

Potential and Actual Dry-Matter Production in Irish Forests

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INTRODUCTION

It is of more than just theoretical interest to enquire about the upper limit to crop production in Ireland, because it is useful in defining objectives to know what the absolute potential in dry-matter production is. It is also useful to consider the factors which cause actual production to fall short of the theoretical, and to enquire about the distribution of dry-matter between the component parts of the total crop biomass.

Photosynthesis is responsible for the primary production of dry matter in higher plant ecosystems. For the present purpose, it is not essential that the detailed biochemical, biophysical or physiological mechanisms be considered, but, since energy capture and energy transfer is a fundamental part of photosynthesis, a consideration, in broad outline, of the nature of the energy aspect is desirable.

In processes involving change two properties, energy and mass, remain constant. Thus, changes in fresh weight or in dry weight of an organism must be balanced in terms of input and output components of mass and of energy.

Although energy is an abstraction, it is recognisable in its forms such as radiant energy. Radiant energy must be absorbed in order to be physiologically useful. The absorbing molecules are known as pigments. Higher plants possess chlorophyll *a*, and other accessory pigments such as chlorophyll *b* and the carotenoids. Radiant energy absorbed by chlorophyll *b* is transferred with an efficiency of almost 100% to the primary photosynthetic pigment, chlorophyll *a*. The transfer from the carotenoids is about 20% efficient. Of the total captured by the pigments, 90 to 95% is directed towards the reduction of an acceptor molecule under optimum conditions.

Radiant energy, or insolation, which is photosynthetically useful occurs almost entirely in the visible range (4000-7000Å) and this latter represents 40-45% of the total radiation. The waves of light are said to be composed of discrete pulsating particles called photons (or quanta, for solar radiation in general). When absorption of light occurs one photon activates one pigment molecule. The quantity of photons absorbed by one mole (molecular weight in grams) of a pigment is a fixed quantity called one einstein and is equivalent to 6.06×10^{23} photons. The energy content per photon, and hence per einstein, is a function of wavelength. Some values per einstein are as follows: ultra-violet (2860Å), 100 k. calories; violet

(4000A), 72 k. cal.; blue-green (5000A), 57 k. cal.; yellow (6000A), 48 k. cal.; red (7000A), 41 k. cal.

THE UPPER YIELD LIMIT

The utilisation of light in photosynthesis is a quantum process confined to the visible region of the spectrum. The mean daily input of total radiation on a horizontal surface at Valentia is approximately 394 g.cal/cm² in the April to September growing period and approximately 119 g.cal/cm² in the October to March period (Anonymous, 1961). The mean daily input averaged over the twelve months is thus 257 g.cal/cm². Loomis and Williams (1963) have used data from Brooks (1961) and Moon (1940) to convert total radiation data into a form which expresses its photosynthetic potential. Accepting their conversion factor (1 g.cal/cm² total radiation = 8.6 micro einsteins/cm² of photosynthetically useful radiation) a mean input of 257 x 8.6 or 2210 micro einsteins/cm²/day is obtained for the twelve month period. If a value of 15% is given to the reflection coefficient (albedo loss for total insolation is generally given as 26% for grassland, 17.5% for oak woodland and 14% for pine forest) and 10% to absorption which is not potentially useful in photosynthesis, it follows that 25% must be deducted from 2210 micro einsteins/cm²/day, giving 1657. The value of 15% given to albedo is probably excessive for photosynthetically useful light (Geiger, 1957).

The number of quanta required to reduce one CO₂ molecule in photosynthesis is generally taken as 10, although some experiments do not support this figure. Accepting this figure as the best available, 1657 micro einsteins/cm²/day will produce 166 micro moles of CH₂O/cm²/day of gross photosynthate.

Respiration losses in forests in temperate regions are often taken as 44% of gross photosynthesis (Boysen-Jensen, 1932; Becking, 1962). Loomis and Williams use a figure of 33%. An examination of the temperature response curves for photosynthesis and respiration (Fig. 1) suggest that for our climate the value selected by Loomis and Williams is closer to the truth. However, without more direct evidence of the extent of respiration loss a compromise value of 40% is chosen. On this basis the amount of net photosynthate produced per cm²/day is approximately 100 μ moles of CH₂O. By confining our calculations, based on the same assumptions, to a six month growing season the potential productivity is approximately 150 micro moles of CH₂O/cm²/day.

As our new forests are principally evergreen a calculation based on the twelve month period is probably best, as there is evidence of photosynthetic activity in evergreen trees in suitable weather during winter (Parker, 1953). One mole of CH₂O is equivalent to 30 grams, so that the conversion from 100 μ

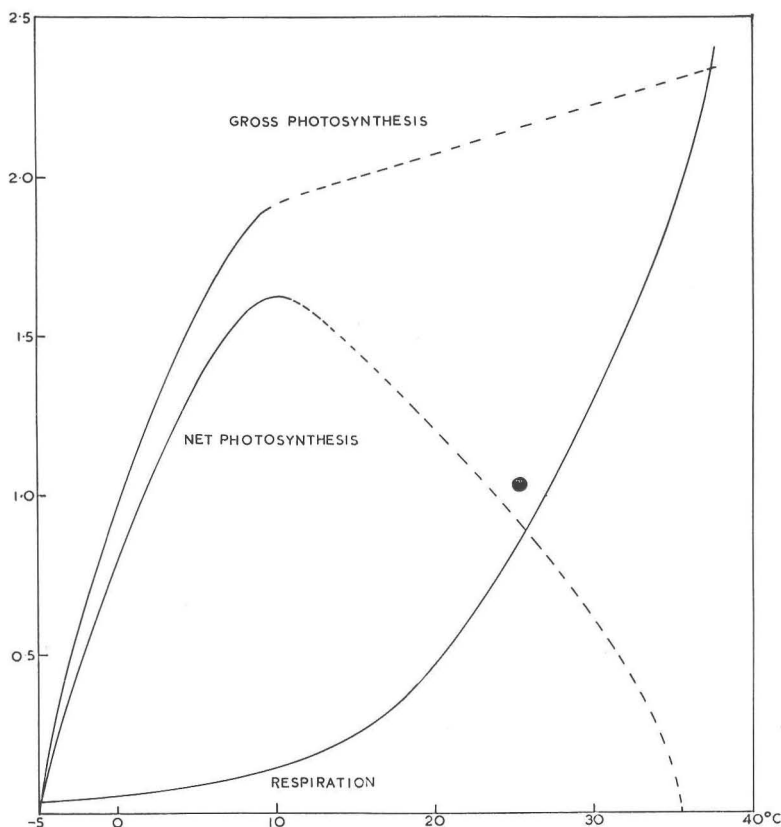


FIG.1 PHOTOSYNTHESIS AND RESPIRATION OF *PINUS CEMBRA* IN RELATION TO TEMPERATURE. (TAKEN FROM TRANQUILLINI 1954).

moles /cm²/day yields 30 g/m²/day over the twelve months and is equivalent to approximately 292 lbs/photosynthate/acre/day, or 47 tons/acre/year. When the minerals absorbed from the soil are added the total dry-matter production potential is approximately 50 tons/acre/year. This represents the upper limit to yield assuming that chlorophyll is distributed in a uniform horizontal layer which intercepts light completely, and that no limiting factors operate to restrict photosynthesis. An examination of these two assumptions is necessary but is deferred until actual yields are compared to the theoretical.

Actual and Potential Dry Matter Yields

On the basis of the assumptions already stated, an annual crop, with an effective growing season of 140 days, will have a potential dry matter production of approximately 30 tons/acre. This production level, and that worked out for a perennial evergreen crop in the previous sections, represents about a 4.4% utilisation of total incident radiant energy or about a 10% utilisation of visible light. Each may be compared with actual records of highest level production (which include estimates of root producton) as follows: pine forest in Britain 14.0 tons/acre, 1.73% conversion of total radiation and 4.32% conversion of visible radiation; deciduous forest in Britan, 6.85 tons/acre, 1.4% and 2.85% conversion levels; sugar beet in Holland, 6.45 tons/acre, 0.83% and 2.07% conversion levels; wheat in Holland, 5.50 tons/acre, 0.73% and 7.83% conversion levels (Odum, 1959). The data for forests do not include the early unproductive years. These production levels may be compared also with the performances of individual leaves under optimum conditions for short periods of time. Conversion levels of 5 to 7% for total radiation and 12 to 16% for visible light are generally recorded (Gaastra, 1962; Holliday, 1966).

It is evident therefore that the highest production levels actually recorded for field and forest crops represent some 18% to 28% of the theoretical maximum. Mean crop performance is of course lower still.

Factors Limiting Photosynthesis

In searching for the causes of the difference between actual and potential yields it is necessary to state that water is generally not a deficiency factor for crop growth in Ireland (Guerrini, 1953, 1957; Curran, 1964). Soil fertility levels are adjustable and this aspect is likewise eliminated from further discussion.

Two broad categories of modifying influence thus remain to be considered

- (a) Factors affecting the component processes of photosynthesis, and
- (a) the characteristics of the light intercepting surface.

(a) the components of photosynthesis

Photosynthesis is looked upon frequently as the reverse of respiration and as such it is conveniently summarised in the form



Three components are recognisable immediately

- (i) the supply of CO_2 ,
- (ii) the fixation of light energy in chemical bonds, and
- (iii) the synthesis of carbohydrate.

The influence of each component has been analysed by Gaastra (1962) and Monteith (1966). The position may be summarised in the following way.

Carbon dioxide has a mean concentration of 300 ppm in normal air. When other limitations are removed, leaves will respond to increasing CO_2 levels by increased photosynthesis up to a level of about 1300 ppm of CO_2 . Therefore, under conditions of high light intensity and satisfactory temperature, photosynthesis is limited by CO_2 supply, and CO_2 is utilised by the chlorophyll units about as rapidly as it arrives at the chloroplast. Consequently, the path of flow of CO_2 from the surrounding air to the point of use is critical in determining photosynthetic rates. The concentration of CO_2 in air may increase with time, by virtue of man's industrial activities, to a level of 400 ppm. Otherwise, and except for the special case of glasshouse horticulture, the level is not subject to man's influence. The rate of flow is not only influenced by concentration differences but also by resistance to flow. A major source of fluctuation in resistance may be the surfaces of the sub-stomatal mesophyll cells of the leaf. A temporary dryness at this point may slow down diffusion considerably. While our crops generally do not suffer from a water deficit at the root, the rate of water entry from a cold soil may not keep pace with the rate of water loss to a drying atmosphere. In which case the plant may suffer physiological stress without displaying morphological symptoms of stress. This aspect also is not controllable. The mechanical disturbance caused by high wind speeds may cause temporary stomatal closure. All of these uncontrollable factors may increase resistance to CO_2 diffusion and thus reduce photosynthesis.

The next major component of photosynthesis is the fixation of light energy in chemical bonds. With factors controlling other components non-limiting, the photosynthetic response of *an individual leaf* to increasing light levels is linear at low light intensities until a level of approximately $6.5 \text{ cal/cm}^2/\text{hr}$ of total radiation or about $3 \text{ cal/cm}^2/\text{hr}$ of visible light is reached. Beyond that level the response is curvilinear, saturation being reached at about $33 \text{ cal/cm}^2/\text{hr}$ of total radiation or about $15 \text{ cal/cm}^2/\text{hr}$ of visible light.

The third component, involving enzyme systems, is responsive to temperature. Forage grasses are considered generally to grow at temperatures above 43°F or 6°C but appreciable growth rates are not reached until temperatures reach 50°F or 10°C . Evergreen conifers probably respond in somewhat similar fashion. Respiration rates climb rapidly at temperatures above 50°F . However, the net response varies widely from one population to another.

(b) *The Characteristics of the Light Intercepting Surface.*

The light intercepting surface is not a uniform layer of chlorophyll, but is a complicated mosaic of surfaces with reflection characteristics. During the establishment phase of the young forest the proportion of light which is usefully intercepted is rather small. The rate at which canopy development proceeds is a function of the vigour of individual plants and the number of such per unit area of ground. The nature of the control of these matters is determined by considerations of timber use and silviculture practices.

Once the closed canopy stage is reached, and indeed long before, the problem of mutual shading of leaves becomes critical. Mutual shading of one chloroplast by another occurs within the individual leaf, but there is some evidence of a regulatory mechanism in the form of protoplasmic movement and chloroplast orientation within the cell. The manner of leaf display is also a determining factor in degree of mutual shading and the regulatory effect of phyllotaxy and angle of leaf is especially evident in annual crop plants and in broadleaf seedling trees. Shape of leaf and angle of inclination of leaf are also important in closed canopies.

The penetrating power of light through foliage is related to its intensity. Although great fluctuations in intensity occur over brief periods of time, seasonal trends are also very pronounced (Anonymous, 1961, Table 2). This fluctuation, coupled with the rhythm of daylength change characteristic of our latitude, has important physiological consequences. The respiratory process, which is essential in all living cells, continues in both light and in darkness at a rate determined by temperature. Photosynthesis proceeds in light at a rate determined by factors already discussed. The point at which organic matter production by photosynthesis balances organic matter destruction by respiration within the individual leaf is called the compensation point. It is the net effect of the physiological activities of a myriad of individual cells. Theoretically at least, a compensation point for the crop or canopy is also conceivable. It is the net effect of the physiological activities of a myriad of individual leaves, all of which are decomposers of organic matter in darkness, and some of which are net producers of organic matter in light. If light were a fixed quantity then it would be possible to arrive at an area of leaf (measuring one surface only) per unit area of ground such that the most deeply shaded leaves are at their compensation point. If the quantity of leaf increases beyond this amount, that is if the leaf area index increases, the lower leaves will be more deeply shaded and their respiratory activities will exceed their photosynthetic activities; they become net users of organic matter and in that condition are parasitic on the crop. If on the other hand the leaf area index remains

unchanged but light quantity (intensity \times time) decreases a similar physiological consequence ensues, the lower leaves become parasitic. Likewise if light quantity increases or leaf area index decreases the lower leaves become less shaded and become net producers of organic matter, but, if light intensity increases beyond the saturation level of lower leaves, light will reach the ground and efficiency of utilisation will drop. It will be apparent that light quantity for lower leaves is not a simple product of intensity and daylength because a certain threshold value of intensity must be exceeded before penetration through the upper foliage is possible. These leaves which are net consumers of organic matter can survive until they have lost more than 50% of their dry weight.

In field crops the optimum leaf area index for economic yield is a function of the variety used and the planting pattern and density used. Another density or planting pattern may result in a higher total biological yield, but in a reduced yield (or reduced quality) of economic product. For kale grown in rows, the optimum leaf area index is about 4, whereas for sugar beet it is about 6. The maximum, but not necessarily the optimum, leaf area index recorded for Scots Pine is 11, and for Spruce 28 (Ovington, 1958).

DISTRIBUTION OF ASSIMILATES WITHIN THE CROP

Total crop biomass is a useful measure of physiological efficiency, but may be of little concern to the practicing forester who is interested in yield of stem wood. Maximum dry-matter production per unit area of ground may not be compatible with maximum yield of timber. Ultimately the problem is one of distribution of assimilates to components of the crop. It has five aspects:

- (1) the nature of the commercial requirement,
- (2) the genetical characteristics of the individuals making up the population,
- (3) the physiological characteristics of the stand at its several phases of growth,
- (4) the ecological characteristics, which involve the morphological and physiological adaptations of the individuals, and soil changes, and
- (5) economic considerations, which determine if certain silvicultural manipulations with biological consequences are justifiable in terms of net returns.

The third aspect has occupied our attention here. Available data suggests that the stem-wood share of total dry-matter produced is about 60% for a variety of mature forest types (Becking, 1962). This constancy may be more apparent than real, although Ovington (1958) found that 60% of the total dry weight of a

55 year *Pinus sylvestris* stand was in the form of bole. For field crops Brouwer (1962) has argued that changes in favour of the relative amount of the economic product generally are associated with a reduction in other organs and of the total product harvested. Holliday (1966) argues that an alteration in distribution of assimilates, such as has been achieved in wheat, is possible in other species without reduction in biological yield and with a consequent increase in economic yield. An intuitive judgement leads one to suspect that Holliday is right.

DISCUSSION

The conversion of the light available in Ireland during an average year into net photosynthetic product has a theoretical maximum of 47 tons/organic matter/acre. The actual yield falls far short of the theoretical because of the limiting effects of CO₂, temperature and the nature of the intercepting surface. On taking these limiting factors into consideration and taking data from field crops for comparison it is suggested that the highest production possible during the closed canopy phase in Irish forests is about 12 tons/dry matter/acre/year. On taking the establishment phase into consideration an upper limit of 9.5 tons/acre/year for a fifty year growth period is suggested, but actual performance data for the establishment phase are required to verify this. If the stem-wood component of the total crop biomass is taken as 60% the above production level yields 5.7 tons of stem-wood/acre/year, averaged over the full growth period of the forest. Complications of a physiological nature such as the relative performance of sun and shade leaves, changes in physiological efficiency of leaves with age, effect of variation in chlorophyll content and the relative efficiency of the chloroplasts from different species or different genotypes have not been considered because their overall significance in practice is highly conjectural.

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