3

Basic Concepts and Terms

3.1 Definitions and the basis of the method

The assimilation of organic matter by a plant community during a certain specified period (e.g. one year), including the amount used up by plant respiration, is called the *gross primary production.* Gross production minus respiration or the formation of plant tissues and reserve substances during the period is the *net primary production,* which may be known simply as primary production. When production is measured as dry weight it includes some mineral salts incorporated into the products of photosynthesis. If ash content is estimated and excluded, or some method is used which estimates only the formation of organic compounds, then *organic production* should be specified. In this Handbook the term production will be used as referring to net annual primary dry matter production unless otherwise specified. The IBP researches to which this Handbook is directed are mainly concerned with net primary production but more developed programmes are likely to involve estimation of other quantities as well.

IBP News 2 (Feb. 1965, p. 12) states: 'A general starting point for comparing photosynthetic primary production is the cumulative course of "net assimilation" (net dry matter production of green parts) over the year(s) or vegetation period(s). This can be determined by the sum total of the following features determined periodically through the year:

(a) Biomass change of photosynthetic plants;

(b) Plant losses by death and the shedding of parts above and below ground;

(c) Man's harvest (in some cases);

(d) Consumption of photosynthesizing plants by animals (botanical and zoological methods will be used to estimate amount lost).'

The unit of study will commonly be a whole biological system, i.e. the sum total of standing crops, which are the populations of living organisms under consideration in a defined area at a defined time. Biomass is the total amount of living matter present at a given moment in a biological system (in this case the photosynthetic plants making up a woodland stand). It is taken to include heartwood and bark (which may no longer be alive) but not dead roots and branches (with no viable buds). In the present context it should be expressed in terms of dry weight, or ash-free dry weight (=organic weight). Biomass may be estimated directly by weighing or indirectly from measurements of the volume and density of the various components concerned.

3.2 Two basic concepts

The basic method quoted from IBP News 2 represents the most fundamental procedure for estimating net production, but another method based on a somewhat different principle may also be used. In terms of mathematical symbols, the two procedures may be expressed as follows. Symbols defined below are used:

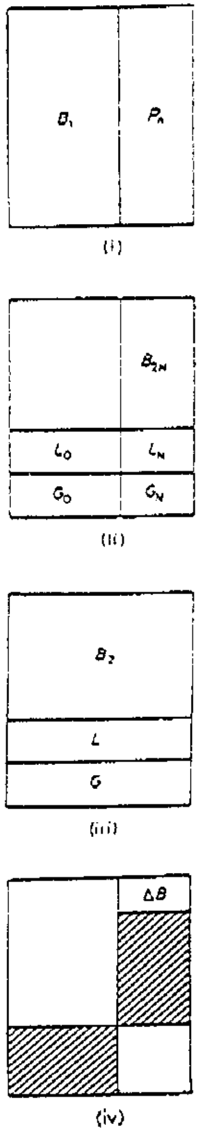
B_1	Biomass of a plant community at a certain time t_1
B_2	Biomass of the same community at t_2 ($= t_1 + \Delta t$)
$\Delta B = B_2 - B_1$	Biomass change during the period $t_1 - t_2$
L	Plant losses by death and shedding during $t_1 - t_2$
G	Plant losses by consumer organisms as herbivorous animals, parasitic plants, etc. during $t_1 - t_2$
P_n	Net production by the community during $t_1 - t_2$

If the amounts, ΔB, L and G, are successfully estimated, we can calculate P_n as the sum,

$$P_n = \Delta B + L + G \text{ (\textit{Method} 1, see Fig. 2 (iv))}$$

Instead of measuring the biomass twice at t_1 and t_2, plants may be harvested only once at the end of the growing season (t_2), and by means of stem analysis (4.61) and by separating the plant matter into current year organs and older parts (4.62), we can estimate the amount of plant matter newly formed in the latest one year period (Δt). The amount obtained by this procedure corresponds to ($P_n - L_N - G_N$), the apparent growth increment (B_{2N}). The net production is then estimated as

$$P_n = B_{2N} + L_N + G_N \text{ (\textit{Method} 2, see Fig. 2 (ii))}$$



During the period t_1–t_2, the amount P_n of new plant body is added to the initial biomass B_1.

On the other hand, a part of B_1, as well as a part of P_n dies and is lost from the biomass. These amounts are respectively designated as L_O and L_N ($L = L_O + L_N$) Similarly G_O and G_N may also be lost by the consumption of heterotrophic organisms from B_1 and P_n respectively ($G = G_O + G_N$). The plant matter newly formed, and remaining to t_2 (i.e. not lost as L_N or G_N), is known as the apparent growth increment B_{2N}.

Therefore $B_2 = B_1 + P_n - (L + G)$

or $B_2 - B_1 = P_n - (L + G) = \Delta B$

(The two hatched portions represent equal quantities, a device for subtracting B_1 from B_2, or alternatively $(L + G)$ from P_n.)

Figure 2

The apparent growth increment (B_{2N}) alone is an underestimate of the real net production whereas ($B_{2N} + L + G$) is an overestimate.

These two methods both have inherent difficulties. In the former the greatest difficulty is that the biomass of the same community must be measured at least twice accurately enough to ensure a reliable estimate of ΔB. In the latter a difficult procedure has to be adopted to separate dead plant material (L) and consumption by heterotrophic organisms (G) into current year and older components.

3.3 Sampling techniques

For either method certain basic principles of sampling apply.

1. Divide the ecosystem into components, such as trees, shrubs, ground vegetation, which can each be considered separately. Within each major physiognomic category, further divisions may include minor layers, species groups or species, and age classes. The intensity of sampling any component should vary according to its importance to the ecosystem as a whole, its inherent variability and the difficulty and cost of sampling.

2. Within each component make some enumeration of what is present. With trees this will involve the measurement of number/unit area, and various dimensions of individual trees of different species (e.g. diameter breast high, DBH or d; canopy area; height; height to first foliage branch). With ground vegetation this may involve estimation of number/unit area, or alternatively frequency of the major species. Where the ground flora is strongly seasonal, this enumeration may have to be repeated in the spring, summer and autumn.

3. Based on this enumeration, design a sampling programme involving three main sorts of samples:

(a) Non-destructive measurements (e.g. measurement of DBH, height, etc.)

(b) Destructive measurements (e.g. cutting of branches or trees, partitioning into leaves, current year's extension growth, main branches, boles, etc. and by use of fresh weights or volumes, with small subsamples for drying, estimating the dry weight of the different components. Partitioning into discrete year's radial growth may often be possible, as suggested for Method 2 above.

(c) Litter fall of various types, see Chapter 6.

4. The object is to obtain correlations (4.8) between a comparatively small destructive sample (which is both time-consuming and destructive of the habitat) with a larger non-destructive sample which is representative of the stand whose production is to be estimated. Often foresters already have a large amount of mensuration data of this non-destructive type which can be used as a basis for production studies. In particular forest plots which have been measured for a good many years are very useful.

3.4 Time scale

Net annual primary production of the tree components of a woodland can be measured on various time scales. Current annual production (which corresponds to the forester's current annual increment, C.A.I.) usually refers to production during the year of study. The actual biomass change over a single year is likely to be small compared with the total biomass present and is therefore difficult to estimate with accuracy. In all woodlands annual production varies greatly from one year to the next, due especially to variation in climate. In even-aged stands production also varies systematically with the age of the stand (as outlined in 2.1).

For purposes of comparison, both within different types of woodland and between woodlands and other types of vegetation, the mean annual production over the whole woodland rotation is the most realistic figure to aim at. This corresponds to the forester's mean annual increment, M.A.I. An alternative value for comparative purposes is the peak mean annual production, which includes the low values early in the rotation, but not those of the senescent stages. This has the advantage of not requiring particularly old stands, and not being dependent upon the length of rotation. In an uneven-aged woodland, the mean periodic annual production, measured over a period of 3–5, or preferably 10, years is probably adequate. In even-aged woodland stands, an age sequence of stands whose thinning history is known can be used to estimate the rate of accumulation of woody biomass through the rotation. It is important to ensure that the stands sampled represent similar species composition on similar sites of similar quality class (Ovington 1957, Cousens & Black 1965). Where this is not possible, estimates of current annual production from one or two stands may be related to a general sequence of production against age of stand for a similar species and region. Foresters are likely to have production tables for different species and site quality classes.

A relatively high degree of accuracy is required in the estimation of stem wood production since this is commonly the largest component of the ecosystem production especially in plantations. In some non-commercial woodlands, although stem wood is still the largest component of biomass, other components of production may sometimes exceed stem production. Annual or rotational variation is taken into account by using radial increments to give average values over the past 5 or 10 years. Branch and large root production can be estimated similarly but separate estimates of leaf, twig and, if methods can be devised, fine root production must be made over at least 3 and preferably 5 seasons.

4

The Estimation of Tree and Shrub Production

The desired estimate of production will be a sum of a number of components, of which the main ones will be:

(a) Bud scales, flowers, fruit and other minor components (Ovington 1963).
(b) Leaves, perhaps with current year's extension growth (twigs).
(c) Branches.
(d) Stems.
(e) Roots.

Ecosystem production will involve the sum of these components for the main layers of the ecosystem, trees, shrubs and ground flora. The annual production of (a) and (b) can either be estimated as litter fall directly in the sample area (Chapter 6) or along with (c) by destructive sampling in the measurement area (4.62, 4.63). Where a good relationship can be obtained between girth or diameter and stem plus branch dry weight, the production of (c) and (d) may be estimated together (4.62). An important new paper (Whittaker & Woodwell, in press), not available when this Handbook was prepared, should be consulted in conjunction with this Chapter.

4.1 The estimation of biomass change

Stem production is the major component, and needs particularly careful attention. The principle of estimation will normally be complete enumeration and measurement of stems within the sample area (4.3), followed by the establishment of a regression between some tree dimension(s) and dry weight. This regression is normally obtained by felling selected trees in the measurement area (4.6). However the actual measurement of biomass change, on which the net production estimate is based may take several forms.

(a) Where it is possible to use a plot on which repeated stem volume estimations have been made over a considerable period, and where good volume tables are available for the species and quality classes concerned, volume increment can be derived accurately from simple DBH and possibly height measurements, and timber volume converted to dry weight by obtaining some values for the specific gravity of the timber concerned.

(b) Where there is no such mensurational framework on which to base the estimates, repeated measurements can be made within the sample plot over a period of 3–5 years. It will then be necessary in effect to construct volume tables and volume/dry weight regressions by felling selected trees in the measurement area. (a) and (b) are versions of Method 1.

(c) If it is necessary to estimate production (albeit less accurately) from a single year's sampling programme, then the estimate of biomass change can be derived from an analysis of the radial increments (for, say, the preceding 5 years) on the stems of the destructive sample taken in the measurement area. The enumeration of the sample area will allow the regressions of dry weight on volume and of dry matter production on some size parameter such as tree volume or DBH, for different species, to be built up into an estimate of stem dry matter production for the sample stand.

(d) If no felling is possible, and there is no mensurational framework, increment cores carefully taken on several radii can be used to obtain an estimate of volume increment over, say, the previous 5 years and also to estimate specific gravity of bark, heartwood and sapwood. (c) and (d) are variants of Method 2.

The principles outlined in (c) and (d) above can only be applied in woodlands where growth is seasonal, and distinct annual rings are formed in the stem timber. Methods (a) and (b) may equally well be applied to seasonal or non-seasonal woodland. Other things being equal (a)–(b)–(c)–(d) represents a series of diminishing accuracy, and (d) should be regarded as a last resort where an inaccurate estimate of production seems better than none at all. There are several basic operations which are common to some or all of these four methods.

4.2 Census of the sample area

Within the sample area the number of living trees of each species are counted and each tree permanently numbered for easy identification. The breast height (1·3 m above ground height on the uphill side of the tree) is permanently marked around each trunk with durable paint.

In all trees the trunk diameter at breast height (DBH) is measured with a steel diameter tape exactly along the paint mark. Diameter tape is better than calipers for the DBH measurements. Each unit graduation measures π cm or π in., so that the value read from the tape represents the circumference of the tree divided by π (3·1416). If a diameter tape is not available, measurements may be made with a normal steel tape and values divided by π. On very small trees a linen tape must be used for circumference or a micrometer type gauge for diameter. Total tree height and tree height to the first major branch (clear-hole height) should also be measured wherever possible, using some optical apparatus (see Hummel 1951, Husch 1963).

In estimating the branch biomass the diameter of the trunk just below the joint of the lowest main branch is often an important measure (see 4.7). This may be measured with tolerable accuracy using a Barr and Stroud Dendrometer* (expensive) based on the rangefinder principle (Jeffers 1956) or some other similar topical instrument (Grosenbaugh 1963). The *Spiegel-relaskop* (see most mensuration textbooks, e.g. Husch 1963, p. 164) may be used. Such instruments also allow direct measurements of taper of the trunk which can be used to give more precision to volume tables. Where the stem is elliptical in section, these optical methods are inevitably inaccurate and a better estimate could be obtained by climbing the tree (with a ladder or a tree bicycle) and measuring girth with a tape.

In multilayered natural forests, the situation of each tree in the stratification is also recorded. The canopy type (dominant, subdominant and suppressed or other convenient grades) is also useful information in forests having relatively simple structure and composition. This inventory can conveniently be mapped on a suitable scale, so that the map shows species, size classes and tree number.

4.3 Recurrent measurements on the sample plot

After the initial census, regular recordings of DBH and height if possible are continued for at least 3–5 years, usually once a year. DBH must always be measured at exactly the same position on each trunk, marked by paint. Greater accuracy can be attained by the use of vernier band dendrometers*, or dendrographs but in quantity these would be expensive and only justifiable where radial growth is very slow, or recurrent measurements are required

over short periods such as a week or perhaps a month. The inexpensive pattern described by Liming (1957) might be useful. It consists of a simple aluminium or zinc band with vernier scales on it held tight around the trunk of the tree by a spring. Other patterns are discussed by Husch (1963), Alm & Brown (1964) and Kern (1961).

If the form factor for the species concerned is known, or suitable volume tables are available, bole volume may be estimated from DBH and height. Young *et al.* (1964, 1965) have published volume and dry weight tables for all components separately for many north-east American tree species. From such tables, dry weight increment of all woody parts can be estimated from height and girth alone.

If it is not possible to make recurrent measurements over 3–5 years, similar information (except that it refers to the previous 5 or 10 years) can be gained from increment cores taken with a Pressler type borer (see Heinrichs 1964, Mesavage 1964, Prestemon 1965). Kurth (1963) and Bunce (1961) both discuss some of the precautions necessary in the interpretation of increment cores. Vins (in press) describes an improved version of the core measurer developed by Eklund (1949) at the Swedish Forest Research Institute. This is based on a low-power microscope, and gives automatic recording of the increment measurements.

From increment cores, radial wood increment for the past 5–10 years, and bark thickness are determined and related to the measurements of DBH and height. From these data it is possible to compute basal areas of wood plus bark, and of wood alone, and bole volume if suitable volume tables are available. When they are not available a preliminary approximation of volume can be obtained from Spurr's (1952) volume equations without species corrections, or by the assumption that the bole approaches a paraboloid of rotations for which the volume is represented by

$$V_p = \frac{\pi r^2 h}{2}$$

in which r is the wood radius at breast height and h is tree height. From the data estimates of tree volume growth are also possible. Basal area increment of a tree may be computed as

$$A_i = \pi[(r^2 - (r - i)^2)]$$

in which i is the radial wood thickness increment per year (normally based on an average of the thickness of the wood growth for the past 5 or 10

---

* The term 'dendrometer' is ambiguous and may refer either to an optical instrument, or to a metal band fixed round the trunk to measure small girth increments.

years). One half basal area increment times tree height provides an estimate of stem wood volume growth 'estimated volume increment', V_i.

$$V_i = \frac{1}{2}(A_i \times h)$$

In many forest trees thickness of wood increment is greater above and below breast height than it is at breast height. Estimated volume increment is consequently often an underestimate; true wood volume growth is generally 1·0 to 1·5 times the estimated volume increment. This difficulty does not apply providing the growth form is consistent with the volume tables being used, which will themselves be based on DBH.

4.4 Conversion of volume to dry weight

If little or no felling is possible, it will be necessary to convert figures for biomass change, in terms of volumes, to dry weight using values for timber specific gravity. Timber density is commonly expressed as basic specific gravity which is the oven dry weight in grammes of 1 cm^3 volume of fresh timber. Values for this can be obtained from increment borings (though there is some danger of compression) or from any trees which have been felled. It will be important to divide the volume figures into heartwood, sapwood and bark. Carlisle & Brown (1966) found for a particular area of oak (*Quercus petraea*) forest that there was a significant correlation between the specific gravities of heartwood, sapwood and bark at 10% up the tree (specific gravities estimated from cores) and the mean specific gravities of these materials for the whole stem. The use of specific gravity estimates based on breast height increment cores is discussed by Stage (1963). Methods of estimating specific gravity from increment cores are discussed by Walters & Bruckmann (1964).

4.5 Selection of trees for destructive sample

Baskerville (1965) has demonstrated clearly the need to select sample trees for felling on the basis of a stand table. In the highly tolerant species Balsam Fir (*Abies balsamifera*) the proportion of the total tree dry weight contributed by each component (e.g. foliage, branches, cones, stem wood, stem bark, roots) varied markedly with the DBH. To derive a reasonably accurate estimate of total tree dry weight, and dry weight of the separate components, using regressions based on more than 100 felled trees it was necessary to derive a stand table using integral DBH classes (1, 2, 3 . . . . . 10 in. in this case) and to solve each component equation for each diameter class. When this was compared with an every tree summation, in which each component equation was solved for each of the 188 trees in the 0·2 acre plot, the stand table approach underestimated total biomass by 1% and the maximum component error was only 2·9%. Other 'short-cut' approaches, based, e.g. on the tree of mean height, mean diameter, mean basal area, mean volume or the average codominant tree, gave total or component estimates which were as much as 50% too high or too low.

While errors would probably be less where an intolerant tree species was concerned, it seems clear that a stand table approach is necessary. Where computer facilities are readily available it may be possible to use the laborious every tree summation techniques as a matter of routine. Shanks & Clebsch (1962) have demonstrated how it is possible to produce computer programmes (in their case in Fortran language for use in an IBM–1620 computer) for the estimation of forest stand weight and mineral content.

The selection of trees for the destructive sample will therefore involve compromise between the large sample desirable and the available commitment of manpower and money. There is no real short-cut and the trees selected must cover the range of size, form and species of the sample plot.

4.6 Estimating biomass and growth increment in destructive samples

In some circumstances it may be desirable to fell sample trees from the sample area after the period of repeated non-destructive measurements. Using the actual trees which have been measured will increase the accuracy of the dry weight estimates but precludes getting any further information from that sample area. More usually the trees to be felled will come from the measurement area and will be selected as suggested above (4.5) to be representative of the range of size, form and species in the sample area. Methods of dealing with destructive samples are set out by Whittaker, Cohen & Olson (1963).

The time of felling depends upon whether information on leaf biomass is required or not. A single sample time will not give reliable information on leaf production, but combined with some fall-out method the assessment of leaf biomass at sample time is valuable. If leaf biomass information is not required, felling should be done in the winter. If it *is* required then time of felling should preferably be near the end of the growing season in deciduous forest, when the current year's growth has already been completed while the leaves still remain green. Conifers often continue to photosynthesize while the leaves still remain green. It would be best during the winter at times when conditions are favourable. It would be best to settle on a sampling time when no photosynthesis is occurring; in some cases in the northern hemisphere, January and February are the months of minimum activity.

The following minimum measurements should be made immediately after felling:

(a) height of top of tree
(b) crown depth
(c) crown diameter (when possible this should be measured before felling)
(d) DBH
(e) stem diameter just below the lowest living branch
(f) total fresh weight of leaves
(g) total fresh weight of branches, current year's extension growth separated
(h) total fresh weight of trunk.

Certain of these measurements, e.g. (b), (c), (e), may not immediately be used in computation. They do tend however to suggest interesting relationships which may subsequently be used to refine analysis or selection of sample.

Four main tree parts (leaves, branches, trunks, roots) can be treated separately and it is necessary to define them. The border line between trunk and root is usually drawn at ground level. It is not always easy to distinguish branches from trunk. The thickest shoot leading more or less straight to the top of the crown is treated as the main trunk. In cases where the distinction is ambiguous, the criteria of separation should be clearly stated. Leaves include leaf stems (petioles). Fruits and flowers, possibly other minor components such as bud scales and pollen may also be separately weighed when necessary.

4.61 Trunk. The diameter of the trunk is measured at 1–3 m intervals according to tree size, for example at 0, 0·3, 1·3, 2·3 m . . . . and so forth from the trunk base. The bole is then cut into corresponding lengths which are individually weighed. Two sets of stout tripod, chain block and spring balance (probably of the capacity of 500 kg) are sufficient in most cases.

The strain gauge apparatus described by Keen & Weetman (1961) is also convenient. Where a chain saw is used, the cut is wide and it may be desirable to make some allowance for the loss of material as sawdust.

If the bole is too heavy or the measuring gear is not available, the weight may be estimated from stem volume. Wood volume for each log should be computed either from the middle wood diameter of the log or from the square-root mean of the end wood diameters.

$$D_m = \sqrt{\frac{(D_1^2 + D_2^2)}{2}}$$

Discs cut from each log not only assist in this measurement of log volume but can also be used for estimating wood increment during the previous 5 or 10 years, the proportions of bark, sapwood and heartwood, and the densities of these three components, where this information is required. These discs may be cut either from the centre point of each log, or from the lower end of each log, in which case two discs are used to describe each log.

Values for density of the different components can be used as suggested in 4.4 to convert volume measurements to dry weight, and to validate or invalidate the use of density values obtained from breast height increment cores.

Radial increments during, say, the last 5 years may be read on four radii on each of the discs. The wood volume (excluding bark) at the time of felling (V_S), that n years ago (V_S') and hence the wood volume increment during the period ($V_S - V_S'$) are thereby obtained. The wood increment in the most recent year (ΔV_S) can be estimated on the basis of either linear or exponential growth.

$$\Delta V_S = (V_S - V_S')/n \text{ linear basis}$$

$$\Delta V_S = V_S\ (1 - e^{-r}),\ r = \frac{1}{n} \log_e\ (V_S/V_S') \text{ exponential basis.}$$

It is to be noted that the former formula may lead to an appreciable underestimation when trees are in an exponential phase of growth. The volume increment is converted to dry weight using the conversion factors obtained as suggested above (4.4).

4.62 Branches. In some instances it is possible from the felled trees to compute the regression of stem plus branch dry weight on girth or diameter so that stem plus branch dry weight can be predicted with considerable accuracy from girth or diameter measurements. In this case, in a minimum programme, no separate estimate need be made of branch production. Where however branch weight is a variable component, not easily correlated with stem diameter, a separate estimate must be made, as described, e.g. by Whittaker (1965). As with stems it will be necessary to make measurements in the sample area which will be converted to dry weight and dry weight increment using regressions developed on the destructive sample taken from the measurement area.

The single most useful branch measurement is diameter measured just above the basal swell into the stem (Attiwill 1962). This can be measured directly by climbing the trees, or possibly with optical apparatus (Grosenbaugh 1963). If none of these are possible, then a relationship must be established between DBH or stem volume and total branch dry weight but this will lead to inaccuracy.

It may be possible to count the number of branches in each of several arbitrary size classes from the ground, and to determine the dry weight of similarly scored branches on the destructive sample.

There are several ways of dealing with the branches in the destructive sample. The basic essential is to estimate total branch dry weight (from fresh weight and conversion factors derived from dried subsample), branch diameter as described above, and to record position on the tree. Also it will be desirable to partition at least a sample of the branches into such components as wood (or wood and bark separately), current year's twigs, leaves and where appropriate flowers or fruit. The proportions of these components may be determined on subsamples and referred to the main sample. One must discover whether or not the proportions of these components vary with position on the tree.

Wherever possible one must estimate branch age. This can be done either from annual rings (often incomplete or very closely spaced) or from successive girdle scars. A combination of both techniques will probably give the most accurate result.

Then one must develop regressions, using branch age or branch basal diameter as the independent variable (x) and branch (wood and bark or each separately) weight, and current twig (with or without leaves, fruits, etc.) as dependent variables (y).

These regressions will usually be of the form

$$\log y = a + b \log x$$

The samples should always contain one of the biggest branches on the sample tree. It is important also to express the results graphically since some of the relationships may not be of this form, and the branches of a particular tree may constitute more than one population (e.g. Whittaker's (1965) branches of fast, medium and slow growth).

The regression above assumes branch growth at the rate

$$\Delta y = by/x$$

and branch production, Δy, can be estimated by multiplying branch dry weight by b/x and summing the results for a given tree.

When stem and branch biomass, and annual stem wood production are known a crude estimate of branch production is possible from the relation

$$\Delta B/B = k(\Delta S/S)$$

where B and ΔB are branch weight and production, S and ΔS are stem weight and production. Whittaker (1965) gives a range of values for k.

There are likely to be greater errors in the estimation of branch production than stem production. However its contribution to the production of the whole woodland ecosystem is smaller than that of the stems so the larger proportional error is tolerable.

4.63 Leaves. There are basically two methods of estimating leaf biomass and production, as part of the branch component (4.62) and as litter fall (Chapter 6). There are also two ways of regarding leaf production:

(a) The maximum dry weight of foliage present on the tree during the year less the minimum quantity. For deciduous species this minimum will be zero (or nearly so as a few leaves may remain).

(b) The dry weight of the tree leaves at the end of the growing season when translocation from leaf to branch has ceased.

The maximum dry weight, (a), is a true measure of leaf production *per se* and represents the quantity of foliage available for phytophagous fauna. Leaf dry weight (g per n leaves) however varies with season, often decreasing before leaf fall. Decreases in leaf dry weight may be due to translocation losses, leaching by rainfall, consumption by insects, and to respiration exceeding assimilation. It is doubtful if this maximum dry weight can be used in calculating the total annual net production (tree stem + branch + root + leaves + etc.) as some of the leaf components become branch components. The better additive value is (b), the dry weight of the leaves at the end of the season. If measurements of leaves and branches are made at the same time, there cannot be translocation from one component to another between measurements.

Maximum leaf production, (a), can be measured by taking representative sample leaves from different parts of the canopy at regular intervals throughout the year, and calculating the maximum dry weight per n leaves. For deciduous trees this can be combined with an estimate of the maximum number of leaves in the stand, derived either from a branch sample (which gives good differentiation of 'sun' and 'shade' leaves) or from litter fall.

Regular measurements of litter fall (collected every 1–4 weeks through the year, see Chapter 6) will give an indication of the total number of leaves or parts of leaves shed throughout the year. Over a period of one year in a deciduous woodland and over a period of 3–5 years in an evergreen woodland this should near enough equal the number of leaves produced. Regular litter and rain wash collections will indicate which causes of leaf loss (e.g. consumption by caterpillars, other invertebrates, aphid dew, wash-out of organic compounds by rain, immature leaf fall, etc. etc.) are important in the particular stand under study. These all represent losses of leaf production, causing leaf fall to be an underestimate of leaf production. It is therefore important to make accurate measurements of any losses which seem to be quantitatively important. Methods of litter collection are discussed in Chapter 6.

When taking the destructive sample, leaves may either be included with the current year's twigs, and the proportion of twig and leaf dry weight determined in subsamples. Or the leaves may all be clipped off and weighed, keeping those from each major branch separate. Weetman & Harland (1964) store the branches and needles at room temperature for some months until they are dry enough for the needles to fall off when shaken; the needles and twigs can then be separated in a mechanical sieve. A dry weight conversion is obtained from representative subsamples. A regression is then calculated for leaf dry weight on branch basal diameter, which will allow estimation of the leaf biomass in the sample area (e.g. Rothacher, Blow & Potts 1954). Subsamples of fresh leaves may also be taken for subsequent estimation of leaf area and chlorophyll content (7.1).

Leaves are sorted into age groups where appropriate. In certain evergreen trees such as pines, an age-leaf survival curve is constructed by which the average longevity of leaf as well as the annual amount of leaf shedding is calculated. Leaf retention may vary from tree to tree and in Scots pine, for example, shoots bearing male inflorescences may retain their leaves for 2–3 times as long as female shoots (Steven & Carlisle 1959).

The estimation of leaf production is complicated where there is lammas growth or where severe defoliation by caterpillars encourages a late flush of resting buds (Carlisle, Brown & White 1966a). This is just one instance where it is important to understand the general ecology and biology of the system under study.

4.64 Estimation of root biomass. The sampling of tree roots is tedious but reasonably reliable estimates of biomass can be obtained. Methods are reviewed by Schuurmann & Goedewaagen (1965), Lieth (in press). The roots with a diameter over 0·5 cm or over 1 cm may be dug or winched or hosed out and weighed (Ovington 1957, Singer & Hutnik 1965, Baskerville 1966). Whittaker (1962) uses regressions of root dry weight on root diameter for sample roots, applied to the broken ends of roots on the root crown to correct for root loss on excavation.

An additional estimate of fine roots can be obtained either by excavation of soil monoliths, or by taking soil cores (e.g. Bray, Lawrence & Pearson 1959) down to a depth of at least 50 cm and washing out the fine roots over a sieve. So far as is possible only live roots should be included. Roots larger than 0·5 cm (or whatever limit was employed) are rejected from these samples as they will have been estimated by excavation. The fine roots will include those of trees, shrubs and ground flora and should therefore be included in the estimate of *stand* biomass. Washed root samples frequently contain mineral soil particles. This can be allowed for by determining the ash content of subsamples in a muffle furnace and correcting the root dry weight estimate to a value (say, 5% ash) appropriate to the species and site. Extensive data on the weights of tree roots were compiled by Ovington (1962), and by Bray (1963). Some shrub root data are given by Whittaker (1962).

4.65 Attempts to estimate root production. There is however no generally acceptable method for estimating root production (Newbould, in press) and it is only possible to suggest some of the directions in which research is, or might be, proceeding and hope that some technique will emerge from IB P initiatives. If it does it may be possible to use subsequent determinations to find a relationship between root biomass and root production, so that meanwhile it is important to estimate root biomass for all stands studied.

The problem is to estimate the turnover of fine roots (Orlov 1955). This turnover is due to organic root secretions, death and decay, consumption, and losses via mycorrhizal fungi. An additional problem, especially in stands which have been thinned, is the presence of root grafts.

One overall simplification would be the assumption that

$$\frac{\text{Above-ground production}}{\text{Above-ground biomass}} = k \times \frac{\text{Below-ground production}}{\text{Below-ground biomass}}$$

Since no accurate figures have yet been obtained for below-ground production, it is difficult to estimate k, though one could simplify further and assume it to be unity.

The production of large roots can be estimated like that of branches (4.62) using radial growth increments where these are visible. However G. C. Head (*in litt*) reports that extra thickening does not occur on all woody roots, and annual rings are not a reliable guide to root age. Many thickish roots do not thicken at all in some years. A root may show, for example, six annual rings but it is not clear to which six years these rings refer. In apple trees secondary thickening of roots is more abundant close to the tree trunk, i.e. roots taper sharply after leaving the trunk.

Other methods which may be worth pursuing are set out below:

(a) Root biomass samples taken by corer at regular time intervals, say once a month, may be sorted into categories (diameter classes; brown, yellow, white; living, dead, perhaps using a vital stain). This should reveal the annual pattern of root development, and it might be possible to deduce root production from the biomass change of particular categories of root. To get enough cores would be laborious and for this method to yield useful results would need a fair degree of mechanization in the coring, washing, sorting and scoring of roots (Fehrenbacher & Alexander 1955, Newman 1966).

(b) Roots can be studied and their elongation growth and thickening measured in a glass-sided root trench (Rogers & Head 1963, Head 1965). The soil/glass interface and the installation of the trench introduce artificial features into the measurement. It is difficult to convert these measurements (mm root extension/m^2 glass wall per time) into dry matter production per unit area of land. The measurement can be made in terms of mm root extension/mm fine root visible. Measurements of root biomass as in (a) above would give values for mm of fine root in the soil below 1 m^2 stratified by depth, so that root extension data could be converted to root production per unit area.

Rates of root browning determined by this method would help in estimating the ages of roots sampled by method (a). Rates of root thickening can also be measured. This method could also suggest but not measure the importance of the loss of cortical tissue from all new roots, the complete rotting away of roots, and losses by consumption. Root extension of seedlings can similarly be studied non-destructively by growing them in glass-sided containers.

(c) Conventional growth analysis of comparatively small plants in containers gives information on root production/shoot production ratios under conditions which can be varied to relate to field problems (e.g. light, mineral nutrients, temperature). This method should be combined with the use of glass-sided containers. There must be many estimates in the literature for the root/shoot ratios of annual or short-lived plants, and a comprehensive review of these would be valuable. Growth analysis experiments lasting more than a couple of years are less numerous and where harvests are infrequent it would not be possible to calculate root production.

(d) The use of radioactive tracers has been suggested, but it is difficult to see how they could be used effectively for estimating production. They are undoubtedly useful for measuring the extent of root systems (Lott, Satchell & Hall 1950, Boggie, Hunter & Knight 1958) Carbon-14 labelling could possibly be used to measure organic root secretions over short periods of time. Such secretions can also be measured in sterile sand or water culture easily enough, and although unnatural may serve to provide maximal values.

An indirect method of measuring translocation of photosynthate to the roots, and thus root production is via the analogue computer models proposed by Olson (1964). Thus gas exchange measurements, combined with information on the rhythms of root and shoot extension and thickening would suggest what proportions of photosynthate were moving to root and shoot respectively at any particular season.

4.7 Correlation between destructive and non-destructive sample

If then we have a suitable estimate of volume change, or even DBH change, and regressions relating these external measurement parameters to total dry weight, or component dry weight, these two sets of information can be combined to develop the estimate of stand production.

The precision of this operation depends markedly on the size and selection of the destructive sample as suggested above.

Kittredge (1944) and Satoo *et al.* (1955–9) proposed the use of the allometric regression on DBH of the weight of different tree components,

$$\log w = a + b \log d$$

in which w stands for the weight of a certain tree component and d for DBH. Once the regression is established from the destructive sample, it is easy to calculate the biomass on the sample area by combining it with the result of the DBH census.

Though this type of regression has proved useful in a number of different forest types (Ovington & Madgwick 1959a, Kimura 1960, Tadaki *et al.* 1960–5, Nomoto 1964, Ogino *et al.* 1964) more accurate estimation can be expected by using d^2h in place of d where h is the tree height (Ogawa *et al.* 1961, 1965a, 1965b, Whittaker *in litt*). In some cases the expression $(d^2 + h + d^2h)$ is to be preferred (Dawkins *in litt*). If tree height is not available for calculation, it may be estimated from the d–h curve empirically obtained by destructive measurements with considerable accuracy (Ogawa *et al.* 1965b, Muller & Nielsen 1965).

Generally trunk weight can be most accurately estimated by such a method. There are indications that this is also true for the root weight (Tadaki & Shidei 1960, Ogawa *et al.* 1965b). As for the weight of branch or leaf, the regression is usually consistent within a stand, but it may vary not only with species but between stands of a single species where age or density of stems is variable (Satoo *et al.* 1958, 1959, Satoo 1962). In such cases the diameter of trunk or the area of trunk cross section at the height just below the joint of the lowest branch is often very useful as a universal parameter, because the weight of leaf or branch per tree tends to be proportional to the area of cross-section of this part of the trunk (Shinozaki *et al.* 1964, Loomis, Phares & Crosby 1966). Its measurement in non-destructive samples is discussed in 4.2.

The change of the foliage amount with tree size is sometimes less regular than in other tree components. The leaf amount per tree tends to approach a ceiling value as trees grow to a very large size. When the regression mentioned above is applied to trees bigger than the sample trees actually felled the amount of their foliage is therefore most likely to be overestimated.

This could be avoided by making the estimation graphically, based on the leaf amount—D^2H (or trunk weight) curve (Muller & Nielsen 1965). The curve may also be formulated by a hyperbolic equation (Ogawa *et al.* 1965).

These regressions or empirical curves are not necessarily peculiar to a single species. Sometimes several tree species of the same life form growing together in a stand have the same regression in common (Kimura 1960, 1963, Ogino *et al.* 1964, Muller & Nielsen 1965, Ogawa *et al.* 1961); in this case the amount of destructive sample and of calculation may be greatly reduced. Using the common regression for 50 species in a tropical rain forest, Ogawa *et al.* (1965b) could successfully estimate the biomass of the forest with satisfactorily high accuracy.

Measurements of DBH and height in all trees of the sample area, probably at an annual interval for 3–5 years, allow the estimation of biomass change during the period. Each tree component should be separately correlated with DBH or other parameters in the calculation, for the correlation is not the same in trunk, branch, root and leaf. It is generally sufficient to carry out destructive measurements only once at the end of, or during, the period of non-destructive measurement. Where the forest is growing very rapidly, the tree weight–stem size regressions may vary within a few years and the destructive sample should preferably be taken twice, both at the beginning and the end of the study period.

The change of biomass plus the amount of litter fall independently measured in the same period is the estimate of net production by Method 1. One component of production missing in this estimate is the turnover of fine roots, which for the present cannot be exactly determined in the field. Except for this omission it involves all other components including the increments of branch and root biomass which are very difficult to determine by Method 2. However the estimate should be checked by the result of Method 2 because these indirect methods of biomass estimation must always involve a considerable error.

In woodlands without a well-defined growing season, as for example tropical rain forest, where no annual growth rings are formed, Method 2 cannot be applied and only Method 1 can be used. (Muller & Nielsen 1965, Kira *et al.* 1967). In mature and stable stands it is likely that the biomass remains more or less constant from year to year and that total production will therefore equal litter fall including branches and dead stems (Nye 1961, Kira *et al.* 1967). It may be possible to estimate the total amount of leaf, branch and stem litter by sampling in a large area (Chapter 6) which may then be regarded as the estimate of net production. Since such equilibrium of forest biomass can only be recognized on a long term because of the irregular and intermittent death of trees, observations must be maintained for quite a long period before the average death rate of trees is correctly estimated. The upper limits of plot size given in 2.2 may need to be at least trebled for this approach. Another difficulty is that in tropical rain forest a lot of decomposition occurs before material reaches the ground.

4.71 Method 2. Apparent growth increments of respective tree components in a tree estimated by the procedures stated in 4.3 can also be correlated with non-destructive parameters. The allometric regression as used in Method 1 may often be used successfully with stem basal area, or leaf weight per tree as the parameters (Tadaki *et al.* 1961–3). The regressions however tend sometimes to be less simple and the estimation of apparent growth increments from DBH etc. could better be made graphically.

It is necessary in Method 2 to estimate the amount of plant tissues which were newly formed during the study period and died before the end of the period, as pointed out in 3.2. In deciduous forests the leaf component of L_N may easily be estimated as litter fall, whereas in evergreen forests it is hardly possible to classify leaf litter into current and older leaves. The greater part of current year production of evergreen leaves may remain alive in the winter months, and can be measured by destructive sampling, so that a small amount of current year leaves shed during the growing season might be disregarded. The same may also be true for current year branches. It is again emphasized that adding the total amount of litter fall (including both L_N and L_O) to apparent growth increment overestimates the net production.

The result obtained by Method 2 is however likely to be a minimum estimate of net production, because such fractions as growth increments in branch and root, losses of current year tissues including the turnover of fine roots, etc. are often difficult to determine and are therefore excluded from the estimate.

4.8 Shrub production

The estimation of shrub production is similar in principle to that of tree production. Full descriptions of methods are given by Whittaker (1961, 1962) and by Ovington, Heitkamp & Lawrence (1963).

5

The Estimation of Other Components of Ecosystem Production

5.1 Production by ground vegetation

Two main methods are possible for estimating production by the ground vegetation (see also the IBP Handbook on *Methods for estimating the primary production of grasslands, arid lands and dwarf shrublands* by Hughes, *et al*; also Scott 1955).

5.11 The individual plant method. Where distinct plants of a single or only a few species are present, the best procedure will be to collect a number of individual plants of each species (preferably including subterranean organs) at monthly intervals through the year. The collected plants are separated into leaves, flowers, stems and roots, which are dried and weighed. These individual plant data can then be combined with density (number of individual plants/area) data for conversion to an area basis. The sum of (Species A max. biomass − min. biomass) + (Species B max. biomass − min. biomass) + ... gives an estimate of net production.

5.12 The harvested quadrat method. Where this procedure is not appropriate, the ground flora can be sampled monthly by harvesting vegetation from random quadrats.

5.13 Location of samples. The quadrats will normally be located in a few representative plots in the measurement area. The sampling principle may be stratified random, i.e. quadrats placed at random (by random number co-ordinates) within a defined sub-plot. It is important to make the area large enough so that n quadrats can be harvested at each of n′ sampling intervals, without this harvesting markedly affecting the growth on quadrats to be harvested subsequently.

5.14 Size of quadrat. The preferred size and shape of quadrat will vary according to the type of vegetation, both mode of growth and uniformity of cover being considered. Suggested sizes range from 100 cm^2 for mosses, 15 cm × 15 cm (225 cm^2) for a uniform fine grass sward to 1 m × 1 m or 0·5 m × 2 m (both = 1 m^2). No general statement is possible as to the number of quadrats to be sampled at each sample interval.

5.15 Frequency of sampling. The areas are resampled at intervals during the year, using a different set of random positions. This will demonstrate the pattern of growth and allow estimation of maximum and minimum values. About 8–12 samples a year would be satisfactory, and the sampling interval may be less during periods of rapid change than, e.g. during the winter.

5.16 Harvesting. So far as possible both above-ground and major below-ground parts should be harvested. This can be done either by digging up entire plants or by clipping combined with root cores. The material must be sorted by species or species groups (e.g. in some cases groupings like 'mosses', 'grasses' will suffice) and into components (at least above- and below-ground). It is then dried and weighed, or if bulky, weighed and subsampled for subsequent drying and weighing.

5.17 Interpretation of results. A crude estimate of production can be made from the difference between the seasonal maximum and minimum dry weight figures. This must include at least underground storage organs, if not the whole root system, since apparent above-ground production may simply be attributable to translocation of stored reserves. Not all species reach their maximum biomass at the same time, so a better estimate would be provided by the sum of maximum-minimum biomass for all species individually. The maximum-minimum estimate may neglect some losses by litter fall, but where production by ground vegetation is less than, say, 5% of the ecosystem production, this is unimportant.

5.2 Climbing plants

Climbing plants, especially woody lianes, play an important role in forest types under a warm moist climate. Adequate methods for estimating wood production by lianes have not yet been developed because of the complicated methods of secondary thickening found in their stems. An indirect method for estimating the biomass of lianes in the tropical rain forest was suggested by Ogawa *et al.* (1965b).

5.3 Epiphytes

The biomass of epiphytes will normally be estimated along with the component upon which they are epiphytic. Where it seems likely that their total contribution to ecosystem production is significant, special methods must be devised for dealing with them.

6

Litter Fall

6.1 Leaves and similar litter

Estimates of litter production in the forests of the world are reviewed by Bray & Gorham (1964). There is considerably diversity of opinion as to the best receptacles for catching litter (Thompson & McGinnes 1963). Suggestions include:

(a) Bags suspended from hoops (Ovington & Murray 1964) about 1 m above the soil. The hoops would be at least 0·5 m in diameter. The bag should be freely permeable to water (nylon mesh, cheese cloth, sail cloth, etc.) to reduce moisture and decomposition inside the bag. Care must be taken with this type of litter trap that the hoop does not incline out of the horizontal and the bag must be pegged or weighted to prevent it blowing inside out.

(b) some receptacle like a plastic dustbin or bucket (e.g. 40 cm diameter), perhaps containing a bag made of terylene gauze fixed in position with a sprung steel rim (Carlisle & Brown 1966).

(c) a more elaborate trap designed by M. W. Shaw (The Nature Conservancy, Bangor, N. Wales) originally for acorns, proved an effective litter trap.

(d) where there is no tendency for the litter to drift, e.g. some conifers, shallow trays may be adequate. Decomposition will be less in these more open containers. Contamination by soil splash may invalidate subsequent chemical analysis of the samples.

The use of 'Fourdrinier' wire screening as used in paper making machines is recommended. It collects the finest particles, shows very rapid drainage and can often be obtained free.

The precise design to be used depends greatly on local circumstances. It is important that the litter fall should drop into the trap, without any aerodynamic effects preventing this, that it should not drop or blow out again, that material from the ground should not get in, and that litter in the trap should not decompose too much before being collected. Whichever

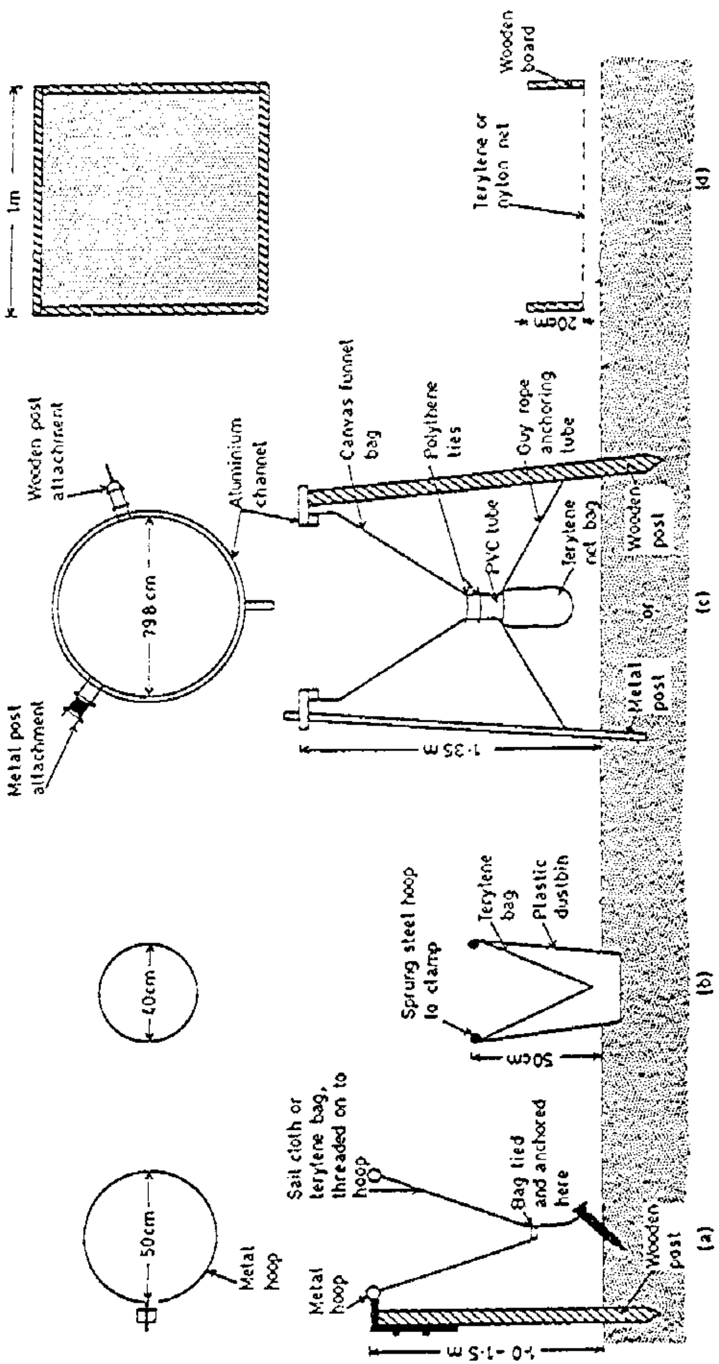


Figure 3. Four suggestions for design of litter trap. For explanation, see text.

litter trap is used, it is important that it should be large enough and that the rim should be level, and well-defined, and well above the soil surface.

The hoops, buckets or trays should be arranged by some stratified random method (e.g. two or more at random within each square of a grid or along each fixed length of a line. Probably not less than 20 would be needed in one sample area, and providing care is taken not to trample too much of the ground vegetation while emptying them, they can be located in the sample area itself. 20 litter traps may give an acceptably low standard error for the total leaf fall, or total non-branch litter, and also for the major components of leaf fall, i.e. the leaves of the dominant species. The standard error for minor species may be large and the frequency distribution heavily skewed. Where special interest attaches to such minor species, more traps must be used, and the frequency distribution examined to see what statistical technique is appropriate.

For preference they should be emptied once a week throughout the year, especially in the humid tropics and after periods of rain. If this frequency is not possible, they should be emptied at least once a month. The frequency of emptying could well be higher during the main litter fall season and lower at other times of year. Particular care is required in the siting of the trap, and the collection and analysis of the material caught where mineral cycling is being studied (7.3). Where chemical analysis is to be done on litter samples, any metal parts of the litter trap should be coated with inert bitumastic paint. It is also necessary to deter birds from perching on the rim.

The material collected from the litter trap should be sorted into appropriate categories (e.g. leaves by species, bud scales, fruits, twigs and general detritus), dried and weighed. For Method 2 of estimating production it is necessary to sort the material into that derived from current year's production (L_N) and that from previous production (L_O).

6.2 Micro-litter

Some of the smaller components of litter may better be sampled using a smaller receptacle, and not allowing water to drain out, i.e. combining this operation with rainfall sampling. This method is described in 7.2.

6.3 Macro-litter

Large items of litter, e.g. branches, are less regular than leaves in their time and space distribution. The amount of branch fall is most relevant in steady state ecosystems where some sort of equilibrium between dry matter production and its fall-out and decomposition is assumed. Where necessary branch fall should be estimated by recording all the branches from relatively large plots, say 20 m × 20 m as a minimum size, at regular intervals, say monthly. Moderate sized branches can be picked up and weighed on site with a subsample for dry weight conversion. Large branches would have to be measured and marked as recorded, with subsequent regression on dry weight. Where fall-out of branches is to be used, in a supposedly steady state system, to estimate branch production, their weight must be corrected for loss by decomposition (by comparing the dry weight/volume relation of living and fallen branches of similar diameter).

7

The Minimum Programme and Additional Measurements

The Minimum Programme so far as woodland production is concerned, consists in carrying out the measurements and calculations suggested in Chapters 4, 5 and 6 on a suitable woodland site. There are no acceptable methods for estimating root production and the minimum programme will just involve getting an estimate of root biomass (4.64), without any attempt at measuring production. If subsequently some general relationships emerge between root biomass and root production, the biomass information can be used. Unless it appears from the leaf litter samples (6.1) that there are important micro- or macro-litter components not otherwise estimated, there is no need in the minimum programme to estimate them (i.e. omit 6.2 and 6.3).

In more highly developed programmes a number of additional measurements will be valuable, and some are discussed briefly in this chapter.

7.1 Characteristics of the photosynthetic system

7.11 Leaf area index. The commonest description of the size of the photosynthetic system is the *leaf area index* which is the *area of leaves carried above a unit area of ground.* By convention, where flat leaves are concerned, only the area of one surface is estimated. Where the leaves are not flat, e.g. pine needles, half the total surface area of the leaves is taken. Methods of estimating the surface area of pine needles are discussed by Madgwick (1964). If a measure other than leaf area index is used, it should be clearly stated and a conversion factor to leaf area index, as defined above, should be given.

The estimate of leaf area index will usually be determined from leaf biomass (either from direct sampling or from litter fall) using a dry weight/leaf area conversion factor determined from a subsample of the leaves to which it is to be applied. The dry weight/leaf area conversion varies not only with time of sampling but also with position in the canopy. Methods of measuring leaf area are summarized by Lieth (1965). In the absence of a photoelectric or airflow device for measuring leaf area, it is best to photostat the leaves, using, for example, Ammonax paper, and to measure their areas with a planimeter, or by cutting them out and weighing. It is often convenient to calculate the regression of some transformation of leaf area on leaf length × width, or length^2, or $\log_{10}$ length and to use this relationship to predict area on subsequent samples. Methods based on punching discs of known area from the leaf, drying and weighing them, tend to be less reliable since the marginal part of the leaf is often under-represented by this procedure.

7.12 Stratified leaf area index. To describe the photosynthetic system further in some detailed studies it is useful to determine the leaf area index as a function of height, and this can be done by dividing the total stand into ten or more horizontal strata, cutting the canopy of felled sample trees into the parts contained in respective strata as illustrated in Fig. 4 and measuring the leaves from each stratum separately. The interval between the strata may vary according to tree size, but it is best to choose an appropriate

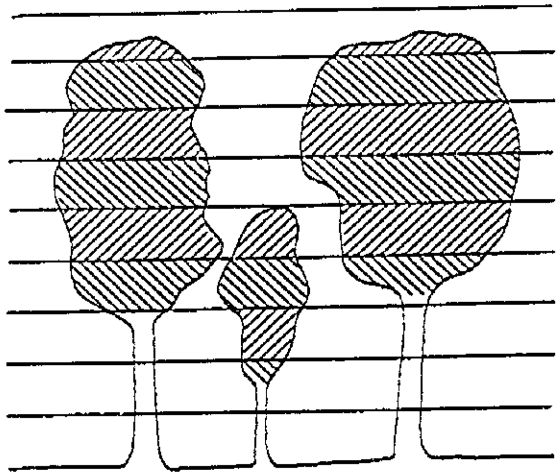


Figure 4. Stratified leaf area index.

length into which the bole can also be cut for stem analysis (4.61). It would be valuable if the light profile in the stand is obtained before felling by recording the relative light intensity at the boundaries between strata (Monsi & Saeki 1953, Saeki 1963). On regularly growing conifers it may be more convenient to treat each branch whorl separately.

7.13 **Chlorophyll.** Another relevant characteristic of the photosynthetic system is the amount of chlorophyll/unit amount of leaf and stem for different strata in the canopy. This must be estimated on fresh leaves and bark, with as little delay as possible. Methods of extraction and analysis are given, *i.a.*, by Mackinney 1941, Arnon 1949, Whittaker & Garfine 1962, Bray 1960, Medina & Lieth 1963, 1964. While there is no suggestion that the amount of chlorophyll limits production, it does represent one measure of the size of the photosynthetic systems. It is useful in bringing the photosynthetic systems of stem and leaf on to a common basis.

7.14 **Canopy photosynthesis.** The canopy characteristics described in 7.11, 7.12 and 7.13 can be combined with measurements of the photosynthetic response curve of individual leaves, and measurements of the radiation climate, to give a model which can predict total photosynthesis under defined conditions (de Wit 1965, Monteith 1965, Monsi in press). Such a model can be tested against short term estimates of net photosynthesis based on CO_2 uptake (Monteith 1962, Bourdeau & Woodwell 1965) and also against long term measurements of production with suitable correction for stem and root respiration, and other losses. The details of this approach, which provides a link between Sections PT and PP, lie outside the scope of this Handbook. Several relevant papers may be found in the UNESCO Montpellier Symposium (1965) and Copenhagen Symposium (in press).

7.2 Leaf losses

The regular litter fall measurements (Chapter 6, also 4.63) will suggest which loss components are important in any particular system. Consumption of attached leaves by invertebrates, especially caterpillars, in some sites and especially in some years may represent an appreciable amount of the primary production estimate (3.2, *G*). Methods for estimating consumption will be described fully in the IBP Handbook by Petrusewicz & Macfadyen. However a few simple suggestions are made here so that the estimate of

primary production may be completed. There are two main methods of measuring consumption. The proportion of hole to entire leaf may be measured in samples taken at intervals through the season (Bray 1961, 1964). Two drawbacks to this are that some leaves may be completely consumed and that holes made in young leaves increase in area as the leaf expands. Alternatively, especially where there are only one or two main defoliating species concerned, frass fall may be collected and counted or

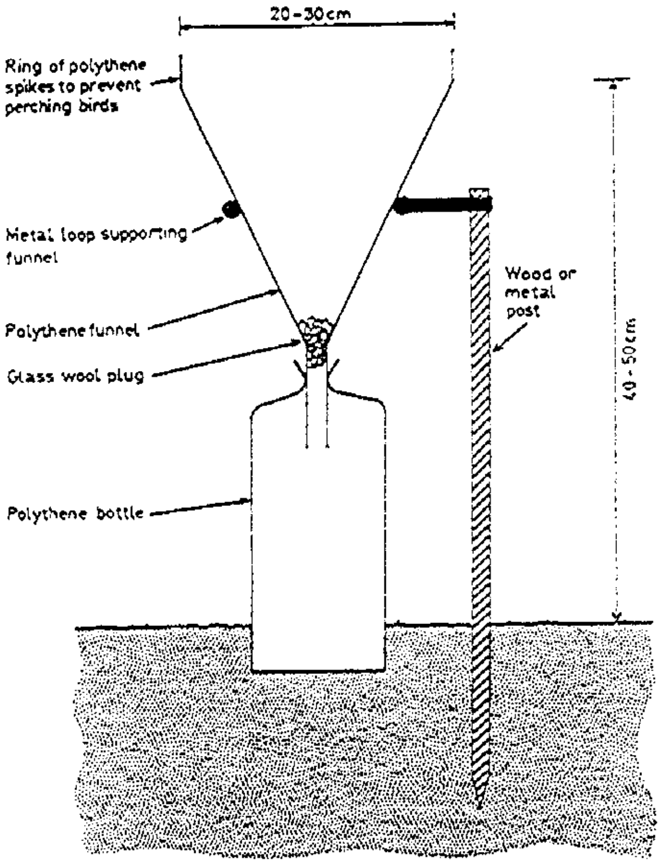


Figure 5. Micro-litter trap.

adequate background information, except that there are insufficient measurements of radiation, especially in the tropics. There are several suitable instruments, e.g. the Kipp's version of the Moll-Gorczynski solarimeter which may be used to give an integrated total (the Siemens electrolytic integrator is suitable) as well as a continuous chart record. Radiation measurements are discussed i.a. by Platt & Griffiths (1964), Gates (1962), Stanhill (1965) and Drummond (1965).

Microclimatological measurements tend to be specialized and expensive and will feature mainly in developed programmes laid on by well-equipped research centres. Records of quantity and quality of rainfall inside and outside woodland areas are useful (7.3).

Similarly information may be needed on the transmission of photosynthetically useful radiation through vegetation, and on the quality and quantity of radiation reaching the woodland floor. There is no agreement about the best and most practical method. Problems include temporal and areal integration, the spectral sensitivity of photocells, and their failure to maintain their calibration. Probably it is best to measure solar energy in the visible spectrum with a thermopile sensitive over the whole solar spectrum (0·4–2 μ) if necessary using a Schott RG 8 filter to find the amount of infra-red radiation at wavelengths longer than 0·7 μ. In most weather energy within the visible spectrum can be taken as 45% of total solar radiation. Other methods, such as selenium or silicon photocells can be calibrated against these instruments.

8

Results

8.1 Data-recording

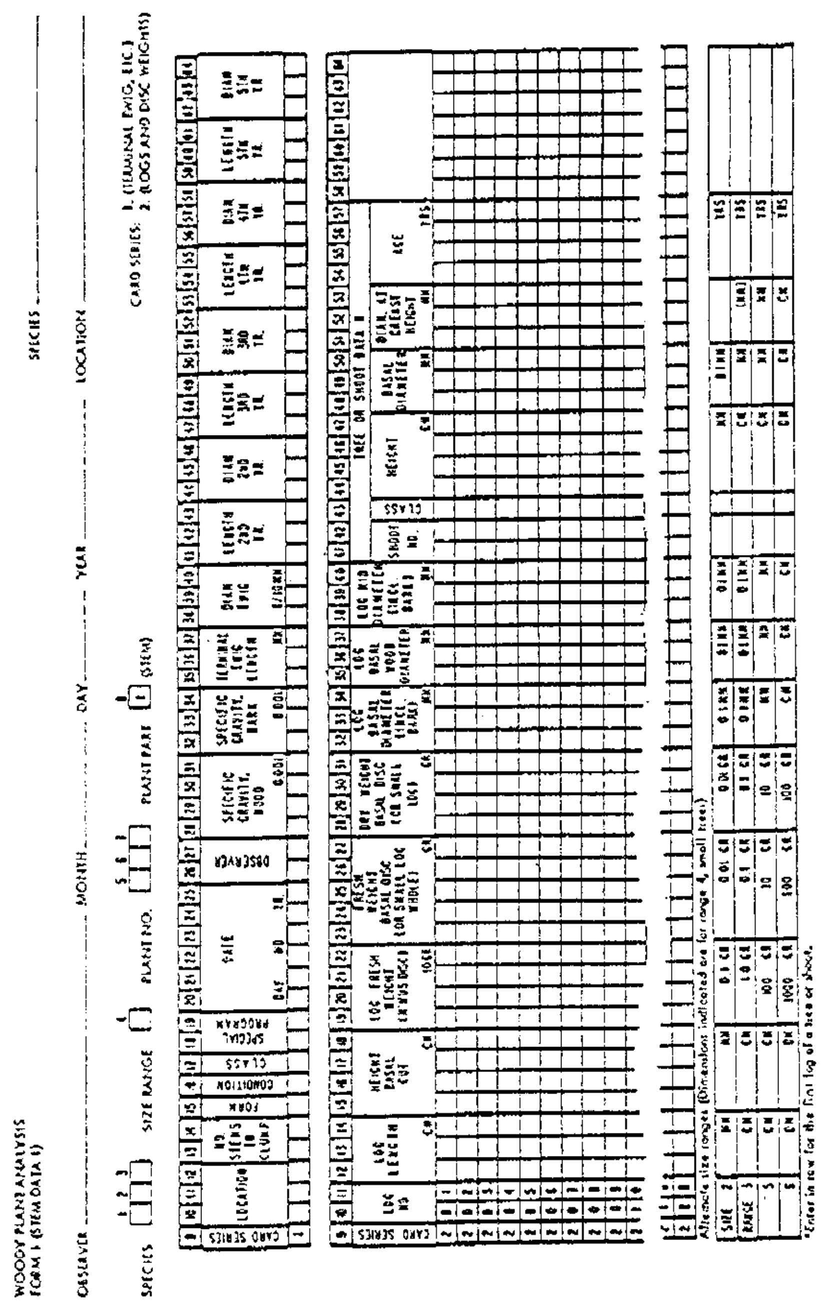
A series of fifteen 'woody plant analysis forms' have been developed at Brookhaven National Laboratory by R. H. Whittaker & G. M. Woodwell. They include field recording, laboratory analysis (e.g. of stem discs) and the compilation of data for the whole forest stand. An example is shown as Fig. 6. The forms are printed on thin cards and measure 28 × 21·5 cm. It is not expected that a given investigator would use all the forms or all the columns on the forms, which allow for a number of special contingencies. They are linked to a programme of computations which is not yet finalized.

The system of analysis involved and full details of the forms are in process of publication (Whittaker & Woodwell, in press). Further details are available from the authors at the Brookhaven National Laboratory, Associated Universities Inc., Upton, Long Island, New York, U.S.A.

8.2 Units

All units should be metric. Dry matter production can be presented as g/m^2 which is the same value as metric tons/km^2, but must be multiplied by 10 to give kg/ha. This latter unit which is generally familiar has the advantage of being quite close to lb/acre (kg/ha × 0·89 = lb/acre). However since the net annual production of woodlands usually lies between 5,000 and 50,000 kg/ha, and accuracy of estimation seldom permits more than three figures to be significant, there is some advantage in using the unit metric tons/ha or 10^3 kg/ha (i.e. 5–50 for the range above).

The term dry weight is itself imprecise since most biological material retains some bound water even at 105°C. The material should be dried to constant weight, either at 85°C or 105°C and it should be clearly stated which temperature has been used. Many ecologists prefer 105°C at which temperature constant weight is achieved more rapidly, but it can lead to combustion in the drying oven, especially where it is over-filled. It would



— 65 —

STEM ANALYSIS - LOGS

WOODY PLANT ANALYSIS
FORM 1 (STEM DATA 1)

OBSERVER ______ MONTH ______ DAY ______ YEAR ______ LOCATION ______

SPECIES ______

CARD SERIES: 1. (TERMINAL TWIG, ETC.) 2. (LOGS AND DISC WEIGHTS)

Figure 6. Sample of the Brookhaven 'woody plant forms'.

be useful in some studies to estimate conversion factors for all types of material from 85°C to 105°C dry weight.

The gram calorie (cal) is the preferred unit of energy despite the adoption by physicists of the joule as the standard unit. The calorie has long been used by biologists and helps, by its association with nutrition, to stress the human welfare aspect of production studies. The solar constant has a convenient value (2·00 cal cm^{-2} min^{-1}). For energy flow studies cal cm^{-2} day^{-1} is a suitable unit. 1,000 calories = 1 kilocalorie (kcal). Nutritionists commonly use kcal units, often representing them simply as Calories.

8.3 Errors

Three major problems in arriving at a precise and accurate estimate of primary production are errors due to measurement, sampling errors and the effects of climatic variation from year to year. The effects of climatic variation on production are poorly understood and cannot easily be corrected for. It is therefore essential to base the production estimate on a minimum period of three years, with five years being preferable, and ten years quite possible for estimates based on radial increments. This is another argument for using long-established sample plots wherever these are available. Components like litter fall should be estimated over a period of at least three and preferably five years (Carlisle, Brown & White 1966a).

In arriving at acceptable production estimates it is best to direct effort towards minimizing the errors in the major components while tolerating larger (sampling and measurement) errors in the minor components. The largest single component will usually be stem growth, and since this is the component which has been most studied by foresters, use of all available mensuration techniques, volume tables, etc. will help to reduce the error in this estimate. It is estimated that figures for the total volume of boles of trees normally come within about 5% of the true value. The measurement and sampling errors in estimating some of the minor components must be quite large. It is seldom if ever possible to present an estimate of annual production with 95% confidence limits which genuinely represent the likelihood that the true annual production of the community under investigations falls within those limits. It is however often possible to give some estimate of the variability of a particular set of measurements involved in the estimate of community production, as for example the dry weight of trees belonging to the same sample unit, or the dry weight of ground flora quadrats clipped at the same time (Whittaker 1966). In such cases the intensity of sampling should aim at a standard error of the mean of ±5% (±10% for 95% confidence limits), though in many cases this is unattainable. It would be valuable, in presenting production data, if authors would give some subjective assessment of the main errors involved in their estimate.

In many cases partitioning of material is arbitrary. There is no rigid or general rule for the separation of root and stem, stem and branch, branch and leaf, living and dead. Stoloniferous grasses, stilt roots, deciduous stem spines, all present their own peculiar problems, for which individual solutions must be worked out. The important thing is to *define the criteria used in any separation* and to *be consistent in applying them.*

8.4 Calculations

The general basis for the calculation of net production has been given in 3.1. In production studies the calculations should be clearly laid out and the assumptions involved clearly stated. If possible the validity of these assumptions should be evaluated and the consequences should the assumptions subsequently prove wrong. Sometimes biases may be accepted as the lesser of two evils. This should also be clearly stated and evaluated.

One should define and describe the dimensions of the amounts calculated. Clear distinction should be made between directly measured and indirectly estimated values. It may be possible in tabulation to put actual measurements in bold figures and calculated values in normal type.

Calculations and mathematical treatments are often greatly facilitated by the use of proper symbols. Care should be taken not to use the same symbol, or confusing symbols for different amounts in a series of studies. A system of notations such as were used by Ogawa *et al.* (1965) is recommended.

8.5 Commitment

Since money and manpower are likely to be the main limiting factors in the IBP, any assessment of the commitment involved in obtaining production data would be very useful.

8.6 Publication

Research falling within the scope of this Handbook should be published in the normal and appropriate journals. It would be appreciated if a reprint

of all publications could be sent to IBP Central Office (7 Marylebone Road, London, N.W.1., U.K.). Original data, where it is inappropriate to include them in full in a published paper, should be preserved, and duplicated copies made available to those who request them.

Acknowledgements

I would like to acknowledge the help of Prof. J. D. Ovington on whose original draft both the draft circulated in January 1966 and this second version are based.

I would like to thank the following for their helpful comments on the first draft. I have incorporated these comments as far as possible but some proved mutually contradictory.

Mr H.W.B.Barlow, East Malling Research Station, U.K.
Dr W.O.Binns, Forestry Commission, U.K.
Dr J.R.Bray, New Zealand.
Dr M.D.Gwynne, E.A.A.F.R.O., Kenya.
Prof. Dr. Ir. G.Hellinga, Wageningen, Netherlands.
Dr B.Hopkins, Ibadan, Nigeria.
Prof. R.J.Hutnik, Dept. of Forestry, Pennsylvania State University, U.S.A.
Dr J.Kvet, Academy of Sciences, Prague, Czechoslovakia.
Dr H.Lieth, Botanisches Institute, Stuttgart-Hohenheim, Germany.
Prof. H.A.I.Madgwick, Dept. of Forestry, Virginia Polytechnic Institute, U.S.A.
Mr P.H.Nye, Dept. of Agriculture, Oxford University, U.K.
Dr J.S.Olson, Oak Ridge National Laboratory, U.S.A.
Dr M.E.D.Poore, The Nature Conservancy, U.K.
Mr M.W.Shaw, The Nature Conservancy, Bangor, U.K.
Mr R.C.Steele, The Nature Conservancy, Monks Wood, U.K.
Prof. Dr Ir.G.J.Vervelde, Wageningen, Netherlands.
Dr B.Vins, Forestry and Game Management Res. Inst., Zbraslav, Czechoslovakia.

Prof. Dr M.Vyskot, Dept. of Silviculture, Brno University, Czechoslovakia.
Dr G.F.Weetman, Pulp and Paper Research Institute, Montreal, Canada.
Dr P.R.Wycherley, Rubber Research Institute, Kuala Lumpur, Malaya.

I would especially like to thank for their full and extended comments Prof. T.Kira of Osaka City University, Japan; Dr A.Carlisle and Mr A.H.F.Brown of the Nature Conservancy Merlewood Research Station, U.K.; Prof. R.H.Whittaker of the Brookhaven National Laboratory, U.S.A.; and Dr H.C.Dawkins of the Forestry Dept., Oxford. Carlisle and Brown produced an extensive duplicated paper on 'The measurement of net primary production in woodlands'. Prof. Whittaker sent extensive comments and details of current work at Brookhaven. Prof. Kira forwarded to me extensive comments which he had summarized, from a meeting of 21 members of the Japanese Working Group on Terrestrial Productivity. I have drawn heavily on these three contributions. I must apologize to their authors for any omissions or misinterpretations which I hope they will correct in due course.

References

Papers included in the symposium on *The Methodology of Plant Ecophysiology,* UNESCO Arid Zone Research 25, held at Montpellier in 1961, and published in Paris in 1965 will be referred to as *UNESCO Montpellier Symposium.*

Papers given at the UNESCO First International Symposium on Ecosystems, held in Copenhagen in 1965, and yet to be published, will be referred to as *UNESCO Copenhagen Symposium.*

Alm A.A. & Brown B.A. (1964). Dendrometer bands to measure stand growth. *Minn. For. Note No.* 156, p. 2.

Arnon D.I. (1949). Copper enzymes in isolated chloroplasts. Polyphenoloxidase in *Beta vulgaris. Pl. Physiol., Lancaster,* 24, 1–15.

Attiwill P.M. (1962). Estimating branch dry weights and leaf area from measurements of branch girth in *Eucalyptus. Forest Sci.* 8, 132–41.

Baskerville G.L. (1965). Estimation of dry weight of tree components and total standing crop in conifer stands. *Ecology* 46, 867–9.

Baskerville G.L. (1966). Dry matter production in immature balsam fir stands: roots, lesser vegetation, and total stand. *Forest Sci.* 12, 49–53.

Boggie R., Hunter R.F. & Knight A.H. (1958). Studies of the root development of plants in the field using radioactive tracers. *J. Ecol.* 46, 621–39.

Bourdeau P.F. & Woodwell G.M. (1965). Measurements of plant CO_2 exchange by infra-red absorption under controlled conditions and in the field. *UNESCO Montpellier Symposium* 283–90.

Bradley R.T., Christie J.M. & Johnston D.R. (1966). *Forest Management Tables. Forestry Commission Booklet* 16, London, H.M.S.O.

Bray J.R. (1960). The chlorophyll content of some native and managed plant communities in central Minnesota. *Can. J. Bot.* 38, 313–33.

Bray J.R. (1961). Measurement of leaf utilization as an index of minimum level of primary consumption. *Oikos* 12, 70–4.

Bray J.R. (1963). Root production and the estimation of net productivity. *Can. J. Bot.* 41, 65-72.

Bray J.R. (1964). Primary consumption in three forest canopies. *Ecology* 45, 165–7.

Bray J.R. & Gorham E. (1964). Litter production in forests of the world. *Adv. Ecol. Res.* 2, 101–57.

Bray J.R., Lawrence D.B. & Pearson L.C. (1959). Primary production in some Minnesota communities for 1957. *Oikos* 10, 38–49.

Bunce H. (1961). A correction table for use when taking increment borings of Western Hemlock to determine total age. *For. Chron.* 37, 158–9.

Carlisle A. & Brown A.H. (1966). *The measurement of net primary production in woodlands.* Mimeographed.

Carlisle A., Brown A.H.F. & White E.J. (1966a). Litter fall, leaf production and the effects of defoliation by *Tortrix viridana* in a sessile oak (*Quercus petraea*) woodland. *J. Ecol.* 54, 65–85.

Carlisle A., Brown A.H.F. & White E.J. (1966b). The organic matter and nutrient elements in the precipitation beneath a sessile oak canopy. *J. Ecol.* 54, 87–98.

Cousens J.E. & Black J.N. (1965). *Utilization of solar energy by forests.* Mimeographed.

Drummond A.J. (1965). Techniques for the measurement of solar and terrestrial radiation fluxes in plant biological research. A review with special reference to the arid zones. *UNESCO Montpellier Symposium* 13–27.

Eklund, B. (1949). Skogsforskningsinstitutets årsringmätningsmaskiner: tillkomst, konstruktion och användning. *Meddn St. SkogsförskInst.* 38, 1–77.

Fehrenbacher J.B. & Alexander J.D. (1955). A method for studying corn root distribution using a soil-core sampling machine and shaker type washer. *Agron. J.* 47, 468–72.

Ferat F. (1958). *Dendrometri.* Kutulmus Matbaasi, Istanbul (Turkish).

Gates D.M. (1962). *Energy exchange in the biosphere.* Harper & Row, N.Y.

Greenland D.J. & Kowal J.M.L. (1960). Nutrient content of the moist tropical forest of Ghana. *Pl. Soil* 12, 154–74.

Grosenbaugh L.R. (1963). Optical dendrometers for out-of-reach diameters; a conspectus and some new theory. *Forest Sci. Monogr.* 4, 1–47.

Head G.C. (1965). Studies of diurnal changes in cherry root growth and nutational movements of apple root tips by time-lapse cinematography. *Ann. Bot.* 29, 219–24.

Heinrichs J.F. (1964). Pocket-sized sharpener for increment borers. *J. For.* 62, 753.

Hughes R.E., Milner C., Slatyer R.O. & Gimingham C.H. (in preparation). *Methods for estimating the primary production of grasslands, arid lands and dwarf shrublands.* IBP, London.

Hummel F.C. (1951). Instruments for the measurement of height, diameter and taper on standing trees. *For. Abstr.* 12, 261–9.

Husch B. (1963). *Forest Mensuration and Statistics.* Ronald Press, N.Y.

Jeffers J.N.R. (1956). Barr and Stroud dendrometer, Type F.P.7. *Rep. For. Res. For. Comm., London* 1954/5, 127–36.

Keen R.E. & Weetman G.F. (1961). Two methods of weighing trees. *Woodlds Res. Index* 123, 1–9.

Kern K.G. (1961). Ein Beitrag zur Zuwachsmessung mit dem Arnberg-Mikrodendrometer. *Allg. Forst-u. Jagdztg.* 132, 206–12.

Kimura M. (1960). Primary production of the warm-temperate laurel forest in the southern part of Osumi Peninsula, Kyushu, Japan. *Misc. Rep. Res. Inst. nat. Resour., Tokyo* 52–53, 36–47.

Kimura M. (1963). Dynamics of vegetation in relation to soil development in northern Yatsugadake Mountains. *Jap. J. Bot.* 18, 255–87.

Kira T., Ogawa H., Yoda K. & Ogino K. (1967). Comparative ecological studies in three main types of forest vegetation in Thailand. IV. Dry matter production, with special reference to the Khao Chong rain forest. *Nature and Life in S.E. Asia* 5, 149–74.

Kittredge J. (1944). Estimation of the amount of foliage of trees and stands. *J. For.* 42, 905–12.

Kurth H. (1963). (Systematic errors in the determination of radial increment from cores). (German). *Arch. Forstw.* 12, 751–63.

Lieth H. (1965). Indirect measurements of dry matter production. *UNESCO Montpellier Symposium* 513–8.

Lieth H. (in press). Methods for the determination of the productivity of the underground organs. *UNESCO Copenhagen Symposium.*

Lieth H. (in press). The measurement of calorific values of biological material and the determination of ecological efficiency. *UNESCO Copenhagen Symposium.*

Liming F.G. (1957). Home-made dendrometers. *J. For.* 55, 575–7.

Loomis R.M., Phares R.E. & Crosby J.S. (1966). Estimating foliage and branchwood quantities in Shortleaf Pine. *Forest Sci.* 12, 30–9.

Lott W.L., Satchell D.P. & Hall N.S. (1950). A tracer element technique in the study of root extension. *Proc. Am. Soc. hort. Sci.* 55, 27–34.

MacKinney G. (1941). Absorption of light by chlorophyll solutions. *J. biol. Chem.* 140, 315–22.

Madgwick H.A.I. (1964). Estimation of surface area of pine needles with special reference to *Pinus resinosa. J. For.* 62, 636.

Medina E. & Lieth H. (1963). Contenido de clorofila de algunas asociaciones vegetales de Europa central y sa relacion con la productividad. *Qualitas Pl. Mater. veg.* 9, 219–29.

Medina E. & Lieth H. (1964). Die Beziehungen Zwischen Chlorophyllgehalt assimilierender Fläche und Trockensubstanzproduktion in einigen Pflanzengemeinschaften. *Beitr. Biol. Pfl.* 40, 451–94.

Mesavage C. (1964). Core examination kit. *J. For.* 62, 635.

Monsi M. (in press). Mathematical models of plant communities. *UNESCO Copenhagen Symposium.*

Monsi M. & Saeki T. (1953). Über den Lichtfaktor in den Pflanzengesellschaften und seine Bedeutung für die Stoffproduktion. *Jap. J. Bot.* 14, 22–52.

Monteith J.L. (1962). Measurement and interpretation of carbon dioxide fluxes in the field. *Neth. J. agric. Sci.* 10, 334–46.

Monteith J.L. (1965). Light distribution and photosynthesis in field crops. *Ann. Bot.* 29, 17–37.

Müller D. & Nielsen J. (1965). Production brute, pertes par respiration et production nette dans la forêt ombrophile tropicale. *Forst. ForsVaes. Danm.* 29, 69–160.

Newbould P.J. (in press). Methods of estimating root production. *UNESCO Copenhagen Symposium.*

Newman E.I. (1966). A method of estimating the total length of root in a sample. *J. appl. Ecol.* 3, 139–45.

Nomoto N. (1964). Primary productivity of beech forest in Japan. *Jap. J. Bot.* 18, 385–421.

Nye P.H. (1961). Organic matter and nutrient cycles under moist tropical forest. *Pl. Soil* 13, 333–46.

Ogawa H., Yoda K. & Kira T. (1961). A preliminary survey on the vegetation of Thailand. *Nature and life in S.E. Asia* 1, 21–157.

Ogawa H., Yoda K, Kira T., Ogino K., Shidei T., Ratanawongse D. & Apasutaya C. (1965). Comparative ecological study on three main types of forest vegetation in Thailand. I Structure and floristic composition. *Nature and Life in S.E. Asia* 4, 13–48.

Ogawa H., Yoda K., Ogino K. & Kira T. (1965). Comparative ecological studies on three main types of forest vegetation in Thailand. II Plant biomass. *Nature and Life in S.E. Asia* 4, 49–80.

Ogino K., Sabhasri S. & Shidei T. (1964). The estimation of the standing crop of the forest in northern Thailand. *The South-east Asian Studies* 4, 89–97.

Olson J.S. (1964). Gross and net production of terrestrial vegetation. *J. Ecol.* 52, *Suppl.* 99–118.

Orlov A. (1955). The role of feeding roots of forest vegetation in enriching the soil with organic matter. *Pochvovedenie* 6, 14–20.

Ovington J.D. (1957). Dry-matter production by *Pinus sylvestris* L. *Ann. Bot.* 21, 287–314.

Ovington J.D. (1962). Quantitative ecology and the woodland ecosystem concept. *Adv. Ecol. Res.* 1, 103–92.

Ovington J.D. (1963) Flower and seed production. A source of error in estimating woodland production, energy flow and mineral cycling. *Oikos* 14, 148–53.

Ovington J.D. (1965a). Organic production, turnover and mineral cycling in woodlands. *Biol. Rev.* 40, 295–336.

Ovington J.D. (1965b). Nutrient cycling in woodlands. *Experimental Pedology*, ed. E. G. Hallsworth & D. V. Crawford, Butterworths, London, 208–18.

Ovington J.D. & Heitkamp D. (1960). The accumulation of energy in forest plantations. *J. Ecol.* 48, 639–46.

Ovington J.D., Heitkamp D. & Lawrence D.B. (1963). Plant biomass and productivity of prairie, savanna, oakwood and maize field ecosytems in central Minnesota. *Ecology* 44, 52–63.

Ovington J.D. & Madgwick H.A.I. (1959a). Distribution of organic matter and plant nutrients in a plantation of Scots Pine. *Forest Sci.* 5, 344–55.

Ovington J.D. & Madgwick H.A.I. (1959b). The growth and composition of natural stands of birch. I. Dry-matter production. *Pl. Soil* 10, 271–88.

Ovington J.D. & Murray G. (1964). Determination of acorn fall. *Q. Jl. For.* 58, 152–9.

Pardé J. (1961). *Dendrometrie.* Imprimerie Louis-Jean, Paris.

Petrusewicz K. & Macfadyen A. (in preparation). *Methods and principles of secondary productivity measurement of terrestrial ecosystems.* IBP, London.

Platt R.B. & Griffiths J. (1964). *Environmental measurement and interpretation.* Reinhold Publ. Corp. New York.

Prestemon D.R. (1965). Improving the power increment borer for hardwoods. *J. For.* 63, 763–5.

Prodan M. *Holzmesslehre* (1965). J. D. Sauerlander Verlag, Frankfurt.

Rogers W.S. & Head G.C. (1963). A new root-observation laboratory. *Rep. E. Malling Res. Stn. for* 1962, 55–7.

Rothacher J.S., Blow F.E. & Potts S.M. (1954). Estimating the quantity of tree foliage in oak stands in the Tennessee Valley. *J. For.* 52, 169–73.

Saeki T. (1963). Light relations in plant communities. In Evans L. T. ed. *Environmental Control of Plant Growth.* Academic Press, N.Y. & London, 79–92.

Satoo T. *et al.* (1955–9). Materials for the studies of growth in stands. 1–5. *Bull. Tokyo Univ. Forests* 48, 69–90; 52, 15–31, 33–51; 54, 71–100; 55, 101–23. (Japanese, Eng. summary).

Satoo T. (1962). Notes on Kittredge's method of estimation of amount of leaves of forest stand. *J. Jap. For. Soc.* 44, 267–72.

Schuurmann J.J. & Goedewaagen M.A.J. (1965). *Methods for the Examination of Root Systems and Roots.* Centre for Agricultural Publications and Documentation. Wageningen.

Special Committee for the International Biological Programme. (1965). *I.B.P. News* 2, Rome.

Scott D.R.M. (1955). Amount and chemical composition of the organic matter contributed by overstory and understory vegetation to forest soil. *Yale Univ. Sch. For. Bull.* 62.

Shanks R.E. & Clebsch E.E.C. (1962). Computer programs for the estimation of forest stand weight and mineral pool. *Ecology* 43, 339–41.

Shinozaki K., Yoda K., Hozumi K. & Kira T. (1964). A quantitative analysis of plant form—the pipe model theory. *Jap. J. Ecol.* 14, 97–105, 133–9.

Singer F.P. & Hutnik R.J. (1965). Excavating roots with water pressure. *J. For.* 63, 37–8.

Spurr S.H. (1952). *Forest Inventory.* Ronald Press, N.Y.

Stage A.R. (1963). Specific gravity and tree weight of single tree samples of Grand Fir. *U.S. For Serv. Res. Pap. Intermt. For. Range Exp. Stn. No. INT–4*, pp. 11.

Stanhill G. (1965). A comparison of four methods of estimating solar radiation. *UNESCO Montpellier Symposium* 55–61.

Steven H.M. & Carlisle A. (1959). *The Native Pinewoods of Scotland*, Edinburgh.

Tadaki Y. & Shidei T. (1960). Studies on productive structure of forest. 1. The seasonal variation of leaf amount and the dry matter production of deciduous sapling stand (*Ulmus parviflora*). *J. Jap. For. Soc.* 42, 427–34.

Tadaki Y., Shidei T., Sakasegawa T. & Ogino K. (1961). Studies on productive structure of forest. 2. Estimation of standing crop and some analyses of productivity of young birch stand (*Betula platyphylla*). *J. Jap. For. Soc.* 43, 19–26.

Tadaki Y., Ogata N. & Takagi T. (1962). Studies on productive structure of forest. 3. Estimation of standing crop and some analyses on productivity of young stands of *Castanopsis cupsidata. J. Jap. For. Soc.* 44, 350–9.

Tadaki Y. (1963). Studies on production structure of forest. 4. Some studies on leaf amount of stands and individual trees. *J. Jap. For. Soc.* 45, 249–56.

Tadaki Y., Ogata N. & Nagatomo T. (1963). Studies on production structure of forest. 5. Some analyses on productivities of artificial stand of *Acacia mollissima. J. Jap. For. Soc.* 45, 293–301.

Tadaki Y. (1965). Studies on production structure of forests. 7. The primary production of a young stand of *Castanopsis cupsidata. Jap. J. Ecol.* 15, 142–7.

Tadaki Y. (1965). Studies on production structure of forest. 8. Productivity of an *Acacia mollissima* stand in higher stand density. *J. Jap. For. Soc.* 47, 384–91.

Thompson R.L. & McGinnes B.S. (1963). A comparison of eight types of mast traps. *J. For.* 61, 679–80.

Vins B. (in press). Foundations, methods and use of annual ring analyses on borings made by increment borer. *UNESCO Copenhagen Symposium.*

Walters C.S. & Bruckmann G. (1964). A comparison of methods for determining volume of increment cores. *J. For.* 62, 172–7.

Weetman G.F. & Harland R. (1964). Foliage and wood production in unthinned Black Spruce in Northern Quebec. *Forest Sci.* 10, 80–8.

Whittaker R.H. (1961). Estimation of net primary production of forest and shrub communities. *Ecology* 42, 177–80.

Whittaker R.H. (1962). Net production relations of shrubs in the Great Smoky Mountains. *Ecology* 43, 357–77.

Whittaker R.H. (1965). Branch dimensions and estimation of branch production. *Ecology* 46, 365–70.

Whittaker R.H. (1966). Forest dimensions and estimated production in the Great Smoky Mountains. *Ecology* 47, 103–21.

Whittaker R.H. & Garfine V. (1962). Leaf characteristics and chlorophyll in relation to production and exposure in *Rhododendron. Ecology* 43, 120–5.

Whittaker R.H., Cohen N. & Olson J.S. (1963). Net production relations of three tree species at Oak Ridge, Tennessee. *Ecology* 44, 806–10.

Whittaker R.H. & Woodwell G.M. (in press). Dimension and production relations of trees and shrubs in the Brookhaven Forest, New York. *J. Ecol.*

Wit, C.T. de (1965). Photosynthesis of leaf canopies. *Versl. Landbouwk. Onderz.* 663, 1–57.

Young H.E., Strand L. & Altenberger R. (1964). Preliminary fresh and dry weight tables for seven tree species in Maine. *Tech. Bull. Me. agric. Exp. Stn, No.* 12, pp. 76.

Young H.E., Hoar, L. & Asheley M. (1965). Weight of wood substance for components of seven tree species. *TAPPI* 48, 466–9.

Further Reading

Aaltonen V.T. (1920). Uber die Ausbreitung und den Reichtum der Baumwurzeln in den Heidewaldern Lapplands. *Acta for. fenn.* 14, 1–55.

Ando T. *et al.* (1959). Estimation of the amount of leaves, twigs and branches of Sugi (*Cryptomeria japonica* D. Don.) by sampling method. *J. Jap. For. Soc.* 41, 117–24.

Ando T. (1965). Estimation of dry-matter and growth analysis of the young stand of Japanese Black Pine (*Pinus thunbergii*). *Advanc. Front. Pl. Sci., New Delhi* 10, 1–10.

Assmann E. & Franz F. (1963). Vorlaufige Fichten-Ertragstafel für Bayern. *Fortwiss. ZentBl.* 84, 1–68.

Attiwill P.M. (1966). A method for estimating crown weight in *Eucalyptus* and some other implications of relationships between crown weight and stem diameter. *Ecology* 47, 795–804.

Bargioni G. (1959). Contributo allo studio del sistema radicale del ciliegio nel Veronese. *Riv. Ortoflorofruttic. ital.* 43, 3–23.

Baskerville G.L. (1962). Production in forests. *Mimeo, Dept. For. Can.* MD–322–62. 83 pp.

Baskerville G.L. (1965). Dry matter production in immature fir stands. *Forest Sci. Monogr.* 9, 1–42.

Becking J.H. (1962). Potential and actual productivity of stem wood in forestry. *Neth. J. agric. Sci.* 10, 354–60.

Bode R.H. (1959). Über den Zusammenhang zwischen Blattenfaltung und Neubildung der Saugwurzeln bei Juglans. *Ber. dt. bot. Ges.* 72, 93–8.

Boysen-Jensen P. (1932). *Die Stoffproduktion der Pflanzen.* Jena G. Fischer Verlag.

Bray J.R. & Dudkiewicz L.A. (1963). The composition, biomass and productivity of two *Populus* forests. *Bull. Torrey bot. Club* 90, 298–308.

Burger H. (1935–54). Series of papers published under general title of Holz, Blattmenge und Zuwachs. *Mitt. schweiz. Anst. Forstl. VersWes.* 15–31.

Cable D.R. (1958). Estimating surface area of ponderosa pine foliage in Central Arizona. *Forest Sci.* 4, 45–9.

Carlisle A., Brown A.H.F. & White E.J. (in press). The measurement of stem biomass and production in uneven-aged oak woodland.

Coker E.G. (1958). Root studies XII: root systems of apple on Malling root stocks on five soil series. *J. hort. Sci.* 33, 71–9.

Dahlman R.C. & Kucera C.L. (1965). Root productivity and turnover in native prairie. *Ecology* 46, 84–9.

Duvigneaud P. ed. (1963). *L'écologie, science moderne de synthèse.* Vol. 2. *Ecosystèmes et biosphère.* Brussels.

Eaton F.M. (1931). Root development as related to character of growth and fruitfulness of the cotton plant. *J. Agric. Res.* 43, 875–83.

Eckhardt F.E. (1966). Groupe d'Étude de la Productivité Primaire des Ecosystèmes Terrestres. *Enquête sur l'opportunité d'un programme integré de recherches.* Programme Biologique International, Comité François. Montpellier, 1–26.

Eidmann F.E. (1943). Untersuchungen über die Wurzelatmung und Transpiration unserer Hauptholzkarten. *SchrReihe Akad. dt. Forstw.* 5, 1–144.

Farrar J.L. (1961). Longitudinal variation in the thickness of the annual ring. *For. Chron.* 37, 323–31.

Ferrill M.D. & Woods F.W. (1966). Root extension in a longleaf pine plantation. *Ecology* 47, 97–102.

Fritts H.C. (1962). Multiple regression analysis of radial growth in indivdual trees. *Forest Sci.* 6, 334–49.

Griffith A.L. & Howland P. (1961). Silviculture research; rate of growth of new roots and new mycorrhiza immediately after planting. *Rep. E. Afr. Agric. For. Res. Org.* 1960, 84–5.

Heikurainen L. (1957). Der Wurzelaufbau der Kiefernbestände auf Reisermoorböden und Seine Beeinflussung durch die Entwässerung. *Acta for. fenn.* 65, 1–85.

Köhnlein J. & Vetter H. (1953). *Enterückstände und Wurzelbild.* Parey Verlag, Hamburg, Berlin.

Kolesnikow E.W. (1960). The study of the root system of fruit trees by the use of the absorption method. (Russian). *Izv. timiryazev. sel.-khoz. Akad.* 4, 34–42.

Kolesnikow E.W. (1962). *Wurzelsysteme von Obst- und Beerengehulzen und Methoden zu ihrem studium.* (orig. Russian). 190 pp. Moskau.

Kozlowski T.T. (1949). Light and water in relation to growth and competition of piedmont forest trees. *Ecol. Monogr.* 19, 207–31.

Kozlowski T.T. & Winget C.H. (1964). Diurnal and seasonal variation in radii of tree stems. *Ecology* 45, 149–55.

Kramer P.J. (1956). Roots as absorbing organs. *Handb. Pflanzenphys. Encyclop. Plant Phys.* 3, 188–214.

Kravcenko V.I. (1964). Dimensions and weight of the aerial and subterranean parts of *Picea abies* trees in stands of different density. (Russian). *Lesn. Z., Arhangel'sk* 7, 45–7.

Kuroiwa S. (1960). Ecological and physiological studies on the vegetation of Mt. Shimagare. V. Intraspecific competition and productivity difference among tree classes in the *Abies* stand. *Bot. Mag., Tokyo* 73, 165–74.

Kutschera L. (1960). *Wurzelatlas mitteleuropäischer Ackerunkräuter und Kulturpflanzen.* 574 pp. DLG Verlag, Frankfurt.

Laitakari E. (1929). Männyn juuristo (the root system of pine, *Pinus sylvestris*). *Acta for. fenn.* 33, 1–380.

Larson M.M. (1962). Construction and use of glass-faced boxes to study root development of tree seedlings. *Res. Notes Rocky Mount. Forest Range Exp. Stn.* 73

Lemke K. (1956). Untersuchungen über das Wurzelsystem der Roteiche auf diluvialen Standortsformen. *Arch. Forstw.* 5, 8–48, 161–202.

Lieth H. (1961). La production de sustancia organica por la capa vegetal terrestre y sus problemas. *Acta cient. venez.* 12, 107–14.

Lieth H. ed. (1962). *Die Stoffproduktion der Pflanzendecke*. Stuttgart, Gustav Fischer Verlag, 156 pp.

Lieth, H. (1964). Versuch einer kartographischen darstellung der Produktivitat der Pflanzendecke auf der Erde. *Geographisches Taschenbuch* 1964/5, 72–80.

Lieth H. (1965) Ökologische Fragestellungen bei der Untersuchung der biologischen Stoffproduktion. *Qualitas Pl. Mater. veg.* 12, 241–61.

Lieth H., Osswald D. & Martens H. (1965). Stoffproduktion, Spross/Wurzel verhältnis, Chlorophyllgehalt und Blattfläche von Jungpoppeln. *Mitt. Ver. Forstl. Standortskunde ForstpflZücht*. 15, 70–4.

Lieth H., Osswald D., Martens H. & Pflanz B. (1963). *Das Arbeitsprogramm zur Untersuchung der Stoffproduktion am Botan*. Inst. der Landw. Hochschule Stuttgart-Hohenheim. Mimeographed.

Maruyama I. & Sato T. (1953). Estimation of the amount of foliage of trees and stands (Report 1)—on the Akamatu of Iwate District. *Bull. Govt. Forest Exp. Stn., Meguro.* 65, 1–10.

McMinn R.G. (1963). Characteristics of Douglas Fir root systems. *Can. J. Bot.* 41, 105–22.

Miller, W.E. (1965). Number of branchlets on Red Pine in young plantations. *Forest Sci.* 11, 42–9.

Möller C.M. (1947). The effect of thinning, age and site on foliage increment and the loss of dry matter. *J. For.* 45, 393–404.

Möller C.M., Müller D. & Nielsen J. (1954). Graphic presentation of dry matter production of European beech. *Forest ForsVaes. Danm.* 21, 327–35.

Moore C.S. (1966). The relationship of increment in trunk girth with shoot growth in Apple trees. *Rep. E. Malling Res. Stn.*, 1964/65, 115–9.

Nanson A. (1962). (Some fundamental points concerning the balance of photosynthetic assimilation in a Beech forest of the Ardennes.) (french). *Bull. Inst. agron. Stns. Rech. Gembloux* 30, 320–31.

Nomoto N., Kasanaga H. & Monsi M. (1959). Dry matter production by *Chamaecyparis pisifera* in winter. *Bot. Mag., Tokyo*, 72, 450–5.

Odum E.P. (1959). *Fundamentals of Ecology*. W. Saunders, Philadelphia, London.

Odum H.T., Copeland B.J. & Brown R.Z. (1963). Direct and optical assay of leaf mass of the lower montane rain forest of Puerto Rico. *Proc. natn. Acad. Sci. U.S.A.* 49, 429–34.

Olson, J.S. (1959). Analysis of forest growth. *Health Physics Division Ann. Progr. Rept. ORNL–2806.*

Osswald D. (1964). *Das Verhältnis der pflanzlichen Stoffproduktion über und unter der Erde*. Zulassungsarbeit dr T. H. Stuttgart, Unpublished.

Ovington J.D. (1956). The forms, weights and productivity of tree species grown in close stands. *New Phytol* 55, 289–304.

Pavlychenko T.K. (1937). Quantitative study of the entire root systems of weed and crop plants under field conditions. *Ecology* 18, 62–79.

Peterken G.F. & Newbould P.J. (1966). Dry matter production by *Ilex aquifolium* L. in the New Forest. *J. Ecol.* 54, 143–50.

Poljakova-Mincenko N.F. (1961). The foliage of broadleaved stands in the steppe zone. (Russian) *Soobshch. Lab. Lesov.* 4, 40–53.

Rees A.R. & Tinker P.B.H. (1963). Dry-matter production and nutrient content of plantation oil palms in Nigeria. I Growth and dry matter production. *Pl. Soil* 19, 19–32.

Reukema D.L. (1961). Crown development and its effect on stem growth of six Douglas-Firs. *J. For.* 59, 370–1.

Rogers W.S. & Booth G.A. (1960). The roots of fruit trees. *Scient. Hort.* 14, 27–34.

Rogerson T.L. (1964). Estimating foliage on Loblolly Pine, *U.S. For. Serv. Note Sth. For. Exp. Stn. No* SO—16, pp. 3.

Saito H., Shidei T. & Kira T. (1965). Dry matter production by *Camellia japonica* stands (Japanese). *Jap. J. Ecol.* 15, 131–9.

Schober R. (1964). Ertragstafeln und Durchforstung der Fichte. *Allg. Forstz.* 19, 293–5, 319–22.

Shidei T. (1963). Productivity of Haimatsu (*Pinus pumila*) community growing in Alpine zone of Tateyama Range. (Japanese). *J. Jap. For. Soc.* 45, 169–73.

Simon W., Eich D. & Zajonz A. (1957). Vorläufiger Bericht über Beziehungen zwischen Wurzelmenge und Vorfruchtwert bei versciedenen Klee- und Grasarten als Hauptfrucht auf leichten Böden. *Z. Acker-u. Pflbau.* 104, 71.

Smirnov V.V. (1961). The foliage and the weight of aerial parts of trees in Birch stands of the coniferous/broadleaved forests subzone. (Russian). *Soobshch, Lab. Lesov.* 4, 86–97.

Smirnov V.V. (1963). The quantities of needles in Spruce stands. (Russian). *Lesn. Hoz.* 16, 17–9.

Smith W.H., Nelson L.E. & Switzer G.L. (1963). The characterization of dry matter and nitrogen accumulation by Loblolly Pine (*Pinus taeda* L.) on poor sites. *Proc. Soil Sci. Soc. Am.* 27, 465–8.

Stephens G.R. Jr. (1963). Organic matter production in forests. *Front. Pl. Sci.*, 16, 6–7.

Switzer G.L., Nelson L.E. & Smith W.H. (1966). The characterization of dry matter and nitrogen accumulation by Loblolly Pine (*Pinus taeda* L.). *Proc. Soil Sci. Soc. Am.* 30, 114–9.

Takase G. (1960). On the prediction of the growth of diameter by the increment borer (Japanese). *J. Jap. For. Soc.* 42, 207–10.

Tamm C.O. (1953). Growth, yield and nutrition in carpets of a forest moss (*Hylocomium splendens*). *Meddn St. SkogsförskInst.* 43, 1–140.

Tamm C.O. & Carbonnier C. (1961). Vaxtnaringen som skoglig produktionsfaktor. *K. Skogs-o. LantbrAkad. Tidskr.* 100, 95–124.

Vyskot M. (1966). *Method of foundation and evaluation of thinning sample plots*. Mimeographed Report.

Weaver J.E. (1926). *Root development of field corps*. New York and London.

Weaver J.E. & Kramer J. (1932). Root system of *Quercus macrocarpa* in relation to the invasion of prairie. *Bot. Gaz.* 94, 51–85.

Weaver J.E. & Zink E. (1946). Annual increase of underground materials in range grasses. *Ecology* 27, 115–27.

Weihe J. (1961). Massen-und Starkenwachstum der Fichte als Funktion des Hohenwachstums. *Allg. Forstz. u. Jagdztg.* 132, 131–6.

Westlake D.F. (1963). Comparisons of plant productivity. *Biol. Rev.* 38, 385–425.

WHITTAKER R.H. (1965). Dominance and diversity in land plant communities. *Science, N.Y.*, 147. 250–60.

WHITTAKER R.H. (1963). Net production of heath balds and forest heaths in the Great Smoky Mountains. *Ecology* 44, 176–82.

WILL G.M. (1964). Dry matter production and nutrient uptake by *Pinus radiata* in New Zealand. *Commonw. For. Rev.* 43, 57–70.

WOODWELL G.M. & BOURDEAU P.F. (1965). Measurement of dry matter production of the plant cover. *UNESCO Montpellier Symposium* 519–27.

YOCUM W.W. (1937). Root development of young Delicious apple trees as affected by soils and by cultural treatments. *Nebr. Agr. Exp. Stn. Res. Bull.* 95, 1–55.

Index

登録番号　2346
参照番号

ODC分類	2	造林
	3	林木の更新と造成

質問内容	Calliandra calothyrsusの淡水魚養殖用飼料としての有効性について
プロジェクト	パナマ森林保全技術開発計画
地域　：　国名	中部アメリカ　：パナマ
キーワード	養殖、アグロフォレストリー、飼料、シルボフィッシャーズ
参考文献	

質問者	高野憲一	回答者	浅川澄彦

個別技術情報支援のための質問書

プロジェクト名　パナマ森林保全技術開発計画
リーダー名　高野憲一

質問技術テーマ：*Calliandra calothyrsus*の淡水魚養殖用飼料としての有効性について

1．質問技術テーマの具体的背景、及びそのプロジェクト活動の中での位置付け
2．プロジェクト側の計画案、解決策案、質問技術テーマの具体的な内容、問題点及びプロジェクト側の期待する回答の範囲
3．その他

1．プロジェクト周辺のコクレ県はパナマ国内でも水田が多い地域で、進んだ農家では水田を利用して（乾期用の避難場所を作るなどして、）テラピアや鯉、手長エビの養殖を行っているものもある。当プロジェクトの課題には養魚と植林を組み合わせた展示があるが、この在野の養魚手法と植林を組み合わせたアグロフォレストリーシステムを展示したいと考えている。

2．ケニア西部Busiaでは、テラピアの養魚池の周辺に*Calliandra calothyrsus*を植栽し、日陰を提供、畦を保全するとともに、このフォダーを養魚池にまいて、餌として活用していた。この手法は林木の保全的な機能と飼料生産の機能を組み合わせた興味深い事例なので、プロジェクトでもこの事例を参考に展示植栽を実施したいと考えているが、他の地域で見たことがなく、またプロジェクトにある文献・資料の中でもこの点についてふれたものがないため、本当に有効であるか疑問が残る。そこで、他に、この手法についてふれた文献があればご紹介願いたい。また、上記手法に関連した別の事例があればご紹介願いたい。

質問のキーワード：

希望資料名：	希望指導委員名：浅川澄彦

パナマ森林保全技術開発計画の質問に対する回答

テーマ：Calliandra calothyrsusの淡水魚養殖用飼料としての有効性について

Calliandra calothyrsusがＭＰＴＳの重要な１種であることは承知していましたが、ケニアで、テラピアの養魚池周辺に植えられているということは知りませんでした。早速、1996.1にインドネシアで開催されたワークショップの論文集（International Workshop on the Genus Calliandra. Evans, D.O.,ed.,FFCTRR Special Issue, Winrock International, Morrilton, Arkansas）を見直してみましたが、このことについては少なくともトピックスとしては載っていません。インドネシアでは1936年にタネが導入されて以来、広く植栽され、いろいろな面で利用されてきたようですが、Silvofisheriesの視点からの用途は少なくともこの論文集には見当たりません。またその他の論文にも、ざっと見た範囲では書かれていないようです。

水産の専門家にも質ねてみましたが、これまで聞いたことはないそうです。その方によりますと、養魚池の近くに樹木を植える場合には、直接影をつくらないように注意する必要があるとのことです。また、その方から紹介されたFish Culture for Small-Scale Farmers(1984)というマニュアルをみますと、Building your pondという章のWhere to build your pondという節にこのことが書かれていますので、その部分のコピーを添えます。このほかにもいくつかの事例を見ましたが、いずれも養魚池の周囲には樹木は植えられていません。ただし Aquaculture Asia の最近号にマングローブ林におけるSilvofisheriesの論文が載っていますが、この場合には両者はかなり接近しており、前記マニュアルの記載とは状況が異なるように思います。もっともCalliandraの場合には、もともと低木のようですから、すこし離して植えれば問題はないかも知れません。

さて一般論として、落葉広葉樹の落葉がプランクトンの増殖に有効であり、従って魚類の生産にも有効であることはかなり以前から言われていますし、そういう文献もみたことがありますが、この場合にも、落葉の分解物がプランクトンに利用され、魚類はプランクトンなどを食べるという流れになっています。従って、フォダーをそのまゝ養魚池にまくのでなく、一旦堆肥のような状態にしてから投入するものゝようです。

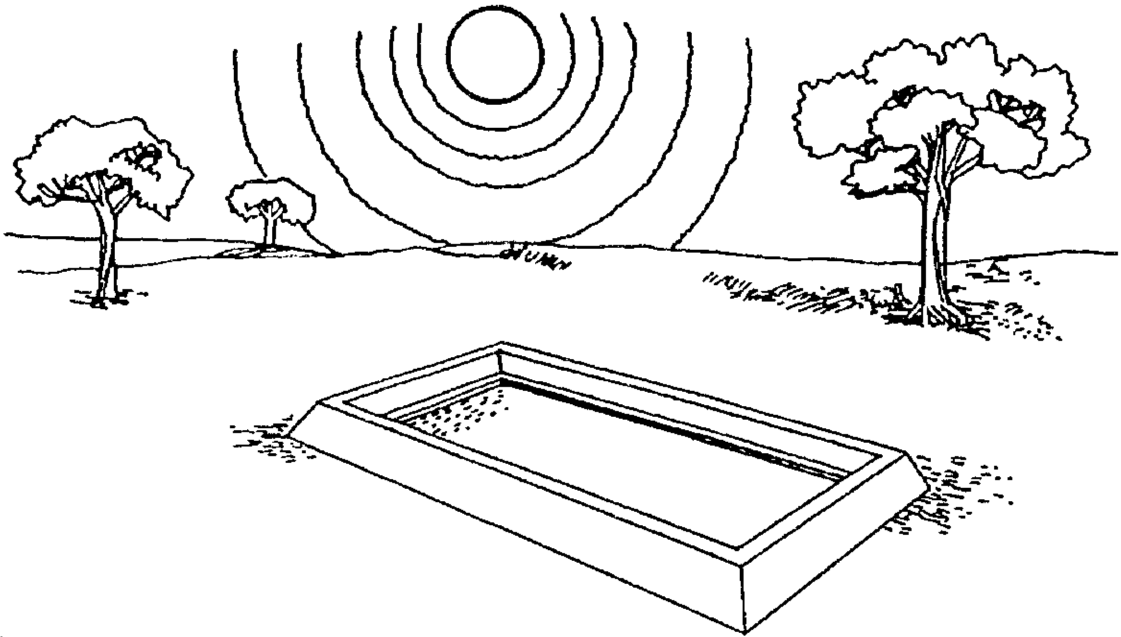
次に、葉の養分組成についてですが、これまで家畜飼料の主力とされてきたギンネムに代わり得る組成だと評価されていますので、おそらくプラントンの培養にも有効なものと思われます。ただし、同じ中米原産のGliricidiaなど、樹種を複数にされたらどうでしょうか？

以上、取り合えずの回答といたしますが、今後もこの種の文献や事例がないものか十分に注意したいと考えます。いずれにしても新しい発想にたった興味ある試みであると思われますので、問題点には留意されて、先進的な展示をされますよう期待しています。

（浅川澄彦）

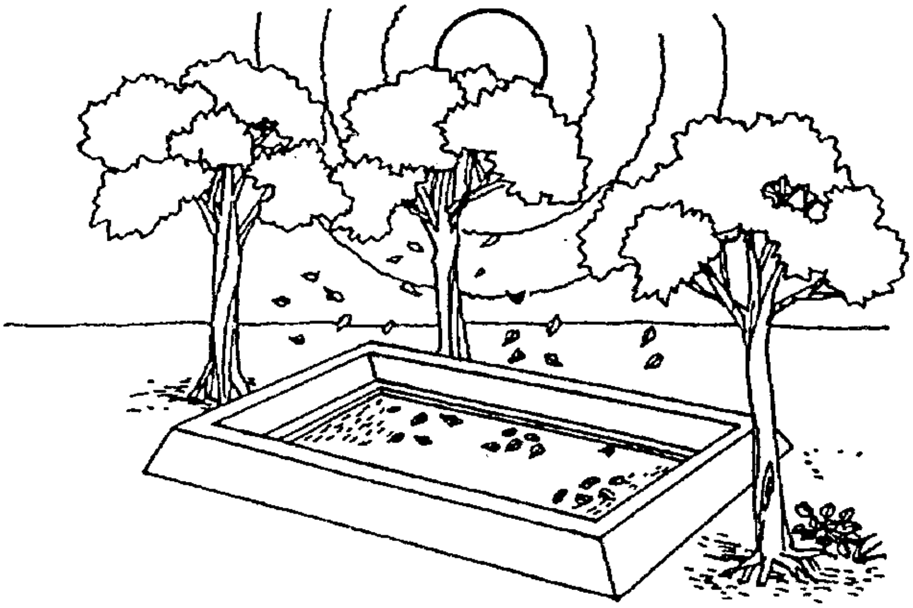
You should build your pond away from trees so it can receive the sun's rays. Light is important for the production of natural food in the pond for your fish.

良い例



Overhanging trees or bamboo will shade the water and also drop leaves into the pond which may make the water quality poor.

悪い例



登録番号　2701
参照番号

ODC分類	2	造林
	3	樹木園　鑑賞目的の樹木栽培　生け垣と生け垣用植物
質問内容	防風林植栽のデザイン	
プロジェクト	パナマ森林保全技術開発計画	
地域　：　国名	中部アメリカ　　　　：パナマ	
キーワード	防風林、アグロフォレストリー、メイズ、植栽間隔、マルチストーリー	
参考文献		

質問者	高野憲一	回答者	工藤哲也

個別技術情報支援のための質問書

プロジェクト名　パナマ森林保全技術開発計画
専門家名　高野憲一

質問技術テーマ：防風林植栽のデザイン

1．質問技術テーマの具体的な背景、及びそのプロジェクト活動の中での位置付け
2．プロジェクト側の計画案、解決策案、質問技術テーマの具体的な内容、問題点及びプロジェクト側の期待する回答の範囲
3．その他

1．プロジェクト周辺のコクレ県は季節風が強く、農作物にたいする影響が大きい。
　このため当プロジェクトは防風林をアグロフォレストリーの重要な一技術として位置付け、訓練コースで研修するとともに、展示用の防風林を造成することを計画している。

2．ＩＣＲＡＦ（国際アグロフォレストリー研究センター）マチャコスステーション（ケニア）での事例を参考に、地域の主要作物であるメイズの農地にマルチストーリーの防風林を造成し、造成しない場合とのメイズのパフォーマンスの違いを比較・対照・展示する予定である。しかし、当プロジェクトで収集したアグロフォレストリー関連の資料の中では、シングル、マルチストーリーの防風林の効用について書かれた文献は多いが、その具体的なデザイン（植栽間隔等）についてふれているものは全くなく、実際の植栽計画作成に支障がある。そのため、熱帯各地で実際に行われている防風林植栽の具体的デザイン（植栽間隔等）をいくつか紹介していただきたい。しかし、あまり防風林に面積をとりすぎるデザインは結果的に農地面積を減らすことになって、農民に普及しにくいデザインになるので、できればあまり幅をとらないものが望ましいかと考えている。

質問のキーワード：

希望資料名：

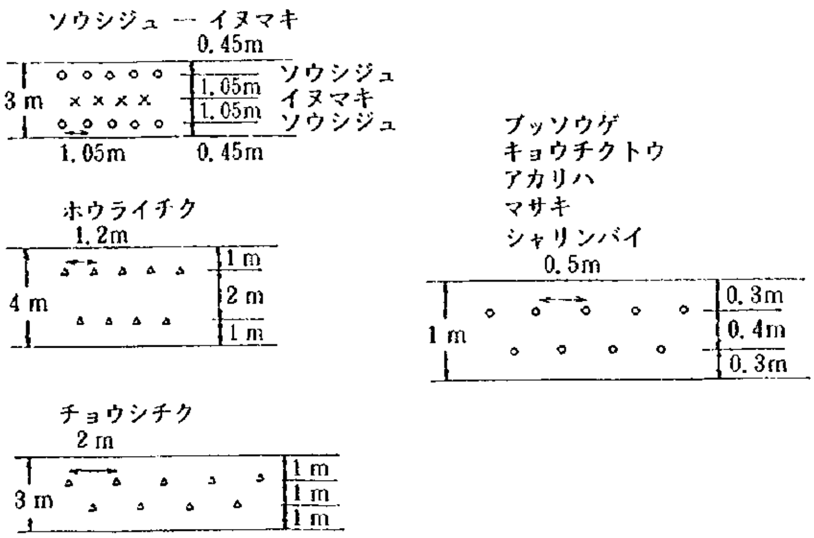
希望指導委員名：工藤哲也

パナマ森林保全技術開発計画における防風林造成計画に対する回答

プロジェクトの希望としては、2～3層程度の複層（複層林）の林帯造成を希望しているようです。複層林の林帯を造成するためには、それなりの広い林帯幅が必要です。そして複層林の林帯でも、林帯の構造によって防風機能は同じではありません（後述）。

貴プロジェクトで計画する防風林造成時の制限条件としては、林帯の配置間隔は30～50mとのことで、ここでは前提条件として配置間隔を50mとします。このような場合、使用可能な林帯幅は10m以上とは考えにくく、妥当な幅は5m以下と考えたらよいでしょうか。また、適度の密閉度（後述）をもつ防風林は、防風効果距離が樹高の20倍程度は期待できますから、この理屈からすれば林帯樹高は 2.5mあれば良いことになります。これは防風林というより防風垣になりますが、実際に成長して樹高が5mに達すれば、防風効果は一層向上します。だから林帯の配置間隔を50mとする場合、以上のような考え方で植栽樹種を選択すれば良いことになります。計画地の土地条件に合うような果樹があるといいですね。

一方、熱帯各地で実際に行われている防風林の植栽例を、との要望ですがあいにく見つけることは出来ませんでした。唯一探し当てたのは、南西諸島の石垣島における植栽計画の例です。この場合の植栽幅は1～4mです（下図）。採用樹種はこのとおりにできないでしょうから、そちらの在来樹種から選択せざるを得ないでしょう。



石垣島における植栽計画の例

以下に記したのは、一般論ですが参考にして下さい。

森林の防風機能

(1) 森林の防風機能

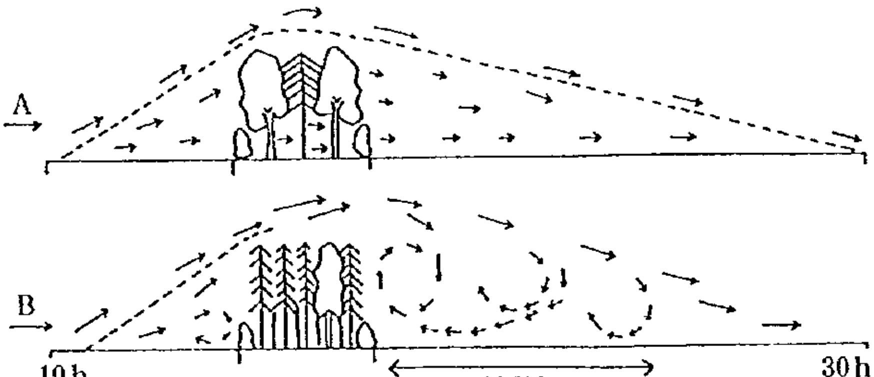
森林は風の流れに対して抵抗物の役割を果たすことで、保護対象物に対する直接の、あるいは間接の加害作用を軽減する機能を持つ。直接的には風速を弱めるとともに風向に変えることにより、間接的には塩分・霧・粉塵等の風によって運搬される微粒子を捕捉したり、冷気流や熱流の移動を防止することにより、本来生じる様々な被害を軽減する。更にこれらの機能の結果として、防風林周辺の微気象を改良する。

防風林は海岸防風林（coastal windbreak）と内陸防風林（inland windbreak）に大別される。海岸防風林は海岸地帯に造成され、その目的は強風および強風による飛砂や海から飛来する塩分を防ぐことにある。内陸防風林は一般的には、農作物や農業施設を強風や飛砂の害から保護するために、農耕地に隣接して設けられる。その効果を及ぼす範囲は、林帯の構造とか樹高（林帯高）・密度（密閉度）等により左右される。

(2) 内陸防風林

1）樹高（林帯高）

防風林の防風効果の及ぶ範囲は、林の樹高が高いほど広くなる。この場合、減風域の程度は、一般的に実距離（m：メートル）よりは樹高・林帯高（h）の倍数で表されることが多く、高倍距離とも称される。生垣を利用した野外観測や風洞実験の結果によると、防風の範囲は高さの約 1.1乗に比例する結果が得られている。しかし林帯高と防風域との関係は、一様に密な林帯とか下枝がなく吹き抜ける林帯とかの林帯の構造によって（図－１）、また風速の垂直分布や接地気層の状態などによっても変化し一定ではない。



図－１　適切な密度の林帯（A）と過密な構造（B）の林帯の風の流れ

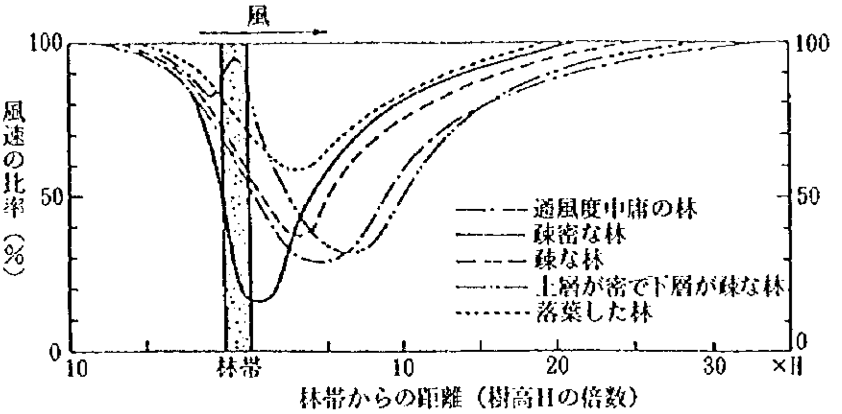
2）密閉度（密度）

森林の防風効果は、林帯の密度により変化する。林帯の密度が高すぎると、林帯の風下直後に逆方向の渦ができるため、その後の風速の回復が早く減風域の範囲が狭くなる。密度の

疎らな林帯では、風下側で減風率が小さくなり、害を及ぼす風速の低下が期待できない（図－２）。

防風林・生垣では、正面から見て幹・枝葉が全面に一様に分布し密閉度が60～70%の時、防風効果は最も大きいとされている。

密閉度の測定法としては、林帯の正面から撮影したモノクロ写真の濃淡を測定する方法とか、方眼に区切った枠を林帯前方に置き、各方眼毎に樹体の占める割合を目測して算出する方法等がある。



図－２　各種の密閉度をもつ林帯の防風効果

３）林体幅

林帯幅が増すことは密閉度が高くなることであるから、結果として林帯風下の減風域の範囲や減風率に影響を与える。幅の広い林帯ほど密閉度が増し風下の減風率は大きくなるものの、減風域は小さくなるので、どの程度の林帯幅が望ましいかが問題となる。以下に最適な林帯幅を試算した例を記す。

（最適林帯幅の試算例）

防風効果に影響を与える林帯の幹・枝葉の量に代わる指標として、測定が容易な胸高直径を用いた。典型的な各種防風林における風速の実測と実験に基づき、林帯を正面から見て10mの範囲に含まれる林木の胸高直径の合計値が、

①　内陸防風林では約 800cm

②　クロマツ海岸防風林では約 3,500cm

③　広葉樹海岸防風林では約 2,000cm

を基準値とした。

これらの値を用いて平均胸高直径10cm、ha当たり立木本数 2,500本の林分を想定すると、

①　内陸防風林では32m

②　クロマツ海岸防風林では 140m

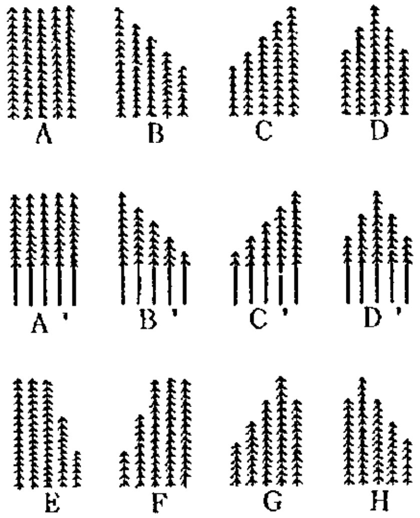
③　広葉樹海岸防風林では80m

が望ましい林帯幅と算定される。

4）林帯の横断形状

風向に沿った防風林の断面の形、横断形状も防風効果に影響を及ぼす一因である。ヒノキの枝で種々の横断形状を作り、防風効果との関係を調べたモデル実験の結果は以下のようである。横断形状としては、矩形のもの（A）、風下側に傾斜をもつもの（B）、風上側に傾斜をもつもの（C）、及び風上側・風下側ともに傾斜をもつもの（D）を基本形とした（図−3）。

得られた結論は、①A、A'、Eの型が書くグループの中で最大の防風効果を示す。しかし成林過程で林帯の風上側が被害を受けやすい。②B型もA型とほぼ同じ短所を持つ。③風下側が最も高いC型では有効範囲はやや低下するが、風による障害が少なく成林しやすい。



図−3　林帯の横断形状（風は左側から吹く）

他のモデル実験例では、風下で風速が半減する距離は矩形では15.5h（h：高倍距離）、三角横断では15h、頭部が丸い形では9hであった。これらの結果から、防風効果の最も高いのは、矩形の断面を持つ林帯であるといえる。

防風林の造成

(1) 植栽樹種と植栽方法

防風林の樹種は、一般的に次のような特徴を備えたものが望ましい。

① 樹幹が強靱である。

② 樹冠が密で枝葉の着生点が低い。

③ 防風が必要な時期に枝葉が十分繁茂している。

④ 成長が早い。

⑤ 深根性である。

⑥ 土地の気候風土に適している。

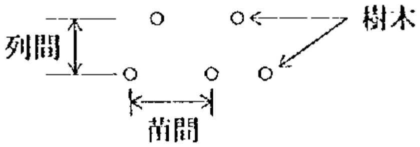
⑦ 病虫害に対して抵抗力がある。

⑧ 作物に対して病虫害の宿主にならない。

防風林は、その樹幹と枝葉が風に対する抵抗物となり防風作用を発現するので、植栽本数は普通の造林地よりも密にすることが望ましい。植栽本数は、一般に肥沃な場所で成長の良い樹種を用いる場合には 3,000本／ha、痩せ地で成長の遅い樹種の場合には 5,000本／ha程度とする。

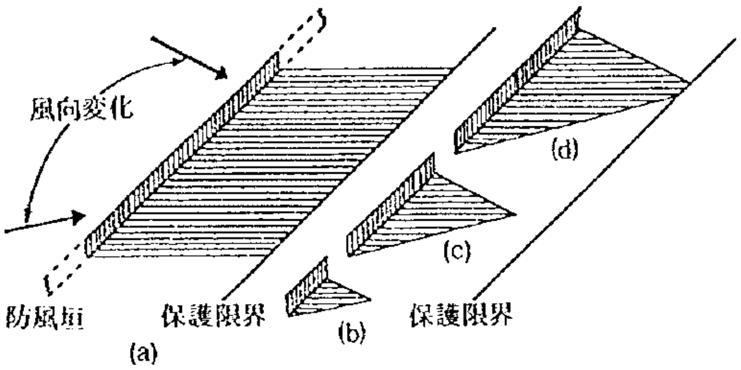
防風林造成では一般に 1.5～2.0 mの正三角形植栽が行われている。表－１に植栽する苗木の間隔から算出した植栽密度を示す。

表－１　苗木の間隔と植栽密度（正三角形植えの場合）

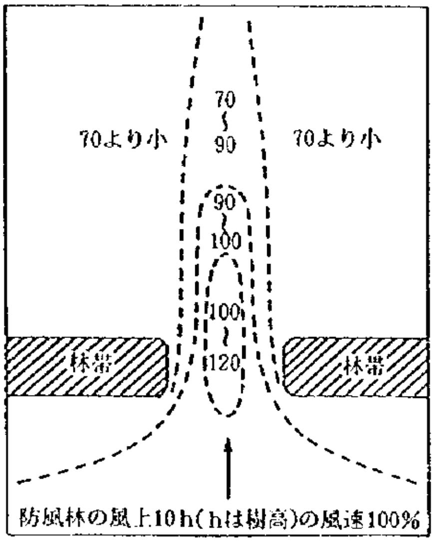
苗間距離（m）	列間距離（m）	１本の割当て面積	植栽本数（ha当り）（本）	備考
0.6	0.52	0.31	32,075	a ：苗間距離（m）
0.8	0.69	0.55	18,042	b ：列間距離（m）
1.0	0.87	0.87	11,547	S ：１本の割当て面積（㎡）
1.2	1.04	1.25	8,019	A ：植栽面積（㎡）
1.4	1.21	1.69	5,891	N ：植栽本数（本）
1.6	1.39	2.22	4,511	
1.8	1.56	2.81	3,564	
2.0	1.73	3.46	2,887	
2.2	1.91	4.20	2,386	$b = \frac{\sqrt{3}}{2} a = 0.866\ a$
2.4	2.08	4.99	2,005	
2.6	2.25	5.85	1,708	$S = a \cdot b$
2.8	2.42	6.78	1,473	$N = \frac{A}{a \cdot b} = \frac{A}{0.866a^2} = 1.1547 \frac{A}{a^2}$
3.0	2.60	7.80	1,283	

⑵ 林帯の長さ

防風林帯は、その長さの方向に直角な風に対して最も有効に作用するが、林帯に対する風向の変化によって、防風効果の範囲も変わってくる。図－４⒜のように林帯が十分長ければ防風範囲は変わらないが、⒝～⒟のように林帯が短い場合には、効果範囲は林帯の長さを底辺とする三角形の範囲に減少する。効果範囲が減少する度合いは、林帯の長さの二乗に比例する。その理由は、⒞⒝のように林帯がさらに短くなると、三角形の底辺と同時に高さも減少していくためである。また風向変化が大きくなると、底辺に対する角度が小さくなるので、効果範囲も減少する。したがって、林帯は風向に直交する長さが長いほど効果が大きい。



図－４　林帯の長さと風向による効果範囲の変化



図－５　林帯の切れ目での風速の増加

林帯の切れ目では風が収斂して逆に風が強まるので（図－５）、切れ目の風下側に補助的な防風林とか生垣を設ける必要がある。

⑶ 林帯の幅

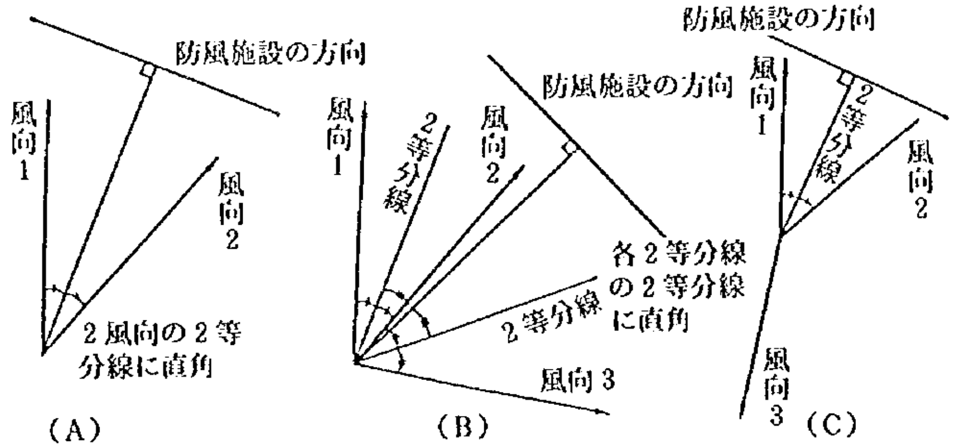
防風機能を最も良く発揮するのは密閉度が60～70％の林であるが、林帯幅については風下林縁における風速が、風上林縁の風速の60％に減少するような幅が最も良いとされており、これは普通の構成の林帯で約30ｍに相当する。また野外観測によると、林帯幅が広いほど防風機能は高いというわけではなく、幅が樹高の５倍以上になると防風効果はかえって低下するとされている。農業地に設置する場合は幅10ｍ程度（３～５列植）までが一般的である。

潮風や霧の被害が及ぶ場所では林帯幅が広いほど効果は大きいが、それに加えて更新のための幅を見込んでおく必要がある。更新に際しては、その機能を低下させないように行うべきである。

⑷ 配　置

防風林は、風害を起こす卓越風向に対して直角に設けることが原則であり、最も効果的であ

る。その効果は風向が斜めになるほど低下し、30°の斜風で最大約15%、45°の風で約20%効果が低下するといわれている。主風向が単一あるいは全く逆な2方向の場合にはその風向に直角でよいが、図－6に示すように2～3方向の風が卓越する場合には、2等分線による方法で林帯の方向を決定する。但し、地形条件・道路・水路・既存防風林などの位置関係から林帯を直角に配置できない場合には、諸事情を総合的に考慮して最も効果的な方向に配置する。



図－6　最多風向に近い風向が2方向、3方向にある場合の防風林設定方向の決定方法

林帯を数列にわたって配置するには、防風効果の及ぶ範囲が林帯前方で5h、林帯後方では20hの場合、以下の方式で配置間隔を算定する。

① 林帯の方向が主風に直角な時

$$D=(5+20)h+(d+d')/2$$

② 林帯の方向が主風に直角でない時

$$D=(5+20)h\sin\alpha+(d+d')/2$$

但し、D　：林帯の中心から次の林帯の中心までの距離（m）
h　：林帯の期待される樹高（m）
d、d'：それぞれの林帯幅（m）
α　：主風向と林帯の方向とのなす角度

本プロジェクトで問題となる要件

(1) 林帯造成にどの程度の幅を用意できるか（特に農地の風上第一線林帯で）。
………林帯の構成に関係する
………防風効果（範囲）に関係する

(2) 林帯造成の植栽樹種として、どのような樹種を採用するか。
………林帯の構成に関係する
………防風効果（範囲）に関係する
………林帯の最終樹高に関係する

　　………林帯成林までの年数に関係する

⑶　林帯成林時に想定される樹高はどのくらいか。

　　………防風効果（範囲）に関係する

　　………林帯の配置間隔に関係する

⑷　林帯成林までに想定される年数はどのくらいか。

　　………植栽樹種の選択に関係する

　　………防風効果発現までの年数に影響する

登録番号　5101
参照番号

ODC分類	5	測樹　生長量　林分の成育課程と林分構造　測量と図化
	1	測定法と測定単位
質問内容	草地の生産性の測定について	
プロジェクト	パナマ森林保全技術開発計画	
地域　：　国名	中部アメリカ　：パナマ	
キーワード	放牧、土地利用、混牧林、草地、Brachiaria decumbens, Tabebuia rosea, Cordia alliodora	
参考文献	生態学実習書	

質問者	高野　憲一	回答者	河原　輝彦

個別技術情報支援のための質問書

プロジェクト名　パナマ森林保全技術開発計画
専門家名　高野憲一

質問技術テーマ：草地の生産性の測定について

1．質問技術テーマの具体的な背景、及びそのプロジェクト活動の中での位置付け
2．プロジェクト側の計画案、解決策案、質問技術テーマの具体的な内容、問題点及びプロジェクト側の期待する回答の範囲
3．その他

1．パナマは他の中南米諸国同様、放牧による粗放な土地利用が一般的に行われており、環境天然資源省はより保全的な土地利用への転換を奨励している。そのため、プロジェクトでも各種の混牧林システムの保全・経済的有効性を試験・展示する事を課題として実施してきている。この中に造林樹種混植下（ha１００本植えとha４００本植えの２密度）での草地の生産性を無立木の草地と比較対照する試験課題があり、１９９７年９月から試験地を造成してきている。

2．混植された林木に関しては一般的な生長量調査を行う予定であるが、草地の生産性を計測する方法が不明なため、一般的に実施されている計測方法をご紹介願いたい。

3．牧草としては、比較的乾燥にも強いといわれる*Brachiaria decumbens*を１９９７年１０月に一律に播種したが、その撫育方法についても特に指摘があればお願いしたい。なお造林樹種は郷土樹種の*Tabebuia rosea*と*Cordia alliodora*である。

質問のキーワード：

希望資料名：	希望指導委員名：

草地の生産性を計測する方法

別添資料の　(5)現存量の測定法　l)草原の場合　に基本的な方法は記述されているが、以下に記述内容に沿って補足を記す。

対象草地は、造林樹種混殖下の草地及び無立木の草地と理解される。両草地とも牧草を播種した草地か、無立木の草地は”放牧による粗放な土地利用”が行われてきた草地か文面からは判断できない。Brachiaria　decumbens はキビ属に近縁のニクキビ属の草種であるが、手近な図鑑等では調べがつかなかった。多年生であろうと推定したが、具体的な特性、草姿は判らない。以上を前提としている。

1．方形枠（コドラート）は牧草地の場合１ｍ×１ｍが一般的あるが、野草地では草種によって群落の姿がかなり異なるので、記述のように、コドラートの大きさを変える。

2．造成した牧草地では層別化する必要ない。野草地では景観的に異質な群落を含む場合は層別化する。(ここでは平面的な層別化を言っており、ii)とは異なる)

3．サンプリング数の”５～１０カ所”は妥当なところである。理論的にはこの数では相当に少なすぎるのが一般だが、作業面を考慮すれば増やすのは難しい場合が多いだろう。

4．コドラートはなにで作ってもよいが、枠を固定し刈り取り作業がやりやすい必要がある。糸は刈るときに切りやすいので臨時的以外には勧められない。２ｃｍ幅くらいの鉄ののべ板を用い、内法を１ｍとし、四隅を溶接したコドラートは丈夫で、ある程度の重さがあって使いやすい。木でも勿論よい。刈り取り作業の時、枠が動き刈り取り面積が狂うのを防ぐためある程度重い方がよい。

5．枠の内側で草を分ける。予め対角に棒をさして枠を固定するとよい。

6．刈り取りには刃渡り２０ｃｍ位の鎌を使うのが一般である。はさみは多労である。刈り取り高さは試験の目的によって変えるが、地際から刈ると再生を期待する草ではダメージが大きいため、生産性を見るには適しない。年１回刈で総生産量を見るにはよい。牧草では一般に再生と家畜の採食する高さを考慮して地上５～１０ｃｍで刈る。草の特性も考慮して決めればよい。

7．コドラートはランダム配置するのが正しいが、現場でこれはなかなか難しい。恣意的にならないような配置法を取る必要がある。機械的に配置する（等間隔をおいて配置等)、枠を投げる等の方法が取られる。枠数が少ないので明らかに特殊な地点に当たったときは枠を移動することもある。

8．刈り取り後の処理は記述の通りでよい。草種毎に区分する、部位別に草分けする、生草と枯れ草を分ける等は試験の目的による。生産量だけを見るなら、全生重を現場で計り、一部を乾物重を出すためのサンプルとして持ち帰る方法で十分である。目的によっては生重だけでもよい。

9．通常牧草は刈り取り又は家畜の採食後再生し、その再生草を再び利用する。このため年間の生産量を求めるには年間に何回か刈り取ってその合計で生産量とする必要がある。草種の再生力や施肥量によるが、年間２～５，６回の刈り取りを行う。刈り取り回数を何回とするかの判断が重要だが、この回数自体が重要な研究テーマであった。

１０．草地の管理については草と利用法が判らないのでコメントできない。初期生育とスタンドの確保が重要なので春～夏の管理（施肥と利用）に十分注意する必要がある。

盛の$\frac{1}{5}$〜$\frac{1}{10}$まで読む．トーションバランスには振動止めがついているが，目盛を読むときには，これを止めない方がよい．葉はそのままトーションバランスにかけて放置する．3）第一回秤量3分後に再び葉重量を測定する．4）乾湿球温度計の目盛を読む．5）実験終了後葉面積を測定する（測定法は114頁参照）．切りとった葉の蒸散量の時間的変化を調べる場合には，測定間隔を最初は1〜3分ごとに行ない，重さの減りが少なくなってきたら，測定間隔をのばす．蒸散量の表示は測定値が相互に比較できるように一定の単位葉面積，時間，および空気の水蒸気飽差に換算する．たとえば $mgH_2O/cm^2/min/10mmHg$ を用いる．これを蒸散速度とよぶ．飽差の算出法は11頁を参照されたい．

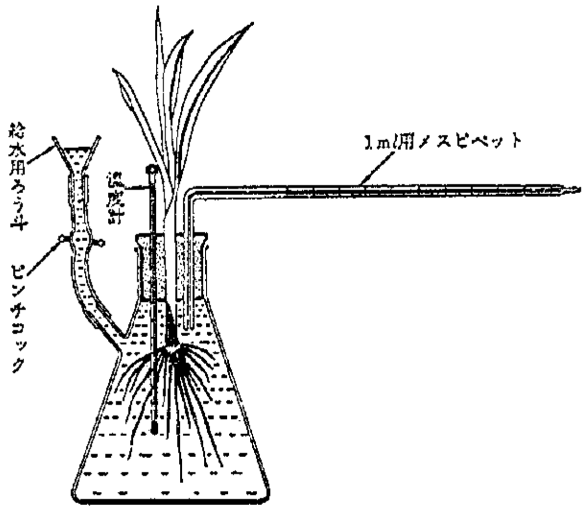


図 I.52 吸水計の一例（佐伯敏郎，1955）
ピンチコックを開き，水を補給しているところ

3）吸水量　植物の生活が正常であれば，吸水量は蒸散量に等しいが，根のおかれている環境が変わると吸水量も変わる．吸水量を直接測定するには吸水計を用いる．図I.52にその一例を示してあるように，切枝または根のついた植物を使用する．植物の吸水とともに側管の水面は次第に左に移動するから，一定時間ごとに水面の位置を読んで吸水量を算出する．また本装置全体の重量の減少量を測定すれば，蒸散量が求まる．植物体を吸水計に固定するには，ゴム栓のほぼ中央に茎の太さ程度の穴をあけ，この穴を通して縦に半割りにする．枝付きコルベンに水をみたし，空気が入りこまないように栓をする．すき間はワセリンで封ずる．実験に使用する水の温度が，実験場所の気温とほぼ等しくなってから測定を開始する．実験に使用する水をあらかじめ煮沸して放冷させておけば，温度が上昇しても気泡が発生しないが，根の呼吸を阻害するおそれがある．吸水計の原理に従って実験植物に適当な形の装置をつくってもよいが，次のことに注意した方がよい．

1）装置全体の容積があまり大きくならないこと．2）読みとりが側管の目盛の範囲内で常にできるように装置に給水管をつける．3）吸水は温度に敏感な生理作用だから，水温測定用の温度計を必ずつけておく．また測定値について温度変化による水の体積変化を補正する．4）気体の膨張は温度に敏感であるから装置内に気泡をいれぬこと．5）切枝を用いる時は水中で茎を切る．空気中で茎を切ると導管内に空気が入りこみ吸水が止まることがある．

4）葉の水分欠差（Čatský，J.，1960による）直径8mmの円板*を10枚，中肋を含まないようにして葉身から切りとり，ただちに秤量**（W_0）する．これらの円板を，直径8mmの穴を10個あけ，水で飽和させたプラスチック製スポンジ（8×5×0.8cm）の穴の中に一枚ずつ置く．このスポンジの両面を穴のないスポンジ板でおさえる．これを大形のシャーレの中におき，蓋をして20°Cの暗室に3時間放置する．3時間後にスポンジ板の間から円板をとり出し，机上に4枚の沪紙（直径12.5cm）を重ねた上に円板をおき，その上に同じ大きさの沪紙4枚をかぶせる．沪紙の上から全面に重量がかかるようにして500gのおもし***をおいて30秒間放置する．円板の生重（W_3）を測定したあと，再び前述と同様にスポンジの間に円板をおき，さらに3時間放置する．その後，生重（W_6）を測定し，85°C，24時間乾燥させたあとで乾重（DW）を測定する．水分欠差は次式で算出する．

$$水分欠差(\%)=\left(\frac{2W_3-W_6-W_0}{2W_3-W_6-DW}\right)\times 100$$

よく切れるコルクボーラーで切抜く．円板の周縁がきれいに切れていないと測定値がふれる．

** 秤量はいずれも0.1mgまで精確に行なう．

*** 蓋付きのプラスチック製容器に水をいれて全体で500gにするとよい．

〔戸　塚　　績〕

（5）現存量の測定法

1）草原の場合

i）サンプリングのしかた　草原の植物現存量を測定するまえに，調査の目的に応じたコドラートの大きさ（面積），サンプリング数およびサンプリングする場所（地点）を決めておかねばならない．その際，できるだけ少ない労力で，調査の精度を高め，信頼度の高い測定値を得るよう細心の注意をはらう必要がある．

コドラートとして普通，方形わくを用いるが，その大きさは群落の高さや均質の度合（生育状態の精密）によって異なる．すなわち，25×25cm，50×50cm，1×1m，および2×2mなど調査する群落の状態によって使いわけるのである．たとえば，草丈の低い，密な生育をしているシバ草原では小さな（たとえば25×25cm）コドラートでよく，ススキ草原のように草丈が高く，大きな株が不均質に分布する群落では大きなコドラート（1×1m，あるいは2×2m）が必要になる．一般に群落の生育状態が粗なものほど大きなコドラートを，また草丈の低いものほど小さなコドラートを使う．

ひと口に草原といっても，局地的にみれば構成種も草の生育状態もかなり異なっている．このような草原で，ただやたらにサンプリングをしたのでは，労力ばかりかかって，意味のある結果は得られない．そこでサンプリングの地点については，まず草原の相観をみて，草原を構成種，均質の度合，あるいはまた採草，火入れ，放牧など人間による処理の違いによって，層別化することが必要である．もちろん厳密に層別化することは困難であるので，おおよその見当である．こうして選んだ均質な群落の中で無作為にサンプリング地点を決める．

サンプリングの数も，群落の面積の大小，均質あるいは不均質の度合，労力の多少によって異なるが，少なくとも5～10ヵ所くらい欲しいところである．現存量を測定する際に，コドラートの周囲がかなり荒され，1 m^2 のサンプリングによって4 m^2 近くの群落がつぶされることがしばしばある．現存量の季節的変化を調査するような際には，このことを十分に考慮してサンプリング数を決めないと，あとで測定できないということになりかねない．

地上部の現存量測定のためのコドラートは木製のわくを使うことが多いが，コドラートの四隅に赤い布をつけた5寸クギをさして固定し，これを太いタコ糸で囲んでもよい．この場合，クギとクギの間に糸をピンと張り，地表の高さでの茎の位置によって，コドラートの内と外の植物を分ける．コドラート内の植物は地表のはえ際から，剪定ばさみを使って切り取り，ただちにポリ袋に詰め，水の蒸発による減量を防ぐ．実験室に持ち帰ってから，種類ごとに分け，生量を測定する．生量をはかった植物は，紙袋に入れ，必要な事項を紙袋に記入した上で，80°C に調節した乾燥機に入れる．試料は恒量になるまで乾燥した後，乾量を測定する．試料の量が大きい時は，野外で全体の生量を測定し，一部をサブサンプルとしてとり，実験室に持ち帰って生量と乾量の比を求め，これから全体の乾量を計算する．なお，生長解析の目的には，葉身（光合成系）と茎・葉柄・花・実（非光合成系）とをわけて秤量し，さらに葉面積の測定を行なう必要もある．

ii）層別刈取法（Stratified crip method）　層別刈取法は植物群落における光合成系と非光合成系の空間的配置を調べるための方法で，これによって明らかにされる群落の階層構造は，物質生産の機能面とも対応するので，群落の“生産構造”とよばれる．また層別刈取の結果得られる生産構造図は，群落を構成する各々の植物種の量と空間的配置を明瞭に示すので，種間競争や遷移などの研究に役立つ．また，生育期間中の生産構造の変化を継続して調べれば，葉の脱落量の推定にも利用できる．

これを実際に行なうには群落の中で割合に均質なところを一定面積（50×50 cm または 1×1 m のコドラート）をとる．コドラートの四隅には高さを目盛ったポールを垂直に立てる．

刈取りは群落の上の方から一定の厚さ（群落の高さにもよるが普通 10 cm，または 20 cm）ごとに順次，剪定ばさみを使って行なう．この際，四隅のポールの間にタコ糸を水平に張り，糸の高さを刈取りの高さに合わせ，上より順次下へずらしていくと，きれいな層別刈取ができる．また刈取りは，できるだけ自然の状態のまま行なうよう心がける．イネ科の植物では斜めになっていた葉が，上部の葉身を切りとることにより立ち上ることがある．この場合には，元の斜めの状態にもどして刈取りを行なうようにする．刈取った植物体は，各層ごとにポリエチレン袋に詰め，実験室に持ち帰る．実験室では植物をまず種類別にし，（種類が多いときは目的に応じて適当なグループ別にしてもよい），さらにそれぞれを光合成系と非光合成系とに分け，生量，乾量の測定を行なう．

表 I．30は，このようにして得られた結果である．これから生産構造図をつくるには，方眼紙を用い，各

表 I．30　霧ケ峯ススキ群落の層別刈取の一例
F：光合成系．　C：非光合成系の乾量．8月上旬測定．

高さ (cm)	ススキ F (g/m^2)	ススキ C (g/m^2)	その他 F (g/m^2)	その他 C (g/m^2)	合計 F (g/m^2)	合計 C (g/m^2)	相対照度 (%)
140 ～ 160	0.6	—	—	—	0.6	—	100
120 ～ 140	3.8	7.3	—	—	3.8	7.3	
100 ～ 120	18.2	14.0	—	—	18.2	14.0	98.0
80 ～ 100	81.8	31.5	—	—	81.8	31.5	
60 ～ 80	68.8	68.6	—	—	68.8	68.6	65.7
40 ～ 60	49.7	84.0	4.3	1.4	54.0	85.4	40.3
20 ～ 40	24.5	89.6	10.8	3.2	35.3	92.8	19.8
0 ～ 20	9.8	93.8	9.8	18.2	19.6	112.0	8.9
計	257.2	388.8	24.9	22.8	282.1	411.6	4.0

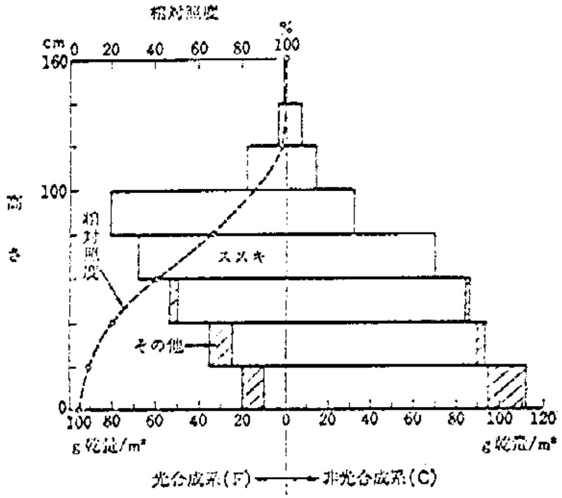


図 I．53　長野県霧ケ峯のススキ群落の生産構造図

通中央の縦線を基準とし，これから左側に光合成系（F），右側に非光合成系（C）の重量をとり，各層別に重さをかき入れる．Cの重量はFにくらべて大きいので，Cの目盛をFの半分にしてとることがある．数種の植物が存在するときは，それぞれを色分けして区別する．

また群落内のいろいろな高さで相対照度を測定し，これを生産構造図にかき入れると，各層の葉群の光合成による生産力をある程度直観的にみてとることができる（図 I.53）．

〔岩　城　英　夫〕

2)　相対生長法による森林現存量の推定

ⅰ）原　理　　相対生長法則（四手井綱英編，1960，1964；吉良竜夫編，1960）とは，大きさの異なる多数の同種個体があるとき，個体のある2つの部分の量 x と z の間に

$$z=Ax^h \tag{1}$$

という関係が成りたつことをいう．A および h は部分の組合せによってきまる定数で，h はとくに相対生長係数とよばれる．この法則は，2部分の量が両対数グラフで直線関係となることにより確認できる．

$$\log z=h\log x+\log A \tag{2}$$

林木では幹重（w_S），枝重（w_B），根重（w_R），葉重（w_L）など単木の各部分の重さ相互間に相対生長法則が成りたつことが多い．また，胸高直径（D）と樹高（H）の間や，w_S，w_B，w_R あるいは w_L と D^2H の間にもこの関係がよく成り立つ．

これらの相対生長関係がわかれば，森林の毎木調査でえられた D と H の値から各個体の各部分の重さを推定し，それらの和として森林の現存量を算出することができる．

同じ林分の林木では，生活形が共通であれば樹種がちがっても同じ相対生長関係を示す場合が多い．

ⅱ）測　定　　森林内に一定面積の調査区を設け，D=4.5 cm 以上の個体について D と H の毎木調査（Ⅲ. 4. a. 参照）を行なう．

胸高（地上1.3 m高）未満の下生えについては，1 m×1 m の方形区を，H=1.3 m以上で D=4.5 cm 未満の木については，5 m×5 m の大きさの方形区をそれぞれ数個調査区内に設け，各方形区内の全個体を地ぎわから刈り取り，種類ごとに個体数および幹，枝，葉の生重を測定する．

D=4.5 cm 以上の木では，なるだけいろいろの直径級を含むように試料木をえらびだす．試料木は10個体以上で，その林分での最大直径級の個体を含むことが望ましい．各試料木は地ぎわから切り倒し，D と H を測定し，幹，枝，葉に切りわけそれぞれの生重を測定する．各部分の一部分をとり乾物率を測定し，生重を乾重に換算する．

ⅲ）整　理　　切り倒した試料木の一覧表（表 I.31）をつくり，D^2H を計算する．表 I.32 のように両軸をとり，両対数グラフ上に各部分間の量の関係をプロットする．

表 I.31　試料木一覧表

個体番号	樹種	D cm	H m	D^2 cm²	D^2H cm²m	w_S kg	w_B kg	w_L kg

表 I.32　両対数グラフにプロットするときの組合わせ方

縦軸	H	w_S	w_B	w_L	w_B	w_L	w_L
横軸	D	D^2H	D^2H	D^2H	w_S	w_S	w_B

グラフ上でまず D～H および w_S～D^2H の相対生長式をきめる．つぎに，w_B～D^2H，w_B～w_S の2式および w_L～D^2H，w_L～w_S の2式を求める．このそれぞれの2式から w_B または w_L を消去してえられる w_S～D^2H の式は，最初に求めた関係式と一致しなければならない．また w_B～D^2H，w_L～D^2H の2式から D^2H を，w_B～w_S，w_L～w_S の2式から w_S を消去してえられる w_L～w_B 関係は，両対数グラフ上のプロットを満足せねばならない．このように，相互に換算できるように各相対生長式を決める．

これらの相対生長関係のうち，w_S～D^2H は一般にばらつきが少ないが，他はばらつくことが多い．ゆえに相対生長式間の関係を検討する場合には w_S～D^2H 関係を固定し，他を操作するのがよい．

毎木調査でえられた D と H から D^2H を計算し，樹種ごとに個体を D^2H の大きさの順にならべた計算表（表 I.33）をつくり，D^2H に対する相対生長式で各個体の各部分の重さを計算する．毎木調査で H が測定できなかった場合には，試料木でえられた H～D 関係から，H を推定し，D^2H を求める．

表 I.33　D=4.5 cm 以上の立木に関する計算表
毎木調査で H が測定された場合には $\log D$ および $\log H$ の欄は不要

樹種	個体番号	D cm	$\log D$	$\log H$	H m	D^2 cm²	D^2H cm² m	$\log D^2H$	$\log w_S$	$\log w_B$	$\log w_L$	w_S kg	w_B kg	w_L kg

表 I.34　現存量の表
y_S：幹，　y_B：枝，　$y_{TC}=y_S+y_B$：地上部非同化部分
y_L：葉，　$y_T=y_{TC}+y_L$：地上部全植物体

樹種	y_S ton/ha	y_B ton/ha	y_{TC} ton/ha	y_L ton/ha	y_T ton/ha

JICA