Abstract. 1. 5054 adult beetles of 144 species were collected in a total of 696 1-m² collecting trays by knockdown insecticide fogging of 36 different oak trees in closed canopy woodland at Richmond Park, U.K., with three of the trees sampled on each of 12 dates, at 2- to 3-week intervals, between April and October 1984.

2. In late spring (April/May), more individuals and species of beetles were collected in trays close to the trunks of trees than in trays more distant from the trunk. The reverse was the case in late September/October. Neither pattern prevailed in the intervening months.

3. Individual species exhibited a variety of patterns, with some species more abundant near the trunk, e.g. *Leiopus nebulosus* (L.), *Strophosoma melanogrammum* (Forster), *Cylindronotus laevioctostriatus* (Goeze), and *Dromius agilis* (Fabricius), and some less abundant near the trunk, e.g. *Curculio pyrrhoceras* (Marsham) and *Rhynchaenus signifer* (Creutzer). For *Adalia decempunctata* (L.), this preference changed with season. The observed species preferences for parts of a tree crown near or distant from the main trunk are discussed with reference to their known biologies.

4. No pronounced pattern of preference for north- or south-facing aspects of trees in closed canopy woodland was observed, however populations of some species exhibited patterns of within-tree distribution that correlate with compass angle; for one species, the ladybird *Adalia decempunctata*, this distribution changed with season and between colour morphs.

Key words. Beetles, canopy fogging, insecticides, oak, spatial distribution.

Introduction

The way in which insects form a community on particular plant species has been examined extensively (e.g. Southwood, 1960, 1961; Kennedy & Southwood, 1984), typically for non-woody biennials and/or annuals. In the last 15 years, many of the physical and logistical problems of studying communities associated with woody trees seem to have been overcome, especially those difficulties involved in obtaining adequate quantitative samples of insects. Recent advances have come primarily through the adoption of knockdown insecticide sampling (e.g. Moran & Southwood, 1982; Southwood et al., 1982a,b; Erwin, 1983a,b, 1990; Adis et al., 1984; Stork, 1987a,b, 1988, 1991; Basset, 1988, 1989, 1990, 1991a,b,c, 1992; Morse et al., 1988; Stork & Brendell, 1990, 1993; Stork et al., 1997). Despite this, with a few notable exceptions (Nielsen & Ejlersen, 1977; Barnard et al., 1986; Basset, 1992; Basset et al., 1992; Koponen et al., 1997; Reynolds & Crossley, 1997; Richardson et al., 1997), knowledge of the basic spatial distribution of insects within trees is scant, coming largely from anecdotal observations, coupled with knowledge of resource requirements of individual species.

European deciduous oaks *Quercus* are among the best known trees in terms of their associated invertebrate faunas (Morris & Perrin, 1974; Patoëka et al., 1999; Hammond & Owen, in press). The beetle fauna of Richmond Park near London, U.K., and in particular of its oak trees, is extremely
well known, with more than a quarter of all 4000+ British species having been recorded there in the last 20 years (Hammond & Owen, in press). In 1984, an intensive arthropod sampling programme using knockdown insecticides was carried out from April to November to examine the arthropod community structure of oak trees in Richmond Park (Stork, 1988; Stork & Hammond, 1997). Barnard et al. (1986) examined the spatial distribution of species of neuropteroids collected as part of this sampling programme and found that Nothochrysa capitata, Sympherobius pellucidus, and Hemerobius humulinus were more abundant in collecting trays positioned near the trunk of fogged trees than in trays positioned towards the edge of the crown.

The work reported here was designed to investigate spatial patterns of the canopy beetle fauna on Richmond Park oak trees, examining whether some species of beetles are associated more closely with the trunk region or outer parts of trees, whether beetles prefer a particular sector of a tree, e.g. the northern or southern part, and whether these preferences change during the year. Where possible, explanations for these patterns are suggested based on the known biology of the beetle fauna.

Methods

Field site and sampling

Three different mature oak trees were fogged every 2 or 3 weeks (depending on suitable weather conditions) on 12 separate occasions between April and October 1984, with a total of 36 different trees sampled overall (26 April (fog 1), 15 May (2), 30 May (3), 12 June (4), 26 June (5), 11 July (6), 25 July (7), 14 August (8), 1 September (9), 11 September (10), 26 September (11), 16 October (12)). Oak trees sampled at the study site were situated in woodland with semi-continuous canopy broken by small to large gaps, both natural and man-made, the most significant being the 5–15 m wide ride running NW–SE across the NW of the wood. Fuller details of the sampling programme, including sampling dates, site map, tree information, and weather conditions, were given by Stork and Hammond (1997).

Arthropods were collected by applying a 1% solution of knockdown insecticide (a synthetic pyrethroid, Reslin E), using an insecticide fogger (Swing Fog SN11), to the canopies of mature oak trees Quercus robur in Richmond Park. Specimens were collected on a series of circular, funnel-shaped, 1-m² trays distributed below the canopy of the sample trees. Ropes were strung at chest-height between available tree trunks from which 12–21 trays were suspended. The trays were not spaced regularly but an attempt was made to ensure that they were positioned such that collections were made from under most areas of the focal tree’s crown. All beetles were extracted from the samples and identified to species.

The horizontal distance from the centre of each tray to the tree trunk (measured to the nearest 0.1 m) and the compass position of each tray in relation to the tree trunk were recorded. No attempt was made to measure the distance of trays from the canopy edge, as tree crowns were of irregular shape. A plan diagram was drawn for each tree showing the arrangement of the trays (Fig. 1).

Statistical analysis

Distance from the trunk of the tree. In order to examine the relationship between beetle abundance and distance from the trunk, beetle abundance was divided into five distance classes: 0–1 m, 1–2 m, 2–3 m, 3–4 m, and 4–5 m. The compass orientation of each tray was recorded in degrees, and the compass orientation was divided into 15° sectors: N, NW, W, SW, S, SE, E, and NE. The abundance of each species was calculated as the number of individuals collected in each distance class and compass orientation sector. The abundance of each species was then tested for significant differences using ANOVA, with distance class and compass orientation as independent variables. The relationship between beetle abundance and distance from the trunk was tested using regression analysis. The regression analysis was performed separately for each species, and the significance of the regression coefficient was tested using the F-test.

Fig. 1. Spatial distribution of collecting trays (open circles) beneath a representative fogged tree in terms of (a) proximity of tray to tree trunk (outer canopy (distance classes indicated by concentric rings)) and (b) compass orientation with respect to the tree trunk (with the tree trunk as centre point).
trunk of the tree, the collecting trays were allocated to the following classes according to the distance measured from the centre of the tree to the nearest point on the trunk: class 1 = 0–1 m, class 2 = 1.1–2 m, class 3 = 2.1–3 m, class 4 = 3.1–4 m, class 5 = 4.1–5 m, class 6 = >5.1 m (Fig. 1a).

The logarithms of overall adult beetle abundances and of beetle species number for each tray were correlated against their distribution in the six distance classes. While this approach has some limitations, the data generated in this study were not suited to analyses using univariate t-tests or ANOVA because of the high level of variation observed in abundances and distribution among sampled trees. This was established through multivariate analyses (not presented here) using PATN: Pattern Analysis Package (Belbin, 1995).

Patterns of spatial distribution were assessed by plotting relative beetle abundance (log \( n_i/n_{tot} \); where \( n_i \) = number of beetles in a tray, \( n_{tot} \) = mean number of beetles in all trays for a given tree) against tray distance class to determine whether beetles were distributed uniformly throughout the crown.

**Beetle preference for compass sectors of the canopy: angle of preferred distribution.** The compass angle of each tray with respect to the tree trunk was measured to the nearest 5° and each tray was allocated to one of the 12 30° sectors on the compass (Fig. 1b). The number of trays in each sector was uneven (mean \( n = 58 \)), with a minimum number of 35 trays in any compass sector across the 12 sampling dates. To ensure even sampling of trays across compass sectors, the beetle frequency of 10 replicate samples of 35 trays was selected randomly for each sector from the data set using SPSS 8.0 (1997). Circular distribution mean angle analyses, as described by Zar (1996) and summarised in the Appendix, were used to determine the distribution of beetles with respect to compass sectors in the canopy.

A mean angle (i.e. compass direction) was determined for each of the 10 replicate data sets (Appendix: eqns 1–8) and a second-order mean of means was calculated (eqns 9–32). The mean of means angles were tested to determine whether the populations of beetles displayed significant mean direction using a parametric one-sample second-order analysis of angles (eqns 33–36). In this way, the angle of preferred direction was calculated for all beetles and individually for the seven commonest species: Dromius quadriracimatus, Dromius quadrimaculatus, Dalopus marginatus, Phyllobius argentatus, Strophosoma melanogrammum, Adalia bipuncata, and Adalia decempunctata. Adalia decempunctata was collected in large enough numbers for analyses of seasonal variation in compass distribution and variation in the compass distribution of its three main colour morphs. The morphs recognised are the typical form (t) – reddish-yellow with small dark spots, the dark or melanic form (d) – largely black with one or more small pale patches, and the intermediate or socks form (s) – many pale spots on a dark background (see Majerus, 1994).

For seasonal analyses, samples were grouped (e.g. fogs 1 and 2, fogs 3 and 4, etc.). Because there were insufficient data for replicated analysis of means as described above, for each of the six resultant groups, a single mean angle, angular dispersion value, and 95% confidence limits for the mean were calculated for each group. Rayleigh’s test was performed to test whether beetle populations were distributed uniformly around the tree (eqns 7–8).

**Results**

**Beetle abundance**

A total of 5054 adult beetles (144 species) and 575 beetle larvae was collected on 696 1-m² trays under the 36 trees sampled on the 12 occasions from April to November, representing an average of 8.09 adult and larval beetles per tray (SD = 7.5), with a maximum of 51 in any 1-m² tray. There were no beetles in 37 of the 696 trays. There was an average of 4.24 species per tray (SD = 3.00, maximum number in a tray = 17), 18.88 species per tree (for an average 13-m² catch), and 33.25 species per fogging occasion (39-m² catch from three trees). Seasonal variation in abundance of individuals and species was considerable. In addition, there were sometimes substantial differences among trees fogged on the same occasion, in part because there were sometimes large differences in the flowering, leaf, and fruiting phenology of the oak trees sampled on each occasion.

**Abundance and species number in relation to distance from the tree trunk**

On average, more adult beetles were found in trays close to the trunks of trees (distance class 1 mean = 11.14) than in trays closer to the edge of the canopy (distance class 6 mean = 7.78) (Table 1). When relative beetle abundance for each of the 696 trays used throughout the sampling period was plotted against tray distance class, the plot had a significant negative slope (regression coefficient = −0.009, SD = 0.002, correlation coefficient = −0.205, \( P < 0.001 \)), indicating greater numbers of beetles in trays closer to the trunk of the tree. When all trays in distance class 1 were excluded, however, the slope was reduced and was not significant (regression coefficient = −0.002, SD = 0.002, \( P > 0.05 \)). This suggests that for the 6-month sampling period as a whole there were, on average,

**Table 1.** Mean number (M) of adult beetles and beetle species per tray in different distance classes (D) from trunk of tree to outer canopy. \( n \) = number of trays for each distance class, SD = standard deviation of the mean.

<table>
<thead>
<tr>
<th>D</th>
<th>( n )</th>
<th>M</th>
<th>SD</th>
<th>M</th>
<th>SD</th>
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<tbody>
<tr>
<td>1</td>
<td>111</td>
<td>11.14</td>
<td>9.25</td>
<td>5.47</td>
<td>3.56</td>
</tr>
<tr>
<td>2</td>
<td>167</td>
<td>7.01</td>
<td>5.69</td>
<td>3.88</td>
<td>2.42</td>
</tr>
<tr>
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<td>146</td>
<td>7.80</td>
<td>7.10</td>
<td>4.21</td>
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<tr>
<td>4</td>
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<td>7.52</td>
<td>6.78</td>
<td>3.92</td>
<td>2.87</td>
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<tr>
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<td>85</td>
<td>7.81</td>
<td>7.00</td>
<td>4.09</td>
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<td>7.78</td>
<td>7.68</td>
<td>3.88</td>
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</table>

significantly more beetles in trays close to the trunk of the sampled trees than in trays away from the tree trunks.

For nine of the 36 trees sampled, the regression coefficient of the mean number of beetles per tray against distance class was significant. The regression coefficient for 29 trees was negative, of which seven were significant (i.e. a preference for the tree trunk), while seven trees exhibited positive slopes, of which two were significant (i.e. a preference for the outer canopy) (Fig. 2a). Plotting the regression coefficients for each tree for the log number of beetles per tray against distance class showed a similar trend (Fig. 2b). The regression coefficients for log species number and for log abundance were highly correlated (correlation coefficient $= 0.84$, $P < 0.001$).

Abundance of individual species in relation to distance from the tree trunk

The relationship of abundance to distance from the trunk of the tree was investigated for adults of 27 of the most common species of beetle collected throughout the year and for the most common larvae (Table 2).

There were no clear relationships between abundance and distance from the trunk for many species, including representatives of the leaf-chewing phytophage guild [e.g. Cryptocephalus pusillus Fabricius, Phyllobius argentatus (L.), P. pyri (L.)], and other foliage or flower-associated species [e.g. Curculio glandium Marsham, C. venosus (Gravenhorst), Malthinus flavomarginatus (Lateille), Anaspis lurida Stephens, A. maculata Fourcroy, and A. regimbarti Schilsky].

A number of species was found to have a significant positive association with the trunk (see Table 2), i.e. their abundances were highest in the trays closest to the trunk. These include the cerambycid *Leiopus nebulosus* (L.), the weevil *Strophosoma melanogrammum* (Forster), the tenebrionid *Cylindronotus laevioctostriatus* (Goeze), and the carabid *Dromius agilis* (Fabricius). The positive association of adult *L. nebulosus* with the trunk is consistent with their bark-like cryptic markings. *Strophosoma melanogrammum* adults feed on shoots and leaves of a wide range of deciduous and coniferous trees (Bevan, 1987), moving at certain times of the year to different tree species when their leaves are most palatable. Adults are completely apterous, so tree to tree movements may entail ground crossings to other tree trunks. This species is also rather bark-like in its colouration. Another flightless species, the tenebrionid *C. laevioctostriatus*, is a nocturnal epiphyte grazer/scavenger, commonly found under loose bark of logs and tree trunks during the day. The highly significant relationship found for this species probably reflects a real preference for the tree trunk where the algae on which the adults feed are mostly found. *Dromius agilis* appeared to be virtually confined to the main trunk of the focal trees. Both the adults and larvae of this species are known to forage on trunks at night and conceal themselves on trunks during the day. Similarly, most of the large beetles collected were distributed close to the trunk of the focal trees [e.g. the carabid *Agonum assimile* (Paykull), the clerid *Opilo mollis* (L.), the elaterid *Stenagostus villosus* (Fourcroy), and the lymexylonid *Lymexylon navale* (L.)]. *Agonum assimile* (Paykull) is a nocturnal woodland-floor predator that is known to rest during the day under loose bark and in crevices on tree trunks (Cook, 1987). *Opilo mollis*,

![Fig. 2. Regression coefficients of (a) log total number of individual beetles per tray and (b) log total number of beetle species per tray, against distance from trunk, and against time of year, for each of 36 trees sampled (on 12 dates between April and October). Significant regression coefficients are indicated with circles.](image-url)
S. villosus, and L. navale, are all saproxylic species and are intimately associated with tree trunks or decaying wood. Many of the rarer saproxylic species regarded as indicators of ancient woodland conditions (Harding & Rose, 1986), while being collected in small numbers, were also only found close to tree trunks [e.g. the elaterid Agrilus pannonicus (Piller & Mitterpacher), the latridiid Corticaria alleni Johnson, the scraptiid Scraptia testacea Allen, the colydiid Synchita humeralis (Fabricius), and the tetratomid Tetrautom flapresti Latreille].

Table 2. Regression coefficients (R) for the commonest species of beetles for number of individuals in trays against each distance class from the trunk of the sampled trees. *P<0.05, **P<0.01, ***P<0.001. T = trunk, OC = outer canopy.

For the coccinellid Adalia decempunctata (L.), there were sufficient data to carry out a seasonal analysis of adult beetle trunk/canopy preferences (Table 2), this species preferring the outer canopy in April and May and being spread more evenly at other times of the year.

The weevils Curculio pyrrocera Marsham and Rhynchaenus signifer (Creutzer) were both present in reasonable numbers in all parts of the tree but were significantly more abundant in trays nearer the canopy edge (Table 2). Another weevil, Phyllobius pyri (L.), on the other hand, was not

Fig. 3. Mean compass angle of distribution of beetles within oak trees with 95% confidence limits (north at top of page).
associated significantly with either the trunk area or the canopy edge but appeared to be more abundant at an intermediate distance between the trunk and the outer canopy.

**Beetle preference for compass sectors of the canopy: angle of preferred distribution**

Of the seven species examined, all except *A. bipunctata* showed significant population directionality (Fig. 3). For most of these, the confidence limits for the mean were narrow, signifying a narrow distribution of individuals around that compass sector. All three morphs of *A. decempunctata*, both separately and combined, and larvae of *A. decempunctata*, also exhibited significant population directionality but the mean direction of these species and groups varied considerably. For example, *D. quadrimaculatus*, *D. marginatus*, *S. melanogrammum*, and *A. decempunctata* morph (d) all displayed significant north-west through to north-easterly mean population directionality, whereas *A. decempunctata* morph (t), *Adalia* larvae, and total *A. decempunctata* adults all had significant southerly mean population directionality.

The distribution of individuals of *A. decempunctata* within the canopy appeared to vary during the year, as indicated by different mean directionalities (Fig. 3b): fogs 1 and 2 (26 April/15 May) south-westerly, fogs 3 and 4 (30 May/12 June) easterly, fogs 5 and 6 (26 June/11 July) westerly, fogs 7 and 8 (25 July/14 August) easterly, fogs 9–12 (1 September/11 September/26 September/16 October) no significant mean direction. *Adalia decempunctata* larvae also displayed a variety of mean population directions at different seasons: fogs 3 and 4 north-easterly, fogs 5 and 6 south-westerly. At other sampling times, no significant mean directionality was found, indicating a more uniform larval distribution.

**Discussion**

The data presented here indicate several patterns of beetle distribution within British oak trees in closed canopy woodland at the time of greatest insect abundance and activity from April to October: (1) some beetle species are more closely associated with the trunk of a tree; (2) others are associated with the outer parts of a tree crown; (3) some species of beetle prefer particular compass sectors of a tree; (4) the distribution patterns (and hence trunk/canopy/compass preferences) for some species change during the year.

As Basset (1992) has shown, there is an enormous range of variables that ultimately influence the spatial distribution of beetles within the crown of an individual tree. The distribution patterns reported here may reflect preferences for the surface of the trunk and large branches or for dense foliage, for warmer or cooler, lighter or shadier parts of the tree. These preferences may in turn reflect particular microclimatic and microhabitat requirements and availability of food resources such as pollen, flowers, fresh leaves, lichens/algae, particular prey species or even availability of enemy-free space.

The complicated patterns of variation in the distribution of individuals of a species at different times of the year is best exemplified by the results for one of the most abundant species, the ladybird *A. decempunctata*. In the early part of the year, adults of this species showed a preference for the outer canopy and for west-facing parts of trees, presumably seeking the warmer parts of trees in search of aphids. Later in the year, there was no clear preference for the outer canopy and the compass preference moved to the east. It appears, however, that the three colour morphs that make up the adult population have different preferences for parts of the tree and that these change during the year: morphs s and t at the beginning of the sampling programme both showed a preference for the west; morph t changed to a south-east preference in fogs 3–4, while morph d exhibited a north-east preference at this time, changing to a south-east preference in fogs 5–6. Non-significant mean directions at other times of the year either indicate no real preferred direction or that if such a preference exists there were insufficient data to reveal such patterns. *Adalia decempunctata* larvae also appeared to exhibit changes in their distribution in the trees observed, as the mean directions changed from north-easterly to south-easterly from cafes 3–4 to cafes 5–6. Geographical variation in the relative incidence of individual morphs of polymorphic ladybird species is well known, and a correlation between high incidence of melanic or dark morphs and low sunshine levels has been reported for several species (Majerus, 1994). Differences in the within-tree distribution of the principal morphs of *A. decempunctata* may also be explained by a greater ability of the darkest individuals to operate in conditions of lower temperature and/or less sunshine. Variation over time may reflect the pattern of adult foraging, seeking out concentrations of aphids that are most likely to be found near points of active growth on the focal trees.

This study demonstrates that careful attention to sampling design is required when carrying out ecological studies of arthropod communities on trees. The arthropod composition of catches will reflect only the arthropod faunas of the parts of the tree sampled, as discussed above. In addition, sampling artefacts, such as leaning of a few tree trunks, asymmetric distribution of foliage, variation in epiphyte load, or the chance occurrence of a single large bracket fungus on a tree, may also distort the picture. Some variation may be due to the genetic variability of the trees or variation in their environment (e.g. soil quality, exposure, etc.). Some individual oaks are more advanced, seasonally, than others (see also Hunter, 1992), sometimes by a matter of several weeks. Surrounding vegetation may also affect faunal load and distribution, particularly for some trees where birch formed an under-canopy. Some beetles, such as members of the broad-nosed weevil phytophage guild (e.g. *Phyllobius*, etc.), move naturally from one species of tree to another (e.g. from birch to oak) at particular times of the year, depending on the palatability of leaves [see Bale (1981) for similar movements between different species of trees for *Rhynchaeus fagi* (L.)]. Birch loses its leaves before oak, and some species therefore move to oak in the autumn. Such movements can alter the abundance and distribution of some species greatly. For
example, in the October/November fogs, the commonest species of Hemiptera collected were species that normally feed on birch (W. R. Dolling, pers. comm.). Stork and Hammond (1997) have also shown that the arthropod fauna collected from trees changes with time of day; early evening samples have more transient (tourist) species than morning samples.

Another possible confounding factor is the influence of edge effects. Murcia (1995) predicted, on theoretical grounds, that there should be bimodal patterns in edge effects. This was confirmed by Didham (1996), who found that in Amazonian lowland rainforest there are two peaks in abundance for leaf litter beetles, one within the first few metres from the edge, the other less than 100 m from the edge. With many trees having canopy widths of tens of metres, within-tree distribution may be complicated by such broad-scale edge effects, particularly in an open woodland with frequent tree gaps such as that at Richmond Park. Finally, it is to be expected that within-tree variation in the abundance of various beetle species is likely to be both more marked and more consistent in pattern in free-standing trees than in continuous woodland. The individual trees sampled at Richmond Park varied substantially in their degree of isolation from neighbouring trees and the extent to which parts of their crowns were exposed. Such differences, rather than seasonal effects per se, may explain some of the differences between sampling dates that are reported above.

In north temperate forests, the low angle of the sun, particularly early in the year, means that the southern parts of the tree are likely to be sunnier and warmer than northern parts. In an earlier unpublished study, N. E. Stork and P. M. Hammond found that almost twice as many beetles were collected after application of knockdown insecticides on the south side of an isolated oak tree than on the north side. Richardson et al. (1997) also found that there were such north/south differences in insect abundance in small trees sampled in forests outside Sydney, Australia. The shift in beetle preference for the more northerly parts of oak trees in May and early June may be related to changes in the light and heat regime such that more beetles were seeking darker, cooler parts of the canopy.

Acknowledgements

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References


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Appendix: Summary of the calculations required to determine the mean angle for beetle distribution in the canopy of oak trees (see Methods: after Zar, 1996)

Part A

Equations 1–8 - Mean angle of each beetle taxon or morph:
The mean angle for each beetle taxon analysed was calculated as follows where $a_i$ is each angle in degrees and $n$ is the number of ‘angles’ (i.e. trays).

\[
X = \sum_{i=1}^{n} \cos a_i / n \\
Y = \sum_{i=1}^{n} \sin a_i / n
\]  

(1)

(2)

\[ r = \sqrt{(X^2 + Y^2)} \]  

(3)

\[ \cos \bar{a} = X/r \]  

(4)

\[ \sin \bar{a} = Y/r \]  

(5)

Angular dispersion/deviation (analogous to a linear standard deviation). Value range is from a minimum of 0° to a maximum of 81.03°

\[ s = \left( \frac{180°}{\pi} \right) \sqrt{2(1 - r)} \]  

(6)

Rayleigh’s R – Rayleigh test. $H_0 = \text{the sampled population is uniformly distributed around the circle (canopy)}$:

\[ R = nr \]  

(7)

Rayleigh z test – $H_0 = \text{no population mean direction}$:

\[ z = \frac{R^2}{n} \text{ or } z = \frac{(nr)^2}{n} \]  

(8)

Equations 9–32 - Second-order analysis: The mean of mean angles:

\[
\bar{X} = \sum_{j=1}^{k} X_j / k
\]  

(9)

\[
\bar{Y} = \sum_{j=1}^{k} Y_j / k
\]  

(10)

Having obtained $\bar{X}$ and $\bar{Y}$, they are substituted for $X$ and $Y$ respectively into eqns 3, 4, and 5 to determine $\bar{a}$, which is the grand mean

95% confidence limits for the second-order mean angle (mean of a set of mean angles):

\[
X_j = r_j \cos \bar{a}_j
\]  

(11)

\[
X_j = r_j \sin \bar{a}_j
\]  

(12)

Where $X_j$ and $Y_j$ are the quantities $X$ and $Y$ respectively applying eqns 1 and 2 to sample $j$; $k$ is the total number of replicates or samples.

\[
\Sigma x^2 = \sum_{j=1}^{k} X_j^2 / k - \left( \sum_{j=1}^{k} X_j \right)^2 / k \]  

(13)

\[
\Sigma y^2 = \sum_{j=1}^{k} Y_j^2 / k - \left( \sum_{j=1}^{k} Y_j \right)^2 / k \]  

(14)

\[
\Sigma xy = \sum_{j=1}^{k} X_j Y_j / k - \left( \sum_{j=1}^{k} X_j \right) \left( \sum_{j=1}^{k} Y_j \right) / k \]  

(15)

\[
A = (k-1) / \Sigma x^2
\]  

(16)

\[
B = (k-1) \Sigma xy / \left( \Sigma x^2 \Sigma y^2 \right)
\]  

(17)

\[
C = (k-1) / \Sigma y^2
\]  

(18)

\[
D = \left[ 2(k-1)[1 - \left( \Sigma xy / \Sigma x^2 \Sigma y^2 \right)] \right] F_{(1,2,k-2)} / \left( k(k-2) \right)
\]  

(19)

\[ H = AC - B^2 \]  

(20)

\[ G = A X^2 + 2B X Y + C Y^2 - D \]  

(21)

\[ U = H X^2 - CD \]  

(22)

\[ V = \sqrt{DH} \]  

(23)

\[ W = H X Y + BD \]  

(24)

\[ b_1 = (W + V) / U \]  

(25)

\[ b_2 = (W - V) / U \]  

(26)

The quantities $b_1$ and $b_2$ are then examined separately, each yielding one of the confidence limits:

For $b_1$

\[ M = \sqrt{1 + b_1^2} \]  

(27)

\[ \sin = b_1 / M \]  

(28)

\[ \cos = 1 / M \]  

(29)

For $b_2$

\[ M = \sqrt{1 + b_2^2} \]  

(30)

\[ \sin = b_2 / M \]  

(31)

\[ \cos = 1 / M \]  

(32)

Part B

Equations 33–36 - Second order mean of means testing:

\[
\sum_{j=1}^{k} x^2 = \sum_{j=1}^{k} X_j^2 - \left( \sum_{j=1}^{k} X_j \right)^2 / k
\]  

(33)

\[
\sum_{j=1}^{k} y^2 = \sum_{j=1}^{k} Y_j^2 - \left( \sum_{j=1}^{k} Y_j \right)^2 / k
\]  

(34)

\[
\sum_{j=1}^{k} xy = \sum_{j=1}^{k} X_j Y_j - \left( \sum_{j=1}^{k} X_j \right) \left( \sum_{j=1}^{k} Y_j \right) / k
\]  

(35)

Test $H_0 = \text{no mean direction}$:

\[ F = \left[ (k(k-2)/2) \right] \left( \sum x^2 \sum y^2 - 2 \sum x \sum y + \sum y^2 \right) / \left( \sum x^2 \sum y^2 - \left( \sum xy \right)^2 \right) \]  

(36)

With the critical value being the one-tailed $F$ with 2 and $k-2$ degrees of freedom.