth was subdivided into eight classes centred on $\phi_L = 0, 45, \ldots, 315°$. The proportions of leaf area in each of the 48 possible combinations of elevation and azimuth defined the distribution of leaf orientation.

The orientation data were used to determine the density functions for leaf inclination, $g'(\theta_L)$, and leaf azimuth, $g''(\phi_L)$. 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, $g''(\phi_L)$ (Lemeur 1973).

The leaf orientation data were analysed using a factorial analysis of variance, with the elements being leaf inclination and azimuth. Where another test was used the statistic is provided in the results. A 5% level of significance is used in all statistical analyses.

RESULTS

Canopy area

The contribution of leaves, wood and fruits to the area of the kiwifruit canopy determined by the sample volume measurements is shown in Table 1. The canopy area index for the areas of the leaves, branches and reproductive organs in the December 1986 measurements was 1.9 and in February 1987 was 3.5, 2.2, and 2.0 for Blocks 1, 2, and 3 respectively; in June 1987 the canopy area index was measured at 2.3 and 1.7 for Blocks 1 and 2 respectively. 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 contributed c. 92% of the total canopy area, the wood contributed 5%, and the fruit and flowers c. 3%. By June many leaves had fallen but leaves still composed over 90% of the total canopy area.

The vertical distribution of the canopy area measured in February is shown in Fig. 3. These are the averaged results from Blocks 1, 2, and 3. The vertical distributions of canopy area for the three blocks were similar. The highest foliage was 0.87 m above the trellis and the lowest was 1.14 m below the trellis. The maximum leaf area density is located in the first 0.2 m above the trellis, and most of the leaf area (c. 80%) is located in the first 0.6 m above the trellis. The branches are mainly located in a layer from 0.2 m below the trellis to 0.2 m above the trellis, although branches are present through the full depth of the canopy. Most of the fruit were found in the layer from 0.2 m below the trellis to 0.2 m above the trellis.

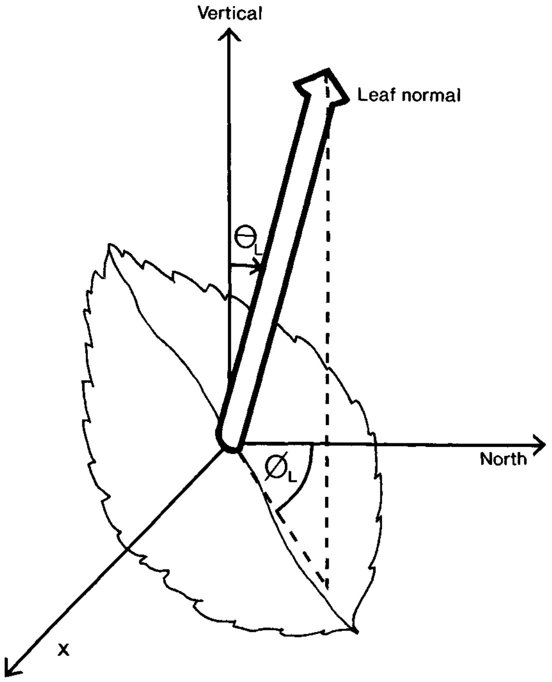

Fig. 2 Diagrammatic representation of the orientation (inclination and azimuth angles) of the normal to a leaf surface in the crop frame of reference. Full details are given in the text.

Table 1 Contribution of each component 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 plan area per unit ground area.

Block		Leaf	Wood	Fruit/flower	Total
Dec 1986		1.72 ± 0.14[a]	0.09 ± 0.02	0.09 ± 0.01	1.90 ± 0.15
Mar 1987	1	3.28 ± 0.22	0.13 ± 0.01	0.09 ± 0.01	3.50 ± 0.22
	2	2.02 ± 0.14	0.11 ± 0.01	0.06 ± 0.01	2.19 ± 0.14
	3	1.85 ± 0.17	0.09 ± 0.01	0.05 ± 0.01	1.99 ± 0.18
Jun 1987	1	2.2 ± 0.1	0.13 ± 0.01[b]	–	2.3 ± 0.1
	2	1.6 ± 0.2	0.11 ± 0.01[b]	–	1.7 ± 0.1

[a]Standard error.
[b]Estimates of wood area are assumed to be the same as those measured earlier in the season.

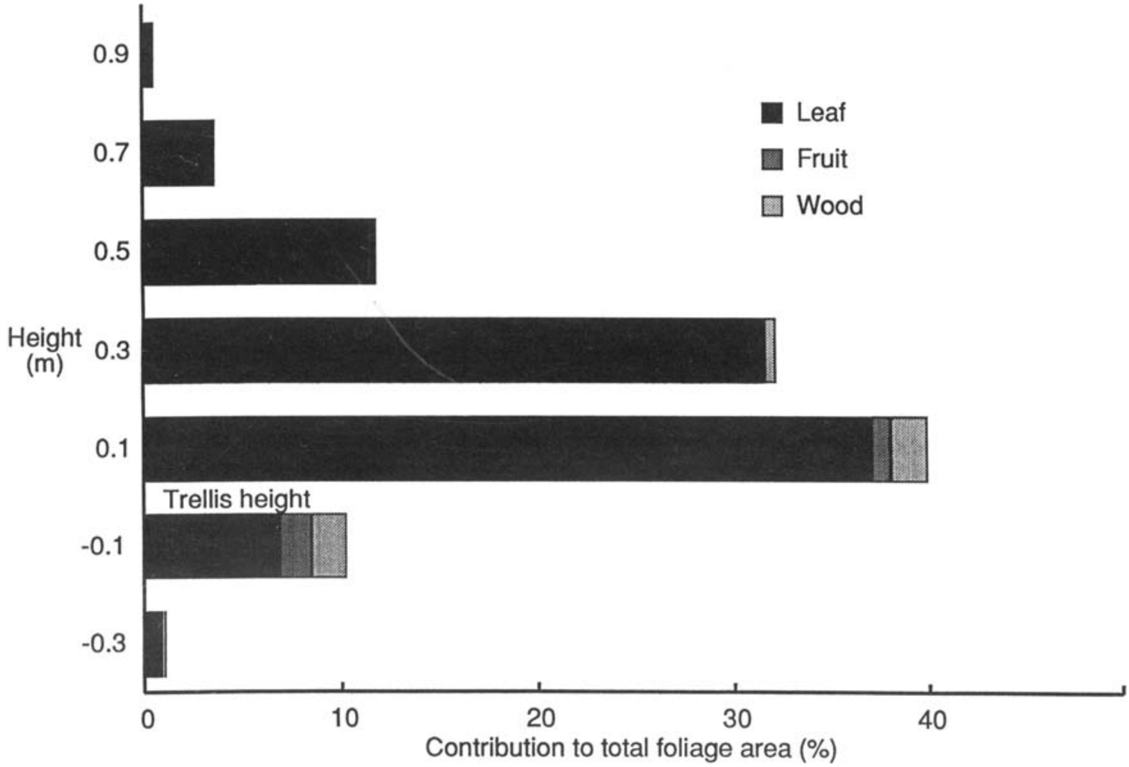

Fig. 3 Vertical distribution of the foliage in the canopy from the measurements made in March 1987. This figure shows the distribution of the leaves, wood, and reproductive organs that comprise the total foliage area and provides a visual representation of the results given in Table 1. The height of the foliage elements is relative to the height of the trellis (height = 0) on which the crop is growing.

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 was most marked in Block 1 where the mean leaf size in the lowest layer was 124 cm^2 and in the top layer it was 180 cm^2. In Blocks 2 and 3 the increase in leaf size between the two layers was from c. 120 cm^2 to c. 140 cm^2. In December the mean size was 97 cm^2 at the bottom of the canopy and 133 cm^2 at the top.

Leaf orientation

The leaf orientation data set was composed of four subsets, one from the set of measurements made in December and three from the three small blocks measured in February. These sets of data were analysed to see if there were significant differences between them. Leaf inclination and azimuth were compared among the four sets of measurements using the chi-square test.

No significant difference was found between the observed frequencies of leaf inclination angles (χ^2 = 21.18, 15 d.f.) or leaf azimuth angles (χ^2 =13.49, 21 d.f.) between the four subsets of data so the results were pooled for further study (Fig. 4).

Examination of the leaf orientation data (Fig. 4) 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.

Over 90° of the leaf area was found to be inclined at angles between 0 and 60°, with most of it (60%) in the range $15 < \theta_L < 45°$ (Fig. 5). Relatively small proportions of the leaf area were found in the classes centred on 62.5 and 82.5°. The mean leaf inclination for the pooled measurements is 33°. The vertical bars (standard error) in Fig. 5 show that there is little variation attributable to azimuth

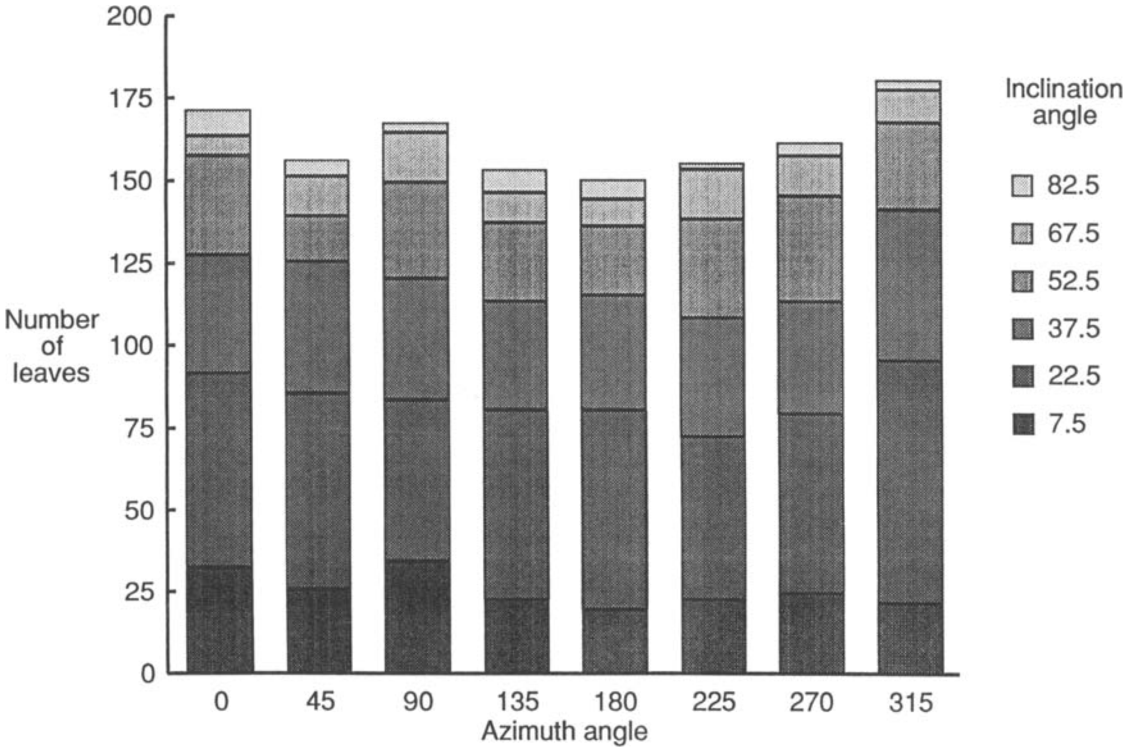

Fig. 4 Orientation of the leaves in a kiwifruit canopy. Columns represent the azimuthal classes of leaf orientation and are divided into six classes of leaf inclination.

in the proportion of foliage in any one class of leaf inclination.

The canopy has a nearly perfect random azimuthal distribution (this occurs when $g''(\phi_L)$ is constant for every value of ϕ_L) (Fig. 6). The azimuthal distribution of the leaves is not different from uniform ($\chi^2 = 4.55$, 7 d.f.); the slight trend for the leaves to orient toward the north is not significant.

The data were analysed to see if leaf orientations varied systematically with depth in the canopy. To do this, data on individual leaves were subdivided into horizontal layers on the basis of cumulative leaf area (as described earlier). The leaf inclination distribution functions were calculated for each layer but no significant differences were found between the different layers.

The whole data set was analysed to see if leaves of different sizes had different leaf inclinations. For this analysis the pooled data for the leaves was divided into four size classes: 0–75, 75–125, 125–175, and over 175 cm^2. The leaf inclination distribution functions were not significantly different between the different size classes ($\chi^2 = 22.61$, d.f. = 15).

The data were analysed to determine whether leaves of different sizes had different azimuth angles. For this analysis the pooled data for leaf orientation was divided into the same four size classes described above. The leaf azimuth distribution functions were not significantly different between the different size classes ($\chi^2 = 26.36$, d.f. = 31).

DISCUSSION

The maximum leaf area density was found in the middle layers of the canopy, and was slightly above the point where fruits and branches are concentrated. 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 (8–10 cm) and large laminae (average size 133 cm^2).

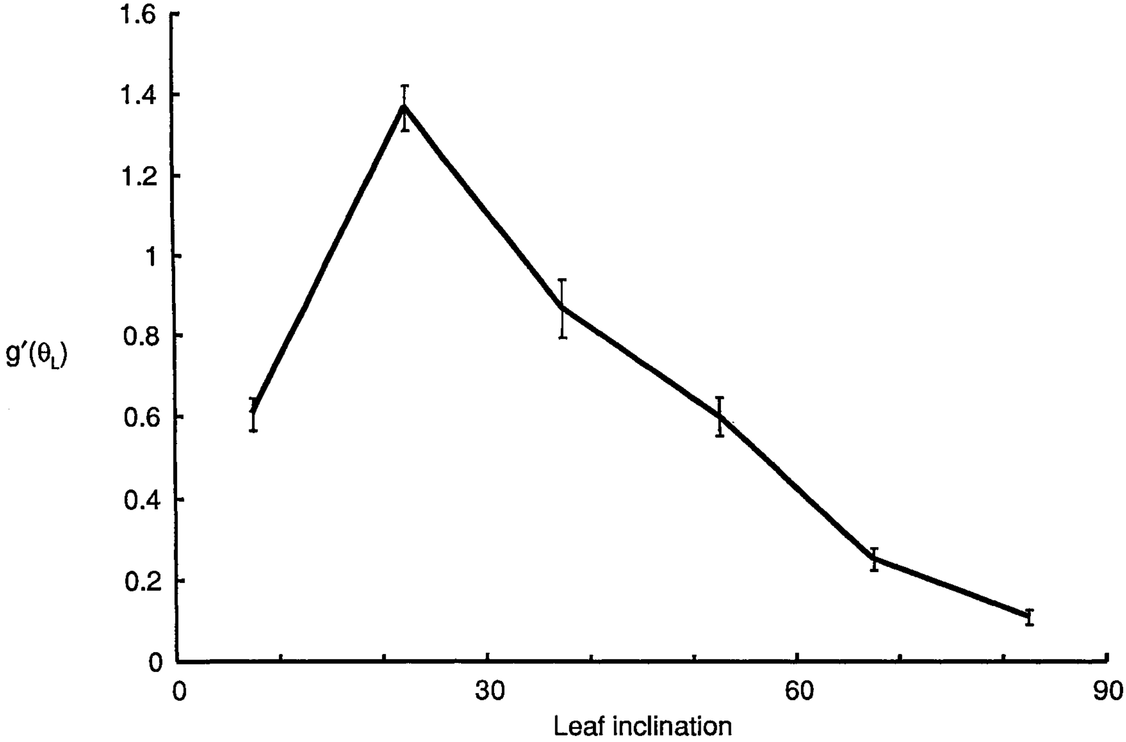

Fig. 5 Leaf angle distribution function calculated for kiwifruit from the orientation data presented in Fig. 4. Error bars show that there is little variation attributable to azimuth in $g(\theta_L)$. From Equation 4, the function $g(\theta_L)$ describes the probability of leaf normals falling within the inclination class described by the angle θ_L.

Observation of leaves and branches in the canopy suggests that laminae are able to grow into positions where they can improve exposure to light through bending and orientation of the petioles.

Leaf angles are inclined closer to the horizontal (more planophilic) than would be the case for a uniform distribution of leaf inclination angles. Kiwifruit with a mean leaf angle of 33° is similar to horse beans (30°, Ross & Nilson 1967), cucumber (c. 32°, Shell et al. 1974), sunflower (29°, Lemeur 1973; 35°, Shell et al. 1974; Shell & Lang 1975), lupin (27–37°, Scott & Wells 1969), and lucerne (31–35°, Scott & Wells 1969). The mean angle is less than that reported for tobacco (40°, Whitfield & Connor 1980), barley (44–53°, Scott & Wells 1969). It is much less than values reported for pepper (47°, Shell et al. 1974) and sorghum (c. 54°, Lang et al. 1985).

Leaf area was distributed uniformly with respect to azimuth. 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 & Nilson 1967), cucumber and young pepper plants (Shell et al. 1974), Jerusalem artichoke 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 T-bar trellises have an asymmetrical azimuthal distribution of leaf area, with leaves being oriented towards the inter-row gaps (Dr R. E. Smart, pers. comm.). With the apparent ability of kiwifruit leaves to orient themselves to improve light reception by phototropic leaf growth (but not heliotropic movements) this is perhaps to be expected as the leaves will orient themselves to the outside of the canopy and in a T-bar a large proportion of the canopy surface area will be facing the inter-row gaps.

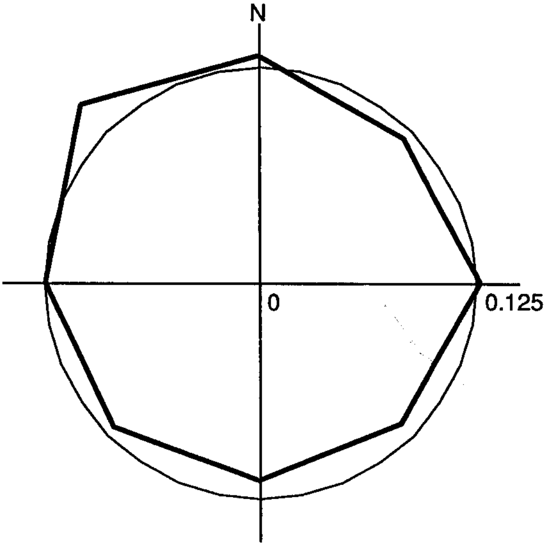

Fig. 6 Azimuthal density function for a kiwifruit canopy. Thick line represents the proportion of foliage in an azimuth distribution based on eight classes. Expected proportion in any one class on the basis of a uniform distribution with respect to azimuth is shown by the circle. North (N) is indicated.

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 symmetry.

The leaf angle distribution is not significantly 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 & Wells (1969) found that in barley the mean leaf angle varied from 44° near the top of the stand to 53° near ground level. For lupin the corresponding values were 27–37° and for lucerne were 35–31°. Lemeur (1973) reported that in sunflower the older leaves tended to be inclined at some angle between 20 and 30°, but the upper part of the canopy was extremely planophile, so that the younger leaves are more horizontal.

In conclusion, the distribution function of leaf area orientation in this kiwifruit canopy grown on a pergola was characterised by an absence of significant azimuthal variation and a mean inclination of 33°. There was no effect of leaf size or depth in the canopy on leaf orientation.

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