# EFFECTS OF LIGHT ENERGY AND TEMPERATURE ON GROWTH OF SUBTERRANEAN CLOVER COMMUNITIES

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# LIST OF ABBREVIATIONS USED IN THE TEXT

| Abbreviation | | Unit |
|---|---|---|
| CGR | crop growth rate | $g/m^2/day$ |
| CLE | current light energy | $MJ/m^2/day$ |
| DDR | daily dark respiration | $g/m^2/day$ |
| DLDM | dead leaf dry matter | $g/m^2$ |
| DLE | daily light energy | $MJ/m^2/day$ |
| DPg | daily gross photosynthesis | $g/m^2/day$ |
| GLDM | green leaf dry matter | $g/m^2$ |
| INS | initial slope of light-gross photosynthesis curve of a community | |
| LAI | leaf area index | |
| LF | light flux | $\mu E/s/m^2$ |
| Pg | gross photosynthetic rate of a community | $gCO_2/m^2/hr$ |
| PgMX | maximum rate of gross photosynthesis of a community | $gCO_2/m^2/hr$ |
| Pn | net photosynthetic rate of a community | $gCO_2/m^2/hr$ |
| SDM | shoot dry matter | $g/m^2$ |
| SLA | specific leaf area | $cm^2/g$ |
| STLF | saturated light flux of photosynthesis of a community | $\mu E/s/m^2$ |
| TDM | total dry matter | $g/m^2$ |
| TLDM | total leaf dry matter | $g/m^2$ |

# SUMMARY

Although it is known that dry matter production of plant communities is strongly influenced by environmental factors, there are few reports of the effects of light energy and temperature on the growth of subterranean clover communities. Experiments reported in this thesis were intended to remedy this deficiency by quantifying responses of subterranean clover communities to light energy and temperature.

Separate effects of light energy and temperature on the growth of subterranean clover communities were examined by growing small communities in temperature-controlled glasshouses at different times of the year, with different degrees of shading and at different constant temperatures. Net $CO_2$ exchange was measured several times during each growth period to examine the effects of growth conditions and the current temperature and light energy environment on growth rate.

Results of $CO_2$ exchange measurements, relationships between plant attributes, and relationship between plant attributes and environmental factors were incorporated in two growth models. A systems analysis was conducted for the total effects of light energy and temperature on the growth of the communities.

Major results found in the study are as follows:

(1) At a given total dry matter, crop growth rate at 20°C increases approximately linearly with increase in daily light energy. The slope of the regression line is higher for a closed canopy than for that of a canopy with an LAI less than 2.5 because of a higher net photosynthetic rate by the closed canopy. However, once a closed canopy is attained, crop growth rate decreases with increase in total

dry matter due to increase in dark respiration rate.

(2) The optimum temperature for growth is relatively high at 20-25°C during the early stages of growth due to high net photosynthetic rate and high rate of leaf area development at that temperature. The optimum decreases with increase in total dry matter mainly because dark respiration rate increases markedly with increase in temperature.

(3) The dark respiration rate of a community is strongly influenced by both total dry matter and ambient temperature and only slightly by light energy and temperature during the growing period.

(4) Net photosynthetic rate at high light flux increases with increase in LAI up to 3; further increase in LAI affects the rate only slightly. The rate at low light flux shows an optimal relation with LAI as dark respiration rate increases with increase in total dry matter. Ambient temperature influences net photosynthetic rate directly at high light flux but inversely at low light flux.

(5) Photosynthesis and respiration calculated from LAI, total dry matter, crop growth rate, ambient temperature and light flux density enable daily net production to be estimated for particular combinations of these plant attributes and environmental factors.

(6) A field experiment involving three planting dates (5 week interval) and three plant densities shows variation in growth curve due to treatments but a similar final dry matter yield between treatments except for the late planting date.

(7) Growth models derived from data generated under controlled conditions can simulate growth in the field with reasonable accuracy from inputs of initial plant attributes, daily light flux and average monthly temperature during growth. Systems analysis reveals

interaction between plant attributes and environmental variables, which affect total dry matter production. Final yield is predicted to be: (i) independent of plant density and planting date up to September; and (ii) inversely related to temperature.

# DECLARATION

This thesis contains no material which has been accepted for the award of any other degree or diploma in any other University, and, to the best of my knowledge and belief, it contains no material previously published or written by another person, except where due reference is made in the text.

S. FUKAI

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## 1.0.0. General Introduction

The growth of plant communities is influenced by both environmental factors and by plant attributes. The effects of environmental factors on growth rate depend on the growth stage (Cocks 1973) due to the changing role of each plant attribute in the community growth process and the changing response of these to environmental conditions. For example, the growth rate of a rice community is markedly increased by the leaf area present up to a certain value of leaf area index (LAI), the actual value depending on daily light energy (Takeda 1961), since net photosynthesis of communities at high light flux density depends strongly on interception of light when the values of LAI are low (Brown, Blaser and Dunton 1966). At low LAI, temperature influences the growth of communities mainly through an effect on the development of leaf area. However once LAI great enough for full light interception is obtained, temperature may influence dry matter production through other plant attributes such as respiration. It is clearly necessary to examine the effect of environmental factors on the growth rates of communities at different growth stages.

The $CO_2$ exchange rate of communities provides an instantaneous measurement of community growth for given conditions and plant attributes. The effect of a specific environmental factor on net photosynthetic rate and dark respiration rate can be analysed and the total effect of the factor on dry matter production can be determined by integrating the rate of $CO_2$ exchange with time.

Some workers (Weihing 1963; Nakaseko and Yoshida 1971) have used correlation techniques for the analysis of the effect of environment on the growth rate of communities in the field. However, interrelations between environmental factors themselves make it difficult to distinguish the effect of an individual factor or to quantitise the relation between factors and growth rate. In contrast to the field situation, controlled environmental facilities can provide conditions in which the level of a single factor can be varied experimentally.

Experiments reported in this thesis were largely conducted in temperature-controlled glasshouses and were aimed at finding the quantitative effects of temperature and light flux density on the growth of subterranean clover communities.

Systems analysis was conducted to provide quantitative relationships between the two environmental factors and the growth of the communities.

# 2.0.0. Review of Literature

## 2.1.0. Introduction

### 2.1.1. Growth of Subterranean Clover

Subterranean clover is the most important annual pasture legume in southern Australia. It is very sensitive to phosphate level in the soil (Biddiscombe, Ozanne, Barrow and Keay 1969) and the introduction of subterranean clover with the application of superphosphate has improved soil fertility over 7 million ha (Donald and Williams 1954). A general description of the species and its history in Australia is given by Morley (1961).

In southern Australia, subterranean clover is sown, or germinates naturally, in the autumn. Rapid growth does not occur until early spring. Maximum crop growth rate ranges from 8 to 20 $g/m^2/day$; maximum dry matter yield ranges from 600 to 1,200 $g/m^2$ according to seasonal conditions (Davidson 1954; Davidson and Donald 1958; Stern 1965). Seeds mature in late spring and most are buried in the ground (Aitken and Mullett 1970).

Canopy structure is planophile (i.e. canopies composed of plants with predominantly horizontal leaves) with an extinction coefficient (k) of approximately 0.9 (Davidson and Philip 1958). Light flux density decreases very rapidly through the canopy to near zero at about half the height of a completely closed canopy (Stern 1965).

Leaf photosynthetic rate at light saturation of 50 klux is 32-35 $mgCO_2/dm^2/hr$ and the shape of the light-leaf photosynthesis curve indicates this species to be a $C_3$ plant (Bouma 1970). Canopy photosynthetic rate of this species is generally low:- 30-35 $mgCO_2/dm^2$

(ground)/hr at 33 klux in canopies with LAI of 4-5 compared with 45 mg$CO_2$/$dm^2$(ground)/hr for wheat canopies under similar conditions (King and Evans 1967). The ratio of respiration rate to photosynthetic rate of canopies of subterranean clover is high at 0.4-0.5 (King and Evans 1967).

### 2.1.2. Growth of the Isolated Plant and Growth of the Community

When the isolated annual plant is young and there is no mutual shading of leaves, plant dry matter increases exponentially with time (Blackman 1919). The rate of dry matter production is influenced strongly by the rate of leaf area development and responds markedly to temperature (Beinhart 1963).

Mutual shading among leaves of the same plant inevitably occurs with increase in plant size. This decreases the rate of photosynthesis per unit leaf area, although the total photosynthesis of the plant still increases with increase in total leaf area (Takeda 1961). In the determinant plant onset of the reproductive stage suppresses the vegetative growth (Friend, Helsen and Fisher 1962a). A decreased ratio of photosynthetic to non-photosynthetic organ dry weight with growth of plant parts other than leaves (Hiroi and Monsi 1963) may result in an increased ratio of total respiration rate to photosynthetic rate. Leaf senescence decreases leaf area and hence the total photosynthetic capacity of the plant (Takeda and Agata 1966a).

The time of onset of mutual shading among leaves is greatly influenced by plant density. If the sowing density is low, the pattern of plant growth is similar to that of the isolated plant (Black 1957). However, if the density is high, mutual shading starts early and growth rapidly ceases to be exponential. Eventually the community develops a closed canopy which intercepts most of the incident light flux. Further increase in leaf area results in only a small increase in daily canopy photosynthesis, particularly in the case of planophile canopies (Duncan 1971). If the increase in respiration associated with increase in leaf area (or total dry matter) exceeds the increase in photosynthesis, net production will decrease with further increase of leaf area (Donald 1963) or of dry matter.

The normal ontogenetic changes apparent in the isolated plant are modified under canopy conditions. Lateral development is often depressed (e.g. tillering in grasses (Knight 1961)). This reduces the possible contributions of these laterals to the total dry matter, but nevertheless decrease in the ratio of photosynthetic to non-photosynthetic organ dry matter is also a characteristic of community development (Iwaki 1958). Senescence of plant organs and death of plants themselves are inevitable in communities, and are more rapid at high plant density (Hiroi and Monsi 1966).

Environmental factors affect the growth of communities differently from that of isolated plants. An example is given from work by Hiroi and Monsi (1963, 1966) in which sunflower plants, both in isolated conditions and in communities, were grown under different shades in the field. At high plant density, plant growth departed from exponential growth at 2 weeks from sowing whilst plant growth was essentially exponential in isolated plants up to 6 weeks after sowing. Results shown in Table 1 demonstrate the effects of low light energy (22 or 23% of incident solar) to be more pronounced under isolated plant conditions than under community conditions.

Table 1. Relative dry weight (%) under shades at different times of growth and different growth conditions (after Hiroi and Monsi 1963, 1966).

| | | Relative light flux density (%) | | | | |
|---|---|---|---|---|---|---|
| | | 22 or 23 | 53 or 50 | 60 | 75 | 100 |
| Third week | isolated plants | 23 | 78 | | 89 | 100 |
| | 25 pl/$m^2$ | 52 | | 69 | | 100 |
| | 400 pl/$m^2$ | 75 | | 81 | | 100 |
| Sixth week | isolated plants | 3 | 32 | | 59 | 100 |
| | 25 pl/$m^2$ | 14 | | 45 | | 100 |
| | 400 pl/$m^2$ | 19 | | 60 | | 100 |

In the following literature review, effects of environmental factors on growth of communities are analysed through their effects on the processes in a plant growth system; e.g. leaf photosynthesis, canopy photosynthesis, respiration, leaf area development, and death and decay. Topics concerned with total dry matter production of communities are reviewed in the last section.

## 2.2.0. Leaf Photosynthesis

### 2.2.1. Processes of Leaf Photosynthesis

(a) The Photochemical Process. The conversion of light energy for reduction of $CO_2$ is limited by the number of incident light quanta and by the amount of chlorophyll present. Net $CO_2$ exchange rate increases linearly with increase in incident light quanta until other processes become rate limiting. The efficiency of the photochemical process is shown by the initial slope of the light energy-photosynthesis curve, and is commonly expressed as

$$\phi = \frac{\text{moles } CO_2 \text{ converted}}{\text{Einsteins absorbed}}$$

The quantum requirement ($\phi^{-1}$) is usually found to be 10-12 (Gaastra 1963). The efficiency of light energy conversion

$$\varepsilon = \frac{\text{gain in free energy}}{\text{incident light energy}}$$

is usually found to be 12-15% of visible solar energy or 6-7% of total solar energy (Gaastra 1963).

The initial slope of the light-photosynthesis curve does not differ much between species when leaves contain chlorophyll at about 4 mg (a+b)/$dm^2$(leaf) (Gabrielsen 1948). In some rice cultivars the initial slope increases with increase in chlorophyll content from 2 to 5 mg/$dm^2$ (Takano and Tsunoda 1970).

The photochemical process is almost independent of leaf temperature and $CO_2$ concentration (Gaastra 1959; Akita, Miyasaka and Murata 1969), but may be affected by severe water stress (Boyer 1971). It may be impaired when leaves adapted to low light are exposed to high light energy (Björkman 1968b).

(b) $\underline{CO_2 \text{ Diffusion}}$. At high light flux photosynthesis is limited by the amount of $CO_2$ available to chloroplasts, the rate increasing with increase of $CO_2$ concentration. Gaastra (1959) introduced the concept of $CO_2$ diffusion resistance.

$$P = \frac{(CO_2)a - (CO_2)chl}{r_a + r_s + r_m}$$

where P is photosynthetic rate, $(CO_2)a$ and $(CO_2)chl$ are the $CO_2$ concentrations in the ambient air and at the chloroplast respectively, and $r_a$, $r_s$ and $r_m$ are the resistances of the leaf boundary layer, the stomata including the intercellular spaces, and the mesophyll cells themselves, respectively.

(c) Biochemical Processes. The biochemical processes of carbon metabolism in photosynthesis are reviewed by Hatch and Slack (1970). In the chloroplasts $CO_2$ is incorporated by RuDP carboxylase in "$C_3$ plants" and PEP carboxylase in "$C_4$ plants".

Forrester, Krotkov and Nelson (1966) demonstrated that the light saturated net photosynthetic rate could be expressed as a product of the carboxylation efficiency and the difference in concentration between $CO_2$ in air and $CO_2$ at the compensation point. Björkman (1968a) related differences in the rate of photosynthesis between ecotypes of *Solidago* to differences in carboxylase activity and Smillie (1962) related it to leaves of different ages.

At high light flux and high $CO_2$ concentration, photosynthesis is considered to be limited solely by the biochemical processes. This is adduced from the fact that the effect of temperature is marked under these conditions (Gaastra 1959, 1962; Akita, Miyasaka and Murata 1969).

### 2.2.2 Physiological Factors Affecting the Rate of Leaf Photosynthesis

(a) Aging. The rate of photosynthesis changes rapidly with aging of a leaf, particularly in annual plants (Saeki 1959). Nevins and Loomis (1970b) found a correlation in nitrogen deficient sugar beet between the rate of photosynthesis at low light fluxes and chlorophyll content of the leaves. However, in nitrogen-sufficient plants, the initial slope of the light-photosynthesis curve seems to change with age less markedly than the saturated rate of photosynthesis (Osman and Milthorpe 1971).

It has been shown in many species that the rate of photosynthesis at high light fluxes increases until about full leaf expansion and decreases thereafter (Saeki 1959; Elmore, Hesketh and Muramoto 1967). Decrease of photosynthetic rate in orchard grass was found to be associated with decrease of chlorophyll content of the leaf by Treharne, Cooper and Taylor (1968) and with decrease in potassium content in maize by Moss and Peaslee (1965). On the other hand, Osman and Milthorpe (1971) found decrease in the rate to be attributable mainly to increased $r_m$. This is in accordance with the finding that change in the rate is associated with change in the activities of photosynthetic enzymes (Smillie 1962).

(b) Chlorophyll Content. A positive correlation between chlorophyll content and the rate of photosynthesis has been shown for leaves of different species (Kariya and Tsunoda 1972) and between leaves of different ages (Sestak and Catsky 1962; Sestak 1966). If this is to be construed as a direct effect of chlorophyll content rather than an indirect effect of nitrogen content, it is likely to be due to an increase in the number of light quanta absorbed by chlorophyll. It is known that light transmission through a leaf depends on the thickness of the leaf and the concentration of leaf pigments (Takano and Tsunoda 1970).

(c) Leaf Morphology. The importance of the area of cell surface in leaf photosynthesis was stressed by El-Sharkawy and Hesketh (1965) and by Wilson and Cooper (1969a). Chonan (1967) determined differences in cell surface area between leaves at different positions on a stem, and suggested that this might account for differences in the rate of photosynthesis. Increase of cell surface area may be considered to decrease $r_m$ by increasing the total internal absorbing surface.

(d) Assimilate Accumulation. Neales and Incoll (1968) reviewed a hypothesis that the rate of photosynthesis is controlled by the assimilates accumulated in a leaf. Ito (1971) found a negative correlation between the rate of photosynthesis and the amount of starch in a leaf of tomato. He suggested that when water content in the leaf decreased in the afternoon, translocation from the leaf was prevented, which resulted in the accumulation of starch in the leaf. It is not known how this affects the rate of photosynthesis.

### 2.2.3. Effects of Light Energy during Growth

(a) Initial Slope. Although the effects of light energy during growth on the initial slope of the light-photosynthesis curve are often considered to be small (Burnside and Böhning 1957), Eagle and Treharne (1969) found a greater initial slope expressed on a chlorophyll basis when orchard grass was grown at a high light energy level. However, this was inconclusive as these authors failed to obtain a correlation between the rate of photosynthesis and phosphorylation and the Hill reaction.

(b) Saturated Rate of Photosynthesis. The rate of photosynthesis at high light flux is higher for many common agricultural species when they are grown under high light energy than when grown under low light (Burnside and Böhning 1957). El-Sharkawy, Hesketh and Muramoto (1965) found higher photosynthetic rates in spring or summer than in winter. Hesketh (1968) showed from growth cabinet experiments that this was neither a daylength effect, nor a temperature effect, but that light flux density was involved.

Several reasons to account for the effects of light energy during growth have been proposed. (1) Hiroi and Monsi (1966), using sunflower, ascribed the difference in saturated rate of photosynthesis to the difference in the number of layers of palisade cells. (2) Pearce and Lee (1969) found that the saturated rate of photosynthesis was related to specific leaf weight (SLW) when plants were transferred several times between different light energy conditions. (3) Holmgren (1968), using *Solidago*, found that the rate was associated with $r_m$ and to a smaller extent with $r_s$. There was a high correlation between SLW and $r_m$. However, Logan (1970) suggested that differences in the rates of photosynthesis could not be ascribed to diffusion resistances as he found the rate of photosynthesis of low light grown yellow birch plants to be low, even when a high $CO_2$ concentration was used. (4) Björkman (1968a) found that sun-adapted species which had a much higher saturated rate of photosynthesis than shade-adapted species, also had a higher activity of carboxydismutase. Hatch, Slack and Bull (1969) showed that some enzymes increased in activity when plants were brought from darker to brighter conditions.

### 2.2.4. Effects of Temperature

(a) Effects of Temperature at Low Light Flux. Gaastra (1959, 1962) found that gross photosynthesis at low light flux is independent of temperature within a wide temperature range. When net photosynthesis at low light flux is concerned, it is slightly and inversely related to temperature (Nevins and Loomis 1970a; Ludlow and Wilson 1971). The temperature-net photosynthesis curve is similar to, but displaced from, the temperature-dark respiration curve (Hiroi and Monsi, 1966). This led Nevins and Loomis (1970a) to state that decrease in net photosynthesis with increase of temperature at low light flux "correlated well with increase in dark respiration which, if "dark" respiration continues in the light ... would largely account for the effect".

There is a possibility that "dark" respiration continues in the light (Downton and Tregunna 1968). Alternatively, the results of Nevins and Loomis (1970a) and others may be due to the rates of photorespiration and dark respiration being similar at low light flux. Hew, Krotkov and Canvin (1969a) found photorespiration at about 4000 lux to be the same as the dark respiration rate when both rates were measured at 22°C.

(b) Effects of Temperature at High Light Flux. Optimum temperature for net photosynthesis increases with increase in light flux (Hiroi and Monsi 1966; Ludlow and Wilson 1971). At high light flux and under normal $CO_2$ concentrations, the net photosynthetic rate has a broad optimum temperature. The temperature-net photosynthetic rate relationship depends on genotype. It may be that plants have a higher optimum temperature than $C_3$ plants at high light fluxes (El-Sharkawy and Hesketh 1964; Björkman, Pearcy and Nobs 1971). Murata and Iyama (1963) and Murata, Iyama and Honma (1965) suggested that differences in the temperature response curves for 20 species of forage crops were related to the original geographical distribution of the species concerned, the plants with wide distribution being less influenced by temperature than those of limited distribution.

The optimum temperature may depend on the technique of measurement. (1) A low optimum temperature may be obtained if air temperature rather than leaf temperature is used to indicate photosynthetic temperature. (2) A stable rate of net photosynthesis may not be obtained for a half hour after a change of temperature

(Raschke, 1970) and errors may arise if temperature is changed continuously (cf. Murata and Iyama 1963). (3) A lower optimum temperature may be obtained if shoot photosynthesis rather than leaf photosynthesis is measured (Murata and Iyama 1963; El-Sharkawy and Hesketh 1964). The ratio of respiration loss to photosynthetic gain is higher in whole shoots than in leaves since respiration rate increases more rapidly than photosynthetic rate with increase in temperature.

(c) Mechanisms of Temperature Effects at High Light Flux Gaastra (1959, 1962) suggested that temperature has a strong effect on the biochemical processes involved in photosynthesis, and only a slight effect on the diffusion processes. This seems to explain satisfactorily the fact that temperature has a strong effect on net photosynthesis at high $CO_2$ concentration and at high light flux when the biochemical processes are limiting the rate of photosynthesis (Gaastra 1959; Hellmuth 1971).

Gaastra's suggestion is supported by the fact that carboxylase activity is involved in the response of photosynthesis to temperature. Björkman and Pearcy (1971) suggested that "probably the carboxylation reaction via ribulose-diphosphate, is rate limiting at low temperatures" in both $C_3$ and $C_4$ plants when they found the activation energy of carboxydismutase to be similar to that of photosynthesis in *Atriplex*. Treharne and Cooper (1969) found the optimum temperature for net photosynthesis to be similar to that for carboxylase enzymes in both $C_3$ and $C_4$ plants. Downes (1970) found increases in the difference between $CO_2$ concentration in the outside air and that of the intercellular spaces with increase of temperature to compensate the increase of $CO_2$ resistance ($r_a + r_s$). It was suggested that the difference in

$CO_2$ concentration reflected enzyme activity in the chloroplast.

There are, however, some reports that photosynthetic response to temperature is related to change in diffusion resistance. An apparent relation between photosynthesis and $r_s$ with change in temperature was found in corn (Raschke 1970) and in brigalow phyllodes (Van den Drissche, Conner and Tunstall 1971).

Another aspect of the temperature-net photosynthesis relation is the response of photorespiration to temperature. It is known that $C_4$ plants (which do not have photorespiration) and $C_3$ plants under low $O_2$ concentration (which suppresses photorespiration), have a high optimum temperature for net photosynthesis (Jolliffe and Tregunna 1968). The optimum temperature for photorespiration, measured as the rate of $CO_2$ evolution into $CO_2$ free air under light, is higher than that for photosynthesis (Hew, Krotkov and Canvin 1969; Hofstra and Hesketh 1969). Therefore the optimum temperature for net photosynthesis may be lower than that of "true" photosynthesis expressed as the sum of net photosynthesis and photorespiration. However, Hellmuth (1971) showed a similarity in peas between the temperature-net photosynthesis curve and the temperature-photorespiration curve, with both optimum temperatures being 28-32°C when photorespiration was calculated by extrapolating the light-photosynthesis curve linearly to zero light flux at low light fluxes.

(d) Effects of Growth Temperature. The relation between temperature and net photosynthesis is influenced by the temperature at which plants are grown. Temperature affects plant growth and the physiological state of the plant, which in turn affect the rate of photosynthesis (see 2.2.2). As the growth responses to temperature are different for different species, it is not surprising to find different effects of growth temperature on net photosynthesis between species. A high photosynthetic rate is reported in corn (Hesketh 1968), sorghum and alfalfa (Murata, Iyama and Honma 1965) and rice (Sato 1970) where plants are grown at relatively high temperature, whilst a high photosynthetic rate occurs in ryegrass (Wilson and Cooper 1969b), orchard grass (Treharne and Eagles 1970) and wheat (Sawada 1970) when plants are grown at low temperature.

The effects of growth temperature on net photosynthesis, however, may depend on the temperature at which the photosynthetic rate is measured (Treharne, Cooper and Taylor 1968) as the optimum temperature may shift according to growth temperature. Charles-Edwards, Charles-Edwards and Cooper (1971), using four temperate grasses, found mean optimum temperatures of 16.9°C and 19.7°C when the plants were grown at 15° and 25°C, respectively. A similar shift of optimum temperature was found in *Mimulus* by Björkman, Nobs and Hiesey(1970). However, some workers have reported a small effect of growth temperature on net photosynthesis except at extreme growth temperatures (Hesketh 1968; Robson 1969).

When plants grow at different localities or at different times of the year, temperature is not the only environmental variable. However, Mooney and West (1964) showed a remarkable acclimation of photosynthesis to growth temperature for plants grown at different elevations on White Mountain in California. Sawada (1970) found a good correlation in wheat seedlings between the optimum temperature for net photosynthesis and the growth temperature when plants were grown at different times of the year.

Temperature adaptation of photosynthesis may occur within a day (Mooney and Shropshire 1967; Mooney and Harrison 1970). A cool night reduces the rate of photosynthesis of the subsequent day (Izhar and Wallace 1967). This quick response suggests that leaf anatomy is not involved in the growth temperature-net photosynthesis relations. Wilson (1970) found the net photosynthetic rate of leaves grown at different temperatures to be associated with cell and with chloroplast size. Chloroplast size was found to change within a day by change in temperature and the importance of this in photosynthesis was suggested by West (1970).

Enzyme activity may be involved in the effects of growth temperature. Treharne and Eagles (1970) suggested carboxydismutase to be important, while Downton and Slatyer (1972) suggested that carbonic anhydrase was involved in $CO_2$ transfer.

Effects of growth temperature on respiration may be another factor to be considered in the relation between growth temperature and net photosynthetic rate (see 2.4.4).

### 2.3.0. Canopy Photosynthesis

The rate of photosynthesis of the canopy is an integration of the rates of photosynthesis of each component leaf. The environment within a canopy differs from that outside especially with respect to light flux the distribution of which is profoundly affected by the canopy itself.

### 2.3.1. Light Penetration through a Canopy

(a) The Monsi-Saeki Equation. Monsi and Saeki (1953) found in certain natural plant communities that light energy decreases exponentially as it passes through successive leaf layers. This is analogous to Beer's law and can be expressed as

$$I = I_o e^{-kF}$$

where $I$ = light energy in a canopy
$I_o$ = outside light energy
$k$ = extinction coefficient
and $F$ = LAI between the top of the canopy and the horizontal level in question.

The equation generally fits well experimental data obtained for many species unless leaves are unevenly distributed as in row plantings (Takeda and Kumura 1957; Agata, Kubota and Kamata 1971b; Luxmore, Millington and Marcellos 1971). The extinction coefficient (k), however, may change with increase in LAI as well as with leaf angle. When k was calculated by measuring light energy at ground level in orchardgrass canopies with varying LAI generated by both thinning and planting density, the value of k decreased with increase in LAI (Brown, Blaser and Dunton 1966). These authors suggested that this decrease might be due to a higher percentage of the leaves "flagging" at low LAI values. A similar result was reported for barley seedlings by Pearce, Brown and Blaser (1967b), but not in white clover and Bermudagrass (Brown, Blaser and Dunton 1966). Ludwig, Saeki and Evans (1965) found no change in the value of k in cotton communities with change in LAI obtained by the progressive upward removal of leaves.

(b) Factors Affecting Light Interception by a Canopy. Light interception by a developing canopy increases with increase of LAI. The LAI at which 95% of the incident light energy is intercepted at local noon has been called the critical LAI by Brougham (1958a). The critical LAI varies among species: it is 2-4 for clover and 4-10 for grasses and cereals (Brougham 1958a; Stern, 1960; Takeda 1961). Planophile canopies intercept more light at low LAI than erectophile canopies and the critical LAI is also low. Pearce, Brown and Blaser (1967a) demonstrated a significant effect of leaf angle on light interception by changing leaf angle artificially in barley seedlings. The critical LAI changed from 11 to 4.5 with change in leaf angle from 90° (vertical) to 18°. A small critical LAI in planophile canopies implies that leaves at the bottom of the canopy receive only a small proportion of the total incident light quanta when the canopy has a high LAI.

Light interception by a canopy changes during the day. Brougham (1958a) found light penetration to the ground to be highest at local noon and to be relatively high in early morning and later afternoon, although the diurnal fluctuation was smaller in clover than in ryegrass. Diurnal change in the proportion of diffuse to total light and change in solar angle were suggested as causes of the diurnal change in light penetration. However, this diurnal change may not be large once the canopy has reached a high LAI (Baker and Musgrave 1964).

### 2.3.2. Factors Affecting Canopy Photosynthesis

(a) Light Energy. Canopy photosynthesis is strongly correlated with the incident light energy under natural conditions; an $R^2$ of 0.90 was reported for corn canopies throughout the growing season (Moss, Musgrave and Lemon 1961). It is therefore necessary to examine the effects of other factors on canopy photosynthesis at specified light energy levels when the canopy is not light saturated. The level of light energy for saturation of the canopy is generally higher than that required for saturation of leaf photosynthesis (Kumura 1965; Brown, Blaser and Dunton 1966) due to mutual shading of leaves and to the angle of leaves to the sun (Kriedemann, Neales and Ashton 1964).

The mechanism of light saturation of canopy photosynthesis is well demonstrated in soybeans by data of Kumura (1965). In his experiment, illuminance at all leaf surfaces in the canopy was measured by small CdS photocells simultaneously to allow a frequency distribution of illuminance at the leaf surface to be constructed. Except in canopies with very small LAI (0.02), there were always some leaves which did not receive sufficient light energy to saturate leaf photosynthesis. However, these leaves remained unsaturated at about the same illumination when incident light energy to the canopy increased from 35 klux to 80 klux. The canopy was thus saturated at 35 klux. A similar phenomenon was observed in sugarbeet canopies (Ito 1965) and in rice canopies with curved and drooped leaves (Tanaka, Matsushima, Kojyo and Nitta 1969).

Different light-photosynthesis curves are obtained at different times during the growth of a canopy (Takeda 1961; Jeffers and Shibles 1969; Robson 1971). When plants are young and LAI is small, the shape of the curve is similar to that of a single leaf. As the canopy becomes mature, the light saturation phenomenon may disappear and the curve becomes almost linear. The initial slope of the light-net photosynthesis curve remains the same once a closed canopy is obtained, but the position of the curve of the mature canopy is often displaced below that obtained from the young canopy due apparently to an increased rate of canopy respiration.

(b) Canopy Structure. Differences in the pattern of light distribution in a canopy between planophile canopies and erectophile canopies results in differences in photosynthetic response to incident irradiance. Net photosynthesis may increase with increase in incident light energy up to very high levels in erectophile canopies whilst the response may be small or negligible in planophile canopies at high light fluxes. This may be seen by comparing the light-photosynthesis curves for soybean (Kumura 1965) with that for rice (Tanaka and Matsushima 1971a).

When droopiness and the angle of rice leaves were varied experimentally, the treated canopy showed light saturation phenomenon whilst the untreated canopy with straight and erect leaves increased in rate of net photosynthesis with increase in incident light energy (Tanaka, Matsushima, Kojyo and Nitta 1969). Light energy inside the canopies decreased more rapidly with depth in the canopy with curved and drooped leaves than in the canopy with straight and erect leaves.

(c) Diffuse Light. A high proportion of diffuse light increased the rate of net photosynthesis in soybean canopies (Kumura 1968a) and in rice canopies (Tanaka, Matsushima, Kojyo and Katsuki 1970) when the canopies had a large LAI. Light energy within the canopy was relatively evenly distributed horizontally and vertically with a high proportion of diffuse light; but was unevenly distributed with direct light, most leaves receiving either very high light energy or very low light energy. The effect of diffuse light was negligible in rice canopies with artificially curved and drooped leaves (Tanaka, Matsushima, Kojyo and Katsuki 1970).

(d) Light Angle. Incident light angle may be expected to affect net photosynthetic rate as light penetration into a plant canopy changes with solar angle (2.3.1). Tanaka and Matsushima (1971b) placed a rice canopy in a photosynthetic chamber which could be rotated vertically as well as horizontally. Net photosynthetic rate at high LAI was much less when the angle of the canopy was $0^{\circ}$ or $30^{\circ}$ to the sun than when the angle was $60^{\circ}$ or $90^{\circ}$. A similar result was obtained by Pearce, Brown and Blaser (1967a) with barley seedlings.

At low LAI a canopy with vertical leaves illuminated vertically intercepts a smaller proportion of the incident light than when it is lit from a low angle, and the rate of canopy photosynthesis may be small (Baker and Musgrave 1964). On the other hand light angle may have only a small effect on photosynthesis of planophile canopies because of a small change of light penetration in the canopy (Brougham 1958a; Ito and Udagawa 1971).

### 2.3.3 Relationship between LAI and Canopy Photosynthesis

Increased percentage light interception by increased LAI results in an increased rate of net photosynthesis (Takeda 1961; Ludwig, Saeki and Evans 1965). However, it has been a matter of controversy whether further increase of LAI above the critical value results in increase in net photosynthetic rate. The conflicting results are partly due to how LAI is generated in experiments. Methods reported in the literature and the likely errors involved are discussed below.

(a) Re-spacing of Plants. McCloud (1964) grew pearlmillet as spaced plants, subsequently moved plants together and measured immediately photosynthesis of the resulting community. Canopy photosynthesis showed an optimum relationship with LAI at low light energy. As light energy increased, the optimum LAI also increased until at very high fluxes a maximal relationship occurred. In the canopies created by this technique, dark respiration rate would be proportional to LAI and it is likely that both the dark respiration rate and the photosynthetic rate of the lower leaves would be higher than in the 'normal' canopy situation where plants grow with mutual shading (see 2.2.3 and 2.4.3).

(b) Removal of Lower Leaves. Ludwig, Saeki and Evans (1965) generated variation in LAI by removing the lower leaves from an established canopy of cotton plants. An optimum relation was found only at low light energy (12 klux) and at high temperatures (30-40°C). This technique of leaf removal results in a low ratio of LAI/total dry matter (TDM) at low LAI. It is therefore likely that the net photosynthetic rate at low LAI was underestimated. The rate of respiration is influenced not only by the weight of leaf which is only approximately expressed by LAI, but also by the weight of other plant organs.

(c) Thinning. Brown, Blaser and Dunton (1966) measured net photosynthetic rate of four pasture species at 59 klux soon after initially dense populations of plants were thinned. The response of net photosynthesis to LAI generated this way was linear in white clover and alfalfa up to an LAI of 3, and in Bermudagrass and orchardgrass up to an LAI of 5.

Leaves which are situated in dim light in the canopy may have the characteristics of 'shade'leaves. When the light flux reaching these leaves is increased by removal of neighbouring plants, they may be unable to respond, and it may be expected that the whole canopy will continue to show a low rate of net photosynthesis. Adjustment to the new environment may subsequently change the relation (Wilfong, Brown and Blaser 1967).

(d) Defoliation of Top Leaves. Pearce, Brown and Blaser (1965) found an approximately linear relationship between net photosynthetic rate and LAI of up to 7 in orchardgrass when variation in LAI was generated by removing different amounts of leaf at the top of the canopy. A canopy cut to 10 cm with an LAI of 1 showed a net efflux of $CO_2$ even in full sunlight.

It is likely that response to increased light flux is smaller in leaves at the bottom of a canopy after defoliation than in leaves at the top. It is also/ /likely that a low ratio of LAI/TDM after defoliation will result in a low ratio of net photosynthesis to respiration. During the regrowth period, gradual adjustment of photosynthetic and respiratory rates may occur, and result in changing relationships between LAI and net photosynthetic rate (Vickery, Brink and Ormrod 1971; Davidson and Birch 1972).

(e) Planting Density. Pearce, Brown and Blaser (1967b) obtained a wide range of LAI of barley seedlings by varying sowing density. $CO_2$ exchange was measured 7 days after sowing by which time, the highest LAI obtained was 18.6. A broad optimum LAI was demonstrated. This result should not be compared with a mature canopy because the specific respiration rate would differ greatly between young seedlings and more mature plants.

(f) Aging. Canopies with different LAI values may be obtained during growth. Puckridge (1971, 1973) measured photosynthesis of wheat canopies at Adelaide from winter through spring at ambient temperature. LAI, however, was partly confounded with temperature in these measurement and LAI-net photosynthesis ($P_n$) relation may have been affected by change in temperature.

Controlled environment facilities may be used to provide constant environmental conditions and may prevent the temperature shift. Robson (1971) measured photosynthesis of ryegrass canopies raised in this way at different growth stages. Net photosynthetic rate at high light fluxes increased with increase of LAI up to 10.6. However, further increase of LAI to 23.3 resulted in decrease of net $CO_2$ uptake at any light fluxes due apparently to increase in respiration rate. Net photosynthetic rate at low light fluxes showed an optimum LAI of less than 10.6.

(g) Combinations of the Above Methods. Jeffers and Shibles (1969) obtained variation in LAI by removing lower leaves as well as by aging. The separate effects of the two methods were not determined. Multiple regression analysis was used to analyse the effects of plant attributes and environmental factors on photosynthesis. The rate of net photosynthesis decreased by 7 $mgCO_2/dm^2/hr$ during a two month growth period. When allowance was made for this aging effect, there was no optimum LAI over a range of solar radiation from 140 to 840 $W/m^2$. Net photosynthesis increased to a maximum value with increase of LAI more sharply at high light fluxes than at low light fluxes. The elimination of the aging effect raises doubt as to the validity of the conclusion drawn above. It is quite likely that respiration increased with increase in total dry matter and if this is a reason for the decreased rate of net photosynthesis with time, the authors were examining the effect of LAI on 'gross' photosynthesis which is different from net photosynthesis.

Plant density and aging were used by Fulwood and Puckridge (1970) to vary LAI in Wimmera ryegrass pastures. There was no sign of an optimum LAI for net photosynthesis with either method even at an incident light flux density of 70 $W/m^2$. The respiration rate was found to be very low at 7% of the daily 'gross' photosynthesis at LAI of 3-5. A low ambient temperature of 10-15°C was suggested as a causal factor.

(h) Conclusions. It is obvious that the relationship between LAI and net photosynthetic rate depends on the species and methods used to generate LAI. Respiration is clearly involved and it is obvious that respiration rate is not linearly related to LAI. Further, the different methods used to generate variation in LAI create different canopy conditions for net photosynthesis and it is not surprising to find different conclusions drawn. It is therefore dangerous to extrapolate results obtained with any particular method. Results obtained from re-spacing of plants (a) and removal of lower leaves (b) should not be used as a basis for general conclusions and results obtained through thinning (c) defoliation of top leaves (d) and high plant densities (e) apply only to specific experimental situations. In the field,variation in LAI is generated mainly by variation in plant density and with time in naturally regenerated pastures, and with time alone after sowing. It is therefore realistic to assess the nature of the $P_n$ - LAI relationship from experiments in which LAI is generated in these ways.

### 2.3.4. Effects of Temperature

Temperature may affect canopy photosynthesis differently from the way in which it affects leaf photosynthesis since in the canopy situation the respiratory response of non-photosynthetic material has to be considered.

(a) Artificial Communities. Ormrod (1964) found a strong interaction between the effects of temperature and light flux in the net $CO_2$ exchange rate of *Phaseolus vulgaris*; optimum temperature increased with increase in light flux. The temperature-net photosynthesis curve at 6 klux was parallel to the temperature - dark respiration curve. A mature canopy with a large dry matter showed a decrease of net photosynthetic rate at

30 klux with increase of temperature from 8 to 32°C, due apparently to increased respiration rate. Bate and Canvin (1971) also showed a decrease of photosynthetic rate of young aspen trees at 48.5 W/$m^2$ (PAR) with increase of temperature from 15 to 30°C. Scott and Menalda (1970) also showed interaction in the effects of temperature and light on net photosynthesis.

(b) Field Experiments. When $CO_2$ exchange measurements are made in the field and the chamber temperature is kept at that of the outside air, interaction between temperature and light flux may not be apparent (Jeffers and Shibles 1969). When the chamber temperature is changed independently from solar radiation, the interaction may be found (Baker 1965). Moss, Musgrave and Lemon (1961) found an increase of net photosynthesis with increase of temperature at various light fluxes in a corn field.

Baker, Hesketh and Duncan (1972) found a decrease in net photosynthesis of cotton communities with increase in temperature above 25°C regardless of the light flux level. An interaction may have been found, however, if net photosynthesis had been measured at lower temperatures. "Day" respiration was estimated by measuring $CO_2$ evolution 6 minutes after darkening the chamber and this is likely to include the $CO_2$ gush. This rate was about the same as dark respiration at about 25°C. "Day" respiration, however, was higher than dark respiration by 20-25% at higher temperatures. "Day" respiration increased almost linearly with temperature up to 42°C.

The rate of photorespiration in measurements of canopy photosynthesis needs to be examined further, as is the case with single leaves.

## 2.4.0. Dark Respiration

### 2.4.1. Contribution of Dark Respiration to Plant Dry Matter Production

(a) Loss of Dry Matter due to Respiration. Dark respiration produces chemical energy at the expense of carbohydrate accumulated through photosynthesis. In the short term, increase of total plant dry matter (d(TDM)/dt) can be obtained as the difference between net photosynthetic gain during the day ($\Sigma Pn$) and dark respiration loss at night ($\Sigma DR$).

$$d(TDM)/dt = \Sigma Pn - \Sigma DR \qquad \text{EQ.1}$$

When an average rate of dark respiration at night ($\overline{DR}$ in $gDM/m^2/hr$) is considered, EQ.1 becomes

$$\begin{aligned} d(TDM)/dt &= \Sigma Pg - 24\overline{DR} \\ &= DPg - DDR \qquad \text{EQ.2} \end{aligned}$$

where Pg is a term for the sum of Pn and $\overline{DR}$,

DPg is daily gross photosynthesis, and

DDR is daily dark respiration rate (24 hr).

The ratio of $\Sigma DR/\Sigma Pn$ or DDR/DPg can be used to indicate the contribution of dark respiration to dry matter production. The ratio changes from day to day due to environmental variation. Agata, Kubota and Kamata (1971a) found the ratio of DDR/DPg to vary daily from 0.25 to 0.79. The ratio of $\Sigma DR/\Sigma Pn$ was 0.3 in wheat for 60 days in a growth cabinet. It increased from 0.4 to 0.5 during an experiment with a subterranean clover canopy (King and Evans 1967). Hogetsu, Oshima, Midorikawa, Tezuka, Sakamoto, Mototani and Kimura (1960), working with *Helianthus tuberosus* found the ratio of DDR/DPg increased up to 0.5 at the later stages of growth. This amounted at maturity to 20-30 gDM/m$^2$/day loss due to respiration.

(b) Optimum LAI for Dry Matter Production. EQ.2 has been used as a basic equation in many theoretical considerations of plant dry matter production. In order to evaluate the respiratory loss, it has been assumed that the rate of respiration is proportional to total dry matter (Monsi and Saeki,1953) or to photosynthetic gain (de Wit 1965). The first assumption introduced the idea of optimum LAI for dry matter production (Monsi and Saeki 1953; Donald 1963). However, it was found that in some communities the rate of dark respiration did not increase linearly with increase in LAI (King and Evans 1967). This was suggested to be due to the low rate of dark respiration of leaves at the bottom of the canopy (Ludwig, Saeki and Evans 1965). It was demonstrated in a computer model that differences in the dark respiration rate of leaves under different light environments are so great that this could easily alter the relationship between LAI and crop growth rate (Loomis, Williams and Duncan 1966).

Although dark respiration can make a marked contribution in plant dry matter production, a quantitative evaluation of dark respiration was conducted only recently (McCree 1970).

### 2.4.2. Physiological Factors Affecting Dark Respiration Rate

(a) Aging. The specific rate of dark respiration of a leaf changes with age; it decreases very rapidly as the leaf expands but is stable afterwards (Dickman 1971; Hoshino, Matsumoto and Okubo 1971). Smillie (1962) found the decrease with age in the rate of respiration expressed per unit fresh weight of a pea leaf to be directly related to enzyme activity. The activity of respiratory enzymes such as enolase, 6-phosphogluconic dehydrogenase, and aconitase decreased as leaves became older. It was concluded that the observed change in the rate of dark respiration reflected the change in the cellular level or activity of the leaf enzymes.

Woledge and Jewiss (1969) suggested that decrease in specific rate of dark respiration of an expanding leaf of tall fescue was due to an increased proportion of cell wall which probably resulted in decrease in soluble carbohydrate levels.

Beevers (1970) suggested in his review paper, that the respiration of plants was regulated mainly by the amount of ADP and phosphopyridine nucleotide (PN). In a young growing cell where ATP and PNH are consumed rapidly, the rate of respiration may be high because of high levels of ADP and PN. It was also suggested that the young cells had an inactive pentose-phosphate pathway which was less efficient (less ATP production per unit of substrate consumed) than the TCA cycle. These can be considered as reasons for the high respiration rates associated with rapid growth in young seedlings.

It has been shown that the specific rate of dark respiration of some plants decreases with age or with increase in total dry matter (Sawada 1970; Razorenova and Nilovskaya 1971). Two reasons for this were given by Kumura and Naniwa (1965); (i) decrease of the specific rate of dark respiration of each organ; and (ii) a decreasing proportion of leaf to total dry matter. As leaves had a higher specific rate of dark respiration than any other organ except pods, a decreasing proportion of leaves resulted in a decreasing specific rate of dark respiration of the whole plant.

(b) Carbohydrate Level. According to Alberda (1970), the rate of respiration of perennial ryegrass is influenced by the level of carbohydrate reserve induced by daylength, temperature and nutrient conditions imposed for periods of 2-5 days.

Pearson and Hunt (1972c) reported that root respiration of alfalfa plants was regulated by the light conditions of the shoot - the rate depending on the amount of substrate from the shoot. Root respiration during the dark period decreased with time at 25°C but was constant at 15°C. It was also suggested that the supply of the substrate to the root was constant at low temperature.

The substrate for dark respiration in corn leaves was found, using $^{14}C$, to be mainly photosynthate produced within three hours before the dark period (Filippova, Voznesenskii and Bogatkina 1964).

(c) Growth Rate. McCree and Troughton (1966a) found the dark respiration rate of white clover to fluctuate during a 24 hour period in a growth cabinet. Average dark respiration rate at night was less than that during the daytime by 20%. When the light energy was changed in the morning, the rate of respiration of the plants changed according to the light environment. It was concluded that the rate of respiration was proportional to the rate of photosynthesis and hence to the net uptake of $CO_2$.

McCree (1970) measured the dark respiration rate of white clover after changing the light energy at different amounts of plant dry matter. Daily dark respiration rate (DDR in $gCO_2/m^2/day$) was linearly related to the daily gross photosynthetic rate (DPg in $gCO_2/m^2/day$) and to the dry weight of the plant (TDM in $g(CO_2$ equivalent$)/m^2$).

$$\text{DDR} = 0.25\text{DPg} + 0.015\text{TDM} \qquad \text{EQ.3}$$

The equation suggests that for any one day, plants lose by respiration 25% of their gain from 'gross' photosynthesis plus 1.5% of their dry weight at that time.

McCree's equation was analysed by Thornley (1970, 1971). Thornley proposed that the substrate produced by photosynthesis ($\Delta S$) can be divided into three parts: substrate respired in maintenance ($\Delta Sm$); substrate respired in synthesis of new material ($\Delta Sr$); and substrate transformed into new plant material ($\Delta St$).

$$\Delta S = \Delta Sm + \Delta Sr + \Delta St \qquad \text{EQ.4}$$

If the maintenance requirement can be expressed as substrate consumed per unit of plant material per unit time as in bacterial cultures, then

$$\frac{\Delta Sm}{\Delta t} = m(TDM) \qquad \text{EQ.5}$$

where m is the maintenance coefficient. When the yield of the process of constructive growth (Yg) was given as

$$Yg = \frac{\Delta St}{\Delta Sr + \Delta St} \qquad \text{EQ.6}$$

then rate of respiration (DR) can be shown as

$$DR = (1-Yg)Pg + mYg(TDM) \qquad \text{EQ.7}$$

where Pg is gross photosynthesis.

The equation is the same form as McCree's equation. It is, however, not known if m and Yg are constant at different values of Pg and TDM.

Hesketh, Baker and Duncan (1971) measured the rate of respiration and dry matter accumulation of growing floral buds, bolls, and leaves of cotton plants. The rate of respiration of each organ was analysed by introducing two respiration components; a 'maintenance respiration' and a 'growth respiration'. An equation was developed on the basis of 'maintenance respiration' being linearly related to dry weight of the organ and the 'growth respiration' being linearly related to the rate of dry matter accumulation.

$$Rd(DM) = Rm(DM) + Gr\ d(DM)/dt \qquad \text{EQ.8}$$

or $$Rd = Rm + Gr(d(DM)/dt)1/DM \qquad \text{EQ.9}$$

where

$Rd$ = specific respiration rate ($gCH_2O/gCH_2O/hr$)

$DM$ = dry matter

$Rm$ = specific rate of maintenance respiration ($gCH_2O/gCH_2O/hr$)

$Gr$ = respiration required to convert $CH_2O$ to dry matter ($gCH_2O/gCH_2O$)

EQ.9 implies, with Rm and Gr assumed to be constant during an experimental period, that the specific rate of respiration is constant if dry weight of the organ increases exponentially and that the specific rate of respiration decreases reciprocally with increase of dry weight of the organ if the dry weight increases linearly.

For the first case, if $DM = DM_0\ e^{Kt}$

then $$(d(DM)/dt)\ 1/DM = K$$

and $$Rd = Rm + Gr \cdot K \qquad \text{EQ.10}$$

For the second case, if $DM = DM_0 + bt$

then $$d(DM)/dt = b$$

and $$Rd = Rm + Gr \cdot b(1/DM) \qquad \text{EQ.11}$$

where K and b are constants.

The experimental data support the above deductions and suggest that EQ.9 describes the relation between respiration rate and the size and the growth rate of the organs.

Thornley and Hesketh (1972) used Yg (EQ.6) in EQ.9, which then becomes

$$Rd = Rm + \left(\frac{1-Yg}{Yg}\right)(1/DM)(d(DM)/dt) \qquad \text{EQ.12}$$

They fitted the logarithm of dry weight of cotton bolls to a polynomial with time as the variable. Specific growth rate was expressed as

$$(1/DM)(d(DM)/dt) = a_1 + 2a_2t + 3a_3t^2$$

The specific respiration rate was also fitted by a polynomial

$$Rd = b_1 + b_2t + b_3t^2$$

From the best fits, the constants ($a_1$, $a_2$, $a_3$, $b_1$, $b_2$, $b_3$) were obtained. Then Yg and Rm were calculated as

$$Yg = 0.74 \pm 0.10 \text{ g (dry matter)/g(substrate)}$$

$$Rm = 0.006 \pm 0.010 \text{ g/g/day}$$

However, the standard errors of the conversion efficiency (Yg) and the specific rates of maintenance respiration (Rm) are too large to determine whether Yg and Rm are constant throughout the period of boll growth.

### 2.4.3. Effects of Light Environment

(a) Direct Effects. Heichel (1970, 1971) found that the rate of respiration of maize leaves decreased during the two hours after illumination. By using $CO_2$ free air when leaves were illuminated, the maximum rate of dark respiration after illumination was found to be quantitatively related to prior illumination, but not to the previous $CO_2$ fixation rate in light. However, this was not observed in tobacco leaves. It was reported by Yamaguchi and Tanaka (1967) with rice and by Helms (1965) with Douglas fir that the rate of dark respiration was highest after sunset. This may, however, reflect the level of carbohydrate available for respiration rather than a direct effect of light.

(b) Light Conditions During Growth. When plants are grown for a long time at low light energy, the specific rate of dark respiration may decrease to very low values (Kumura 1968b; Schmidt and Blaser 1969). This effect may be more pronounced if the rate of leaf respiration is expressed on an area basis because leaves grown under low light energy have a high specific leaf area (SLA) (Hiroi and Monsi 1963, 1964).

Woledge (1971) obtained contrasting results in her experiments. When tall fescue plants were grown in the field during summer the specific rate of leaf respiration was less at 23% shade than when plants were grown under full sunlight. However, the specific rates of leaf respiration of plants grown in a growth cabinet were not significantly different at 72 compared with 18 $W/m^2$ (PAR). The cabinet experiment was conducted at lower light energy than the field experiment, and temperature differences between the two experiments may be another reason for the different results. Woledge (1972) suggested that the decreased rate of dark respiration observed for shaded leaves was related to their rapid aging.

### 2.4.4 Effects of Temperature

(a) Responses of Dark Respiration to Temperature. Early work on the relation between temperature and dark respiration is well documented by James (1953). In many species the rate of dark respiration increases almost exponentially with increase in temperature at low temperature ranges; a less rapid increase occurs at high temperature ranges. The temperature coefficient ($Q_{10}$) of respiration is about 2.0 with slightly higher values at low temperatures and slightly lower values at high temperatures.

James (1953) found the optimum temperature for many species to be 35-45°C. The temperature-respiration relationship differs between species (Murata and Iyama 1963) and between populations within a species (Eagles 1967).

Semikhatova (1970) found that a high rate of respiration at high temperature had the same efficiency (ATP produced/substrate consumed) as that at low temperature. It was suggested that the increased ATP production through high respiration rate at the high temperature was used for the increased energy requirement for cell repair and re-synthesis of destroyed compounds at the high temperature, instead of the synthesis of new material. Tajima (1971) found the optimum temperature for the efficiency of oxidative phosphorylation (in terms of ADP consumed/$O_2$ consumed) in mitochondria of several plants to be about 25°C.

(b) Growth Temperature. The effects of growth temperature on the $Q_{10}$ of dark respiration are not clear. Several views have been expressed: (i) $Q_{10}$ increases slightly when plants are grown at low temperature or in winter (Wager 1941; Sawada 1970); (ii) $Q_{10}$ is almost independent of growth temperature (Fukui, Ojima and Watanabe 1965; Strain and Chase 1966); (iii) $Q_{10}$ is increased when plants are grown at high temperature (Pearson and Hunt 1972c); (iv) there is no consistent relation between $Q_{10}$ and growth temperature (Scott 1970).

When the dark respiration rates of plants grown at different temperatures are compared, the temperature at which respiration is measured should be considered. An example of the need for this may be seen in the results of Pearson and Hunt (1972c). Dark respiration rate measured at 10°C was higher for plants grown at 20/15°C than for those grown at 30/25°C, but the rate measured at 30°C was lower for plants grown at 20/15°C than for those grown at 30/25°C.

Effects of growth temperature on the specific rate of dark respiration are complicated by the fact that temperature influences a large number of interacting processes. Plants grown at near optimum temperature and consequently with a relatively high total dry matter may have a relatively small specific rate of dark respiration. This is particularly apparent when experiments are conducted with young plants (cf. Fukui, Ojima and Watanabe 1965; Rook 1969). Similarly, Geronimo and Beevers (1964) ascribed the low specific rate of respiration of pea leaves to acceleration of aging by high temperature when the plants were grown at high temperatures. On the other hand, when plants are grown at near optimum temperature, they have a high crop growth rate and a high photosynthetic rate, which tend to increase the rate of specific dark respiration. This may compensate for the effect of high dry matter (cf. Wager 1941; Strain and Chase 1966). Low temperature increases the level of soluble carbohydrate in the leaves (Warren Wilson 1966) which may increase dark respiration rate (Strain 1969; Woledge and Jewiss 1969).

When the respiration of mature plants of similar dry matter (Murata, Iyama and Honma 1965) or respiration of leaves of the same physiological age (Woledge and Jewiss 1969) were compared for plants grown at different temperatures, specific respiration rate was slightly higher for plants grown at low temperatures than those grown at high, when dark respiration rate was measured at a common temperature.

Adaptation of dark respiration to a new temperature regime may occur within a few days - within two days in *Pinus radiata* seedlings (Rook 1969) and within one day in Italian ryegrass and in orchard grass (Tajima 1965). Rook (1969) and Woledge and Jewiss (1969) suggested these rapid changes were due to the change in carbohydrate level.

(c) Dark Respiration Rate Measured at Growth Temperature. Although dark respiration rate increases almost exponentially with temperature when measurements are made immediately after temperature change, the effect of temperature is much less when plants are grown at a range of temperatures and measurements made at the growth temperature (Murata, Iyama and Honma 1965; Rook 1969). An explanation for this difference may be found in the fact that plants grown at low temperature have in general a rather high specific respiration rate. Sawada (1970) found the specific rate of leaf respiration of wheat plants grown in the field to be constant when measured at a temperature optimal for photosynthesis. Optimal temperature for photosynthesis was linearly related to the mean growth temperature.

However, the above results were obtained with young seedlings and the situation may be different for mature plants or a mature canopy. Ludwig, Saeki and Evans (1965) grew cotton plants at 30°C until 1-2 weeks prior to $CO_2$ exchange measurement when plants were moved to 20°, 30° and 40°C growth cabinets. The dark respiration rate measured at growth temperature was directly related to temperature; plants at 40°C had double the respiration rate of those at 20°C. However, these comparisons were made at the same LAI, and LAI is not a good basis for the expression of dark respiration rate since the relation between LAI and total dry matter may change with the growth temperature.

Takeda and Agata (1964b, pers. comm.), working with white clover, found the specific rate of dark respiration to be directly related to growth temperature. They suggested that the high dark respiration at high temperature causes a reduction of growth through acceleration of aging of leaves and through exhaustion of carbohydrate content.

A quantitative evaluation of respiration loss due to high temperature for plant communities does not appear to have been reported.

## 2.5.0 Development of Leaf Area

### 2.5.1 Dry Matter Distribution among Plant Parts

(a) Introduction. Total leaf lamina area is influenced by both the distribution of dry matter between plant parts (distribution ratio to each organ) and the ratio of individual leaf lamina area to leaf lamina dry weight (specific leaf area, SLA). Monsi and Murata (1970) discussed the role of the distribution ratio to leaves in increasing potential total photosynthesis and hence dry matter production. Shibles and MacDonald (1962) also stressed the role of the distribution ratio to leaves when they found differences in seedling dry weight between cultivars of birdsfoot trefoil in the absence of differences in leaf photosynthesis.

The distribution of dry matter between plant parts is also important in dry matter production processes as it determines the economic yield (i.e. grain or tuber, etc.) of the crop and influences nutrient and water supply through root/shoot ratio. Further, different plant parts may have different specific rates of respiration and such differences will influence the total plant respiration.

### (b) Factors Influencing the Distribution Ratio

(1) Aging and Total Dry Matter. Iwaki (1958) showed in field grown buckwheat communities that the distribution ratio to leaves was high when plants were young. During the middle growth stages the distribution ratio to stems increased and at later stages that to the reproductive organs was very high. These results agree with the findings that root and leaf are the primary "sinks" for photosynthate when plants are young, and that stem becomes a major "sink" with aging (Balasko and Smith 1973).

The distribution ratio changes with increase of total dry matter of plants or communities. Moriya (1970) found a quadratic relation between green leaf dry matter (GLDM) and total dry matter (TDM) for rice and soybean:

$$\mathrm{GLDM} = a(\mathrm{TDM}) - b(\mathrm{TDM})^2 \qquad \text{EQ.13}$$

This indicates that the distribution ratio to leaves decreases continuously with increase of dry matter. In sugar beet and sugar cane, the relation was best expressed as a cubic function and the distribution ratio to leaf increased slightly when total dry matter was very large.

The distribution of dry matter to plant parts is best analysed when the dry matter of each part is expressed in relation to total dry matter rather than as a function of time as was shown by Moriya (1970). This is because functions relating GLDM and TDM can give the distribution ratio by differentiation. In EQ.13, for example,

$$d(GLDM)/d(TDM) = a - 2b(TDM)$$

Furthermore, ontogenetic drift associated with environmental conditions may be minimized (Evans 1972).

(2) Light Energy. "Sun" and "shade" plants respond differently to light energy. "Shade" plants show a constant or slightly increased distribution ratio to leaf with decreased growth light energy (Evans and Hughes 1961; Kuroiwa, Hiroi, Takada and Monsi 1964) when comparisons are made at the same total dry matter. As SLA generally increases with decrease in light energy, shade plants grown at low light energy have a larger leaf area than those grown at high light energy again at the same total dry matter. Sun plants, on the other hand, show decreased distribution to leaf with decreased growth light energy at the same total dry matter (Hiroi and Monsi 1964; Kuroiwa, Hiroi, Takada and Monsi 1964) and here increased SLA at low light energy may compensate partially or completely for the decreased distribution ratio to leaf (Terry 1968). Hiroi and Monsi (1964) discussed differences in distribution ratio between species as causes of shade tolerance and shade intolerance.

The ratio of root dry matter to total dry matter is generally high under high light energy conditions (Evans and Hughes 1961; Hughes and Cockshull 1971). This agrees with the results of an experiment with radioactive carbon ($^{14}C$) showing the rate of translocation of photosynthate to root to be high under high light energy (Ryle 1970).

However, Terry (1968) found no effect of light energy level on the root/total dry matter ratio of sugar beet.

(3) Temperature. Friend, Helson and Fisher (1965) showed the leaf/total dry matter ratio to be highest at 20-25°C in wheat for the first five week growth period, but a different result is obtained if the ratio is calculated for the data at the same total dry matter. There appears to be little data available on temperature effects on the distribution ratio to leaf.

The root/total dry matter ratio is high when plants are grown at low temperature when the comparison is made at the same total dry matter (Brouwer 1962; Terry 1968). $^{14}C$ studies show the rate of translocation to root and the proportion of $^{14}C$ retained in leaves to be high under low temperature conditions (Sekioka 1961; Hartt 1965).

### 2.5.2 Effects of Environmental Factors on Plant Morphology

Leaf area per plant or per unit ground area can be expressed as

leaf area = leaf size X number of leaves

= leaf size X number of leaves on a tiller X number of tillers

Most studies of the effects of environmental factors on development of the area of individual leaves are limited to isolated plants and the results may not be directly applicable to the community situation except for the early stages of community growth during which individual plants in the community grow essentially as isolated plants.

(a) Leaf Appearance Rate on a Single Stem. The effects of light energy on leaf appearance rate on a single stem are not clear. Some workers have found a high leaf appearance rate under high light energy conditions (Mitchell 1953; Friend, Helson and Fisher 1962b) while others reported no effects of light energy on leaf appearance rate (Aspinall and Paleg 1964; Bean 1964).

The rate of leaf appearance on a single stem is accelerated in many species by increase in temperature (Mitchell 1956; Raguse, Fianu and Menke 1970).

(b) Leaf Expansion Rate. The rate of increase in area of a leaf increases with increase in light energy in wheat and cucumber (Friend, Helson and Fisher 1962b; Milthorpe and Newton 1963).

25°C was the optimum temperature for leaf expansion in cocksfoot and ryegrass (Davidson and Milthorpe 1965; Robson 1972).

(c) Leaf Size. The final area attained by a leaf increases with increase in the level of insertion and a leaf at a higher level of insertion is more responsive to environmental factors than one at a low level (Friend, Helson and Fisher 1962b; Taylor, Cooper and Treharne 1968).

The length of a grass leaf decreases with increase in light energy whilst the width generally increases (Friend, Helson and Fisher 1962b; Wilson and Cooper 1969c; Friend and Pomeroy 1970). However, the resultant effects of light energy on final leaf size are not completely clear; a positive effect of light energy was reported in cucumber by Milthorpe and Newton (1963) whilst a negative effect is seen in wheat in the results of Friend and Pomeroy (1970). The optimum temperature for final leaf size was 18-25°C in cucumber and ryegrass. In ryegrass this was due to effects on leaf length rather than leaf width (Milthorpe 1959; Robson 1972).

(d) Branching (Tillering). High light energy accelerates lateral production (Mitchell 1953; Friend 1965). Cooper and Tainton (1968) suggested that the ample amount of carbohydrate produced by high light energy stimulated tiller initiation. Low temperature hastens the production of laterals (Mitchell and Lucanus 1960; Beinhart 1963). This is attributed to a high percentage of water soluble carbohydrate in plants at low temperature (Sato and Ito 1969; Robson 1972).

### 2.6.0 Death and Decay

Senescence, death, and decay of both plant parts and of plants themselves occur with increase in age and as a result of competition. These processes are important aspects of plant growth but are often neglected, especially in the standing crop.

### 2.6.1 Senescent and Dead Matter

Senescent and dead matter comprises a considerable proportion of the total leaf weight particularly under canopy situations (Brougham 1958b). McCree and Troughton (1966b) reported the longevity of a leaf to be reduced when the plant canopy was heavily shaded. Hopkinson (1966), working with cucumber, and Woledge (1972), with ryegrass, found a rapid aging of leaves under very low light energy (21 $W/m^2$ PAR or 10% of full light). The lower leaves in a canopy are often in a state of advanced senescence and receive very little light energy (Brougham 1958b; Hunt 1965; Taylor, Cooper and Treharne 1968). The leaf longevity decreases with increase in temperature (Takeda and Agata 1966a).

Stern (1960) traced the pattern of leaf growth in subterranean clover and found that weight may decline to 50% of the maximum just prior to complete disintegration. A similar trend was observed in white clover by Brougham (1958b, 1962). Both carbohydrate and nitrogen are known to be exported from leaves during senescence (Brougham 1958b; Hirose 1971). Hopkinson (1966) suggested that mineral nutrients moved from old leaves to younger parts of the plant when he found that the removal of old photosynthetically inactive leaves reduced the total growth of cucumber.

If the number of green leaves on a stem is constant for a long period of time, the rate of leaf loss through senescence would be the same as that of leaf appearance. Hunt (1965) found this to be the case in Italian ryegrass in winter in New Zealand. He also calculated the daily loss of living dry matter falling to the ground to be 0.8 $g/m^2$. Hunt and Brougham (1966) reached a slightly higher estimate of 1.2 $g/m^2$/day for a mature Italian ryegrass canopy.

Dead leaf dry matter may also be estimated by clipping a uniform canopy in strata at different times (Iwaki, Takada and Monsi 1969). The loss of dry matter may be approximated by the decrease of dry matter within each stratum. This technique is valid only when no new leaves appear in the stratum between measurements. No translocation out of the stratum is assumed to occur. Iwaki, Takada and Monsi (1969) found, after several clippings in a *Solidago altissima* community that 280 $g/m^2$ of dead material disappeared over a 7 month period of growth, during which time the standing crop reached 1200 $g/m^2$.

### 2.6.2 Decomposition of Dead Material

The rate of leaf decomposition may be estimated either by observing the rate of disappearance of a sample of dead material enclosed in bag on ground (Bocock, Gilbert, Capstock, Twinn, Waid and Woodham 1960), or by measuring the amount of dead material at different times at the same site (Wiegert and Evans 1964). However, the most reliable method involves the use of $^{14}C$ (Grossbard 1969). Hunt (1965) found that the dead material of Italian ryegrass decomposed more quickly on wet land than on dry.

Since decomposition of dead material always occurs in closed plant canopies, measurement of the standing crop including dead material on the ground, does not accurately estimate the total dry matter accumulated. Total 'gross' production can be estimated by collecting dead plant material before decomposition (leaf trap technique) and by adding this to the dry weight of the standing crop. It is difficult, however, to collect dead plant material in pasture communities without disturbing canopy structure.

McCree and Troughton (1966b) collected all dead material from a white clover plant in a growth cabinet. After 70 days, 50-60% of the total dry matter produced was present as green material; the rest was mainly dead leaves, some of which may have been decomposed had they not been removed. Hunt (1970) collected dead leaves from perennial ryegrass - white clover pasture every 2 days in spring or 4 days in autumn using tagged plants which were not harvested. Standing crop dry matter was estimated by sequential harvesting and 'gross' growth by adding the weight of the dead leaves to that of the standing crop. 'Gross' growth may have been overestimated since the standing crop was likely to contain some undecomposed dead leaves. Accumulated dead leaf dry matter increased almost linearly with time during the last stages of growth. There was accumulated dead leaf dry matter of 250 $g/m^2$ at 80 days after planting in spring and of 67 $g/m^2$ at 61 days after planting in autumn. Clover had more dead leaves than did ryegrass. The total amount of accumulated dead leaf was such that the 'gross' growth curve was considerably different from the 'net' growth curve obtained by sequential harvest. The 'gross' growth curve had a longer linear phase than the net growth curve.

## 2.7.0. Total Dry Matter Production

### 2.7.1. Growth Curves

Several mathematical functions are found to fit the canopy dry matter/time relationship. Common functions reported in the literature are:

(1) a third degree polynomial

$$\mathrm{TDM} = a + bt + ct^2 + dt^3$$

(Williams 1964; Cocks 1973; Egli and Leggett 1973)

(2) autocatalytic function

$$\mathrm{TDM} = \frac{A}{1 + be^{-Kt}}$$

(Williams 1964; Brougham and Glenday 1967)

(3) von Bertalanffy function

$$(\mathrm{TDM})^{1-m} = A^{1-m}(1 \pm be^{-Kt})$$

(Friend, Helson and Fisher 1962a)

The use of these growth functions in biology is discussed by Richards (1959, 1969). For each function the crop growth rate (CGR) can be calculated by differentiating with respect to time.

Each growth curve has a period of an initial low CGR (Stage I) followed by a period of rapid growth (Stage II). Thereafter (Stage III), crop growth rate may decrease continuously to zero which results in the occurrence of a ceiling TDM (autocatalytic and von Bertalanffy functions) or may become negative and TDM decreases (cubic polynomial). When each growth stage is considered separately, the TDM/time relationship may be well expressed by an exponential at Stage I (Cocks 1973) and by a linear function at Stage II (Alberda and Sibma 1968). If dark respiration is considered to increase with TDM or leaf area, a ceiling yield can be expected to be obtained at Stage III under constant environment and constant photosynthetic rate conditions (Davidson and Philip 1958).

Williams (1964) has pointed out that the TDM/time relation is complex and different equations may be used to approximate the system at different times. However, although the biological meaning of a mathematical function may not be clear, the usefulness of the exercise is justified if it allows quantitative comparisons of the growth of different genotypes or of the same genotype under different conditions.

### 2.7.2. Analysis of Effects of Environmental Factors in the Field

(a) Limitation of Correlation Technique. Some of the effects of natural environmental variation on the dry matter production of plants can be adduced from correlations between plant growth and levels of climatic factors (Gregory 1926).

Correlation techniques have general faults and need to be applied with caution for the following reasons. (1) The responses of plants to climatic factors may differ in degree at different growth stages. (2) Climatic factors are generally interrelated and it is often difficult to separate individual factors, although partial correlations may be useful if the correlations between the climatic factors themselves are not strong. (3) It is often difficult to select the level of a continuously varying factor such as temperature that best represents average conditions over a given period. A maximum day temperature, for example, is obtained at a particular time of the day and may not represent the temperature of the major part of the day. (4) A given level of any factor, e.g. total solar radiation, may be obtained by variation in two contributing factors, such as flux density and day length. (5) The range in the level of a climatic factor must be considered carefully - plants may respond to temperature within certain ranges but not in others.

Black (1955) used multiple linear regression analysis to study the effects of climatic factors on growth attributes of subterranean clover seedlings. His conclusion that the growth of subterranean clover plants was independent of temperature was criticized by Morley (1961) on the grounds of there being a strong correlation between solar radiation and temperature and the response to temperature being non-linear. In any case the results should not be applied to mature canopies as done by Black (1964). 'Bacchus Marsh', the cultivar which Black used in his experiment was found to be unique in its growth response to temperature when compared to four other cultivars of subterranean clover (Morley 1958).

(b) Growth in Stage I. Changes in relative growth rate (RGR) with season were examined for young plants of *Lolium perenne*, *Dactylis glomerata* and *Festuca arundinacea* (MacColl and Cooper 1967) and for young tomato plants (Goodall 1945). The highest RGR was found to occur in summer with lower values in autumn, spring and winter.

Bunt (1972) showed that both the CGR and RGR of young carnation plants from cuttings were affected by solar radiation and temperature. Growth rate responded more to the change in daily solar radiation than to change in mean temperature over ranges of 0.8 - 14.7 $MJ/m^2$/day and 12-21°C. Growth rates of plants established from cuttings, however, are difficult to assess because of the possibility of translocation from the cutting to the new growing tissue and the variation in cutting size. A similar problem arises when considering regrowth (e.g. Weihing 1963).

(c) Growth in Stage II. Nakaseko and Yoshida (1971) divided corn growth into six stages. Silking was proposed as the centre of the whole growth period with each stage consisting of 3 weeks. In the vegetative stages, CGR was correlated with the product of LAI and solar energy. Deviation from the fitted regression was positively correlated with temperature (range 17-22°C). At an early reproductive stage, CGR was positively correlated with the amount of rainfall, suggesting that at that time plants were suffering from water stress.

When crop growth rate is constant with time in Growth Stage II, as was the case with grassland in the Netherlands (Alberda and Sibma 1968), the coefficient of linear regression obtained in different seasons can be correlated with environmental factors. However, these authors did not use regression analysis. Comparison of actual data with de Wit's growth model (1959) which did not include a temperature factor, showed the actual production to be much less than the calculated potential production throughout a year, the difference being more pronounced in the spring than in the autumn. It was concluded that this difference was due to temperature, because the temperature was much lower in spring than in autumn.

(d) Work by Brougham and Glenday. One of the problems in examining the effects of climate on plant growth is short term fluctuation in weather. The fluctuation can cause large deviations from a smooth growth curve. Such effects were analysed by Brougham and Glenday (Brougham 1955, 1959; Glenday 1955, 1959; Brougham and Glenday 1969). The basic idea of the analysis is to produce several growth curves within a short period and if there are simultaneous deviations from each smoothed growth curve, these are considered to be due to weather fluctuations. Smoothed growth curves after removing the deviations could be analysed with respect to climate. In one of their experiments with ryegrass dominant pasture, the deviations due to weather fluctuations showed positive significant correlations with radiation ($r = 0.360^{**}$) and daily temperature range ($r = 0.308^{*}$). The seasonal trend of growth after removing the deviations was significantly correlated with radiation ($r = 0.979^{***}$), maximum temperature ($r = 0.734^{***}$), minimum temperature ($r = 0.611^{**}$), and daily temperature range ($r = 0.844^{**}$). It was found that plant growth was regulated by climatic factors mainly and by weather fluctuations to a smaller extent. These results were obtained from six weeks growth which resulted in 250 $g/m^2$ in spring. Growth rate of amounts of dry matter greater than 250 $g/m^2$ was not analysed because of considerable variation.

### 2.7.3. Analysis of the Specific Effects of Some Environmental Factors

(a) Light Energy. Shading cloth is sometimes used in the field to examine the effects of light energy on the growth of plants. It is necessary to interpret results with caution since shading inevitably changes other environmental factors such as temperature and soil moisture status. Day temperature under shade may be lower by 5°C than that without shade (Ampofo and Lawson 1972) and soil moisture is often relatively high under shades because of low evapotranspiration rate (Campbell, Pelton and Nielsen 1969). It is also necessary to consider the change in the absolute light energy during an experiment under shade, even though the relative light energy under shades, compared with no shade, may be constant during the experiment.

Watson, Motomatsu, Loach and Milford (1972) found in sugar beet under ample water conditions that shading resulted in the reduction of yield for all organs at any stage of growth. The effect of light energy on the development of leaf area was relatively small, suggesting a major effect of light energy on photosynthetic rate itself. The reduction in the yield due to shading depended on the period of shading. Similar results to those obtained with sugar beet by Watson *et al.* are to be found in many other species (Blackman and Wilson 1951; Cooper 1966).

(b) Temperature. The effects of temperature on dry matter production of plants have been examined extensively in controlled environments, mostly with single plants.

(1) Shift of Optimum Temperature with Time in Isolated Plant Growth. The growth response of plants to temperature depends to some extent on the stage in ontogeny. Growth at high temperature is suppressed at later stages of growth (Pearson and Hunt 1972a) and optimum temperature may shift to lower temperature with time (Friend, Helsen and Fisher 1962a; Takeda and Agata 1966a).

Suppression of growth at high temperature at later stages of growth is suggested to be due: (1) to increased rate of respiration at high temperature (Ito and Takeda 1962); and (2) to the early occurrence of the reproductive stage at high temperature (Brouwer 1962).

Friend, Helsen and Fisher (1962a) found in wheat that the maximum crop growth rate at the time of the inflection of a fitted von Bertalanffy curve was highest at 20°C at high light energy levels; and at 15°C at low light energy levels. However, the calculated maximum dry weight of a plant was inversely related to temperature because of the long growth period at low temperatures. It was suggested that the short growth period of plants grown at high temperature was due to the early occurrence of floral development.

(2) Dynamics of Plant Growth at Different Temperatures. Although results are limited to isolated plants, work by Takeda and Agata (1964a, b; 1966a, b, c) reveals the dynamics of plant growth at different temperatures. Results of $CO_2$ exchange measurements showed that gross photosynthetic rate per unit leaf area at 60 klux measured at growth temperature was independent of growth temperature. Total gross photosynthetic rate per unit ground was strongly affected by leaf area. Leaf area development was affected by temperature; low growth temperature promoted leaf area development through large leaf size and a large leaf number. This was caused by a high branching rate, a low flowering rate and a low rate of leaf senescence. A high growth temperature, on the other hand, promoted leaf area through a high rate of leaf appearance and a high leaf expansion rate. High temperature ($25^oC$) resulted in a large leaf area in the early stages of growth when senescence of leaves and branching were, presumably, not very prominent. It was also argued that one of the disadvantages of high growth temperature was increased rate of respiration which resulted in decreased level of carbohydrate in the plants and hence decreased uptake of nutrients, particularly nitrogen and potassium.

(3) Canopy Growth. Davidson, Gibson and Birch (1970) found almost no difference between the shoot dry weights of subterranean clover swards grown for 16 weeks at $12^o$ and at $22^oC$. Plants grown at $12^o$ had more root dry weight than those at $22^oC$. The result was completely different from that obtained by Morley (1958) who found the growth rate of isolated subterranean clover plants to decrease sharply below $19^oC$. Davidson *et al.* (1970) suggested that once the

canopy becomes mature with full light interception, there was no need for further development of leaf area and hence the advantage of high growth temperature disappeared.

Recent work by Cocks (1973) shows an interaction between temperature and LAI on growth rate of subterranean clover. When plants were grown at a low density of 180 plants/m$^2$ in a growth cabinet, growth was essentially exponential and plants at 27/22°C and 22/17°C showed higher growth rates than those at lower temperatures. At a high density of 8,360 plants/m$^2$, dry matter increase was similar to that at the low density of 180 plant/m$^2$ when plants were very young. However with increase of dry weight, crop growth rate at the high temperatures was suppressed which resulted in the same dry weight as that obtained at 17/12°C at day 35. When crop growth rate was plotted against LAI for each temperature, crop growth rate was directly related to temperature at small LAI but inversely related to temperature at large LAI. Crop growth rate was apparently independent of temperature at a medium LAI of 3-4. Cocks explained the phenomenon of suppressed growth at high temperature from the frequency distribution of plant size; skewness increased with increase in growth temperature and small plants at high temperature decreased their weight while at low temperature all plants increased their weight.

The literature reviews suggests that effects of light energy and temperature on growth of a community have not been fully understood although a bulk of fragmentary information on each process of the total dry matter production system is available. The experiments described hereafter were designed to show the effects of light energy and temperature on individual processes, and on the whole community growth system of subterranean clover communities.

## 3.0.0. Programme of the Investigation

A brief outline of each experiment is given to provide a general view of the study.

A field experiment with three planting times and three planting densities was conducted to examine the growth of subterranean clover communities in the field. Growth rates of the communities were calculated from growth curves constructed through frequent dry matter harvesting. Effects of the variation in environmental factors on the growth rate of the communities were examined by the use of correlation techniques.

Experiments were also conducted in temperature-controlled glasshouses to examine the separate effects of light energy and temperature on the growth of subterranean clover communities. Small communities were grown in a large number of square-section pots and growth rates calculated from dry matter data. Effects of variation in light energy and temperature were examined by growing communities at different times of the year and under different degrees of shading, and at different constant temperatures under similar light conditions.

Net $CO_2$ exchange of communities grown in the temperature-controlled glasshouses was measured in a photosynthesis chamber at different light flux densities and temperatures. Since net $CO_2$ exchange rate of communities was expected to be strongly influenced by LAI and total dry matter, comparisons were made at similar levels of these attributes.

Deterministic models to describe the growth of subterranean clover communities under different light energy and temperature conditions were constructed from results of the $CO_2$ exchange measurements; from relationships between plant attributes and the environmental factors; and from relationships between plant attributes themselves. The effects of light energy and temperature on several growth processes were incorporated in the models. Simulated dry matter growth curves were compared with growth curves obtained in the field as well as those obtained in the temperature-controlled glasshouses.

## 4.0.0. Field Experiment

### 4.1.0. Introduction

Effects of planting density on the pattern of growth of subterranean clover communities are well established in the literature (Donald 1951; Davidson 1954; Stern 1965). In the early stages of growth, growth rate is directly related to density over a wide range of sowing rates; but at late stages, it is inversely related to density except at low densities of less than about 10 plants/m$^2$. Final dry matter yield is approximately constant once planting density exceeds about 500 plants/m$^2$. Variation in sowing rate can thus result in different growth curves but a similar final yield of dry matter.

Effects of planting date on the pattern of growth of subterranean clover communities, on the other hand, are not clear. However, it can be expected that late planting will result in a high initial growth rate due to favourable environmental conditions in spring. This may result in final yield being similar to that of early planting as long as planting is not delayed until very late in the season. This possibility is examined in this study through sowing at different times of the year.

Since the effects of a particular environmental factor on growth rate may depend on growth stage, these effects were examined at similar dry matter yields independently of time and rate of sowing.

### 4.2.0. Experimental Methods

### 4.2.1. Experimental Design

Treatments comprised 3 plant densities x 3 planting dates, with 6 replicates. Plot size was 5 m x 5 m with provision for 16 primary harvests of sub-plots each 50 cm x 50 cm. A distance of 50 cm separated the edges of neighbouring sub-plots. The total area was 30 m x 50 m. A randomized block design was used and the experiment was located on a slightly sloping site at the Waite Institute, on 'Urrbrae Loam' soil.

Densities of 1,000, 2,000 and 4,000 plants/m$^2$ were chosen because: (1) 4,000 plants/m$^2$ was about the sowing density beyond which considerable self-thinning occurred in an experiment reported by Davidson (1954); and (2) 1,000 plants/m$^2$ would contrast with 4,000 plants/m$^2$ early in the season and yet give an equivalent dry matter yield at the end of the growing season (Davidson 1954).

In 1971 the break of season occurred in late April and the first planting of 3 densities was made on May 19. After the first planting, all unsown plots were covered with straw to prevent weed growth and maintain a good tilth. The straw was removed just before sowing. Seedlings of the second planting were damaged by birds which necessitated replanting this treatment on June 30 after use of a herbicide to kill the seedling plants. The third planting was made on August 2.

### 4.2.2. Planting

Seeds were not selected for size, the thousand seed weight at each planting being about 9 g. Seed size was greater than that used in the subsequent temperature-controlled glasshouse experiments. Seed was broadcast by hand, live seed being mixed with dead at the two lower densities to assist even spreading.

Establishment was estimated about 30 days after each planting (Table 2).

**Table 2.** Seed rate at planting and plant number at establishment

| | Planting | | Establishment | | |
|---|---|---|---|---|---|
| | Planting date | Seed rate kg/ha | Date counted | No. of plants /m$^2$ | Establishment % |
| **Early Planting** | | | | | |
| Density low | 19.5.71 | 136 | 14.6.71<br>(26 days) | 869 | 61 |
| medium | " | 271 | " | 1688 | 59 |
| high | " | 543 | " | 4018 | 70 |
| **Middle Planting** | | | | | |
| Density low | 30.6.71 | 173 | 28.7.71<br>(28 days) | 1330 | 73 |
| medium | " | 345 | " | 2805 | 77 |
| high | " | 691 | " | 5628 | 77 |
| **Late Planting** | | | | | |
| Density low | 3.8.71 | 123 | 7.9.71<br>(35 days) | 973 | 68 |
| medium | " | 246 | " | 1900 | 67 |
| high | " | 492 | " | 4156 | 73 |

The middle planting was expected to have the lowest percentage establishment because of low winter temperature; higher seed rates were therefore used at that time. However, the highest percentage establishment was obtained at this time and resulted in established plant number being 1.5 times greater than that at the other plantings.

No fertilizer was applied as the phosphate status of the soil was considered to be adequate - 300 kg/ha superphosphate had been applied over the previous three years.

### 4.2.3. Plant Growth and General Cultivation

Seedlings were inoculated soon after each planting by watering with a suitable culture of rhizobium. Examination of the roots confirmed that plants had healthy nodules. There were no symptoms of any nutrient deficiency throughout the experiment. Weeds were removed by hand.

Soil moisture status until the end of October appeared adequate for growth. Sprinkler irrigation was then used 2-3 times per week. A slight water stress occurred at the end of October for 2-4 days just before the installation of the sprinklers.

### 4.2.4. Harvesting

The first harvest was made about 30 days after sowing in each case with subsequent harvests at 9-15 day intervals, all 3 densities being cut on the same day.

Harvesting of the early sown treatment was terminated in November because of weed invasion and damage by clover wilt (*Kabatiella caulivora* (Kirchn). Karak). Harvesting of the middle and late sown treatments was terminated in December.

Plants were cut by hand at ground level and all dead and senescent material on the ground included in the sample. After flowering, burrs were also recovered from below the soil surface. Root weight was not estimated.

Straw, weeds, and soil were removed from the sample in the laboratory. Only total shoot dry weight was measured in winter. After early September, subsamples were taken for estimation of dry weight of petiole, stem and pod, green leaves, and dead leaves. Leaf lamina area was measured by an electronic planimeter. Dry matter of each fraction was measured after drying at 85°C for 24 hr.

Plant number per unit area was calculated from a sub-sample of 10 individual plants which were dried and weighed separately. However, when the plant canopy became mature and plants developed laterals plant number was not measured as it was not possible to distinguish single plants from laterals. During the period over which plant number was recorded (until September), there was no decrease in plant number with time except at the highest densities in the early and late sowing. It is remarkable that the high plant density plot of the middle planting time showed no decrease in plant number between day 28 and day 70.

### 4.3.0. Weather

1971 was a very wet year but comparison with long term monthly means showed it to have average solar radiation and monthly temperatures The patterns of solar radiation, air temperature (mean of maximum air temperature and minimum air temperature), soil temperature (mean of maximum soil temperature and minimum soil temperature), evaporation and rainfall during the experimental period are shown in Fig. 1.

Each point is an average of values for 10 days. All data were obtained at the Waite Meteorological Station located about 0.5 km from the experimental site. Solar radiation was measured with a Kipp solarimeter. Soil temperature was measured at 2.5 cm under bare ground.

### 4.4.0. Results

### 4.4.1. Shoot Dry Matter

Changes in shoot dry matter with time are shown in Fig. 2. All treatments display similarly shaped growth curves, typical of those of many crop communities.

<u>Figure 1</u>. Meteorological station records of environmental changes during the 1971 field experiment. (Soil temperature at 2.5 cm.)

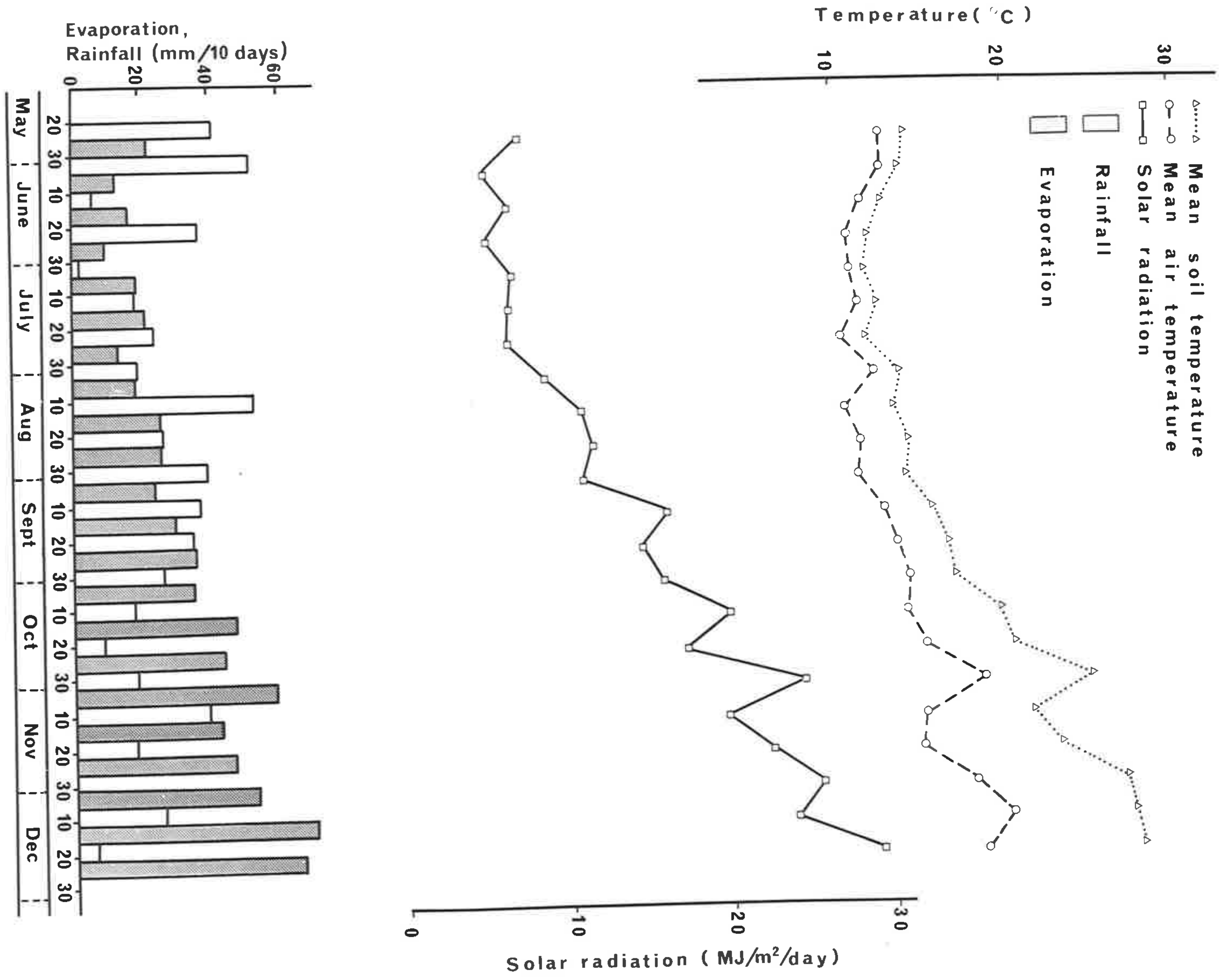
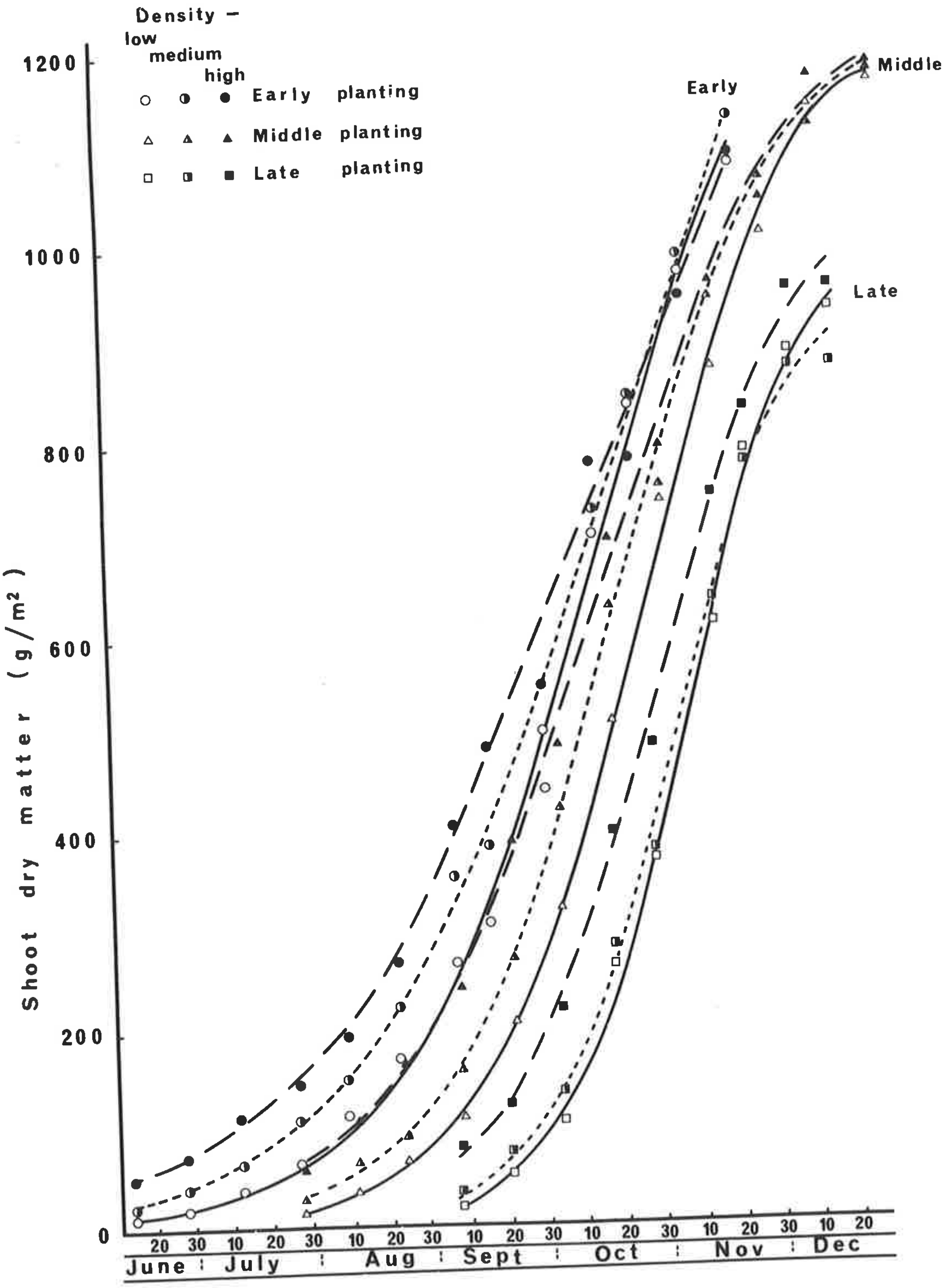

Temperature( °C )
10
20
30
Mean soil temperature
Mean air temperature
Solar radiation
Rainfall
Evaporation
Evaporation,
Rainfall (mm/10 days)
0
20
40
60
May
June
July
Aug
Sept
Oct
Nov
Dec
20
30
10
20
30
10
20
30
10
20
30
10
20
30
10
20
30
10
20
30
10
20
30
0
10
20
30
Solar radiation ( MJ/m²/day )

Figure 2. Shoot dry matter production in the field for three densities and three planting times. The curves are from logistic equations fitted to experimental points for each treatment.


Density –
low
medium
high
○ ◑ ● Early planting
△ ▲ ▲ Middle planting
□ ◨ ■ Late planting
Early
Middle
Late
Shoot dry matter (g/m²)
1200
1000
800
600
400
200
0
20 30 10 20 30 10 20 30 10 20 30 10 20 30 10 20 30 10 20
June : July : Aug : Sept : Oct : Nov : Dec

Plant growth can be divided into 3 stages.

I. From seeding to shoot dry matter of 150 g/$m^2$. Growth was slow but shoot dry matter increased exponentially with time.

II. The linear phase in which growth rate was almost constant.

III. The final phase in which growth rate decreased and shoot dry matter approached an asymptote.

The late planting treatment had a higher growth rate than the early and the middle planting treatments during Stages I and II. Stage III occurred relatively early after the late planting and resulted in a lower final dry matter for this treatment. In Stage I, crop growth rate was highest in the high density treatment for all planting dates. Differences in dry matter between densities therefore initially increased with time. This trend was reversed during Stages II - III so that dry matter yield between densities tended toward a common value at the end of the season within each planting date.

A logistic curve was fitted by an iterative method to each empirical growth curve. The equation is

$$\text{SDM} = \frac{A}{1 + Be^{-cT}}$$

where SDM = shoot dry matter (g/$m^2$)

T = days after planting

A,B,C = constants

According to Richards (1959), this logistic equation is symmetrical with the time of inflection at SDM = $\frac{A}{2}$ where the constant A defines maximum dry matter yield at infinite time. B and C define the shape of the curve. The following functions may be derived from the equation:

$\frac{AC}{4}$ ... maximum crop growth rate (Max CGR) (g/m$^2$/day)

$\frac{A}{2}$ ... dry matter at Max CGR (g/m$^2$)

$\frac{1}{C}\log_e B$ ... number of days after planting when Max CGR occurs

Maximum crop growth rate is close to the constant crop growth rate of Stage II, and the number of days after planting when Max CGR occurs is determined by the lengths of Stages I and II.

A good fit was obtained in all cases and estimates of the parameters characterizing each growth curve are shown in Table 3.

Table 3. Calculated values of growth attributes from fitted logistic curves in the field experiment

| Treatment | | (1) Maximum yield g/m $^2$ | (2) Max CGR g/m$^2$/day | (3) Dry wt at Max CGR g/m$^2$ | (4) Max CGR day | (5) Date at Max CGR |
|---|---|---|---|---|---|---|
| **Early planting** | | | | | | |
| Density | low | 1347 | 13.1 | 674 | 149 | 15 Oct. |
| | medium | 1567 | 11.9 | 783 | 155 | 21 Oct. |
| | high | 1493 | 9.8 | 746 | 151 | 17 Oct. |
| **Middle planting** | | | | | | |
| Density | low | 1233 | 14.2 | 617 | 118 | 26 Oct. |
| | medium | 1231 | 13.4 | 616 | 112 | 20 Oct. |
| | high | 1281 | 11.4 | 641 | 109 | 17 Oct. |
| **Late planting** | | | | | | |
| Density | low | 1027 | 15.6 | 514 | 96 | 7 Nov. |
| | medium | 967 | 14.5 | 484 | 92 | 3 Nov. |
| | high | 1066 | 13.4 | 533 | 88 | 30 Oct. |

$$Y = \frac{A}{1 + Be^{-CT}}$$

(1) $A$

(3) $\frac{A}{2}$

(2) $\frac{AC}{4}$

(4) $\frac{1}{C}\log_e B$

Estimated maximum dry matter yield was influenced by plant density only for the first planting, but decreased with successive planting dates. Max CGR was influenced by both planting date and plant density; low plant density and late planting increased Max CGR. The number of days to Max CGR was greater after early planting than after late planting. This resulted in small differences in the actual date at which Max CGR occurred.

Max CGR was linearly and inversely related to dry matter within each planting density (Fig. 3). It was also inversely related to plant density at a given dry matter. As Max CGR occurred within a short period of time among the different treatments (Table 3, column 5), climatic environments were similar to each other at Max CGR for the different treatments. Plant density and shoot dry matter therefore had a direct influence on the value of Max CGR.

Crop growth rate (CGR), calculated by differentiating the sigmoid equation with respect to time, is plotted for each 10 day interval against the corresponding shoot dry matter (SDM) in Fig. 4. A common numeral indicates CGR and SDM values for all treatments calculated on the same day.

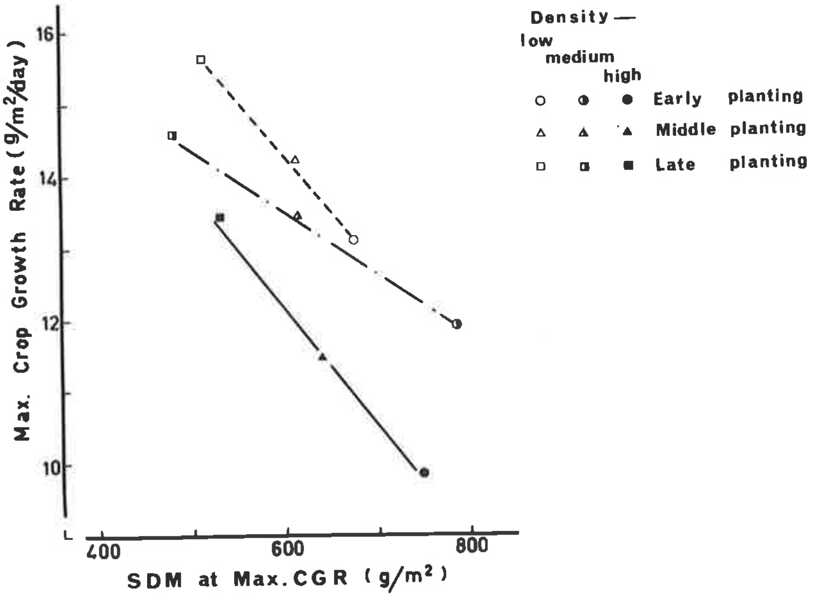
In general CGR shows a broad optimal relationship with SDM over the whole range of SDM. However, when crop growth rates over all treatments are examined at particular times, a family of curves can be discerned. These curves show that: (1) CGR increases with SDM in the early part of the experiment (Nos. 1-8); (2) CGR and SDM appear to be optimally related in the middle part of the experiment (Nos. 9-13); and (3) CGR decreases with increase in SDM in the late stages of the experiment (Nos. 14-18). Change in the relation between CGR and SDM with time (indicated by the separate 'numeral curves') may be ascribed to variation in environmental conditions during the whole season since a common numeral indicates essentially a common

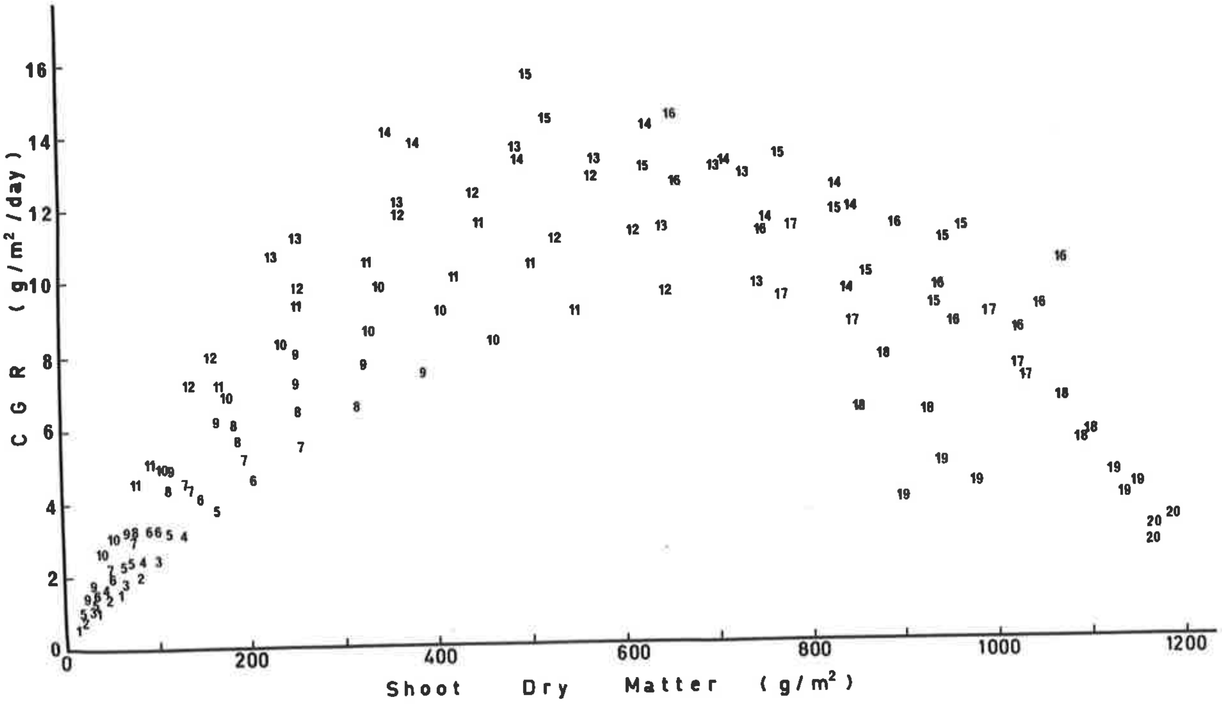
**Figure 3.** (Top)

Comparison of maximum crop growth rate (Max. CGR) calculated from the fitted logistic equation and shoot dry matter (SDM) at Max. CGR for the 9 treatments. Regression lines are drawn for each plant density treatment.

**Figure 4.** (Bottom)

The relationship between calculated crop growth rate (CGR) and corresponding shoot dry matter (SDM) at different times during the field experiment. Numerals on the graph indicate the last day of successive ten day periods from June 10 to December 26.


Density —
low
medium
high
○ ◑ ● Early planting
△ ▲ ▲ Middle planting
□ ◨ ■ Late planting
Max. Crop Growth Rate (g/m²/day)
16
14
12
10
400
600
800
SDM at Max.CGR (g/m²)


C G R (g/m² /day)
16
14
12
10
8
6
4
2
0
0
200
400
600
800
1000
1200
Shoot Dry Matter (g/m²)

environment. The fact that communities may exhibit a range of values of CGR for the same SDM shows there to be no exact relation between CGR and SDM.

### 4.4.2. Leaf Area

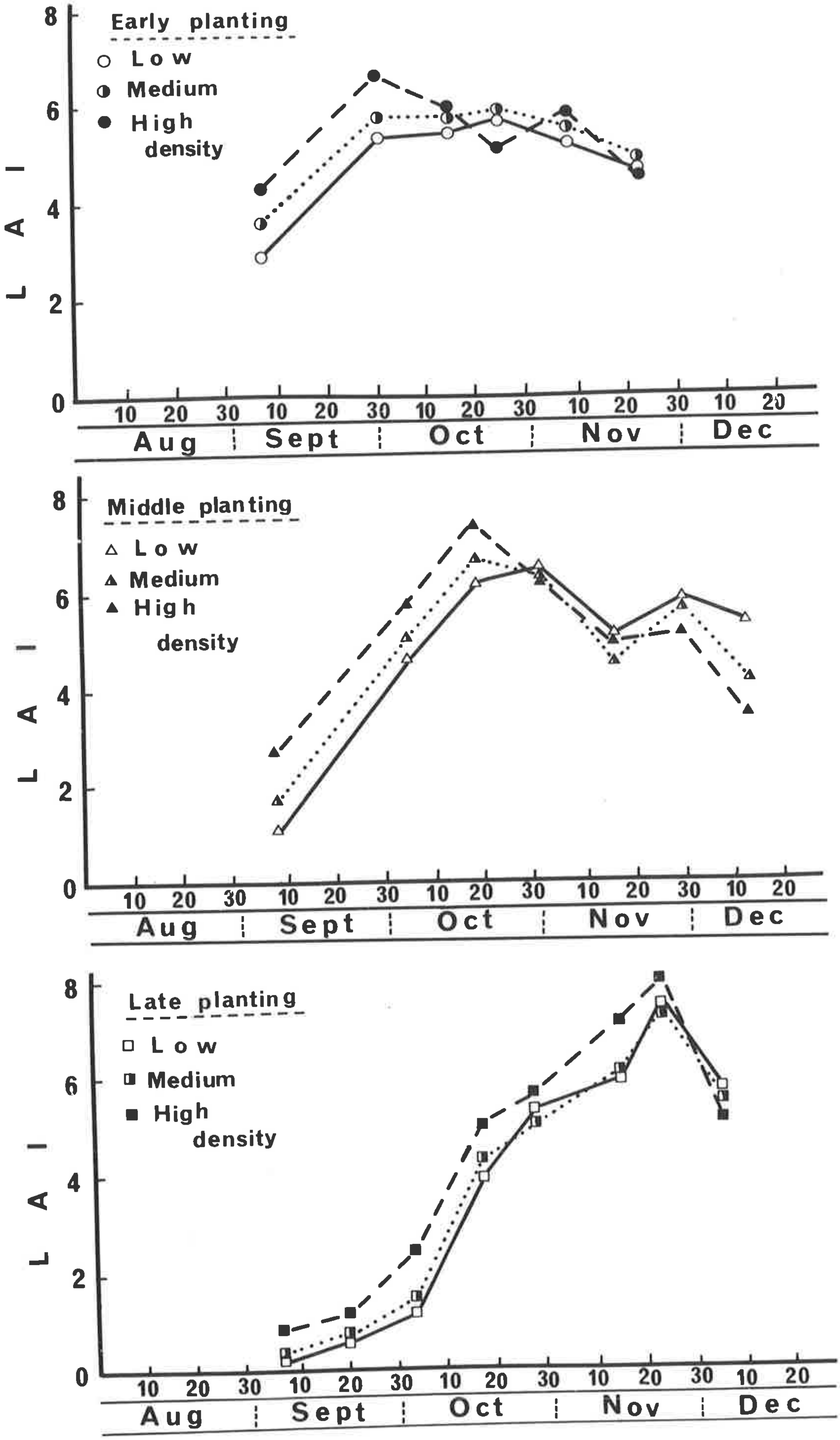
Leaf area was measured from September 7. LAI for each treatment is plotted against time in Fig. 5. A slow increase of LAI during the early stages of growth in the late planting was followed by a rapid increase until a maximum was obtained. The maximum occurred earlier for the early planting than for the late planting. Generally, the maximum value of LAI is positively related to plant density within each planting date. Late planting resulted in the highest maximum LAI.

LAI declined after attaining a maximum value, slowly in the case of early planting and rapidly in that of late planting. However, LAI values of between 6 and 4 were maintained after the maximum was reached. Canopies were composed mainly of old leaves after the maximum LAI was reached.

Relationships between LAI and SDM are shown in Fig. 6. LAI increased linearly with SDM up to about 500 $g/m^2$ although LAI was very variable around 700 $g/m^2$. As SDM increased further, LAI gradually decreased. There is no obvious effect of either density or time of sowing on the relationship between LAI and SDM.

LAI can be expressed as: SDM x percentage of leaf dry matter x specific leaf area (SLA). Early in September the early planting had an average SLA of approximately 300 $cm^2/g$, whilst late planting was less than 200 $cm^2/g$. The difference is likely to be due to differences in SDM and to age of the community, since both treatments had experienced similar environments for 35 days before measurement. After about October 10, SLA varied between 260 $cm^2/g$ and 420 $cm^2/g$. When SLA is plotted against SDM (Fig. 7) it appears that SLA increased

**Figure 5.** Change of leaf area index (LAI) with time for the 9 treatments in the field experiment.



Early planting
○ Low
◑ Medium
● High density
L A I
0
2
4
6
8
10
20
30
Aug
Sept
Oct
Nov
Dec
Middle planting
△ Low
◭ Medium
▲ High density
Late planting
□ Low
◫ Medium
■ High density

Figure 6. (Top)

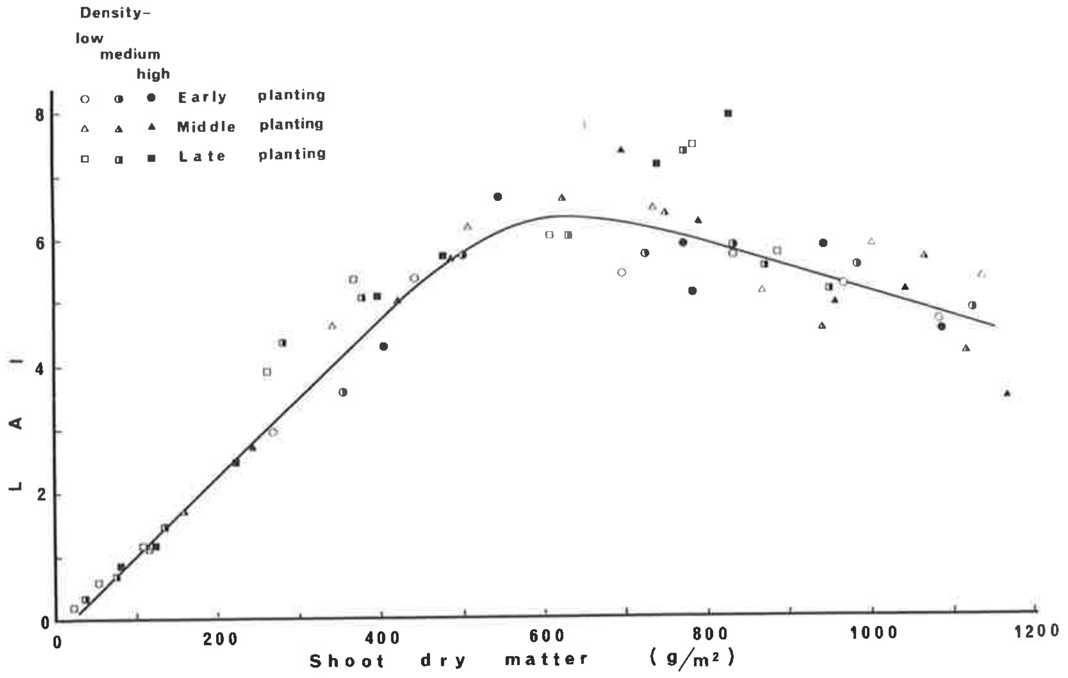
The relationship between leaf area index (LAI) and shoot dry matter for the 9 treatments in the field experiment.

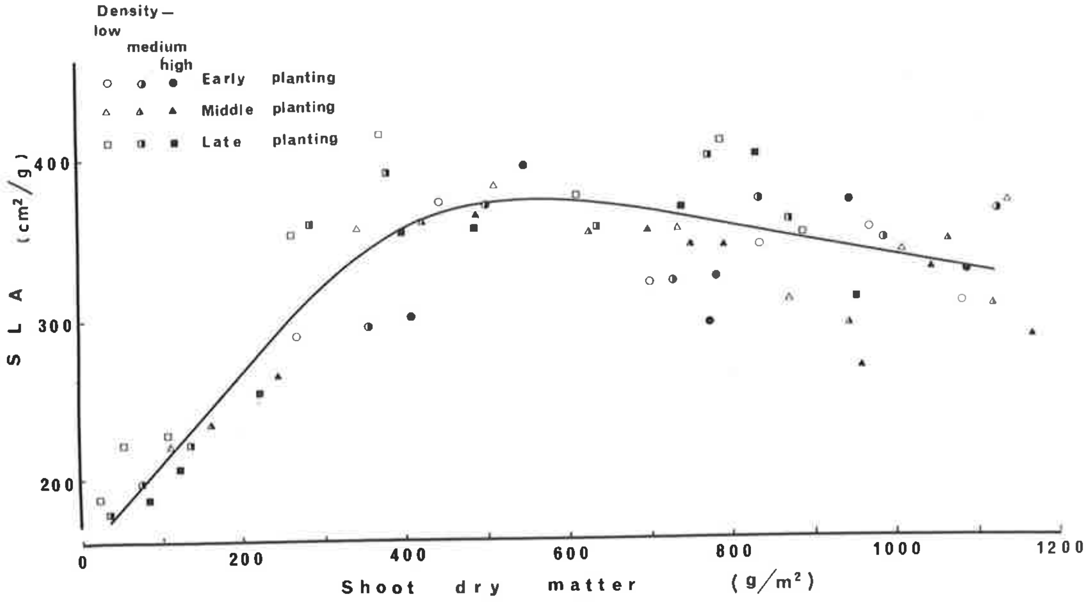
The curve is fitted by eye.

Figure 7. (Bottom)

The relationship between specific leaf area (SLA) and shoot dry matter for the 9 treatments in the field experiment.

The curve is fitted by eye.


Density-
low
medium
high
○ ◑ ● Early planting
△ ▲ ▲ Middle planting
□ ◧ ■ Late planting
L A I
0
2
4
6
8
0
200
400
600
800
1000
1200
Shoot dry matter (g/m²)


Density—
low
medium
high
○ ◑ ● Early planting
△ ▲ ▲ Middle planting
□ ◧ ■ Late planting
S L A (cm²/g)
200
300
400
0
200
400
600
800
1000
1200
Shoot dry matter (g/m²)

linearly with SDM up to about 400 g/m$^2$. After SDM reached about 600 g/m$^2$, SLA decreased slightly with further increase in SDM although the variation is large.

Fig. 8 shows the percentages of SDM as: (i) leaf lamina; and (ii) as stem, petiole, and pod. The lamina proportion decreased almost linearly with SDM. There is no apparent effect of treatment on these attributes, the leaf lamina proportion being entirely a function of SDM.

The rapid increase in LAI with SDM up to 500 g/m$^2$ can partly be attributed to increase in SLA. After a SDM of 500 g/m$^2$, SLA decreased slightly and the percentage of leaf continued to decrease. This resulted in a small decrease in LAI after 700 g/m$^2$.

### 4.4.3. Environmental Factors

The role of environmental factors in influencing the time course of dry matter was first considered by examining deviations from the fitted growth curve.

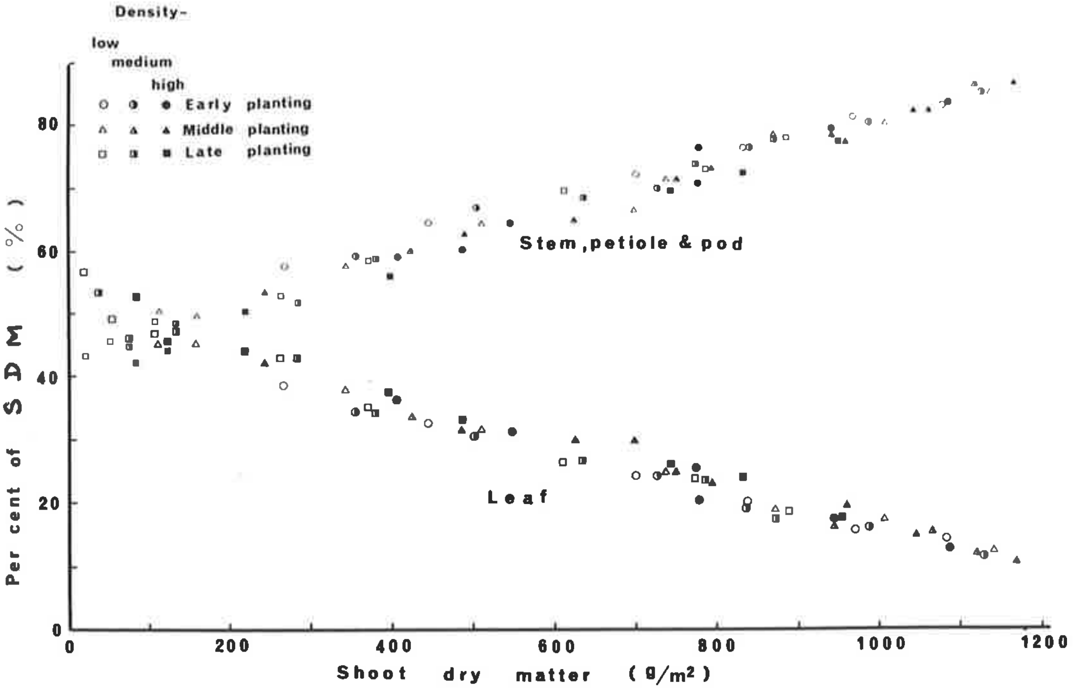
Average values for five environmental factors, namely solar radiation (SE), maximum air temperature (ATH), minimum air temperature (ATL), maximum soil temperature (STH), and minimum soil temperature (STL) were computed for each 10 day interval prior to each harvest. A second degree polynomial was then fitted to the data for each environmental factor with time as the independent variable ('environmental factor curve'). Deviation at each harvest date from the fitted polynomial for each environmental factor was compared with deviation from the fitted logistic growth curve at the same date. Deviation from the growth curve was related to that from the 'environmental factor curve' in very few cases. It is concluded that the growth curves fitted for each treatment approximate the actual

<u>Figure 8</u>. (Top)

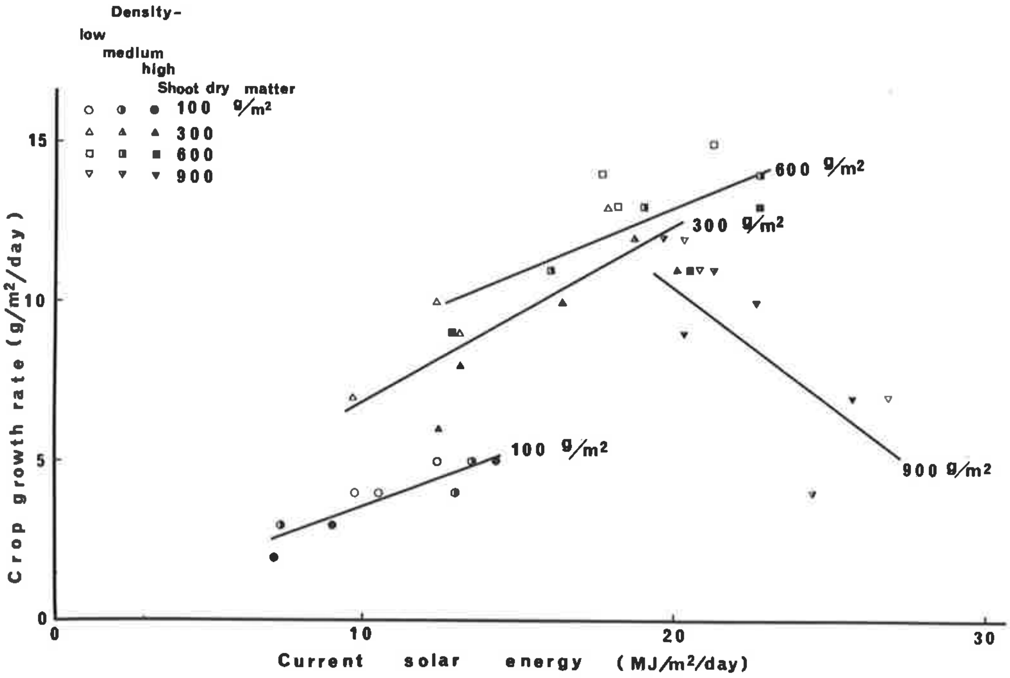
Plant part as a percentage of shoot dry matter (SDM) plotted as a function of shoot dry matter.

<u>Figure 9</u>. (Bottom)

The effect of solar energy level on crop growth rate for different amounts of shoot dry matter. Current solar energy is a mean of daily solar energy for 10 days prior to the day at which crop growth rate is calculated.



Density-
low
medium
high
○ ◑ ● Early planting
△ ▲ ▲ Middle planting
□ ◨ ■ Late planting
Stem, petiole & pod
Leaf
Per cent of SDM (%)
0
20
40
60
80
0
200
400
600
800
1000
1200
Shoot dry matter (g/m²)



Density-
low
medium
high
Shoot dry matter
○ ◑ ● 100 g/m²
△ ▲ ▲ 300
□ ◨ ■ 600
▽ ▼ ▼ 900
600 g/m²
300 g/m²
100 g/m²
900 g/m²
Crop growth rate (g/m²/day)
0
5
10
15
0
10
20
30
Current solar energy (MJ/m²/day)

growth curve without any serious systematic error. The fitted curves could therefore be used to analyse relations between environmental factors and crop growth rates in the field.

Crop growth rates were calculated from the fitted logistic curve at shoot dry matter values of 100, 200, 300, ..., 1,100 g/m$^2$. Average solar energy was calculated for 10 days prior to the day at which the given shoot dry matter was obtained from the fitted curve. Some representative results to indicate the effect of solar energy on crop growth rate are shown in Fig. 9.

When shoot dry matter was 100 g/m$^2$ (LAI = 1), crop growth rate increased linearly from 2 to 5 g/m$^2$/day with increase of solar energy from 7 to 14 MJ/m$^2$/day. At 300 g/m$^2$ (LAI = 3.5), crop growth rate increased from 7 to 12.5 g/m$^2$/day with increase in daily solar energy from 10 to 20 MJ/m$^2$/day. The correlation coefficient (r) between crop growth rate and solar energy decreased with increase of shoot dry matter (r = 0.908** at 100 g/m$^2$; r = 0.816** at 300 g/m$^2$ and r = 0.601* at 600 g/m$^2$). At 900 g/m$^2$ (LAI = 5-6), crop growth rate decreased with increase of daily solar energy, although this was not significant at the 5% level (r = 0.594$^{NS}$).

From Fig. 9 it appears that solar radiation affected crop growth rate and that the effect was dependent on the dry matter present. Solar energy and temperature were highly correlated during each 10 day period, especially during the early part of the season (SDM up to 600 g/m$^2$). This apparently resulted in there being a similar correlation coefficient between crop growth rate and temperature as between crop growth rate and solar energy (Table 4).

It was considered that the sprinkler irrigation used late in the season lowered the temperature over the plots. Correlations between temperature and crop growth rate above 900 g/m$^2$ have therefore been excluded.

**Table 4.** Correlation matrix with crop growth rate

SE : solar radiation
ATL : minimum air temperature
ATH : maximum air temperature
ATM : mean air temperature
ATD : difference between maximum and minimum air temperature
STL : minimum soil temperature
STH : maximum soil temperature
STM : mean soil temperature
STD : difference between maximum and minimum soil temperature

| Shoot DM ($g/m^2$) | SE | ATL | ATH | ATM | ATD | STL | STH | STM | STD | Period |
|---|---|---|---|---|---|---|---|---|---|---|
| 100 | 0.908 | 0.486 | 0.750 | 0.683 | 0.802 | 0.704 | 0.864 | 0.862 | 0.400 | 10 July - 1 October |
| 200 | 0.876 | 0.727 | 0.859 | 0.835 | 0.862 | 0.865 | 0.869 | 0.902 | 0.693 | 7 August - 14 October |
| 300 | 0.816 | 0.539 | 0.876 | 0.802 | 0.915 | 0.837 | 0.872 | 0.881 | 0.714 | 26 August - 23 October |
| 400 | 0.716 | 0.530 | 0.841 | 0.801 | 0.824 | 0.949 | 0.872 | 0.931 | 0.456 | 9 September - 30 October |
| 500 | 0.714 | 0.660 | 0.666 | 0.678 | 0.554 | 0.827 | 0.754 | 0.791 | 0.607 | 21 September - 6 November |
| 600 | 0.601 | -0.281 | 0.458 | 0.181 | 0.736 | 0.723 | 0.729 | 0.752 | 0.674 | ( 3 October - 13 November (SE)<br>( 3 October - 25 October (T) |
| 700 | -0.071 | 0.623 | 0.736 | 0.759 | 0.379 | 0.782 | 0.685 | 0.760 | 0.244 | (12 October - 19 November (SE)<br>(12 October - 31 October (T) |
| 800 | 0.364 | 0.349 | 0.128 | 0.235 | -0.492 | 0.390 | 0.255 | 0.313 | 0.026 | (23 October - 29 November (SE)<br>(23 October - 7 November (T) |
| 900 | -0.594 | | | | | | | | | 1 November - 17 December |
| 1000 | -0.532 | | | | | | | | | 9 November - 27 November |
| 1100 | -0.867 | | | | | | | | | 19 November - 11 December |

It is apparent that the correlation between crop growth rate and environmental factors decreased with increase in shoot dry matter and that at shoot dry matter of 800 $g/m^2$ the correlation was poor. Solar energy and temperature increased continuously from July to the end of the experimental period, whilst crop growth rate increased only until late October or early November after which crop growth rate decreased.

Multiple linear regressions revealed that the inclusion of factors additional to that with the highest correlation coefficient did not increase the multiple correlation coefficient significantly at the 5% level.

The highest correlation coefficient with crop growth rate at 100 $g/m^2$ was found for solar energy. This was obtained in the period when increase in temperature was small while daily solar energy was doubled. At shoot dry matter of 200 $g/m^2$, the correlation coefficient was more or less the same for most environmental factors. Above 300 $g/m^2$, the correlation coefficient for soil temperatures was generally high.

# 5.0.0. Experiments in the Temperature-controlled Glasshouses

## 5.1.0. Introduction

The separate effects of light energy and temperature on the growth of communities can be examined if these factors are varied independently of each other under controlled conditions. This technique will be of use if growth rates in controlled environment are comparable with those in the field under similar conditions. Further, measurements of $CO_2$ exchange rate of communities grown under specific conditions of light energy and temperature may reveal the effects of growth conditions on the $CO_2$ exchange rate.

Clover communities reach full light interception at relatively small values of LAI of 2-4 (Stern 1960). It is therefore likely that rates of photosynthesis of the communities are only slightly affected by increase in LAI above a value of 4. Under these conditions, community growth rate may be influenced strongly by dark respiration loss. Some of the features of dark respiration were therefore investigated in detail.

## 5.2.0. Techniques and Methods

### 5.2.1. General Procedure

#### 5.2.1.1. Planting

In the main experiments conducted in the temperature-controlled glasshouses subterranean clover (*Trifolium subterraneum*) c.v. Woogenellup plants were grown in square section galvanized metal pots, 15 cm x 15 cm x 45 cm (deep). The pots were lined with plastic tube before filling with soil to prevent possible zinc toxicity. A plastic plate with 5 holes was used as a bottom to the pot with a layer of gravel above to assist drainage. UC Mix compost (1 sand : 1 peat) was used as a root medium in all experiments. A tonne of this compost contained: $K_2SO_4$ 113 g, $KNO_3$ 142 g, dried blood (source of phosphate) 1219 g, $MgCO_3$ 198 g, $CaCO_3 + Ca(OH)_2$ 2155 g, $CaSO_4$ 1134 g and 'reverted super' ($Ca(H_2PO_4)_2 + CaCO_3$) 1134 g. Careful packing of the pots with soil was conducted to obtain an even bulk density. Each pot contained about 14 kg of soil.

Two seeds were placed in each position of a 7 x 7 matrix in each pot and covered with UC Mix soil to about a half centimetre. Sieved seed of diameter 1.6 mm - 2.2 mm was used. This fraction weighed 5.6 g for 1,000 seeds. A few days after emergence plants were thinned to 49 per pot. Each plant therefore had a distance of 2 cm from the four surrounding plants. Plant density was 2,120/$m^2$.

After planting, the pots were packed close together in a controlled temperature glasshouse so that there was no gap between them. Experimental pots were surrounded by one row of border pots which were not harvested.

### 5.2.1.2. Cultivation of Plants

Plants were watered with tap water several times a day until emergence. After emergence, a modified Hoagland* solution was flushed through in the morning, and tap water in the afternoon. The pots were flushed through once a week with a large volume of tap water. Plants were nodulated by the appropriate culture of rhizobium in all experiments.

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* The solution contained:

| | |
|---|---|
| $K^+$ | 145 μg/l |
| N as $NH_4^+$ | 7 |
| N as $NO_3^-$ | 112 |
| P as $PO_4^{---}$ | 16 |
| S as $SO_4^{--}$ | 32 |

micronutrients (B, Zn, Cu, Mb and Mn) and Fe - EDTA.

Aphids and mites were controlled when necessary by application of 'metasystox' and 'kelthane' respectively.

Leaf appearance and leaf senescence were examined in some experiments by recording new leaves and senesced leaves every 5-7 days. Sixteen to twenty plants in the community were identified at the beginning of the experiment by coloured thread to mark leaves.

### 5.2.1.3. Harvesting

For harvests at which the $CO_2$ exchange of a canopy was not measured, 4 or 5 pots were taken out of the plant canopy and the canopy re-formed by closing up the remaining pots. When the $CO_2$ exchange was to be measured, 8 pots were removed and put into the photosynthetic chamber (see 5.2.2). After measuring $CO_2$ exchange, 5 of the 8 pots were harvested and the rest returned to the original canopy.

Plants in a pot were cut at soil level. Roots were washed out thoroughly with tap water. The shoots were washed and sub-sample plants taken. These were separated into green leaf; dead leaf; and stem, petiole and pod (if any).

Leaf area was measured by an electronic planimeter (Paton Industries Pty Ltd, South Australia), at least twenty leaves being used for each measurement. All plant parts were dried at 85°C for 24 hr, and then weighed. All yield data were converted to $g/m^2$.

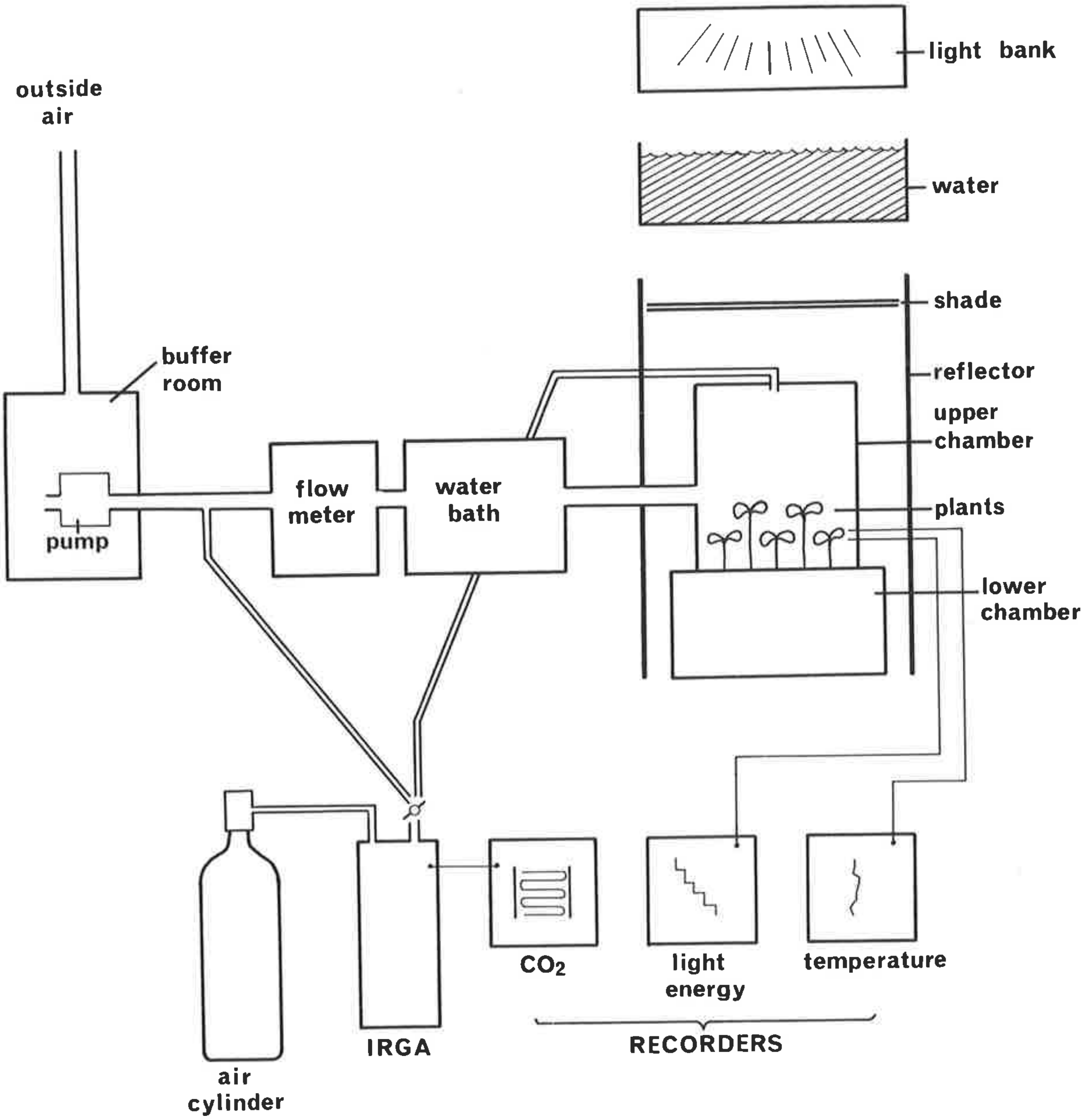
## 5.2.2. Measurement of $CO_2$ Exchange

### 5.2.2.1. Apparatus

An open system, illustrated in Fig. 10, was used for the measurement of the $CO_2$ exchange of each community.

The photosynthetic chamber consisted of a lower metal box, 45 cm x 45 cm x 50 cm (deep) to contain 8 pots and an upper aluminium

Figure 10. A flow diagram showing the method of measurement of $CO_2$ exchange rate of subterranean clover communities.



light bank
water
shade
reflector
upper chamber
plants
lower chamber
outside air
buffer room
pump
flow meter
water bath
air cylinder
IRGA
CO2
light energy
temperature
RECORDERS

section 45 cm x 45 cm x 50 cm (high) to enclose shoots. The top of the chamber was covered with transparent 'melinex'. Copper tubes were attached to the aluminium walls to assist in control of chamber temperature. Chilled water was circulated through the tubes.

A water filter was placed between the chamber and the light source of 4 x 1,000 W quartz-iodine lamps. Various light flux densities were obtained by interposing 'Tygon' shades. Light flux density at the top of the plant canopy in the chamber was measured with a 'Kipp' thermopile. Variation in irradiance between the centres of all pots was less than 4%. Photosynthetically active radiation (PAR) in the chamber was measured by use of an interference filter (Chance-Pilkington HA, 3 mm thick) with allowance for the heat absorption and light transmission of the filter. The proportion of PAR varied slightly about a value of 0.44 with the depth of water in the filter. Ultra-violet radiation from the quartz iodine lamps was considered to be negligible (McCree 1972b). The shade cloths used to reduce irradiance did not affect the proportion of PAR. The maximum irradiance possible was 300 $W/m^2$ (PAR).

A controlled temperature glasshouse was used as an air-supply buffer room with a vent to the outside to admit fresh air. Air mixing in the buffer room reduced small fluctuations in $CO_2$ concentration, but it was impossible to prevent drift in $CO_2$ concentration throughout the day.

The temperature of the air in the buffer room was maintained at about 15°C. The pump to the chamber was a major source of heat but this was reduced by the use of a long lead to the chamber. Control of temperature was achieved principally by changing the temperature of the waterbath and the walls of the chamber. Air temperature in the chamber was usually within 0.5°C of that desired.

Flow rate of air pumped to the photosynthetic chamber was measured by a 'Fisher and Porter' rotameter of low pressure drop design. The air, after passing through a controlled temperature waterbath, entered the photosynthetic chamber through a perforated pipe maintained just above the plant canopy. Velocity across the canopy was fairly uniform at about 3 m/sec.

Air and leaf temperatures were measured with shielded copper-constantan or chrome-constantan thermocouples. Leaf temperature was measured by pressing a thermocouple junction against the lower surface of a leaf. Leaf temperature was usually higher than air temperature by 1-3 degrees when the air temperature was about 16°C, but was about the same as air temperature when the latter was at 20-24°C. A leaf situated at the top of the canopy had a temperature 1-2°C higher than that of a leaf in a lower layer. In the dark, all leaves were very close to air temperature.

Air samples at the entry and exhaust parts of the chamber were freeze dried, warmed, and the $CO_2$ concentration of each air sample measured by a 'Beckman' (Model 215B) infra-red gas analyser. The IRGA was used as a differential type, the reference gas being air from a cylinder with known $CO_2$ concentration. Each air sample entered the IRGA every alternate minute by use of a solenoid switch and the difference in $CO_2$ concentration with the reference air was recorded on a 'Leeds and Northrup' recorder.

The IRGA was calibrated every day with 'Wösthoff' gas mixing pumps. These pumps could provide concentrations of $CO_2$ in $N_2$ from 250-350 µl/l in 10 µl/l steps.

#### 5.2.2.2. General Procedure for Each Measurement

Eight pots were taken out of the community, put in the lower part of the photosynthetic chamber without the top and allowed to regain the original canopy structure. Young plants required one day; old plants required 2-4 days.

Penetration of lateral light into the canopy was prevented by four black plastic boards containing a number of small holes which also confined the canopy to the same surface area as that of the 8 pots.

The plants were positioned under the light bank and the lower chamber was filled with tap water to soil level to eliminate $CO_2$ exchange with the soil. Replacement of all the air space in the soil took about 20 minutes. The aluminium top was then placed in position with a water seal between the two parts; the air stream was started and the light turned on.

One hour was usually necessary to attain equilibrium. During this time temperature was adjusted to the desired level and the IRGA was calibrated.

When the difference in $CO_2$ concentration between inlet air and outlet air was constant, net $CO_2$ exchange rate was read and a shade was placed on the chamber to provide a new level of irradiance. Fifteen minutes was usually sufficient to attain equilibrium. The procedure was repeated for 5-6 levels of irradiance. Air flow was adjusted at each light flux density so that the difference in $CO_2$ concentration between inlet and outlet air was less than 25 µl/l.

In the experiment described in 5.4.0. completion of a series of measurements for different irradiances at one temperature was followed by the same sequence at other temperatures. All photosynthesis measurements were finished before 1800 hr and were followed by dark respiration measurements after equilibration for one hour in the dark. About 5 different temperatures between 9° and 29°C were used in the temperature experiments (5.4.0.). Temperatures were changed in increasing order with at least 20 minutes allowed for stabilisation.

Plants were harvested immediately after the dark respiration measurements.

### 5.2.2.3. Accuracy of the Measurement

According to Catsky, Janac and Jarvis (1971), the net $CO_2$ exchange rate (Pn) can be calculated from the following equation* when a rotameter is used.

$$Pn = \frac{\Delta C \times 10^{-6}}{A} \times \frac{44 \cdot J}{22.414} \times \frac{273}{T} \times \frac{P}{1013} \times \sqrt{\frac{T}{T_1}} \times \sqrt{\frac{P_1}{P}}$$

where

$\Delta C$ = change in $CO_2$ concentration (µl/l).
J = air flow rate through the assimilation chamber (l/hr).
A = ground area ($m^2$).
P = barometric pressure at the time of observation (mb.).
$P_1$ = pressure at which the rotameter was calibrated (mb.).
T = temperature of the flow meter at the time of observation (K).
and $T_1$ = temperature at which the rotameter was calibrated (K).

The pressure in the system was taken as that of air for, although the air pressure fluctuated from time to time, the difference was small - a 10 milibar difference, which would occur rarely during the measurement of Pn, affects Pn by less than 1%. Thus the equation becomes:

$$Pn = \frac{\Delta C \times 10^{-6}}{A} \times \frac{44 \cdot J}{22.414} \times \frac{273}{T} \times \sqrt{\frac{T}{T_1}}$$

---

* The equation was adopted here for the rate of canopy photosynthesis in g $CO_2/m^2$ (ground)/hr.

In this system $T_1 = 294$ and $T = 308$ in most cases. T fluctuated by less than ± 5°C which would produce an error of less than ± 1%.

The equation actually used for the calculation was:

$$Pn = 1.87 \times 10^{-6} \times \frac{\Delta C \times J}{A}$$

The reproducibility of results is shown in Fig. 11. Three measurements on one day were on the same light - net photosynthesis curve. Similar results were obtained using different plant canopies. It can be seen also from the figure that the variation of each measured point from the hand fitted curve was very small.

The flow rate to the chamber could affect the net $CO_2$ exchange rate; i.e.

(1) when the flow rate was so small that the depletion of $CO_2$ concentration was larger than 35 μl/l the net $CO_2$ exchange rate decreased;

(2) as the flow rate decreased, the air temperature in the chamber increased, which had a measurable effect on the net $CO_2$ exchange rate (see 5.4.0.).

However, by working within these limits the effect of the flow rate* on the net $CO_2$ exchange was found to be negligible as is shown in Fig. 12.

The actual $CO_2$ concentration in the chamber changed from time to time during the day and from day to day due to the change of $CO_2$ concentration in the outside air; the buffer room eliminated only small fluctuations in the $CO_2$ concentration. The absolute $CO_2$

---

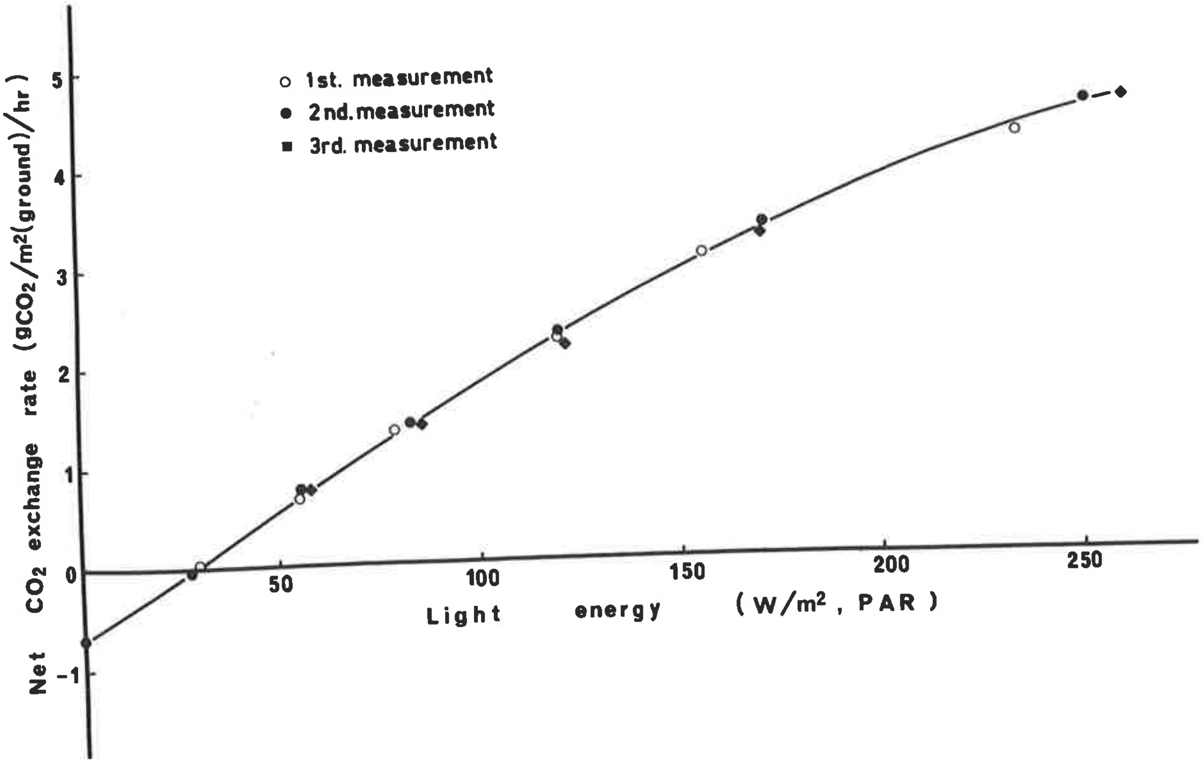
* The accuracy of the rotameter was specified to be ± 1% of a full scale of 417 l/min.

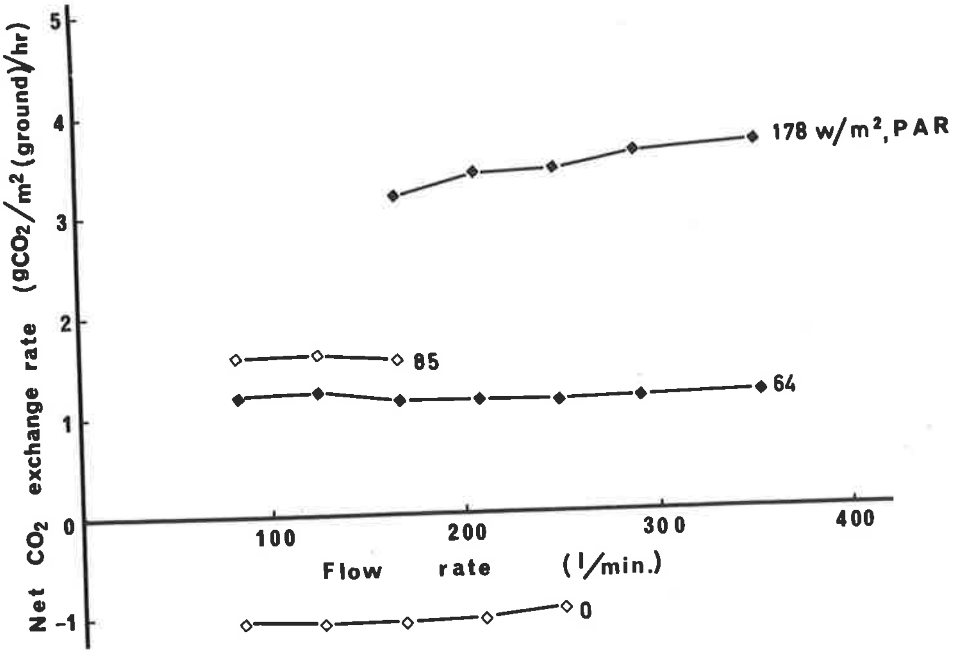
**Figure 11.** (Top)

Light - net photosynthesis curve of a community showing consistent values obtained from 3 separate measurements at 10 a.m., 1 p.m. and 4 p.m. on same day.

**Figure 12.** (Bottom)

Effects of flow rate to the photosynthetic chamber on net $CO_2$ exchange rate in the dark and three different light energy levels.


○ 1st. measurement
● 2nd.measurement
■ 3rd. measurement
Net CO$_2$ exchange rate (gCO$_2$/m$^2$(ground)/hr)
5
4
3
2
1
0
-1
50
100
150
200
250
Light energy (W/m$^2$, PAR)


Net CO$_2$ exchange rate (gCO$_2$/m$^2$(ground)/hr)
5
4
3
2
1
0
-1
100
200
300
400
Flow rate (l/min.)
178 w/m$^2$, PAR
85
64
0

concentration at the inlet to the chamber was between 320 and 350 µl/1 in most measurements. No correction was made for this, although it could result in an error not greater than 10%.

### 5.2.3. Light Energy Experiments

#### 5.2.3.1. General Growth Conditions

Plants were grown at an air temperature of 20 ± 1°C in a controlled temperature glasshouse under natural daylight. A summary of the experimental conditions is given in Table 5. The symbols Sp, Su, A and W stand for spring, summer, autumn and winter. Different light energy levels were obtained by growing plants at different times of the year and by using 'Tygon' shade cloth positioned over some of the pots. Dry matter production was examined in 9 different light energy conditions and leaf number was recorded in 3 different light energy conditions.

The sieved U.C. Mix used with fertilizer in Su72 resulted in nutrient toxicity at early stages of growth. The plants recovered after a large amount of water had been added each afternoon for 10 days. At this early stage of growth, leaves had a higher specific leaf area than that obtained in other experiments. Photosynthetic rates were also found to be lower than in normal plants and therefore the growth and $CO_2$ exchange data obtained over this period have been disregarded.

Sp70 and Sp72 are 'temperature experiments' described in 5.4.0.

#### 5.2.3.2. Light Energy Levels

Daily solar energy inside the glasshouse was measured by 'Kipp' thermopiles on many days throughout the experimental period.

Table 5. Light energy and growth conditions in the light energy experiments

| Experiment No. | Time | Duration (days) | Range in daily solar flux* (MJ/m$^2$/day) | % of outside solar flux⁄ | Rooting medium | Fertilizer added to Mix (+) or not (-) |
|---|---|---|---|---|---|---|
| Sp 70<br>(Spring 70) | 20 July<br>- 1 November 1970 | 104 | 4.4 - 13.4 | 50-60 | Unsieved U.C. Mix | + |
| Su 71<br>(Summer 71) | 13 January<br>-27 February 1971 | 45 | 18.5 - 12.4 | 50-60 | Unsieved U.C. Mix | + |
| W 71<br>(Winter 71) | 14 May<br>-15 September 1971 | 124 | 2.5 - 7.5 | 50 | Unsieved U.C. Mix | + |
| Su 72a | 27 December<br>- 3 March | 67 | 8.4 - 15.5 | 40-65 | Sieved U.C. Mix | + |
| Su 72b | 27 December<br>-14 February | 49 | 3.3 - 7.8 | 20-30<br>(by shade cloth) | Sieved U.C. Mix | + |
| Su 72c<br>(Summer 72) | 27 December<br>-21 February 1971-72 | 56 | 3.4 - 5.2 | 10-20<br>(by shade cloth) | Sieved U.C. Mix | + |
| A 72a | 13 February<br>-13 May | 90 | 15.5 - 6.1 | 50-60 | Sieved U.C. Mix | - |
| A 72b | 13 February<br>- 6 May | 83 | 6.3 - 2.9 | 20-25<br>(by shade cloth) | Sieved U.C. Mix | - |
| A 72c<br>(Autumn 72) | 13 February<br>-12 May 1972 | 89 | 2.9 - 1.0 | 10-15<br>(by shade cloth) | Sieved U.C. Mix | - |
| Sp 72<br>(Spring 72) | 17 July<br>24 November | 130 | 4.2 - 15.9 | 40-60 | Unsieved U.C. Mix | + |

* Range of daily solar flux in glasshouses for 7 day periods during the experiment.

⁄ Percentage of daily transmitted solar energy on to plant canopies.

Otherwise flux was estimated from the solar energy reading at the nearby Waite Meteorological Station.

To evaluate the light energy which plants received, the daily solar energy inside the glasshouse was averaged for 7 days prior to each harvest (Fig. 13) and the averaged light energy is called current light energy (CLE). In Su72, the daily energy was high and constant after an early low period. In A72, the daily solar energy decreased with time after the commencement of the experiment, while in Sp70 and Sp72 it increased almost linearly with time. In W71, the daily solar energy was very low and constant during the early part of the experiment but increased over the latter part.

The relative magnitude of the daily fluctuation was similar under shade to that in the unshaded part of the glasshouse.

Daily light energy inside the glasshouse fluctuated from 50 to 65% of that outside. The percentage transmission tended to be higher on days of high solar energy. In some experiments the glasshouses were sprayed lightly with white paint to help keep the internal temperature on days of high solar radiation close to that required. This procedure reduced the solar energy in the glasshouse by up to 20% compared with unsprayed.

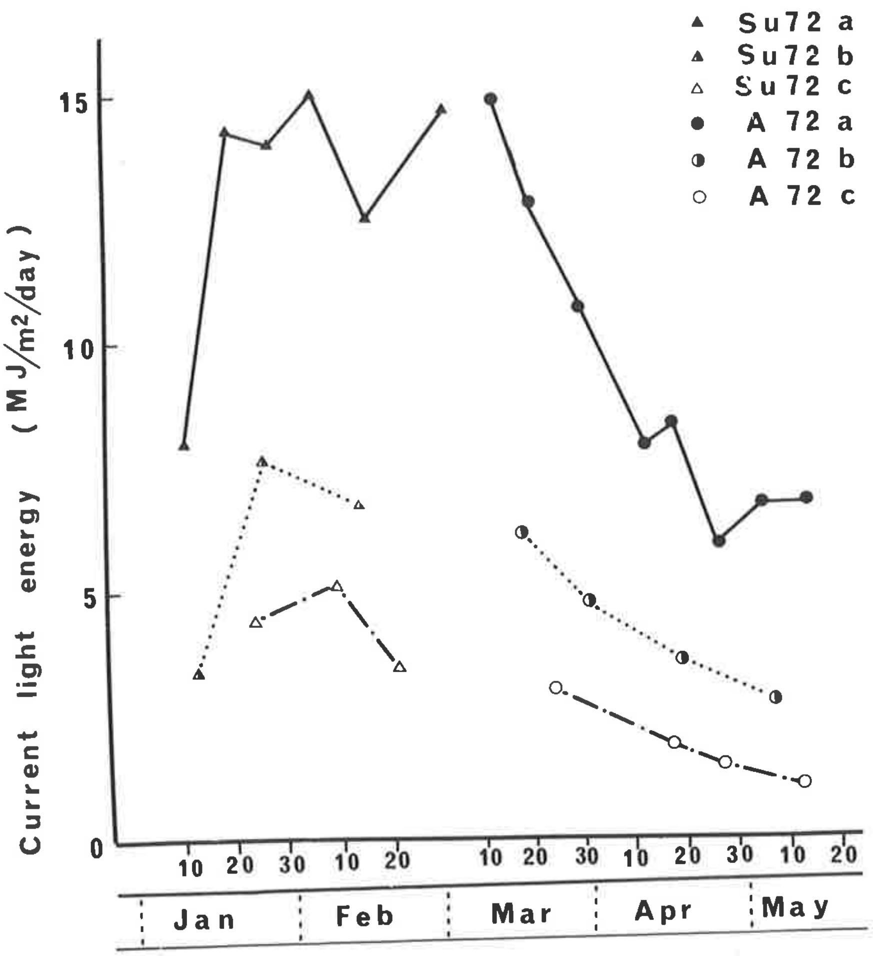
The daily course of light flux under shade was similar to that without shade. The heavy shade in A72c provided a lower daily solar energy than that of W71. The seasonal change in daylength (sunrise to sunset) at Adelaide is from 14.5 hr to less than 10 hr. As the daylength under shade would be close to that outside, plants in Su72b and c experienced a long daylength although the daily light energy was low.

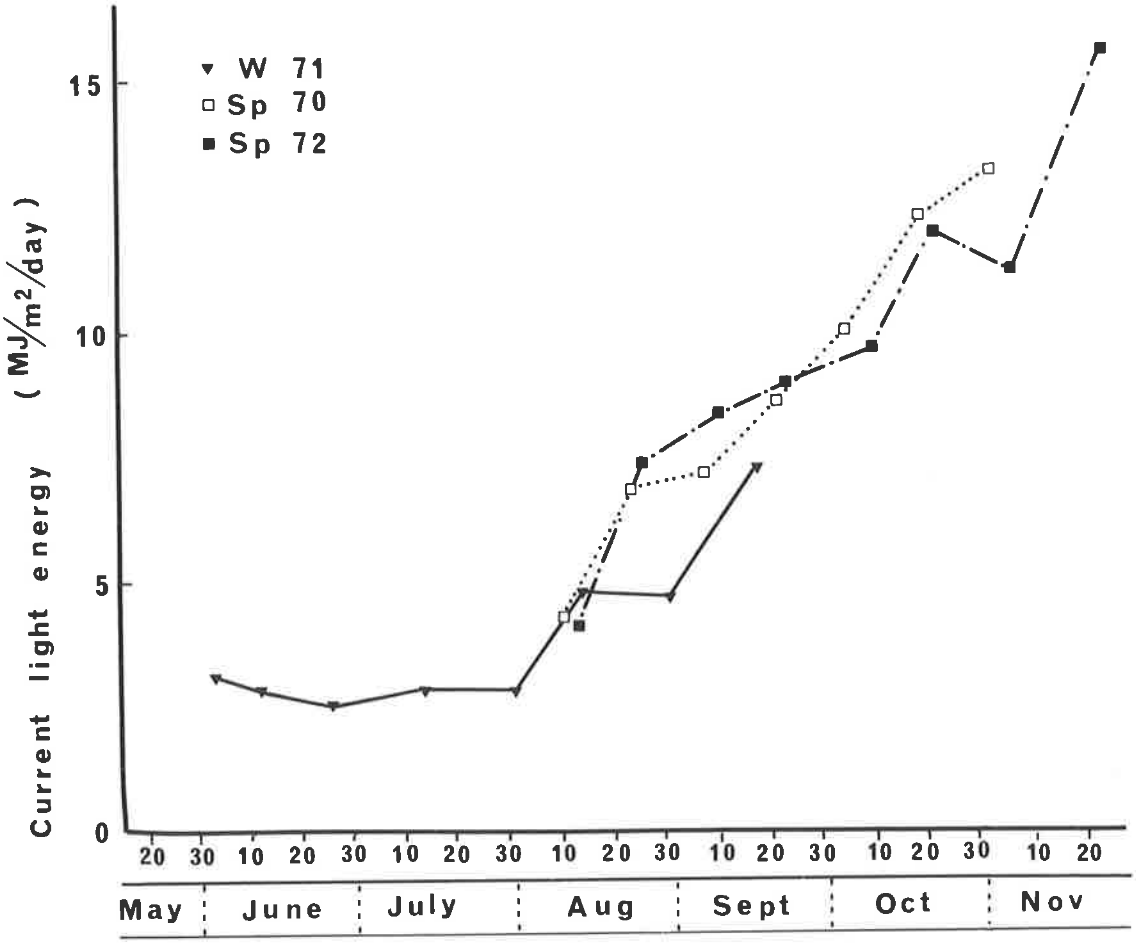
The ratio of diffuse to direct light may change during the day and from day to day under natural light. The proportion of diffuse

Figure 13. Change in current light energy during the light energy experiments. The current light energy is a mean of daily solar energy for 7 days prior to a harvest.

Top: Summer and Autumn Experiments.

Bottom: Winter and Spring Experiments.


▲ Su72 a
▲ Su72 b
△ Su72 c
● A 72 a
◐ A 72 b
○ A 72 c
Current light energy ( MJ/m²/day )
0
5
10
15
10
20
30
10
20
10
20
30
10
20
30
10
20
Jan
Feb
Mar
Apr
May


▼ W 71
□ Sp 70
■ Sp 72
Current light energy ( MJ/m²/day )
0
5
10
15
20
30
10
20
30
10
20
30
10
20
30
10
20
30
10
20
30
10
20
May
June
July
Aug
Sept
Oct
Nov

light was not measured, but it is expected that plants under shade (in Su72b and c, and A72b and c) and plants in a white-painted glasshouse (in Su72, in the early part of A72 and in the late part of Sp72) were grown under a higher proportion of diffused light than plants in other conditions.

### 5.2.4. Temperature Experiments

Two experiments were conducted to examine the effects of temperature on the growth of subterranean clover communities. Planting methods, general culture, harvesting methods and $CO_2$ exchange measurement techniques are described in 5.2.1. Light conditions in the glasshouses used for these experiments are described in 5.2.3.2. Humidity was not controlled but relative humidity was rarely less than 60% at any temperature.

#### (a) 1970 Experiment

Plants were germinated and grown at 20°C constant temperature for 14 days before transfer to constant temperatures of 15°, 20°, 25° a 30°C. At the two higher temperatures a control of ± 1°C was achieved. At the two lower temperatures day temperature reached 2-3°C above set point for 3-4 hours near noon on days of high solar energy flux. Dry matter increase and changes in plant morphology with time were examined, all temperature regimes being sampled on the same day.

#### (b) 1972 Experiment

Plants were germinated and grown at 8°-10°C night temperature and 15°-22°C day temperature in an ordinary glasshouse for 13 days before transfer to constant temperatures of 12°, 16°, 20° and 24°C As in 1970 a general control to within 1°C of set point was achieved at the higher temperatures. However, 12°C could not be maintained under peak solar load. Better control at this temperature was achieved after painting the inside of all the glasshouses with a thin white paint, reducing solar energy input by 20%. Dry matter increase and $CO_2$ exchange were measured at various times during growth.

## 5.3.0. Results of the Light Energy Experiments

### 5.3.1. Dry Matter and Crop Growth Rate

Change in total dry matter with time after planting is shown for each experiment in Fig. 14.

A growth curve was fitted to each set of growth data: a sigmoid curve was calculated for Sp70 and Sp72; a curve fitted by eye for the other experiments, except Su72b and c in which a straight line was drawn between the two harvests. Crop growth rate was calculated by differentiating the sigmoidal function, by reading the 10 days increase in dry matter about the harvesting date in the case of eye-fitted growth curves; and from the slopes of the straight lines in the other cases.

Dry matter increased almost linearly with time in Su72 where the daily solar energy was constantly high. During most of the experimental period, crop growth rate was about 13 $g/m^2$/day which resulted in 686 $g/m^2$ at day 67 when the experiment was terminated. This however may be an underestimate for the given light conditions since the plants showed symptoms of nutrient toxicity in the early stages of growth (see 5.2.3.1). Plants grew less rapidly under shade (Su72b and c).

In A72a where daily solar energy and daylength decreased with time, plant dry matter increased almost linearly from day 30 to day 50 but was nearly constant after day 60. A similar trend of dry matter change is evident in A72b and c except that after day 60, total dry matter decreased slightly. Maximum dry matter was obtained between

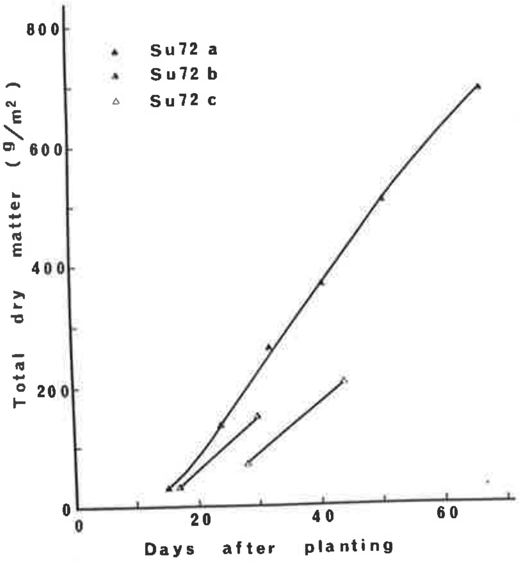
Figure 14. Change in total dry matter with time for communities grown in glasshouses at 20°C under 9 different light energy conditions.

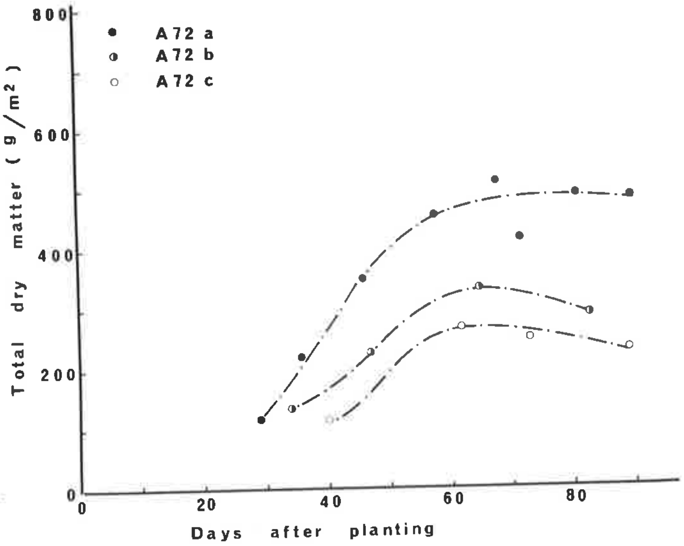
Top left: Summer Experiments.

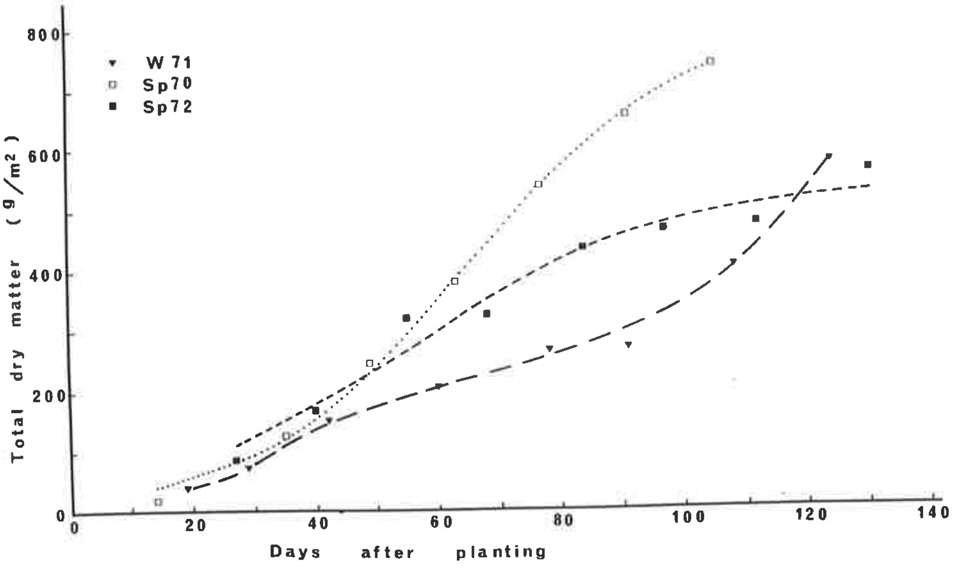
Top right: Autumn Experiments.

Bottom: Winter and Spring Experiments.

A logistic curve was fitted for the growth data in the two spring experiments. The other curves are fitted by eye.


Su72 a
Su72 b
Su72 c
Total dry matter ( g/m² )
800
600
400
200
0
0
20
40
60
Days after planting


A72 a
A72 b
A72 c
Total dry matter ( g/m² )
800
600
400
200
0
0
20
40
60
80
Days after planting


W 71
Sp70
Sp72
Total dry matter ( g/m² )
800
600
400
200
0
0
20
40
60
80
100
120
140
Days after planting

days 65 and 75. This was 580, 330 and 270 g/m$^2$ for A72a, b, and c, respectively, showing maximum dry matter to be directly related to daily solar radiation.

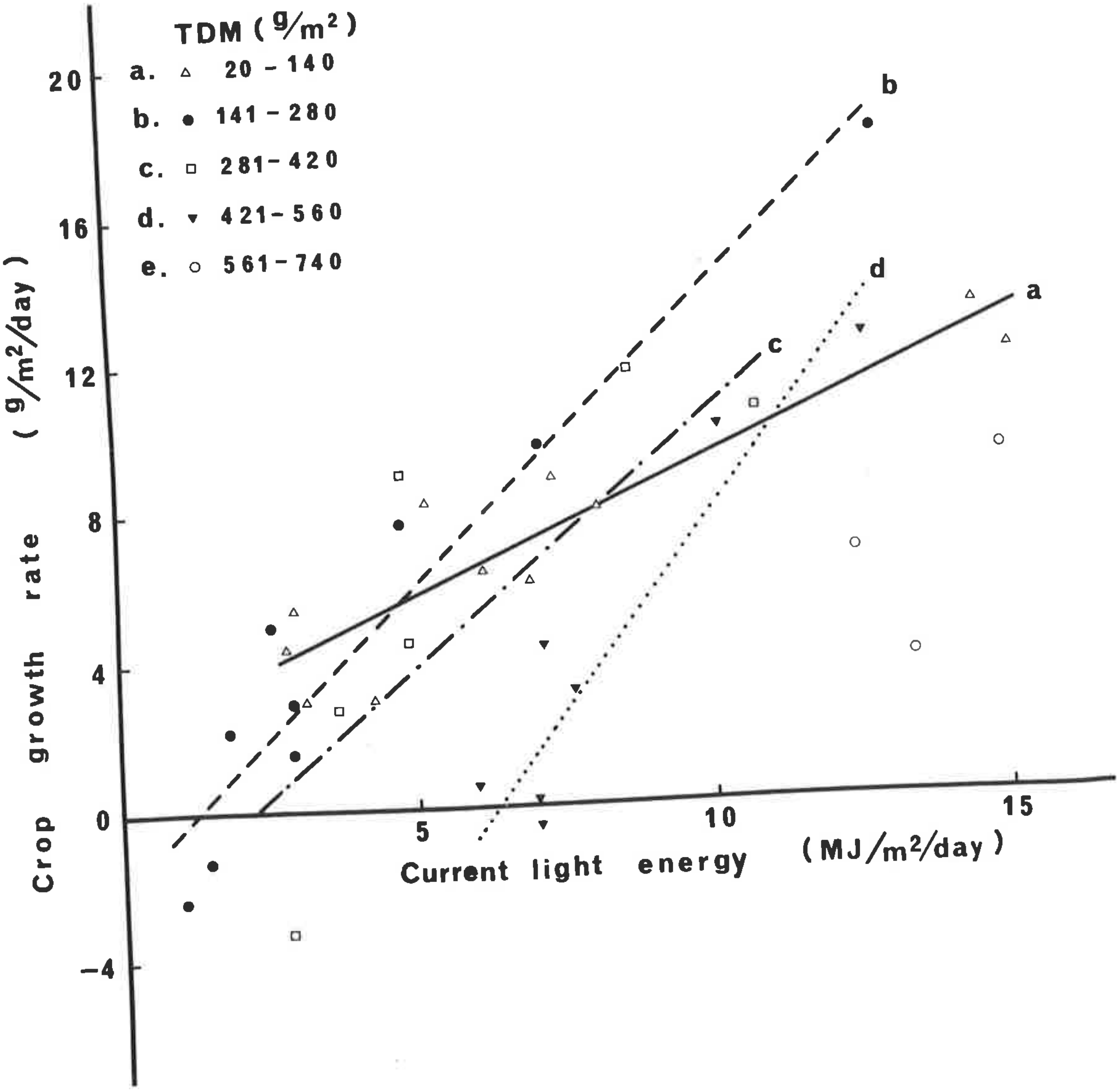
In Sp70 and Sp72, growth rates were low during the early stages, subsequently accelerated and finally decreased. The actual growth rates were different in the two spring experiments. This may be ascribed to a slight difference in the solar energy input at the late stages of growth and to slight nutrient problems in Sp72.

Growth during the early stages of W71, was very slow at 2-5 g/m$^2$/day up to day 90. The rapid increase during the last 30 days in this experiment is associated with increase in daily solar energy (see Fig. 13). Data for this last period are not included in subsequent calculations as the growth rate could not be estimated accurately.

Crop growth rate is plotted against current light energy for different amounts of dry matter in Fig. 15. In Su72b and Su72c light energy was obtained by averaging all daily solar energies between the two harvests. The results of Sp72 were excluded from the figure as crop growth rate of the experiment was lower than that of the other experiments due probably to nutrient problems and to the fact that plant mortality was higher in this experiment than in the others.

Crop growth rate generally increased with increase in daily light energy ($r = 0.74^{***}$), although the variation is considerable. This variation is partly accounted for by differences in dry matter. Five ranges of total dry matter (TDM) are designated on the graph, and it is shown that plant canopies with TDM above 561 g/m$^2$ have a lower crop growth rate for a given daily light energy than canopies with TDM of less than 560 g/m$^2$. Analysis of covariance conducted over TDM values of less than 560 g/m$^2$ show that the slopes of 4 regression lines are significantly different ($F = 7.423^{**}$ with d.f. of 3, 25). A 't'

**Figure 15.** Effects of current light energy on crop growth rate at 20°C for communities with different amounts of total dry matter.


TDM (g/m²)
a. △ 20 - 140
b. ● 141 - 280
c. □ 281 - 420
d. ▼ 421 - 560
e. ○ 561 - 740
Crop growth rate (g/m²/day)
20
16
12
8
4
0
-4
5
10
15
Current light energy (MJ/m²/day)
a
b
c
d

test shows the slope of regression line (a) to be significantly smaller than that of the others, but there is no significant difference in slope among (b), (c) and (d). Analysis of covariance conducted for regression lines (b), (c) and (d) shows that there is a significant difference in displacement of regression lines (F = 14.29** with d.f. of 2, 18).

### 5.3.2. Partition of Dry Matter and Leaf Area

#### (a) Partition of Dry Matter

Plants were separated at harvest into green leaf lamina, dead leaf lamina, stem and petiole, and root. The dry weight of each part was calculated as a percentage of the whole and is plotted in Fig. 16 as a function of TDM. Results of Su72 and A72 are shown in the graph. It is evident that increase in total dry matter was associated with a decrease in both leaf lamina and root percentage; an increase in stem and petiole percentage; and an increase of dead leaf lamina percentage. However, the light environment affects the relationship considerably, particularly with respect to root percentage and stem and petiole percentage. High light energy increased green leaf lamina percentage and root percentage, while low light energy (Su72c, A72b and A72c) increased stem and petiole percentage and dead leaf lamina percentage. Medium light energy (Su72b) showed intermediate values for each attribute.

The percentages of green and dead leaf lamina were added and are plotted against total dry matter in Fig. 16c. The graph shows a slight decrease in the total leaf lamina percentage with increase in total dry matter. It is evident that light conditions had little effect on the total leaf lamina percentage.

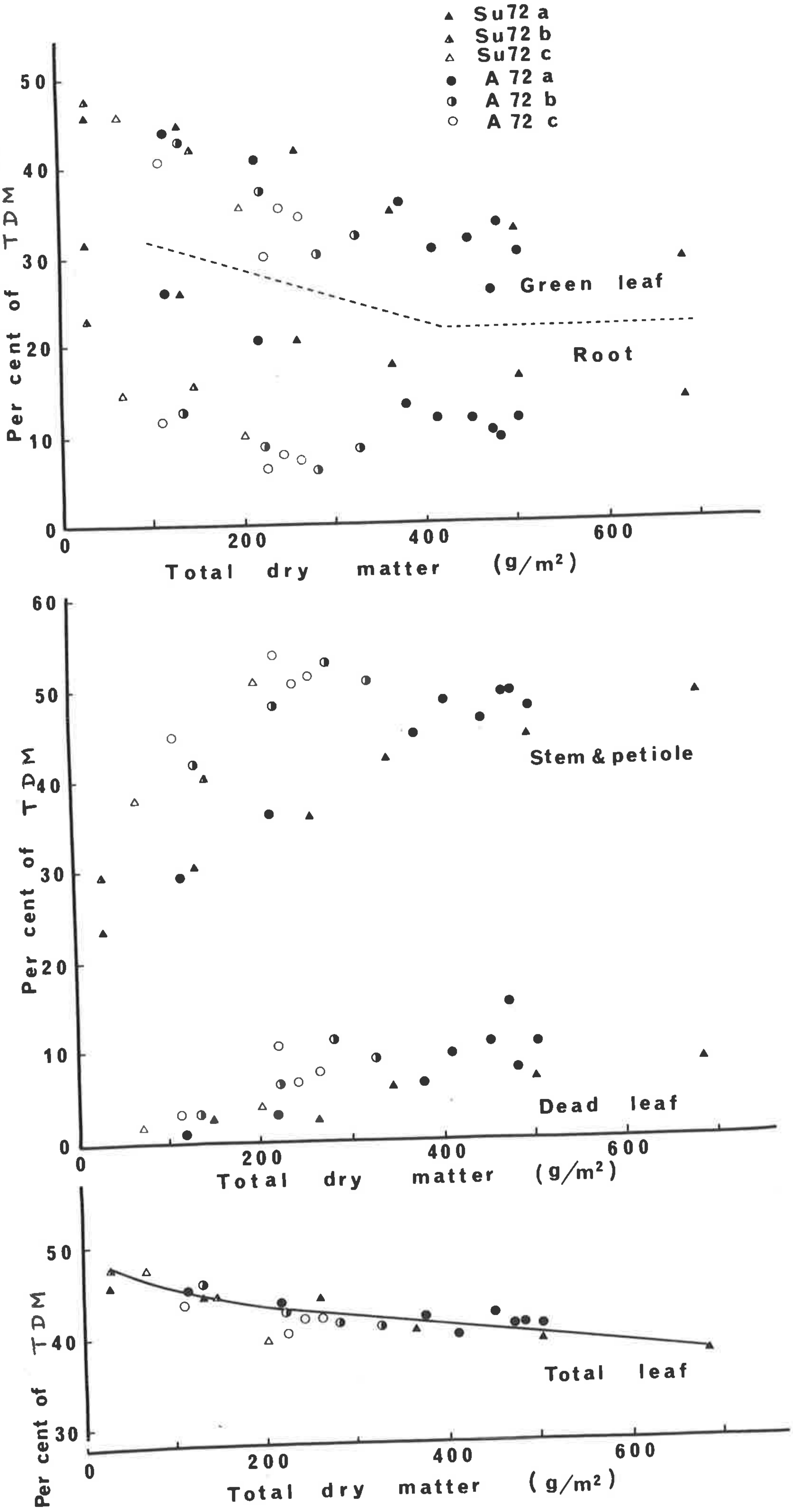
The results of Sp70, W71 and Sp72 were similar to those shown in the graph except: (i) Sp70 showed a high percentage of root and a

Figure 16. Plant part as a percentage of total dry matter (TDM) plotted as a function of total dry matter.

Top: Green leaf lamina and root

Middle: Stem and petiole and dead leaf lamina

Bottom: Total leaf lamina.


▲ Su72 a
▲ Su72 b
△ Su72 c
● A 72 a
◐ A 72 b
○ A 72 c
Per cent of TDM
0
10
20
30
40
50
0
200
400
600
Total dry matter (g/m²)
Green leaf
Root
Per cent of TDM
0
10
20
30
40
50
60
0
200
400
600
Total dry matter (g/m²)
Stem & petiole
Dead leaf
Per cent of TDM
30
40
50
0
200
400
600
Total dry matter (g/m²)
Total leaf

low percentage of stem and petiole; and (ii) W71 showed a slightly high percentage of total leaf. The former was considered to be due to drier soil conditions during the experiment.

### (b) Specific Leaf Area

The relation between SLA and light conditions under which the plants were grown is shown in Fig. 17. Current light energy was calculated as shown in Fig. 13. It may be seen that SLA tends to decrease with increase in the light energy although the value of SLA differs considerably between experiments. Apparently, some other factor contributes to variation in SLA. In Sp70 small values of SLA ($300\ cm^2/g$) was found, whilst Sp72 showed a high value of SLA ($500\ cm^2/g$).

### (c) Leaf Area Index

The relationship between LAI and total dry matter (TDM) is shown in Fig. 18. LAI may be expressed as

$$LAI = TDM \times (\text{percent total leaf} - \text{percent dead leaf}) \times SLA.$$

In general, LAI increases with increase in TDM. In Sp70 a small LAI for given TDM was obtained due mainly to a low SLA. In A72, plants grown without shade (A72a) tended to have smaller LAI than those with heavy shade (A72c) for a given TDM. High SLA obtained under low light energy compensated more than the reduction of green leaf lamina percentage caused by high percentage of dead leaf.

### (d) Crop Growth Rate and LAI

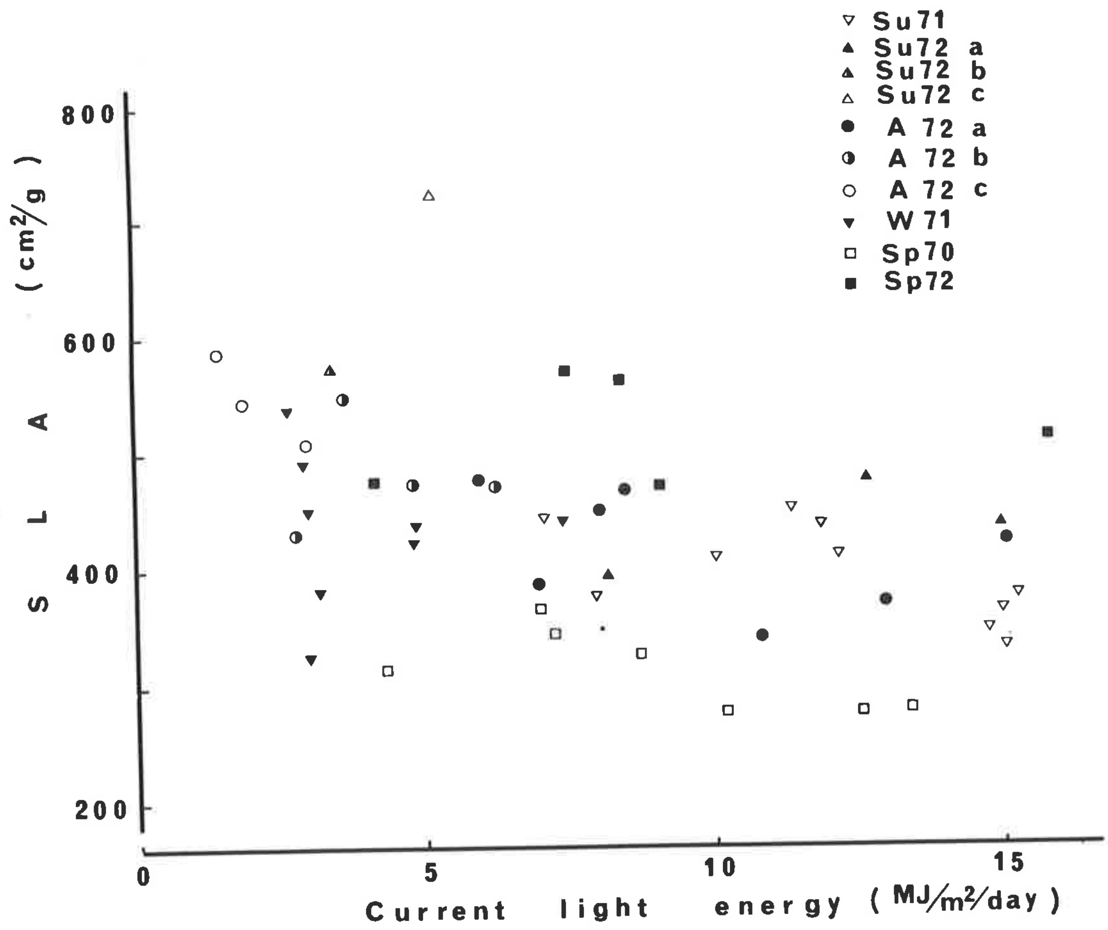
Crop growth rate (excluding data for Sp72) is plotted against LAI for each range of current light energy (CLE) in Fig. 19. A high

**Figure 17.** (Top)

Relationship of current light energy to specific leaf area (SLA).

**Figure 18.** (Bottom)

The relationship between leaf area index (LAI) and total dry matter at 20°C. One curve is shown for Sp70 and the other curve for the rest of the data.


▽ Su71
▲ Su72 a
▲ Su72 b
△ Su72 c
● A 72 a
◐ A 72 b
○ A 72 c
▼ W 71
□ Sp70
■ Sp72
800
600
400
200
S L A ( cm²/g )
0
5
10
15
Current light energy ( MJ/m²/day )

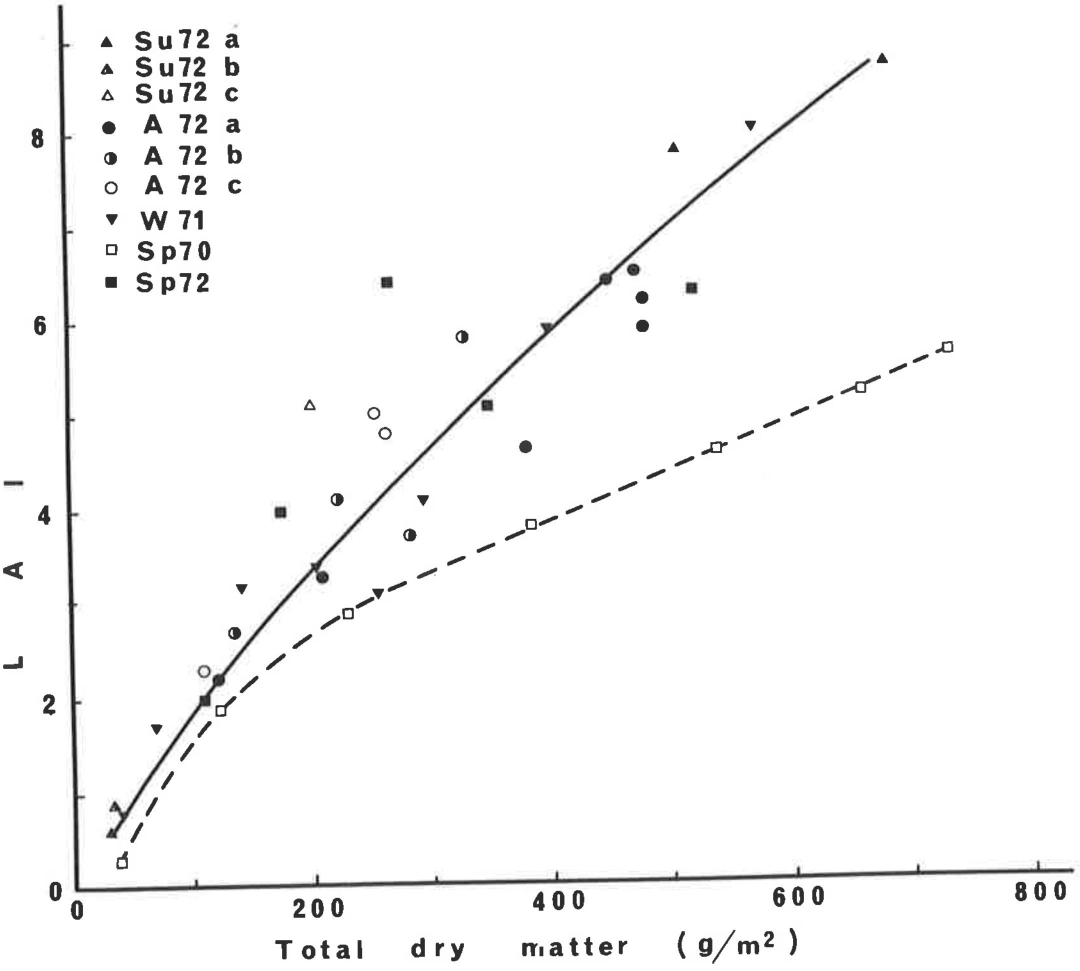
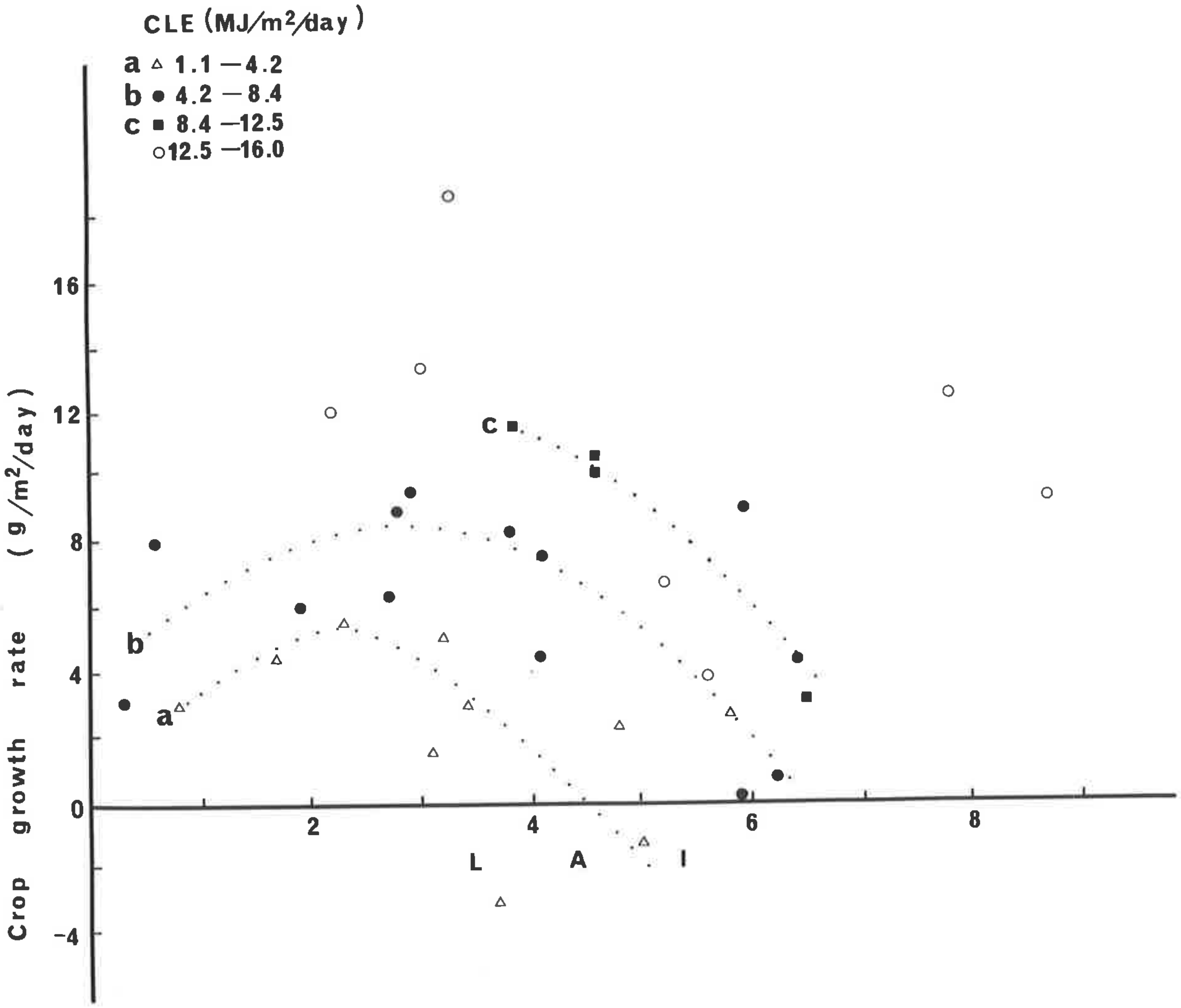

▲ Su72 a
▲ Su72 b
△ Su72 c
● A 72 a
◐ A 72 b
○ A 72 c
▼ W 71
□ Sp70
■ Sp72
8
6
4
2
0
L A I
0
200
400
600
800
Total dry matter ( g/m² )

**Figure 19.** The relationship between crop growth rate and leaf area index (LAI) at 20°C for different current light energies (CLE). Curves for the three lowest ranges of CLE were fitted by eye.


CLE (MJ/m2/day)
a △ 1.1 —4.2
b ● 4.2 —8.4
c ■ 8.4 —12.5
○12.5 —16.0
Crop growth rate (g/m2/day)
16
12
8
4
0
-4
2
4
6
8
L A I
a
b
C

level of current light energy resulted in a high crop growth for a given LAI. For any specified light energy level, crop growth rate increases with LAI up to a maximum and then decreases, although at the highest levels of CLE, the relationship between crop growth rate and LAI is not clear. Two points obtained at the highest range of daily light energy with LAI of 5.2 and 5.6 showed a smaller crop growth rate than might be expected from the other points. These two points were obtained in Sp70 where plants had a low ratio of LAI to corresponding total dry matter (see Fig. 18).

### 5.3.3. Leaf Number

The rate of leaf appearance, the rate of leaf senescence, and the number of laterals per plant were measured in Sp70, Su71 and W71.

The number of green leaves per plant is shown in Fig. 20. Plants in Su71 had more green leaves than those in Sp70 and W71. This was mainly due to increased number of laterals at a high solar energy level as shown in Fig. 21. Laterals appeared early and increased very rapidly in number between 25 and 35 days after planting in Su71. No senescent laterals were apparent by day 45. The number of laterals per plant was small in Sp70 and W71 and resulted in almost no live laterals (0.1 per plant) at later stages of these experiments.

Current number of green leaves on the main stem on the other hand, showed small differences between the experiments as is shown in Fig. 22. The number of green leaves per main stem increased until it reached a constant number of 4.8 for Sp70 and W71, while in Su71 it increased to 7 at day 29 decreasing subsequently to 5.4. A constant leaf number on a main stem in Sp70 and W71 was obtained because of a constant rate of leaf appearance and a constant rate of leaf senescence as is shown in Fig. 23.

Figure 20. (Top)

Change with time in current green leaf number on plants grown at 20°C.

Curves are fitted by eye.

Figure 21. (Middle)

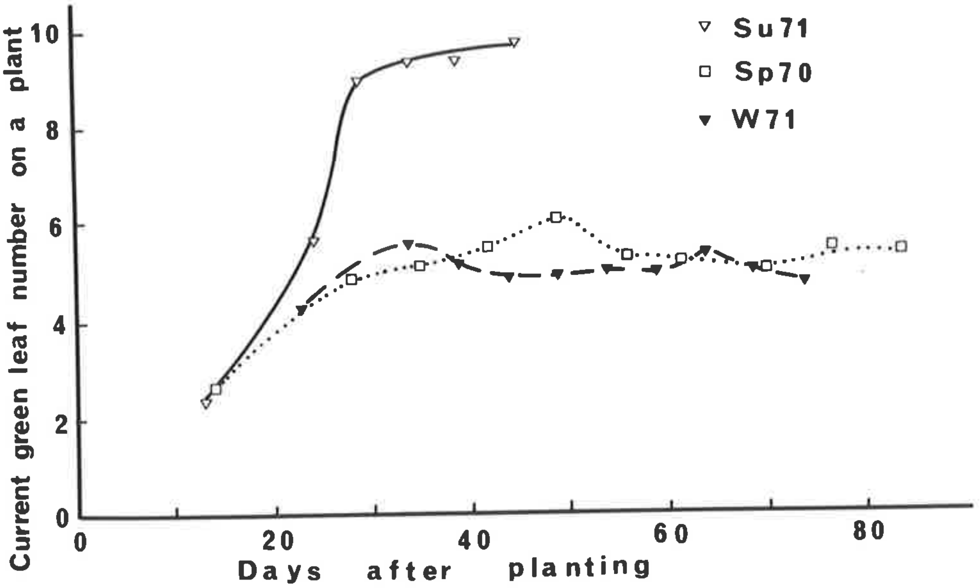
Change with time in accumulated total or dead laterals on plants grown at 20°C.

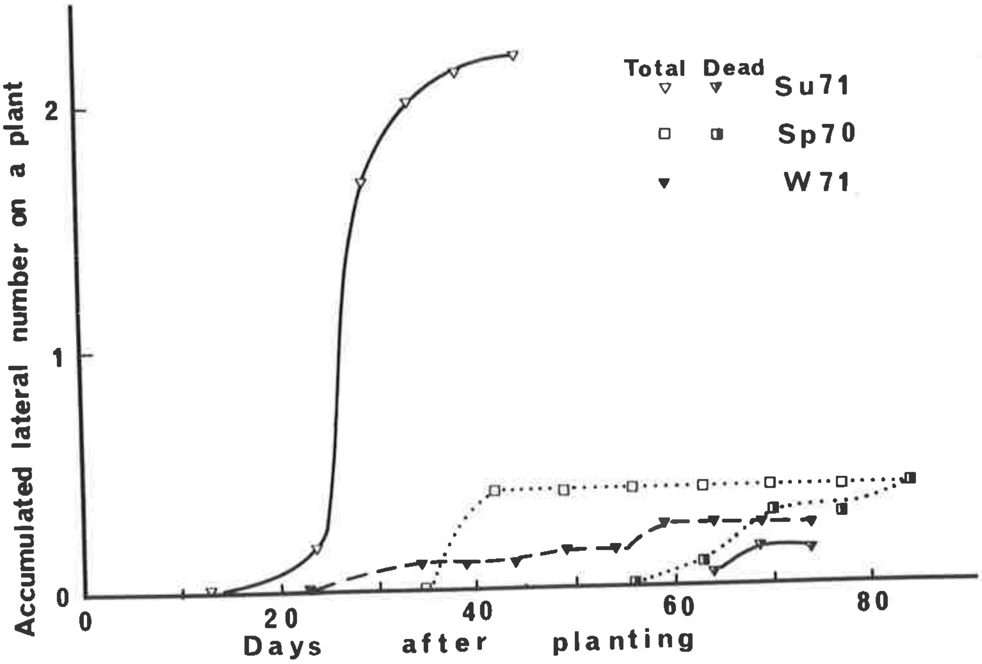
Curves are fitted by eye.

Figure 22. (Bottom)

Change with time in current green leaf number on a main stem of plants grown at 20°C.

Curves are fitted by eye.


▽ Su71
□ Sp70
▼ W71
Current green leaf number on a plant
0
2
4
6
8
10
0
20
40
60
80
Days after planting


Total Dead
▽ ▼ Su71
□ ◧ Sp70
▼ W71
Accumulated lateral number on a plant
0
1
2
0
20
40
60
80
Days after planting

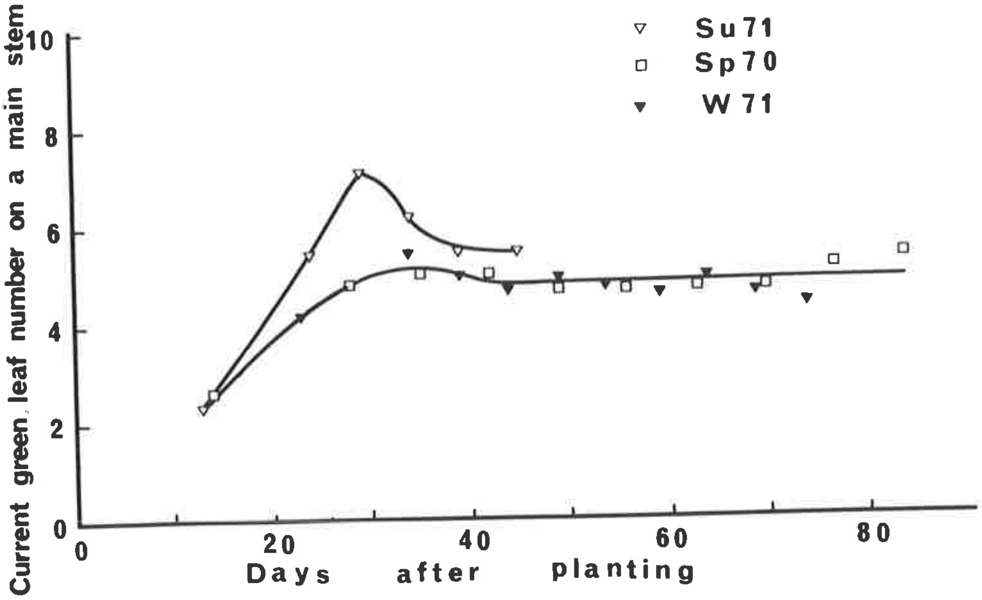
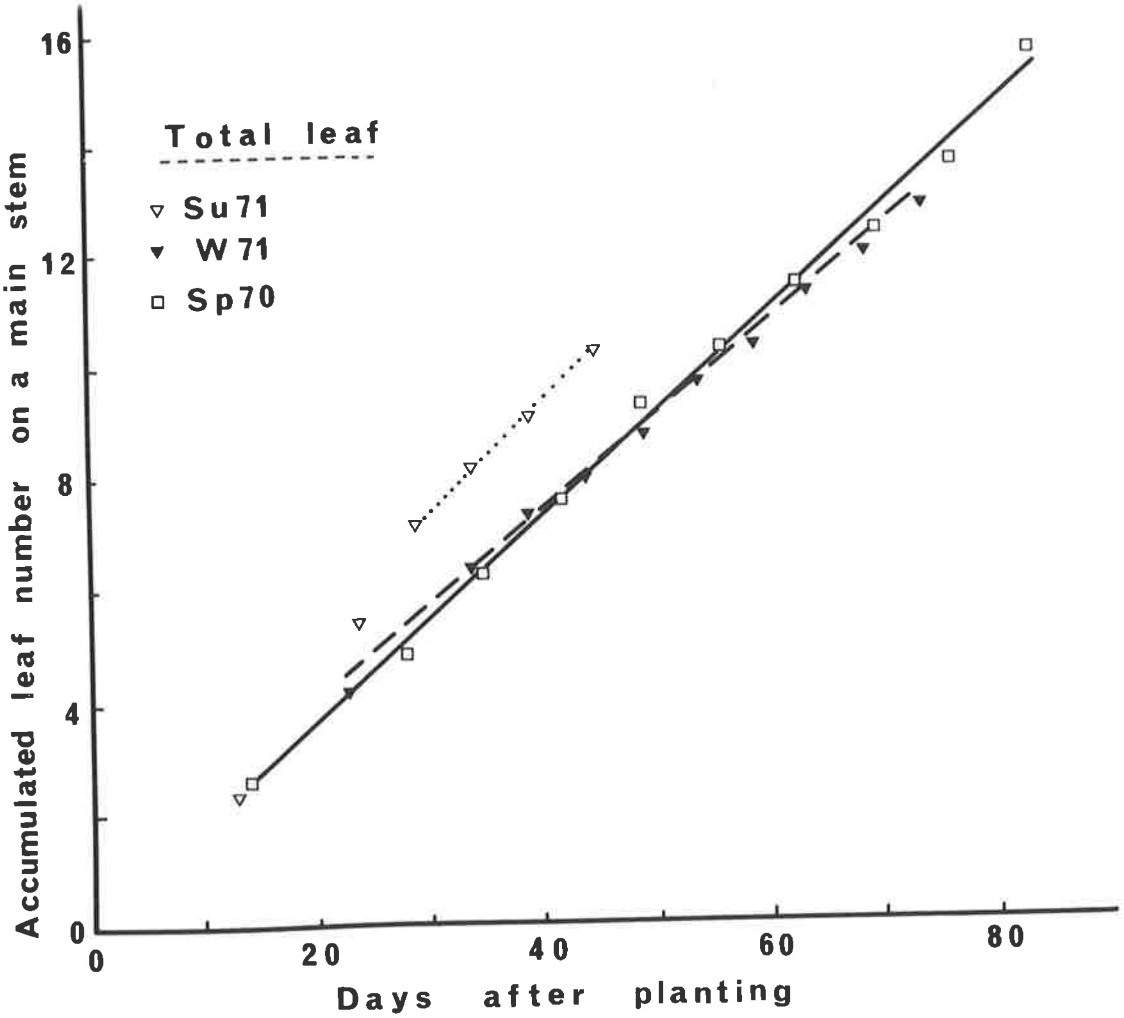
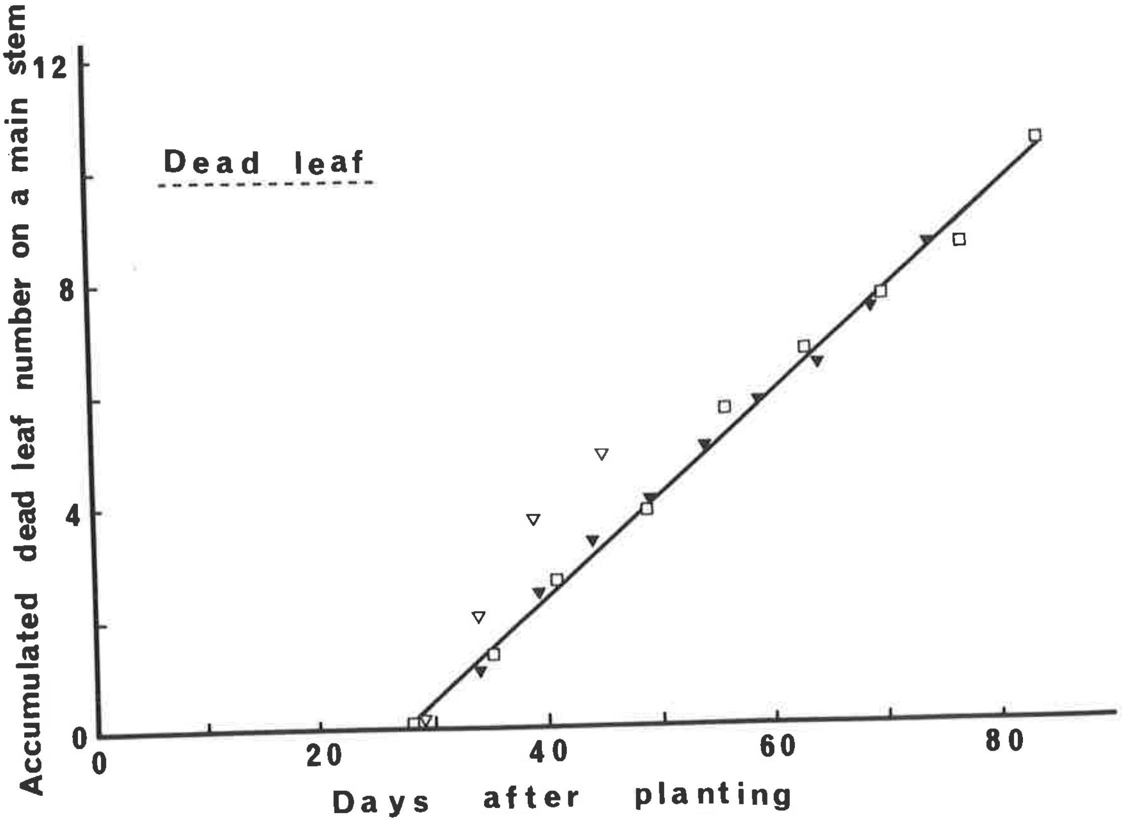

▽ Su71
□ Sp70
▼ W71
Current green leaf number on a main stem
0
2
4
6
8
10
0
20
40
60
80
Days after planting

Figure 23. Fitted regressions of leaf number on the main stem against time. Equations given in Table 6. Total leaves include dead leaves.


Total leaf
Su71
W71
Sp70
Accumulated leaf number on a main stem
0
4
8
12
16
0
20
40
60
80
Days after planting


Dead leaf
Accumulated dead leaf number on a main stem
0
4
8
12
0
20
40
60
80
Days after planting

Su71 showed a slightly higher accumulated total leaf number as well as senesced leaves. Linear regressions of accumulated total leaf number and accumulated dead leaf number on the main stem with time are shown in Table 6.

Table 6. Accumulated total leaf number and accumulated dead leaf number on a main stem

(1) Leaf appearance on a main stem

($x$ = days after planting;
$y$ = accumulated number of leaves)

Su71 $y = 1.3 + 0.200x$ $(29 < x < 45)$

W71 $y = 0.67 + 0.166x$ $(23 < x < 74)$

Sp70 $y = -0.02 + 0.181x$ $(14 < x < 84)$

(2) Leaf senescence on a main stem

Su71 $y = -8.23 + 0.296x$ $(29 < x < 45)$
W71 $y = -4.67 + 0.177x$ $(34 < x < 74)$
Sp70 $y = -4.91 + 0.180x$ $(28 < x < 84)$

Increasing light energy promoted leaf appearance rate on the main stem only slightly. The short period of the observations of leaf senescence in Su71 makes it difficult to assess the effect of light energy on the rate of leaf senescence. There were no differences in the rate between the other two experiments. The leaf appearance interval on the main stem was 5-6 days for the 3 experiments; this was the same as that of the leaf senescence in W71 and in Sp70 but was longer than that of leaf senescence in Su71.

### 5.3.4. Dark Respiration

Dark respiration rates of plant communities were measured in W71, Su72, A72 and Sp72 at $20^\circ \pm 1^\circ$C, the same temperature as that at which the plants were grown. The early stages of Su72 are not included because of fertilizer toxicity. The results are shown in Fig. 24.

The rate of dark respiration is shown per unit ground area in (a) and per unit dry matter in (b). The rate of dark respiration per unit ground area is linearly related to shoot dry matter.

$$DR = 0.156 + 0.00128SDM \qquad \text{EQ.14}$$

$$(R^2 = 0.875)$$

where DR : dark respiration rate ($gCO_2/m^2$ (ground)/hr)

and SDM : shoot dry matter ($g/m^2$).

The rate of dark respiration per unit dry matter (specific respiration rate) is high for young plants and decreases with increase of shoot dry matter. From EQ.14 the rate of dark respiration per unit dry matter is expressed as

$$Rd = 156/SDM + 1.28 \qquad \text{EQ.15}$$

where Rd : specific dark respiration rate ($mgCO_2/g.DM/hr$)

and SDM : shoot dry matter ($g/m^2$)

Variation about the general regression line relating DR with SDM can be explained by variation in the crop growth rate (CGR) induced by different growth conditions. When four ranges of CGR are recognized and designated on the graph, it can be seen that low values of CGR tend to be below the general regression and high values above. An equation can approximate this relation:

$$DDR = 1.94 + 0.022\ SDM + 0.11\ CGR \qquad \text{EQ.16}$$

$$(R^2 = 0.895)$$

where SDM : shoot dry matter ($g/m^2$)

CGR : crop growth rate ($g/m^2$/day)

and DDR : 24 hr dark respiration ($g/m^2$/day)

Dark respiration rate was converted to a dry matter loss per $m^2$ per 24 hr, assuming 1 g of $CO_2$ to be equivalent to 0.7 g of plant dry matter.

Measured 24 hr dark respiration rates are compared with corresponding rates calculated from the equation in Fig. 25. Nearly 90% of the variation is accounted for by the equation. The inclusion of CGR in the equation increased the multiple regression coefficient slightly but significantly.

When the current light energy (CLE) was used instead of crop growth rate to account for variation about the general regression line in Fig. 24, the multiple regression coefficient, after inclusion of current light energy, was as high as that when crop growth rate was included. There was a positive correlation between crop growth rate and current light energy as is seen in Fig. 15. The equation is given below:

$$DDR = 2.21 + 0.020\ SDM + 0.13\ CLE \qquad EQ.17$$

$$(R^2 = 0.898)$$

where SDM : shoot dry matter ($g/m^2$)

CLE : current light energy ($MJ/m^2$/day)

DDR : 24 hr dark respiration ($g/m^2$/day)

### 5.3.5. Photosynthesis

Photosynthesis was measured in W71, Su72, A72 and Sp72. As the plants were slightly affected by fertilizer in the early stages of Su72, the results of the photosynthesis measurements at this time are disregarded. The results of Sp72 will be seen in 5.4.0 with the

**Figure 24.** (Top)

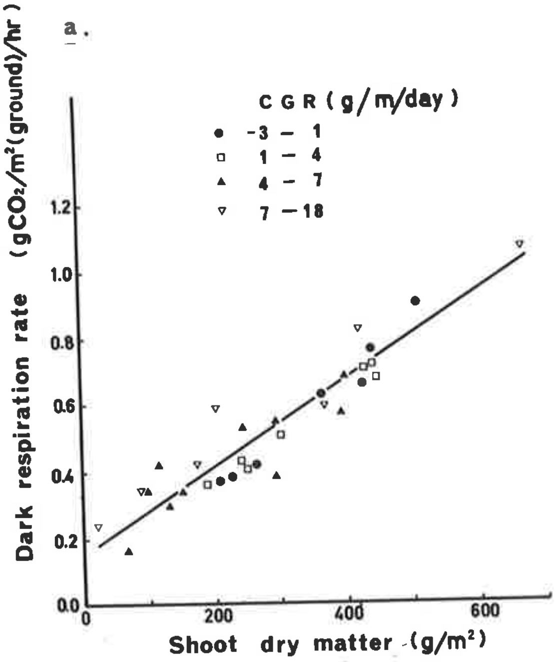
The relationship between dark respiration rate and shoot dry matter of communities with different crop growth rates induced by different light energy conditions.

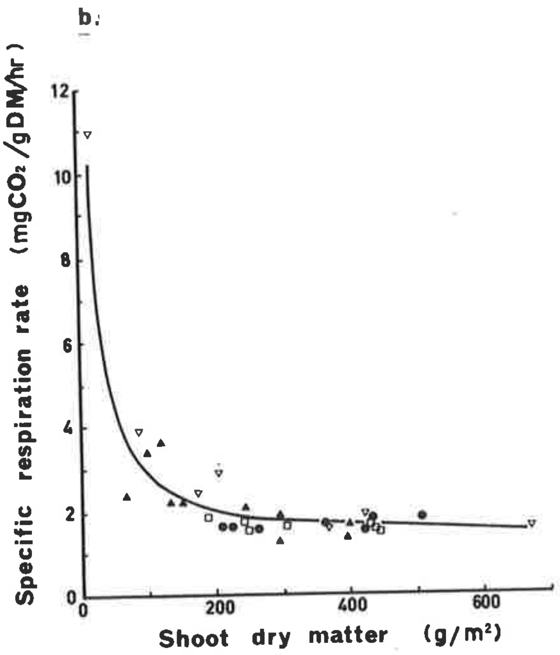
(a) Left: total dark respiration rate

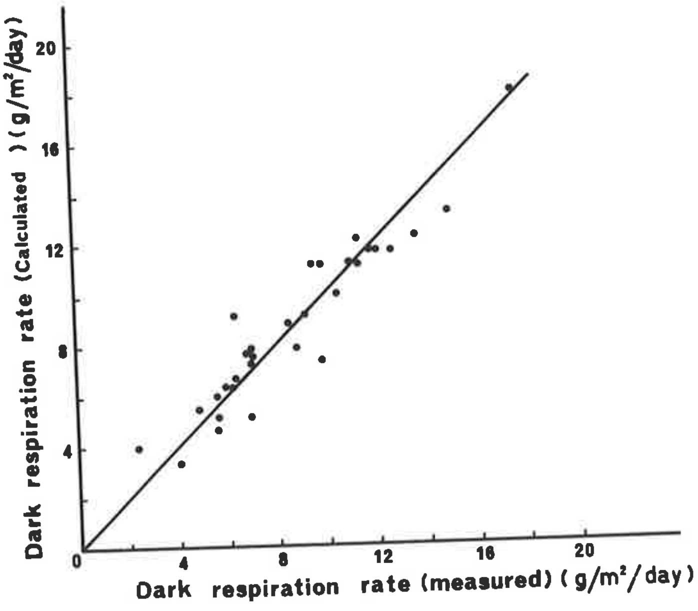
(b) Right: specific respiration rate

**Fig. 25.** (Bottom)

Comparison of calculated daily dark respiration rates (DDR) with measured rates. Calculated rates were obtained from EQ.16 using values for shoot dry matter (SDM) and crop growth rate (CGR) from the experimental data.


a.
CGR (g/m/day)
● -3 – 1
□ 1 – 4
▲ 4 – 7
▽ 7 – 18
Dark respiration rate (gCO₂/m²(ground)/hr)
0.0
0.2
0.4
0.6
0.8
1.0
1.2
0
200
400
600
Shoot dry matter (g/m²)


b.
Specific respiration rate (mgCO₂/gDM/hr)
0
2
4
6
8
10
12
0
200
400
600
Shoot dry matter (g/m²)


Dark respiration rate (Calculated) (g/m²/day)
4
8
12
16
20
0
4
8
12
16
20
Dark respiration rate (measured) (g/m²/day)

results of the other temperature experiments.

Canopy temperature was maintained at 22 ± 2°C as was described in 5.2.2. Gross photosynthesis is defined as the sum of net $CO_2$ uptake and respiration under darkness.

The relationship between net $CO_2$ exchange rate and light energy expressed as $W/m^2$ of PAR, measured at different stages of growth for A72a and W71 are shown in Fig. 26 (a) and (b) respectively.

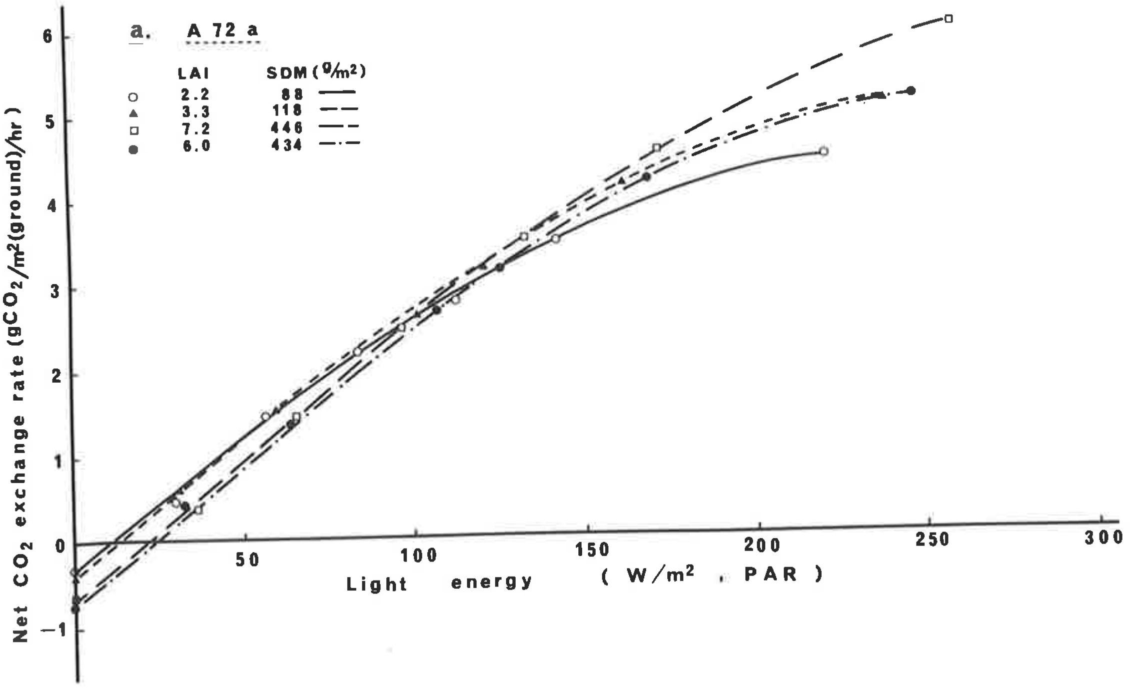
Some representative results only are shown in the graph to avoid complexity. For light fluxes from 0 to 100 $W/m^2$, net $CO_2$ exchange rate increased almost linearly with increase in light flux density. At higher light fluxes, curvature became apparent. Complete light saturation of net $CO_2$ exchange rate was not obvious in any experiment except for canopies with LAI less than 1.

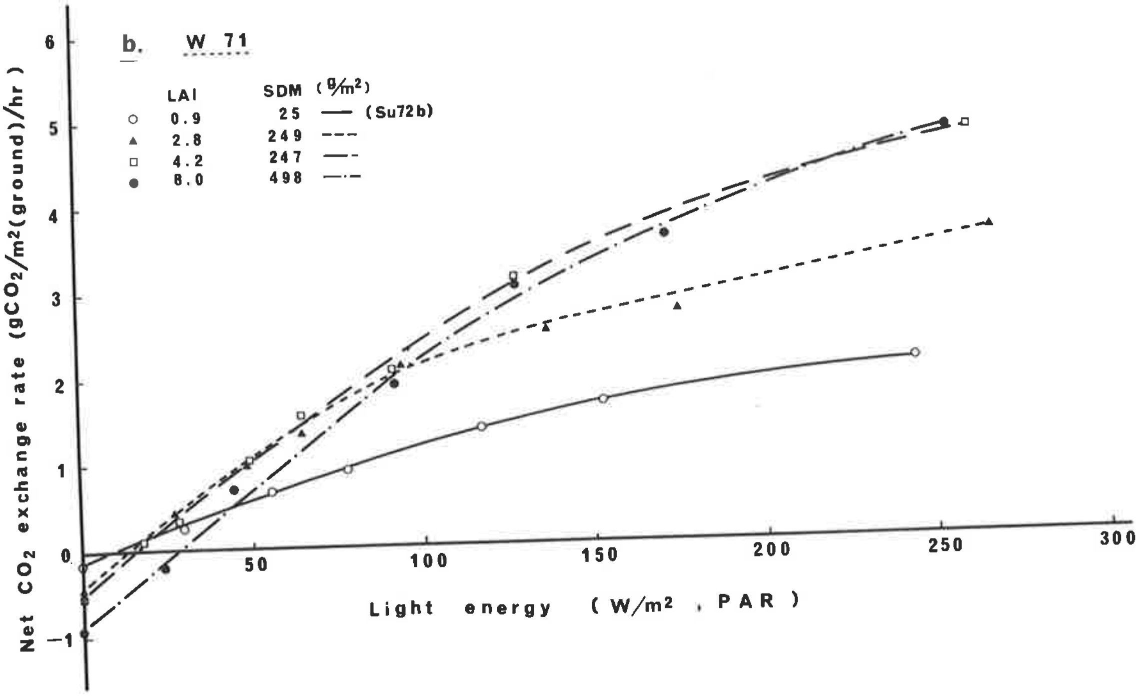
The results of A72a show that young canopies with LAI between 2.2 and 3.3 had higher rates of net $CO_2$ exchange rate at low light fluxes than older canopies with higher LAIs and high dry matter. The difference is mainly accounted for by difference in the dark respiration rate. At light fluxes of more than 150 $W/m^2$ the youngest plant canopy with LAI of 2.2 showed the lowest net $CO_2$ exchange rate. The canopy with LAI of 7.2 on the other hand had a low net $CO_2$ exchange rate at low light fluxes, but had the highest rate of net $CO_2$ exchange at high light fluxes. An old canopy with LAI of 6.0 had a low rate of net $CO_2$ exchange at low light flux like the LAI 7.2 canopy, but a lower rate than the LAI 7.2 canopy at high light flux. A relatively low rate of net $CO_2$ exchange of old canopies at high light fluxes was also observed in A72b and c. In these communities the daily light energy decreased with the aging of the plants and there was no increase of dry matter at the late stages of the growth (see Fig. 14).

Figure 26. Light-net photosynthesis curve of communities with different values of leaf area index (LAI) and shoot dry matter (SDM).

(a) Top: Autumn 72a

(b) Bottom: Winter 71


a. A 72 a
LAI SDM (g/m²)
○ 2.2 88 ——
▲ 3.3 118 – –
□ 7.2 446 — —
● 6.0 434 —·—
Net CO₂ exchange rate (gCO₂/m²(ground)/hr)
6
5
4
3
2
1
0
−1
50
100
150
200
250
300
Light energy (W/m², PAR)


b. W 71
LAI SDM (g/m²)
○ 0.9 25 —— (Su72b)
▲ 2.8 249 - - -
□ 4.2 247 — -
● 8.0 498 —·—
Net CO₂ exchange rate (gCO₂/m²(ground)/hr)
6
5
4
3
2
1
0
−1
50
100
150
200
250
300
Light energy (W/m², PAR)

The results of W71 show a similar relationship to those of A72a between net $CO_2$ exchange rate and light flux. A result of Su72b is included in the graph to show a light - net photosynthesis (P/I) curve of a young community with a small LAI. Su72b was shaded and current light energy levels were similar to those of W71*.

The youngest plant canopy with LAI of 0.9 showed the lowest respiration rate, but the initial slope of the light photosynthesis curve was much smaller than that of older canopies with higher LAIs and the rate at high light flux much lower than in older canopies with LAI > 2.

The oldest canopy with LAI of 8.0 had a low net $CO_2$ exchange rate at low light flux. However, the rate at the high light flux was high. This result is in contrast with that of A72a as described above. In W71 the daily light energy increased in the late stages of the experiment and the growth rate responded.

Gross photosynthetic rate is plotted against light energy in Fig. 27. The gross photosynthetic rate was almost the same for all canopies in A72a at low light flux with perhaps a slightly lower rate for the youngest canopy with LAI of 2.2. At high light flux gross photosynthetic rate increased with increase of LAI up to 7.2; older canopies with similar LAI show a decreased rate of gross photosynthesis.

Similar results were obtained from plant canopies grown at low daily light energy levels (W71). The young canopy with a small LAI (0.9) had a very low rate of gross photosynthesis over the whole range of light flux employed. The gross photosynthetic rate generally increased as plants became older and developed a higher LAI. The

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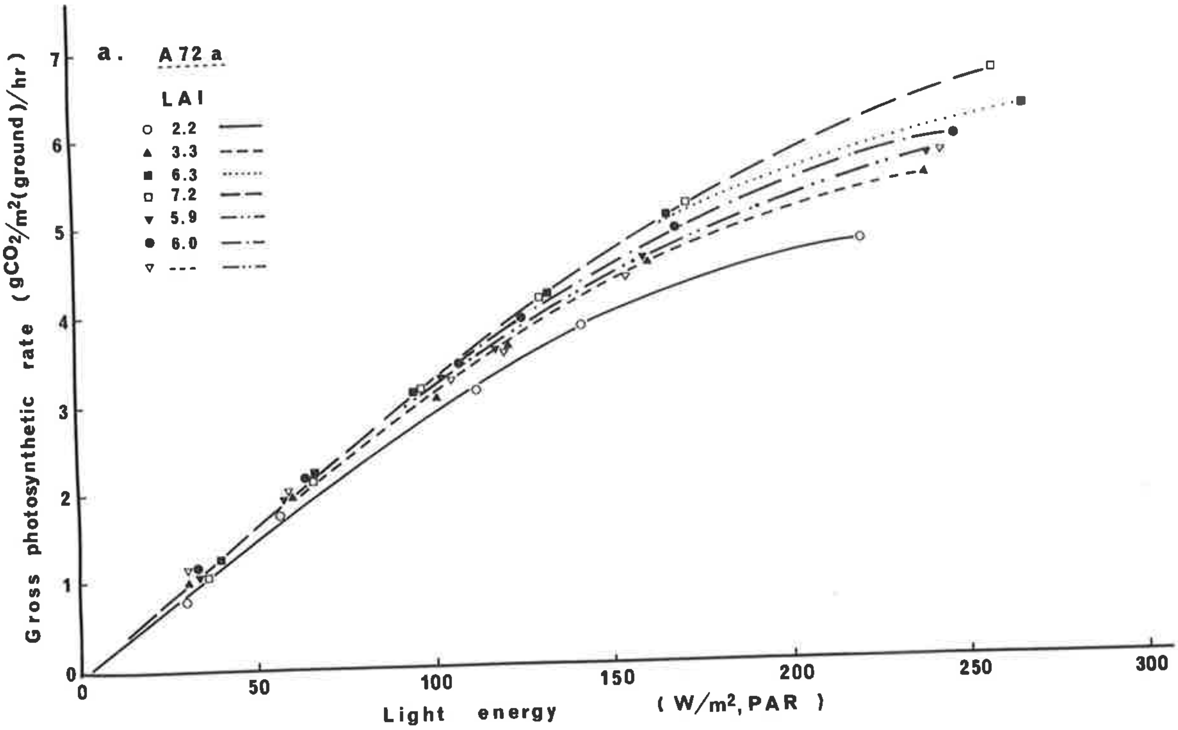
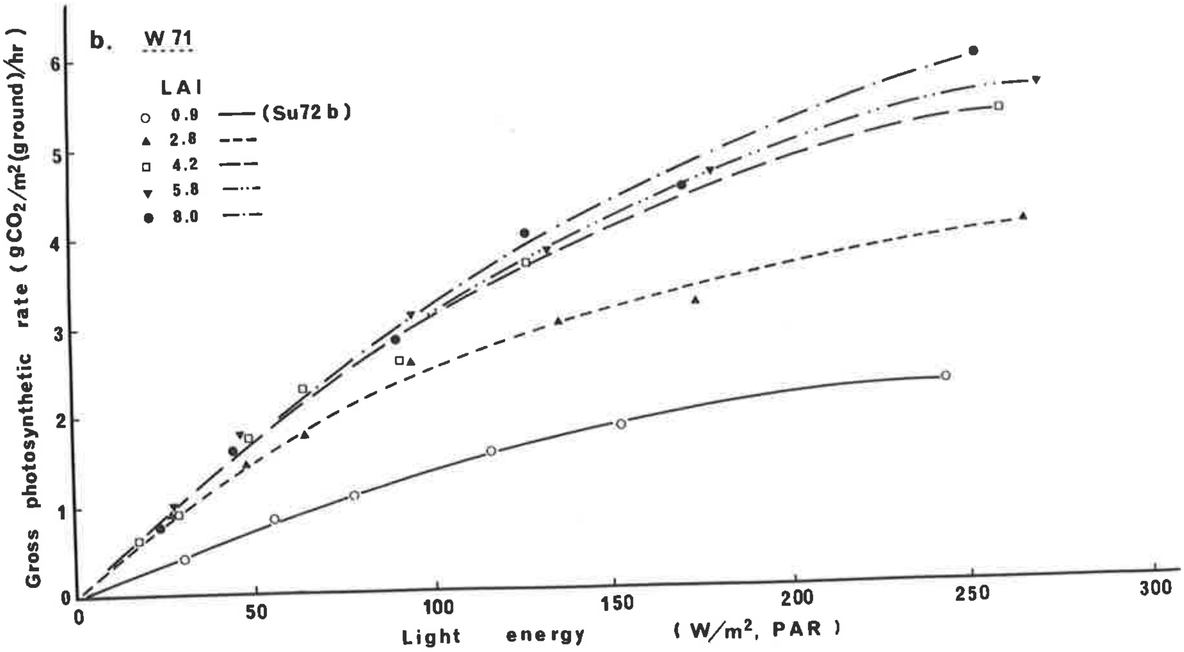
* Net $CO_2$ exchange rate was not measured under the quartz-iodine lamps in W71 when the plants were young.

Figure 27. Light-gross photosynthesis curve of communities with different values of leaf area index (LAI).

(a) Top: Autumn 72a

(b) Bottom: Winter 71


a.
A 72 a
LAI
○ 2.2
▲ 3.3
■ 6.3
□ 7.2
▼ 5.9
● 6.0
▽ ---
Gross photosynthetic rate ( $gCO_2/m^2$(ground)/hr )
0
1
2
3
4
5
6
7
0
50
100
150
200
250
300
Light energy
( $W/m^2$, PAR )


b.
W 71
LAI
○ 0.9 (Su72 b)
▲ 2.8
□ 4.2
▼ 5.8
● 8.0
Gross photosynthetic rate ( $gCO_2/m^2$(ground)/hr )
0
1
2
3
4
5
6
0
50
100
150
200
250
300
Light energy
( $W/m^2$, PAR )

rate of gross photosynthesis at low light flux was the same for different canopies once they attained an LAI of about 3. However, the rate at high light flux increased with the increase of LAI up to 8. The plants were growing rapidly at the time and this would contribute to the high gross photosynthetic rate at high light flux, as will be discussed later.

Net $CO_2$ exchange rates at 0, 50, 150, and 250 $W/m^2$ of PAR were read from the fitted curves of Fig. 26. These rates are plotted against LAI of the canopy concerned for each light flux in Fig. 28. Supplementary measurements to A72 and W71 are included to provide data for low LAI values.

It is clear from the figure that at 250 $W/m^2$ (PAR) the rate of net photosynthesis increases with increase of LAI up to about 4. Further increase of LAI resulted in little change in the rate of net photosynthesis. Net photosynthesis rate at 50 $W/m^2$ on the other hand, showed an optimum LAI of 3-4 at which the rate was maximal. Decrease in net photosynthetic rate with further increase of LAI was associated with increase in dark respiration rate with increase in LAI.

When the results of A72a and W71 are compared, it is apparent that plants grown under high daily light energy (A72a) had a higher rate of net photosynthesis at 250 $W/m^2$ than those grown under low daily light energy (W71). The difference was 0.5 - 0.6 $gCO_2/m^2$ (ground)/hr at LAI of above 3. The rate of net photosynthesis at 50 $W/m^2$ was about the same for both experiments for plants from different light conditions.

Net photosynthetic rate at 150 $W/m^2$ was intermediate in its relation with LAI between those at 50 and 250 $W/m^2$. The rate was slightly higher for plants grown at high light energy.

Figure 28. (Top)

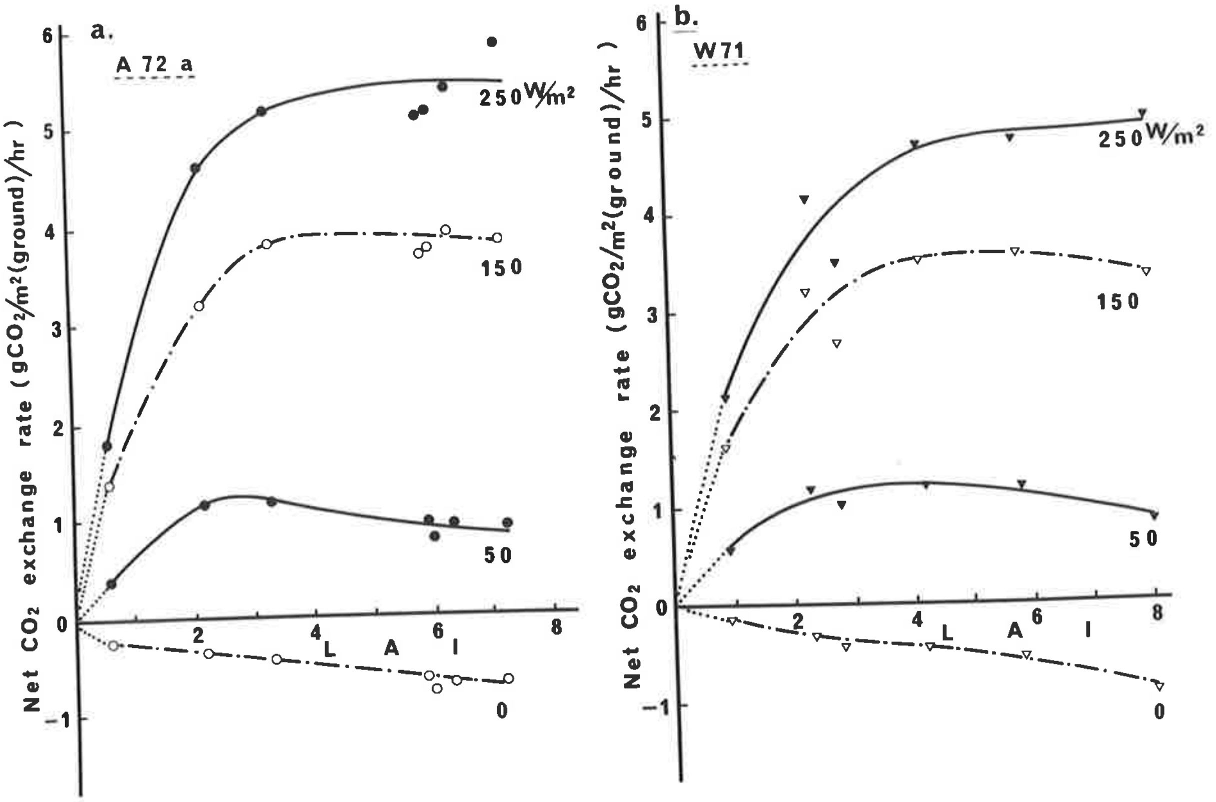
The relationship between net $CO_2$ exchange rate of communities and LAI at 4 levels of light energy ($W/m^2$, PAR).

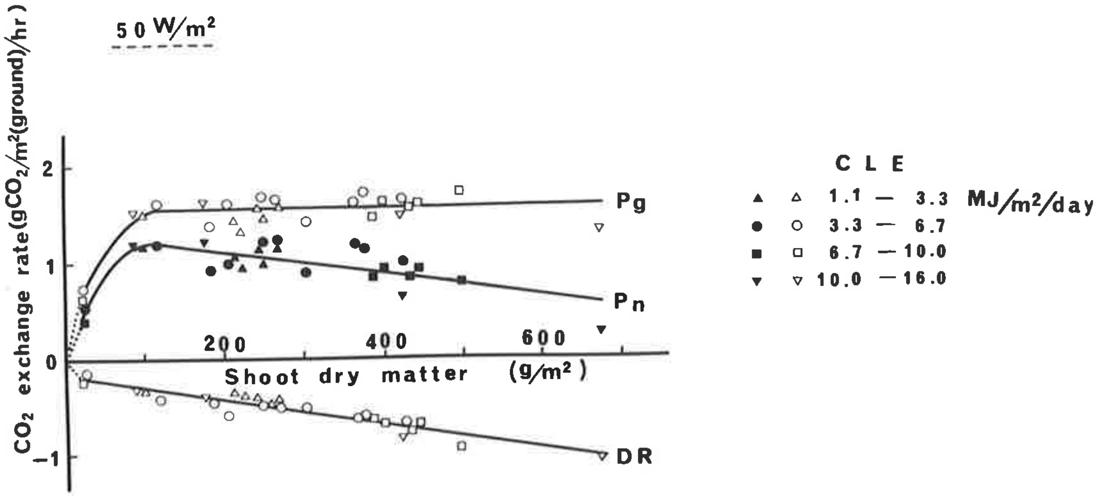
Curves are fitted by eye.

Figure 29. (Bottom)

Gross photosynthetic rate (Pg) and net photosynthetic rate (Pn) at 50 $W/m^2$ PAR, and dark respiration rate (DR) as a function of shoot dry matter for 4 ranges of current light energy (CLE).

Curves are fitted by eye.


a.
A 72 a
Net CO2 exchange rate (gCO2/m²(ground)/hr)
250 W/m²
150
50
0
L A I
-1
0
1
2
3
4
5
6
2
4
6
8
b.
W71
Net CO2 exchange rate (gCO2/m²(ground)/hr)
250 W/m²
150
50
0
L A I
2
4
6
8


50 W/m²
CO2 exchange rate (gCO2/m²(ground)/hr)
Pg
Pn
DR
Shoot dry matter (g/m²)
200
400
600
2
1
0
-1
C L E
▲ △ 1.1 — 3.3 MJ/m²/day
● ○ 3.3 — 6.7
■ □ 6.7 — 10.0
▼ ▽ 10.0 — 16.0

The rates of gross photosynthesis (Pg) and net photosynthesis (Pn) at 50 $W/m^2$ were read from all eye-fitted curves for each measurement. These rates as well as dark respiration rate (DR) are plotted against shoot dry matter in Fig. 29.

Net photosynthetic rate at 50 $W/m^2$ increased rapidly with increase of shoot dry matter up to about 100 $g/m^2$. Further increase of shoot dry matter resulted in decreased rate of net photosynthesis. This decrease is linear and the slope is about the same as that obtained when dark respiration rate is plotted against shoot dry matter. These parallel relationships resulted in the rate of gross photosynthesis at 50 $W/m^2$ being constant (1.55 $gCO_2/m^2/hr$) once shoot dry matter attained 100 $g/m^2$.

Four ranges of current light energy levels at which the plants were grown are designated on the graph to examine the effect of current light energy on the rates of photosynthesis at 50 $W/m^2$. No effect of current light energy on the rates of photosynthesis can be shown by analysis of variance.

The rates of net $CO_2$ exchange and gross photosynthesis at 250 $W/m^2$ were read for all measurements from fitted P/I curves. These points are plotted against LAI of the corresponding canopy in Fig. 30 in (a) for gross photosynthetic rate and in (b) for net photosynthetic rate.

The rate of gross photosynthesis increased with increase in LAI up to 4, and further increase in LAI resulted in only a slight further increase of the rate of gross photosynthesis.

The relation between net $CO_2$ exchange rate and LAI was similar to the relation between gross photosynthetic rate and LAI. There was apparently no increase of net $CO_2$ exchange rate with increase in LAI above 4.

<u>Figure 30.</u> (Top)

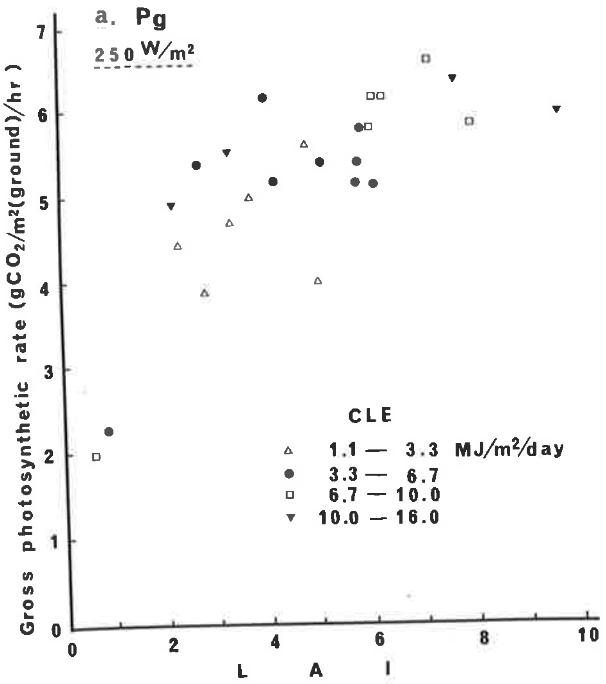
The relationship between photosynthetic rate at 250 W/m$^2$, PAR and leaf area index (LAI), for canopies grown under different levels of current light energy (CLE).

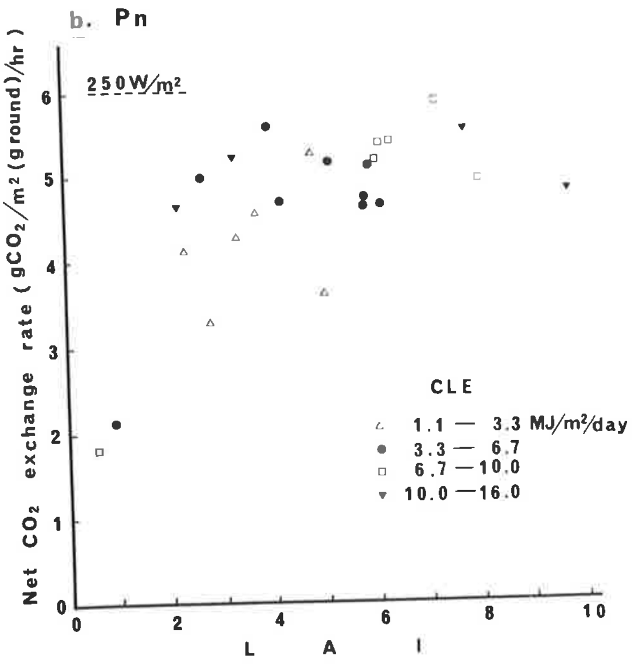
(a) Left: gross photosynthetic rate

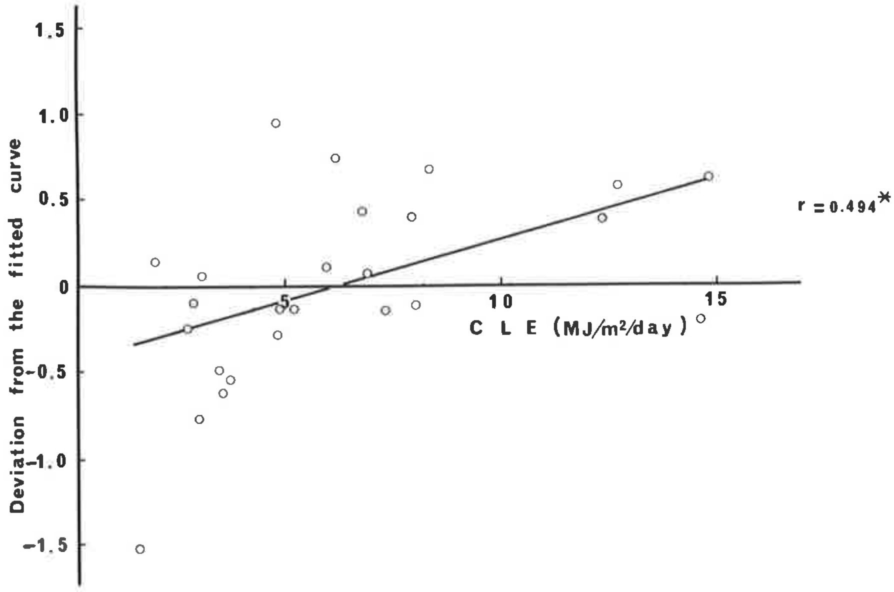
(b) Right: net photosynthetic rate

<u>Figure 31.</u> (Bottom)

The relationship between current light energy (CLE) and deviation from a hyperbola fitted to data of gross photosynthetic rate (Pg) and leaf area index (LAI) shown in Figure 30a.


a. Pg
250 W/m²
Gross photosynthetic rate (gCO₂/m²(ground)/hr)
0
1
2
3
4
5
6
7
L A I
0
2
4
6
8
10
CLE
△ 1.1 — 3.3 MJ/m²/day
● 3.3 — 6.7
□ 6.7 — 10.0
▼ 10.0 — 16.0


b. Pn
250 W/m²
Net CO₂ exchange rate (gCO₂/m²(ground)/hr)
0
1
2
3
4
5
6
L A I
0
2
4
6
8
10
CLE
△ 1.1 — 3.3 MJ/m²/day
● 3.3 — 6.7
□ 6.7 — 10.0
▼ 10.0 — 16.0


Deviation from the fitted curve
1.5
1.0
0.5
0
−0.5
−1.0
−1.5
5
10
15
C L E (MJ/m²/day)
r = 0.494*

Four ranges of current light energy were designated as in the previous figure. It may be seen that the plant canopies grown under the higher light energies always had high gross photosynthetic rate. To analyse this point in more detail a hyperbola was fitted by the least squares method to the gross photosynthetic rate - LAI relationship and the residual from the fitted curve was plotted against current light energy in Fig. 31. A significant correlation ($r = 0.494^*$) was found between the residual and CLE. Similarly, significant correlation ($r = 0.481^*$) was also found between the residual and CGR. However, there was no significant correlation ($r = -0.333^{N.S.}$) between the residual and SLA.

## 5.4.0. Results of the Temperature Experiments

### 5.4.1. Total Dry Matter and Crop Growth Rate

Total dry matter per square meter of ground for each temperature is plotted against days after planting for each experiment in Fig. 32.

Statistical analysis (Table 7) was conducted for only the 1970 data since the plants for different treatments were not harvested on the same day in 1972.

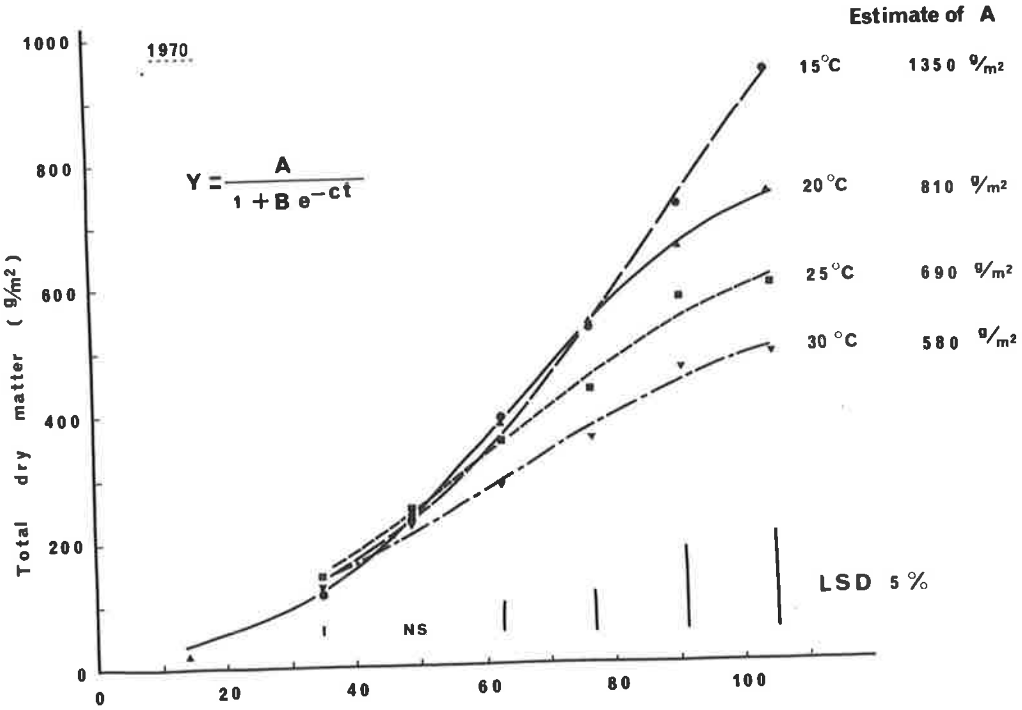
At day 35, total dry matter is significantly greater at 25°C than at 15°, 20° and 30°C. There is no significant difference between temperature treatments at day 49. At day 63, total dry matter is least at 30°C. Dry weight at day 105 is inversely related to temperature. The effect of temperature on increase in dry matter was similar in 1972 to that in 1970.

Figure 32. Change in total dry matter with time for communities grown at different temperatures.

Top: 1970 experiment

Bottom: 1972 experiment

Curves are drawn by fitting sigmoidal equations to the change in total dry matter with time for each temperature. Estimated values of maximum yield (A) are shown on the right side of each graph.


Estimate of A
1970
$Y = \frac{A}{1 + B e^{-ct}}$
Total dry matter ( g/m² )
1000
800
600
400
200
0
0
20
40
60
80
100
15°C
1350 g/m²
20°C
810 g/m²
25°C
690 g/m²
30 °C
580 g/m²
LSD 5 %
NS

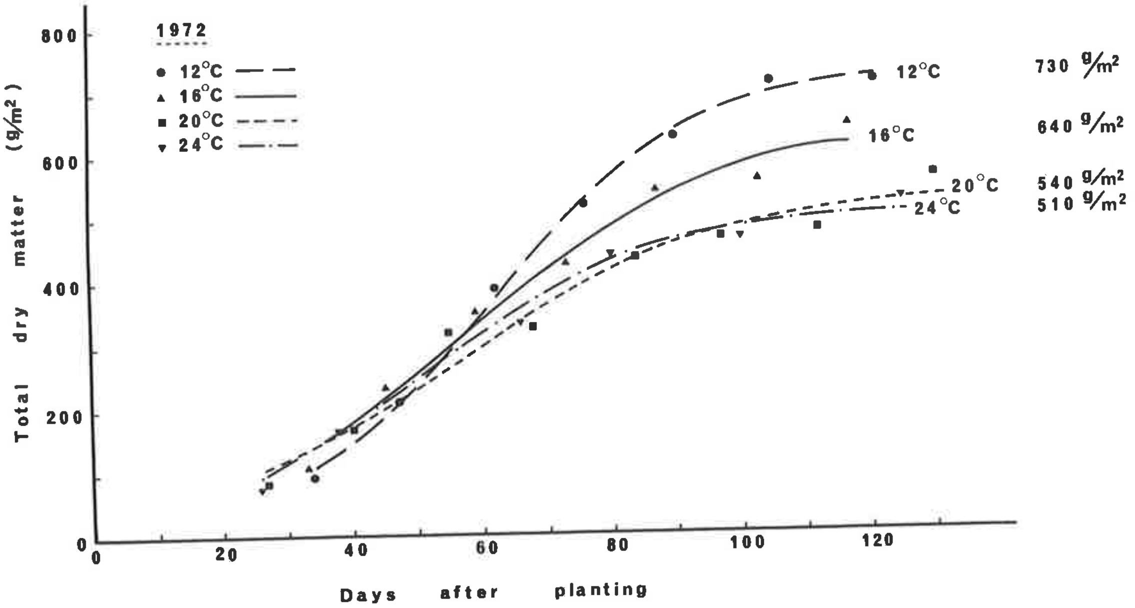

1972
● 12°C
▲ 16°C
■ 20°C
▼ 24°C
Total dry matter (g/m²)
800
600
400
200
0
0
20
40
60
80
100
120
Days after planting
12°C
730 g/m²
16°C
640 g/m²
20°C
540 g/m²
24°C
510 g/m²

Table 7. Analysis of variance of mean dry matter for each harvest in 1970 temperature experiment

| Days after planting | Mean dry matter (g/pot) | | | | F values | L.S.D. at 5% |
|---|---|---|---|---|---|---|
| | $15^oC$ | $20^oC$ | $25^oC$ | $30^oC$ | | |
| 35 | $2.64^a$ | $2.93^a$ | $3.39^b$ | $2.94^a$ | 5.54* | 0.41 |
| 49 | $5.38^a$ | $5.67^a$ | $5.80^a$ | $5.30^a$ | $1.67^{NS}$ | - |
| 63 | $9.08^a$ | $8.81^a$ | $8.19^a$ | $6.62^b$ | 8.75** | 1.15 |
| 77 | $12.36^a$ | $12.50^a$ | $10.05^b$ | $8.29^c$ | 17.48** | 1.49 |
| 91 | $16.85^a$ | $15.24^{a,b}$ | $13.36^{b,c}$ | $10.84^c$ | 8.93** | 3.07 |
| 105 | $21.69^a$ | $17.16^b$ | $13.88^{b,c}$ | $11.34^c$ | 14.67** | 3.60 |

The general growth pattern follows a logistic curve. A sigmoid curve of the form

$$TDM = \frac{A}{1 + Be^{-CT}}$$

where TDM : total dry matter ($g/m^2$)

T : days after planting

A, B and C : constants

was fitted to the dry weight - time data for each temperature treatment in each year. A generally good fit was obtained except at the early stages where the fitted curves overestimate dry matter in some cases. From the three constants in the equation, parameters characterizing each growth curve were obtained (Table 8).

Within each year the following points are apparent from Table 8. (1) Maximum yield is inversely related to temperature. In 1970 maximum yield was more than doubled by decreasing the temperature from 30° to 15°C, while in 1972 the yield at 12°C was 1.5 times that at 24°C. (2) Maximum crop growth rate is also inversely related to

Table 8. Calculated growth attributes from fitted logistic curves in the temperature experiments

| Year | Temperature | (1) Maximum yield ($g/m^2$) | (2) Max CGR ($g/m^2/day$) | (3) Dry wt at Max CGR ($g/m^2$) | (4) Days after planting at Max CGR |
|---|---|---|---|---|---|
| 1970 | 15°C | 1354 | 14.3 | 677 | 87 |
| | 20 | 805 | 11.6 | 403 | 65 |
| | 25 | 694 | 8.0 | 347 | 63 |
| | 30 | 578 | 6.1 | 289 | 63 |
| 1972 | 12°C | 731 | 12.0 | 365 | 61 |
| | 16 | 638 | 8.6 | 319 | 58 |
| | 20 | 539 | 6.5 | 270 | 55 |
| | 24 | 513 | 7.5 | 256 | 51 |

$$Y = \frac{A}{1 + Be^{-CT}}$$

(1) $A$

(3) $\frac{A}{2}$

(2) $\frac{AC}{4}$

(4) $\frac{1}{C}\log_e B$

temperature. (3) Plants grown at low temperature took longer to reach the point of inflection. Daily solar energy increased with time in these experiments (see Fig. 13) and delay in occurrence of inflection favoured a high maximum crop growth rate. However, this does not account for all of the difference in maximum crop growth rate between different growth temperatures, as the increase in daily solar energy was not large. There was only a two day difference in the date of occurrence of maximum crop growth rate between 20° and 30°C in 1970, although the actual maximum crop growth rate differed by a factor of about 2.

Comparing the results for the two years in Table 8 and in Fig. 32, it is obvious that plants grew much better in 1970 than in 1972. Maximum yield in 1970 was twice that in 1972 at low temperatures; the difference was smaller at high temperatures, one reason for this difference being differences in growth periods which may be seen by comparing days after planting to maximum crop growth rate (Table 8, column 4). Maximum crop growth rate was also higher in 1970 although dry matter production up to day 65 was about the same in the two years. Reduced daily light energy as a result of painting the glasshouses in the middle of the experiment in 1972 may be a reason for this early occurrence of maximum yield. Another reason may be a slight nutrient deficiency inducing a low photosynthetic rate; also SLA was relatively large in 1972 (see Fig. 17).

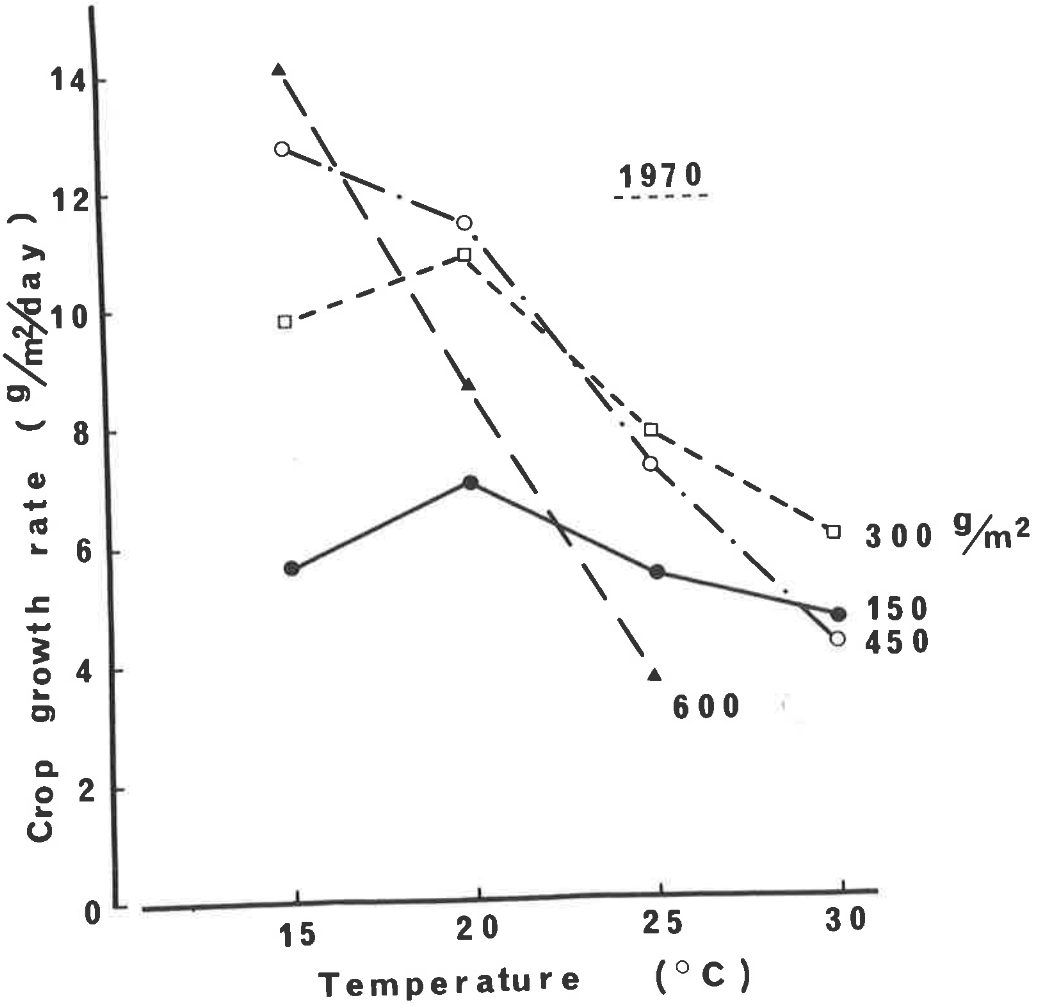
Crop growth rate was calculated from each fitted sigmoid curve by differentiating the equation with respect to time:

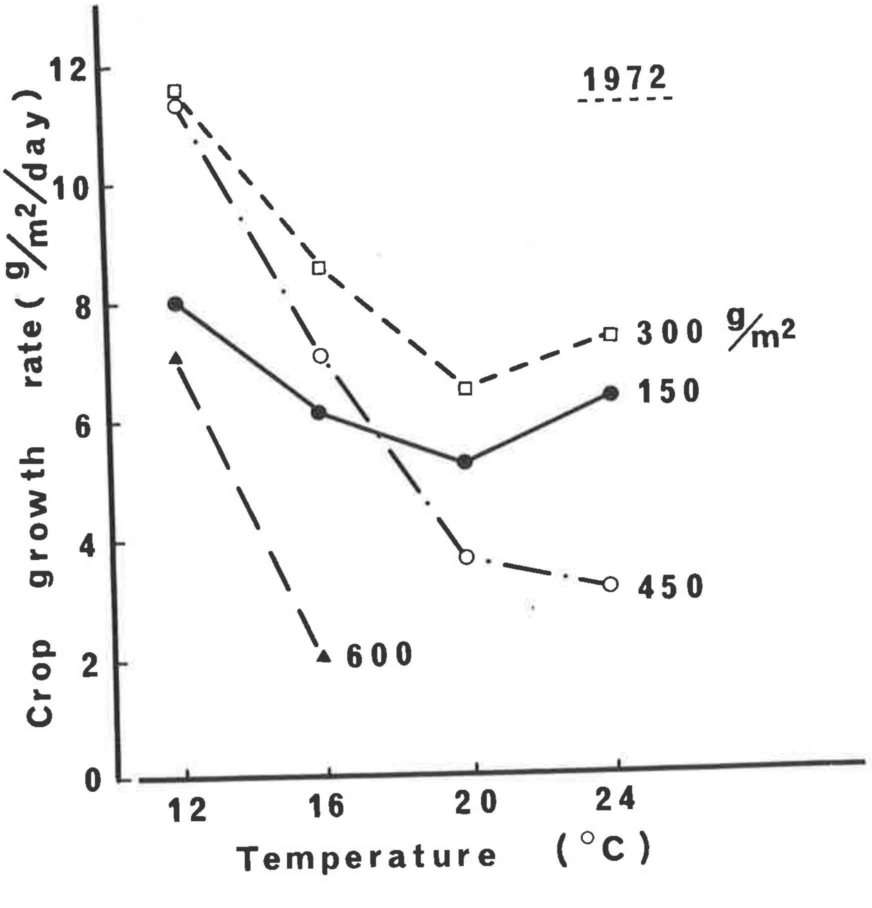
$$\frac{d(\mathrm{TDM})}{dt} = \frac{C}{A}\left(\mathrm{TDM} - \frac{A}{2}\right)^2 + \frac{AC}{4}$$

Crop growth rates at total dry matter of 150, 300, 450 and 600 g/m$^2$ were calculated and this is plotted against growth temperature in Fig. 33. Crop growth rate was less dependent on temperature at a total dry matter of 150 g/m$^2$ than at 450 or 600 g/m$^2$ where the rate decreased very rapidly with increase in temperature. Plants grown at different temperatures reached these specified levels of plant dry matter at different dates, and therefore under different light conditions (see Fig. 32 and Fig. 13). However, the difference in light conditions would be small since there was only 10 days difference between treatments to reach 150 or 300 g/m$^2$. Furthermore, as plants grown at high temperatures reached high dry matter considerably later than those at low temperatures, the light conditions would therefore be

**Figure 33.** The relationship between growth temperature and crop growth rate calculated from the fitted sigmoidal curves for total dry matter levels of 150, 300, 450 and 600 g/m$^2$.

| | |
|---|---|
| Top: | 1970 experiment |
| Bottom: | 1972 experiment |


1970
Crop growth rate ( g/m2/day )
0
2
4
6
8
10
12
14
15
20
25
30
Temperature (°C)
300 g/m2
150
450
600


1972
Crop growth rate ( g/m2/day )
0
2
4
6
8
10
12
12
16
20
24
Temperature (°C)
300 g/m2
150
450
600

better for high temperature plants than for low temperature plants. In spite of this, plants grown at high temperatures showed a low crop growth rate when the plant dry matter was large.

### 5.4.2. LAI and Crop Growth Rate

Leaf area index is plotted against time and curves are fitted by eye in Fig. 34. The trend of increase in LAI with time is different from that of total dry matter. In 1970, at day 35 LAI was greater at 25°C than at 15°, 20° and 30°C. At days 63-91, LAI was greatest at 20° - 25°C. During the last half of the experiment, the rate of increase of LAI declined steadily with time at 25° and 30°C, decreased slightly at 20°C, and increased with time at 15°C. In 1972 LAI increased rapidly at first at all temperatures to a plateau of about 6 at day 55. Thereafter 20° and 24°C showed little change but 12° and 16°C increased again after about day 70.

Relationships between LAI and TDM are shown in Fig. 35. In 1970 LAI increased approximately linearly with increase of dry matter except where TDM > 200 $g/m^2$ and at 30°C. LAI per unit TDM was much higher at 20° and 25°C than at 15°C. At 30°C the relation between LAI and TDM was curvilinear. Plants at 12°C in 1972 also showed a low LAI in relation to TDM. However, there was not a consistent relationship between LAI and TDM for plants grown at and above 16°C.

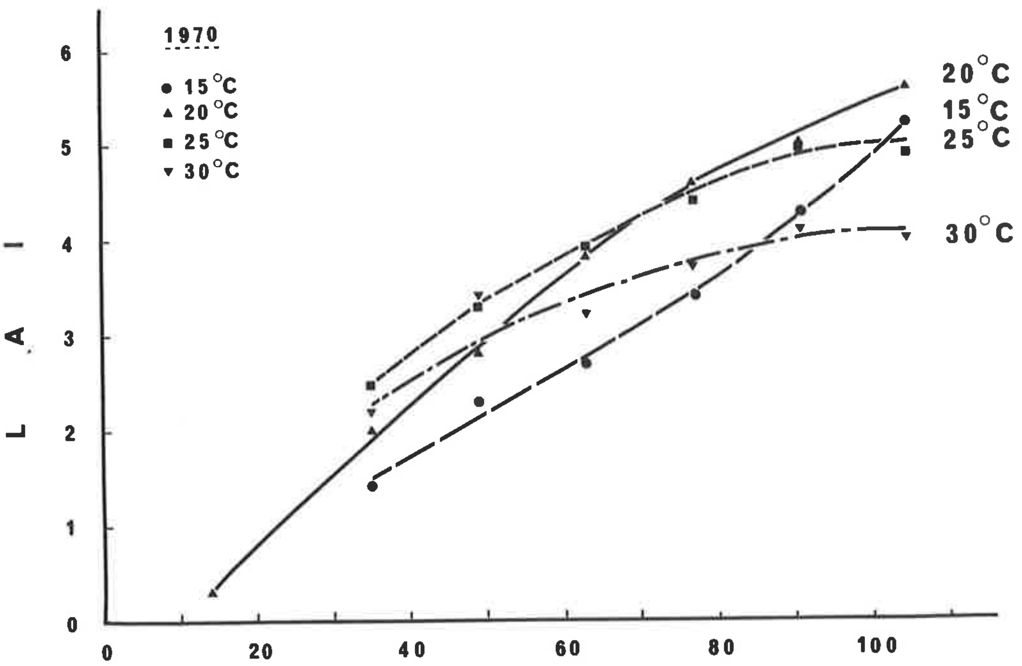
Crop growth rate (CGR) in 1970 is plotted against the corresponding estimate of LAI from the fitted curve of LAI with time at each harvest (Fig. 36). CGR was optimally related to LAI at each temperature, the maximum growth rate being inversely related to temperature, and the optimal LAI of about 4 being scarcely affected by temperature. CGR decreased rapidly with increase in LAI beyond the optimum. A similar but much less clear trend is evident in 1972.

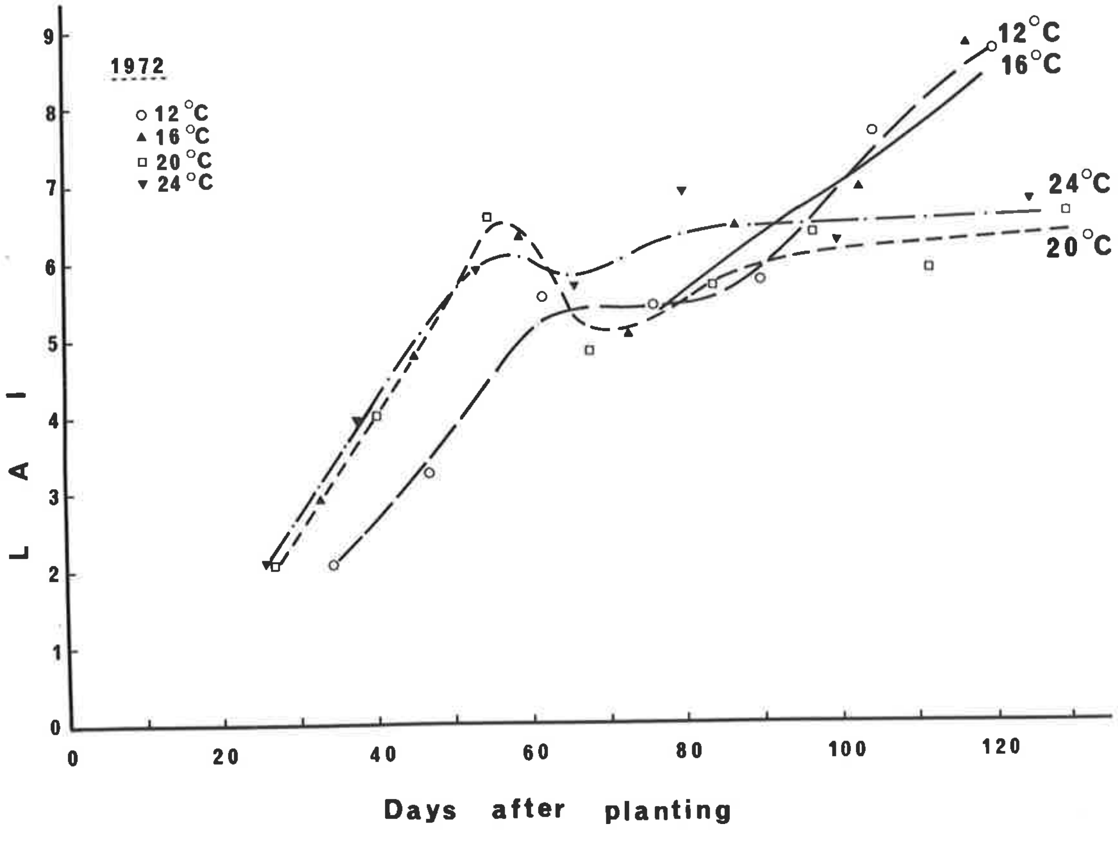
Figure 34. Change in values of leaf area index (LAI) with time for communities grown at different temperatures.

Top: 1970 experiment

Bottom: 1972 experiment

Curves are fitted by eye.


1970
● 15°C
▲ 20°C
■ 25°C
▼ 30°C
L A I
0
1
2
3
4
5
6
0
20
40
60
80
100
20°C
15°C
25°C
30°C

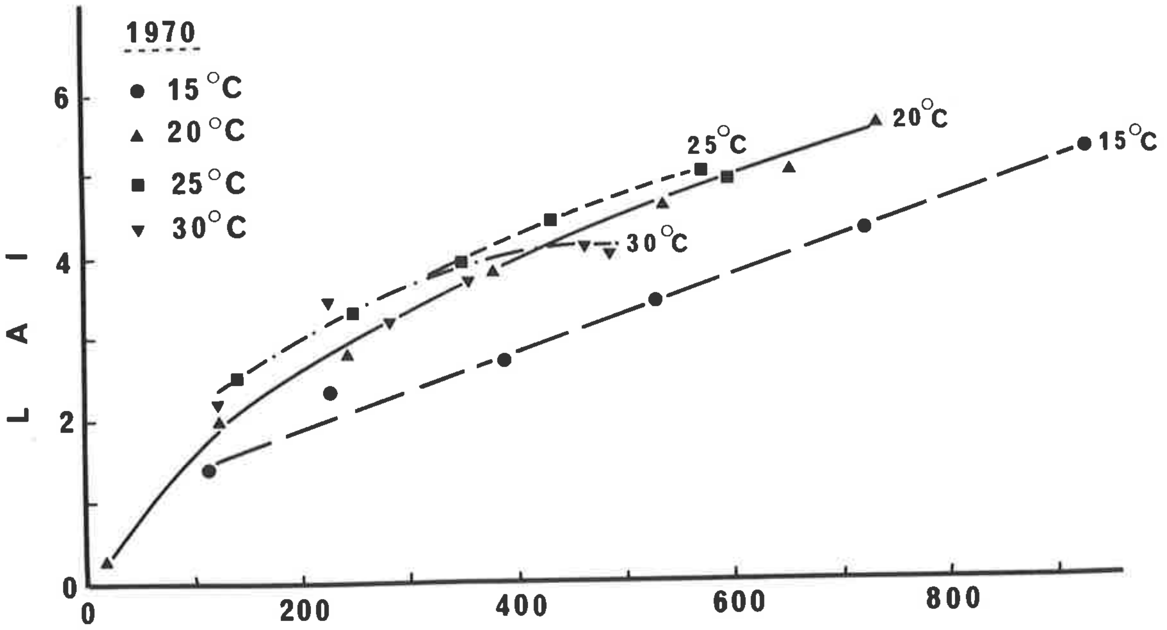

1972
○ 12°C
▲ 16°C
□ 20°C
▼ 24°C
L A I
0
1
2
3
4
5
6
7
8
9
0
20
40
60
80
100
120
Days after planting
12°C
16°C
24°C
20°C

<u>Figure 35.</u> The relationship between leaf area index (LAI) and total dry matter for communities grown at different temperatures.

Top: 1970 experiment

Bottom: 1972 experiment

Curves are fitted by eye.


1970
● 15 °C
▲ 20 °C
■ 25 °C
▼ 30 °C
L A I
0
2
4
6
0
200
400
600
800
25 °C
20 °C
15 °C
30 °C

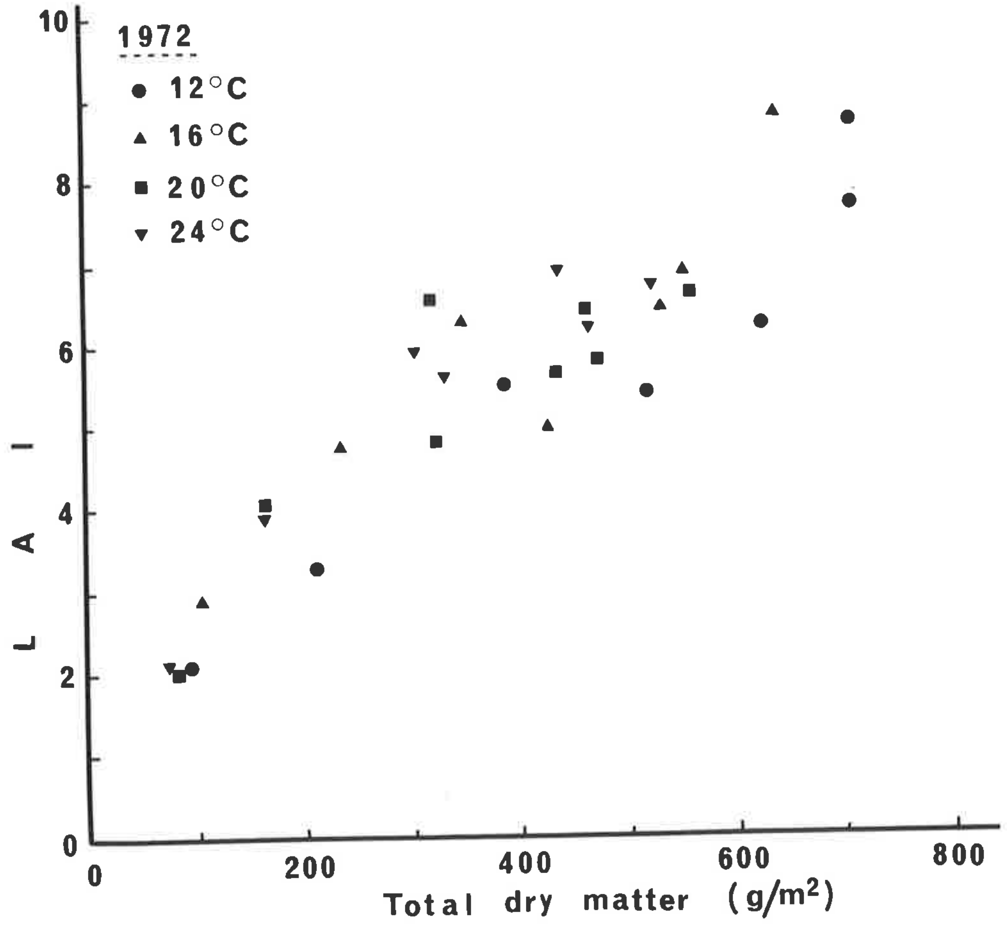
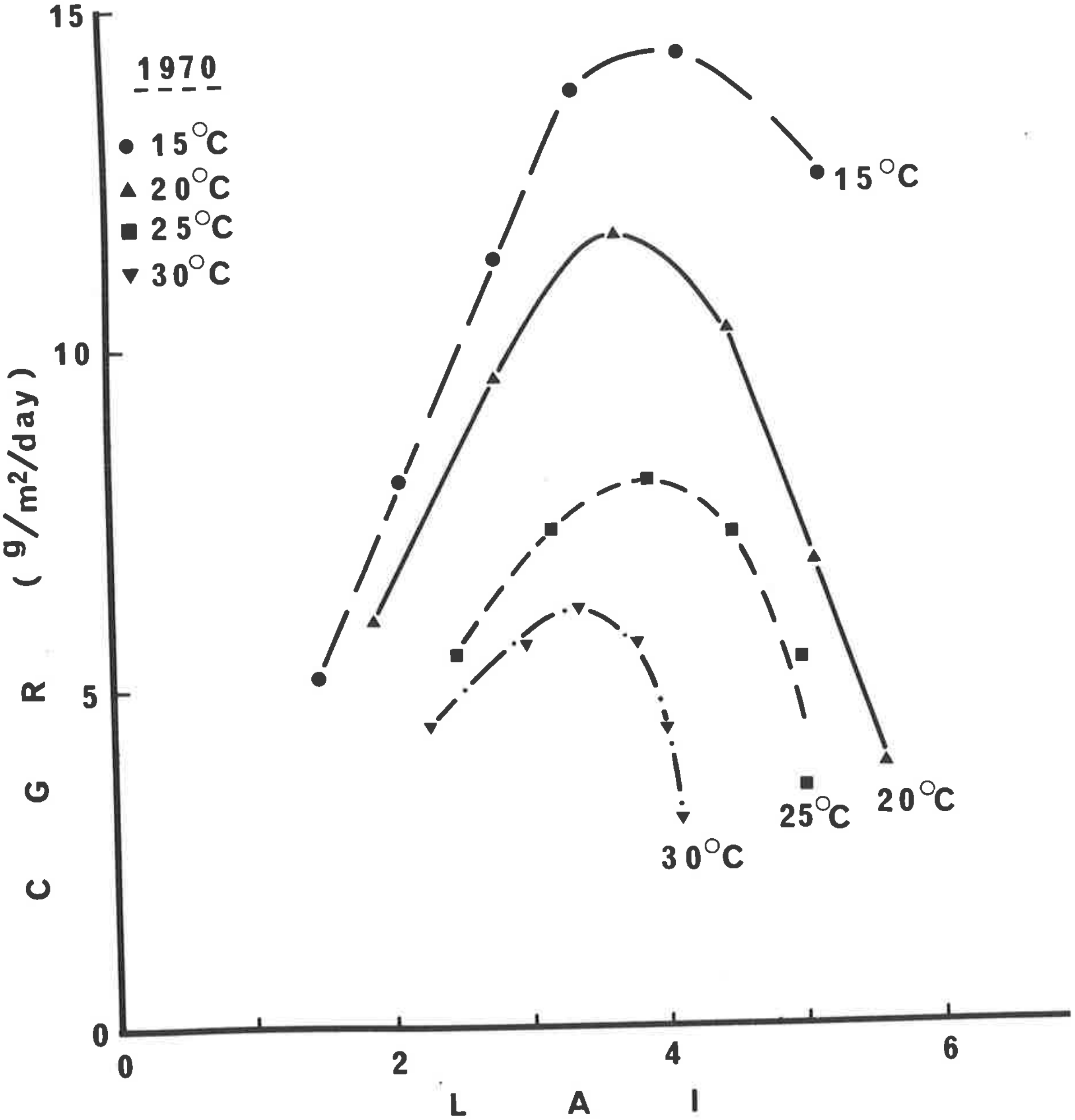

1972
● 12 °C
▲ 16 °C
■ 20 °C
▼ 24 °C
L A I
0
2
4
6
8
10
0
200
400
600
800
Total dry matter (g/m²)

**Figure 36.** The relationship between crop growth rate (CGR) and corresponding leaf area index (LAI) for communities grown at 4 different temperatures in 1970. Equal LAI's did not occur at the same date for different temperatures.


15
10
5
0
1970
● 15 °C
▲ 20 °C
■ 25 °C
▼ 30 °C
C G R ( g/m²/day )
15 °C
20 °C
25°C
30 °C
0
2
4
6
L A I

Where LAI was less than 5 CGR was highest at 12°C. Optimum LAI was about 5.

Plants growing at different temperatures reached the same LAI at different dates (see Fig. 34) and hence under different light conditions. For example, in 1970 an LAI of 3.5 was reached on approximately 80, 60, 55 and 75 days from sowing at 15°, 20°, 25° and 30°C respectively. The corresponding average daily solar energies were 10.5, 8.0, 7.6, 9.7 $MJ/m^2$/day, respectively. Therefore it may be expected that differences in CGR at LAI of 3.5 between 15° and 20°C and 15° and 25°C would be smaller if corrected for differences in light energy.

### 5.4.3. Morphology

Morphological aspects relating mainly to the development of leaf area were examined at different temperatures in more detail in 1970 than in 1972 and the results obtained in 1970 only are shown here.

#### (a) Percentage Dry Matter

The percentage of stem and petiole and that of dead leaf lamina increased with increase in dry matter but the percentage of green leaf lamina and that of root decreased (Fig. 37).

The percentage of stem and petiole was not affected by temperature. Plants at lower temperature had a high proportion of root dry matter, but there is an obvious trend toward a common value above about 600 $g/m^2$. The root percentage at high dry matter was about 20% in 1970 while it was 10% in 1972. This difference may be due to the level of soil moisture being lower in 1970 than in 1972.

The effect of temperature on green leaf lamina percentage in 1970 is not clear. 15°C plants showed slightly less green leaf lamina than the others. 30°C plants showed slightly more dead leaf

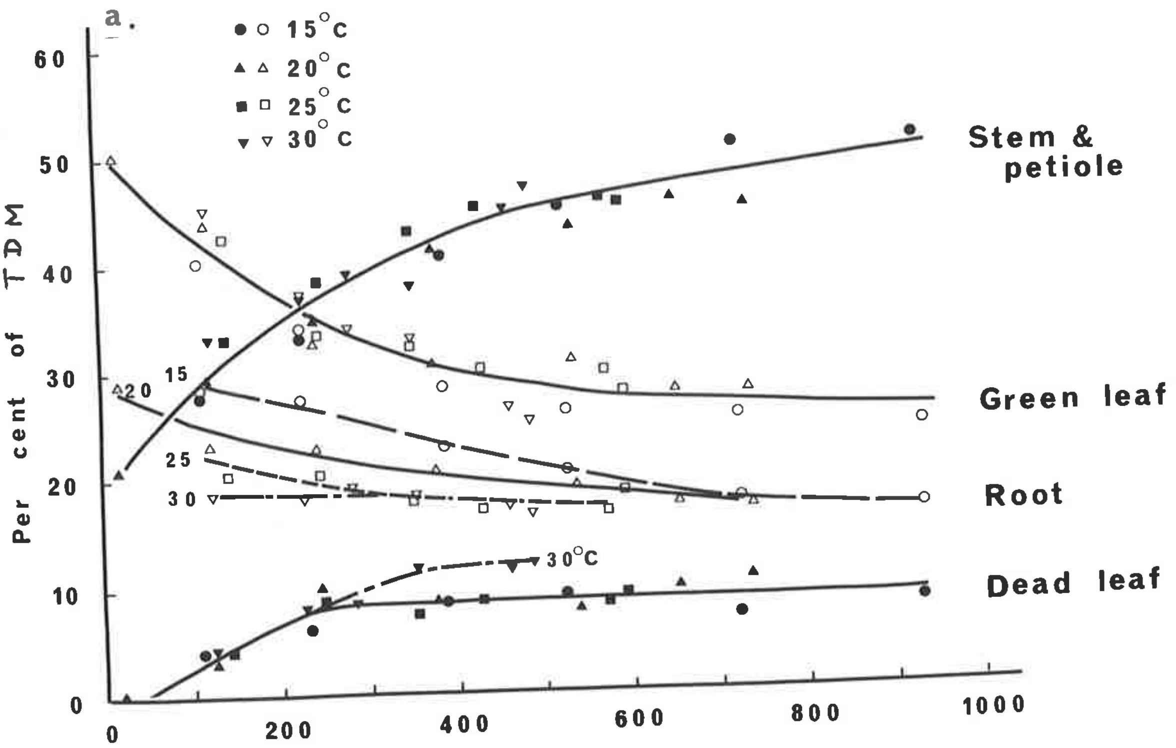
**Figure 37.** Plant part as a percentage of total dry matter (TDM) plotted as a function of total dry matter for communities grown at 4 different temperatures in 1970.

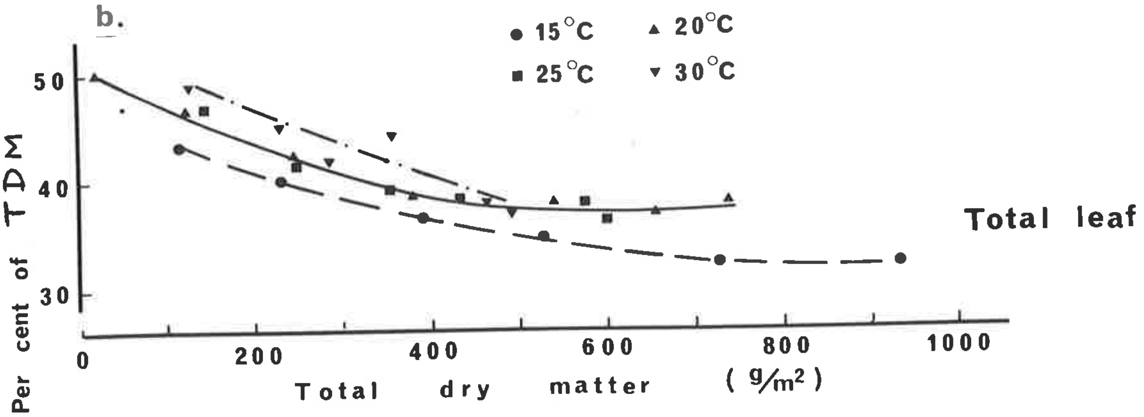
(a) Top: stem and petiole, green leaf lamina, root and dead leaf lamina

(b) Bottom: total leaf lamina

Curves are fitted by eye.

1970


a.
● ○ 15°C
▲ △ 20°C
■ □ 25°C
▼ ▽ 30°C
Per cent of TDM
60
50
40
30
20
10
0
Stem & petiole
Green leaf
Root
Dead leaf
15
20
25
30
30°C
0
200
400
600
800
1000


b.
● 15°C
▲ 20°C
■ 25°C
▼ 30°C
Per cent of TDM
50
40
30
Total leaf
0
200
400
600
800
1000
Total dry matter (g/m²)

lamina than the others and when total leaf lamina percentage is calculated as a sum of green leaf lamina and dead leaf lamina this was directly related to temperature as shown in Fig. 37b.

### (b) SLA

SLA in 1970 is plotted against days after planting for each temperature (Fig. 38). SLA decreased at each temperature until about day 80 after which it remained roughly constant, the value being directly related to temperature. SLA was much higher in 1972 than in 1970. The difference in light conditions between the two years was not probably great enough to account for the difference in SLA and possible nutrient deficiency and ample watering in 1972 may be involved as causal factors.

### (c) Growth of Laterals

The accumulated number of laterals and the pattern of their senescence are shown in Fig. 39. Laterals appeared earlier on plants at high temperature but ceased to appear after day 42. Plants at 15°C, on the other hand, increased lateral number until day 56 when each plant had an average of 2.1. Laterals contributed 21, 6, 5 and 14% to the total shoot dry weight at 15°, 20°, 25° and 30°C respectively, at day 63 when their number was about maximal: contribution to LAI was about the same percentage.

### (d) Leaf Appearance and Senescence

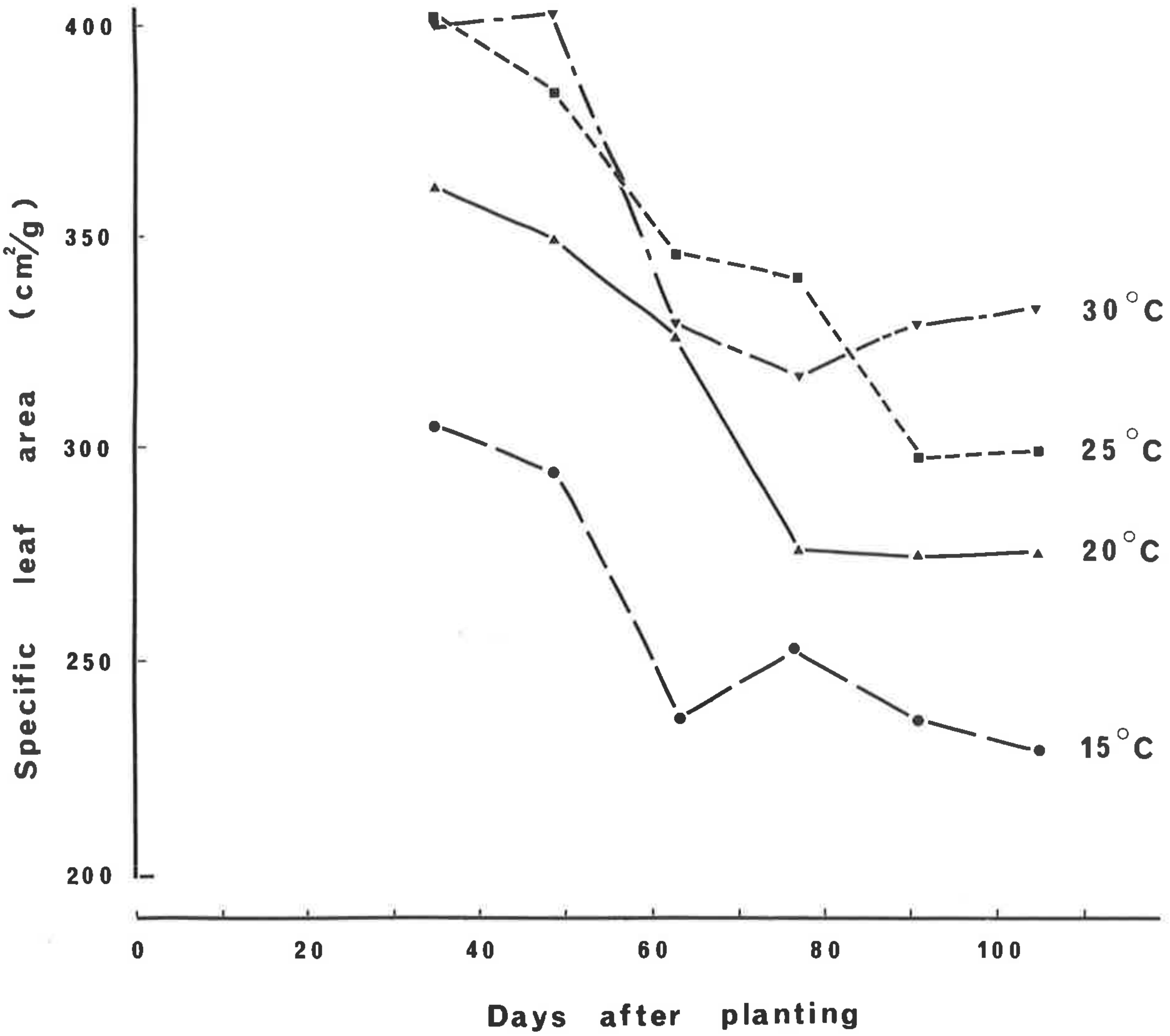
Accumulated number of leaves, leaf appearance and leaf senescence on a main stem is plotted against time in Fig. 40. For each temperature the rates of leaf appearance and senescence were almost constant throughout the experiment and were directly related to temperature. Linear regression coefficient for each temperature was calculated for the period over which no death of plants occurred.

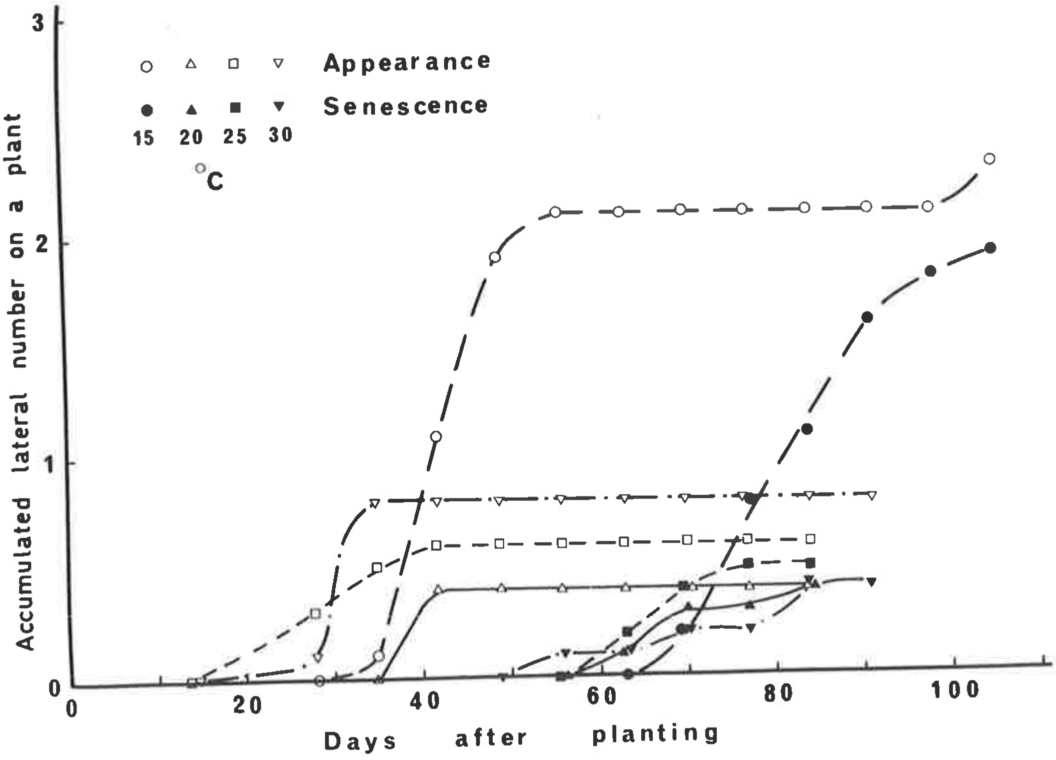
Figure 38. (Top)

Change of specific leaf area (SLA) with time for communities grown at 4 different temperatures in 1970.

Figure 39. (Bottom)

Change in average numbers of total accumulated laterals and of senescent laterals per plant for communities grown at 4 different temperatures in 1970.


Specific leaf area (cm²/g)
400
350
300
250
200
0
20
40
60
80
100
Days after planting
30 °C
25 °C
20 °C
15 °C

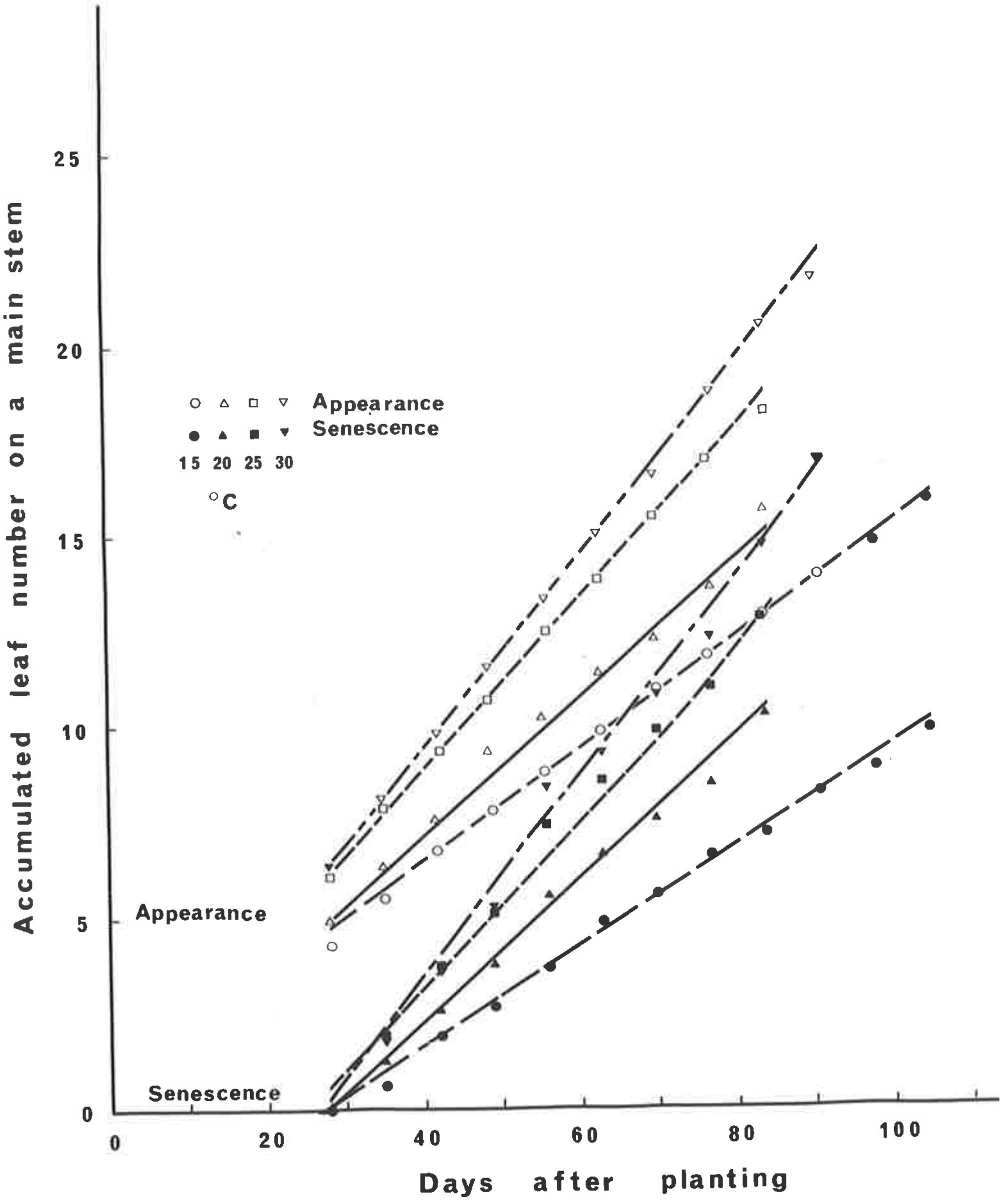

Accumulated lateral number on a plant
3
2
1
0
○ △ □ ▽ Appearance
● ▲ ■ ▼ Senescence
15 20 25 30
°C
0
20
40
60
80
100
Days after planting

<u>Figure 40.</u> (Top)

Change in average numbers of total accumulated leaves (total green and senescent) and of senescent leaves on a main stem with time for communities grown at 4 different temperatures in 1970. Regression equations are shown in Table 8.

<u>Figure 41.</u> (Bottom)

Change in average numbers of total accumulated leaves (total green and senescent) and of senescent leaves on a plant with time for communities grown at 4 different temperatures in 1970.


Accumulated leaf number on a main stem
25
20
15
10
5
0
○ △ □ ▽ Appearance
● ▲ ■ ▼ Senescence
15 20 25 30
°C
Appearance
Senescence
0
20
40
60
80
100
Days after planting

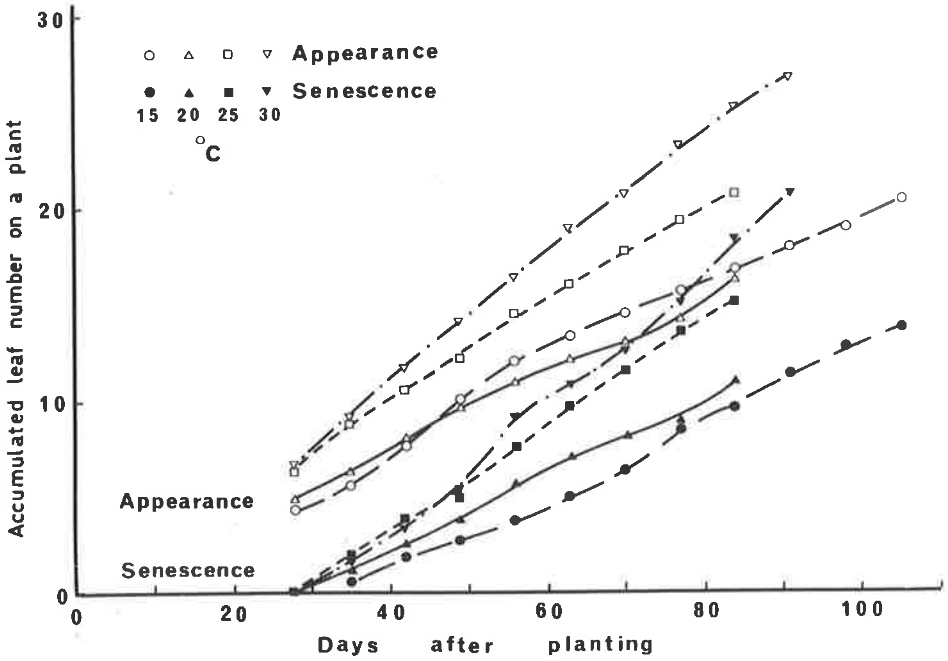

Accumulated leaf number on a plant
30
20
10
0
○ △ □ ▽ Appearance
● ▲ ■ ▼ Senescence
15 20 25 30
°C
Appearance
Senescence
0
20
40
60
80
100
Days after planting

Table 9 shows the rate of leaf appearance to range from 6.7 days/leaf at 15°C to 4.0 days at 30°C. The rate of leaf senescence ranged from 7.7 days/leaf at 15°C to 3.8 days at 30°C.

Table 9. Rates of leaf appearance and senescence at 4 temperatures

(1) Leaf appearance ($x$ : days after planting; $y$ : accumulated number of leaves)

| | | |
|---|---|---|
| 15°C | $y = 0.37 + 0.149\,x$ | (6.7 days/leaf) |
| 20°C | $y = -0.02 + 0.181\,x$ | (5.5 days/leaf) |
| 25°C | $y = 0.32 + 0.214\,x$ | (4.7 days/leaf) |
| 30°C | $y = -0.58 + 0.247\,x$ | (4.0 days/leaf) |

(2) Leaf senescence ($x$ : days after planting; $y$ : accumulated number of dead leaves)

| | | |
|---|---|---|
| 15°C | $y = -3.62 + 0.130\,x$ | (7.7 days/leaf) |
| 20°C | $y = -4.91 + 0.180\,x$ | (5.6 days/leaf) |
| 25°C | $y = -6.01 + 0.229\,x$ | (4.4 days/leaf) |
| 30°C | $y = -7.25 + 0.261\,x$ | (3.8 days/leaf) |

(3) Longevity of a leaf ($y$ : accumulated number of leaves ($y$th leaf); $w$ : longevity of a leaf (days))

| | |
|---|---|
| 15°C | $w = 30.3 + 0.98\,y$ |
| 20°C | $w = 27.2 + 0.03\,y$ |
| 25°C | $w = 27.7 - 0.31\,y$ |
| 30°C | $w = 25.4 - 0.22\,y$ |

(4) Current green leaf number ($x$ : days after planting; $z$ : number of leaves)

| | |
|---|---|
| 15°C | $z = 3.99 + 0.019\,x$ |
| 20°C | $z = 4.89 + 0.001\,x$ |
| 25°C | $z = 6.33 - 0.015\,x$ |
| 30°C | $z = 6.67 - 0.014\,x$ |

The longevity of a leaf was calculated from the regressions of leaf appearance and leaf senescence. Longevity was inversely related to temperature, the difference between temperature increasing with leaf number on the main stem.

The number of current green leaves calculated from the regressions of leaf appearance and leaf senescence with time increased with time at 15°C, was constant at 20°C, and decreased with time at 25° and 30°C. The increase in green leaves with time at 15°C was such that plants at 15°C had the largest number of green leaves at the late stages of the growth in spite of the lowest number at the temperature when plants were young.

Both the accumulated total leaf number and the accumulated total number of dead leaves showed similar trends with time for the plant and for the main stem except that plants at 15°C had more leaves appearing than those at 20°C during the later parts of the experiment, due to development of laterals (Fig. 41). This resulted in an increased number of current green leaves per unit ground area during the same period (Fig. 42).

Up to about day 80 the number of green leaves per unit area was higher at 30°C than at 20°C. The number of green leaves decreased during the late stages of growth at all temperatures due to death of laterals and plants.

### (e) Leaf Size

Average leaf size calculated from LAI and the number of green leaves per unit ground area (Fig. 43) was maximal at 20°C.

### 5.4.4. Dark Respiration

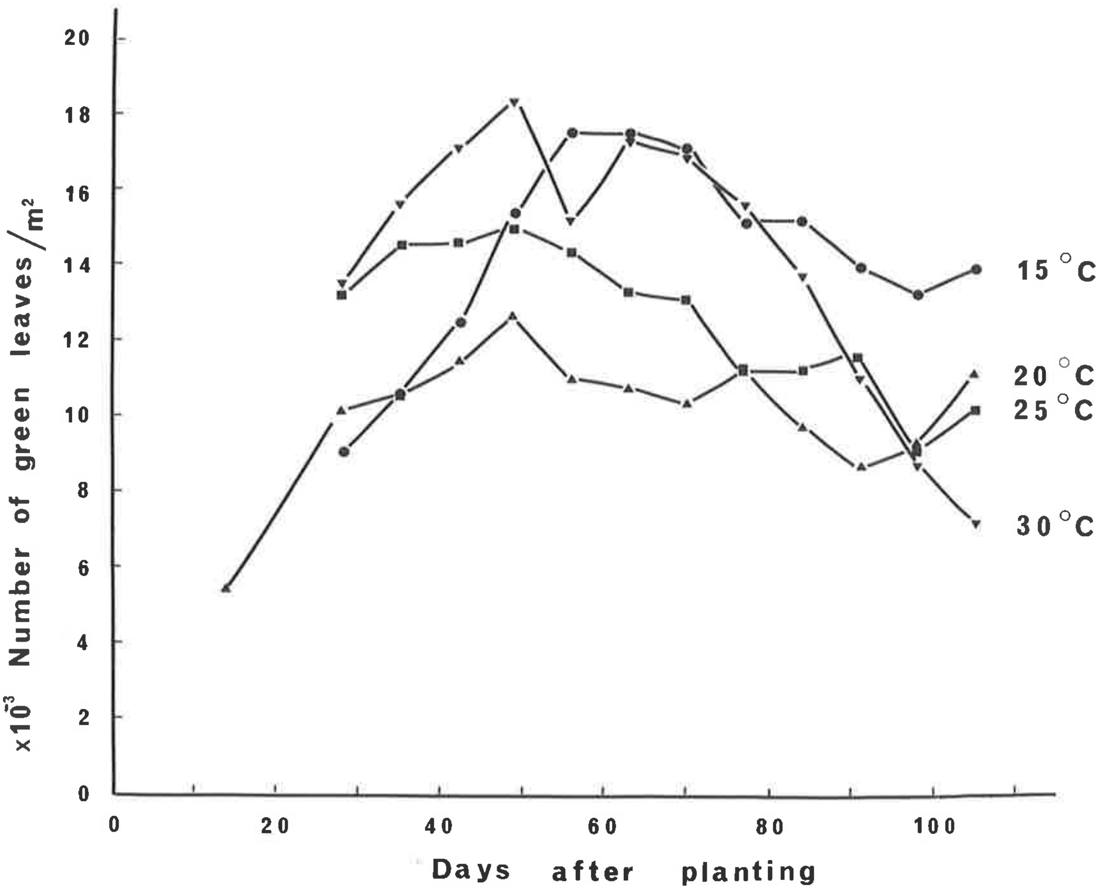
In 1972 the dark respiration rates of communities were measured after photosynthesis at 5 temperatures between 9° and 29°C. Measurements were taken at least 20 minutes after each new temperature was attained. Air temperature and leaf temperature were similar during darkness; the former is used to indicate plant temperature.

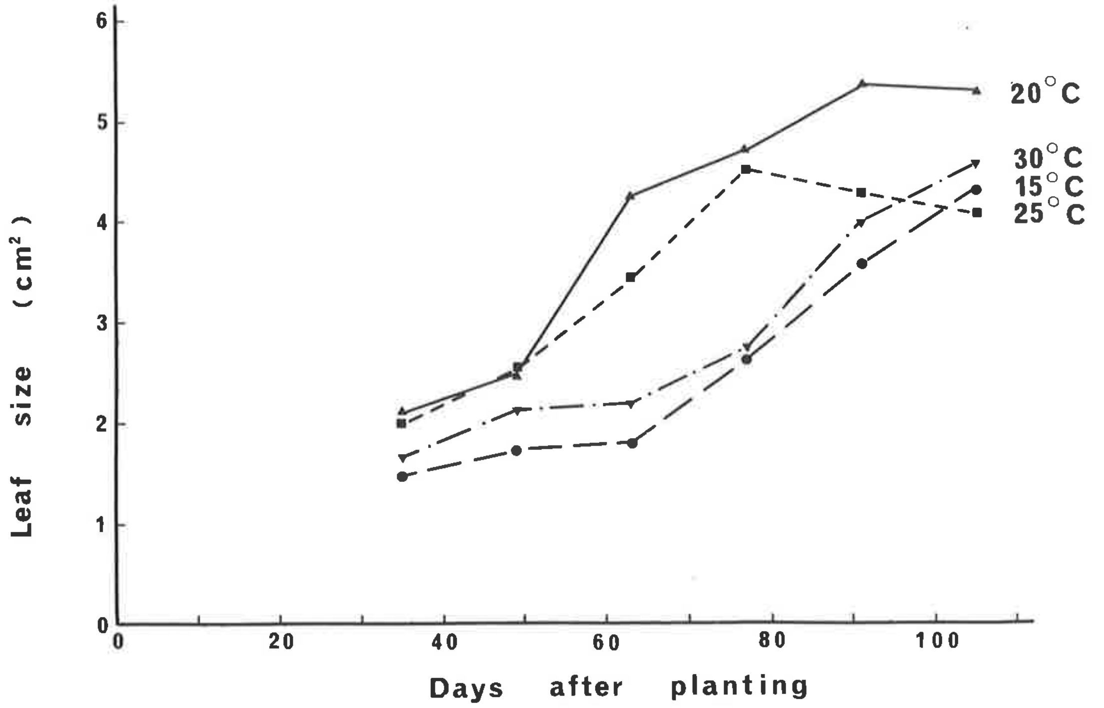
<u>Figure 42.</u> (Top)

Change in number of existing green leaves per $m^2$ of ground with time for communities grown at 4 different temperatures in 1970.

<u>Figure 43.</u> (Bottom)

Change in average leaf size with time for communities grown at 4 different temperatures in 1970.


x10$^{3}$ Number of green leaves/m$^{2}$
0
2
4
6
8
10
12
14
16
18
20
0
20
40
60
80
100
Days after planting
15 °C
20 °C
25 °C
30 °C


Leaf size (cm$^{2}$)
0
1
2
3
4
5
6
0
20
40
60
80
100
Days after planting
20°C
30°C
15°C
25°C

The drift in dark respiration rate between 1 and 4 hours of darkness was very small. No drift could be detected with a young plant community and was at most 10% for older plants. In a preliminary cabinet experiment dark respiration fluctuated ± 7% from the initial value over an 8 hour period. In the following calculations the rate of dark respiration is assumed to be constant with time.

### (a) Dark Respiration Rates at Growth Temperature

Dark respiration rate measured at each growth temperature at different times is plotted against the corresponding shoot dry matter for that temperature in Fig. 44. The relationship between dark respiration and shoot dry matter is linear and slopes of the regression lines are significantly different between the temperature treatments (F = 3.35* with d.f. of 3 and 21). Dark respiration rate increased with increase in SDM more rapidly at 24°C than at 12°C, but 16°, 20° and 24°C did not differ significantly.

The analysis given by Seale (1971) to test the significance of displacement of regression lines when the slopes are significantly different shows significant differences in displacement between the temperature treatments (F = 3.30* with d.f. of 3 and 21).

The rates of dark respiration at 100, 300 and 500 g DM/$m^2$ were read for each growth temperature from the regression lines and converted to g DM for a 12 hour period (assuming 1 g $CO_2$ = 0.7 g DM). These 12 hour rates are plotted against growth temperature in Fig. 45, and provide a measure of the loss of dry matter at night for plants grown at different constant temperatures with different amounts of dry matter. Dry matter loss during the night was considerable, particularly with large amounts of dry matter at high temperature. This could amount to 8 g/$m^2$ per night of 12 hours.

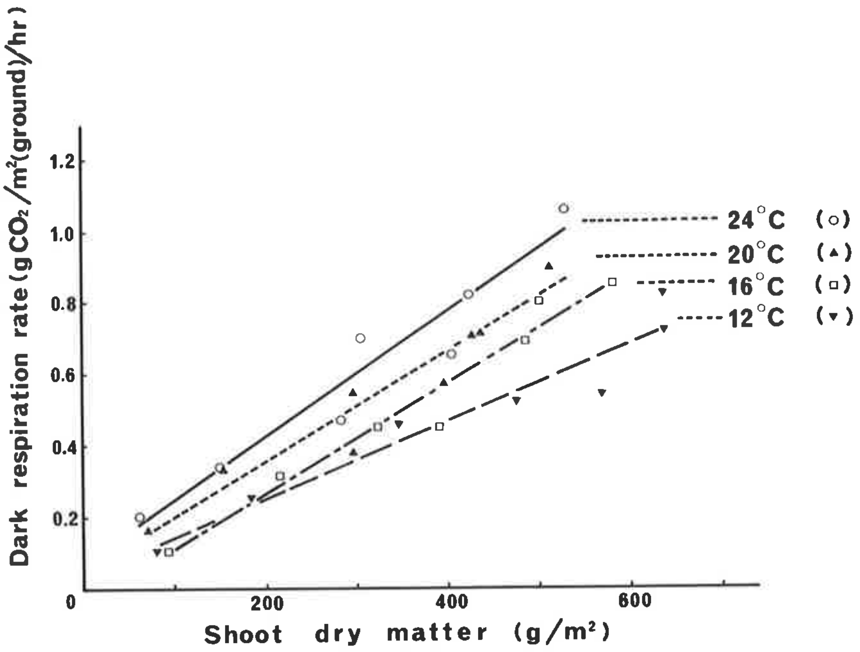
A multiple linear regression analysis of the data given in

Figure 44. (Top)

The relationship between dark respiration rate, measured at growth temperature, and shoot dry matter for communities grown at 4 different temperatures.

Figure 45. (Bottom)

Effects of temperature on 12-hour dark respiration rate of communities with different shoot dry matter. Respiration was measured at growth temperature. Regression lines are drawn from EQ.18.


Dark respiration rate (g CO₂/m²(ground)/hr)
1.2
1.0
0.8
0.6
0.4
0.2
0
200
400
600
Shoot dry matter (g/m²)
24°C (○)
20°C (▲)
16°C (□)
12°C (▼)

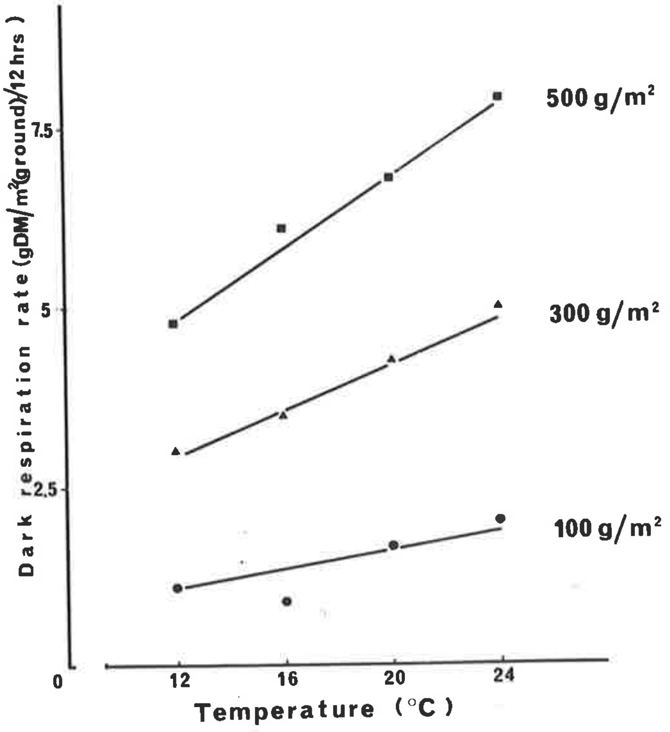

Dark respiration rate (gDM/m²(ground)/12 hrs)
7.5
5
2.5
0
12
16
20
24
Temperature (°C)
500 g/m²
300 g/m²
100 g/m²

Fig. 44 was conducted. The overall equation relating dark respiration rate to shoot dry matter and temperature is

$$DDR = \frac{SDM}{100}(0.89 + 0.089T) + 0.073T - 0.91 \qquad \text{EQ.18}$$

$$(R^2 = 0.933)$$

where T : temperature (°C)

SDM : shoot dry matter ($g/m^2$)

DDR : daily dark respiration ($g/m^2$/day)

The equation indicates that 24 hour dark respiration increases linearly with temperature at any shoot dry matter, the slope being 0.073 + 0.00089 SDM. The regression lines drawn in Fig. 45 were obtained from this equation.

### (b) Temperature Coefficient ($Q_{10}$) of Dark Respiration

When dark respiration was measured at temperatures other than that at which the community was grown, the rate increased exponentially with increase in temperature. In most cases the correlation coefficient was of the order of 0.99. Typical results are shown using a logarithmic scale for dark respiration in Fig. 46.

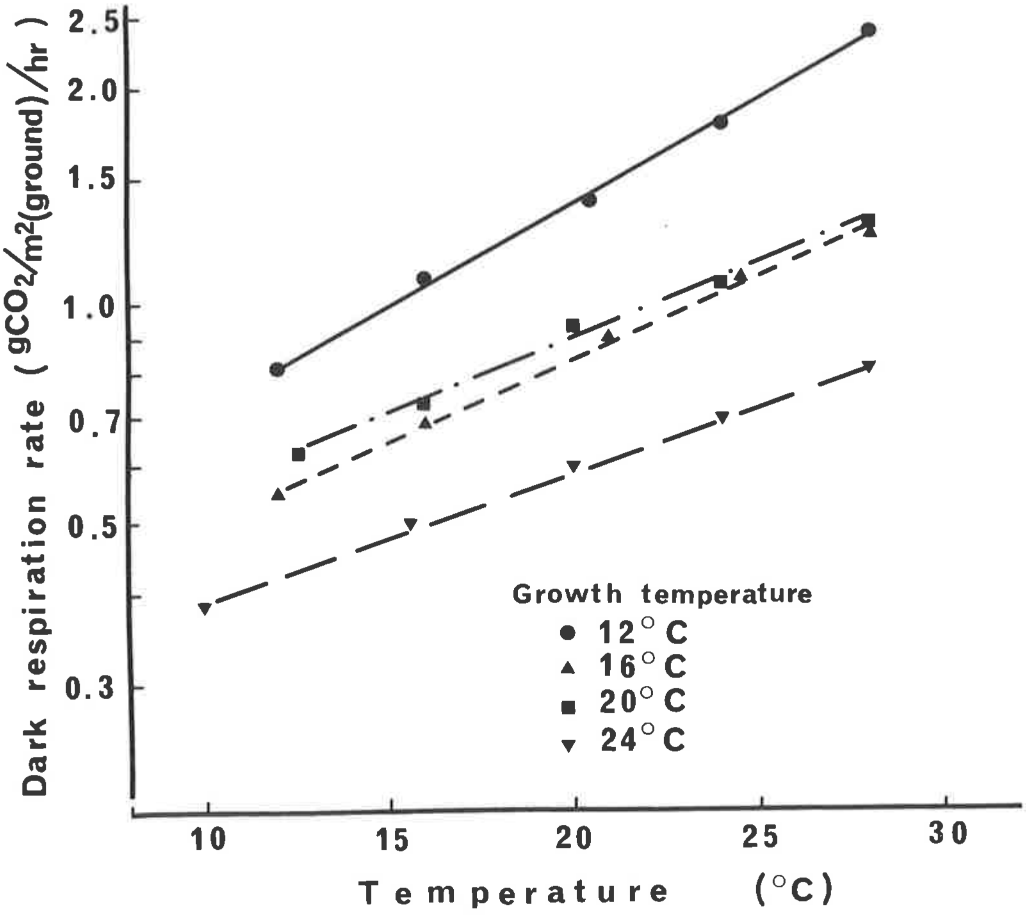
There was no consistent trend of the $Q_{10}$ of the dark respiration rate with time and an average $Q_{10}$ was calculated for each growth temperature (Fig. 47). Analysis of variance showed $Q_{10}$ to be significantly affected by growth temperature; the LSD at 5% is indicated on the figure. There is no significant difference in $Q_{10}$ between plants grown at 12° and 16°C and between plants grown at 20° and at 24°C.

Figure 46 (Top)

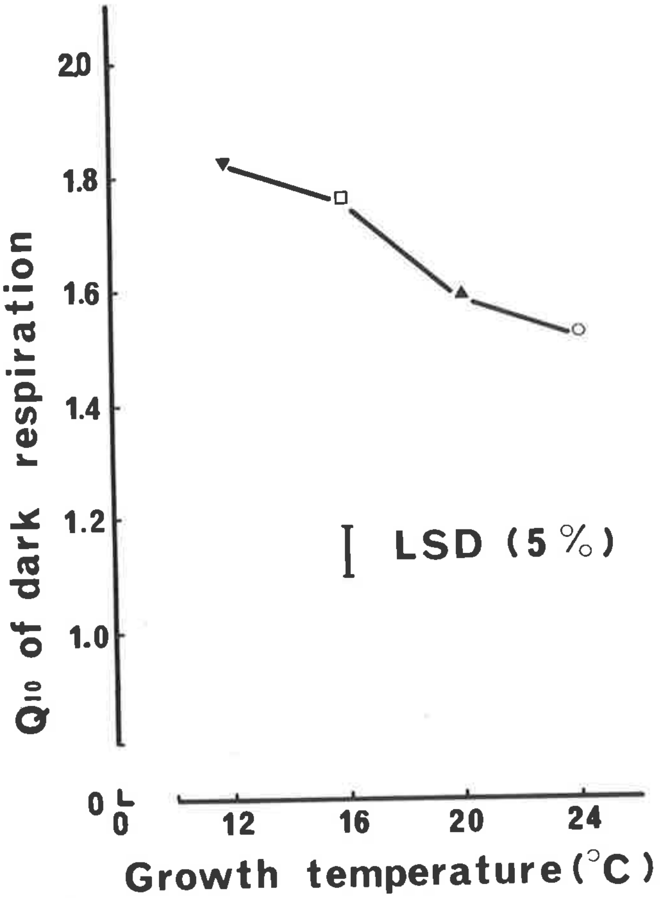
Response of dark respiration to change of temperature for communities grown at 4 different temperatures. Linear regressions are drawn for logarithm of dark respiration rate on temperature.

Figure 47. (Bottom)

The relationship between average values of temperature coefficient of dark respiration of communities ($Q_{10}$) and growth temperature.



Dark respiration rate ( gCO2/m2(ground)/hr )
2.5
2.0
1.5
1.0
0.7
0.5
0.3
10
15
20
25
30
Temperature (°C)
Growth temperature
● 12° C
▲ 16° C
■ 20° C
▼ 24° C



Q10 of dark respiration
2.0
1.8
1.6
1.4
1.2
1.0
0
0
12
16
20
24
Growth temperature (°C)
LSD (5 %)

### (c) Dark Respiration Rates of Communities Grown at Different Temperatures Compared at the Same Temperature

Rates of dark respiration at 12°, 20° and 28°C for communities grown at four different temperatures were calculated from regressions of the logarithm of dark respiration on temperature at different amounts of shoot dry matter. Each rate is plotted as a function of the corresponding shoot dry matter in Fig. 48.

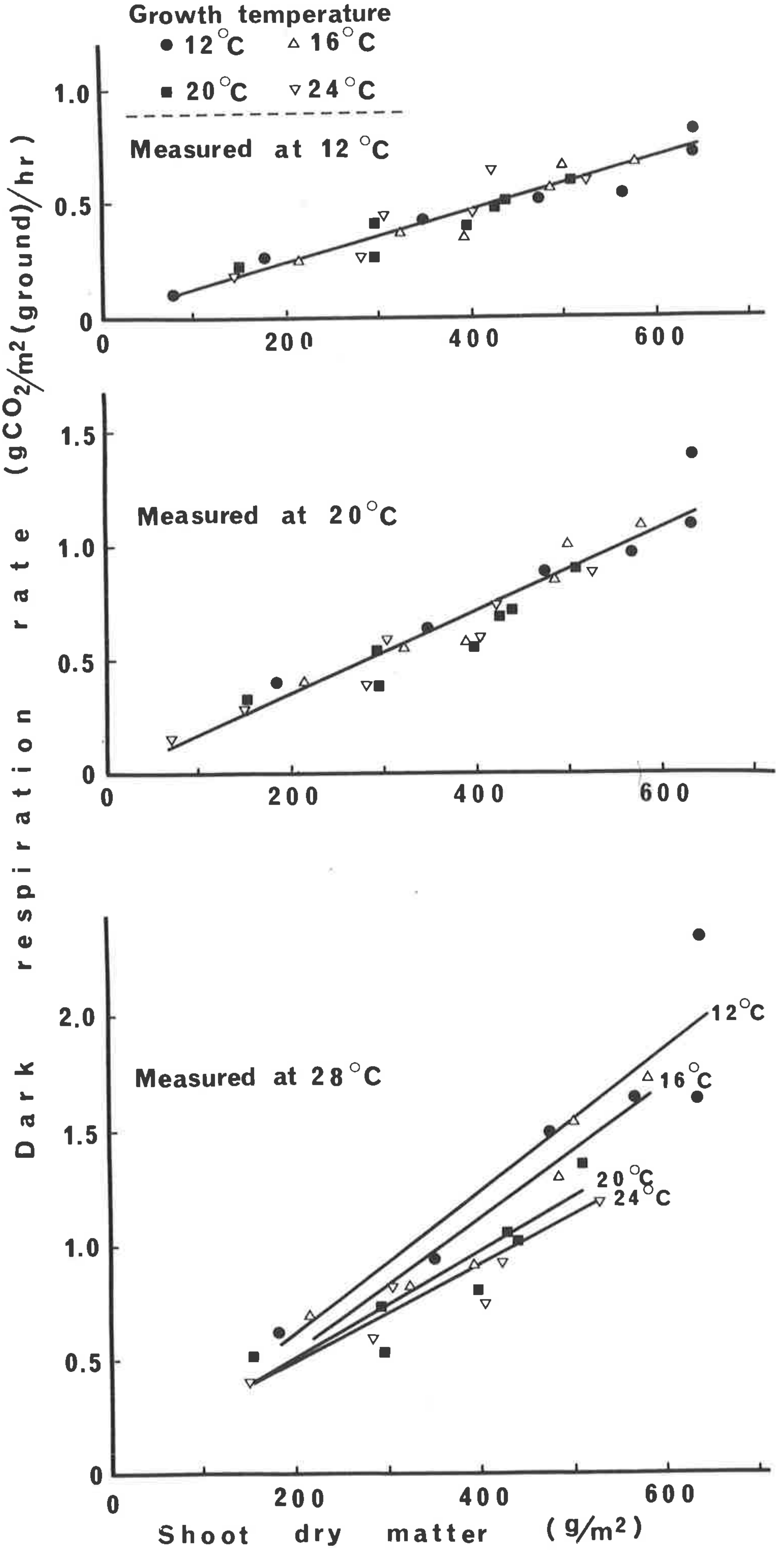
Growth temperature had no significant effect on the dark respiration rate measured at 12° or at 20°C, but the linear regression coefficient of the dark respiration rate with shoot dry matter measured at 28°C was significantly higher for plants grown at low temperature (F = 4.737* with d.f. of 3 and 18).

It is now possible to modify the equation relating dark respiration (DR), dry weight and growth temperature to that which includes variation in measured temperature using $Q_{10}$ (Fig. 47). In Fig. 49 DR calculated from a known growth temperature, shoot dry matter and measured temperature is compared with the actual measured rate. The calculated value was fairly close to the measured rate.

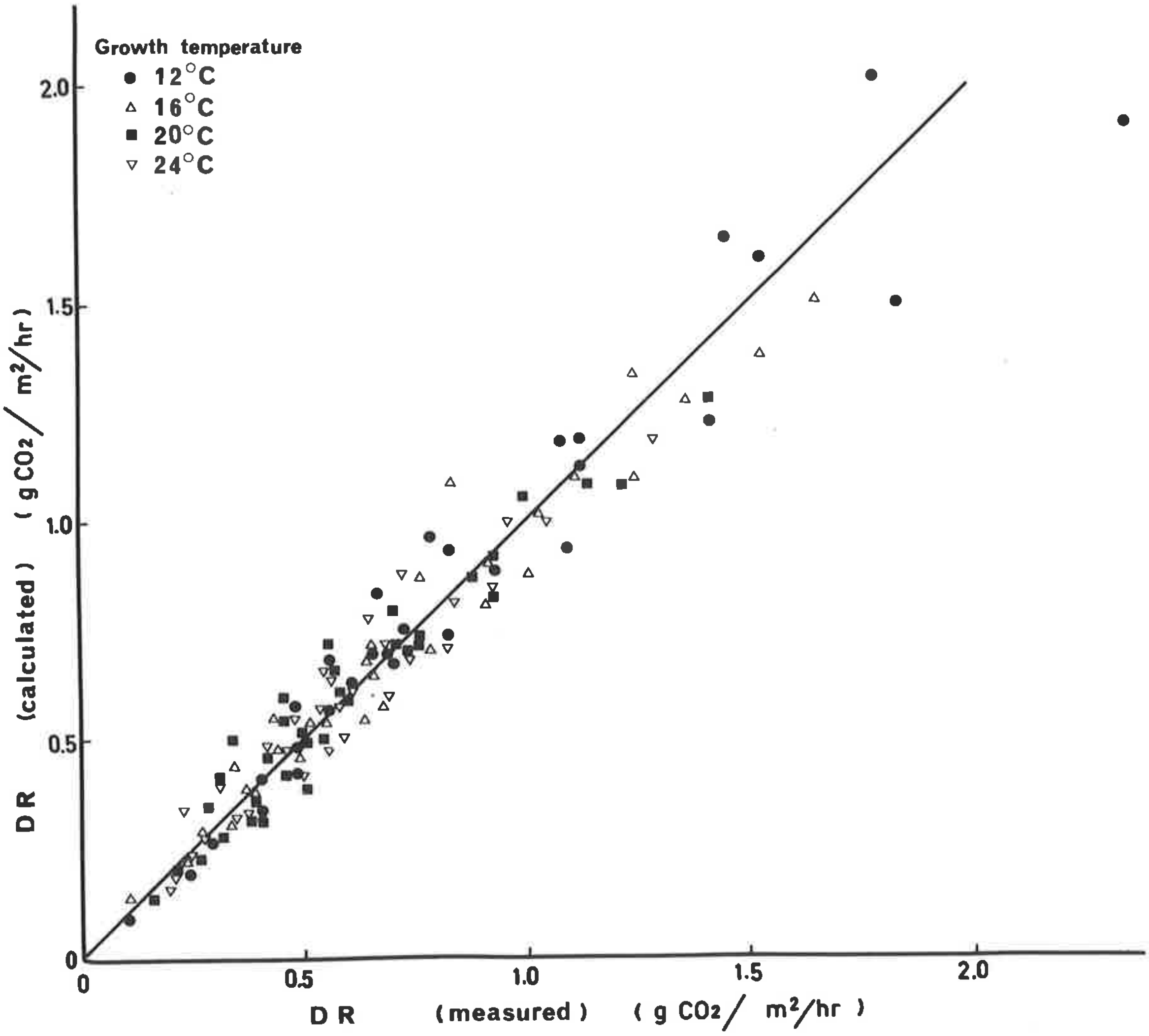
### 5.4.5. Photosynthesis

Net $CO_2$ exchanges of the plant communities were measured in the 1972 experiment. Air temperatures in the photosynthetic chamber could be maintained to within 0.5°C of desired temperature at temperatures between 16° and 28°C but not at 12°C (see 5.2.2). Air temperature is used to indicate the temperature of the system; this was 1-2°C higher than leaf temperature in the top layer in the canopy at 28°C and 1-3°C lower at 16°C. It was found that photosynthetic responses to temperature were the same when temperature was changed at constant light flux and when light flux was changed at different temperatures.

Figure 48. The relationship between shoot dry matter and dark respiration rate measured at 3 different temperatures for communities grown at 4 different temperatures.


Growth temperature
● 12°C
△ 16°C
■ 20°C
▽ 24°C
Measured at 12 °C
1.0
0.5
0
0
200
400
600
Measured at 20°C
1.5
1.0
0.5
0
0
200
400
600
Measured at 28°C
2.0
1.5
1.0
0.5
0
0
200
400
600
12°C
16°C
20°C
24°C
Dark respiration rate (gCO2/m2(ground)/hr)
Shoot dry matter (g/m2)

<u>Figure 49</u>. The relationship between calculated dark respiration rate (DR) and measured rate for communities grown at 4 different temperatures. Dark respiration rate was measured at 5 temperatures at each of 6-8 times during growth of each community. Calculated values were obtained by using EQ.18 and $Q_{10}$ values shown in Figure 47.


Growth temperature
● 12°C
△ 16°C
■ 20°C
▽ 24°C
2.0
1.5
1.0
0.5
0
DR (calculated) ( g CO₂ / m²/hr )
0
0.5
1.0
1.5
2.0
D R (measured) ( g CO₂ / m²/hr )

## (a) Photosynthetic Responses to Light Energy at Growth Temperature

Net $CO_2$ exchange was first measured at the growth temperature, except that plants grown at 12°C were measured at 16°C. Relationships between net $CO_2$ exchange rate and light energy at different amounts of dry matter are shown in Fig. 50 for plants grown at 24°C and 16°C: the curves were eye-fitted. Results for plants grown at 12°C and 20°C were similar to those obtained at 16°C and 24°C and were omitted. Representative results only are shown in the figure. The shapes of the light net photosynthesis curves are very similar to those obtained in the solar energy experiment (Fig. 26), and are remarkably similar to each other over a range of LAI values from 4 to 8 for each temperature. There are only small differences in net photosynthetic rate at high light energy between plant canopies varying in dry matter. Old canopies with a high dry matter yield (LAI 6-9) had a low net $CO_2$ exchange rate at low light energy. This could largely be accounted for by high dark respiration rates.

Gross photosynthetic rate is plotted against light energy in Fig. 51. All the data at 24° and 16°C are included in the figure. Gross photosynthetic rates were calculated from the net photosynthetic rates as shown in Fig. 50 and from calculated dark respiration rates, using the equations relating dark respiration rate with shoot dry matter (Fig. 44). Each curve is drawn to pass through the calculated dark respiration rate at 0 $W/m^2$.

Gross photosynthetic rate at light energy levels up to 100 $W/m^2$ is almost independent of LAI above LAI 4; it is directly proportional to light energy up to 100 $W/m^2$ but at higher fluxes the relation becomes curvilinear.

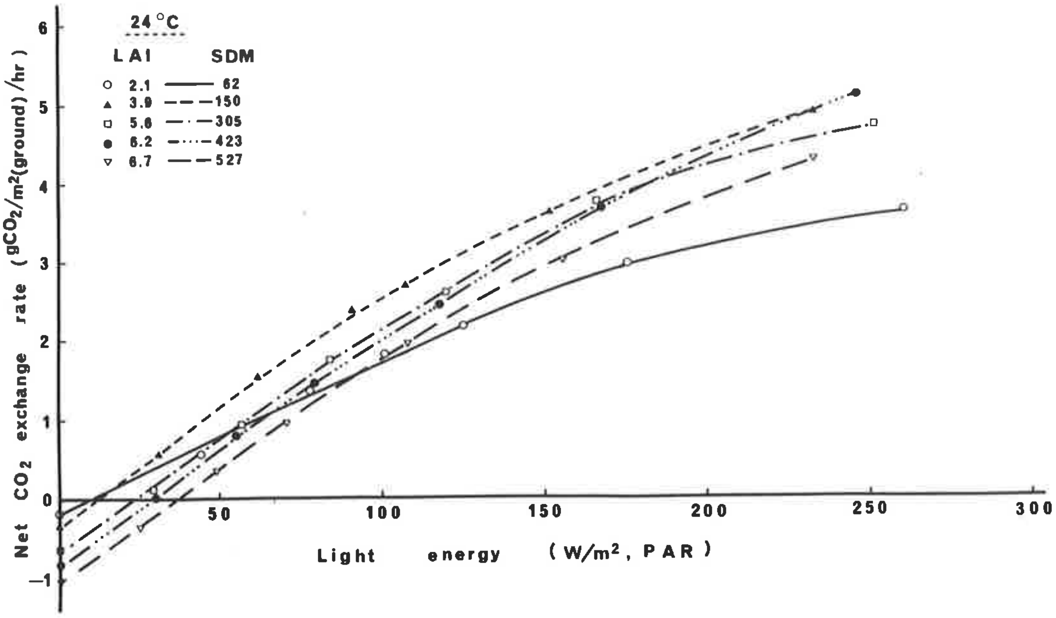
To examine the effects of temperature and some plant attributes on photosynthesis in more detail, net $CO_2$ exchange rates and the gross photosynthetic rates at light energies of 0, 50 and 250 $W/m^2$ were read

Figure 50. Light-net photosynthesis curves of communities with different values of leaf area index (LAI) and shoot dry matter (SDM).

Top: communities grown at 24°C and net $CO_2$ exchange rate measured at 24°C.

Bottom: communities grown at 16°C and net $CO_2$ exchange rate measured at 16°C.

Curves are fitted by eye.


24 °C
LAI SDM
○ 2.1 62
▲ 3.9 150
□ 5.6 305
● 6.2 423
▽ 6.7 527
Net CO2 exchange rate (gCO2/m2(ground)/hr)
6
5
4
3
2
1
0
−1
50
100
150
200
250
300
Light energy (W/m², PAR)

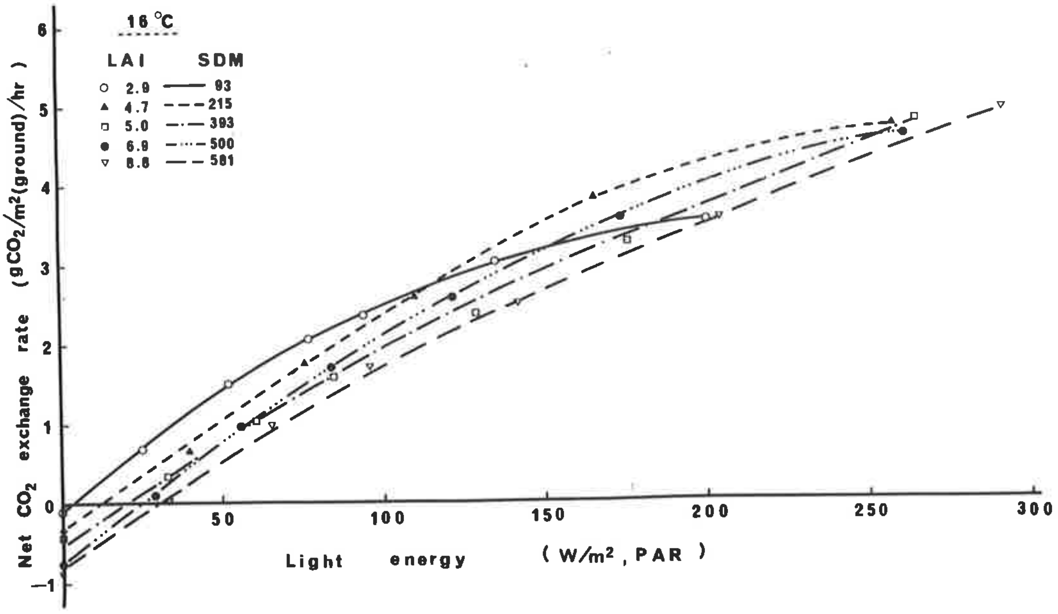
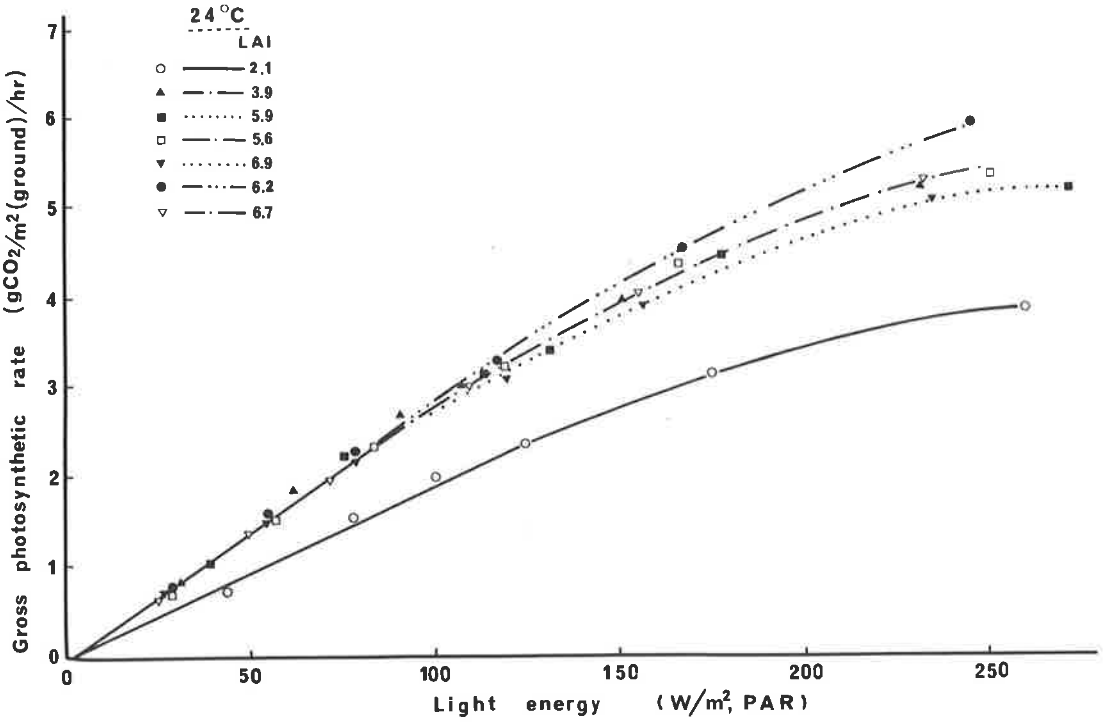

16 °C
LAI SDM
○ 2.9 93
▲ 4.7 215
□ 5.0 393
● 6.9 500
▽ 8.6 581
Net CO2 exchange rate (gCO2/m2(ground)/hr)
6
5
4
3
2
1
0
−1
50
100
150
200
250
300
Light energy (W/m², PAR)

**Figure 51.** Light-gross photosynthesis curves of communities with different values of leaf area index (LAI).

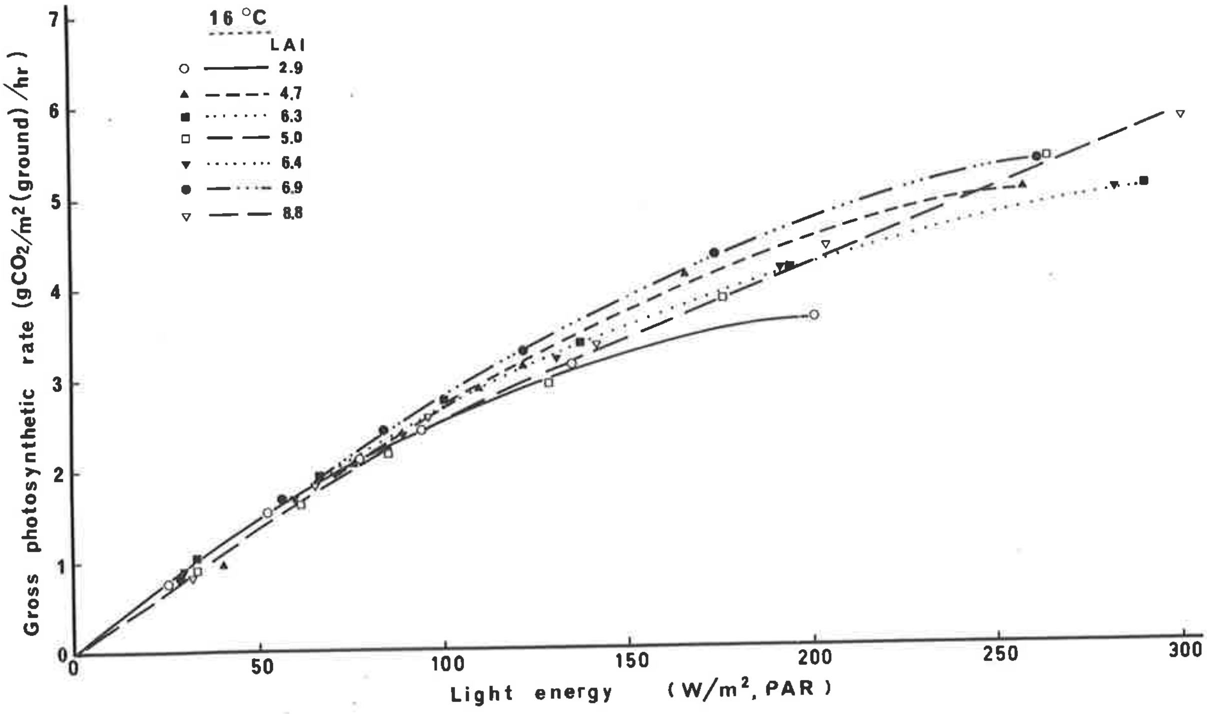
Top: communities grown at 24°C and gross photosynthetic rate measured at 24°C.

Bottom: communities grown at 16°C and gross photosynthetic rate measured at 16°C.

Curves are fitted by eye.



24 °C
LAI
○ 2.1
▲ 3.9
■ 5.9
□ 5.6
▼ 6.9
● 6.2
▽ 6.7
Gross photosynthetic rate (gCO2/m2(ground)/hr)
0
1
2
3
4
5
6
7
0
50
100
150
200
250
Light energy (W/m², PAR)



16 °C
LAI
○ 2.9
▲ 4.7
■ 6.3
□ 5.0
▼ 6.4
● 6.9
▽ 8.8
Gross photosynthetic rate (gCO2/m2(ground)/hr)
0
1
2
3
4
5
6
7
0
50
100
150
200
250
300
Light energy (W/m², PAR)

from the original light photosynthesis curves. These are plotted in Fig. 52 against LAI (a) and against SDM (b). In a few cases, the value at 250 W/m$^2$ was read by extrapolating the light-photosynthesis curve. Dark respiration rates for plants grown at 12°C were measured at 16°C. All growth temperature treatments are included in the figure. Net $CO_2$ exchange rate at 50 W/m$^2$ decreased with increase in LAI above 4 and with increase in SDM above 200 g/m$^2$, the decrease being accounted for largely by increase in dark respiration. The exchange rate was slightly higher for plants measured at 16°C than for those measured at higher temperatures. Net $CO_2$ exchange rate at 250 W/m$^2$ increased with increase of LAI up to 3 and with increase of SDM up to 150 g/m$^2$. Further increase of LAI or SDM resulted in little difference in the net $CO_2$ exchange rate. At very high LAI or high SDM, the rate at 250 W/m$^2$ may even have decreased.

Analysis of variance to examine the effect of temperature on the rate of $CO_2$ exchange at 250 W/m$^2$ for canopies with LAI greater than 3 is shown in Table 10.

Growth temperature had a significant effect on the net $CO_2$ exchange rate when measured at growth temperature. 24°C plants had a significantly higher rate when compared with pooled data for 12° and 16°C. This was done as plants grown at 12° and 16°C were measured at 16°C. 12° plants are likely to have a lower exchange rate if measured at 12°C.

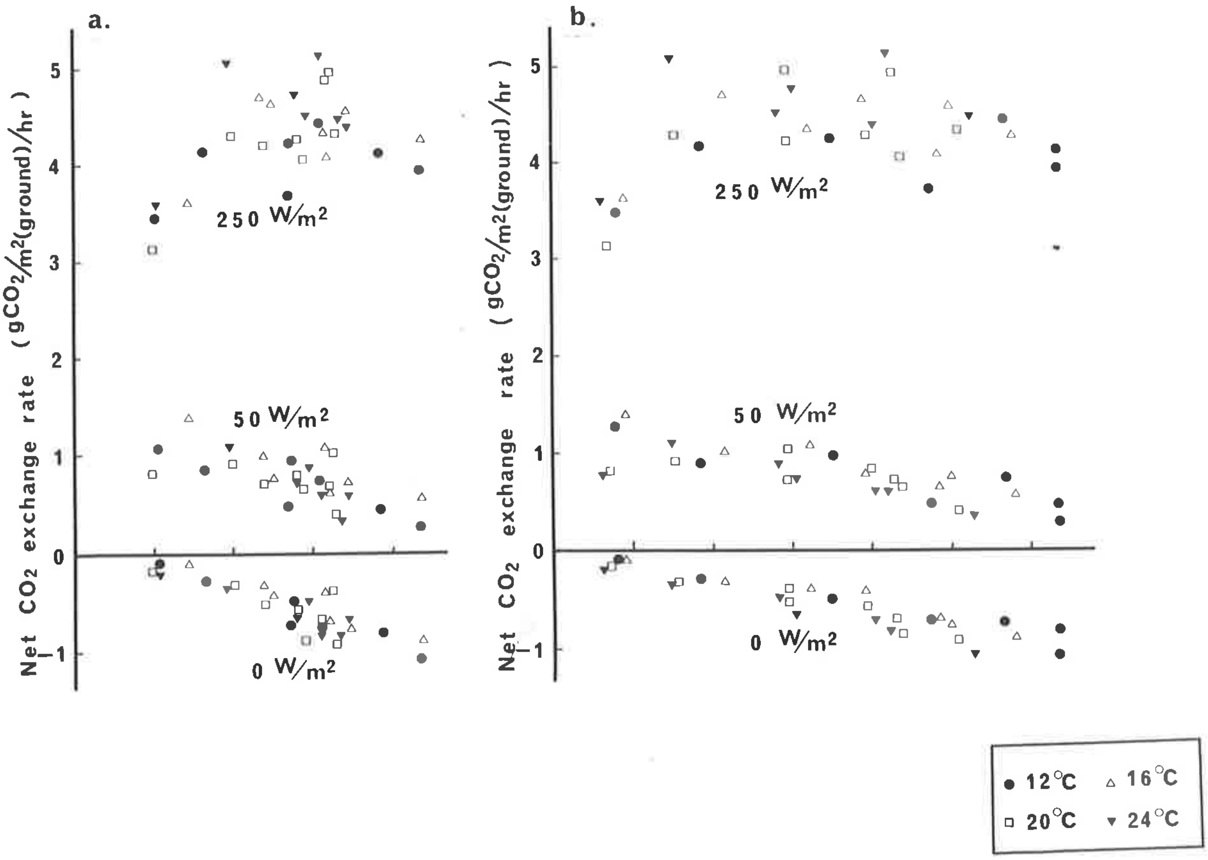
Gross photosynthetic rates at 50 W/m$^2$ and at 250 W/m$^2$ are plotted against LAI and against SDM in Fig. 53 (a) and (b). At 50 W/m$^2$ gross photosynthetic rate increased up to LAI of 3-4, and up to SDM of 150 g/m$^2$. The rate was constant at 1.4 g $CO_2$/m$^2$ (ground)/hr once an LAI of 4 was attained. Analysis of variance showed no significant effect of temperature on the gross photosynthetic rate at 50 W/m$^2$.

<u>Figure 52.</u> (Top)

Effects of temperature on the relationships between net $CO_2$ exchange rate and leaf area index (LAI) (left) and between net $CO_2$ exchange rate and shoot dry matter (right) for darkness and 2 different light energies ($W/m^2$). Temperature effects were significant at 250 and 0 $W/m^2$.

<u>Figure 53.</u> (Bottom)

Effects of temperature on the relationships between gross photosynthetic rate and leaf area index (LAI) (left) and between gross photosynthetic rate and shoot dry matter (right) at 2 different light energies ($W/m^2$). Temperature effects were significant where no lines are shown.


a.
b.
Net CO2 exchange rate ( gCO2/m2(ground)/hr )
250 W/m2
50 W/m2
0 W/m2
5
4
3
2
1
0
-1
● 12°C
△ 16°C
□ 20°C
▼ 24°C

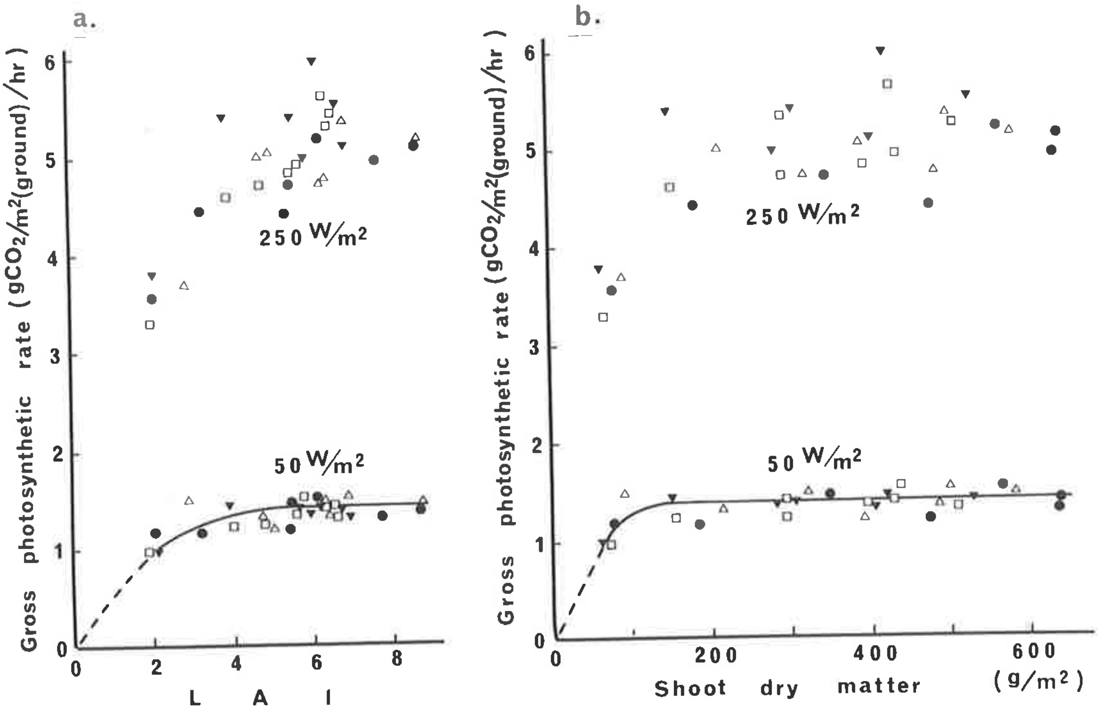

a.
b.
Gross photosynthetic rate ( gCO2/m2(ground)/hr )
250 W/m2
50 W/m2
6
5
4
3
2
1
0
0
2
4
6
8
L A I
0
200
400
600
Shoot dry matter (g/m2)

Table 10. Analysis of variance of net $CO_2$ exchange rate at 250 $W/m^2$ of communities with LAI > 3

(a) Individual

| | S.S. | d.f. | M.S. | F |
|---|---|---|---|---|
| Treatment | 119.48 | 3 | 39.83 | 4.41* |
| Error | 189.63 | 21 | 9.03 | |

LSD (5%) for ($12^o$, $16^o$ and $24^oC$) = 3.61
LSD (5%) for ($20^oC$ and others) = 3.48

| | Growth Temperature | | | |
|---|---|---|---|---|
| | $12^oC$ | $16^oC$ | $20^oC$ | $24^oC$ |
| mean | $40.80^a$ | $44.13^{a,b}$ | $44.24^{a,b}$ | $47.10^b$ |

(b) Pooled for $12^o$ and $16^oC$

| | S.S. | d.f. | M.S. | F |
|---|---|---|---|---|
| Treatment | 86.14 | 2 | 43.07 | 4.25* |
| Error | 222.97 | 22 | 10.135 | |

LSD (5%) for ($16^o$ and $20^oC$) = 3.15
LSD (5%) for ($20^o$ and $24^oC$) = 3.68
LSD (5%) for ($16^o$ and $24^oC$) = 3.31

| | $16^oC$ | $20^oC$ | $24^oC$ |
|---|---|---|---|
| mean | $42.47^a$ | $44.24^{a,b}$ | $47.10^b$ |

At 250 $W/m^2$ gross photosynthetic rate increased rapidly with increase of LAI up to 3 and SDM of 150 $g/m^2$. Above these values the picture is not entirely clear although it seems that further increase of LAI or SDM results in little increase in gross photosynthetic rate.

Analysis of variance for the rate of 250 W/m$^2$ for canopies with LAI greater than 3 (Table 11) shows growth temperature to have a significant effect on the gross photosynthetic rate; 24°C plants had a significantly higher gross photosynthetic rate than 12° or 16°C plants.

Table 11. Analysis of variance of gross photosynthetic rate at 250 W/m$^2$ of communities with LAI > 3

(a) Individual

| | S.S. | d.f. | M.S. | F |
|---|---|---|---|---|
| Treatment | 111.84 | 3 | 37.28 | 3.501* |
| Error | 223.62 | 21 | 10.65 | |

LSD (5%) for (12°, 16° and 24°C) = 3.92
LSD (5%) for (20°C and others) = 3.78

| | 12°C | 16°C | 20°C | 24°C |
|---|---|---|---|---|
| mean | 47.93$^a$ | 50.00$^a$ | 50.36$^{a,b}$ | 53.93$^b$ |

(b) Pooled for 12° and 16°C

| | S.S. | d.f. | M.S. | F |
|---|---|---|---|---|
| Treatment | 99.02 | 2 | 49.51 | 4.61* |
| Error | 236.44 | 22 | 10.747 | |

LSD (5%) for (16° and 20°C) = 3.24
LSD (5%) for (20° and 24°C) = 3.79
LSD (5%) for (16° and 24°C) = 3.41

| | 16°C | 20°C | 24°C |
|---|---|---|---|
| mean | 48.97$^a$ | 50.36$^{a,b}$ | 53.93$^b$ |

Note: Means with different superscripts were significantly different.

## (b) Photosynthetic Responses to Light Energy at Different Temperatures

After the net $CO_2$ exchange rate was measured at several light energy levels at the growth temperature, the temperature was changed and a new light-photosynthesis relationship was obtained. In this way light-photosynthesis curves could be constructed for 4 different temperatures in one day. An example of typical results is shown in Fig. 54 for a canopy grown at $16^{\circ}$, LAI of 6.9 and SDM of 560 $g/m^2$. Up to 100 $W/m^2$ the net $CO_2$ exchange rate was highest at $16.5^{\circ}C$, differences between temperatures in net $CO_2$ exchange rate being accounted for by differences in dark respiration rate. At higher levels of irradiance (e.g. 250 $W/m^2$), net $CO_2$ exchange rate was highest at $28^{\circ}$ and $24^{\circ}C$.

Other canopies, differing from the above in LAI, SDM and growth temperature showed a similar response of the light-photosynthesis curve to temperature. From each light-photosynthesis curve in the previous figure the net $CO_2$ exchange rate was read at 0, 50, 100, 150, 200 and 250 $W/m^2$. These values are plotted against the measured temperature in Fig. 55. It is evident that the net $CO_2$ exchange rate is inversely and linearly related to temperature at 50 $W/m^2$, but is directly and curvilinearly related to temperature at 250 $W/m^2$. The light-gross photosynthesis curve of the canopy used in the previous figure is shown in Fig. 56. The gross photosynthetic rate is independent of measured temperature up to about 100 $W/m^2$, but is directly related to temperature at higher light energies. Plants grown at temperatures other than $16^{\circ}C$ showed similar results.

## (c) The Effects of Growth Temperature and Measured Temperature on Gross Photosynthesis at High Light Flux

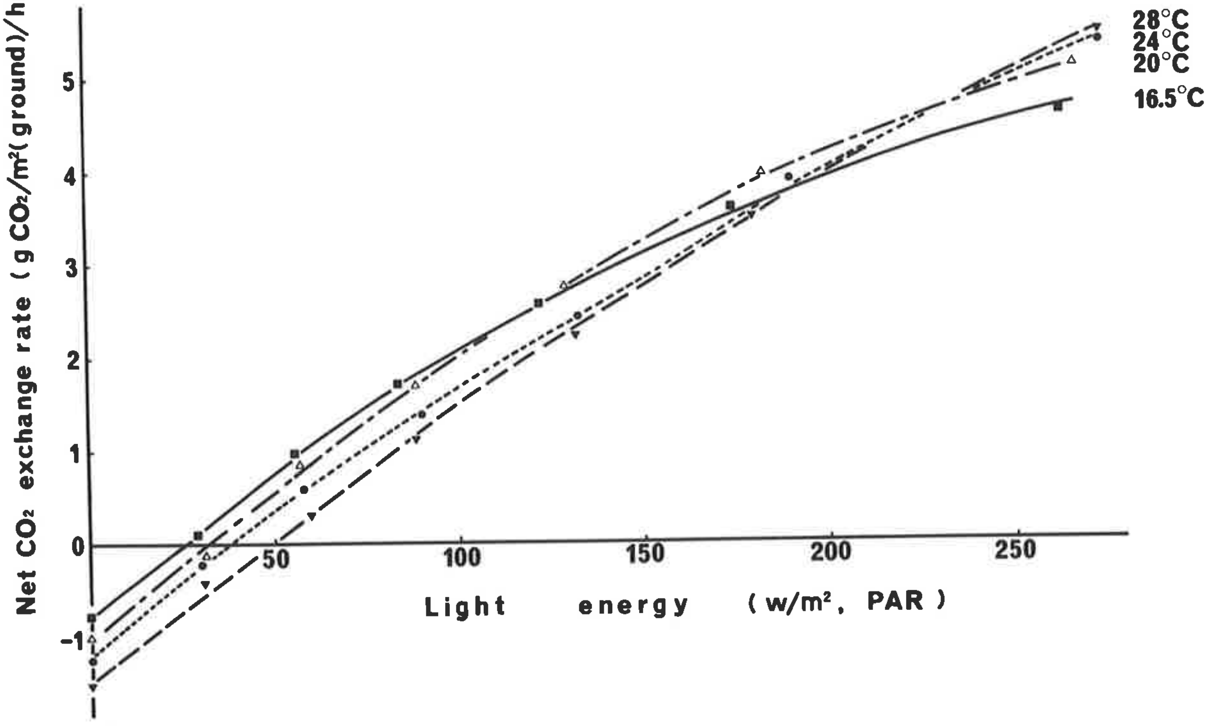
Gross photosynthetic rate at 250 $W/m^2$ was read from each light-

**Figure 54.** Light-net photosynthesis curves of a community (LAI 6.9 and shoot dry matter 500 g/m$^2$) measured at 4 different temperatures.

Curves are fitted by eye.

**Figure 55.** The relationship between net $CO_2$ exchange rate and measured temperature at different light energies (W/m$^2$ PAR). Figure 54 was used to construct this figure.

Curves are fitted by eye.


Net CO2 exchange rate ( g CO2/m2(ground)/hr )
5
4
3
2
1
0
-1
50
100
150
200
250
Light energy (w/m², PAR )
28°C
24°C
20°C
16.5°C

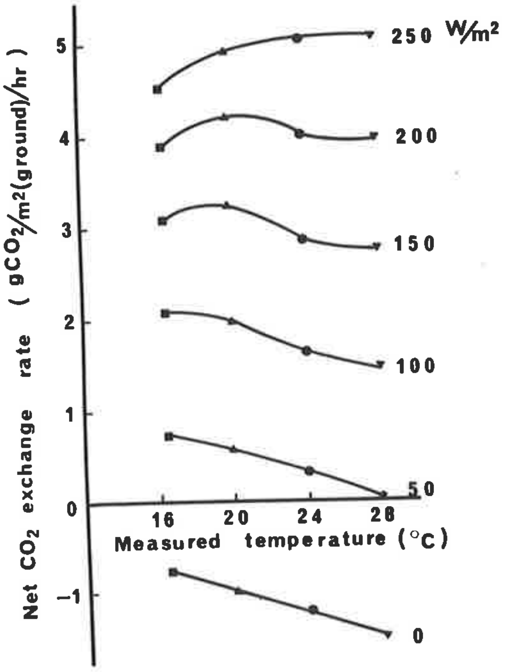

Net CO2 exchange rate ( gCO2/m2(ground)/hr )
5
4
3
2
1
0
-1
16
20
24
28
Measured temperature (°C)
250 W/m²
200
150
100
50
0

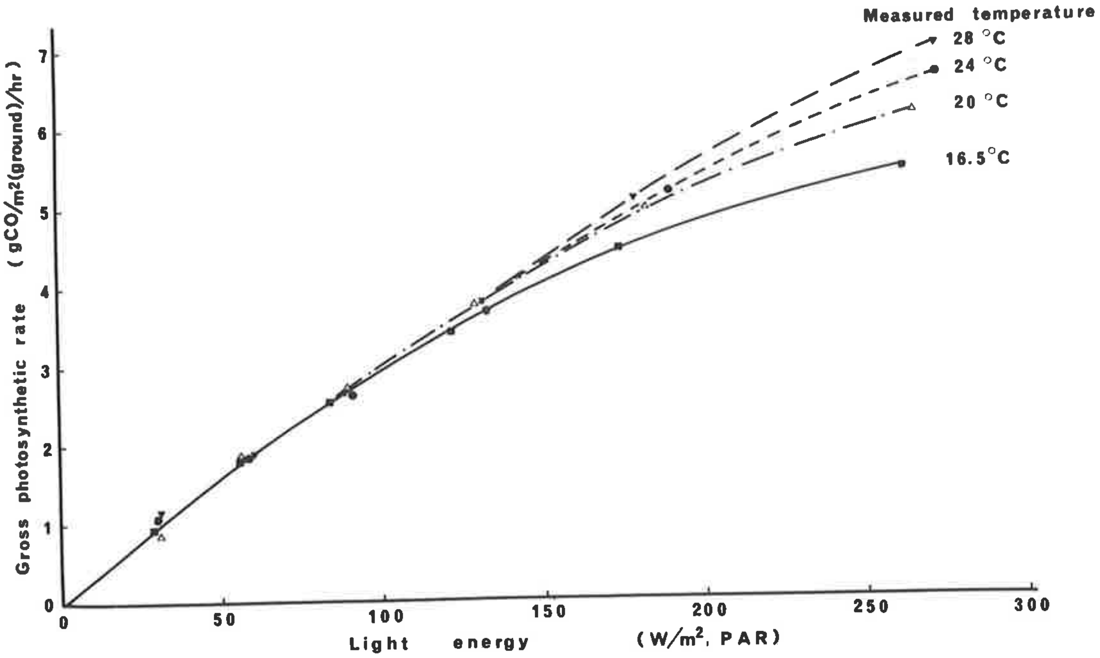
Figure 56. (Top)

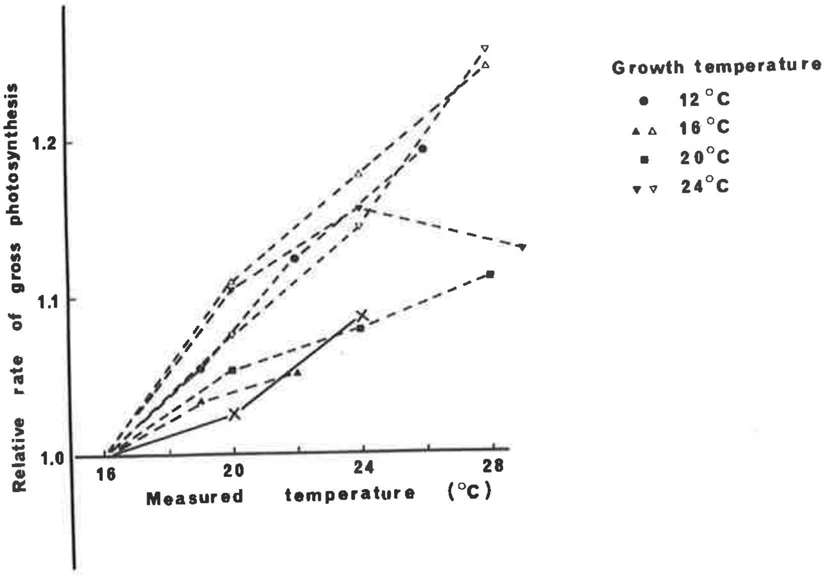
Light-gross photosynthesis curves of a community (LAI 6.9 and shoot dry matter 500 $g/m^2$) measured at 4 different temperatures.

Curves are fitted by eye.

Figure 57. (Bottom)

Relative rate of gross photosynthesis of communities measured at different temperatures, the rate at 16°C being given a value of 1.0. Communities were grown at 4 different temperatures and relative rate is calculated for each community. Gross photosynthetic rates of plants grown and measured at 20° and 24°C are also shown relative to that of plants grown and measured at 16°C (solid line).


Measured temperature
28 °C
24 °C
20 °C
16.5°C
Gross photosynthetic rate ( gCO/m2(ground)/hr )
0
1
2
3
4
5
6
7
0
50
100
150
200
250
300
Light energy (W/m², PAR)


Growth temperature
● 12 °C
▲ △ 16 °C
■ 20°C
▼ ▽ 24°C
Relative rate of gross photosynthesis
1.0
1.1
1.2
16
20
24
28
Measured temperature (°C)

photosynthesis curve obtained at different temperatures. In some cases it was necessary to extrapolate the curve slightly. For each growth temperature, its photosynthetic rate at different temperatures was compared to its own rate of photosynthesis at 16°C which was given a value of 1.00. This is shown as a relative rate of gross photosynthesis in Fig. 57. Increase of gross photosynthetic rate with increase of measured temperature is not consistently associated with growth temperature.

The relative rates of photosynthesis of communities grown at 16°, 20° and 24°C and measured at their growth temperature are also shown in the figure. It may be that increase in gross photosynthetic rate at growth temperature with increase in growth temperature from 16° to 24°C is less than that of a community measured immediately from 16° to 24°C.

# 6.0.0. A Systems Approach to Growth of Subterranean Clover Communities under Constant Temperature Conditions

## 6.1.0. Introduction

Dry matter production by plant communities is consequent on operation of a complex system. The total system consists of a large number of interacting sub-systems or growth processes such as photosynthesis, respiration, dry matter distribution, nutrient uptake and water transport.

In this Chapter plant dry matter production models are constructed from the experimental data given in 5.0.0. These experiments involved variation in light flux density and temperature and the models employ these factors as environmental variables. The purpose is to construct a simple model that adequately describes dry matter production by a subterranean clover community in different temperature and light energy environments with mineral nutrients and water at optimum levels of supply.

The effects of each environmental factor on dry matter production is determined through its influence on growth processes. Statistical analyses are used to show significant relationships between environmental factors and growth processes, and between growth processes and plant attributes. Multiple linear regression techniques and curve fitting by the iterative method are used to select the most important environmental and plant variables and to find the best mathematical function relating them quantitatively.

The models constructed in this way are tested by comparing simulated dry matter growth curves with those obtained under experimental conditions. A general application is sought in defining relationships between environmental factors and the growth of the community.

## 5.2.0. Net Photosynthesis Models

### (a) Construction of Models

Canopy photosynthesis, measured under an artificial light source, is used to provide a basic relationship between light flux and net photosynthesis. It is simpler to use canopy rather than leaf photosynthesis for this purpose as it does not involve the estimation of light distribution functions in the canopy. Two models (PHS-1 and PHS-2) are constructed.

PHS-1, constructed from experimental data (5.3.0), calculates net canopy photosynthesis (Pn) at given light fluxes (LF) over a range of values of LAI, total dry matter (TDM) and crop growth rate (CGR) at a constant temperature of $20^{\circ}C$.

PHS-2, constructed from experimental data (5.4.0), calculates Pn over a range of values of LAI and TDM, at constant temperatures ranging from constant $10^{\circ}$ to constant $30^{\circ}C$.

### (b) The Unit of Light Flux

Quartz-iodine lamps were used as a light source in the experiments described in 5.0.0 for the measurement of $CO_2$ exchange rate, the unit of light flux being $W/m^2$ photosynthetic active radiation (PAR). However, similar light flux densities generated by different sources do not have similar photosynthetic rates due to variation in spectral composition especially at low light flux (McCree 1972b). Quantum flux is therefore used as the unit of irradiance since the quantum yield is much less dependent on wavelength than is the relative action yield based on light energy. McCree (1972b) found the photosynthetic rates of an "average plant" at similar quantum fluxes in natural light and in quartz-iodine light to differ by about 8%. Differences in photosynthetic rate between light sources can be corrected by correcting the light flux reading when the quantum yield of the test plant is the same as that of the "average plant". Tables III, IV and Fig. 13 in McCree's paper (1972a) show that the relative quantum yield of white clover differs much from his "average plant". It was decided not to correct further for light source for subterranean clover as it is likely that the relative quantum yield of subterranean clover differs from "average plant". Table II of McCree's paper (1972b) is used for the conversion of light energy ($W/m^2$) to quantum flux ($\mu E/s/m^2$) or the reverse.

### (c) Calculation of Gross Photosynthesis

Several mathematical equations were examined for goodness of fit to quantify the relation between quantum flux and gross photosynthesis using the data given in 5.0.0. The best fit for each type of function was determined by the least squares method. Representative data giving the residual sums of squares for three types of equation are shown in Table 12.

The addition of a constant term reduces the residual sums of squares of a hyperbola only slightly. As the shape of a light-net photosynthesis curve was the same as that obtained for a light-gross photosynthesis curve with a constant term, the small difference in residual sums of squares between the two equations indicates that the shape of the light-net photosynthesis curve is almost identical to that of the light-gross photosynthesis curve.

Leaf photosynthesis and light flux are often related by a hyperbola; Puckridge and Ratkowsky (1971) used this function for canopy net photosynthesis and light flux in wheat canopies. For the present data it was found that a second degree polynomial gave the smallest residual sum of squares in most cases. This function gives a more realistic estimate of the light saturated rate of gross photosynthesis (PgMX) than does the hyperbola. PgMX calculated by the

Table 12. Comparison of residual sums of squares for different functions fitted to light-gross photosynthesis data ($\times 10^2$ (g $CO_2/m^2/hr)^2$)

| Curve number | Polynomial | Hyperbola | | Mitcherlich |
|---|---|---|---|---|
| | (1) $y=ax+bx^2$ | (2) $y=\frac{PgMX\cdot x}{K+x}$ | (3) $y=\frac{PgMX\cdot x}{K+x}+b$ | (4) $y=PgMX(1-e^{-bx})$ |
| (Light energy experiments) | | | | |
| W71 (6) | 11.5 | 11.6 | - | - |
| W71 (7) | 6.6 | 2.1 | - | - |
| W71 (8) | 12.7 | 11.6 | - | - |
| Su72a (1) | 1.4 | 2.4 | 2.4 | 2.1 |
| Su72a (5) | 6.4 | 9.1 | 7.7 | 8.1 |
| A72a (2) | 2.2 | 6.2 | 5.6 | 4.6 |
| A72b (2) | 0.8 | 0.7 | 0.7 | 0.6 |
| A72a (5) | 8.2 | 12.5 | 10.1 | 10.9 |
| A72c (3) | 1.1 | 5.0 | 4.6 | 2.9 |
| (Temperature Experiment 1972) | | | | |
| 16.6.16 | 0.2 | - | 2.2 | 1.2 |
| 20 | 4.3 | - | 6.6 | 6.7 |
| 24 | 4.2 | - | 3.5 | 4.0 |
| 28 | 3.4 | - | 2.7 | 3.2 |
| 12.6.16 | 0.9 | - | 4.7 | 1.7 |
| 20.6.16 | 2.5 | - | 2.1 | 4.4 |
| 24.6.16 | 6.2 | - | 14.8 | 13.0 |
| 20 | 4.0 | - | 6.5 | 6.4 |
| 24 | 1.1 | - | 1.7 | 1.7 |
| 28 | 6.9 | - | 6.6 | 7.9 |

second degree polynomial defined below, was almost always less than 10 g $CO_2/m^2$ (ground)/hr whereas values of PgMX estimated from a hyperbola (and also from a Mitcherlich equation) were very much greater.

A second degree polynomial of the form

$$y = ax + bx^2 \qquad \text{EQ.19}$$

is used in the models. A diagram of a light-gross photosynthesis curve fitted by such a function is shown in Fig. 58. The following parameters are used to characterize the equation:

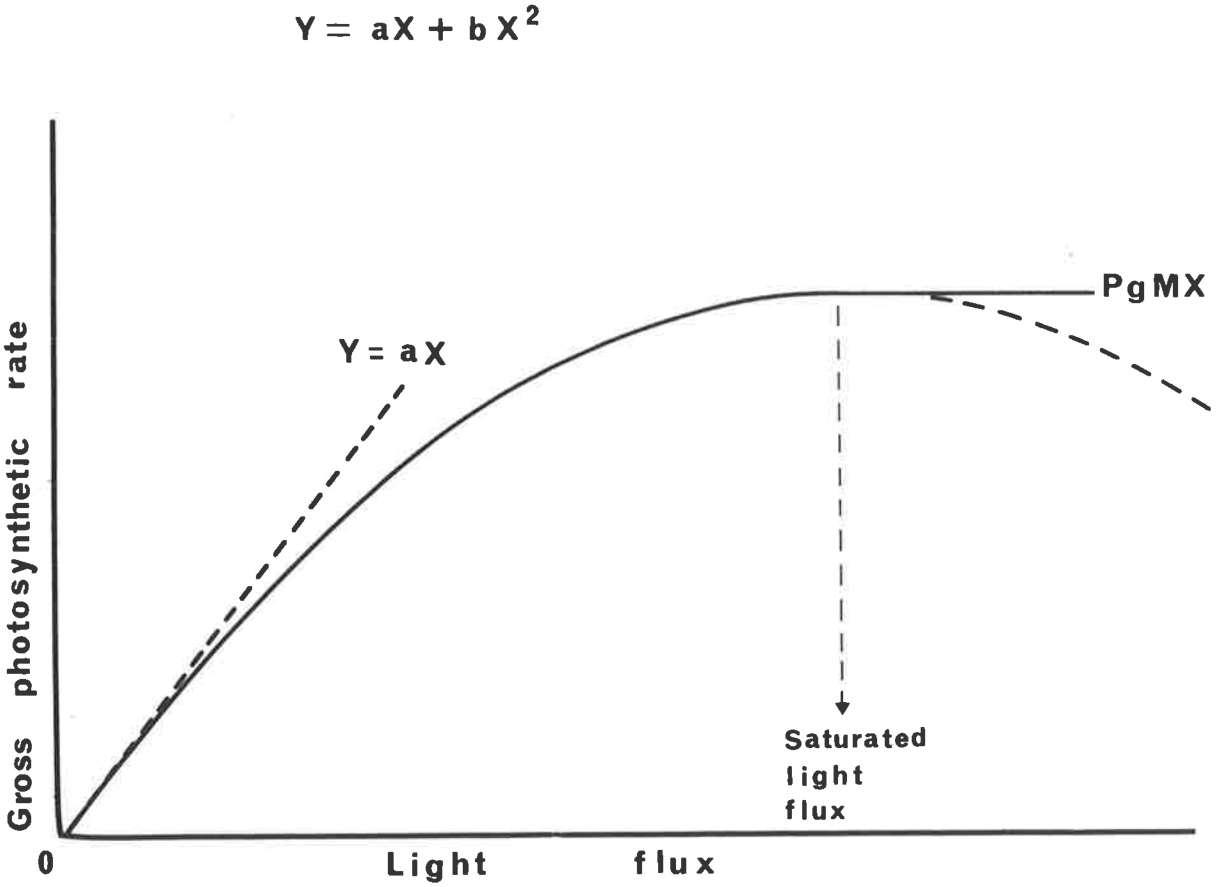

$Y = aX + bX^2$
$Y = aX$
PgMX
Saturated light flux
Gross photosynthetic rate
0
Light flux

**Figure 58.** The general relationship indicated as a continuous line between gross photosynthetic rate and light energy used in the models, PHS-1, PHS-2, CLO-GRO 1 and CLO-GRO 2.

INS ... initial slope of light-gross photosynthesis curve

... a

PgMX ... estimated maximum rate of gross photosynthesis

... $\frac{-a^2}{4b}$

STLF ... saturated light quantum flux at which PgMX occurs

... $-\frac{a}{2b}$

The models assume the gross photosynthetic rate (Pg) to be constant at light quantum fluxes above that estimated at STLF. Since all the experimental data lie to the left of this point potential errors introduced by use of the polynomial are avoided.

(d) Dark Respiration

Dark respiration rate (DR) can be calculated in two ways.

(i) At constant 20°C. Extensive growth data at 20°C are available so an equation is derived for that temperature involving shoot dry matter and crop growth rate:

$$DR = a + b\ (SDM) + c\ (CGR)$$

If it is assumed that the specific root respiration is the same as specific shoot respiration (Pearson and Hunt 1972b), the equation can be written in a particular form for 20°C (see EQ.16) as

$$DR = 0.1155 + 0.00132\ TDM + 0.00664\ CGR \qquad EQ.20$$

$$(\text{with } R^2 = 0.895)$$

However, when TDM is less than 30 g/m$^2$ the use of a constant term is not realistic; a quadratic function over the range 0-30 g/m$^2$ is introduced giving, assuming crop growth rate to be zero,

$$DR = 0.00595\ TDM - 0.00002645\ (TDM)^2 \qquad EQ.21$$

(ii) At constant temperatures between 10° and 30°C. Net $CO_2$ exchange rate was measured in the temperature experiments at different values of SDM and at different temperatures (see 5.4.5). DR is estimated from this data using SDM and current temperature (CT).

$$DR = a + b\ (SDM) + c\ (CT) + d\ (SDM)\ (CT)$$

Again assuming similar specific respiration rates for shoot and root, the equation can be written in a particular form (see Fig. 44) as

$$DR = -0.0535 + 0.00053\ TDM + 0.00436\ CT + 0.000053\ (TDM)\ (CT) \qquad EQ.22$$

At 20°C, the equation gives similar values of DR to those given by EQ.20 for a range of TDM and CGR values; the difference in DR given by the two equations is generally less than 0.1 g $CO_2/m^2$ (ground)/hr.

(e) The Actual Models

(i) PHS-1 (for constant 20°C). INS and PgMX were calculated for 25 light-gross photosynthesis curves at 20°C. Since LAI was known to contribute to variation in these quantities, values are plotted against the corresponding LAI in Fig. 59. It may be seen that INS is constant at values of LAI of 2-10. A hyperbola does not fit the data well; two linear regressions are therefore used to relate INS and LAI, assuming INS increases linearly with increase in LAI at LAI less than 1.7.

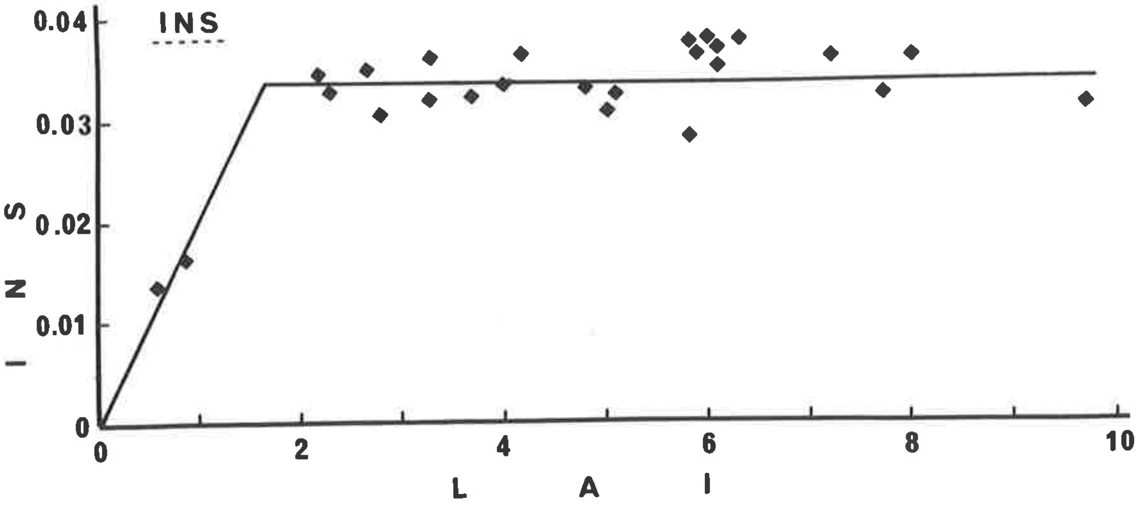
Figure 59. (Top)

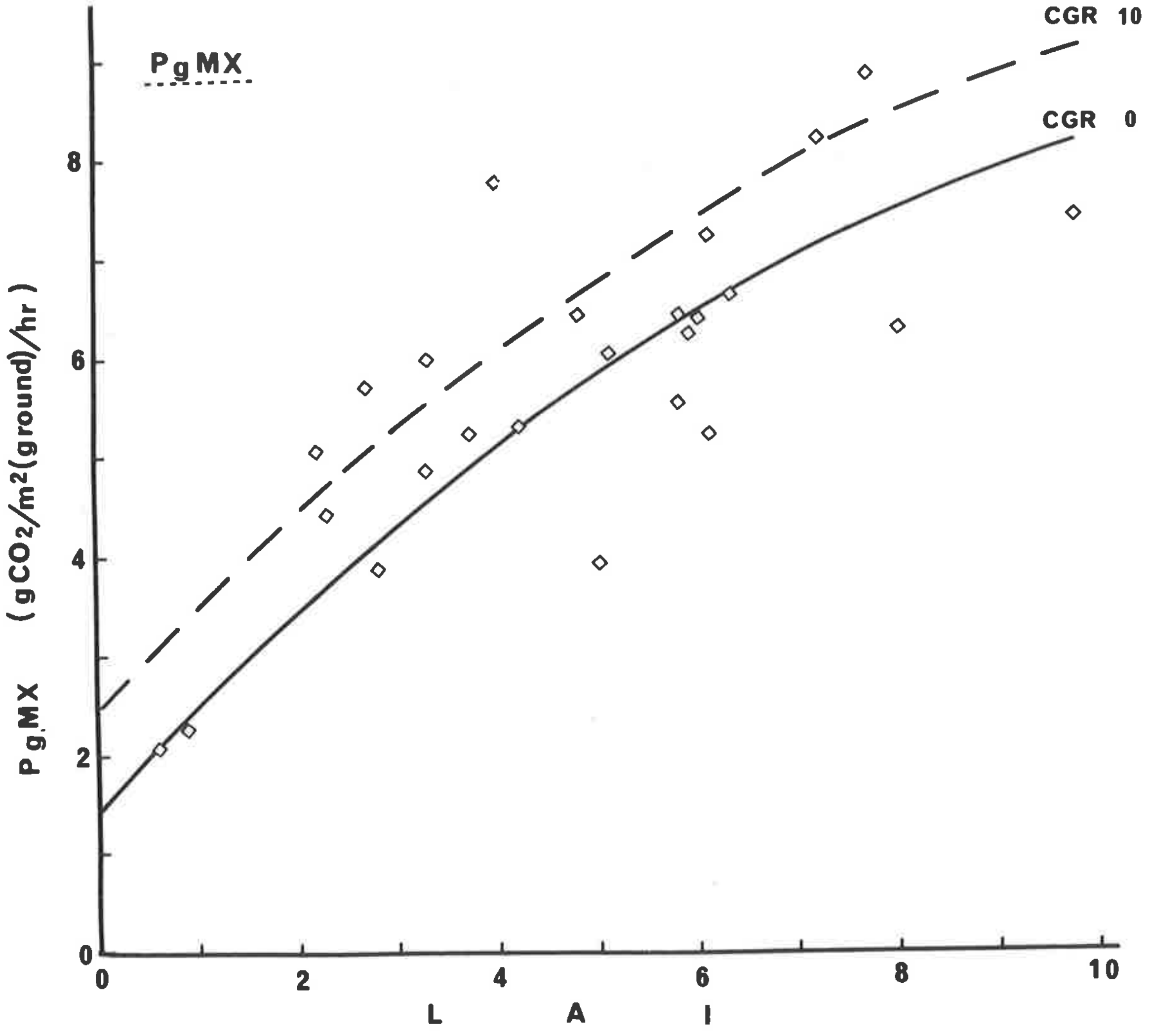
Plot of INS (initial slope) on leaf area index (LAI) for 25 light-gross photosynthesis curves obtained in the light energy experiments. The two straight lines used to relate INS and LAI in PHS-1 are shown.

(Bottom)

Plot of PgMX on leaf area index (LAI) for 25 light-gross photosynthesis curves obtained in the light energy experiments. Two curves are drawn from calculated data for crop growth rates (CGR) of 0 and 10 $g/m^2$/day to show the effect of variation in CGR on the relationship.

**PHS 1**


INS
0.04
0.03
0.02
0.01
0
I N S
0
2
4
6
8
10
L A I


PgMX
CGR 10
CGR 0
8
6
4
2
0
PgMX ( gCO2/m2(ground)/hr )
0
2
4
6
8
10
L A I

$$\text{INS} = 0.020\ \text{LAI} \quad \text{if} \quad \text{LAI} < 1.7$$

and EQ.23

$$\text{INS} = 0.034 \quad \text{if} \quad \text{LAI} > 1.7$$

Deviation from the two regression lines in EQ.23 (and from a fitted hyperbola) were calculated for each point in the figure. Analysis of variance showed the deviation to be not related to the current light energy (CLE) nor to CGR at that time so no allowance is made for effects of these factors.

Estimates of PgMX were analysed by multiple linear regression with LAI, CGR, CLE and SLA as variables. The two major contributors to variation in PgMX were LAI and CGR. The equation of best fit is:

$$\text{PgMX} = 1.433 + 1.059\ (\text{LAI}) - 0.03758\ (\text{LAI})^2 + 0.1066\ \text{CGR} \qquad \text{EQ.24}$$

$$(\text{with } R^2 = 0.689)$$

The relationship between PgMX and LAI at two levels of CGR is shown in Fig. 59 with experimental points. For any given LAI and CGR, INS (EQ.23) and PgMX (EQ.24) and the constants a, and b in EQ.19 can be calculated. Pg at any light quantum flux (LF) can be calculated as

$$\text{Pg} = a\ (\text{LF}) + b\ (\text{LF})^2 \quad \text{if LF} < \text{STLF}$$

and EQ.25

$$\text{Pg} = \text{PgMX} \quad \text{if LF} > \text{STLF}$$

Net $CO_2$ exchange rate (Pn) at a given light quantum flux (LF) is calculated as the difference between Pg and DR in EQ.20.

(ii) PHS-2 (for different constant temperatures). INS and PgMX were calculated from the data obtained in 5.4.0, and are plotted against the corresponding LAI in Fig. 60. No significant effect of temperature on INS was found by analysis of variance and a temperature factor is therefore not included for the estimation of INS. Two linear regressions were used:

$$\mathrm{INS} = 0.01224\ \mathrm{LAI}$$

$$\text{if}\quad \mathrm{LAI}\quad 2.5$$

and EQ.26

$$\mathrm{INS} = 0.0306$$

$$\text{if}\quad \mathrm{LAI}\quad 2.5$$

A hyperbola was fitted to the plot of PgMX on LAI excluding one point obtained at 16°C as this had an extremely high STLF. The equation of best fit is:

$$\mathrm{PgMX} = \frac{8.5532\ \mathrm{LAI}}{2.68 + \mathrm{LAI}} \qquad \text{EQ.27}$$

Deviations from the fitted lines were significantly related to temperature (F = 6.44** with d.f. of 2 and 18). A temperature factor for PgMX is therefore included in this model.

$$\mathrm{PgMX} = \frac{8.5532\ \mathrm{LAI}}{2.68 + \mathrm{LAI}} + 0.1458\ \mathrm{CT} - 2.934 \qquad \text{EQ.28}$$

When LAI is very small (< 1.0), the use of a constant term is not realistic, particularly at low CT and this is adjusted for the range of LAI 0 - 1.0 as follows:

$$\mathrm{PgMX} = \frac{8.5532\ \mathrm{LAI}}{2.68 + \mathrm{LAI}} \times \frac{1.458\ \mathrm{CT} - 6.11}{23.24} \qquad \text{EQ.29}$$

The relationship used in the model between LAI and PgMX at 16° and 24°C are also illustrated in Fig. 60.

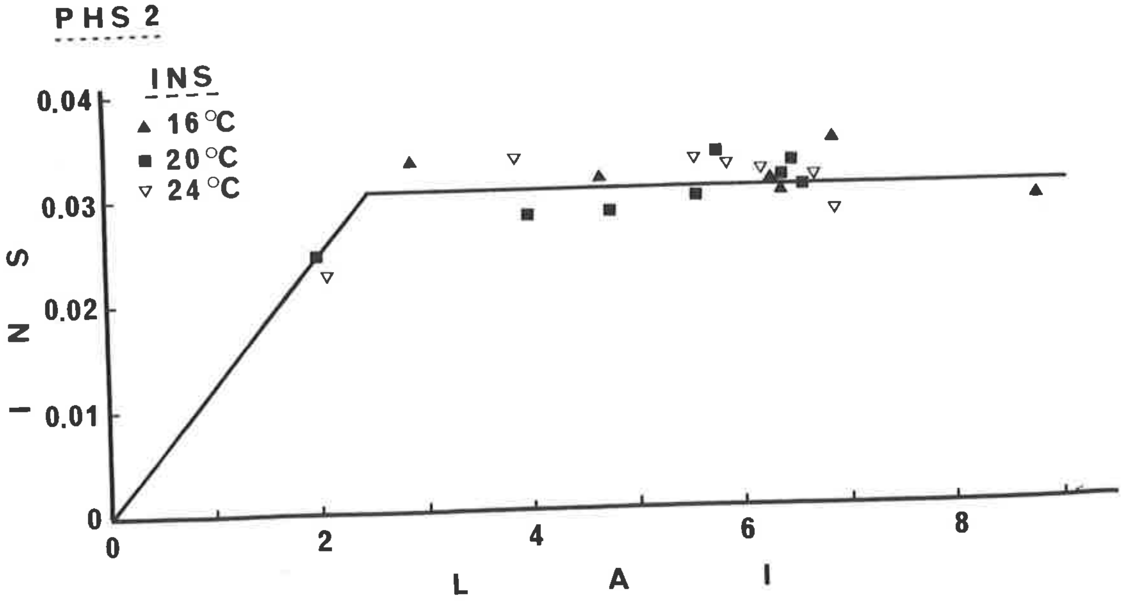
INS (EQ.26), PgMX (EQs.27, 28) and the constants a and b in EQ.19 for given values of LAI and CT can be calculated. Pg at any

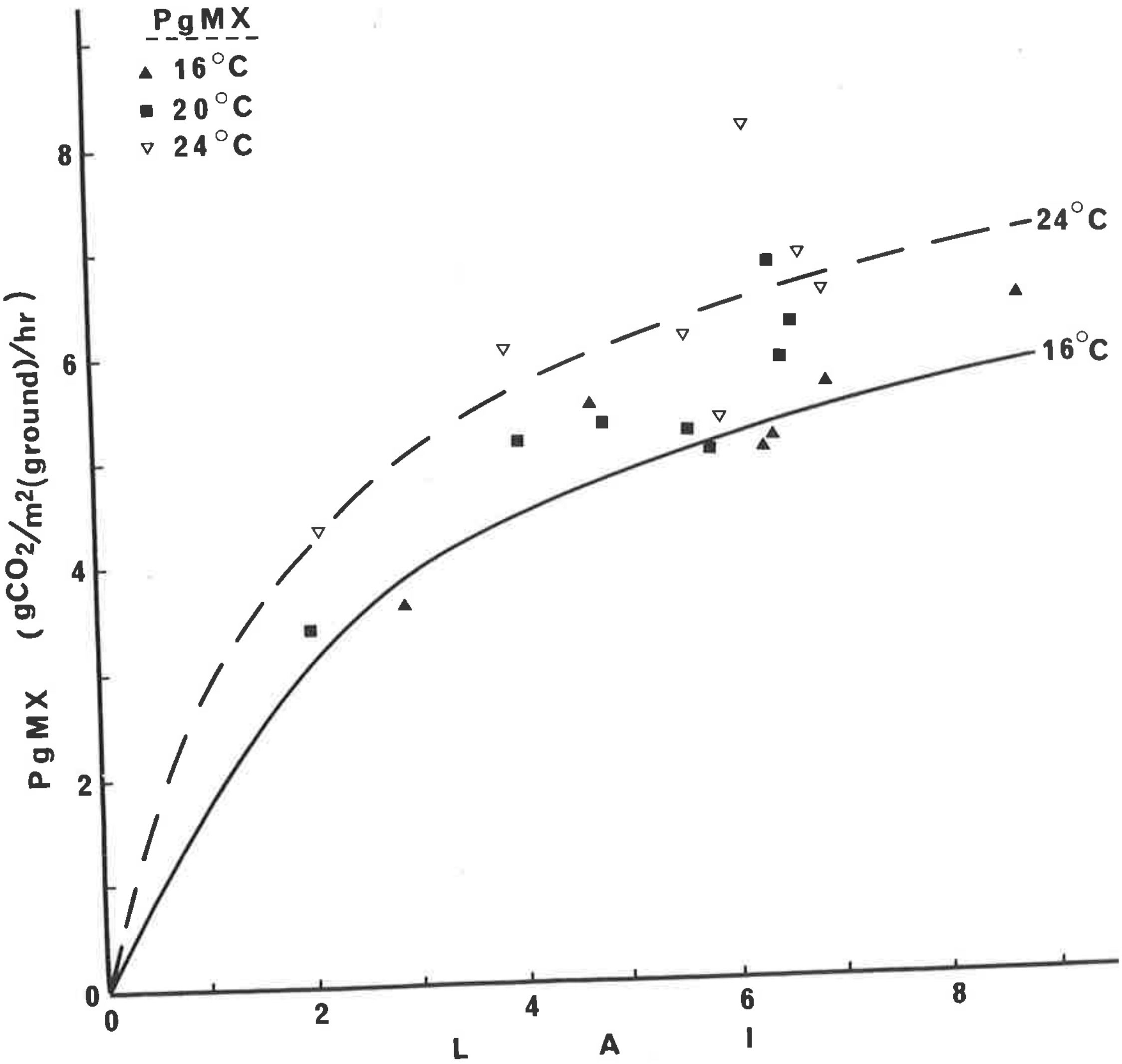
**Figure 60.** (Top)

Plot of INS (initial slope) on leaf area index (LAI) for 21 light-gross photosynthesis curves obtained in the temperature experiments. The two straight lines used to relate INS and LAI in PHS-2 are shown.

(Bottom)

Plot of PgMX on leaf area index (LAI) for 21 light-gross photosynthesis curves obtained in the temperature experiments. Two curves are drawn from calculated data, one for 24°C and the other for 16°C, to show the effect of growth temperature on the relationship.


PHS 2
INS
▲ 16°C
■ 20°C
▽ 24°C
0.04
0.03
0.02
0.01
0
I N S
0
2
4
6
8
L A I


PgMX
▲ 16°C
■ 20°C
▽ 24°C
8
6
4
2
0
PgMX (gCO₂/m²(ground)/hr)
24°C
16°C
0
2
4
6
8
L A I

light quantum flux (LF) can be calculated from EQ.25. Pn is the difference between Pg and DR.

### (f) Testing the Models

Accuracy of the models is tested by comparing the Pn data obtained in the experiments and those calculated from the models with particular values of variables obtained in the experiments.

(i) PHS-1 (for constant 20°C). Light-net photosynthesis curves were constructed by calculating Pn from the general equations at several values of LF for each of 25 experimental conditions with particular values of LAI, CGR and SDM. These are shown in Fig. 61 with the observed Pn values. The goodness of fit of each calculated curve to the data was judged by means of the ratio of the residual sum of squares from the fitted curve to the number of observations for each curve. Of the 25 possible comparisons, three are illustrated in the figure. One comparison shows the poorest fit and one the best fit. The remaining 23 curves were intermediate between them and one of the 23 curves is also shown in Fig. 61 as an intermediate fit.

In general, the calculated Pn curves fit the experimental results reasonably well. The fit is particularly good when LF is small as here DR and INS are estimated with considerable accuracy, but Pn at large LF is not reliably estimated because of the less accurate estimate of PgMX.

(ii) PHS-2 (for different constant temperatures). Pn was calculated from the general equations for each of 22 experimental conditions with particular values of LAI, SDM and CT. The light-net photosynthesis curve from the general equations was then compared with that obtained in the experiment. Three representative graphs selected in the similar way in PHS-1 out of 22 measurements are shown in Fig. 62.

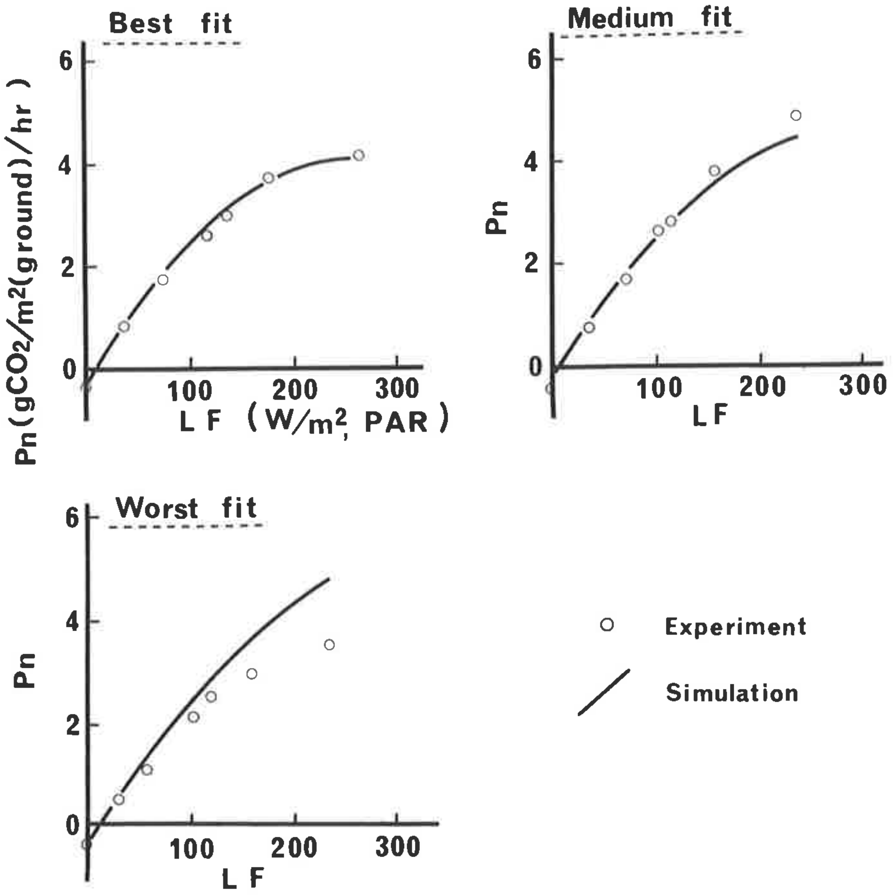
Figure 61. (Top)

Reproducibility of light-photosynthesis curve by PHS-1. The 3 graphs show the range of goodness of fit from 25 comparisons of calculated curves with experimental points.

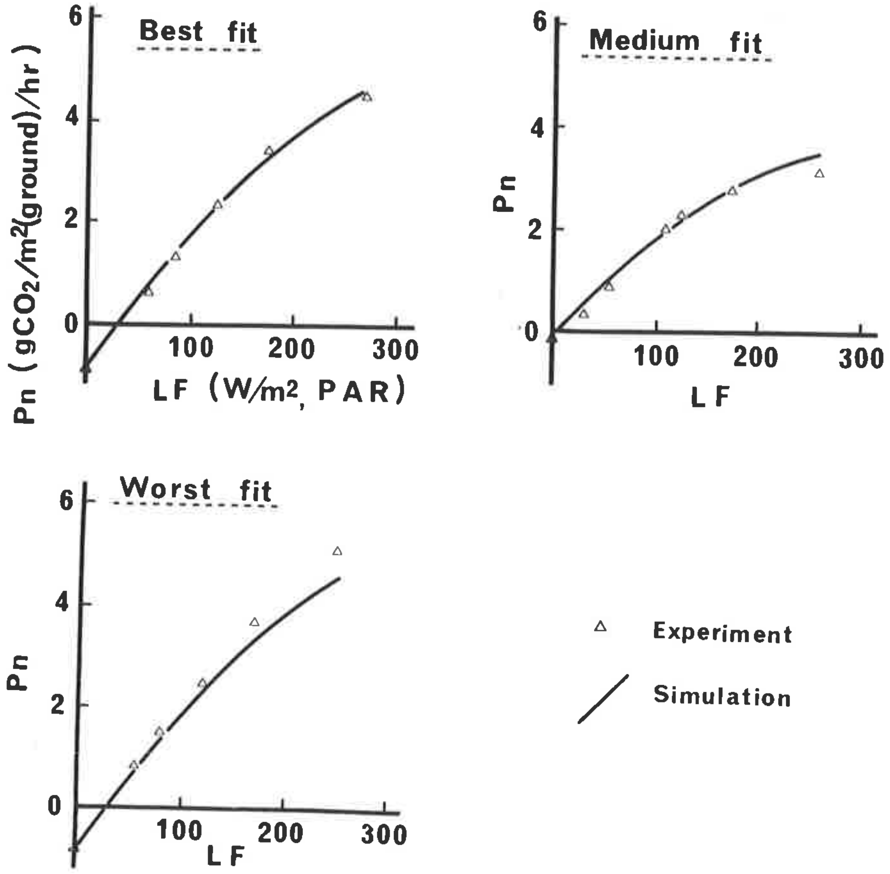
Figure 62. (Bottom)

Reproducibility of light-photosynthesis curve by PHS-2. The 3 graphs show the range of goodness of fit from 22 comparisons of calculated curve with experimental points.

PHS 1


Best fit
Medium fit
Worst fit
Pn (gCO2/m2(ground)/hr )
Pn
0
2
4
6
100
200
300
L F (W/m2, PAR )
L F
Experiment
Simulation

PHS 2


Best fit
Medium fit
Worst fit
Pn ( gCO2/m2(ground)/hr )
Pn
0
2
4
6
100
200
300
LF (W/m2, PAR)
L F
Experiment
Simulation

xperimental data are well reproduced by the model particularly at small LF.

(g) Application of the Models

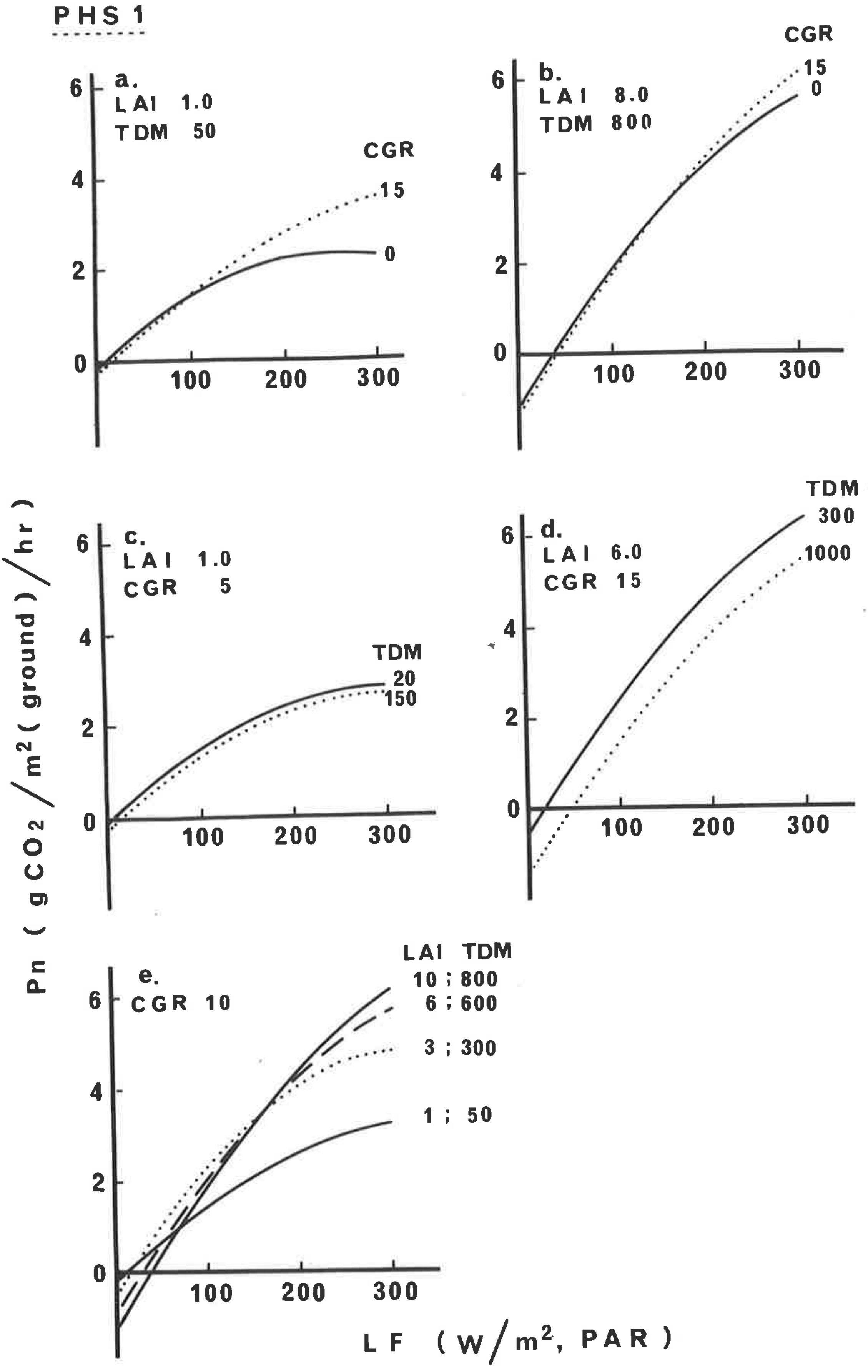
(i) PHS-1 is used to determine quantitative relationships between Pn and each of LAI, CGR and TDM at 20°C. In Fig. 63 (a) and (b) the effect of variation in CGR is shown for given values of LAI and TDM. LF is instantaneous flux, hence it is possible to examine a community with zero CGR at a range of light flux although the community may encounter high light flux very rarely. The value of TDM is chosen from Fig. 18 as an average value to be expected for the corresponding LAI. The effect of variation in CGR is small except at large LF and at small LAI.

In Fig. 63 (c) and (d) the effect of variation in TDM alone is shown for given LAI and CGR values. Two extreme values of TDM for a given LAI are chosen from Fig. 6 (after adjusting from SDM to TDM), Fig. 18 and Fig. 35. The effect of TDM on Pn can be seen to be considerable over a wide range of LF.

The effects of variation of LAI and TDM together are examined for a given CGR in Fig. 63 (e). The value of TDM is chosen as above. At large LF Pn is strongly influenced by LAI whilst at small LF Pn is strongly influenced by the value of DR.

(ii) PHS-2 is used to determine quantitative relationships between Pn and each of LAI, TDM and CT (Fig. 64). Values of TDM for a given LAI at 12°, 20° and 30°C were selected from data obtained in the 1970 and 1972 experiments. At small LAI and TDM, temperature has a negligible effect at low LF, but has a large effect at large LF. At large LAI and TDM, Pn at low LF is inversely related to CT. Pn at any CT is affected by the ratio of LAI/TDM: if TDM is large for a

Figure 63. Calculated light-net photosynthesis curves by PHS-1 for different values of leaf area index (LAI), total dry matter (TDM) and crop growth rate (CGR) to show effects of CGR (a, b), effects of TDM (c, d) and effects of LAI and TDM (e) on the relationship.


P H S 1
a.
L AI 1.0
T DM 50
CGR
15
0
b.
L A I 8.0
TDM 800
CGR
15
0
c.
L A I 1.0
C GR 5
TDM
20
150
d.
L A I 6.0
CGR 15
TDM
300
1000
e.
CGR 10
LAI TDM
10 ; 800
6 ; 600
3 ; 300
1 ; 50
0
2
4
6
100
200
300
Pn ( g CO2 / m2 ( ground ) / hr )
L F ( W / m2, P A R )

given LAI, a small Pn will be obtained as shown by PHS-1 in Fig. 63 (c) and (d).

## 6.3.0. Systems Analysis of Growth of Subterranean Clover Communities (CLO-GRO)

Two models to calculate dry matter production of subterranean clover communities over a given period of time are constructed; one, CLO-GRO 1 uses PHS-1 to calculate net photosynthetic rate (Pn) with particular initial values of LAI, TDM and CGR and variable solar energy inputs at 20°C. CLO-GRO 2 uses PHS-2 to calculate Pn with particular initial values of LAI and TDM and variable solar energy inputs at any constant temperature between 10° and 30°C. The light fluxes used are those occurring naturally at Adelaide but those for any locality can be written into the programme.

### 6.3.1. CLO-GRO 1

(a) Construction

A diagram (Fig. 65) shows the environmental and plant variables incorporated in the model.

(i) Daily Net Production (DNP). Instantaneous light fluxes are read at 15 minute intervals and Pn calculated for each flux value using PHS-1. DNP is obtained by summing all Pn values over 24 hours. DNP is expressed as g DM/m$^2$/day. Daily gross photosynthesis (DPg) is obtained as the sum of Pg for a day. DNP can also be obtained as the difference between DPg and daily (24 hour) dark respiration (DDR).

(ii) Current Light Energy (CLE) for day n is obtained by averaging total daily light energy (DLE) (a sum of LF for a day) for the

Figure 64. Calculated light-net photosynthesis curves from PHS-2 showing the effects of current temperature on the relationship at different values of leaf area index (LAI) and total dry matter (TDM). Values of TDM were selected for each temperature from Figure 34 for each value of LAI.

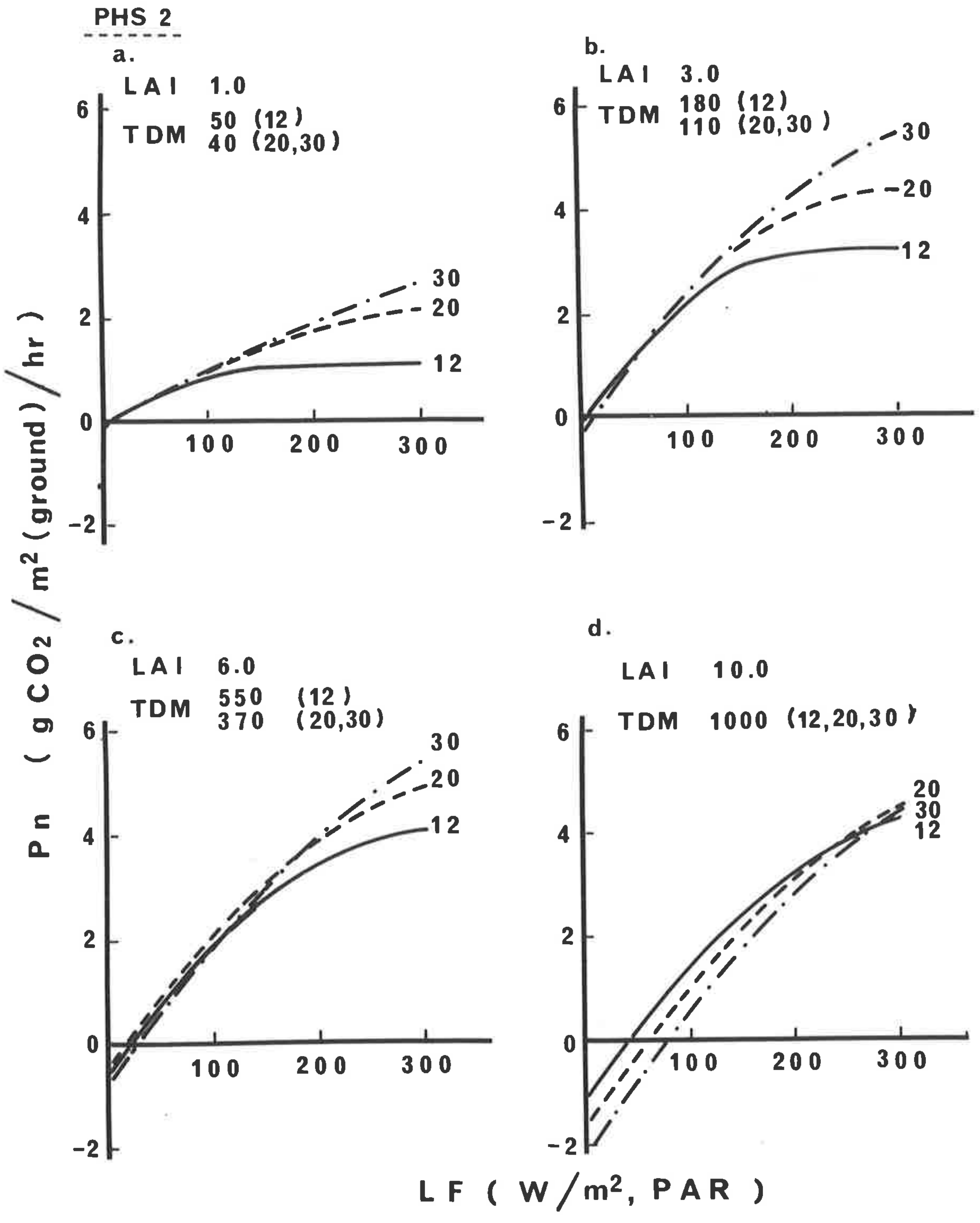
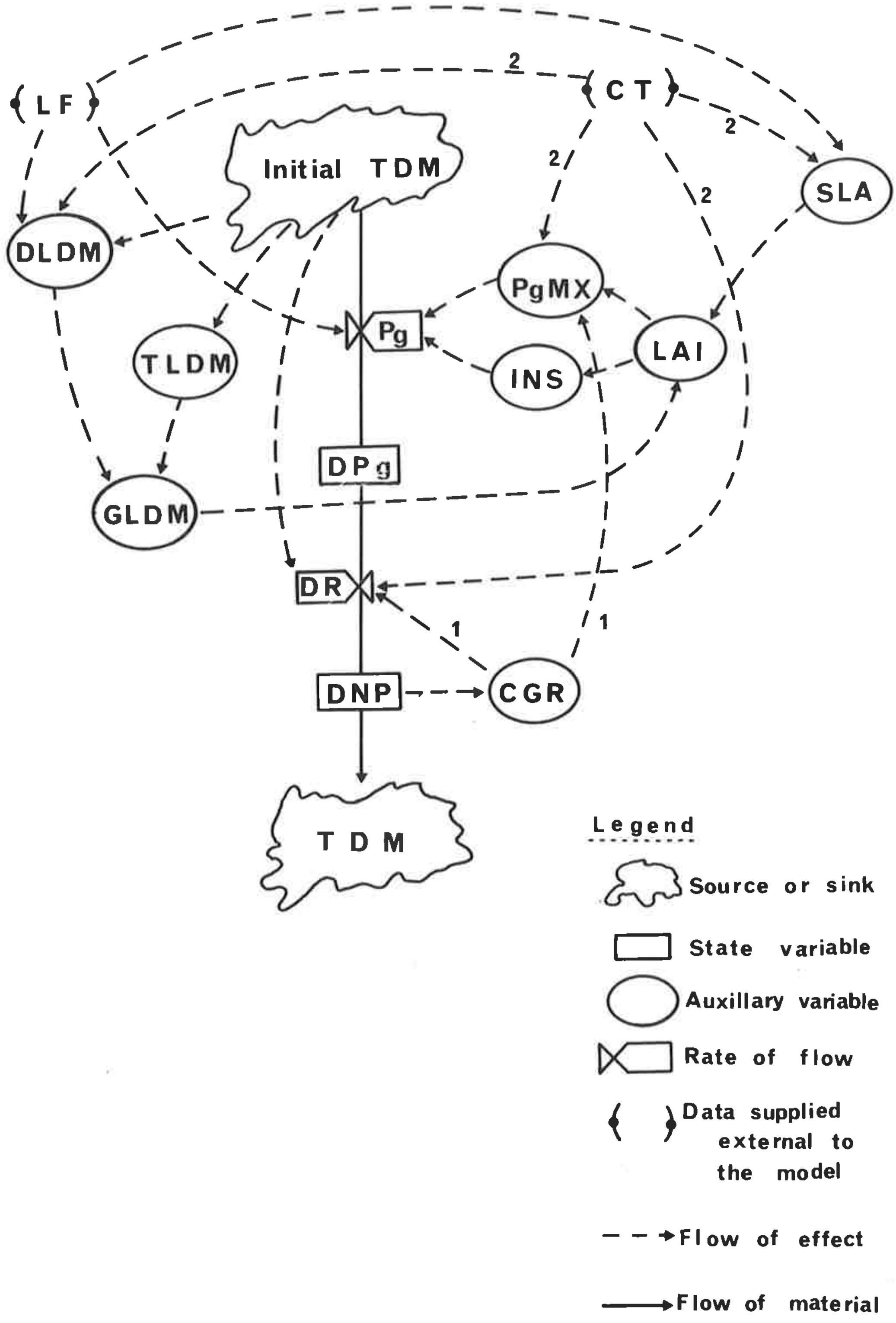

PHS 2
a.
LAI 1.0
TDM 50 (12) 40 (20,30)
b.
LAI 3.0
TDM 180 (12) 110 (20,30)
c.
LAI 6.0
TDM 550 (12) 370 (20,30)
d.
LAI 10.0
TDM 1000 (12,20,30)
30
20
12
6
4
2
0
-2
100
200
300
Pn (g CO2 / m2 (ground) / hr)
LF (W/m2, PAR)

Figure 65. Flow diagram showing the relationships between plant attributes and environmental variables, and between plant attributes as used in CLO-GRO. 1 in the graph indicates the relationship used only in CLO-GRO 1 and 2 indicates the relationship used only in CLO-GRO 2.


LF
CT
2
2
2
2
Initial TDM
SLA
DLDM
PgMX
Pg
TLDM
LAI
INS
DPg
GLDM
DR
1
1
DNP
CGR
TDM
Legend
Source or sink
State variable
Auxillary variable
Rate of flow
Data supplied external to the model
Flow of effect
Flow of material

previous 7 days. CLE rather than DLE is used in the model to reduce daily fluctuation. If n is less than 8, CLE is calculated as an average value of DLE for the whole period.

(iii) Specific Leaf Area (SLA) is expressed as

$$\text{SLA} = 309 + \frac{1449}{4.225 + \text{CLE}} \qquad \text{EQ.30}$$

The equation was obtained from the three autumn experiments (Fig. 17) as the data were intermediate for the whole ten experiments.

(iv) Dead Leaf Dry Matter (DLDM). The best equation for the estimation of DLDM obtained from the results shown in Fig. 16 is:

$$\text{DLDM} = (5.34 + 0.01946\ \text{TDM} - 0.4748\ \text{CLE}) \times \text{TDM} \times 10^{-2} \qquad \text{EQ.31}$$

This allows for increase in DLDM with increase in TDM and with decrease in CLE.

(v) Total Leaf Dry Matter (TLDM) is calculated as

$$\text{TLDM} = \left(29.08 + \frac{10582}{519 + \text{TDM}}\right) \times \text{TDM} \times 10^{-2} \qquad \text{EQ.32}$$

The proportion of TLDM to TDM decreases with increase in TDM but is not affected by CLE (see Fig. 16).

(vi) Green Leaf Dry Matter (GLDM) is the difference between TLDM and DLDM.

(vii) LAI for day n is calculated as the product of SLA and GLDM.

(viii) Crop Growth Rate (CGR) for day n is calculated as an average of DNP for the 7 days prior to day n. If n is less than 8, CGR is calculated as an average DNP for the whole period.

(ix) Total Dry Matter (TDM) for day n is the sum of TDM at day n-1 and DNP at day n-1.

Three canopy attributes, TDM, LAI and CGR calculated after simulation for day n, are used in PHS-1 to calculate Pg (or Pn) at 15 minute intervals at day n + 1. Plant attributes themselves are updated at the end of each day.

Fortran program CLO-GRO 1 is shown in Appendix 1.

### (b) Testing the Model

The growth experiments involving variation in light energy described in 5.3.0 were simulated by CLO-GRO 1 with initial values of TDM, LAI and estimated CGR obtained at the first or at any subsequent harvest. Nine simulations were run for up to 130 days and the growth curves constructed in this way compared with the actual curves obtained by dry matter harvesting to test if the model could reproduce the experimental results.

The model growth curves are similar in shape to the actual growth curve with varying degrees of accuracy in the estimated value of TDM at particular times. Each of the nine curves may be classified into one of three groups according to the accuracy of prediction: (1) a poor fit (overestimation) during the middle-late growth period (Su72a, Sp71); (2) a poor fit (underestimation) during early stages of growth (A72c, W71, Su72c); and (3) a good fit in general (A72a, Sp70, Su72b, A72b). Three of these curves are shown in Fig. 66 and simulated plant attributes affecting growth are shown in Fig. 67 with actual data.

(i) Su72a. In this curve TDM is overestimated after Harvest 2 but when the simulation starts from Harvest 4, TDM is accurately predicted. Thus the main difference between simulation and experiment

Figure 66. Comparison of dry matter growth curves obtained by harvesting in the light energy experiments and by simulation by CLO-GRO 1.

Top: Su72a, an example of overestimation of total dry matter by simulation when started from 1st harvest.

Middle: A72c, an example of underestimation of total dry matter by simulation when started from 1st harvest.

Bottom: A72a, an example of good fit of total dry matter by simulation.

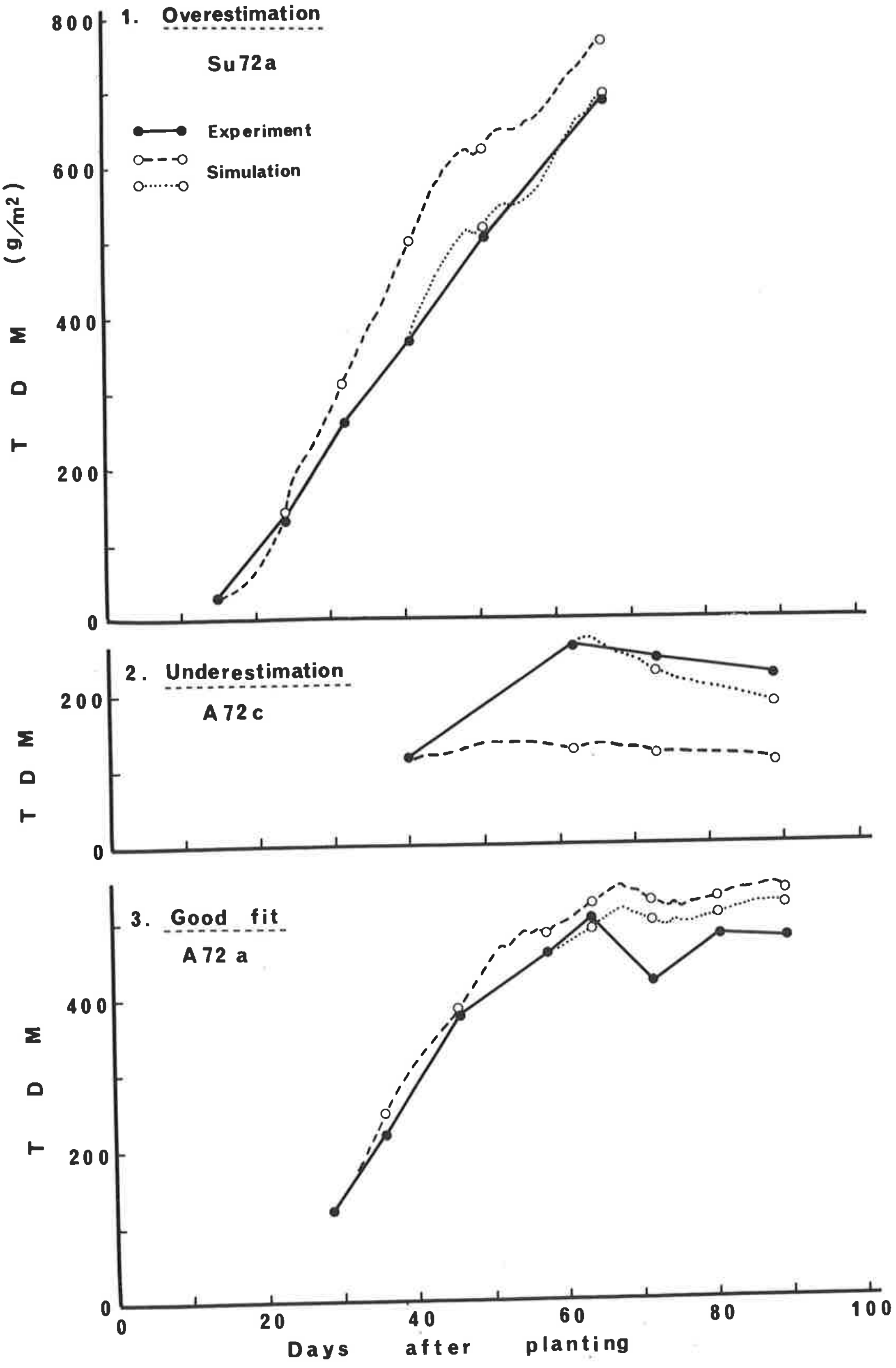
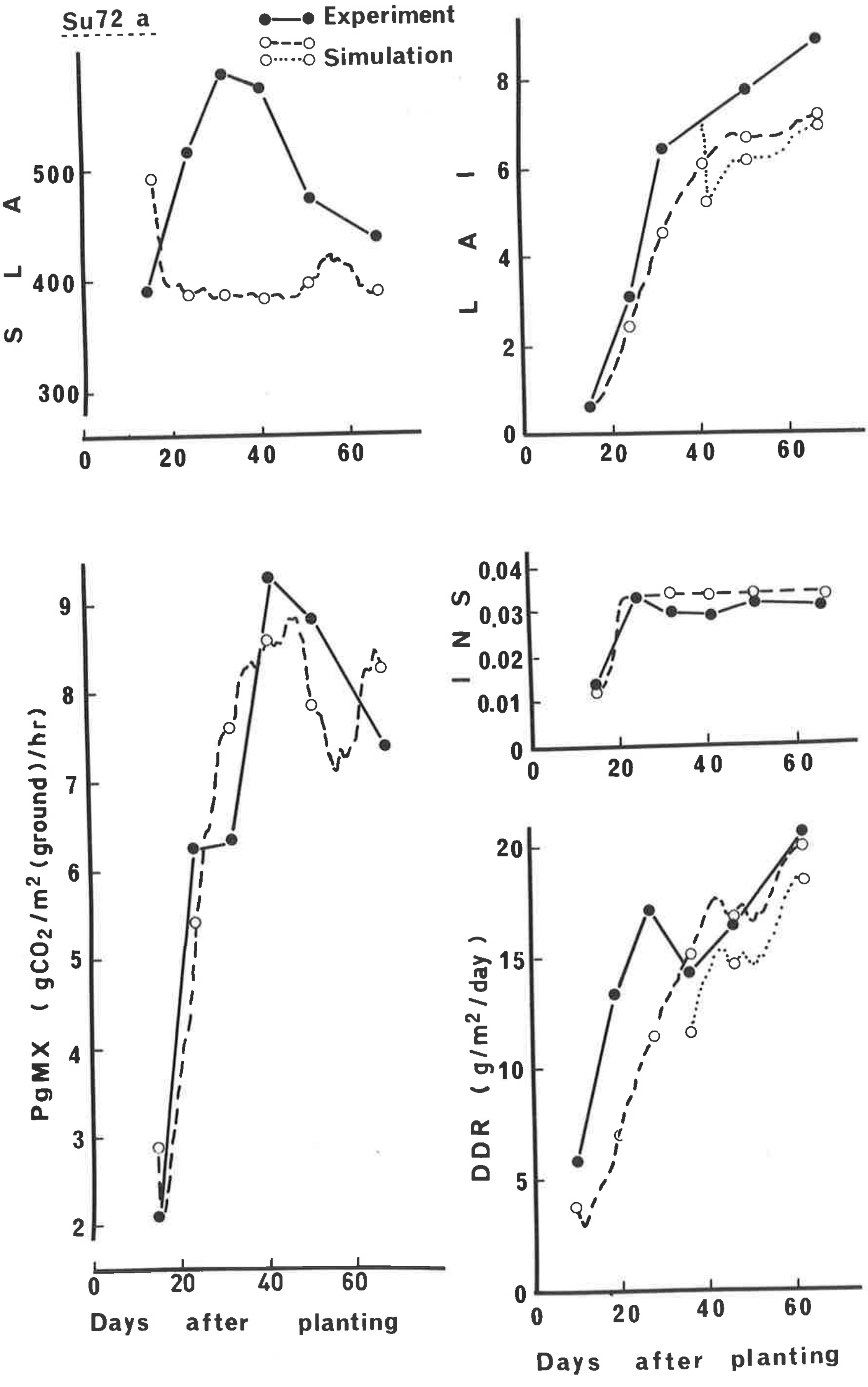

1. Overestimation
Su72a
Experiment
Simulation
800
600
400
200
0
T D M (g/m²)
2. Underestimation
A72c
200
0
T D M
3. Good fit
A72 a
400
200
0
T D M
0
20
40
60
80
100
Days after planting

Figure 67. Change in some plant attributes with time as simulated by CLO-GRO 1 compared with values obtained in the light energy experiments.

Su72a - an example of overestimation of total dry matter by the model.


Su72 a
●—● Experiment
○--○ ○·····○ Simulation
SLA
300
400
500
0 20 40 60
LAI
0 2 4 6 8
0 20 40 60
PgMX ( gCO$_2$/m$^2$ (ground)/hr)
2 3 4 5 6 7 8 9
0 20 40 60
Days after planting
INS
0 0.01 0.02 0.03 0.04
0 20 40 60
DDR ( g/m$^2$/day )
0 5 10 15 20
0 20 40 60
Days after planting

<u>Figure 67.</u> A72c – an example of underestimation of total dry matter by the model.

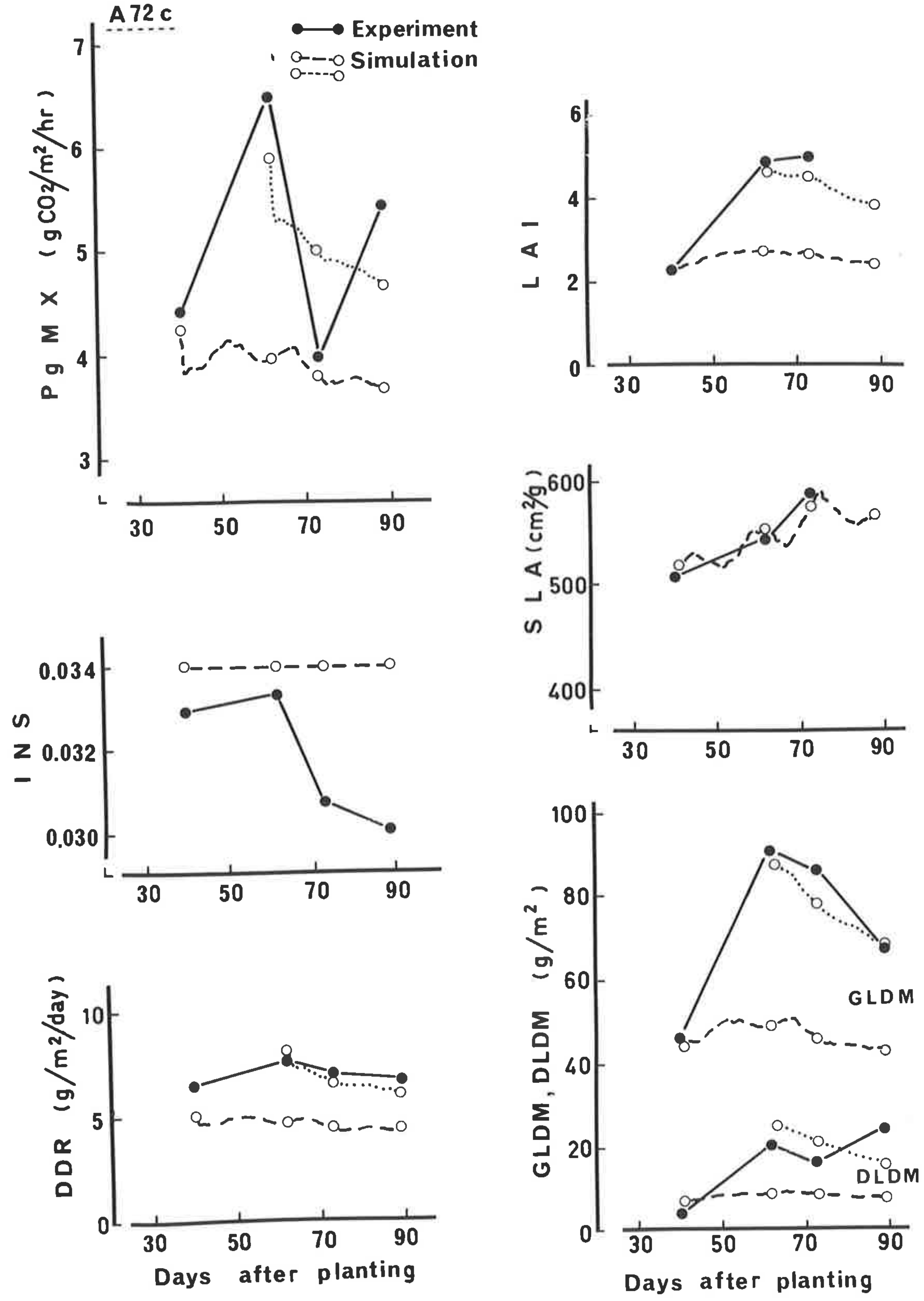
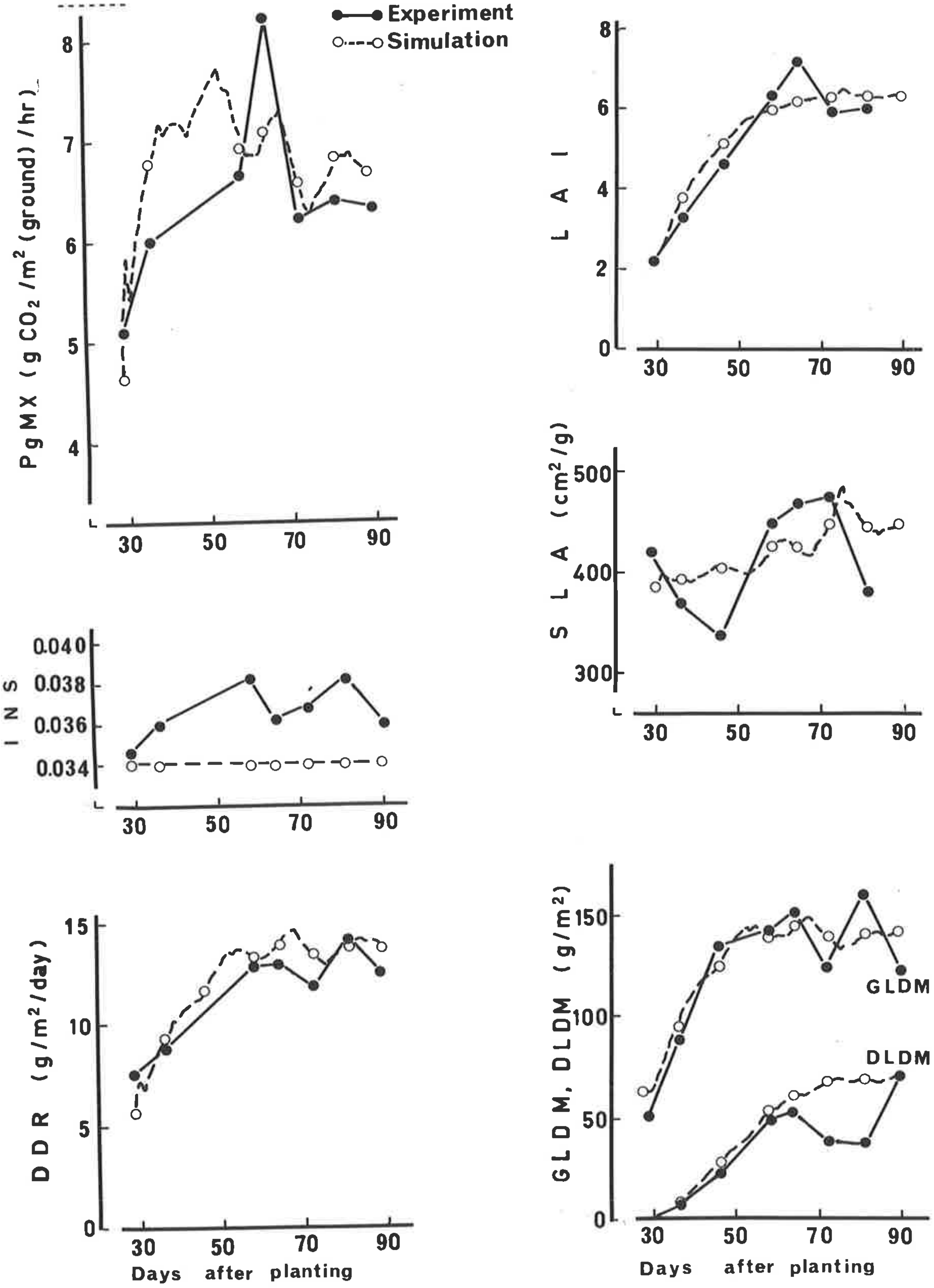

A 72 c
Experiment
Simulation
P g M X ( g CO2/m2/hr )
7
6
5
4
3
30
50
70
90
L A I
6
4
2
0
S L A (cm2/g)
600
500
400
I N S
0.034
0.032
0,030
DDR (g/m2/day)
10
5
0
GLDM, DLDM (g/m2)
100
80
60
40
20
0
GLDM
DLDM
Days after planting
Days after planting

Figure 67. A72a - an example of good fit of total dry matter by the model.

A72 a


Experiment
Simulation
PgMX (g CO₂ /m² (ground) /hr)
8
7
6
5
4
30
50
70
90
L A I
8
6
4
2
0
S L A (cm²/g)
500
400
300
I N S
0.040
0.038
0.036
0.034
D D R (g/m²/day)
15
10
5
0
Days after planting
GLDM, DLDM (g/m²)
150
100
50
GLDM
DLDM

occurred between Harvest 2 and Harvest 4. The experimental plants had an exceptionally high SLA, and a high LAI. At Harvest 3, PgMX and INS, however, were smaller than that predicted. This was considered to be due to poor nutrient supply in the experiment (see 5.2.3), which also increased DDR up to Harvest 3. At the later stages of the experiment when the problem of nutrient supply was solved, these plant attributes as well as TDM are accurately predicted by the model.

(ii) A72c. TDM is always underestimated by the model, particularly from Harvest 1 to Harvest 2. This is probably due partly to a small PgMX in the model at the early stages of growth which results in small LAI. However, when simulation was started from Harvest 2, TDM was still under-estimated despite the fact that INS was overestimated in the model. This suggests that some other factors, not included in the model, may be involved in determining dry matter production.

(iii) A72a. TDM is fairly well predicted by the model in this curve although the model slightly overestimates TDM at the second half of growth period. All plant attributes except INS are reasonably well predicted. High PgMX in the model probably does not explain the slightly high TDM in the second half of the growth period. Decomposition of dead leaves may be involved in the apparent low TDM in the experiment.

### (e) Application of the Model

A reasonably good fit by the model to actual dry matter curves under known conditions indicates that a wider application may be sought. It is of interest to determine patterns of growth in response to seasonal variation in solar radiation at constant temperature. With this objective, simulation is started at different times of the year 1971 (i.e. variation in planting date) and with different initial amounts of TDM (i.e. variation in planting density) with 100% solar energy. Although growth at 100% solar energy is an extrapolation from the 55% solar energy which was obtained in the glasshouses, this simulation is conducted to estimate growth in the field under ideal conditions. Although a canopy with high initial TDM has the characteristics of a mature canopy in the simulation it is recognised that the canopy and plant attributes resulting from high planting density may not be exactly similar to those of a mature canopy at the same dry matter.

It may be seen in Fig. 68 that when the simulation starts in June, crop growth rate at the early stages of growth is highest for communities where the initial TDM is 50-100 g/m$^2$. Subsequently growth rate is inversely related to initial TDM and this results in almost no differences in TDM after 200 days simulation for different initial amounts. Simulations started on August 1, September 1 and October 1 show a high growth rate to occur and that 'planting' up to the end of September results in the same amount of dry matter at the end of December as that obtained when 'planting' occurs in June. Thus it is clear that at a moderate temperature of 20$^o$C and with no restrictions on growth other than radiation, a theoretical upper limit of about 15 tonne/ha dry matter yield is achieved, independent of plant density and time of planting from June 1 to October 1.

When, during a simulation, a particular day had a CLE within $\pm$ 0.21 MJ/m$^2$/day at each of 7 selected values between 0 and 30 MJ/m$^2$/day, CGR at that day was calculated and the corresponding TDM read from the curve. The relationship between CGR and TDM is shown for each level of CLE in Fig. 69. Results obtained from simulation with 55% solar energy are also shown for a comparison with those obtained with 100% solar energy.

It can be seen that CGR increases with increase in TDM up to a

<u>Figure 68</u>. Simulated growth curves for 20°C by CLO-GRO 1 for different times of planting and different plant densities. Light energy levels used for the simulation were those measured at Adelaide in 1971.

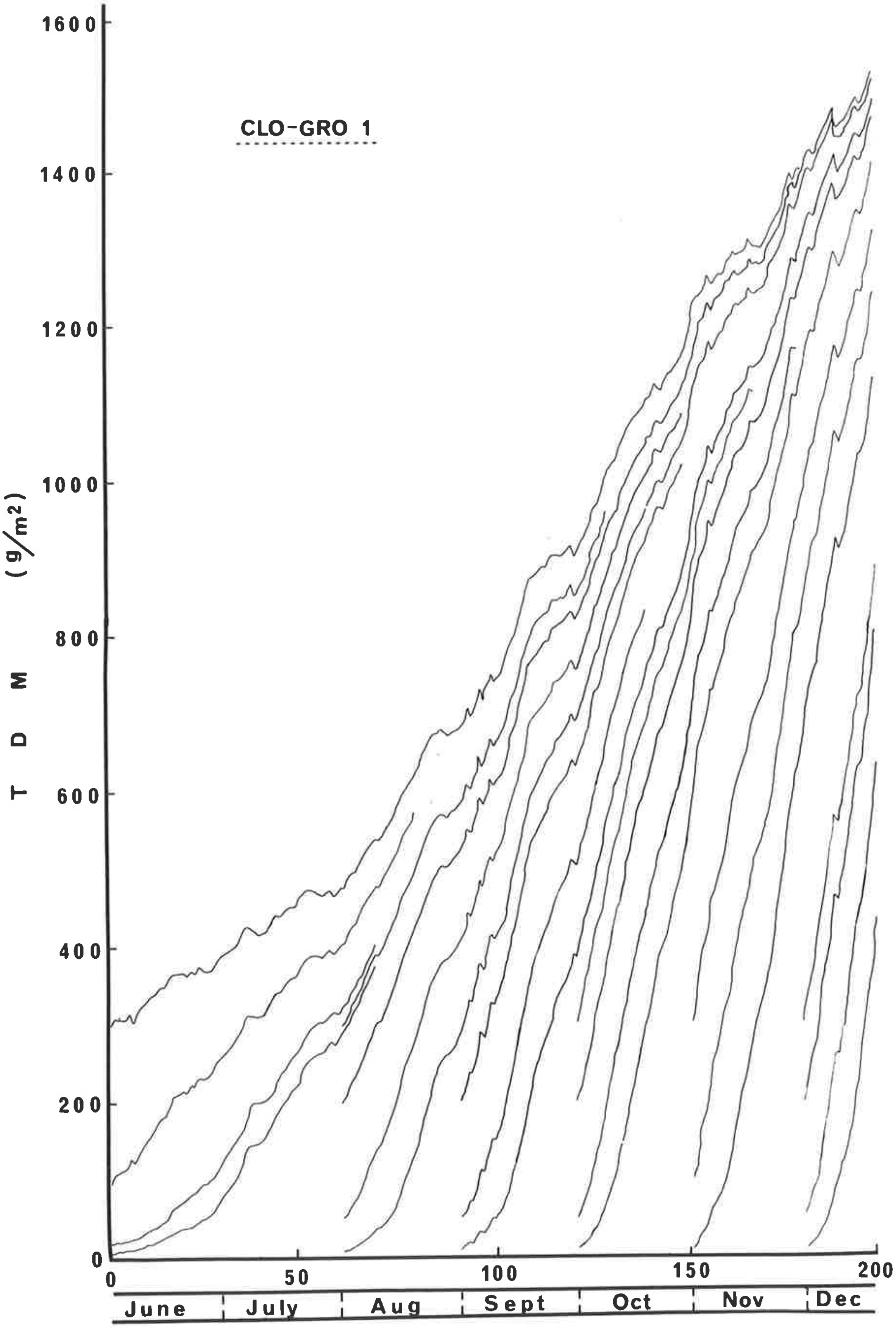
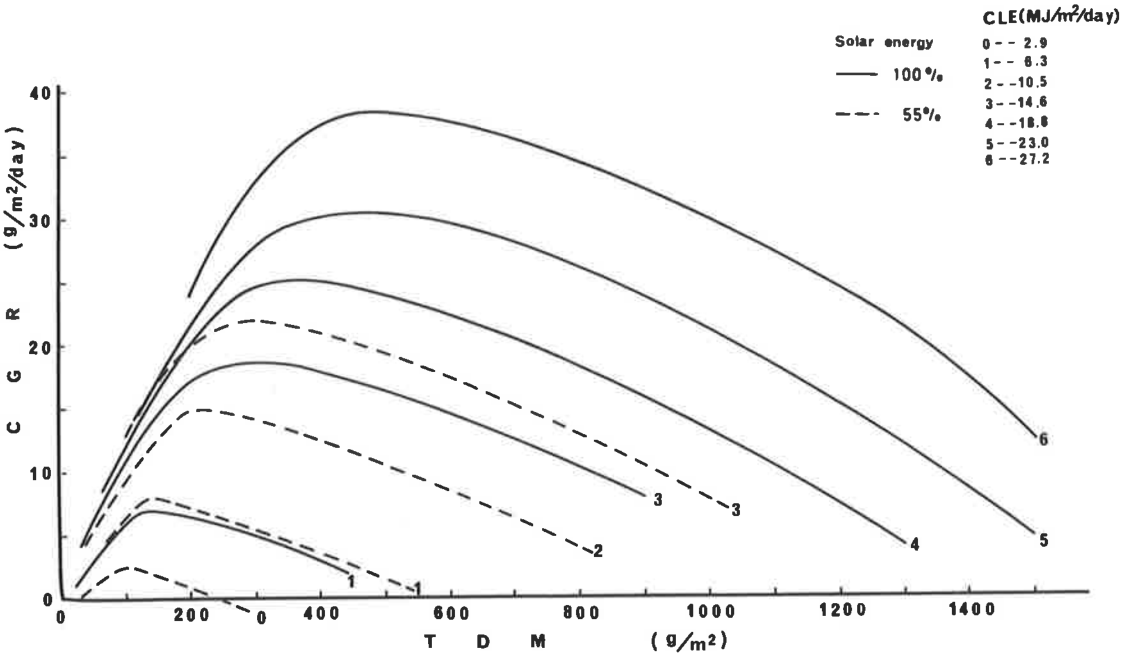

CLO-GRO 1
T D M (g/m²)
1600
1400
1200
1000
800
600
400
200
0
0
50
100
150
200
June
July
Aug
Sept
Oct
Nov
Dec

**Figure 69.** (Top)

The relationship between crop growth rate (CGR) and total dry matter (TDM) at different current light energy levels (CLE) obtained from simulation by CLO-GRO 1. Smoothed curves were obtained after plotting values of CGR and TDM for a simulation "day" with CLE values ± 0.21 MJ/m$^2$/day of the designated values shown for each curve. Simulations under 55% solar radiation (dotted lines) are shown for comparison with 100% solar radiation (solid lines).

**Figure 70.** (Bottom and Following Page)

Comparison of total dry matter growth curves at 4 temperatures by CLO-GRO 2 with experimental results in 1972.


Solar energy
100%
55%
CLE(MJ/m²/day)
0 -- 2.9
1 -- 6.3
2 -- 10.5
3 -- 14.6
4 -- 18.8
5 -- 23.0
6 -- 27.2
CGR (g/m²/day)
0
10
20
30
40
0
200
400
600
800
1000
1200
1400
TDM (g/m²)
0
1
1
2
3
3
4
5
6

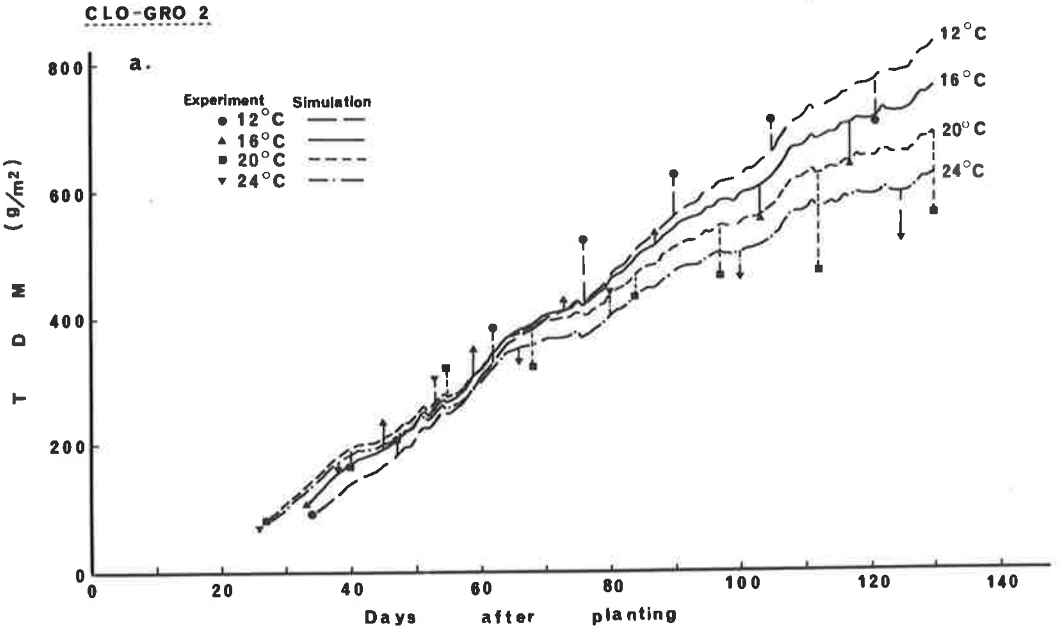
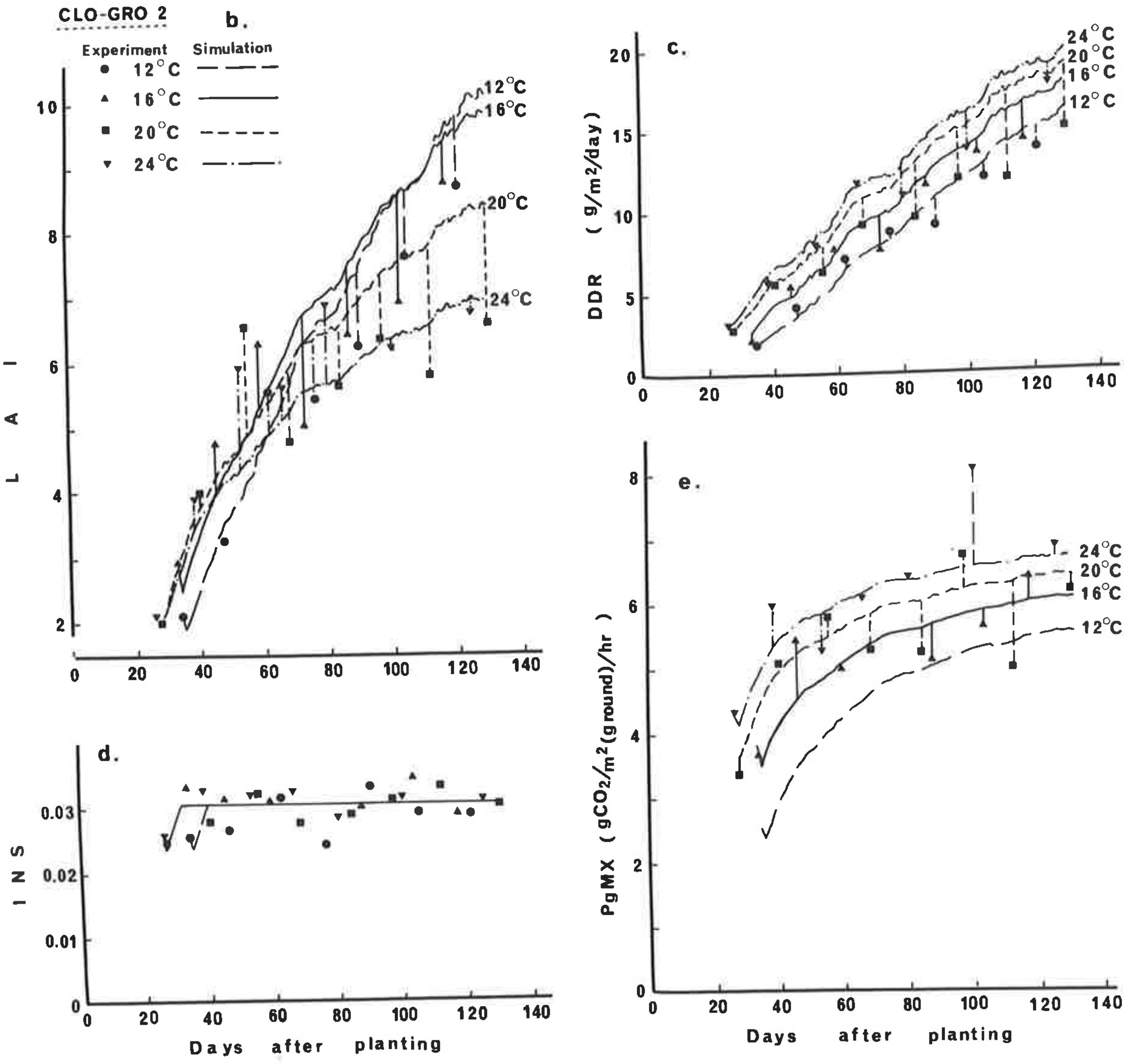

CLO-GRO 2
a.
Experiment
Simulation
● 12°C
▲ 16°C
■ 20°C
▼ 24°C
12°C
16°C
20°C
24°C
TDM (g/m²)
0
200
400
600
800
0
20
40
60
80
100
120
140
Days after planting

Figure 70. Comparisons of change in some plant attributes with time (leaf area index (LAI), daily dark respiration (DDR), initial slope of light-gross photosynthetic rate (INS) and maximum rate of gross photosynthesis (PgMX)) with that obtained by the temperature experiment.


CLO-GRO 2
b.
Experiment
Simulation
● 12°C
▲ 16°C
■ 20°C
▼ 24°C
L A I
2
4
6
8
10
12°C
16°C
20°C
24°C
0
20
40
60
80
100
120
140
c.
DDR ( g/m2/day)
0
5
10
15
20
24°C
20°C
16°C
12°C
d.
I N S
0
0.01
0.02
0.03
Days after planting
e.
PgMX ( gCO2/m2(ground)/hr )
0
2
4
6
8
24°C
20°C
16°C
12°C
Days after planting

maximum, then decreases almost linearly with further increase in TDM. However, as the model predicts a small CGR under low light energy particularly at small TDM, CGR may be underestimated at low light energy in the figure. The figure shows that the optimum TDM for CGR and the value of maximum CGR increase linearly with increase in CLE. The values of TDM at which CGR = 0 or DPg = DDR may be obtained by extrapolation. These values are also linearly related to CLE.

It can also be seen that CGR at 55% of the solar energy flux is slightly higher than that at 100% for the same daily input of energy. This can be ascribed to the fact that at 55% of the solar energy flux a much longer daylength is required to obtain the same total daily energy input.

### 6.3.2. CLO-GRO 2

(a) <u>Construction</u>

The model to calculate dry matter production of subterranean clover communities at any constant temperature between $10^{\circ}$ and $30^{\circ}$C is substantially the same as CLO-GRO 1 with temperature adjustment for the following processes:

(i) Temperature effects on SLA (see Fig. 38) are corrected by adding

$$CF = -\sqrt{9200 - 640CT} - 60 \text{ if } CT < 14.374$$

or EQ.33

$$CF = \sqrt{640CT - 9200} - 60 \text{ if } CT > 14.375$$

to the SLA/CLE relation used in CLO-GRO 1. This correction factor (CF) is the only approximation available from the data.

(ii) DLDM is expressed as:

$$\text{DLDM} = \left(11.21 - \frac{2770}{194 + \text{TDM}}\right) \times \left(\frac{\text{CT}}{8} - 1\right) \times \text{TDM} \times 10^{-2}$$

if TDM > 55

and EQ.34

$$\text{DLDM} = 0 \qquad \text{if TDM} < 55$$

This allows for increase in DLDM with increase in CT (see Fig. 37).

(iii) LAI is affected by temperature through SLA and through DLDM and is calculated as:

$$\text{LAI} = \text{SLA} \times (\text{TLDM} - \text{DLDM}) \times 10^{-4}$$

(iv) Two canopy attributes TDM and LAI and the environmental variables CT and LF are fed to PHS-2 to calculate Pg or Pn at 15 minute intervals. DPg, DDR and DNP are calculated every day and all plant attributes are updated every day as in CLO-GRO 1. Fortran program CLO-GRO 2 is shown in Appendix II.

### (b) Testing the Model

Validity of the model was examined by comparing simulated growth curves with actual points at each of four temperatures for conditions described in 5.4.0. Results of simulation for the 1972 experiment are shown in Fig. 70. SLA in the simulation was adjusted since the 1972 experiment had a higher SLA than that obtained in the 1970 experiment. It was found, however, that such adjustment changed the simulated growth curve only slightly. Results of the simulation show a similar trend in the effect of temperature on dry matter production to that apparent from the experimental results - optimum temperature for growth decreases with time and the final dry matter yield is inversely related to temperature.

At $12^{o}$ and $16^{o}$C, the model underestimated TDM over the major experimental period while it overestimated TDM at the three high temperatures after day 90 (Fig. 70). Simulation of plant attributes are shown in Fig. 70 b-e. With the adjustment of SLA, the results of the simulation for LAI agrees with those of the experiment at the early stages of the simulation (Fig. 70b). DDR at all temperatures at later stages of simulation is overestimated, which is associated with an overestimation of TDM (Fig. 70c). INS is the same for different temperatures (Fig. 70d). PgMX at any day is directly related to temperature although high temperature reduces LAI at later stages of simulation (Fig. 70e). A large PgMX at high temperatures results in a large DPg. This, however, does not result in large DNP and hence large TDM, since DDR is inversely related to temperature on any day during the simulation. At early stages of growth when LAI and TDM are small, the effect of temperature in increasing PgMX is so large that it almost compensates for a parallel increase in DDR with the result that DNP is only slightly responsive to temperature. At later stages of growth, at large TDM the relatively smaller LAI at high temperature results in a small difference in PgMX among the temperature treatments, and the differences are largely due to differences in DDR.

### (c) Application of the Model

In the following section, coefficients used in PHS-2 to calculate INS and PgMX (EQs.26, 27) are adjusted to those in PHS-1. This is done because measured photosynthetic rates in the temperature experiments from which PHS-2 was constructed, may have been low due to nutrient problems.

(i) Planting Date and Plant Density Simulation. An example of the application of CLO-GRO 2 is shown in Fig. 71 in which simulation is started at different times of the year 1971 (i.e. variation in planting date) and with different initial amounts of TDM (i.e. variation in planting density) with 100% of solar energy at 12°, 20° and 30°C.

The effects of dates of commencement of the simulation at each temperature are similar to those found in Fig. 68 by CLO-GRO 1 at 20°C. The results show that when simulation is started in winter with TDM of 200 $g/m^2$ initial dry matter production at 30°C is lower than that at the other temperatures, but is higher than that at 12°C when simulation is started with TDM of 20 $g/m^2$. Initial dry matter production at 12°C is always lower than that at the other temperatures when simulation is started with TDM of 20 $g/m^2$. Plants at 12°C have a longer linear phase of growth and dry matter yield at December is inversely related to temperature when simulation is started by September 1.

When a day during the simulation has a CLE within ± 0.21 $MJ/m^2$/day of three selected values of CLE, CGR on that day is calculated and the corresponding TDM read from the curve. The relationship between CGR and TDM is shown for each level of CLE and for each temperature in Fig. 72. At 12°C, there is a broad optimum TDM and decrease in CGR above the apparent optimum is gradual while at 30°C, there is a much more obvious optimum TDM and decrease in CGR above the optimum is rapid. For a given level of CLE, CGR is directly related to temperature when TDM is small while it is inversely related to temperature when TDM is large. The value of optimum TDM is inversely related to temperature for each level of CLE.

Figure 71. Simulation of growth curves at 3 different constant temperatures by CLO-GRO 2 for different times of planting and different plant densities. Light energy levels used for the simulation were those measured at Adelaide in 1971.

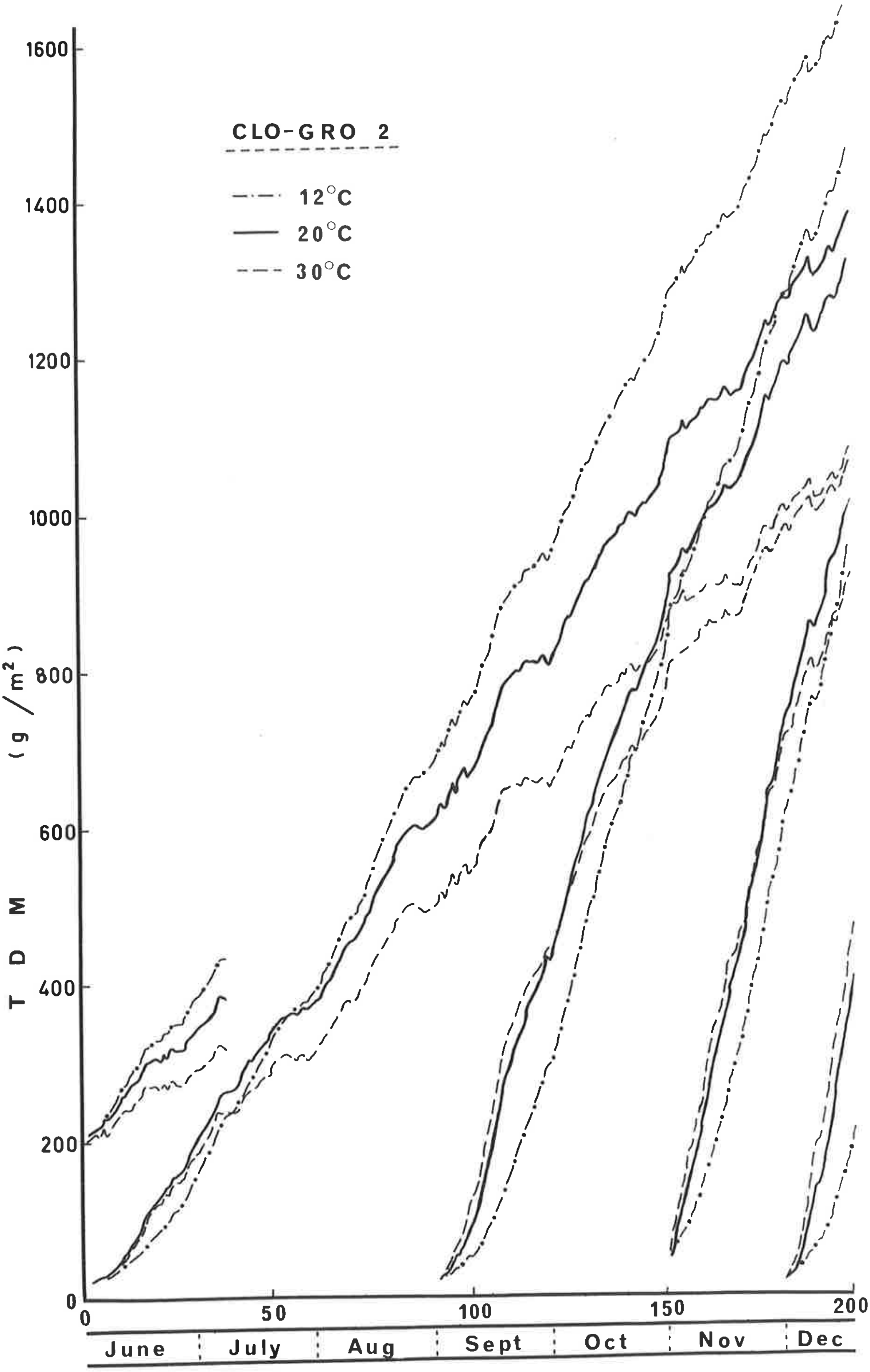
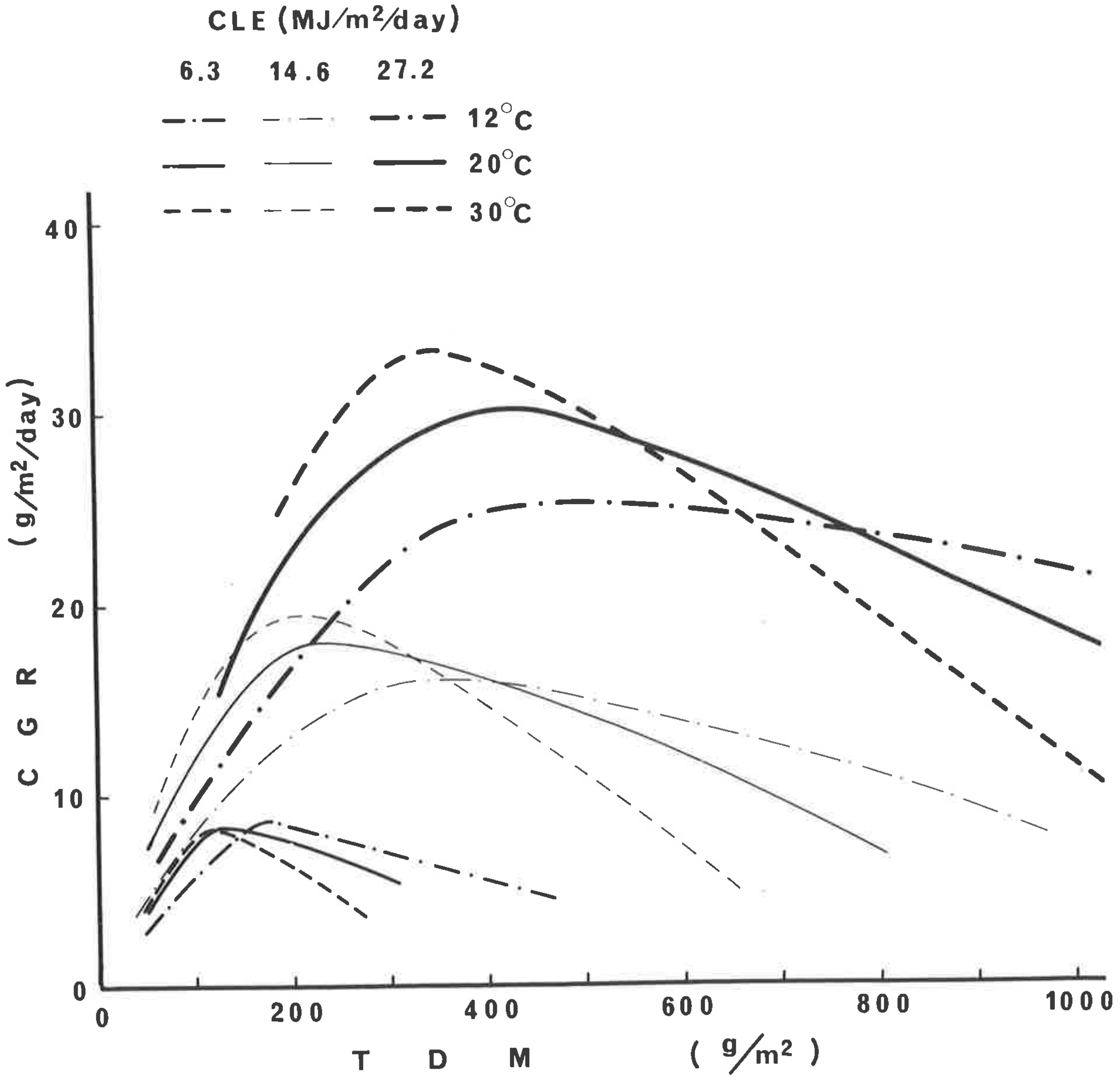

CLO-GRO 2
12°C
20°C
30°C
T D M (g / m²)
1600
1400
1200
1000
800
600
400
200
0
0
50
100
150
200
June
July
Aug
Sept
Oct
Nov
Dec

Figure 72. The relationship obtained from simulation by CLO-GRO 2 at 3 different temperatures between crop growth rate (CGR) and total dry matter (TDM) at 3 different current light energy levels (CLE). Smoothed curves are obtained after plotting values of CGR and TDM for a simulation "day" with CLE values ± 0.21 MJ/m$^2$/day of one of designated values shown at the top of the graph.


CLE (MJ/m²/day)
6.3
14.6
27.2
12°C
20°C
30°C
40
30
20
10
0
C G R (g/m²/day)
0
200
400
600
800
1000
T D M (g/m²)

(ii) Simulation for the Field Experiment. Simulation was conducted for the field experiment (4.0.0). Root dry matter (RDM) was assumed to be 30% of TDM at the first harvest and to be 20% from the second harvest onward (see Fig. 37). When LAI was not measured at the particular harvest at which simulation was commenced, the value of LAI was estimated from the relationship between LAI and shoot dry matter shown in Fig. 6.

Simulation of the early stages of growth results in overestimation of TDM (Fig. 73). It was found that SLA was also overestimated in the simulation; calculated SLA was 300-350 in winter whereas a value of 200 was obtained at that time in the field. This overestimation of SLA resulted in overestimation of LAI in the model which would result in large TDM. The equations (EQs. 30, 33) relating SLA to CT and CLE in CLO-GRO 2 was then changed so that the values of SLA calculated in the model were close to those obtained in the field. Results of a new simulation with adjusted SLA are also shown in Fig. 73. The accuracy of prediction is improved by the adjustment of SLA, although the model still overestimates TDM particularly at the late planting suggesting that factors other than those used in the model may be involved in growth.

Simulation was also started with initial TDM values of about 200 $g/m^2$. The original equations (EQs. 30, 33) relating SLA to CLE and CT was used.

The results (Fig. 74) show a reasonably good approximation to the experimental data, although simulation again overestimated TDM initially particularly in the case of early planting. This is probably partly caused by overestimation of LAI as shown also in Fig. 74 but other factors may also be involved.

Figure 73. Simulated total dry matter production at an early growth stage in the field compared with experimental results. Mean temperatures over the simulation periods shown in the figure were used in the model. Simulation after adjustment of specific leaf area to the values obtained for field data is also shown.

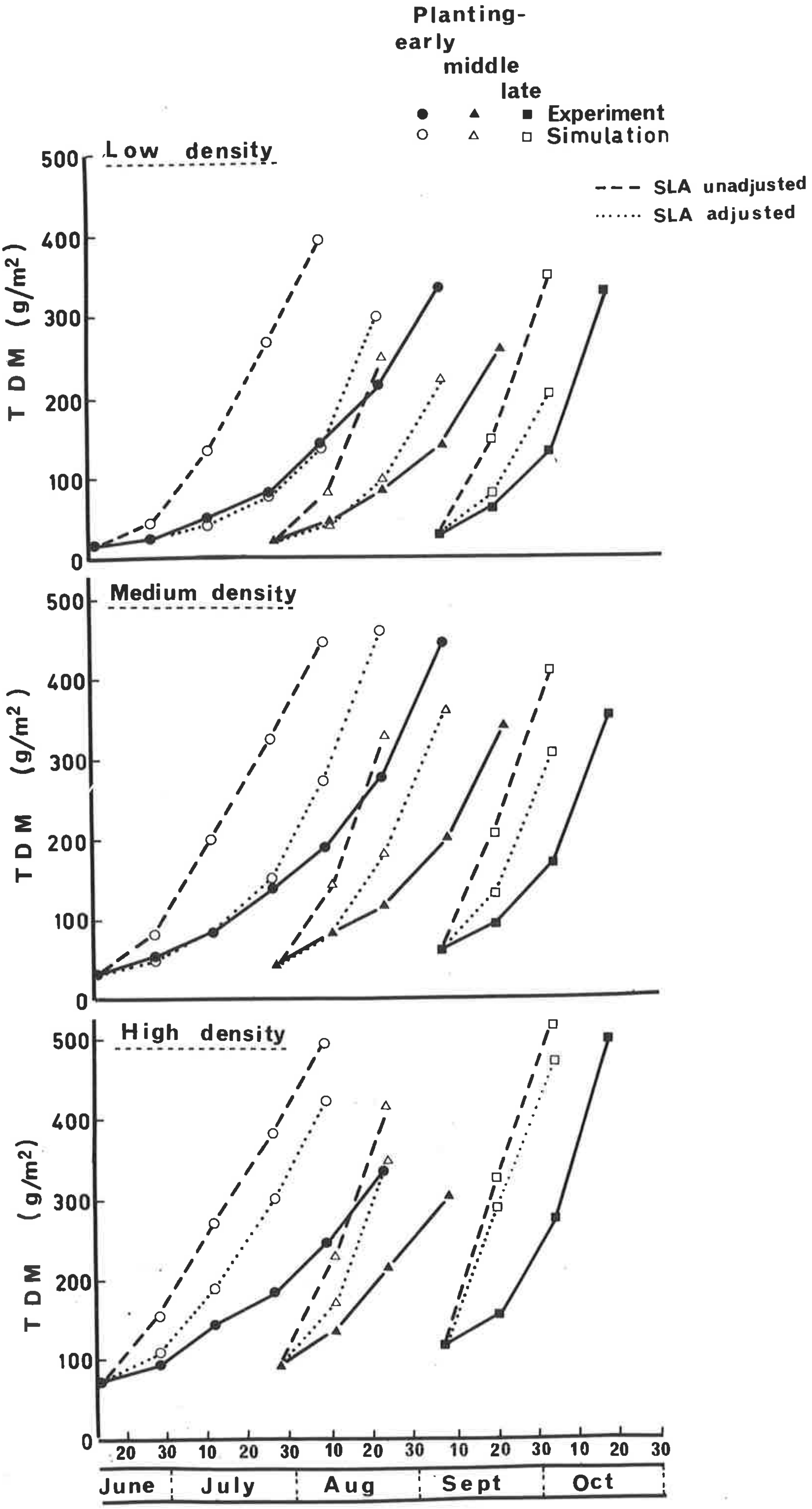

Planting-
early
middle
late
● ▲ ■ Experiment
○ △ □ Simulation
– – – SLA unadjusted
······ SLA adjusted
Low density
Medium density
High density
TDM (g/m$^2$)
0
100
200
300
400
500
20
30
10
20
30
10
20
30
10
20
30
10
20
30
June
July
Aug
Sept
Oct

Figure 74a. Comparison of total dry matter growth simulated by CLO-GRO 2 with that obtained for mature communities in the field in 1971. Mean temperature calculated for each month is used for the simulation. Three planting dates shown for each density.

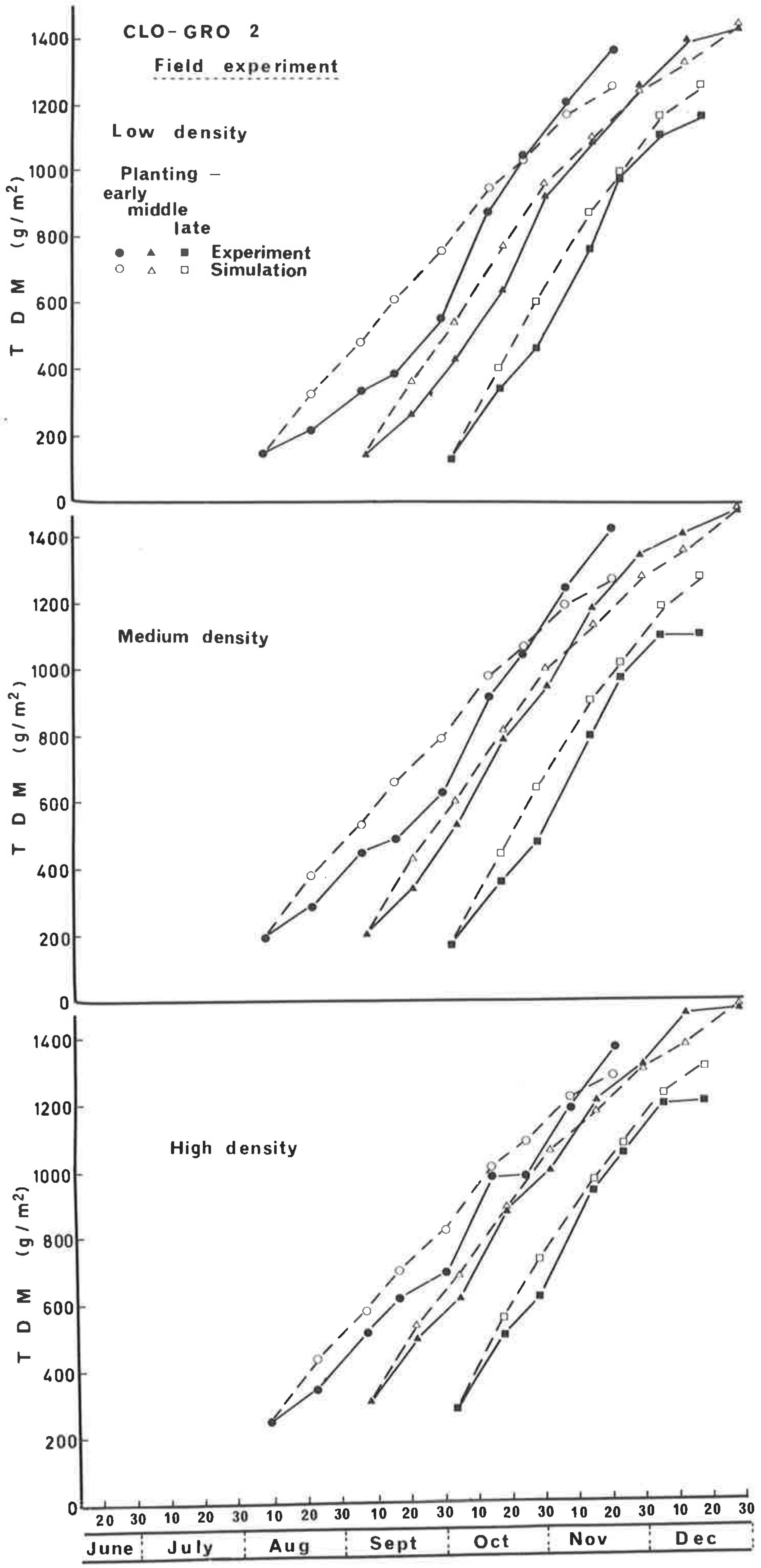
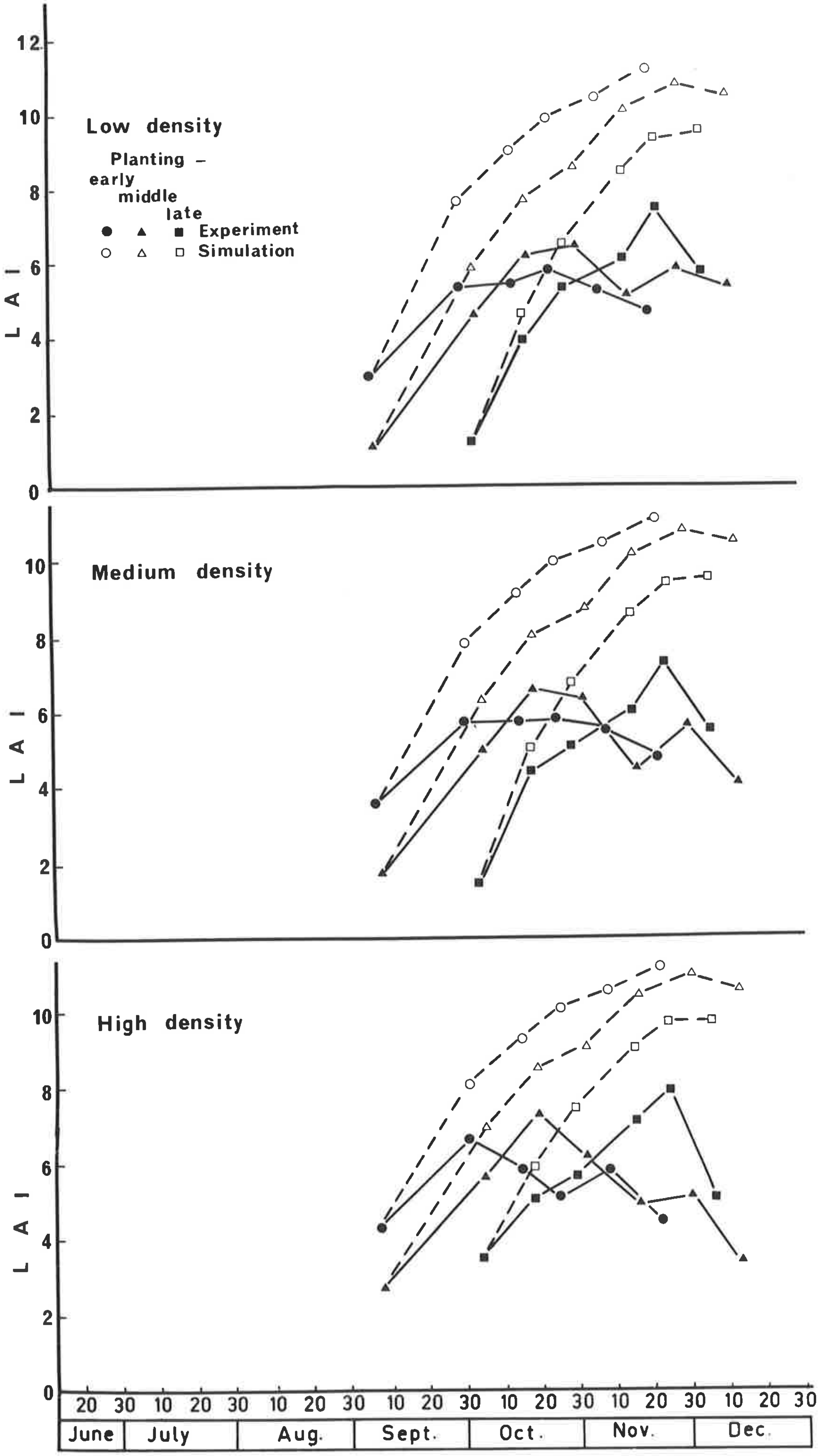

CLO-GRO 2
Field experiment
Low density
Planting –
early
middle
late
● ▲ ■ Experiment
○ △ □ Simulation
Medium density
High density
T D M (g/m²)
0
200
400
600
800
1000
1200
1400
20 30 10 20 30 10 20 30 10 20 30 10 20 30 10 20 30 10 20 30
June
July
Aug
Sept
Oct
Nov
Dec

Figure 74b. Simulated changes in leaf area index (LAI) for different planting dates and plant densities compared with experimental data.

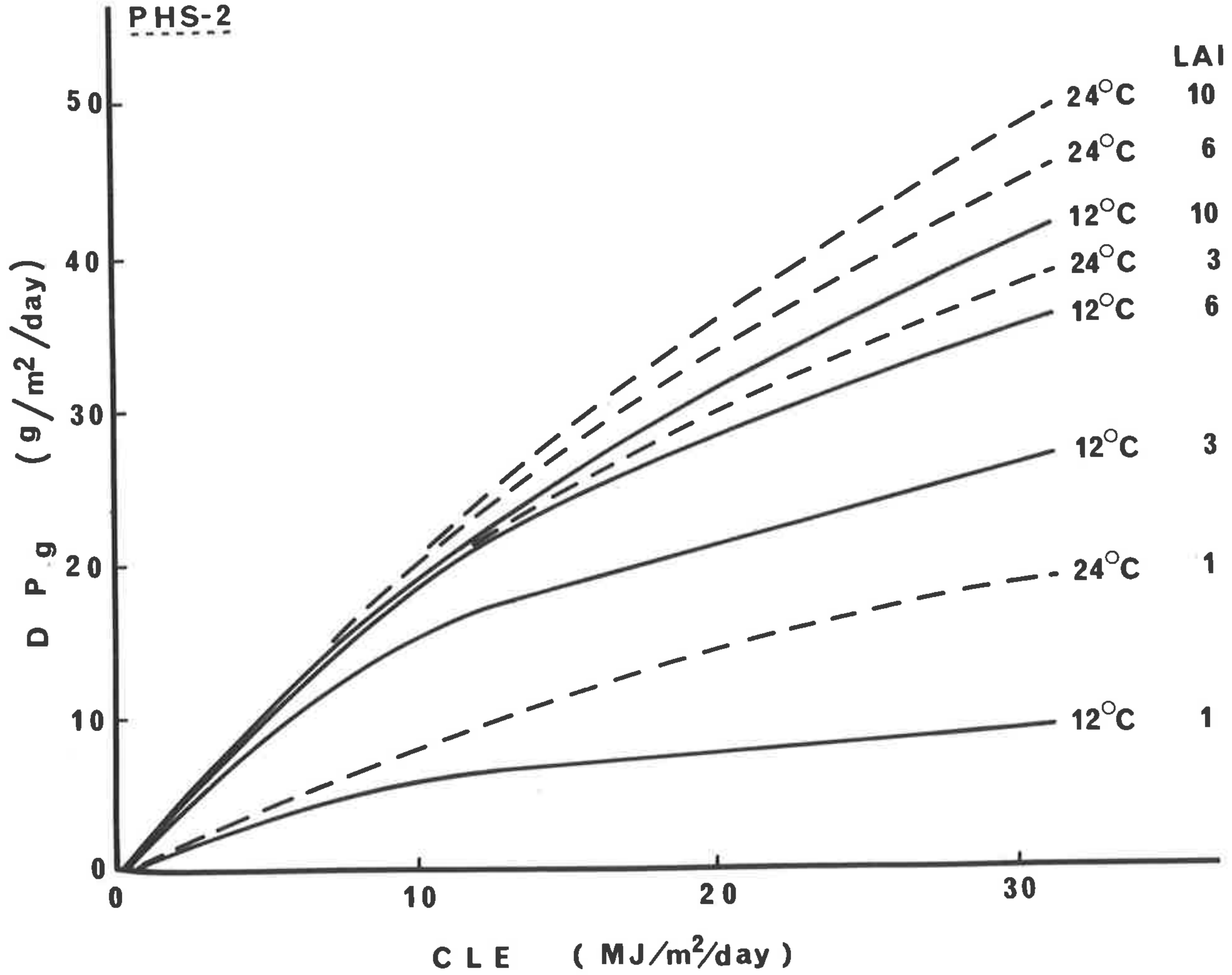

Low density
Planting –
early
middle
late
● ▲ ■ Experiment
○ △ □ Simulation
Medium density
High density
L A I
0
2
4
6
8
10
12
20 30 10 20 30 10 20 30 10 20 30 10 20 30 10 20 30 10 20 30
June
July
Aug.
Sept.
Oct.
Nov.
Dec.

It is unlikely that overestimation of LAI by the model at later stages of growth results in overestimation of TDM for the following reasons.

(1) Calculation by PHS-2 shows (Fig. 75) that increase in DPg with increase in LAI from 6 to 10 is 1-3 g/m$^2$/day at 24°C and 2-5 g/m$^2$/day at 12°C for CLE of 15-30 MJ/m$^2$/day. The increase in CGR will be smaller than that of DPg indicated above, since DDR will be greater for the large LAI and the large TDM canopy. Therefore variation in LAI above about LAI 6 is unlikely to be associated with variation in CGR.

(2) The model does not include fluctuation in temperature during the day. This results in underestimation of DPg since Pg is directly related to CT as can be seen from Fig. 64. This underestimation is probably large in spring when there is a large daily fluctuation in temperature; the difference between monthly maximum air temperature and monthly minimum air temperature increased from 5.4°C in June to 10.3°C in December in 1971. These two factors may have compensated each other with the result of a reasonably good prediction of TDM by the model at later stages of growth although decomposition of leaves is another factor which is not considered in the model. The amount of current dead leaves in the field ranged from 30 to 50 g/m$^2$ in November and December while the model predicted this to be 50-200 g/m$^2$ at that time. As the model was constructed from data with relatively small TDM, decomposition of plant material may have to be taken into account when predicting CGR at large TDM values.

Figure 75. The relationship obtained from CLO-GRO 2 between daily gross photosynthesis (DPg) and current light energy (CLE) at 2 temperatures and at different values of leaf area index (LAI).


PHS-2
LAI
24°C 10
24°C 6
12°C 10
24°C 3
12°C 6
12°C 3
24°C 1
12°C 1
DP$_g$ (g/m$^2$/day)
0
10
20
30
40
50
0
10
20
30
CLE (MJ/m$^2$/day)

## 7.0.0. Discussion

Applicability of the experimental techniques. The controlled environments in which growth and photosynthesis were measured in the present experiments differed from the field in several notable respects. The temperature regime was constant, the solar radiation was about half that outside and the radiation much more diffuse. Plants in the glasshouses experienced no water stress and had a constant, high level of nutrient supply. It is likely that root growth was influenced by the size of the containers used as, during most experiments, roots emerged from the bottom of the containers. Communities in the glasshouses grew at maximum rates similar to those obtained in the field and the levels of total dry matter produced in the glasshouse (up to 900 g/m$^2$) are comparable with those obtained in the field, where ungrazed subterranean clover pastures can be expected to produce 600-1,200 g/m$^2$ (Davidson 1954; Stern 1965). Growth in the glasshouses may therefore be taken as being representative of growth in the field in terms of total dry matter.

Among the problems arising from the use of photosynthetic chambers is that of the relevance of the measured values of net $CO_2$ exchange to growth in the field. Conditions in the chamber may differ from those in the field notably with respect to air movement and to canopy structure. In the present experiments canopy boundary layer resistances were probably low due to the use of reasonably high wind velocity across the canopy. Transfer of pots to the uncovered chamber several days before measurement was intended to allow the canopy to recover its original structure. No attempt was made to change the incident angle of artificial light during the 'day' in the chambers and the proportion of diffuse to direct light was constant. The fact that canopy photosynthesis data were successfully incorporated into a predictive model indicates that the values of net $CO_2$ exchange rate were close to those occurring in the field, or were balanced by the operation of other factors.

Temperature. New information has been obtained in this study concerning the effects of temperature on both dry matter production and total dry matter yield. Results of the two temperature experiments clearly showed that the dry matter production of a subterranean clover community depends on ambient temperature (Fig. 32). Under the light conditions employed, the optimum temperature was 20-25°C when plants were young, but the optimum temperature decreased during growth and final dry matter yield was inversely related to temperature over the range of 12-30°C. These results are similar to those obtained in a growth cabinet by Cocks (1973) with 'Mount Barker' subterranean clover although he used only a short experimental period (i.e. 35 days at high temperatures) and plant dry matter did not exceed 500 $g/m^2$. The present study was conducted with an experimental period of over 105 days and the results extend the relation between growth and temperature to 900 $g/m^2$. Cocks grew plants at different constant temperatures from sowing and the suppression of growth at early stages was therefore much more pronounced at low temperature than was found here in which plants of different treatments were grown at the same temperature for 14 days after sowing. Cocks attributed the low growth rate at high temperature at later stages of growth to a skewness in the frequency distribution of plant size at that temperature. However, it is difficult to judge if the skewness is a causal factor in the suppression of growth of the community or a result of the suppression.

Suppression of growth at high temperature can largely be ascribed to increased respiration rate (see 5.4.4. and below) but it is clear that temperature also influences several aspects of morphology to a marked degree (see 5.4.3.) and the total effects of temperature on development of leaf area are the combined effects of temperature on each component of total leaf area development. High temperature tends to increase leaf appearance rate, individual leaf size and specific leaf area. The advantages of low temperature in leaf area development, on the other hand, are increased lateral development and low rate of leaf senescence. In the early stages when there are no fully senescent leaves, total leaf area development is favoured by high temperature, while at later stages of growth when laterals appear and plants at high temperature lose green leaves rapidly, total leaf area development is favoured by low temperature. The above results extend to a community situation, the correlation between temperature and leaf area development of isolated white clover plants, reported by Takeda and Agata (1964a, 1966b).

The low ratio of LAI to total dry matter at low temperature, due to low values of SLA, results in the value of optimum LAI (of about 4) being almost independent of temperature (Fig. 36). However, the value of TDM at which the crop growth rate is maximal is inversely related to temperature (Table 8).

Light (Daily Solar Energy). The crop growth rate (CGR) of a subterranean clover community has been found in this study to increase linearly with increase in light energy (CLE) from zero to 15 $MJ/m^2/day$, the growth response depending on the amount of dry matter present (Fig. 15). When total dry matter was less than 140 $g/m^2$, the relation was $CGR = 2.15 + 0.71\ CLE$; above 140 $g/m^2$ $CGR = -2.24 + 1.17\ CLE$. Although the slope of the regression line was unaffected by further increase in dry matter, the displacement of the regression line was affected by the amount of dry matter. Since 140 $g/m^2$ corresponded to an LAI of about 2.5 it is clear that a closed canopy responded to light energy in a different manner from one that did not intercept all the solar radiation. At PAR levels of 150 and 250 W/m$^2$ net $CO_2$ exchange rates of communities with LAI above 2.5 was higher than those with LAI less than 2.5 (Fig. 28). This would result in more rapid growth response to light energy in a closed canopy with LAI above 2.5. However, once a closed canopy was attained, a further increase in LAI did not result in increase in net photosynthetic rate at 150 or 250 W/m$^2$, but it resulted in decrease in net photosynthetic rate at 50 W/m$^2$. The increased amount of total dry matter results in an increased dark respiration rate (Fig. 24) which accounts for decreased crop growth rate at TDM above 280 g/m$^2$.

A linear increase of crop growth rate with increase in daily light energy can be considered to be due to the frequent occurrence of low light fluxes where the net $CO_2$ exchange rate responds linearly to variation in light flux. It is also likely that days with low light energy, in the experiments due to shading or in the winter conditions, had a higher percentage of diffuse to total light than clear days with high light energy. The higher percentage of diffuse light would result in a relatively high photosynthetic rate (Kumura 1968a) and hence a relatively high crop growth rate in days with low light energy.

The growth responses to light energy obtained in this study support the conclusions of Stern and Donald (1962) that the growth rates of subterranean clover communities with high values of LAI are influenced by the level of solar energy and that optimum LAI increases with increase in light energy. Stern and Donald, however, suggested that at LAI 2 the maximum growth rate would occur when the radiation was 2 MJ/m$^2$/day, which is in contrast with the results of this study which shows linear growth response up to 15 MJ/m$^2$/day. The results of

Stern and Donald were inconclusive as the interrelationship between growth rate, LAI and daily light energy was constructed from a small number of experimental points. Their experiments were conducted with pure clover stands and in mixed stands with grasses in the field in winter when temperature was reasonably constant, 12.5° ± 1.5°C, and under low light energy conditions ($< 9$ MJ/m$^2$/day).

Similar conclusions were reached by different methods by Black (1963). He planted 'Bacchus Marsh' subterranean clover at 8 planting densities ranging from 500 to 20,000 plants/m$^2$ at 3 times of the year. Variation in incident light energy was obtained by using shades imposed two weeks before the first harvest which was followed by a second harvest after 14-21 days growth. Crop growth rates for given values of LAI and light energy obtained by Black are generally in good agreement with those obtained in this study. However, Fig. 7 of his paper which shows interrelationship of crop growth rate, leaf area index and light energy must be accepted with caution since: (1) mean temperature during growth varied from 15° to 26°C during the year: (2) extremely high plant densities with rapid decrease in plant number with time were used to create high LAI. Communities of extremely high plant density may not grow as well as those of low plant density (Hiroi and Monsi 1966).

The results of this study (Fig. 44) show that a difference in mean temperature of 11°C during the year, as in Black's experiments, would result in a difference in dark respiration loss during a night of about 3 g/m$^2$ for communities of 500 g/m$^2$ total dry matter (LAI of approximately 6). The difference in daily net photosynthesis between 15°C and 26°C depends on the level of light energy (Fig. 51); if it is less than 10 MJ/m$^2$/day, the community grown at 15°C would have a higher daily net photosynthesis than one at 26°C as may be anticipated from Fig. 75, which shows daily gross photosynthesis at different temperature and light energy conditions, allowing for the difference in dark respiration loss between the two communities due to temperature.

Black concluded that temperature had little effect on the relationship between crop growth rate and LAI. However close examination of Figs. 1-3 of his paper reveals that a different ratio of TDM/LAI was obtained in different seasons. In the summer a large ratio of TDM/LAI would result in a large dark respiration loss. In the winter a small ratio of TDM/LAI would result in a small dark respiration loss. It therefore may be calculated that for a given daily light energy the crop growth rate of a community with LAI of 6 in the winter is higher than under shade in the summer by more than 3 $g/m^2/day$.

It is difficult to see why Black did not obtain a significant effect of temperature on growth of subterranean clover communities. It may be that the high rate of mortality in the community, i.e. up to 50% for a period of 21 days, of the winter experiments under shade suppressed growth and compensated for the small dark respiration loss of the community in winter. On the other hand, the species which Black used may be as insensitive to temperature when grown in communities as Morley (1958) found to be the case for the individual plant.

The ratio of LAI/total dry matter (TDM) may affect the growth of communities since LAI strongly influences net photosynthetic rate at high light flux and TDM influences dark respiration rate and net photosynthetic rate at low light flux. The ratio was found to be slightly higher for plants grown under low light energy than it is for plants grown at high light energy (Fig. 18), due to an inverse relationship between specific leaf area (SLA) and light energy, although the values of SLA obtained in the different experiments vary greatly with a range of about 200 $cm^2/g$. The other component affecting the ratio of LAI/TDM is the proportion of green leaf dry matter which is directly related to light energy. This is apparently due to the increased proportion of dead leaf dry matter at low light energy since the total leaf dry matter proportion is found to be independent of light energy.

The non response of the proportion of total leaf dry matter to increase in light energy suggests preferential distribution of photosynthate to the formation and growth of new leaves (Ryle 1970). The fact that the rate of leaf appearance on a main stem was not affected by light conditions (Fig. 23) supports this suggestion. On the other hand high light energy increases the root proportion whilst it decreases the stem and petiole proportion (Fig. 16). However, these particular responses to light energy should be interpreted with caution since they may simply reflect the fact that decomposition occurs in a mature canopy. It would be necessary to study translocation of photosynthate before firm conclusions could be drawn.

Dark Respiration. Quantitative relationships of dark respiration rate of subterranean clover communities to shoot dry matter (SDM), crop growth rate (CGR), growth temperature, and current temperature (CT) were obtained in this study. The most important factors affecting dark respiration rate were SDM and CT.

When dark respiration of subterranean clover communities is measured at growth temperature, the rate at given plant dry matter is approximately linearly related to temperature. A direct relationship between temperature and dark respiration of communities measured at growth temperature was reported by Ludwig, Saeki and Evans (1965) on cotton. However, the results in cotton communities were not obtained at the same dry matter for plants grown at different temperatures and the removal of leaves at low position in the canopy to vary LAI would make the ratio of LAI/total dry matter (TDM) different from that of 'normal' communities. It is difficult, therefore, to assess these results. The study of subterranean clover communities on the other hand, clearly shows the effect of temperature on dark respiration loss; e.g. for communities with 500 g/m$^2$ TDM, and grown at 12° and 24°C, the difference in dark respiration loss at growth temperature during a night of 12 hours would be 3 g/m$^2$/12 hr (Fig. 45).

The $Q_{10}$ of dark respiration of subterranean clover decreased with increase in growth temperature from 1.8 at 12°C to 1.5 at 24°C (Fig. 47). This result is similar to that obtained by Wager (1941) and by Rook (1969) and contrasts with results obtained by Pearson and Hunt (1972c). No workers have offered an explanation for differences in $Q_{10}$ between plants grown at different temperatures. In this study the lack of a consistent trend in change of the $Q_{10}$ value with time suggests that $Q_{10}$ is independent of aging or growth rate.

A high $Q_{10}$ induced by a low growth temperature of 12°C or 16°C means that dark respiration rate is high when the temperature is raised to 28°C (Fig. 48). Plants grown at low temperature will lose appreciable dry matter when they are subjected suddenly to high temperature. It is not known, however, from this study how long $Q_{10}$ values take to adjust to new temperature regimes. If the value of $Q_{10}$ changes rapidly, a high respiration rate may be induced by high temperature after a cool period in the field. There was, however, no significant effect of growth temperature on dark respiration rate at a given shoot dry matter when the rate was measured at temperatures of 12° and 20°C (Fig. 48).

An equation obtained in the light energy experiments relating daily dark respiration (DDR) to shoot dry matter (SDM) and crop growth rate (CGR) was:

$$\text{DDR} = 1.94 + 0.022\ \text{SDM} + 0.11\ \text{CGR} \qquad \text{EQ.16}$$

However, the constant term in the equation suggests that the relation does not hold as SDM approaches zero. A positive constant term was also found in the temperature experiment (Fig. 44) except at 16°C. It possibly indicates that the specific rate of dark respiration decreases with increase in SDM (Fig. 24), a phenomenon found in several plant species, e.g. soybean (Kumura and Naniwa 1965). It is unlikely that the constant term represents soil respiration since this was suppressed by water in these experiments.

McCree (1970), working with white clover, found a constant term in an equation relating DDR with TDM and DPg (daily gross photosynthesis), but he considered this to be due to soil respiration and neglected it in his equation where:

$$\text{DDR} = 0.25\ \text{DPg} + 0.015\ \text{TDM} \qquad \text{EQ.3}$$

By substituting DPg = CGR + DDR, this may be changed to

$$\text{DDR} = 0.020\ \text{TDM} + 0.33\ \text{CGR} \qquad \text{EQ.35}$$

Thornley (1970, 1971) interpreted EQ.3 as showing that dark respiration consisted of 'growth' respiration and 'maintenance' respiration. The significant effect of crop growth rate on dark respiration rate obtained in this study supports the view that 'growth' respiration is contributing to the total respiration rate. However, comparing EQ.16 and EQ.35, it is evident that the contribution of CGR to DDR is approximately three times higher in white clover than in subterranean clover. CGR values used to generate EQ.16 were obtained by dry matter harvest and are likely to be less than those generated by differences between the sum of DPg and the sum of DDR during the same period because of loss of dry matter from leaf senescence and death of plants (Hunt 1970). Correction of EQ.16 for senescence and death would, therefore, increase the difference between the two equations in the size of the contribution of CGR to DDR. The difference may be attributed to difference in the generation of variation of daily light energy and hence CGR. In McCree's experiments, daily light energy was changed daily, whereas in this study variation in daily light energy occurred naturally throughout the year. Consequently, plants may have become adapted to successive light environments so that DDR was close to constant for a given DM. Plants may respond differently in DDR to a rapid change in light energy compared with a slow change through the difference in response in 'growth' respiration.

EQ.16 shows dry matter to be a major factor influencing the rate of dark respiration for a given temperature. A range of CGR from 0 to 15 $g/m^2$/day, which is roughly the seasonal variation shown by a closed canopy of subterranean clover in the field at Adelaide, results in a difference in DDR of only 1.7 $g/m^2$/day, while each increase in DM of 100 $g/m^2$ results in a difference in DDR of 2.2 $g/m^2$/day.

The small number of associated observations of dark respiration rate and shoot dry matter at each temperature in the temperature experiments precludes the possibility of including CGR in equations relating DDR and TDM. It is possible that the equations relating DDR and TDM at different temperatures will be affected by variation in CGR. The effect of CGR, however, will be relatively small, the major factors being TDM and growth temperature even where crop growth is maximal. The small contribution of CGR to DDR can be explained by considering 'growth' and 'maintenance' respiration. As shown early in this section, the contribution of 'growth' respiration to total respiration in subterranean clover is small, the major contributor to total respiration being 'maintenance' respiration which is likely to be directly related to temperature. Semikhatava (1970) suggests that the ATP produced through high respiration rate at high temperature is used mainly for the increased energy requirement for repair of cell structure and re-synthesis of destroyed compounds. Thus, a high rate of respiration of subterranean clover communities at high growth temperature need not necessarily result in a high growth rate.

Photosynthesis. At LAI values of about 1, photosynthesis readily became light saturated but at LAI above 3, saturation was not achieved at the highest fluxes generated (250 W/m$^2$, PAR).

The change in the shape of the light-net photosynthesis curve with the change in LAI obtained here confirms the published results from experiments in which variation in LAI was obtained by canopy aging (Jeffers and Shibles 1969; Robson 1971).

Net photosynthesis at high light flux density increased with increase in LAI, the increase being very small once an LAI of 3 was attained (Fig. 28). This is in contrast with the results of ryegrass communities reported by Robson (1971) in which net photosynthetic rate at high flux density is higher in a community with LAI 10.6 than that with LAI 3.0. Photosynthesis of the ryegrass communities was measured under similar experimental conditions to those of this study, and it is likely that the difference between the two can be ascribed to the difference in canopy structure. The increase in light interception by a planophile canopy with increase in LAI is small once an LAI of 3 is attained (Stern 1960).

At low light flux density net photosynthesis has a clear optimum LAI. Decrease in the net photosynthetic rate at low flux density with further increase in LAI or SDM is apparently associated with increase in dark respiration rate (Fig. 29). This suggests that at low flux density, either photorespiration rate equals dark respiration rate or its contribution to the total respiration is small. The latter may occur because the proportion of photosynthetic tissue to TDM decreases with increase in TDM (see Figs. 8, 16, 37). Further, leaves low in the canopy receive low light energy particularly in the case of planophile canopies (Kumura 1965) and therefore it is likely that the total photorespiration of the canopy is small in comparison with total canopy respiration.

The fact that the shape of the temperature - net photosynthesis curve at low light energy is very similar to that of temperature - dark respiration curve (Fig. 55) again indicates the probability of 'dark' respiration being the major contributor to $CO_2$ loss from a subterranean clover canopy at low light energy.

Photosynthesis of a community appears to be affected not only by temperature and LAI but also by the growth conditions. The rate of net photosynthesis of a closed canopy at high light energy was higher when grown at high light energy than when grown at low light energy (Figs. 28, 30). The difference, however, is small - it was of the order of 0.5 g $CO_2/m^2$ (ground)/hr between the autumn experiment without shade (A72a) and the winter experiment (W71) (Fig. 28). This is in contrast to the situation with single leaves. Kumura (1968b) showed a difference of the order of 1.0 g $CO_2/m^2$/hr between soybean leaves grown at high and low solar energy. The small differences shown for the canopy can be attributed to the fact that clover leaves emerge through a dark zone in the canopy (Stern 1960; Brougham 1962). When leaves reach the top of the canopy and receive full sunlight they still may possess the photosynthetic system of 'shade' leaves.
Depending on the time taken for adaption, some of the leaves at the top

of the canopy will have a low net photosynthetic rate even at high light flux. Also, since leaves in the lower strata of the canopy receive low light energy they probably show the characteristics of shade leaves even when the top of the canopy is illuminated by full light. Thus only a small proportion of the total leaf population has the attributes of high light grown leaves even in a canopy grown at high light.

It is not possible in this study to separate the effects of current light energy from those of crop growth rate on net photosynthetic rate since the two are correlated ($r = 0.739$). Both factors had about the same correlation coefficients with dark respiration rate (5.3.4.) and gross photosynthetic rate at 250 $W/m^2$ (PAR) (5.3.5.). The effect of current light energy or crop growth rate on net photosynthesis depends on light flux density. Rapid growth may influence net photosynthetic rate directly through 'sink' effects; rapid growth requires a large supply of photosynthate and rapid transport of the photosynthate from the leaf with a resultant high rate of photosynthesis (King, Wardlaw and Evans 1967).

An interaction between light energy and temperature on net photosynthetic rate is evident when net photosynthesis of a canopy was measured at temperatures other than growth temperature (Figs. 54, 55). This may be due to two separate effects of temperature; one a positive effect through gross photosynthesis and the other a negative effect through dark respiration. Similar interactions have been reported in the literature (e.g. Ormrod 1964). In this study the similar interaction between light energy and temperature on net photosynthetic rate was also found when net photosynthesis was measured at growth temperature in canopies with different growth temperatures (Fig. 52). This is in contrast with results reported by Ludwig, Saeki and Evans (1965) where net photosynthetic rate of cotton communities at 3 light fluxes measured at growth temperature was inversely related to growth temperature between 20° and 40°C. The range of growth temperature at which net photosynthesis was measured in this study with subterranean clover communities was 16-24°C and the difference in the range of temperature may be a reason for the different results between experiments with cotton and subterranean clover communities.

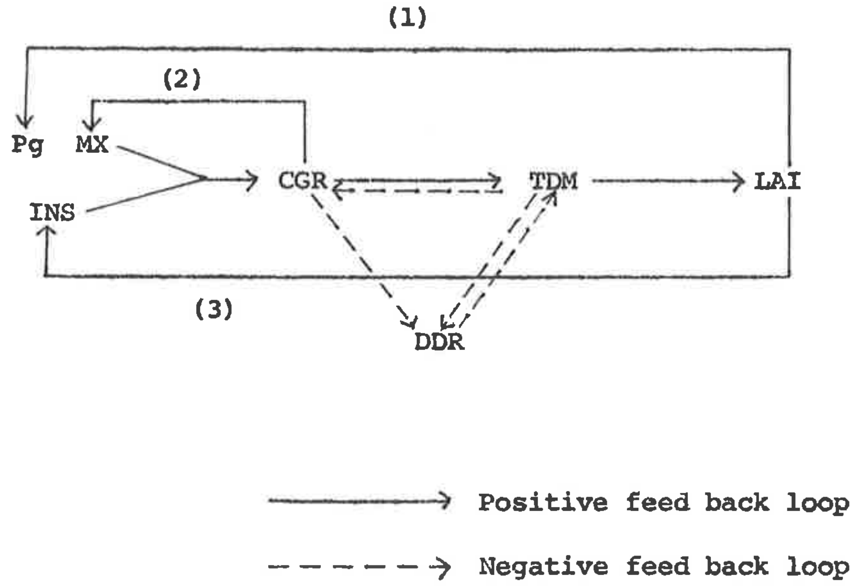
Models. Models of dry matter production by plant communities can synthesize relationships between interacting variables which affect community growth, and can examine community growth quantitatively under different environmental conditions. Although the interactions between variables on one part of the whole community dry matter production system can be examined experimentally under specified conditions, it is difficult, without models, to estimate the effects of these interactions on community growth outside the range used in the experiments.

It is preferable to construct empirical models such as PHS and CLO-GRO from a small number of biologically-significant variables so that the contribution of each variable in the system can be examined easily.

In the photosynthesis models, PHS-1 and PHS-2, constructed from experimental results to quantify the relationship between net photosynthesis (Pn) and environmental variables (current temperature (CT) and light flux (LF)), gross photosynthesis (Pg) was calculated conventionally as the sum of Pn and dark respiration (DR). This procedure makes calculation of Pn possible from relatively few plant variables. In PHS-1, Pn for a given LF can be calculated from only LAI, crop growth rate (CGR) and total dry matter (TDM); in PHS-2 for given values of LF and CT, Pn can be calculated from LAI and TDM.

Pn can be calculated with reasonable accuracy (Figs. 61, 62) and interactions between the effects of CGR and LF, and between those of CT and LF, on Pn are readily shown (Figs. 63, 64). Increase in CGR or CT increases both Pg and DR and thus the effect of CGR or that of CT depends on LF. Both models show Pn to be strongly influenced by LAI at high LF and by TDM at low LF.

The experimental results suggest the operation of feed back loops in the system of community growth. These are shown in the following diagram as used in CLO-GRO 1.



Three positive feed back loops are indicated in the diagram. When TDM is increased by positive daily net production (DNP), LAI is also increased which in turn results in increased maximum rate of gross photosynthesis (PgMX) and initial slope (INS). Pn will then be increased to give increased CGR and TDM. An increase in CGR also tends to increase PgMX, which in turn results in increased CGR.

The contribution of the positive feed back loops in determining DNP depends on the actual value of LAI. INS is affected by LAI only when the value of LAI is small (Fig. 59). Further, the increase in PgMX associated with increase in LAI becomes small when LAI is large (Fig. 59). Thus increase in DPg with increase in LAI becomes small at large LAI.

Two negative feed back loops are used in CLO-GRO 1. The TDM/DDR negative loop becomes progressively important in determining DNP and CGR with increase in TDM.

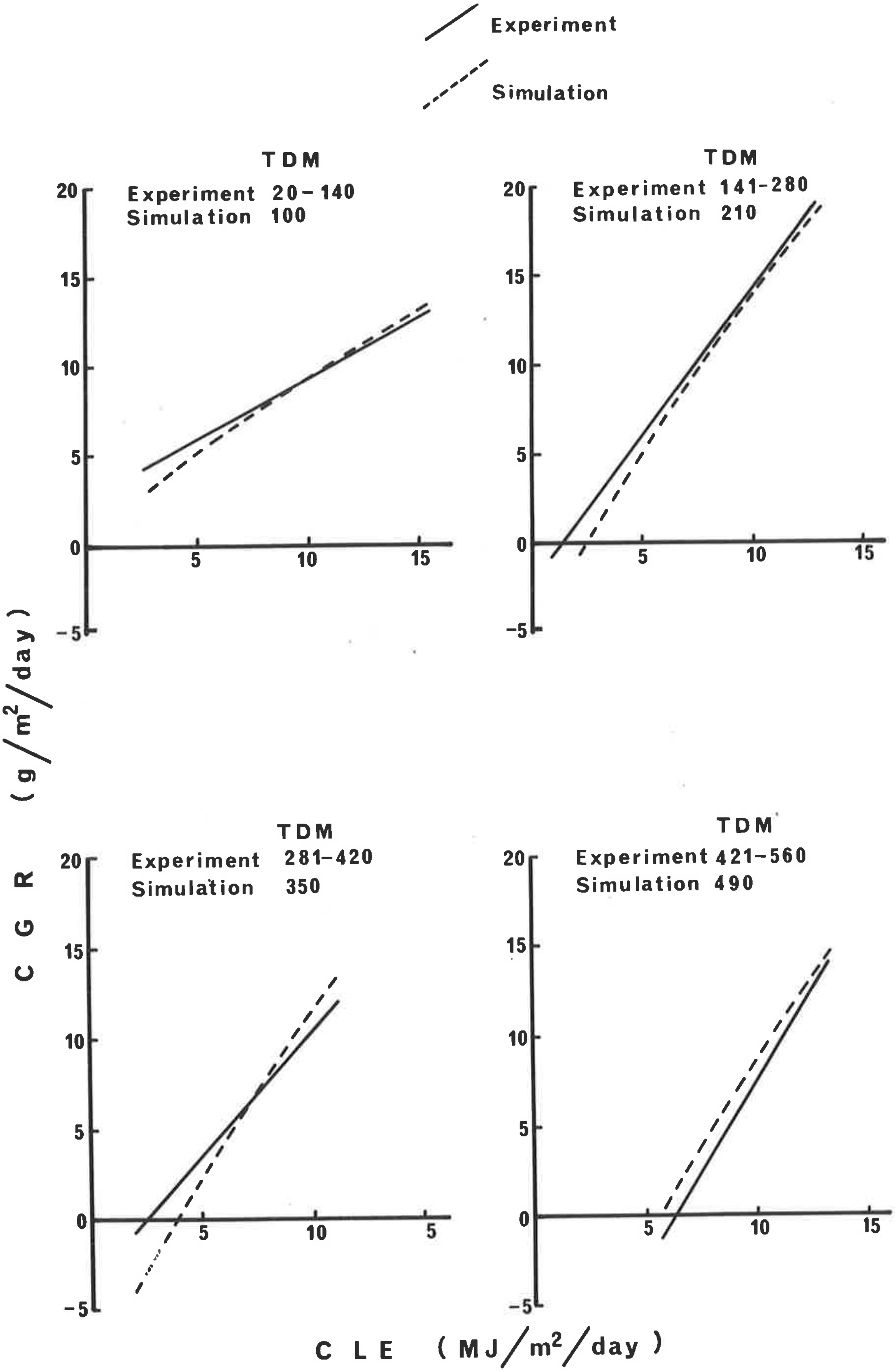
At small TDM, the effect of the positive feed back loops exceeds that of the negative feed back loops and results in increased CGR, increased TDM and increased LAI. With increase in TDM, the effect of the negative feed back loops becomes dominant and CGR decreases with increase in TDM. With further increase in TDM, CGR becomes zero when DDR equals DPg and dry matter increase ceases. The dry matter yield at which this occurs is linearly related to current light energy (CLE) (Fig. 69).

From the experimental results and from PHS-1 and CLO-GRO 1, it appears that the major plant attributes affecting the growth of subterranean clover communities at 20°C are LAI through DPg and TDM through DDR.

Under optimum water and nutrient supply conditions, the relationship between LAI and TDM at 20°C is not strongly affected by light energy level (CLE) (Fig. 18), and the two become interchangeable plant attributes affecting growth rate. LAI is to be preferred to TDM at small TDM as growth rate is strongly influenced by DPg through LAI. It is preferable, however, to use TDM rather than LAI at large TDM since the negative feed back loop involving DDR becomes the major system influencing growth rate and TDM therefore has more direct biological meaning than LAI.

Experimental results relating CGR with CLE at different values of TDM are well reproduced by CLO-GRO 1. In Fig. 76 regression lines relating CGR and CLE obtained in the experiments (Fig. 15) are compared with corresponding curves obtained from CLO-GRO 1. Except

Figure 76. Comparison of simulated growth responses of communities to current light energy (CLE) at 4 different amounts of total dry matter, calculated by CLO-GRO 1, and values obtained from the light energy experiments.


Experiment
Simulation
TDM
Experiment 20-140
Simulation 100
TDM
Experiment 141-280
Simulation 210
TDM
Experiment 281-420
Simulation 350
TDM
Experiment 421-560
Simulation 490
20
15
10
5
0
-5
5
10
15
CGR (g/m²/day)
CLE (MJ/m²/day)

at small CLE at which the model underestimates CGR, the model can estimate CGR from CLE for given values of TDM with considerable accuracy. It is evident that for the range of values of CLE indicated in Fig. 76, CGR decreases with increase in TDM above 210 g/m$^2$ due to increased DDR. CLO-GRO 1 shows the optimum TDM and Max CGR at the optimum TDM to be linearly related to current light energy (Fig. 69).

There are several reasons for the discrepancies between experimental and simulated values of TDM at low CLE, particularly when TDM is small (see Figs. 66, 67). It is probable that the proportion of diffuse to total light energy was high in the glasshouses when CLE was low; this is not considered in the model. Incident light angle may also be involved since the model was constructed from experimental results with fixed incident light angle. Another factor may be quantitative errors in the relationships between the plant variables themselves or between plant variables and environmental factors due to the small number of observations.

Feed back loops involving CGR were not used in CLO-GRO 2. Temperature has two effects on the positive feed back loops included in this model: i.e., an increase in PgMX (Fig. 60); and a rapid increase of LAI due to increased SLA for a given amount of photosynthesis at high temperature. When LAI is small and the positive feed back loops have a major effect on the whole dry matter production system, CGR particularly at high CLE is affected by temperature through the operation of the above factors.

Temperature, on the other hand, also affects DDR in the negative feed back loop. The role of the loop in the total dry matter production system is small at small TDM and optimum temperature for growth at this stage is high, the actual value being dependent on CLE (see Fig. 72). The effect of temperature at this stage is essentially the same as that on the growth of isolated plants before maturity at which the optimum temperature is high (e.g. Friend, Helsen and Fisher 1962a).

With increase in TDM, the negative feed back loop becomes dominant and largely determines the growth rate. Although DPg is still positively related to temperature, as seen in Fig. 70 (d), (e), the difference in DDR between temperature levels is far more important in determining CGR than is the difference in DPg. This results in TDM being inversely related to temperature at later stages of growth (Fig. 70a).

The difference in TDM between the simulation in CLO-GRO 2 and the results of the temperature experiment (1972) at later stages of growth (Fig. 70), suggests that the rate of decomposition of dead plant material may be important. The number of dead plants, as well as the dry matter of dead leaves, was larger in 1972 than in 1970 and the drier conditions in 1970 may have resulted in less decomposition of dead material. Decomposition was neglected in this study but it appears that it can have a considerable role in determining plant dry matter production particularly at high TDM (see 2.6.2.).

Although CLO-GRO neglects decomposition and fails to predict TDM accurately at low CLE when TDM is small, it generally describes growth under different light and temperature conditions with reasonable accuracy. A systems approach can be useful once the results of simulation are found to be close to experimental results under different conditions. General advantages of the use of systems analysis are considered below with particular reference to the CLO-GRO model.

(1) The level of the final product (total dry matter) can be predicted for a given time and given external variables (Figs. 68, 70).

(2) The quantitative effects of external variables on the rate of attainment of final product (crop growth rate) can be shown with possible interactions between variables (Fig. 72).

(3) The contributions of sub-systems can be recognized for different conditions, e.g. the great contribution of dark respiration rate to plant growth when total dry matter is large (Fig. 70).

(4) The quantitative relationships between plant variables which affect the final product can be understood, e.g. the effect of total dry matter on dead leaf dry matter.

(5) Factors not incorporated in the model, but which may have significant effects on the system, may be considered when discrepancies between experimental results and simulation are found, e.g. the possible effects of nutrient toxicity and decomposition.

The special features of CLO-GRO are considered below in comparison with a photosynthesis model by Duncan, Loomis, Williams and Hanau (1967) and with growth models by de Wit (1965) and de Wit, Brouwer and Penning de Vries (1970).

(1) The major relationships between plant attributes and environmental factors, and between plant attributes themselves, used in CLO-GRO were obtained from experiments with communities grown in temperature-controlled glasshouses in which light energy and temperature were known for each experiment. An advantage of this approach is that effects of growth conditions on plant attributes affecting community growth can be quantitatively evaluated.

Duncan _et al._ constructed their photosynthesis model from single leaf photosynthesis data and from the theoretical light penetration within a community; they did not consider effects of previous growth conditions on leaf photosynthesis. In de Wit's model, some equations were obtained from experimental results but the others were derived from theoretical consideration.

(2) Net $CO_2$ exchange of communities rather than single leaves was used in the CLO-GRO model, with actual values of light flux recorded at 15 minute intervals to calculate daily net production of communities. This approach minimizes errors due to estimating incident light flux and light distribution within a community. Daily and yearly variation in growth due to variation in light flux can be examined.

Both Duncan's and de Wit's models calculate incident light flux for different latitudes, times of the year and times of the day from the physical nature of direct and sky light. Leaf photosynthesis is used to calculate community photosynthesis with theoretical consideration of light distribution within each of the different canopy structures. Effects of incident light angle and those of the proportion of diffuse to total light flux on net $CO_2$ exchange of erectophile canopies can be considered to be greater than those of planophile canopies (Tanaka, Matsushima, Kojyo and Katsuki 1970).

(3) Precise estimates of dark respiration rate of communities used in CLO-GRO involve total dry matter (TDM), current temperature (CT), and crop growth rate (CGR) of the community in question. Although for a given community an immediate change of temperature results in exponential change in dark respiration rate, the dark respiration rate of subterranean clover communities measured at different growth temperatures was linearly related to temperature, due probably to adaptation to the growth conditions.

In the Duncan model, daily respiration is assumed to be 40% of daily net photosynthesis. The de Wit model calculates dark respiration rate as a sum of maintenance and growth respiration rate, using coefficients reported by McCree (1970) for white clover. Dark respiration rate is considered in the de Wit model to increase nearly exponentially with increase in temperature up to 35°C.

(4) In the CLO-GRO model effects of temperature on the relationships between plant attributes were obtained experimentally and were incorporated to provide a measure of the total effect of temperature on the growth of communities.

In the Duncan model, no consideration was given for the temperature factor. In the de Wit model, effects of immediate change of temperature on photosynthetic rate are incorporated by a multiplying coefficient for each temperature, but no interaction between temperature and light flux on photosynthetic rate is adopted. The model assumes that temperature has an effect on growth stages of leaves and on dark respiration rate.

The differences in assumptions and equations used in these models would result in differences in simulated dry matter when applied to the same crop and conditions. A quantitative assessment of these differences has not been made.

It would be possible to incorporate other variables such as nutrient level in the CLO-GRO model leading to an understanding of the effects of nutrient level on dark respiration, photosynthesis and leaf development and ultimately on the growth of the community. The model could also be extended to simulate pasture growth under defoliation or grazing.

## APPENDIX I

```
   PROGRAM CLOGRO1 (INPUT,OUTPUT)
   DIMENSION EL(60),DLE(30),CGR(30), TDM(30),DNP(30)
 C CLOGRO IS A GROWTH MODEL OF SUBTERRANEAN CLOVER COMMUNITIES BY SHU FUKAI
 C CLOGRO1 PROGRAM TO PREDICT DM PRODUCTION OF SUBTERRANEAN CLOVER COMMUNITIES
 C AT 20 DEGREES
 C PLANTING DATE TRIAL START FROM 26/9/71
 C TRANSMISSION RATE IN THIS SIMULATION IS 55 PERCENT NOTE A AND B VALUES
 C FOLLOWING ABBREVIATION IS USED ONLY IN THE
 C PROGRAM.   CORRESPONDING
 C ABBREVIATION USED IN THE TEXT IS SHOWN IN
 C PARENTHESES;  AIL(LAI),EL(LF),SIN(INS),
 C UNITS USED IN THE PROGRAM DIFFER FROM THOSE
 C IN THE TEXT
   READ 1,ND
 1 FORMAT (I3)
   PRINT 20
20 FORMAT (1HO,20X,*DAT 1*)
   READ 2,TDM(1),AIL,CGR(1)
   PRINT2,TDM(1),AIL,CGR(1)
 2 FORMAT (3F10.1)
   READ 3,DATE,(EL(I),I=1,60)
 3 FORMAT (F6.0,12F5.0/(6X,12F5.0))
   PRINT 19,DATE
   CALL PHS1 (CGR(1),TDM(1),AIL,EL,DNP(1),DLE(1))
   DO 4 N=2,ND
   PRINT 9,N
 9 FORMAT (1HD,20X,*DAY*I3)
   CGR(N)=CLE=0
   JD2=N-1
   IF(N.LE.8)GO TO 5
   DIV=7.
   JD1=N-7
   GO TO 6
 5 JD1=1
   DIV=N-1
 6 DO 7 J=JD1,JD2
   CGR(N)=CGR(N)+DNP(J)/DIV
 7 CLE=CLE+DLE(J)/DIV
   TDM(N)=TDM(N-1)+DNP(N-1)
   DLDM=(5.34+0.01946*TDM(N)-0.01986*CLE)*TDM(N)*0.01
   IF(DLDM.LT.0.0)26,27
26 DLDM=0.0
27 TLDM=(29.08+10582./(519.+TDM(N)))*TDM(N)*0.01
   GLDM=TLDM-DLDM
   SLA=309.+34638./(101.+CLE)
   AIL=GLDM*SLA*0.0001
   PRINT 8,CLE,SLA,TDM(N),DLDM,TLDM,GLDM,AIL,CGR(N)
 8 FORMAT(1HO,10X*CLE*F10,2/11X*SLA*F10.2/11X*TDM*F10,2/11X*DLDM*F10,
  1 2/11X*TLDM*F10.2/11X*GLDM*F10.2/11X*LAI*F10.2/11X*CGR*F10.2)
   READ 3,DATE,(EL(I),I=1,60)
   PRINT 19,DATE
19 FORMAT (10X,F6.0)
   CALL PHS1 (CGR(N),TDM(N),AIL,EL,DNP(N),CLE(N))
 4 CONTINUE
   END
```

```
      SUBROUTINE PHS1 (CGR,TDM,AIL,EL,DNP,CLE)
      DIMENSION EL(60),PG(60)
      NN=60
      PRINT 14,(EL(J),J=1,NN)
 14   FORMAT (6X,10F10.2)
      IF(AIL,LT,1,7)6,7
  6   SIN=0.2*AIL
      GO TO 18
  7   SIN=0.34
 18   IF(AIL,LT,14.09)8,9
  8   PGMX=14.33+10.59*AIL-0.3758*AIL*AIL+1.066*CGR
      GO TO 17
  9   PGMX=90.94+1.066*CGR
 17   B=-0.25*SIN*SIN/PGMX
      B=404.44*B
      A=20.114*SIN
      PRINT 10,K,SIN,PGMX,B,A
 10   FORMAT (1HO,20X,*CURVE*I4,*INS=*F6.3,*PGMX=*F7.3,*B=*F8.5,*A=*F8.3)
      AB=-A/2./B
      DPG=0
      DO 11 J=1,NN
      IF(EL(J).LT.AB)12,13
 12   PG(J)=A*EL(J)+B*EL(J)*EL(J)
      GO TO 11
 13   PG(J)=PGMX
 11   DPG=DPG+PG(J)*7./400.
      IF(TDM.LT.30.0)40,41
 40   DDR=0.1*TDM-TDM*TDM*4.0/9000.0
      GO TO 42
 41   DDR=1.94+0.022*TDM+0.11*CGR
 42   DNP=DPG-DDR
      DLE=0
      DO 38 I=1,NN
      DLE=DLE+EL(I)
 38   CONTINUE
      DLE=DLE/7.82*15
      DLE=DLE/100.*55
      PRINT 15,DPG,DDR,DNP,DLE      DDR
 15   FORMAT(20X,*DPG=*F10.2,10X*=*F10.2,10X*DPR=*F10.2,10X*DLE=*F10.
     *2)
      RETURN $ END
```

# APPENDIX II

```
      PROGRAM CLOGRO2(INPUT,OUTPUT)
      DIMENSION EL(60),DLE(152),CGR(152),TDM(152),DNP(152)
C     CLOGRO2 TO PREDICT GROWTH OF SUBTERRANEAN CLOVER COMMUNITIES AT CONSTANT
C     TEMPERATURE
C     BETWEEN 10 AND 30 DEGREES
C     1972 SPRING EXPT START TDM 20.7 LAI 0.3 CT 24.0 FROM 31772
C     TRANSMISSION RATE IN THIS SIMULATION IS 55 PERCENT NOTE A AND B VALUES
C     FOLLOWING ABBREVIATION IS USED ONLY IN
C     THE PROGRAM.   CORRESPONDING ABBREVIATION
C     USED IN THE TEXT IS SHOWN IN PARENTHESES:
C     AIL(LAI), EL(LF), SIN(INS),
C     UNITS USED IN THE PROGRAM DIFFER FROM
C     THOSE IN THE TEXT
      READ 1,ND
    1 FORMAT(I3)
      PRINT 20
   20 FORMAT(1HO,20X,*DAY 1*)
      READ 2,TDM(1),AIL,CT
      PRINT2,TDM(1),AIL,CT
    2 FORMAT(3F10.1)
      READ 3,DATE,(EL(I),I=1,60)
    3 FORMAT(F6.0,12F5.0/(6X,12F5.0))
      PRINT 19,DATE
      CALL PHS2 (CT,TDM(1),AIL,EL,DNP(1),DLE(1))
      DO 4 N=2,ND
      PRINT 9,N
    9 FORMAT (1HO,20X,*DAY*I3)
      CGR(N)=CLE=0
      JD2=N-1
      IF(N.LE.8) GO TO 5
      DIV=7,
      JD1=N-7
      GO TO 6
    5 JD1=1
      DIV=N-1
    6 DO 7 J=JD1,JD2
      CGR(N)=CGR(N)+DNP(J)/DIV
    7 CLE=CLE+DLE(J)/DIV
      TDM(N)=TDM(N-1)+DNP(N-1)
      IF(TDM(N).LT.55.0)30,31
   30 DLDM=0.0
      GO TO 32
   31 DLDM=(11.21-2770./(194.+TDM(N)))*(CT/8.-1.)*TDM(N)*0.01
   32 TLDM=(29.08+10582./(519.+TDM(N)))*TDM(N)*0.01
      GLDM=TLDM-DLDM
      IF(CT.LT.14.1)26,25
   25 CF SQRT(640.0*CT-9200.0)-60.0
      GO TO 27
   26 CF=-SQRT(9200.0-640.0*CT)-60.0
   27 SLA=309.+34638./(101.+CLE)+CF
      AIL=GLDM*SLA*0.0001
      PRINT 8,CLE,SLA,TDM(N),DLDM,TLDM,GLDM,AIL,CGR(N)
    8 FORMAT (1HO,10X*CLE*F10.2/11X*SLA*F10.2/11X*TDM*F10.2/11X*DLDM*F10.
     1 2/11X*TLDM*F10.2/11X*GLDM*F10.2/11X*LAI*F10.2/11X*CGR*F10.2)
      READ 3,DATE,(EL(I),I=1,60)
      PRINT 19,DATE
   19 FORMAT(10X,F6.0)
      CALL PHS2 (CT,TDM(N),AIL,EL,DNP(N),DLE(N))
    4 CONTINUE
      END
```

```
      SUBROUTINE PHS2 (CT,TDM,AIL,EL,DNP,DLE)
      DIMENSION EL(60),PG(60)
      NN=60
      PRINT 14,(EL(J),J=1,NN)
   14 FORMAT(6X,10F10.2)
      IF(AIL.LT.2.5)6,7
    6 SIN=0.1224*AIL
      GO TO 18
    7 SIN=0.306
   18 IF(AIL.LT.1.0)29,28
   29 PGMX=(85.532*AIL/(2.68+AIL))/23.24*(1.458*CT-6.11)
      GO TO 17
   28 PGMX=85.532*AIL/(2.68+AIL)+1.458*CT-29.34
   17 B=-0.25*SIN*SIN/PGMX
      B=404.44*B
      A=20.114*SIN
      PRINT 10,K,SIN,PGMX,B,A
   10 FORMAT(1HO,20X,*CURVE*I4,*INS=*F6.3,*PGMX=*F7.3,*B=*F8.5,*A=*F8.3)
      AB=-A/2./B
      DPG=0
      DO11 J=1,NN
      IF(EL(J).LT.AB)12,13
   12 PG(J)=A*EL(J)+B*EL(J)*EL(J)
      GO TO 11
   13 PG(J)=PGMX
   11 DPG=DPG+PG(J)*7./400.
      DDR=(TDM/100.0)*(0.89+0.089*CT)+0.073*CT-0.91
      DNP=DPG-DDR
      DLE=0
      DO 38 I=1,NN
      DLE=DLE+EL(I)
   38 CONTINUE
      DLE=DLE/7.82*15.
      DLE=DLE/100.*55.
      PRINT 15,DPG,DDR,DNP,DLE
   15 FORMAT(1HO,20X,*DPG=*F10.2,10X*DDR=*F10.2,10X*DNP=*F10.2,10X*DLE=*
     *F10.2)
      RETURN $ END
```

# BIBLIOGRAPHY

Agata, W., Kubota, F. and Kamata, E. (1971a)

Dry matter production of forage plants. 1. Comparison of the amount of dry matter calculated from $CO_2$ balance with one observed in forage plant populations.
J. Jap. Soc. Grassld Sci. 17 : 223-28.

Agata, W., Kubota, F. and Kamata, E. (1971b)

Dry matter production of forage plants. 3. Influences of light extinction coefficient (k) on dry matter production and optimum frequency of cutting in forage plant populations.
J. Jap. Soc. Grassld Sci. 17 : 235-42.

Aitken, Y. and Mullett, J.H. (1970)

Patterns of seasonal development in the main pasture species used in Southern Victoria, 38°S.
Proc. 11th Int. Grassld Congr. 1970 : 300-05.

Akita, S., Miyasaka, A. and Murata, Y. (1969)

Studies on the differences of photosynthesis among species. I. Differences in the response of photosynthesis among species in normal oxygen concentration as influenced by some environmental factors.
Proc. Crop Sci. Soc. Jap. 38 : 507-24.

Alberda, Th. (1970)

The influence of carbohydrate reserves on respiration. photosynthesis, and dry matter production of intact plants.
Proc. 11th Int. Grassld Congr. 517-22.

Alberda, Th. and Sibma, L. (1968)

Dry matter production and light interception of crop surfaces. 3. Actual herbage production in different years as compared with potential values.
J. Br. Grassld Soc. 23 : 206-15.

Ampofo, S.T. and Lawson, G.W. (1972)

Growth of seedlings of *Afrormosia elata* Harms in relation to light intensity.
J. appl. Ecol. 9 : 301-06.

Aspinall, D. and Paleg, L.C. (1964)

Effects of daylength and light intensity on growth of barley. III. Vegetative development.
Aust. J. Biol. Sci. 17 : 807-22.

Baker, D.N. (1965)

The effects of certain environmental factors on net assimilation in cotton.
Crop Sci. 5 : 53-56.

Baker, D.N., Hesketh, J.D. and Duncan, W.G. (1972)

Simulation of growth and yield in cotton. I. Gross photosynthesis, respiration and growth.
Crop Sci. 12 : 431-35.

Baker, D.N. and Musgrave, R.B. (1964)

Photosynthesis under field conditions. V. Further plant chamber studies of the effects of light on corn (*Zea mays* L.)
Crop Sci. 4 : 127-31.

Balasko, J.A. and Smith, D. (1973)

Carbohydrates in grasses: V. Incorporation of $^{14}C$ into plant parts and nonstructural carbohydrates of timothy (*Phleum pratense* L.) at three developmental stages.
Crop Sci. 13 : 19-22.

Bate, G.C. and Canvin, D.T. (1971)

The effect of some environmental factors on the growth of young aspen trees (*Populus tremuloides* Michx) in controlled environments.
Can. J. Bot. 49 : 1443-53.

Bean, E.W. (1964)

The influence of light intensity upon the growth of an S.37 cocksfoot (*Dactylis glomerata*) sward.
Ann. Bot. (N.S.) 28 : 427-43.

Beevers, H. (1970)

Respiration in plants and its regulation. In "Prediction and measurement of photosynthetic productivity". pp. 209-14.

Beinhart, G. (1963)

Effects of environment on meristematic development, leaf area, and growth of white clover.
Crop Sci. 3 : 209-13.

Biddiscombe, E.F., Ozanne, P.G., Barrow, N.J. and Keay, J. (1969)

A comparison of growth rates and phosphorus distribution in a range of pasture species.
Aust. J. Agr. Res. 20 : 1023-33.

Björkman, O. (1968a)

Carboxydismutase activity in shade-adapted and sun-adapted species of higher plants.
Physiol. Pl. 21 : 1-10.

Björkman, O. (1968b)

Further studies on differentiation of photosynthetic properties in sun and shade ecotypes of *Solidago virgaurea*.
Physiol. Pl. 21 : 84-99.

Björkman, O., Nobs, M.A. and Hiesey, W.M. (1970)

Growth, photosynthetic, and biochemical responses of contrasting *Mimulus* clones to light intensity and temperature.
Carnegie Inst. Year Book 68 : 614-20.

Björkman, O. and Pearcy, R.W. (1971)

Effect of growth temperature on the temperature dependence of photosynthesis *in vivo* and on $CO_2$ fixation by carboxydismutase *in vitro* in $C_3$ and $C_4$ species.
Carnegie Inst. Year Book 70 : 511-20.

Björkman, O., Pearcy, R.W. and Nobs, M.A. (1971)

Hybrids between *Atriplex* species with and without β-carboxylation photosynthesis. Photosynthetic characteristics.
Carnegie Inst. Year Book 69 : 640-48.

Black, J.N. (1955)

The interaction of light and temperature in determining the growth rate of subterranean clover (*Trifolium subterraneum* L.).
Aust. J. Biol. Sci. 8 : 330-43.

Black, J.N. (1957)

Seed size as a factor in the growth of subterranean clover (*Trifolium subterraneum* L.) under spaced and sward conditions.
Aust. J. Agr. Res. 8 : 335-51.

Black, J.N. (1963)

The interrelationship of solar radiation and leaf area index in determining the rate of dry matter production of swards of subterranean clover.
Aust. J. Agr. Res. 14 : 20-38.

Black, J.N. (1964)

An analysis of the potential production of swards of subterranean clover (*Trifolium subterraneum* L.) at Adelaide. South Australia.
J. appl. Ecol. 1 : 3-18.

Blackman, G.E. and Wilson, G.L. (1951)

Physiological and ecological studies in the analysis of plant environment. VII. An analysis of the differential effects of light intensity on the net assimilation rate, leaf area ratio, and relative growth rate of different species.
Ann. Bot. (N.S.) 15 : 373-408.

Blackman, V.H. (1919)

The compound interest law and plant growth.
Ann. Bot. 33 : 353-60.

Bocock, K.L., Gilbert, O., Capstock, C.K., Twinn, D.C., Waid, I.S. and Woodhan, M.J. (1960)

Changes in leaf litter when placed on the surface of soils with contrasting humus types. I. Losses in dry weight of oak and ash leaf litter.
J. Soil Sci. 11 : 1-9.

Bouma, D. (1970)

Effects of nitrogen nutrition on leaf expansion and photosynthesis of *Trifolium subterraneum* L. II. Comparison between nodulated plants and plants supplied with combined nitrogen.
Ann. Bot. (N.S.) 34 : 1143-53.

Boyer, J.S. (1971)

Recovery of photosynthesis in sunflower after a period of low leaf water potential.
Pl. Physiol. 47 : 816-20.

Brougham, R.W. (1955)

A study in rate of pasture growth.
Aust. J. Agr. Res. 6 : 804-12.

Brougham, R.W. (1958a)

Interception of light by the foliage of pure and mixed stands of pasture plants.
Aust. J. Agr. Res. 9 : 39-52.

Brougham, R.W. (1958b)

Leaf development in swards of white clover (*Trifolium repens* L.).
N.Z. J. Agr. Res. 1 : 707-18.

Brougham, R.W. (1959)

The effects of season and weather on the growth rate of a ryegrass and clover pasture.
N.Z. J. Agr. Res. 2 : 283-96.

Brougham, R.W. (1962)

The leaf growth of *Trifolium repens* as influenced by seasonal changes in the light environment.
J. Ecol. 50 : 449-59.

Brougham, R.W. and Glenday, A.C. (1967)

Grass growth in mid-summer: a re-interpretation of published data.
J. Br. Grassld Soc. 22 : 100-07.

Brougham, R.W. and Glenday, A.C. (1969)

Weather fluctuations and the daily rate of growth of pure stands of three grass species.
N.Z. J. Agr. Res. 12 : 125-36.

Brouwer, R. (1962)

Distribution of dry matter in the plant.
Neth. J. Agr. Sci. 10 : 361-76.

Brown, R.H., Blaser, R.E. and Dunton, H.L. (1966)

Leaf area index and apparent photosynthesis under various microclimates for different pasture species.
Proc. 10th Int. Grassld Congr. 108-13.

Bunt, A.C. (1972)

Effect of season on the carnation (*Dianthus caryophyllus* L.)
I. Growth rate.
J. hort. Sci. 47 : 467-77.

Burnside, C.A. and Böhning, R.H. (1957)

The effect of prolonged shading on the light saturation curves of apparent photosynthesis in the sun plants.
Pl. Physiol. 32 : 61-63.

Campbell, C.A., Pelton, W.L. and Nielsen, K.F. (1969)

Influence of solar radiation and soil moisture on growth and yield of Chinook wheat.
Can. J. Plant Sci. 49 : 685-700.

Catsky, J., Janac, J. and Jarvis, P.G. (1971)

General principles of using IRGA for measuring $CO_2$ exchange rates.
In "Plant Photosynthetic Production Manual of Methods" pp. 161-67. Ed. by Sestak, Catsky and Jarvis.

Charles-Edwards, D.A., Charles-Edwards, J. and Cooper, J.P. (1971)

The influence of temperature on photosynthesis and transpiration in ten temperate grass varieties grown in four different environments.
J. Expt Bot. 22 : 650-62.

Chonan, N. (1967)

Studies on the photosynthetic tissues in the leaves of cereal crops III. The mesophyll structure of rice leaves inserted at different levels of the shoot.
Proc. Crop Sci. Soc. Jap. 36 : 291-96.

Cocks, P.S. (1973)

The influence of temperature and density on the growth of communities of subterranean clover (*Trifolium subterraneum* L. cv. Mount Barker).
Aust. J. Agr. Res. 24 : 479-95.

Cooper, C.S. (1966)

Response of birdsfoot trefoil and alfalfa to various levels of shade.
Crop Sci. 6 : 63-66.

Cooper, J.P. and Tainton, N.H. (1968)

Light and temperature requirements for the growth of tropical and temperate grasses.
Herb. Abstr. 38 : 167-76.

Davidson, J.L. (1954)

The effect of density of sowing on the growth of *Trifolium subterraneum* (subterranean clover).
Hons. B.Ag.Sc. Thesis, Univ. of Adelaide.

Davidson, J.L. and Birch, J.W. (1972)

Effects of defoliation on growth and carbon dioxide exchange of subterranean clover swards.
Aust. J. Agr. Res. 23 : 981-93.

Davidson, J.L. and Donald, C.M. (1958)

The growth of swards of subterranean clover with particular reference to leaf area.
Aust. J. Agr. Res. 9 : 53-72.

Davidson, J.L., Gibson, A.H. and Birch, J.W. (1970)

Effects of temperature and defoliation on growth and nitrogen fixation in subterranean clover.
Proc. 11th Int. Grassld Congr. 542-45.

Davidson, J.L. and Milthorpe, F.L. (1965)

The effect of temperature on the growth of cocksfoot (*Dactylis glomerata* L.).
Ann. Bot. (N.S.) 29 : 407-17.

Davidson, J.L. and Philip, J.R. (1958)

Light and pasture growth.
Symp. Climatology and Microclimatology, Canberra, 1955.
pp. 181-87 (Unesco : Paris).

Dickmann, D.I. (1971)

Photosynthesis and respiration by developing leaves of cottonwood (*Populus deltoides* Bartr.).
Bot. Gaz. 132 : 253-59.

Donald, C.M. (1951)

Competition among pasture plants. I. Intraspecific competition among annual pasture plants.
Aust. J. Agr. Res. 2 : 355-76.

Donald, C.M. (1963)

Competition among crop and pasture plants.
Adv. Agron. 15 : 1-118.

Donald, C.M. and Williams, C.H. (1954)

Fertility and productivity of a podzolic soil as influenced by subterranean clover and superphosphate.
Aust. J. Agr. Res. 5 : 664-87.

Downes, R.W. (1970)

Effect of light intensity and leaf temperature on photosynthesis and transpiration in wheat and sorghum.
Aust. J. Biol. Sci. 23 : 775-82.

Downton, J. and Slatyer, R.O. (1972)

Temperature dependence of photosynthesis in cotton.
Pl. Physiol. 50 : 518-22.

Downton, W.J.S. and Tregunna, E.B. (1968)

Photorespiration and glycolate metabolism: a re-examination and correlation of some previous studies.
Pl. Physiol. 43 : 923-29.

Van den Drissche, R., Connor, D.J. and Tunstall, B.R. (1971)

Photosynthetic response of brigalow to irradiance, temperature and water potential.
Photosynthetica 5 : 210-17.

Duncan, W.G. (1971)

Leaf angles, leaf area, and canopy photosynthesis.
Crop Sci. 11 : 482-86.

Duncan, W.G., Loomis, R.S., Williams, W.A. and Hanau, R. (1967)

A model for simulating photosynthesis in plant communities.
Hilgardia 38 : 181-205.

Eagles, C.F. (1967)

Apparent photosynthesis and respiration in populations of *Lolium perenne* from contrasting climatic regions.
Nature, Lond. 215 : 100-01.

Eagles, C.G. and Treharne, K.J. (1969)

Photosynthetic activity of *Dactylis glomerata* L. in different light regimes.
Photosynthetica 3 : 29-38.

Egli, D.E. and Leggett, J.E. (1973)

Dry matter accumulation patterns in determinate and indeterminate soybeans.
Crop Sci. 13 : 220-22.

Elmore, C.D., Hesketh, J.D. and Muramoto, H. (1967).

A survey of rates of leaf growth, leaf aging and leaf photosynthetic rates among and within species.
J. Ariz. Acad. Sci. 4 : 215-19.

El-Sharkawy, M.A. and Hesketh, J.D. (1964)

Effects of temperature and water deficit on leaf photosynthetic rates of different species.
Crop Sci. 4 : 514-18.

El-Sharkawy, M.A. and Hesketh, J.D. (1965)

Photosynthesis among species in relation to characteristics of leaf anatomy and $CO_2$ diffusion resistances.
Crop Sci. 5 : 517-21.

El-Sharkawy, M., Hesketh, J. and Muramoto, H. (1965)

Leaf photosynthesis and other growth characteristics among 26 species of *Gossypium*.
Crop Sci. 5 : 173-75.

Evans, G.C. (1972)

"The quantitative analysis of plant growth."
Blackwell Scientific Publications.

Evans, G.C. and Hughes, A.P. (1961)

Plant growth and the aerial environment. I. Effect of artificial shading on *Impatiens parviflora*.
New Phytol. 60 : 150-80.

Filippova, L.A., Voznesenskii, V.L. and Bogatkina, V.F. (1964)

Utilization of the products of photosynthesis in respiration.
Sov. Pl. Physiol. 11 : 37-41.

Forrester, M.L., Krotkov, G. and Nelson, C.D. (1966)

Effect of oxygen on photosynthesis, photorespiration and respiration in detached leaves. I. Soybeans.
Pl. Physiol. 41 : 422-27.

Friend, D.J.C. (1965)

Tillering and leaf production in wheat as affected by temperature and light intensity.
Can. J. Bot. 43 : 1063-76.

Friend, D.J.C., Helson, V.A. and Fisher. J.E. (1962a)

The rate of dry weight accumulation in Marquis wheat as affected by temperature and light intensity.
Can. J. Bot. 40 : 939-55.

Friend, D.J.C., Helson, V.A. and Fisher, J.E. (1962b)

Leaf growth in Marquis wheat as regulated by temperature, light intensity, and daylength.
Can. J. Bot. 40 : 1299-311.

Friend, D.J.C., Helson, V.A. and Fisher, J.E. (1965)

Changes in the leaf area ratio during growth of Marquis wheat, as affected by temperature and light intensity.
Can. J. Bot. 43 : 15-28.

Friend, D.J.C. and Pomeroy, M.E. (1970)

Changes in cell size and number associated with the effects of light intensity and temperature on the leaf morphology of wheat.
Can. J. Bot. 48 : 85-90.

Fukui, J., Ojima, M. and Watanabe, I. (1965).

Studies on the seed production of soybean I. Effect of temperature on photosynthesis of soybean.
Proc. Crop Sci. Soc. Jap. 33 : 432-36.

Fulwood, P.G. and Puckridge, D.W. (1970)

Photosynthesis of Wimmera ryegrass (*Lolium rigidum* Gaud.) in the field.
Proc. 11th Int. Grassld Congr. 530-34.

Gaastra, P. (1959)

Photosynthesis of crop plants as influenced by light, carbon dioxide, temperature, and stomatal diffusion resistance.
Mededel. Landbounhogesch. Wageningen 59 : 1-68.

Gaastra, P. (1962)

Photosynthesis of leaves and field crops.
Neth. J. Agr. Sci. 10 : 311-24.

Gaastra, P. (1963)

Climate control of photosynthesis and respiration.
In "Environmental control of plant growth". (Ed. L.T. Evans) pp. 113-38. Academic Press, Inc., New York.

Gabrielsen, E.K. (1948)

Effect of different chlorophyll concentrations on photosynthesis in foliage leaves.
Physiol. Pl. 1 : 5-37.

Geronimo, J. and Beevers, H. (1964)

Effect of aging and temperature on the respiratory metabolism of green leaves.
Pl. Physiol. 39 : 786-93.

Glenday, A.C. (1955)

The mathematical separation of plant and weather effects in field growth studies.
Aust. J. Agr. Res. 6 : 813-22.

Glenday, A.C. (1959)

Mathematical analysis of growth curves replicated in time.
N.Z. J. Agr. Res. 2 : 297-305.

Goodall, D.W. (1945)

The distribution of weight change in the young tomato plant. I. Dry-weight changes of the various organs.
Ann. Bot. (N.S.) 9 : 101-39.

Gregory, F.G. (1926)

The effect of climatic conditions on the growth of barley.
Ann. Bot. 40 : 1-26.

Grossbard, E. (1969)

A visual record of the decomposition of 14C -labelled fragments of grasses and rye added to the soil.
J. Soil Sci. 20 : 38-51.

Hartt, C.E. (1965)

The effect of temperature upon translocation of $^{14}C$ in sugarcane.
Pl. Physiol. 40 : 74-81.

Hatch, M.D. and Slack, C.R. (1970)

Photosynthetic $CO_2$-fixation pathways.
Ann. Rev. Pl. Physiol. 21 : 141-61.

Hatch, M.D., Slack, C.R. and Bull, T.A. (1969)

Light induced changes in the content of some enzymes of the $C_4$-dicarboxylic acid pathway of photosynthesis and its effect on other characteristics of photosynthesis.
Photochem. 8 : 697-706.

Heichel, G.H. (1970)

Prior illumination and the respiration of maize leaves in the dark.
Pl. Physiol. 46 : 359-62.

Heichel, G.H. (1971)

Response of respiration of tobacco leaves in light and darkness and the $CO_2$ compensation concentration to prior illumination and oxygen.
Pl. Physiol. 48 : 178-82.

Hellmuth, E.O. (1971)

The effect of varying air $CO_2$ level, leaf temperature and illuminance on the $CO_2$ exchange of the dwarf pea, *Pisum sativum* L. var. Meteor.
Photosynthetica 5 : 190-94.

Helms, J.A. (1965)

Diurnal and seasonal patterns of net assimilation in Douglas fir, *Pseudotsuga menziesii* (Mirb) Franco, as influenced by environment.
Ecol. 46 : 698-708.

Hesketh, J.D. (1968)

Effect of light and temperature during plant growth on subsequent leaf $CO_2$ assimilation rates in standard conditions.
Aust. J. Biol. Sci. 21 : 235-41.

Hesketh, J.D., Baker, D.N. and Duncan, W.G. (1971)

Simulation of growth and yield in cotton: respiration and the carbon balance.
Crop Sci. 11 : 394-98.

Hew, C.-S., Krotkov, G. and Canvin, D.T. (1969a)

Determination of the rate of $CO_2$ evolution by green leaves in light.
Pl. Physiol. 44 : 662-70.

Hew, C.-S., Krotkov, G. and Canvin, D.T. (1969b)

Effects of temperature on photosynthesis and $CO_2$ evolution in light and darkness by green leaves.
Pl. Physiol. 44 : 671-77.

Hiroi, T. and Monsi, M. (1963)

Physiological and ecological analysis of shade tolerance of plants. 3. Effect of shading on growth attributes of *Helianthus annuus*.
Bot. Mag. 76 : 121-29.

Hiroi, T. and Monsi, M. (1964)

Physiological and ecological analysis of shade tolerance of plants. 4. Effect of shading on distribution of photosynthate in *Helianthus annuus*.
Bot. Mag. 77 : 1-9.

Hiroi, T. and Monsi, M. (1966)

Dry-matter economy of *Helianthus annuus* communities grown at varying densities and light intensities.
J. Fac. Sci. Univ. Tokyo III. 9 : 241-85.

Hirose, T. (1971)

Nitrogen turnover and dry matter production of a *Solidago altissima* population.
Jap. J. Ecol. 21 : 18-31.

Hofstra, G. and Kesketh, J.D. (1969)

Effects of temperature on the gas exchange of leaves in the light and dark.
Planta 85 : 228-37.

Hogetsu, K., Oshima, Y., Midorikawa, B., Tezuka, Y., Sakamoto, M., Mototani, I. and Kimura, M. (1960)

Growth analytical studies on the artificial communities of *Helianthus tuberosus* with different densities.
Jap. J. Bot. 17 : 278-305.

Holmgren, P. (1968)

Leaf factors affecting light-saturated photosynthesis in ecotypes of *Solidago virgaurea* from exposed and shaded habitats.
Physiol. Pl. 21 : 676-98.

Hopkinson, J.M. (1966)

Studies on the expansion of the leaf surface. VI. Senescence and the usefulness of old leaves.
J. Expt Bot. 17 : 1762-70.

Hoshino, M., Matsumoto, F. and Okubo, T. (1971)

Studies on the assimilation and translocation of $^{14}CO_2$ in ladino clover. V. Relation between leaf age and ability of assimilation and translocation.
Proc. Crop Sci. Soc. Jap. 40 : 468-73.

Hughes, A.P. and Cockshull, K. (1971)

The effects of light intensity and carbon dioxide concentration on the growth of *Chrysanthemum morifolium* cv. Bright Golden Anne.
Ann. Bot. (N.S.) 35 : 899-914.

Hunt, L.A. (1965)

Some implications of death and decay in pasture production.
J. Br. Grassld Soc. 20 : 27-31.

Hunt, L.A. and Brougham, R.W. (1966)

Some aspects of growth in an undefoliated stand of Italian ryegrass.
J. appl. Ecol. 3 : 21-28.

Hunt, W.F. (1970)

The influence of leaf death on the rate of accumulation of green herbage during pasture regrowth.
J. appl. Ecol. 7 : 41-50.

Ito, A. and Udagawa, T. (1971)

Phytometrical studies of crop canopies. (1) Geometrical structure of soybean canopy and sunlight penetration.
J. Agr. Meteorol. (Tokyo) 26 : 187-96.

Ito, K. (1965)

Studies on photosynthesis in sugar beet plant.
III. Photosynthesis in the community.
Proc. Crop Sci. Soc. Jap. 33 : 492-98.

Ito, K. and Takeda, T. (1962)

Studies on the effect of temperature on the sugar production in sugar beet. I. The effect of temperature on the growth.
Proc. Crop Sci. Soc. Jap. 31 : 272-76.

Ito, T. (1971)

Photosynthetic activity of vegetable plants and its horticultural significance. II. The time course of photosynthesis in the tomato plant as influenced by some external and internal factors, especially by water and starch contents in the leaf.
J. Jap. Soc. Hort. Sci. 40 : 41-47.

Iwaki, H. (1958)

The influence of density on the dry matter production of *Fagopyrum esculentum*
Jap. J. Bot. 16 : 210-26.

Iwaki, H., Takada, K. and Monsi, M. (1969)

Studies on the dry matter production of *Solidago altissima* community I. The plant biomass and annual net production.
Bot. Mag. 82 : 215-25.

Izhar, S. and Wallace, D.H. (1967)

Effect of night temperature on photosynthesis of *Phaseolus vulgaris* L.
Crop Sci. 7 : 546-47.

James, W.O. (1953)

"Plant respiration."
Oxford : Clarendon Press.

Jeffers, S.L. and Shibles, R.M. (1969)

Some effects of leaf area, solar radiation, air temperature and variety on net photosynthesis in field-grown soybeans.
Crop Sci. 9 : 762-64.

Jolliffe, P.A. and Tregunna, E.B. (1968)

Effect of temperature, $CO_2$ concentration and light intensity on oxygen inhibition of photosynthesis in wheat leaves.
Pl. Physiol. 43 : 902-06.

Kariya, K. and Tsunoda, S. (1972)

Relationship of chlorophyll content, chloroplast area index and leaf photosynthesis rate in *Brassica*.
Tohoku J. Agr. Res. 23 : 1-14.

King, R.W. and Evans, L.T. (1967)

Photosynthesis in artificial communities of wheat, lucerne, and subterranean clover plants.
Aust. J. Biol. Sci. 20 : 623-35.

King, R.W., Wardlaw, I.F. and Evans, L.T. (1967)

Effect of assimilate utilization on photosynthetic rate in wheat.
Planta 77 : 261-76.

Knight, R. (1961)

The relation between tillering and dry matter production in cocksfoot (*Dactylis glomerata* L.) grown under spaced and sward conditions.
Aust. J. Agr. Res. 12 : 566-77.

Kriedemann, P.E., Neals, T.T. and Ashton, D.H. (1964)

Photosynthesis in relation to leaf orientation and light interception.
Aust. J. Biol. Sci. 17 . 591-600.

Kumura, A. (1965)

Studies on dry matter production of soybean plant. 2. Influence of light intensity on the photosynthesis of the population. Part 1. Relation between photosynthesis and light receiving aspect of the population in case where light intensity varies with weather condition.
Proc. Crop. Sci. Soc. Jap. 33 : 473-81.

Kumura, A. (1968a)

Studies on dry matter production of soybean plant.
3. Photosynthetic rate of soybean plant population as affected by proportion of diffuse light.
Proc. Crop. Sci. Soc. Jap. 37 : 570-82.

Kumura, A. (1968b)

Studies on dry matter production of soybean plant.
4. Photosynthetic properties of leaf as subsequently affected by light condition.
Proc. Crop. Sci. Soc. Jap. 37 : 583-88.

Kumura, A. and Naniwa, I. (1965)

Studies on dry matter production of soybean plant.
I. Ontogenetic changes in photosynthetic and respiratory capacity of soybean plant and its parts.
Proc. Crop. Sci. Soc. Jap. 33 : 467-72.

Kuroiwa, S., Hiroi, T., Takada, K. and Monsi, M. (1964)

Distribution ratio of net photosynthate to photosynthetic and non-photosynthetic systems in shaded plants.
Bot. Mag. 77 : 37-42.

Logan, K.T. (1970)

Adaptions of the photosynthetic apparatus of sun- and shade-grown yellow birch (*Betula alleghaniensis* Britt.).
Can. J. Bot. 48 : 1681-88.

Loomis, R.A., Williams, W.A. and Duncan, W.G. (1966)

Community architecture and the productivity of terrestrial plant communities.
In "Harvesting the sun". pp. 291-308.

Ludlow, M.M. and Wilson, G.L. (1971)

Photosynthesis of tropical pasture plants. I. Illuminance, carbon dioxide concentration, leaf temperature, and leaf-air vapour pressure difference.
Aust. J. Biol. Sci. 24 : 449-70.

Ludwig, L.J., Saeki, T. and Evans, L.T. (1965)

Photosynthesis in artificial communities of cotton plants in relation to leaf area. 1. Experiments with progressive defoliation of mature plants.
Aust. J. Biol. Sci. 18 : 1103-18.

Luxmoore, R.J., Millington, R.J. and Marcellos, H. (1971)

Soybean canopy structure and some radiant energy relations.
Agron. J. 63 : 111-15.

McCloud, D.E. (1964)

Light relations and photosynthesis within plant communities.
Proc. 9th Int. Grassld Congr. 511-17.

MacColl, D. and Cooper, J.P. (1967)

Climate variation in forage grasses. III. Seasonal changes in growth and assimilation in climate races of *Lolium, Dactylis* and *Festuca*.
J. appl. Ecol. 4 : 113-28.

McCree, K.J. (1970)

An equation for the rate of respiration of white clover plants grown under controlled conditions.
In "Prediction and measurement of photosynthetic productivity". pp. 221-29.

McCree, K.J. (1972a)

The action spectrum, absorptance and quantum yield of photosynthesis in crop plants.
Agric. Meteorol. 9 : 191-216.

McCree, K.J. (1972b)

Test of current definitions of photosynthetically active radiation against leaf photosynthesis data.
Agric. Meteorol. 10 : 443-53.

McCree, K.J. and Troughton, J.H. (1966a)

Prediction of growth rate at different light levels from measured photosynthesis and respiration rates.
Pl. Physiol. 41 : 559-66.

McCree, K.J. and Troughton, J.H. (1966b)

Non-existence of an optimum leaf area index for the production rate of white clover grown under constant conditions.
Pl. Physiol. 41 :1615-22.

Milthorpe, F.L. (1959)

Studies on the expansion of the leaf surface. I. The influence of temperature.
J. Expt Bot. 10 : 233-49.

Milthorpe, F.L. and Newton, P. (1963)

Studies of the expansion of the leaf surface. III. The influence of radiation on cell division and leaf expansion.
J. Expt Bot. 14 : 483-95.

Mitchell, K.J. (1953)

Influence of light and temperature on the growth of ryegrass *Lolium* spp. I. Pattern of vegetative development.
Physiol. Pl. 6 : 21-46.

Mitchell, K.J. (1956)

Growth of pasture species under controlled environment.
I. Growth at various levels of constant temperature.
N.Z. J. Sci. Tech. A38 : 203-16.

Mitchell, K.J. and Lucanus, R. (1960)

Growth of pasture species under controlled environment.
II. Growth at low temperatures.
N.Z. J. Agr. Res. 3 : 647-55.

Monsi, M. and Murata, Y. (1970)

Development of photosynthetic systems as influenced by distribution of matter.
In "Prediction and measurement of photosynthetic productivity" pp. 115-30.

Monsi, M. and Saeki, T. (1953)

Über den Lichtfaktor in den Pflanzengesellschaften und seine Bedeutung für die Stoffproduktion.
Jap. J. Bot. 14 : 22-52.

Mooney, H.A. and Harrison, A.T. (1970)

The influence of conditioning temperature on subsequent temperature-related photosynthetic capacity in higher plants.
In "Prediction and measurement of photosynthetic productivity". pp. 411-18.

Mooney, H.A. and Shrophshire, F. (1967)

Population variability in temperature related photosynthetic acclimation.
Oecologia Plantarum 2 : 1-13.

Mooney, H.A. and West, M. (1964)

Photosynthetic acclimation of plants of diverse origin.
Amer. J. Bot. 51 : 825-27.

Moriya, M. (1970)

On the dry matter distribution in several crop plants.
Proc. Crop Sci. Soc. Jap. 39 : 259-68.

Morley, F.H.W. (1958)

Effects of strain and temperature on the growth of subterranean clover (*Trifolium subterraneum* L.).
Aust. J. Agr. Res. 9 : 745-53.

Morley, F.H.W. (1961)

Subterranean clover.
Adv. Agron. 13 : 57-123.

Moss, D.N., Musgrave, R.B. and Lemon, E.R. (1961)

Photosynthesis under field conditions. III. Some effects of light, carbon dioxide, temperature and soil moisture on photosynthesis, respiration and transpiration of corn.
Crop Sci. 1 : 83-87.

Moss, D.N. and Peaslee, D.E. (1965)

Photosynthesis of maize leaves as affected by age and nutrient status.
Crop Sci. 5 : 280-81.

Murata, Y. and Iyama, J. (1963)

Studies on the photosynthesis of forage crops. II. Influence of air-temperature upon the photosynthesis of some forage and grain crops.
Proc. Crop Sci. Soc. Jap. 31 : 315-22.

Murata, Y., Iyama, J. and Honma, T. (1965)

Studies on the photosynthesis of forage crops. 4. Influence of air-temperature upon the photosynthesis and respiration of alfalfa and several southern-type forage crops.
Proc. Crop Sci. Soc. Jap. 34 : 154-58.

Nakaseko, K. and Yoshida, M. (1971)

Effects of climatic factors on the dry matter production in corn
Memoirs Fac. Agr. Hokkaido Univ. 8 : 40-48.

Neales, T.F. and Incoll, L.D. (1968)

The control of leaf photosynthesis rate by the level of assimilate concentration in the leaf: a review of the hypothesis.
Bot. Rev. 34 : 107-25.

Nevins, D.J. and Loomis, R.S. (1970a)

A method for determining net photosynthesis and transpiration of plant leaves.
Crop Sci. 10 : 3-6.

Nevins, D.J. and Loomis, R.S. (1970b)

Nitrogen nutrition and photosynthesis in sugar beet (*Beta vulgaris* L.).
Crop Sci. 10 : 21-26.

Ormrod, D.P. (1964)

Net carbon dioxide exchange rates in *Phaseolus vulgaris* as influenced by temperature, light intensity, leaf area index and age of plants.
Can. J. Bot. 42 : 393-401.

Osman, A.M. and Milthorpe, F.L. (1971)

Photosynthesis of wheat leaves in relation to age, illuminance and nutrient supply. II. Results.
Photosynthetica 5 : 61-70.

Pearce, R.B., Brown, R.H. and Blaser, R.E. (1965)

Relationships between leaf area index, light interception and net photosynthesis in orchardgrass.
Crop Sci. 5 : 553-56.

Pearce, R.B., Brown, R.H. and Blaser, R.E. (1967a)

Photosynthesis in plant communities as influenced by leaf angle.
Crop Sci. 7 : 321-24.

Pearce, R.B., Brown, R.H. and Blaser, R.E. (1967b)

Net photosynthesis of barley seedlings as influenced by leaf area index.
Crop Sci. 7 : 545-46.

Pearce, R.B. and Lee, D.R. (1969)

Photosynthetic and morphological adaptation of alfalfa leaves to light intensity at different stages of maturity.
Crop Sci. 9 : 791-93.

Pearson, C.J. and Hunt, L.A. (1972a)

Effects of temperature on primary growth of alfalfa.
Can. J. Pl. Sci. 52 : 1007-15.

Pearson, C.J. and Hunt, L.A. (1972b)

Studies on the daily course of carbon exchange in alfalfa plants.
Can. J. Bot. 50 : 1377-84.

Pearson, C.J. and Hunt, L.A. (1972c)

Effects of pretreatment temperature on carbon dioxide exchange in alfalfa.
Can. J. Bot. 50 : 1925-30.

Puckridge, D.W. (1971)

Photosynthesis of wheat under field conditions. III. Seasonal trends in carbon dioxide uptake of crop communities.
Aust. J. Agr. Res. 22 : 1-9.

Puckridge, D.W. (1973)

A quantitative account of the influence of solar radiation, water and nitrogen supply on the photosynthesis of wheat communities in the field.
In "Plant response to climatic factors". Proc. Uppsala Symp. 1970. pp. 519-25.

Puckridge, D.W. and Ratkowsky, D.A. (1971)

Photosynthesis of wheat under field conditions. IV. The influence of density and leaf area index on the response to radiation.
Aust. J. Agr. Res. 22 : 11-20.

Raguse, C.A., Fianu, F.K. and Menke, J.W. (1970)

Development of subterranean clover (*Trifolium subterraneum* L.) at very early stages.
Crop Sci. 10 : 723-24.

Raschke, K. (1970)

Temperature dependence of $CO_2$ assimilation and stomatal aperture in leaf sections of *Zea mays*.
Planta 91 : 336-63.

Razorenova, T.A. and Nilovskaya, N.T. (1971)

Age and species characteristics of dark respiration of several vegetables.
Sov. Pl. Physiol. 18 : 423-27.

Richards, F.J. (1959)

A flexible growth function for empirical use.
J. Expt Bot. 10 : 290-300.

Richards, F.J. (1969)

The quantitative analysis of growth.
In "Plant Physiology V.5A." Ed. by Stewart. pp. 3-76.

Robson, M.J. (1969)

Light temperature and the growth of grasses.
Rep. Grassld Res. Inst. 1968: 111-23.

Robson, M.J. (1971)

The use of simulated swards in growth rooms.
Rep. Grassld Res. Inst. 1970 : 158-68.

Robson, M.J. (1972)

The effect of temperature on the growth of S.170 tall fescue (*Festuca arundinacea*). I. Constant temperature.
J. appl. Ecol. 9 : 643-53.

Rook, D.A. (1969)

The influence of growing temperatures on photosynthesis and respiration of *Pinus radiata* seedlings.
N.Z. J. Bot. 7 : 43-55.

Ryle, G.J.A. (1970)

Partition of assimilates in an annual and a perennial grass.
J. appl. Ecol. 7 : 217-28.

Saeki, T. (1959)

Variation of photosynthetic activity with aging of leaves and total photosynthesis in a plant community.
Bot. Mag. (Tokyo) 72 : 404-08.

Sato, K. (1970)

Effects of environmental conditions of long and short duration on subsequent leaf $CO_2$ assimilation rates of rice plant under a definite standard condition.
Proc. Crop Sci. Soc. Jap. 39 : 370-75.

Sato, K. and Ito, M. (1969)

Responses of orchardgrass plant to photoperiod and air-temperature.
Proc. Crop Sci. Soc. Jap. 38 : 43-52.

Sawada, S. (1970)

An ecophysical analysis of the difference between the growth rates of young wheat seedlings grown in various seasons.
J. Fac. Sci. Univ. Tokyo. Sci. III 10 : 233-63.

Schmidt, R.E. and Blaser, R.E. (1969)

Effect of temperature, light and nitrogen on growth and metabolism of 'Tifgreen' Bermudagrass (*Cynodon* spp.).
Crop Sci. 9 : 5-9.

Scott, D. (1970)

$CO_2$ exchange of plants. 3. Temperature acclimatisation of three species.
N.Z. J. Bot. 8 : 369-79.

Scott, D. and Menalda, P.H. (1970)

$CO_2$ exchange of plants. 2. Response of six species to temperature and light intensity.
N.Z. J. Bot. 8 : 361-68.

Seale, S.R. (1971)

"Linear models". Wiley.

Sekioka, H. (1961)

Effect of temperature on the translocation of sucrose - $^{14}C$ in the sweet potato plant.
Proc. Crop Sci. Soc. Jap. 30 : 27-30.

Semikhatova, O.A. (1970)

Energy efficiency of respiration under unfavourable conditions.
In "Prediction and measurement of photosynthetic productivity". pp. 247-50.

Sestak, Z. (1966)

Limitations for finding a linear relationship between chlorophyll content and photosynthetic activity.
Biol. Pl. 8 : 336-46.

Sestak, Z. and Catsky, J. (1962)

Intensity of photosynthesis and chlorophyll content, as related to leaf age in *Nicotiana sanderae hort.*
Biol. Pl. 4 : 131-40.

Shibles, R.M. and MacDonald, H.A. (1962)

Photosynthetic area and rate in relation to seedling vigor of birdsfoot trefoil (*Lotus corniculatus* L).
Crop Sci. 2 : 299-302.

Smillie, R.M. (1962)

Photosynthetic and respiratory activities of growing pea leaves.
Pl. Physiol. 37 : 716-21.

Stern, W.R. (1960)

The light factor in grass and clover swards.
Ph.D. thesis, University of Adelaide.

Stern, W.R. (1965)

The effect of density on the performance of individual plants in subterranean clover swards.
Aust. J. Agr. Res. 16 : 541-55.

Stern, W.R. and Donald, C.M. (1962)

The influence of leaf area and radiation on the growth of clover in swards.
Aust. J. Agr. Res. 13 : 615-23.

Strain, B.R. (1969)

Seasonal adaptions in photosynthesis and respiration in four desert shrubs growing *in situ*.
Ecol. 50 : 511-13.

Strain, B.R. and Chase, V.C. (1966)

Effect of past and prevailing temperature on the carbon dioxide exchange capacities of some woody desert perennials.
Ecol. 47 : 1043-45.

Tajima, K. (1965)

Studies on the physiology of crop plants in response to the effect of high temperature. I. Effect of high temperature on growth and respiration of crop plants.
Proc. Crop Sci. Soc. Jap. 33 : 371-74.

Tajima, K. (1971)

Effect of temperature on the activity of respiratory enzymes and oxidative phosphorylation in crop yields.
Proc. Crop Sci. Soc. Jap. 40 : 261-66.

Takano, Y. and Tsunoda, S. (1970)

Light reflection, transmission and absorption rates of rice leaves in relation to their chlorophyll and nitrogen contents.
Tohoku J. Agr. Res. 21 : 111-17.

Takeda, T. (1961)

Studies on the photosynthesis and production of dry matter in the community of rice plants.
Jap. J. Bot. 17 : 403-37.

Takeda, T. and Agata, W. (1964a)

Analysis of the growth in forage crops. 1. Effects of high temperature on dry matter and leaf production of Ladino clover. Proc. Crop Sci. Soc. Jap. 33 : 1-6.

Takeda, T. and Agata, W. (1964b)

Analysis of the growth in forage crops. 2. Effects of high temperature on photosynthesis, respiration, chemical composition and regrowth of Ladino clover. Proc. Crop Sci. Soc. Jap. 33 : 7-16.

Takeda, T. and Agata, W. (1966a)

Analysis of the growth in forage crops. 3. Effect of temperature on organ formation in Ladino clover with special reference to photosynthetic organ formation. Proc. Crop Sci. Soc. Jap. 34 : 264-74.

Takeda, T. and Agata, W. (1966b)

Analysis of the growth in forage crops. 4. Effect of temperature on organ formation in Ladino clover with special reference to non-photosynthetic organ formation. Proc. Crop Sci. Soc. Jap. 34 : 275-80.

Takeda, T. and Agata, W. (1966c)

Analysis of the growth in forage crops. 5. Effect of the repeated treatment of "cut and regrowth" on the growth responses of Ladino clover under various temperatures. Proc. Crop Sci. Soc. Jap. 34 : 281-86.

Takeda, T. and Kumura, A. (1957)

Analysis of grain production in rice plant. I. Influence of nitrogen levels on leaf area, photosynthetic ability and respiration rate. II. Influence of nitrogen on light receiving coefficient and dry matter production. Proc. Crop Sci. Soc. Jap. 26 : 165-75.

Tanaka, T. and Matsushima, S. (1971a)

Analysis of yield-determining process and its application to yield-prediction and culture improvement of lowland rice. 102. Relations between the leafiness of rice plant communities and their light-curves of carbon assimilation. Proc. Crop Sci. Soc. Jap. 40 : 356-65.

Tanaka, T. and Matsushima, S. (1971b)

Analysis of yield-determining process and its application to yield-prediction and culture improvement of lowland rice. 103. On factors affecting the light-curves of carbon assimilation in rice plant communities. Proc. Crop Sci. Soc. Jap. 40 : 366-75.

Tanaka, T., Matsushima, S., Kojo, S. and Katsuki, Y. (1970)

Analysis of yield-determining process and its application to yield-prediction and culture improvement of lowland rice. 91. On the relation between the percentage of the amount of diffused light to the total amount of sunlight and the light-curve of carbon assimilation in a rice plant population.
Proc. Crop Sci. Soc. Jap. 39 : 319-24.

Tanaka, T., Matsushima, S., Kojyo, S. and Nitta, H. (1969)

Analysis of yield-determining process and its application to yield-prediction and culture improvement of lowland rice. 90. On the relation between the plant type of rice plant community and the light-curve of carbon assimilation.
Proc. Crop Sci. Soc. Jap. 38 : 287-93.

Taylor, T.H., Cooper, J.P. and Treharne, K.J. (1968)

Growth response of orchardgrass (*Dactylis glomerata* L.) to different light and temperature environments. 1. Leaf development and senescence.
Crop Sci. 8 : 437-40.

Terry, N. (1968)

Developmental physiology of sugar beet. I. The influence of light and temperature on growth.
J. Expt Bot. 19 : 795-812.

Thornley, J.H.M. (1970)

Respiration, growth and maintenance in plants.
Nature 227 : 304-05.

Thornley, J.H.M. (1971)

Energy, respiration and growth in plants.
Ann. Bot. (N.S.) 35 : 721-28.

Thornley, J.H.M. and Hesketh, J.D. (1972)

Growth and respiration in cotton bolls.
J. appl. Ecol. 9 : 315-17.

Treharne, K.J. and Cooper, J.P. (1969)

Effect of temperature on the activity of carboxylase in tropical and temperate Gramineae.
J. Expt Bot. 20 : 170-75.

Treharne, K.J., Cooper, J.P. and Taylor, T.H. (1968)

Growth response of orchardgrass (*Dactylis glomerata* L.) to different light and temperature environments. 2. Leaf age and photosynthetic activity.
Crop Sci. 8 : 441-45.

Treharne, K.J. and Eagles, C.F. (1970)

Effect of temperature on photosynthetic activity of climatic races of *Dactylis glomerata* L.
Photosynthetica 4 : 107-17.

Vickery, P.J., Brink, V.C. and Ormrod, D.P. (1971)

Net photosynthesis and leaf area index relationships in swards of *Dactylis glomerata* under contrasting defoliation regimes.
J. Br. Grassld Soc. 26 : 85-90.

Wager, H.G. (1941)

On the respiration and carbon assimilation rates of some arctic plants as related to temperature.
New Phytol. 40 : 1-19.

Warren Wilson, J. (1966)

An analysis of plant growth and its control in arctic environments.
Ann. Bot. (N.S.) 30 : 383-402.

Watson, D.J., Motomatsu, T., Loach, K. and Milford, G.F.J. (1972)

Effects of shading and of seasonal differences in weather on the growth, sugar content and sugar yield of sugar-beet crops.
Ann. Appl. Biol. 71 : 159-85.

Weihing, R.M. (1963)

Growth of ryegrass as influenced by temperature and solar radiation.
Agron. J. 55 : 519-21.

West, S.H. (1970)

Biochemical mechanism of photosynthesis and growth depression in *Digitaria decumbens* when exposed to low temperatures.
Proc. 11th Int. Grassld Congr. 514-16.

Wiegert, R.G. and Evans, F.C. (1964)

Primary production and the disappearance of dead vegetation on an old field in south-eastern Michigan.
Ecol. 45 : 49-63.

Wilfong, R.T., Brown, R.H. and Blaser, R.E. (1967)

Relationships between leaf area index and apparent photosynthesis in alfalfa (*Medicago sativa* L.) and Ladino clover (*Trifolium repens* L.).
Crop Sci. 7 : 27-30.

Williams, R.F. (1964)

The quantitative description of growth.
In "Grasses and Grasslands". pp. 89-101.
Ed. C. Bernard, London : Macmillan

Wilson, D. (1970)

Starch and apparent rate of photosynthesis of leaves of *Lolium perenne* grown at different temperatures.
Planta 91 : 274-78.

Wilson, D. and Cooper, J.D. (1969a)

Effect of light intensity and $CO_2$ on apparent photosynthesis and its relationship with leaf anatomy in genotypes of *Lolium perenne* L.
New Phytol. 68 : 627-44.

Wilson, D. and Cooper, J.P. (1969b)

Effect of temperature during growth on leaf anatomy and subsequent light-saturated photosynthesis among contrasting *Lolium* genotypes.
New Phytol. 68 : 1115-23.

Wilson, D. and Cooper, J.P. (1969c)

Effect of light intensity during growth on leaf anatomy and subsequent light-saturated photosynthesis among contrasting *Lolium* genotypes.
New Phytol. 68 : 1125-35.

de Wit, C.T. (1959)

Potential photosynthesis of crop surfaces.
Neth. J. Agric. Sci. 7 : 141-49.

de Wit, C.T. (1965)

Photosynthesis of leaf canopies.
Agric. Res. Rep. (Wageningen) 663 : 1-57.

de Wit, C.T., Brouwer, R. and Penning de Vries, F.W.T. (1970)

The simulation of photosynthetic systems.
In "Prediction and measurement of photosynthetic productivity".
pp. 47-70.

Woledge, J. (1971)

The effect of light intensity during growth on the subsequent rate of photosynthesis of leaves of tall fescue (*Festuca arundinacea* Schreb).
Ann. Bot. (N.S.) 35 : 311-22.

Woledge, J. (1972)

The effect of shading on the photosynthetic rate and longevity of grass leaves.
Ann. Bot. (N.S.) 36 : 551-61.

Woledge, J. and Jewiss, O.R. (1969)

The effect of temperature during growth on the subsequent rate of photosynthesis in leaves of tall fescue (*Festuca arundinacea* Schreb).
Ann. Bot. (N.S.) 33 : 896-914.

Yamaguchi, J. and Tanaka, A. (1967)

The effect of light on respiratory rate of the rice plant.
Pl. Cell Physiol. Tokyo 8 : 343-46.