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IBP HANDBOOK No. 2

Methods for Estimating the Primary Production of Forests

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The Handbook series of IBP has a specific purpose. It is for volumes which are urgently needed by biologists around the world who wish to participate in the programme. Some volumes, such as No. 1 *Guide to the Human Adaptability Proposals*, deal with a whole section of IBP; others, such as this and a number of others in active preparation (see back cover), deal with methods of research in a comparatively narrow branch of the programme. Some of these handbooks, like this one, are brief, written by one scientist, who has been selected by the international section concerned and has consulted many specialists in the process of drafting. Other volume will be larger, with chapters written by a number of different specialists under the guidance of a general editor.

It must be emphasized that the methods described in this and other handbooks are *recommended* for the purpose of IBP, not *agreed*. To obtain universal agreement on any particular method, if it could be achieved at all would take a long time. Moreover, it might retard rather than advance biology, because the methodology in a great many subjects within IBP is evolving rapidly. The methods described in these handbooks are recommended to scientists who themselves do not think they have better method. They provide some guarantee that the results obtained by their use all over the world will be comparable.

A further point of importance is that all IBP handbooks are to some extent provisional. Those concerned with methodology in particular may need alteration as a result of practical experience and distribution to numerous specialists. Indeed it is hoped that revised and more definitive editions of these books will be called for before the conclusion of IBP in 1972.

The author, P.J. Newbould, has just been elected to the Chair of Biology in the new University of Coleraine in Northern Ireland. He took his first degree at Oxford, his doctorate in London with W. H. Pearshall. For a number of years past, as lecturer in botany at University College, London, he has been in charge of the Conservation Course. This is organized in consultation with the Nature Conservancy of the United Kingdom, in order to train postgraduate students in the sciences which underlie conservation and the rational use of biological resources. Since IBP commenced, Professor Newbould has taken a prominent part in Section PT, both nationally within the UK, and internationally.

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Preface

This methodological outline for estimating the primary production of forest and woodlands as part of IBP is based on preliminary documents circulate to more than seventy scientists directly concerned with such studies and incorporates many of their comments. The current version undoubtedly could be improved further but revision can be a never ending process. Rather than trying to produce a polished and generally acceptable version which might not have been ready before the end of IBP it was decided to publish at this stage and to issue corrections and revisions later. Suggestions for these should be sent to the author at the address below.

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I have taken the opportunity in this reprint to correct a few minor errors, and to introduce a few more references.

P.J.N.

1

Objectives

The outline of the PT programme in IBP News 9 states: 'General investigations of primary production should be made at a global network of sites' This Handbook suggests some of the methods that can be used in forest and woodlands to fulfil this aim. Forests and woodlands are here taken as synonymous and the term woodland is generally used. Woodlands include all vegetation in which trees (more than 5 m tall) play a predominant part. These methods would also be applicable to the tree component of vegetation in which the trees have a minor role.

The actual investigations to be carried out within this theme will vary from place to place; precise objectives and the availability of sites, fun and manpower will determine which methods are to be used in any particular investigation. Objectives may include the provision of primary production estimates as a basis for complete ecosystem studies, comparisons (within woodlands) between species, geographical regions, management technique and comparisons between woodlands and other types of vegetation or systems of agriculture. In general it is difficult to set up meaningful comparisons without proper experimental design. It is essential in these comparisons to reduce the number of independent variables to the absolute minimum, for example by comparing one species over a range of climate but with similar management regimes and soil types.

Woodland production has been measured by foresters for many years, and their current methods are outlined in several textbooks of forest mensuration (Prodan 1965, 1968, Husch 1963, Parde 1961, Ferat 1958 Spurr 1952). In general they concentrate upon the economic product, stem wood. Studies of biological production are concerned with the whole dry matter production of the trees, shrubs and ground vegetation. The total dry matter production in any ecosystem is a measure of its efficiency of energy fixation. It also represents the energy input to the system; the energy will subsequently be dissipated by the respiration of all the organism in the ecosystem, the plants themselves, the consumers including carnivores and the decomposers.

This Handbook does not aim to describe the standard mensuration techniques used by foresters; local advice and tables describing the growth of the main tree species will normally be available in each country (e.g. Bradley, Christie & Johnston 1966). What is required is to convert the foresters' production from timber volume to dry weight and to add to it estimates of the production located in the non-useful parts of the tree and in other parts of the ecosystem. The methods for doing this are indicated in this Handbook.

Complete standardization of methods is undesirable and impracticable but wide adoption of certain general Principles will help to make the results of different investigations comparable. This Handbook is intended only as a guide from which appropriate methods can be selected and is especially for the use of institutions where productivity studies are not currently in progress. Reference is made to papers which contain further details of suitable methods.

2

Forest Type and Site Selection

2.1 Forest types

The number of forest types chosen for study in a given geographical area may depend upon the amount of funds and manpower available. It is however hoped that all representative or major types of forest found within the area, either natural or artificial, will be covered as far as possible. At the outset it is important to distinguish between two situations. The annual production of uneven-aged 'climax' woodland, although varying from year to year, probably fluctuates about some comparatively steady mean. Current production of a woodland stand, measured over 3-5 years, provides a value genuinely representative of that site and stand.

By contrast an even-aged woodland shows a regular change in production, which increases to a maximum value and then gradually declines (Ovington 1957). Here the most realistic value for annual production is the mean production over a whole rotation or the whole life-span of the stand. This implies making measurements on an age sequence of even-aged stands.

It is important in each region to compare the best available approximation to natural climax woodland with the main types of plantations. It may also be useful for intercontinental comparisons of production to choose plantations of such widely cultivated genera as *Pinus* (especially *P. radiata*), *Larix*, *Eucalyptus*, etc. It is always important to understand as much as possible of the ecology of the system being studied, especially the seasonal changes in activity.

2.2 Site selection

It may be useful to envisage four sorts of areas as shown in [Figure 1](#).

1. *Sample area*: initially used only for measurements which will not affect it. Climatic measurements and regular growth recording are carried out here. Ultimately it could be felled as a final sample or preferably conserved inviolate as a reference site (0.1-1 ha).
2. *Buffer area*: an area of at least two tree heights in width, around the sample area; not subjected to any disturbance which could affect the sample area.
3. *Measurement area*: large enough to permit felling of trees, digging of soil pits and root trenches; so far as possible felling should not exceed 5% of the trees to minimize effect on sample and buffer areas (1-10 ha).
4. *Study area*: acts mainly as a large scale buffer zone; may be necessary for the associated study of mammals and birds (10-100 ha).

The methods used depend upon the degree of destructive sampling permissible; often one must make non-destructive measurements on a considerable number of trees (perhaps all those in 1) while cutting down a smaller number of trees (from 3) for dry weight determination. Felling should be so organized (possible with reference to the prevailing wind direction) that it does not markedly affect the climate of the sample and buffer areas. The sample area is usually regular in shape, but need not be square. The study and measurement areas need not be regular.

2.21 Size of areas

The size of the areas depends upon the sites available, the size of the trees, the structural complexity of the woodland, its general heterogeneity, the accuracy and the manpower available. No vegetation is homogeneous but the heterogeneity of 1 and 3 should be kept as small as possible while in 4 which may be used for related ecosystem

investigations, as for example on vertebrates, more heterogeneity can be accepted. Heterogeneity may involve species composition, age and height structure of the woodland and site conditions, e.g. slope, soil and climate, often indicated by the ground flora. The smaller areas should as far as possible constitute a representative sample of the larger areas (i.e. 1 of 3, and 3 of 4).

The minimum sizes shown above are barely adequate and are intended for areas where woodland sites are small and few and far between. Probably in uneven-aged or mixed woodlands the sample area should not be less than 0-5 ha. In tropical rain forest the areas might have to be as much as five times as large as the maximum sizes given above. Where adequate areas cannot be found, it may be necessary to use measurement areas which are not adjacent to the sample areas, but which are within the same region and are as closely comparable as possible. In some cases more than one sample and measurement area may be located within the same study area, either as replicates, or as an experiment involving different tree species or management regimes.

2.22 Existing research plots

Existing research plots should be used wherever possible. In particular it would be of immense value to locate these studies in or adjacent to a mensuration plot on which long term recurrent girth measurements have been made on numbered trees. This will allow much more precision in the estimation of wood production which is the major component. It may also make it possible to relate, (with care and suitable reservations) the total dry matter production (via mensuration data and volume tables where available) to other stands in the same region. The extent to which the stand sampled is thought representative of larger areas of woodland should be stated, giving corroborative detail if possible.

2.23 Replication

Replication is highly desirable where comparisons are to be made between stands. In some cases it may be impracticable due to site heterogeneity and shortage of manpower. Replication of non-destructive measurements (girth, height, etc.) may be simpler than replication of destructive measurements and may serve to indicate the amount of variation involved. Subdivision of the sample area and the measurement area will provide additional information on the variability of the stand.

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 6 4 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 Principal may also be used. In terms of mathematical symbols, the two procedures may be expressed as follows (Kira & Shidei 1967). 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 $t_2 (= t_1 + Dt)$

$DB = B_2 - B_1$ 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, DB , L and G , are successfully estimated, we can calculate P_n as the sum,

$$P_n = DB + L + G \text{ (Method 1, see [Figure 2](#) (iv))}$$

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 (Dt). 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

$$P_n = B_{2N} + L_N + G_N \text{ (Method 2, see [Figure 2](#) (ii))}$$

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 DB . 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, an 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 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.T. 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 evenaged 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 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

d.

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 1968), 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 Principal 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 p cm or p in., so that the value read from the tape represents the circumference of the tree divided by p ($3 \cdot 1416$). If a diameter tape is not available, measurements may be made with a normal steel tape and values divided by p . 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 optical 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.

* 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.

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 aluminum 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 (1968) 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

$$V_p = p r^2 h / 2$$

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

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

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

$$V_i = 1/2(A_i \times h)$$

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 cm³ 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 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.

$$D_m = \{[D_1^2 + D_2^2]/2\}^{-2}$$

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 (DV_s) can be estimated on the basis of either linear or exponential growth.

$$DV_s = (V_s - V'_s)/n \text{ linear basis}$$

$$D V_s = (V_s (1 - e^{-r}), r = 1/n \log_e (V_s / V'_s) \text{ exponential basis.}$$

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

$$Dy = by/x$$

and branch production, Dy , 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

$$DB/B = k(DS/S)$$

where B and DB are branch weight and production, S and DS 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. Rotliacher, Blow & Potts 1954, Holland 1968). 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 lammis 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 (1968). 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). Whittaker (1962) has given some shrub root data.

4.65 Attempts to estimate root production

There is however no generally acceptable method for estimating root production (Newbould 1968) 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 IBP 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

$$\begin{aligned} & \text{Above-ground production} / \text{Above-ground biomass} = \\ & k * \text{Below-ground production} / \text{Below-ground biomass} \end{aligned}$$

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' 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 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 root production cannot be calculated.

(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. Further suggestions on root production and biomass are in the USSR Academy of Sciences symposium volume on the subject (1968).

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*). However Bunce (1968) showed that the inclusion of height only marginally improved his estimate of tree dry weight. 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 nondestructive 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 I 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 Principal to that of tree production. Full descriptions of methods are given by Whittaker (1961, 1962), Ovington, Heitkamp & Lawrence (1963) and Gimingham & Miller (1968).

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 No 6 on *Methods for the measurement of the primary production of grassland*, by Milner & Hughes; 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 Principal 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 cm² for mosses, 15 cm x 15 cm (225 cm²) for a uniform fine grass sward to 1 m x 1 m or 0.5 m x 2 m (both = m²). 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 belowground 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.

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 (Figure 3):

(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 Shaw (1968) 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 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-Utter

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 x 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 x width, or length', or log, o 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 [Figure 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 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 7.1.1, 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 1968). Such a model can be tested against short term estimates of net photosynthesis based on CO₂ 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 (1968).

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 are described fully in IBP Handbook No 13 by Petruszewicz & Macfadyen (1970). 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 weighed. Simple feeding experiments are carried out on the main defoliating species, in jam jars or beakers, to find out the relationship between weight of leaf consumed and weight or number of frass pellets produced, (values of frass production = 40 - 50 % leaf material are quite common). From this figure and the estimate of frass fall, leaf consumption in the field may be calculated (Carlisle & Brown 1966). Care must be taken to avoid atypical feeding behaviour in these experiments. Further details will be found in IBP Handbook No 13 on *Productivity of Terrestrial Animals: Principles and methods* by Macfadyen & Petruszewicz (1970).

Frass fall is best collected in rather smaller containers than are used for leaf litter (Chapter 6). 'Polythene rain-gauges' (Figure 5) used for measuring rainfall inside the woodland, and providing samples for chemical analysis (7.5) may serve a dual function as traps for frass and other micro-litter (Carlisle, Brown & White 1966b). Fine solid material is caught on a glass wool plug and analysed separately. Other components caught in these small impermeable traps include soluble organic matter washed out of the leaves, fine particles of organic matter including pollen grains and aphid dew (melezitose), Carlisle, Brown & White (1966b). In many cases these minor items will not be significant in the final production estimate, but it is necessary to make approximate estimates of them to ensure that this is the case.

Where plant material is consumed on the tree by, e.g. monkeys or birds, the estimation of loss is difficult and would necessarily be derived from a study of the vertebrates concerned and their average food intake.

Where material largely decomposes before falling to the ground, as is the case in humid tropical forests, these losses will also be difficult to measure. The Principal will be to count leaf tips or leaf midribs, to measure twigs, to count seeds, etc. and then to convert these items to the full dry weight of an undecomposed and unconsumed leaf, twig, fruit, etc.

7.3 Chemical and calorific analysis and mineral cycling

Plant samples collected and dried in order to estimate dry matter production often represent a considerable manpower commitment and could yield much additional information on energy flow and mineral cycling if they were subjected to calorific and chemical analysis.

It is especially useful to determine the energy content of the material formed. The annual production expressed in energy units can be compared with records of the available radiation (7.4) to give some estimate of efficiency. Also the annual energy production represents the starting point of ecosystem metabolism and functioning; it is the energy source for all the consumer and decomposer organisms.

In practice the difference between the energy content (cal/g) of different plant components may be small compared with the errors in estimates of production (Ovington & Heitkamp 1960). Where it is not possible to determine energy content, a value of 4700 cal/g dry weight of plant material may be used. The term biocontent is suggested as meaning the total energy content (calorific value) in a standing crop, corresponding to the term for mass, biomass.

Lieth (1968) discusses the precautions necessary in sample preparation (drying, milling and pressing into tablets) and in the calibration and use of the bomb calorimeter.

In some programmes there will be emphasis on the study of mineral cycles (Ovington 1965a, 1965b, Greenland & Kowal 1960, Nye 1961). Details of methods are beyond the scope of this Handbook. In addition to the chemical analysis of samples collected for biomass measurement, it would be necessary to carry out chemical analysis of rainfall penetrating the woodland (7.2), of stem flow and of rainfall collected either outside the woodland or on a tower above the canopy (Carlisle, Brown & White 1966b). Most interest will attach to analysis of N, P, K, Ca and Mg. Where there is no immediate prospect of carrying out chemical or calorific analysis, it may still be worth storing subsamples of all the dry matter components. Components such as leaves, fine roots, twigs, may conveniently be milled before storage, but subsamples of main stem and branches are best stored whole. It may be possible to reduce the number of separate samples by bulking material from several samples. The amount stored can be quite small (10 g dry weight would be enough for most purposes).

7.4 Climate

There will probably be an IBP Handbook on climatological methods. Meanwhile a few comments are added here based on a document entitled 'Climatological Measurements for the International Biological Programme' produced by Dr. J.L. Monteith for the British National Committee for IBP.

In general the existing network of climatological stations will provide 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-Gorczyński 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 m if necessary using a Schott RG 8 filter to find the amount of infra-red radiation at wavelengths longer than 0.7 m. 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.

8.1 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 [Figure 6](#). The forms are printed on thin cards and measure 28 x 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 1968). 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 ($\text{kg}/\text{ha} \times 0.89 = \text{lb}/\text{acre}$). 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 $10^3 \text{ kg}/\text{ha}$ (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 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 ($2.00 \text{ cal cm}^{-2} \text{ min}^{-1}$). For energy flow studies $\text{cal cm}^{-2} \text{ day}^{-1}$ 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 investigation 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 $\pm 5\%$ ($\pm 10\%$ 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, e.g. Bunce (1968) says that a tree of 104 cm girth can be felled, weighed and subsampled in two days by three people using a power saw for large branches and trunk sections. 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 I BP, 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 I BP 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.

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